Life history, behaviour and social structure of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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GMIT

INSTITIÚID TEICNEOLAÍOCHTA NA GAILLIMHE-MAIGH EO
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I hereby certify that this material, which I now submit for assessment on the programme of study leading to the award of PhD is entirely my own work and has not been taken from the work of others save and to the extent that such work has been cited and acknowledged within the text of my work.

Signed: Isabel Baker , the candidate.

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Date: 30th November 2017

For my grandparents

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ABSTRACT

Bottlenose dolphins are a complex intelligent species with great diversity and variability in behaviours and social systems across populations, but site-specific information on many aspects of the bottlenose dolphin population in the Shannon Estuary was previously limited or unavailable. The major objectives of this research were (1) to determine baseline reproductive parameters for bottlenose dolphins in Ireland; (2) to establish a full suite of observed behaviours; (3) to better understand the social structure of the population; and (4) to explore dolphin sociality at an individual level. By combining photo-identification and sightings data with novel data collection methods using focal follows, these questions could be addressed. This thesis is divided into six chapters: an introductory chapter (Chapter 1) outlining the research background, four analytical chapters written as scientific manuscripts, and a discussion which reflects on the results of these studies and outlines proposals for future research. The first data chapter (Chapter 2, Manuscript I) presents female reproductive parameters for the first time, together with new population demographics. Chapter 3 (Manuscript II) presents the first ethogram for dolphins in Ireland, validates its use using a video test, and presents new data on activity states and behavioural events. Chapter 4 (Manuscript III) analyses the social structure of the population, revealing age- and area-related associations and demonstrating the presence of long-term associations. Chapter 5 (Manuscript IV) investigates fine-scale sociality from the first focal follows of dolphins in Ireland, revealing female-male affiliations and the absence of male alliances. The general discussion (Chapter 6) brings together results from Chapters 2-5 to consider their implications and to propose ideas for further research and conservation management. It is essential for understanding diverse complex species that data are gathered and analysed for specific populations. By providing new information and analyses of bottlenose dolphin reproductive rates, behaviour, social structure and sociality in Ireland, this research increases our understanding of bottlenose dolphin populations globally.

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Chapter 1

Introduction


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1 Introduction

1.1 The importance of site-specific science

Bottlenose dolphins (*Tursiops* spp.) are the most extensively studied cetacean species in the world and are also one of the most diverse, occupying a wide geographical range worldwide (Connor *et al.* 2000b). They have the second largest relative brain size (*i.e.*, brain mass/body mass) of any animal on Earth and are thus arguably one of the most intelligent species on the planet (Marino 1998, Connor 2007, Whitehead & Rendell 2015). Their high level of social intelligence has likely been one of the drivers in the formation of the many varied and complex societies apparent among well-studied resident populations (Connor 2007). Despite being well-studied, information on bottlenose dolphins is often generalised in behavioural studies of the species by using data from the most well-studied resident populations in long-term study sites, particularly Sarasota Bay, Florida, USA (47 yr; Wells 2014), Shark Bay, Western Australia, Australia (33 yr; Connor *et al.* 2000b) and the Moray Firth, Scotland (27 yr; Wilson *et al.* 1999). However, the substitution of data from other study sites is not good practice as it can lead to errors in the results generated for specific populations (Patterson & Murray 2008, Arso Civil *et al.* 2017).

To conserve and protect a specific population of this complex species, it is essential to establish baseline data for that population in particular, ideally from detailed long-term research on identifiable individual animals inhabiting the specific study site. In addition, behavioural research on such populations, especially using novel research techniques, contributes to the global scientific knowledge of the species. It is essential to establish empirical baseline datasets before further investigations into a population can occur. The knowledge gained helps to inform conservation and management priorities and thus has important implications for future research on such populations.

1.2 General characteristics of bottlenose dolphins from global research

1.2.1 Taxonomy, distribution and resident populations

There are currently two recognised species of bottlenose dolphin in the world, the common bottlenose dolphin (*Tursiops truncatus*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Committee on Taxonomy 2017). Both species are slate grey in colour with lighter ventral pigmentation and have robust bodies and moderately falcate dorsal fins; one of the main differences in their morphology is their size in that the common bottlenose dolphin is about twice as large as the Indo-Pacific bottlenose dolphin, with the largest *T. truncatus* individuals found in colder temperate waters (Wells & Scott 1999, Connor *et al.* 2000b). These species also differ genetically, as well as morphologically (Wang *et al.* 1999). A division of *T. truncatus* into inshore and offshore "ecotypes" has been described based on morphological, ecological and genetic differences (Duffield *et al.* 1983, Louis *et al.* 2014). Bottlenose dolphins range across the globe in tropical and temperate waters, but not extending into the polar regions (Hammond *et al.* 2012; Fig. 1.1). It is estimated that a minimum of 600,000 bottlenose dolphins exist worldwide, occupying coastal, estuarine, shelf and pelagic waters (Wells & Scott 1999, Hammond *et al.* 2012).

Figure 1.1 World map illustrating the global distribution (yellow) of *Tursiops truncatus*. The species is found throughout the world's oceans, excluding polar regions (Hammond *et al.* 2012).

In many regions, coastal populations of resident bottlenose dolphins have been discovered, wherein specific individuals exhibit long-term site fidelity to a particular area (Wells & Scott 1999). These populations have facilitated long-term research on the species (*e.g.*, in Sarasota Bay, USA (Wells 2014) and in Shark Bay, Western Australia (Connor *et al.* 2000b)). These coastal study sites vary widely in their geographical form, from small estuarine inlets (*e.g.*, Swan Canning River, Australia (Chabanne *et al.* 2012)) to large river estuaries (*e.g.*, Patos Lagoon Estuary, Brazil (Fruet *et al.* 2015)), linear lagoon systems (*e.g.*, Indian River Lagoon, USA (Titcomb *et al.* 2015)), fjords (*e.g.*, Doubtful Sound, New Zealand (Lusseau *et al.* 2003)), enclosed bays (*e.g.*, Sarasota Bay, USA (Wells 2014)) and more open bays (*e.g.*, Bay of Islands, New Zealand (Tezanos-Pinto *et al.* 2015) and Shark Bay, Western Australia (Connor *et al.* 2000b)).

Resident populations of bottlenose dolphins around the world vary in size considerably. For example, the small population of bottlenose dolphins in the Sado Estuary, Portugal, comprises only 24 individual dolphins, whereas the study population in the Bay of Islands, New Zealand is estimated to consist of about 408 individuals (Augusto *et al.* 2011, Tezanos-Pinto *et al.* 2015). Wells (2013) described geographical regions with resident populations as “natural laboratories” for international research, presenting ideal conditions to carry out behavioural studies.

A key feature of bottlenose dolphins as a study species is their individual distinctiveness. Bottlenose dolphins have nicks and notches in their dorsal fins, along with secondary features such as scars and lesions, which make them individually identifiable (Würsig & Würsig 1977, Würsig & Jefferson 1990). Thus, researchers can recognise each individual dolphin’s unique identity, allowing for the development and management of photo-identification catalogues (see section 1.5) wherein every individual in the population is accounted for (Hammond *et al.* 1990, Wells & Scott 1990).

1.2.2 Life history and reproduction

The life history or reproductive parameters of a species help to explain the developmental stages of its lifetime from birth to eventual death. In addition, the cycles of these births and deaths and the pace at which they occur can indicate the growth or decline of an animal population. Because of the variation in animal populations, it is important to calculate species-specific and population-specific reproductive parameters.

In particular, for highly social species like bottlenose dolphins, it is of scientific value to discern similarities and differences in these reproductive traits between the diverse societies in which these animals live. However, the production of reliable life history parameters is dependent on longitudinal studies with consistent continuous data collection and management (Wells 1991, Mann & Karniski 2017). In cetaceans, information on these reproductive rates is known only for a relatively small number of populations, primarily due to the difficulty in obtaining the longitudinal datasets necessary to estimate these parameters (Arso Civil 2015).

The longest-running study on free-ranging bottlenose dolphins is the Sarasota Dolphin Research Program in Sarasota, Florida, USA, where research has been conducted since 1970 (Wells 2014). This longitudinal study has been the source for much of the information currently known for *T. truncatus*, particularly with respect to the life history of the species. Bottlenose dolphins are long-lived mammals and reproduce relatively slowly (Connor *et al.* 2000b); therefore it can take many years to gain a thorough understanding of the general reproductive traits of the species. Bottlenose dolphins have relatively long life expectancies; in Sarasota Bay in 2013, the oldest resident female was 63 years old and the oldest resident male was 50 years old (Wells 2014). Females typically reach reproductive maturity at around 5-12 years of age whereas males are thought to reach reproductive maturity a little later at 10-13 years of age (Wells & Scott 1999). The reproductive lifespan of female dolphins is prolonged, with some females in Sarasota Bay still successfully producing and rearing calves at age 48 and males siring calves up to age 40 (Duffield & Wells 2002, Wells 2014). Wells and Scott (1990) calculated a mean annual crude birth rate of 5.5% for bottlenose dolphins in Sarasota Bay, and a mean first-year calf mortality rate and maximum adult mortality rate of 18.9% and 3.8%, respectively.

Bottlenose dolphins have a gestation period of 12 months and generally give birth to a single calf at a time whom they nurse with milk secreted from mammary glands located within mammary slits on their ventral surfaces (Schroeder 1990). Studies of captive bottlenose dolphins report an 18-month lactation period but field studies have reported lactation periods of twice that duration (Mann *et al.* 2000a). There is considerable variation among individuals for both nursing duration and the period of calf dependency, thus the point at which calves gain full nutritional dependence from their mothers is also likely to vary along with these factors (Connor *et al.* 2000b). Although female bottlenose dolphins are seasonally polyestrous (Schroeder 1990), temporal patterns in reproduction are apparent in many populations with peaks in calving during summer months (*e.g.*, in Bunbury, Western Australia (Smith *et al.* 2016) and Cardigan Bay, Wales (Veneruso & Evans 2012)). As with other long-lived mammal species, bottlenose dolphins undergo a relatively long juvenile period between weaning from their mothers and becoming sexually mature, and this has been shown to be an important developmental stage in terms of behaviour and social organisation (McHugh 2010).

Population demographics are determinant factors in the structure and viability of a population. For example, a mammal population containing individuals of only one sex will not succeed in long-term survival (if the population is closed with no access to individuals from other populations). Likewise, if a population contains a low proportion of calves and has low recruitment levels (*e.g.*, the Sado Estuary, Portugal, dolphin population (Augusto *et al.* 2011)), long-term viability becomes less likely. In Sarasota, the ratio for individuals of known sex is about 1:1 female to male, and individuals of known age class are 42% subadult and 58% adult (Wells 2014). Manlik *et al.* (2016) report sex ratios of 50:50 in Shark Bay and 55:45 female to male in Bunbury, Western Australia.

Reproductive parameters can indicate the reproductive fitness and tempo of a population. For example, if female dolphins in a population reproduce, on average, every two years, the population will grow faster than one in which the females reproduce every six years. These inter-birth intervals (IBIs) vary by individual and by population (Fruet *et al.* 2015; see Chapter 2, Table 2.4), with minimum individual IBIs of 1.1 years in the Port River estuary, Australia (Steiner & Bossley 2008) to maximum IBIs of 11 years in Sarasota Bay (Wells & Scott 1999) and the Sado Estuary, Portugal (Gaspar 2003). Mean population IBIs range from 3.0 (Adriatic Sea, Bearzi *et al.* 1997, Patos Lagoon Estuary, Brazil, Fruet *et al.* 2015) to 5.4 years (Sarasota Bay, Wells & Scott 1999). Fecundity rates range from 0.11 in the Patos Lagoon Estuary, Brazil (Fruet *et al.* 2015) to 0.25 in the Bay of Islands, New Zealand (Tezanos-Pinto *et al.* 2015). First-year mortality rates for bottlenose dolphin calves can be quite high; for example, mortality rates of 45% and 33% have been recorded for young-of-year (YOY) calves in the Moray Firth, Scotland (Robinson *et al.* 2017) and Doubtful Sound, New Zealand (Henderson *et al.* 2014), respectively, and can be especially high for calves of primiparous females (Wells 2014). Knowledge of life history and population demographics is essential to the scientific study, conservation and management of wild animal populations (Mann & Karniski 2017).

1.2.3 Behavioural studies

The study of behaviour is central to the scientific understanding of animal species (Lehner 1996, Slater 1999). To begin behavioural research on animals in a population, it is essential to establish clear definitions of behavioural categories and types (Masatomi 2004). An ethogram, a list of behavioural descriptors, helps to outline these definitions and can be used by multiple researchers observing the behaviour of the species under study (Mann *et al.* 2000b). In addition, the precise descriptions and definitions in an ethogram coupled with quantification of the outlined behaviours can provide a valuable basis for further systematic and quantitative research on a species and/or specific population (Martin & Bateson 1986). These baseline data on the behavioural repertoire of a species must be produced before more complex analyses can be carried out (Lehner 1996).

Distinguishing between “behavioural states” and “behavioural events” is important for defining behaviours, but especially for recording and analysing behavioural data (Altmann 1974). States are usually long-duration behaviours whereas events are almost instantaneous (Mann *et al.* 2000b). Nowacek (2002) provides a good example of this distinction by comparing the behavioural *state* “eyes open” to the behavioural *event* “blinking”.

Previous research on bottlenose dolphin behaviour has resulted in various ethograms from specific studies, mostly for activity states, but also for behavioural events (incorporating surface behaviours) in some cases (*e.g.*, Weaver 1987, Shane 1990, Bearzi *et al.* 1999). However, there have been few detailed behavioural studies of dolphins in temperate waters and no ethograms have been produced for bottlenose dolphins in Ireland or for the two geographically closest resident populations in the Moray Firth, Scotland and Cardigan Bay, Wales.

Bottlenose dolphin activity states are generally defined in a mutually exclusive way and studies almost always include the four main states: “travel”, “social”, “forage” and “rest” (Mann *et al.* 2000b). Differences in the activity state budgets of bottlenose dolphins within and between populations can provide interesting insights into the behavioural patterns and life history of those populations (Karniski *et al.* 2015). For example, dolphins in Shark Bay allocate a large proportion (37%) of their activity budget to resting (Gero *et al.* 2005, Karniski *et al.* 2015) compared to bottlenose dolphins in the Patos Lagoon Estuary, Brazil and Sarasota Bay where only 1% of the daytime activity budget is allocated to resting (Waples 1995, Mattos *et al.* 2007, McHugh *et al.* 2011) (see Chapter 3, Table 3.9, for further comparison between study sites).

Examples of bottlenose dolphin surface behaviours include “leaps”, “snags” and “tailslaps”, the definitions of which can vary by study (see Chapter 3, Table 3.10, for comparable descriptors). These behavioural events can occur during different activity states. For example, in a study of bottlenose dolphins in Doubtful Sound, New Zealand, Lusseau (2006) revealed that leaps played different roles in several behavioural categories and were used as a form of non-vocal communication between focal dolphin groups. Similarly, Pearson (2017) found that leaping in dusky dolphins (*Lagenorhynchus obscurus*) in Admiralty Bay, New Zealand had an effect on fission-fusion grouping patterns and foraging behaviour, and was potentially also used as a signalling mechanism.

Bottlenose dolphins exhibit many types of social behaviours, involving other conspecifics in social activity contexts. In Shark Bay in 2011, two male dolphins were recorded (by the author, IB) engaging in “head-to-head” behaviour, where individuals face one another rostrum-to-rostrum for a prolonged period, often jerking their heads up and down and making audible quacking-like low frequency vocalisations (Connor *et al.* 2000b). Social behaviours, like this one, can be either affiliative or agonistic/aggressive. For example, bottlenose dolphins often express affiliation by physical proximity or synchronous movement, with social behaviours such as “rubbing” or “petting” (Connor *et al.* 2000b). In contrast, social behaviours such as “biting” (one dolphin bites another) and “headbutt” (two dolphins jump simultaneously and hit their heads together) are often used by bottlenose dolphins during aggressive interactions (Lusseau 2006).

International research has shown that bottlenose dolphins feed on a wide variety of prey, such as octopus in Bunbury, Australia and soniferous fish in Sarasota Bay, and use an inventive set of foraging strategies to do so (Berens McCabe *et al.* 2010, Sprogis *et al.* 2017). Dolphins also exhibit a multitude of foraging specialisations, at individual and group levels (Nowacek 2002, Sargeant *et al.* 2006). For example, a subset of dolphins in Shark Bay uses marine sponges to access fish living below the substrate (Smolker *et al.* 1997, Patterson & Mann 2011), and an even smaller number of dolphins there have developed a potentially innovative foraging strategy described as "conching" or "shelling" (Allen *et al.* 2011). In Cedar Key, Florida, individual dolphins take on the same specific roles during group hunting, some individuals assuming the role of "driver", driving fish against those playing the role of "barrier" (Gazda *et al.* 2005). Many other fascinating foraging behaviours have been described, including strand feeding by hydroplaning dolphins (Sargeant *et al.* 2005), "kerplunking" (Connor *et al.* 2000a) and "fish-whacking" (Wells *et al.* 1987).

With these many specialisations, it is important to define the key universal behavioural events that occur during foraging activity. For example, ethogram definitions such as "catch fish" and "with fish in mouth" are likely to apply in almost every foraging context. Using behavioural event types that can be observed in all dolphin populations allows for comparison between different populations and study sites. The true diversity of bottlenose dolphin foraging strategies has yet to be revealed through further more extensive research (Whitehead & Rendell 2015). The range of specialisations apparent from studies so far reinforces the scientific importance of defining behavioural repertoires for specific populations, to understand similarities and differences among populations and to pave the way for observations of population-, group- or individual-specific behaviours at specific study sites.

1.2.4 Social structure and sociality

Bottlenose dolphins live in extremely dynamic societies with complex social structures, comparable to those of human populations (Connor 2007). These societies are fission-fusion social systems in which populations are composed of individuals associating in small groups that frequently change in size and composition (Connor *et al.* 2000b). Fission-fusion grouping is one of the most complex types of social organisation systems seen in the animal kingdom (Smolker *et al.* 1992).

Social structure is a fundamental component of the biology of an animal population and can affect population growth, genetics and animal movements (Lusseau *et al.* 2006, Whitehead 2008). The study of social structure involves analysing associations and interactions between identifiable individual animals within and/or between populations (Whitehead 2009). Social structure has been studied in many bottlenose dolphin populations around the world; research from the two longest running studies of wild bottlenose dolphin populations in Sarasota, Florida (*e.g.*, Wells 1991) and Shark Bay, Australia (*e.g.*, Connor *et al.* 2000b) has revealed fascinating complexities in bottlenose dolphin social structure, and many other populations have been analysed in recent years (*e.g.*, in Golfo Dulce, Costa Rica, Moreno & Acevedo-Gutiérrez 2016, and Brittany, France, Louis *et al.* 2017).

The social structure of a whole population can be analysed, or individual members of a population can be classified and their social structure analysed within that population. Whole population studies on bottlenose dolphins in the Moray Firth, Scotland have revealed a remarkable social structure entailing long- and short-term associations and a split in the population with two socially distinct communities (Lusseau *et al.* 2006). In Brittany, France, the study of a geographically isolated bottlenose dolphin community of 31 individuals yielded one of the highest mean half-weight association indices (HWI = 0.5) reported for bottlenose dolphins worldwide, with strong bonds between most individuals (Louis *et al.* 2017). In Ireland, Oudejans *et al.* (2015) reported that dolphins using the coastal waters of western Ireland appeared to be socially distinct from dolphins using offshore waters. The development of sophisticated statistical tests has allowed for association matrices of individuals within populations to be permuted to test for preferred or avoided companions (Bejder *et al.* 1998, Whitehead 2008). Much of the previous work has been focused on finding preferred companions among individual dolphins; however recent work has highlighted the importance of detecting social avoidance patterns too (Strickland *et al.* 2017).

In research studies where individuals in a population were of known sex, interesting results have included sex differences in patterns of association among adults (Smolker *et al.* 1992) and among juveniles in the way that they associate with their mothers and other conspecifics (Samuels 1996, McHugh 2010). In the bottlenose dolphin societies of Shark Bay, Australia and Sarasota Bay, USA, strong long-term associations between adult individuals of the same sex are exhibited (Connor *et al.* 1992, Smolker *et al.* 1992, Connor *et al.* 2000b, Owen *et al.* 2002, Wells 2014, Connor & Krützen 2015). These associations are characterised by dramatic sex differences in association patterns comprising long-term bonds between males and looser network associations among female dolphins. Male dolphins in these populations form strong associations (termed “alliances”) whereas female dolphins do not form alliances, but instead form large social networks (Connor *et al.* 2000b). In a stark contrast between study sites, male bottlenose dolphins in Shark Bay tend to form trios (although some pairs occur) whereas male bottlenose dolphins in Sarasota Bay form pairs and no trios have been observed (Connor *et al.* 1992, Owen 2003). Remarkably, second-order alliances, that is, associations between two or more first-order male subgroups, may last as long as 20 years in Shark Bay (Connor & Krützen 2015). Bottlenose dolphins in Shark Bay also form third-order alliances with this population’s male dolphins forming the most complex nested alliances known outside of humans (Connor *et al.* 2017).

Associations between female and male dolphins seem to be less common (long-term associations between individuals of different sexes are not found in Sarasota Bay or Shark Bay (Connor *et al.* 2000b)), but have been observed in some populations. In Doubtful Sound, New Zealand, Lusseau *et al.* (2003) recorded some female-male associations that were stable over the course of several years. Similarly, stable long-term female-male associations were recorded for bottlenose dolphins in Port Stephens, Australia, where constant companionships occur between females and males (Wiszniewski *et al.* 2010).

In addition to sex-related patterns of association, the different age classes in bottlenose dolphin societies have been reported to influence social association preferences. For example, in Shark Bay, consistent preferential associations were exhibited between juveniles, with the top-ranked associates of juvenile males being other juvenile males (Smolker *et al.* 1992, Samuels 1996). Similarly, juvenile bottlenose dolphins in Sarasota Bay show a marked preference for associating with other juveniles, especially of their own sex (McHugh 2010).

In some populations, associations related to area use have also been found. In the Moray Firth, Lusseau *et al.* (2006) identified two separate social units that mainly used two different parts of the study area. Titcomb *et al.* (2015) noted a relationship between spatial distribution and association strength for individuals in the bottlenose dolphin population inhabiting the Indian River Lagoon, Florida, USA, with the lowest association indices among individuals at the study site’s northern and southern boundaries.

Because they are so long-lived, and studies have shown some associations to last decades, it is of scientific interest to conduct long-term research on the social structure of bottlenose dolphin populations; and similarly to reproductive parameters, the continuous collection of detailed longitudinal data makes the patterns and the evolution of such relationships more discernible (Connor *et al.* 2000b, Mann & Karniski 2017).

1.2.5 Connecting long-term studies

Although the topics of life history, female reproduction, behaviour and social structure are analytically distinct, they are closely interconnected. They all tend to rely heavily on the existence of long-term datasets in which the relevant data are systematically recorded. But there are also important substantial connections among these questions, since they are all related to establishing a holistic understanding of the dynamics of a given population. Population estimates and demographics provide a basic insight into the population as a whole, and its stability or variability over time. Within this basic picture, reproductive parameters indicate the patterns through which the population sustains itself over time. Behavioural research reveals the repertoire of behaviours and activity budgets that have proved adaptive to a particular population in a particular setting. Additionally, the investigation of social structure provides a deeper insight into how the members of the population relate to each other, giving a more detailed picture of the forms of association that sustain the population over time. It is therefore not surprising that all of these features of dolphin populations are studied within the long-term research programmes discussed above, insofar as resources permit. They are all components of a broader attempt to understand the population as a whole, as well as the general characteristics of the species.

1.3 Bottlenose dolphin conservation and management

Globally, bottlenose dolphins are listed as of “Least Concern” by the International Union for Conservation of Nature (IUCN) (Hammond *et al.* 2012). The species is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS or Bonn Convention (1983)), within which they are also included in the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS).

At the European level, bottlenose dolphins are listed under Appendix II of the Bern Convention which aims to conserve wild flora and fauna and their natural habitats, and to promote cooperation between European member states. The European Union Habitats Directive (92/43/EEC) lists bottlenose dolphins under both Annex IV, which stipulates “strict protection” for all cetacean species, and Annex II, which requires the designation of Special Areas of Conservation (SACs) by member states. Thus, Ireland is obliged to designate SACs for bottlenose dolphins. As part of a European strategy (the Natura 2000 network of European protected sites), this legislation also requires Ireland to maintain all populations of whale and dolphin species at a “Favourable Conservation Status”.

Within Ireland’s Exclusive Economic Zone (EEZ), bottlenose dolphins are protected by a number of legislative instruments including the Wildlife Act (1976) and the Wildlife (Amendment) Act (2000), which prohibit the hunting, injury, wilful interference and destruction of breeding places of cetaceans. In addition, the governmental Marine Notice No. 15 of 2005 provides guidelines to boat operators in Ireland for correct procedures when encountering whales and dolphins, including instructions to maintain a distance of 100 m between vessels and cetaceans (Maritime Safety Directorate 2005).

There are two designated SACs in Ireland which include bottlenose dolphins as a qualifying interest – the Lower River Shannon SAC (Site Code: 002165; National Parks and Wildlife Service (NPWS) 2012) and the West Connacht Coast SAC (Site Code: 002998; NPWS 2015). The bottlenose dolphin population in the Shannon Estuary is the only resident population of bottlenose dolphins in Ireland and thus warrants particular conservation and protection (O’Brien *et al.* 2009).

1.4 Previous bottlenose dolphin research in the Shannon Estuary

The Lower River Shannon SAC study site contains the survey areas used in previous research on bottlenose dolphins in the Shannon Estuary and in the present study. It extends from Limerick in the east to its border with the Atlantic Ocean in the west between Loop Head, Co. Clare and Kerry Head, Co. Kerry (Chapter 2, Fig. 2.1), incorporating many species and habitat types across its range (NPWS 2012). A variety of vessel activities occur in the study area, with an average of four large ships transiting per day, one/two car ferries operating between Killimer, Co. Clare and Tarbert, Co. Kerry, small recreational vessels and fishing boats, and two dolphin-watching tour boats (O'Brien *et al.* 2016).

A dolphin-watching tourism industry has built up in the area since the 1990s and has enabled systematic long-term data collection on this population, with the two commercial dolphin-watching boats providing opportunistic platforms for research

(Berrow *et al.* 1996, Berrow & Holmes 1999). Additionally, dedicated surveys have been conducted using small ~6 m RIBs (Rigid-hulled Inflatable Boats); for example, Berrow *et al.* (2012) conducted small-scale dedicated line transect surveys as part of a capture-recapture study of the dolphin population in 2010.

Previous research on bottlenose dolphins in the Shannon Estuary has largely focused on abundance/distribution, acoustics and genetics. Photo-identification studies have been conducted since the early 1990s, resulting in the identification of many recognizable individuals (Berrow *et al.* 1996, Ingram 2000, Berrow *et al.* 2012). Mark-recapture abundance estimates have been reported by six separate studies between 1997 and 2015, indicating that the number of animals in the population has remained relatively stable over these 19 years. These studies yielded extant population size estimates of 113 ± 14 in 1997 (Ingram 2000), 121 ± 14 in 2003 (Ingram & Rogan 2003), 140 ± 12 in 2006 (Englund *et al.* 2007), 114 ± 17 in 2008 (Englund *et al.* 2008), 107 ± 12 in 2010 (Berrow *et al.* 2010, Berrow *et al.* 2012), and 114 ± 14 in 2015 (Rogan *et al.* 2015). In contrast to population censuses based on a comprehensive knowledge of all of the individuals in a population, such as those conducted in Sarasota Bay, these studies have all been based on mark-recapture abundance estimates, and therefore dependent on a set of general assumptions about the population.

Indications of year-round presence, referred to as residency, have been published; for example, Berrow (2009) conducted winter surveys of the estuary and found dolphins on most occasions. Ingram (2000) also recorded dolphins in autumn and winter months. Ingram and Rogan (2002) revealed the use of “hotspots” in the estuary – core areas where dolphins were more concentrated during surveys. The Shannon Estuary has a very complicated geometry and bathymetry (O'Brien *et al.* 2016) and Ingram and Rogan (2002) showed that bottlenose dolphins regularly occur in two core areas with the greatest slope and depth. Encounter locations and minimum convex polygons of known ranges for permanently marked individual dolphins suggested a degree of habitat partitioning with potentially fewer individuals using the inner estuary (Ingram & Rogan 2002, Ingram & Rogan 2003). Additionally, Barker and Berrow (2016) recently showed that bottlenose dolphin group size varies significantly between different areas in the estuary and between months.

There is no published evidence that bottlenose dolphins recorded in the Shannon Estuary use areas of the coastline more than 25 km outside the estuary and thus they appear to be spatially confined to the estuary and adjacent Tralee Bay and Brandon Bay (Ryan & Berrow 2013, Levesque *et al.* 2016 (Appendix D)).

Following the analysis of 46 genetic samples from bottlenose dolphins in the Shannon Estuary, and their comparison to genetic samples taken from live dolphins and from dead stranded animals around the coast of Ireland, Mirimin *et al.* (2011) concluded that the dolphins in the Shannon Estuary were genetically discrete from two other populations in Ireland – a coastal population of *ca.* 171 individuals (Ingram *et al.* 2009, Nykänen 2016) and a putative offshore population inhabiting the waters between the coast and continental shelf (samples from animals stranded around the coastline excluding the Shannon Estuary).

Two studies of contaminant burdens in Shannon Estuary bottlenose dolphins have been conducted. Berrow *et al.* (2002) analysed samples from eight free-swimming Shannon Estuary bottlenose dolphins; the maximum recorded polychlorinated biphenyls (PCB) concentration in the blubber of 18.3 mg kg^{-1} wet weight suggested low-level organochlorine contamination in the population. More recently, in a study of PCB concentrations across European cetacean populations, Jepson *et al.* (2016) used results from the same samples and concluded that PCB levels in Shannon Estuary dolphins were lower than those of other bottlenose dolphins in European waters, but still above PCB toxicity thresholds for marine mammals, and high enough to pose a risk to the health of the animals and to cause reproductive impairment.

Extensive acoustic research has been carried out on bottlenose dolphins in the Shannon Estuary. An initial investigation into whistle production by bottlenose dolphins in the estuary by Berrow *et al.* (2006) led to the classification of the whistle types produced by the dolphins into five categories. Following this, Hickey *et al.* (2009) constructed an ethogram of whistle types and compared the whistles of Shannon Estuary bottlenose dolphins to those in Cardigan Bay, Wales, concluding that whistles unique to each site could be representative of behavioural, environmental or morphological differences between regional areas or dialects. O'Brien *et al.* (2016) conducted the first assessment of the effects of vessel activity on the bottlenose dolphins in the Shannon Estuary, highlighting potential anthropogenic disturbances to the acoustic communication of the dolphins from shipping noise. Berrow *et al.* (2006) linked several activity states (“travelling”, “travel/feeding”, “foraging” and “milling”) to whistle types produced by dolphins in the Shannon Estuary, with whistle type A, described as a rise, the most frequently recorded whistle during foraging, and whistle type E, described as a fall, the most common whistle recorded during travelling activity. Thus, the authors suggested that certain whistle types were likely associated with certain behaviour types.

Leeney *et al.* (2007) assessed the effectiveness of acoustic deterrents on bottlenose dolphins in the Shannon Estuary by using underwater pingers which emitted an acoustic alarm when activated by an echolocation click train. They found that dolphin detection rates were significantly greater when continuously sounding pingers were inactive than when they were active. Although this was a focused behavioural response study, Leeney *et al.* (2007) did define seven behavioural categories which they used to assess the potential effects of the acoustic disturbance: group formation, surfacing mode, directionality, direction, speed, distance from boat and overall behaviour (which included the activity states "travelling", "foraging", "socializing", and "aerial behaviour"). The researchers reported a dramatic change in behaviour following the deployment of active pingers, most notably, sudden and speedy movements away from the boat. Berrow *et al.* (2002) also described behavioural reactions of bottlenose dolphins in the Shannon Estuary to biopsy darting, including one individual dolphin who breached several times.

The first recorded live stranding of a bottlenose dolphin in the Shannon Estuary occurred in June 2012, when a female adult dolphin (ID# 242) stranded during a fast-ebbing tide (O'Brien *et al.* 2014 (Appendix E)). Through photo-identification following her successful refloat, she has been monitored and recorded 85 times since her release (unpublished data, this study). Remarkably, she gave birth to a calf in September 2012 indicating that she had been nine months pregnant at the time of her stranding (O'Brien *et al.* 2014 (Appendix E)). Subsequent monitoring of this adult female and her calf has yielded detailed records of their association patterns (Appendix F, Poster 2), the calf's weaning age and behaviour, and the birth of her next calf in 2016 (Chapter 2, Table 2.1).

The two previous studies of the social structure of bottlenose dolphins in the Shannon Estuary determined that the population lives in a fission-fusion society, with no apparent evidence of sexual segregation (based on division of individuals into probable sex classes; Ingram 2000, Foley *et al.* 2010).

Prior to the beginning of this research project, little research had been conducted in Ireland on dolphin surface behaviour and no life history parameters were available for bottlenose dolphins in Irish waters. It was clear from the cited works that dolphins in the Shannon Estuary existed both alone and in groups, composed of adults, juveniles, mother-calf pairs, or a combination, but the demography of the population had not been examined. Calves with foetal folds were reported, indicating that reproductive females (and presumably males) were present in the population, but nothing was known about calf survival, inter-birth intervals or reproductive rates. No previous research had sought to quantify these vital life history characteristics. O'Brien *et al.* (2009) recommended that future research target the reproductive biology of cetaceans in Irish waters, with a focus on bottlenose dolphins in particular. Other than the studies mentioned above that touched on dolphin behaviour, no behavioural research had ever been conducted on bottlenose dolphins in Ireland. The two studies which included social structure had comparatively small quantities of data, lacked demographic data, and thus did not classify individuals within the population.

The bottlenose dolphins in the Shannon Estuary, Ireland are a unique study population with a high dolphin encounter rate, year-round presence and long-term site fidelity (Berrow *et al.* 2012, Levesque *et al.* 2016 (Appendix D)). They therefore presented an ideal opportunity for further investigative research. Thus, this research project was born from knowledge gaps identified specific to reproductive parameters, behaviour, social structure and sociality of bottlenose dolphins in Ireland, and sought to create valuable baseline data for this population and for comparisons with other populations globally.

1.5 Photo-ID catalogue and database development

In this section and the next, I set out the steps I took as a researcher in creating the databases and managing the research effort that went into this project.

Photographic systems and the advancement in dedicated software have led to the creation of databases where photo-id and sightings data can be stored side by side (Adams *et al.* 2006). The selection, development and adaptation of the two major databases used in this study, “*IMatch*” and “*FinBase*”, and the protocols associated with their use (Baker 2015 (Appendix G)), formed a key integral basis for data management and acquisition.

Initially, I reviewed a number of potential programs used by other research projects, protocol documents, database systems, volunteer recruitment and management plans. Then, over the course of five years (2012-2016), I created and developed a photographic database within the software environment *IMatch* (Fig. 1.2) which now contains 87,634 photos (most of which I processed and all of which I independently checked and validated), drawn from 216,760 original files.

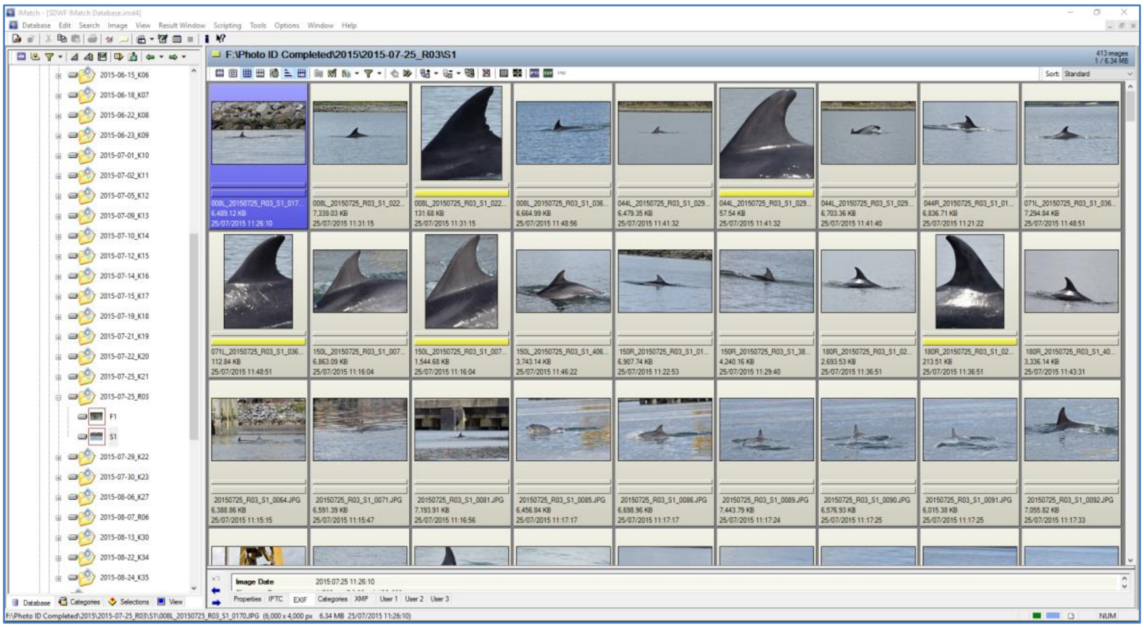
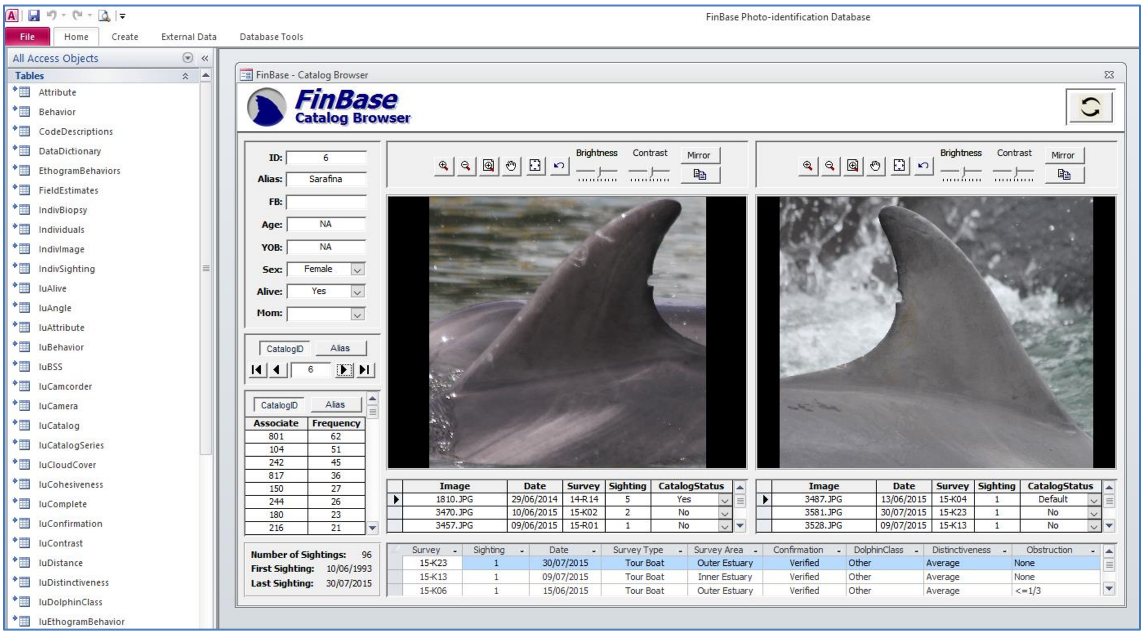


Figure 1.2 Screenshot of the *IMatch* software environment used for photographic data entry and processing.

In conjunction with *IMatch*, starting with a relational sightings database designed by Jeff Adams at NOAA for dolphin research (*FinBase*, Fig. 1.3), I adapted and developed a database specifically for this project with his assistance. This database currently contains 4,469 individually entered records with photographic and sightings information attached to each individual dolphin. *IMatch* and *FinBase* were used for dorsal fin photo-identification, photo processing and analysis, and the maintenance of a relational sightings database. In addition to the 467 surveys carried out for this project between 2012 and 2016, I incorporated historical data collected by the Shannon Dolphin and Wildlife Foundation (SDWF) between 1993 and 2011, resulting in a total of 1,120 surveys.



ID: 6
Alias: Sarafina
FB:
Age: NA
YOB: NA
Sex: Female
Alive: Yes
Mom:

Associate	Frequency
801	62
104	51
242	45
817	36
150	27
244	26
180	23
216	21

Number of Sightings: 96
First Sighting: 10/06/1993
Last Sighting: 30/07/2015

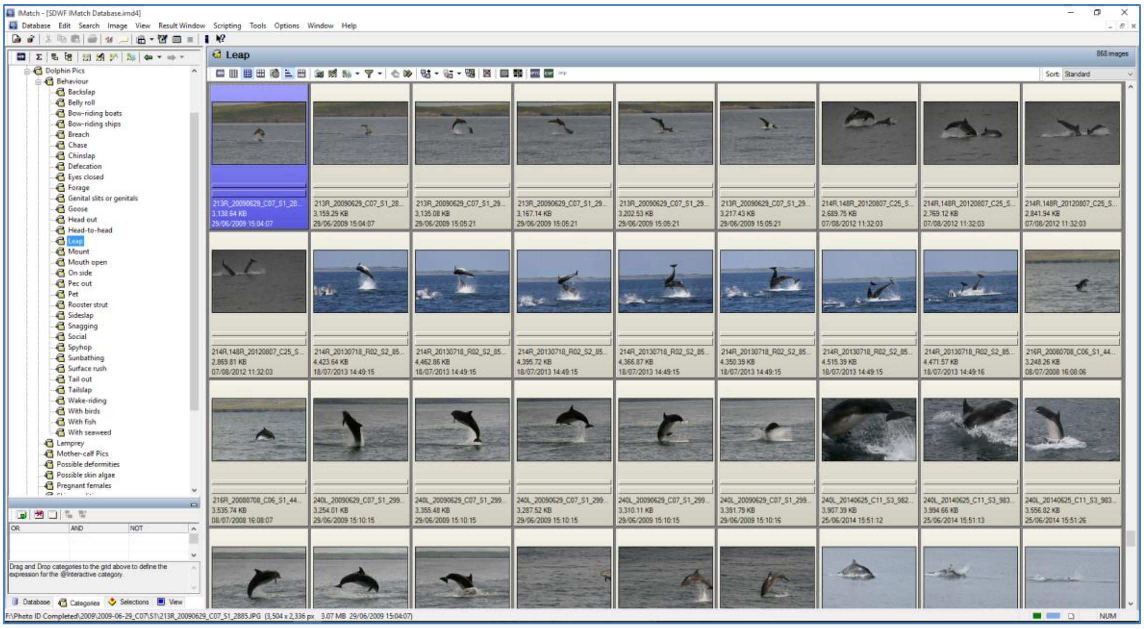
Image	Date	Survey	Sighting	CatalogStatus
1810.JPG	29/06/2014	14-R14	5	Yes
3470.JPG	10/06/2015	15-K02	2	No
3457.JPG	09/06/2015	15-R01	1	No

Image	Date	Survey	Sighting	CatalogStatus
3487.JPG	13/06/2015	15-K04	1	Default
3581.JPG	30/07/2015	15-K23	1	No
3528.JPG	09/07/2015	15-K13	1	No

Survey	Sighting	Date	Survey Type	Survey Area	Confirmation	DolphinClass	Distinctiveness	Obstruction
15-K23	1	30/07/2015	Tour Boat	Outer Estuary	Verified	Other	Average	None
15-K13	1	09/07/2015	Tour Boat	Inner Estuary	Verified	Other	Average	None
15-K06	1	15/06/2015	Tour Boat	Outer Estuary	Verified	Other	Average	<=1/3

Figure 1.3 Screenshot of the relational sightings database in *FinBase* showing the catalogue summary for ID# 006.

I incorporated behavioural definitions into *IMatch* (where every photo of every behaviour (Chapter 3, Tables 3.2-3.4) is categorised) and *FinBase* (where we specially developed an ethogram form so that all behavioural information is connected to every sighting). As part of this research project, 10,863 photos were individually categorised in *IMatch* to illustrate 49 different kinds of behaviours (Fig. 1.4). Additional categories for photos of dolphins with possible deformities and skin lesions were also maintained.



Drag and Drop categories to the grid above to define the expression for the @Interactive category.

Figure 1.4 Screenshot of *IMatch* software environment with Categories window displayed. On the left, the user can select a category to which photos have been assigned, while on the right all photos from the category are displayed. The example shown is the behaviour “leap”.

I entered the life history measures of this population, particularly known calf ages, into *FinBase* from a separately maintained matrilines record. This record of reproductive females and their calves currently contains information on 37 females and 69 calves in the Shannon Estuary population, including the first records of known weaned individual dolphins in Ireland.

I investigated location data from surveys and follows using “ArcGIS” mapping software. The integration of the *FinBase Mapping Tools* toolbox in ArcGIS (Fig. 1.5) provided another resource for investigation into this population’s life history and behaviour. This toolbox connects to the *FinBase* database and allows for the presentation of GPS location records within ArcMap, including queries based on:

i) Individuals
ii) Surveys
iii) Age Class and Group Size
iv) Behaviours (Activity States); and
v) Custom Queries.

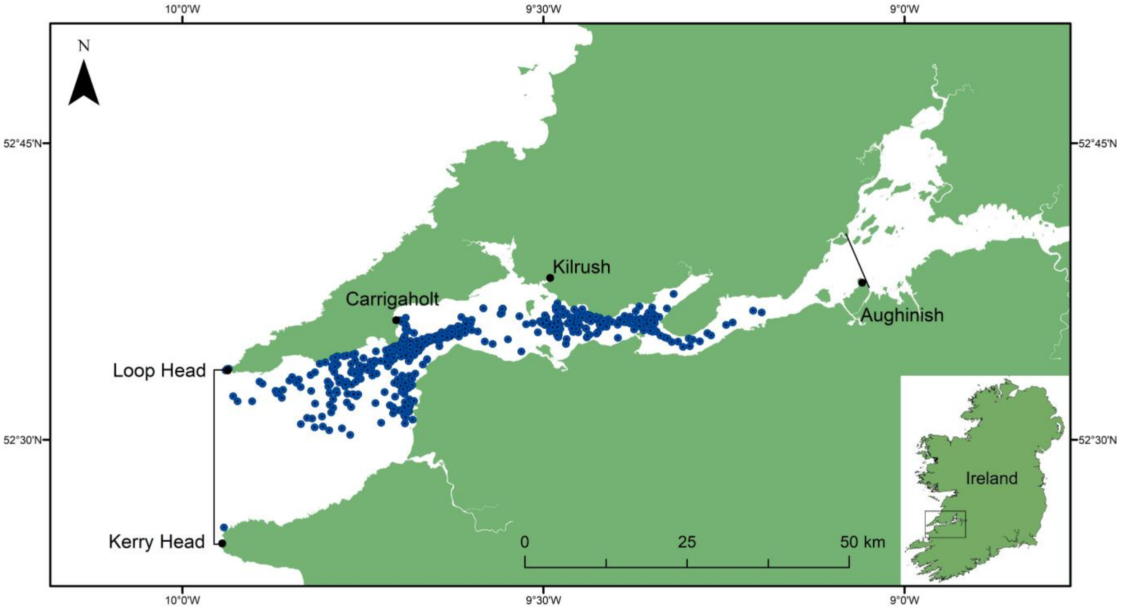


Figure 1.5 Map of the Shannon Estuary study site with 551 location points (blue circles) for bottlenose dolphin sightings with GPS records from 2012 to 2016. The *FinBase Mapping Tools* toolbox allows for custom queries to be mapped directly from the *FinBase* database along with preset options for specific behavioural and demographics displays of data.

Bottlenose dolphins have individually recognisable dorsal fins and this allows for the development and management of photo-identification catalogues wherein every individual in a resident population is recognised and identified (Wells *et al.* 1987, Hammond *et al.* 1990). I built a digital photo-id catalogue using cropped dorsal fin photographs from the *IMatch* database, to aid comparisons of known identifiable individuals with those photographed during surveys in the field. I updated this digital photo-id catalogue every year, with left and right side images of adults, juveniles and calves.

More information on data management and analysis can be found in the Methods sections of Chapters 2-5.

1.6 Project management

This PhD research was based in the Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology (Oct-Apr) and the Shannon Dolphin and Wildlife Centre (during field seasons, May-Sep). Through collaboration with the Shannon

Dolphin and Wildlife Foundation (SDWF), this research combined the ongoing collection of long-term data by the organisation with novel data collection methods specific to the PhD research project. In this section, I describe the voluntary work that I did in managing the research team, as well as the educational, fundraising and administrative work that was an essential part of sustaining that research effort.

In 2012, I began volunteering with the SDWF, and in 2013, I initiated a research assistant programme which I led and developed over the years that followed. The initial goal of creating this programme was to put into place a system whereby the SDWF would have access to a dedicated team of volunteers every summer for the research and education strands of the organisation. However, the system proved invaluable to my PhD project too, in that it helped to provide a research station, cover for many essential research costs (by way of fundraising by the volunteers), access to multiple researchers (necessary for collecting the large amounts of data sought in this study) and the crew I needed to support me in the dedicated behavioural research we conducted from our research vessel (the IWDG’s RIB, *Muc Mhara*). Had this system not been in place, this PhD project could not have occurred.

However, as with any new system, development and ongoing project management was required, and some parts of the project management improved considerably in later years as I developed my skillset. Every year, I engaged in volunteer recruitment through advertisement, application assessment, interviews with short-listed candidates via Skype and final recruitment of 4-6 research assistants. I maintained a weekly rota/team schedule and work record, in which I could account for the activities that every researcher engaged in on every day during my time as their supervisor and mentor. In doing so, I ensured, as far as possible, that every team member had an equal opportunity to participate in fieldwork on each of the dolphin-watching boats and our research vessel and in each type of research/educational task. I also organised local housing and dealt with all renting and housing issues that came along. This was one part of an important relationship I endeavoured to build with the local community and stakeholders in the area, which also took time and perseverance.

At the beginning of each 4-month field season, I embarked on a two-week training programme with the new research assistants. I supplied them each with a protocols document I wrote for fieldwork and data entry (Baker 2015 (Appendix G)). I held workshops in equipment use, including the correct use and maintenance of DSLR cameras, optical equipment (binoculars and a monocular), computers and a camcorder.

Research assistants used the equipment in the dolphin centre, then outside on land and then on the boats. In the first two years, I accompanied each researcher on the boats multiple times to ensure that they were comfortable handling the equipment and filling out datasheets before they went alone. In the remaining two years, a returning research assistant also helped with this training; for example, if two boats were going out at the same time, I would go with a research assistant on one trip, and the experienced researcher went on the other with another new research assistant. The research assistants were also trained in how to liaise with the dolphin-watching tour boat operators and how to behave with members of the public when they were on board the boats.

On the dedicated research vessel, I provided initial training in the marina, including lessons about embarking and docking, some important basic knots, correct use of lifejackets and on-board safety equipment, and procedures associated with the launch, retrieval and towing of the boat on its trailer. During each survey from the research vessel, I captained the boat and helped the research assistants to put the fieldwork protocols they had diligently learnt into action. They learned a range of important techniques in cetacean fieldwork, including spotting dolphins, collecting several types of data in the field, equipment use on a moving platform, visual recognition of individually identifiable dolphins and appropriate vessel conduct around marine mammals.

Back in the lab, I provided training and ongoing supervision in data management, data collation and entry, photographic categorisation and matching and several forms of database use. As their mentor, I offered individual weekly progress meetings during which they could discuss areas of fieldwork or data processing that they were having trouble with, or anything else that they wished to bring to my attention.

In addition, the research assistants had the opportunity to learn, under my supervision, about cetacean strandings and associated protocols whenever the opportunity arose. Together with the research assistants, I developed my skills in sample collection and cetacean necropsies. I led the successful refloat of a live-stranded common dolphin mother-calf pair in 2016, an achievement that required careful team management, expert consultation and public communication.

All of this research effort was integrated with and dependent on a substantial programme of education and public outreach. To support that programme, I devised a guided tour layout and provided training to the research assistants in the provision of educational guided tours to members of the public, which resulted in the research assistants' ability to provide special individually-catered tours to every person/group that entered the dolphin centre, seven days a week. I also devised a school tour which we collectively provided to various school groups during arranged visits. I set up new video slides and developed new educational materials and interactive games. Together, we redesigned many of the educational information boards in the centre. I set up social media accounts for the SDWF on Facebook, Twitter and Instagram and encouraged the research assistants to post new information daily.

We created fundraising events and scheduled them across each summer to take place in the dolphin centre and surrounding towns. I arranged our presence at a number of public events including the Ballybunion Seaweed Festival, Clare Environmental Network Fair, Vandeleur Walled Garden craft fairs, Whale Watch Ireland events and Heritage Week days at the Cliffs of Moher visitor centre, where we presented information on the Shannon dolphins and engaged with interested members of the public. I also set up promotional pages for the visitor centre on, for example, the Discover Ireland and Wild Atlantic Way websites, and TripAdvisor.

I wrote 14 grant applications at the beginning of my PhD project in an effort to gain funding for the project; unfortunately these were not successful. However, in my final year, I was successful in obtaining Local Agenda 21 funding for the SDWF. I also received two Marine Institute researcher travel awards and a Society for Marine Mammalogy (SMM) student travel grant. In 2015, the research team ran a successful crowd-funding campaign with a video on Kickstarter.com to fundraise for the repainting of the outside wall of the dolphin centre with an artist's mural. During my PhD project, I also successfully acquired a sponsored berth for our research vessel from L&M Keating (Maritime) Ltd, GPS equipment from Garmin, optical equipment from Minox, and many other donated items from local suppliers which helped with the running of the research and visitor centre.

In 2015, we were successful in gaining recognition in the newspaper, *The Clare Champion*, where an article in the Living Section was written entitled "Shannon dolphin research project leads the way in Europe" (published 03 Jul 2015). A newspaper article was also written about our successful live-stranding refloat (mentioned above) in 2016. Our research was also highlighted by my participation in several TV programmes (RTE Nationwide (broadcast 11 Oct 2013), an independent documentary called Nature's

Keepers (to be released), UTV Ireland's Lesser Spotted Journeys (broadcast Oct 2016)), a Heritage Week video and a radio show (RTE Radio Mooney Goes Wild).

I was also in charge of many administrative tasks including website management (www.shannondolphins.ie), accounting, merchandise ordering, stock management (including databasing), sales (and merchandise database protocols), product checklists, restock lists, visitor numbers data collection, graphic design (of flyers, posters, etc.) and I set up a successful Adopt-a-Dolphin Scheme.

Over the course of the project, I chaired over 30 team meetings to discuss the larger team mission of combining research with successful education and fundraising. Following the completion of each field season, I sent out evaluation forms to all of the research assistants and provided references for job applications.

For my PhD behavioural research, I also wrote two permit applications and two licence reports for the National Parks and Wildlife Service (NPWS) to gain permission for conducting behavioural research on bottlenose dolphins in the Shannon Estuary SAC.

In summary, I independently ran four 4-month field seasons with teams of 6-8 researchers, supervising early career stage scientists. Overall, I trained, supervised, and mentored 22 full-time research assistants and volunteers. We collectively conducted 467 boat-based surveys (47% of the research conducted by SDWF up to the end of 2016), including 57 days of dedicated behavioural research from IWDG's RIB *Muc Mhara* amounting to 90.8 hours of focal follow data. I was captaining the research vessel or on board dolphin-watching boats for 155 of these surveys. In addition to behavioural research, I managed the SDWF's research and education centre which included organising and participating in long-term monitoring surveys from tour boats, public outreach events, data processing, visitor centre tours, administration, merchandising and fundraising. I include all this information here to indicate the range and volume of the activity that lies in the background of the more succinct discussions of Methods in Chapters 2-5.

1.7 Aims of this dissertation

1.7.1 Specific objectives

The main aim of this study was to establish scientifically rigorous life history and behavioural data for this unique population, generally for the very first time, and in all cases with the most extensive and reliable dataset so far assembled, thus providing valuable data for global comparisons, putting this population on the map with other long-term studies and making site-specific population data available for conservation and management. The specific objectives of this project were:

A. To determine baseline reproductive parameters for bottlenose dolphins in Ireland using new data collection and processing methods to query a long-term dataset.

Before this study was initiated, there were no reproductive parameters available from sightings of live dolphins in Ireland. Although all age classes of individual had been observed in the Shannon Estuary population, the demographics of the population were relatively unknown. This resulted in many studies using surrogate data from populations in very different geographical locations with different societal makeups and/or different population sizes. Life history parameters such as female reproductive success and inter-birth intervals are important for the conservation management of long-lived marine mammal species. Based on the techniques of other studies, this research quantitatively assesses similar variables for the Shannon Estuary bottlenose dolphin population (Chapter 2 (Manuscript I)).

B. To establish a full list of observed behaviours, creating an ethogram for behavioural research, and assessing the use of such an ethogram by multiple observers and by untrained marine biologists.

The study of animal behaviour, particularly of individually recognisable animals, must begin with baseline data before the introduction of more complex analytical procedures. The behavioural research in this study therefore commences (Chapter 3 (Manuscript II)) with the production of an ethogram to describe activity states and behavioural events in the population before quantifying the behavioural data recorded for this population. This is important to the field of dolphin behavioural research by beginning to establish a scientific record of the behaviour of this population and also by providing results which could be used to compare the Shannon Estuary dolphins with other long-term bottlenose dolphin study populations.

C. To better understand the social structure of the population using a larger dataset, classification of the population by age, sex and area use, and revised analytical techniques.

Extremely dynamic societies of bottlenose dolphins with complex social structures have been described elsewhere. Sophisticated studies of vertebrate social structure, especially when individuals are individually identifiable, can lead to the provision of detailed measures and displays of social systems. In bottlenose dolphin societies, differences in patterns of association have been discovered in relation to sex and age class. In other studies where bottlenose dolphin groups do not seem to be segregated by sex or age class, some of these demographically mixed groups have formed socially distinct communities within populations. Previous work on the social structure of the population by Foley *et al.* (2010) and Ingram (2000) used much smaller datasets for analysis and did not have access to information on individual age, sex or area use to investigate the structure of the bottlenose dolphin society in detail. Chapter 4 (Manuscript III) investigates the overall population structure and then examines the social organisation in relation to individuals classed by sex, age and area use.

D. To explore fine-scale sociality by conducting individual focal follows on cetaceans in Ireland for the first time and analysing these behavioural observations at the individual level.

While network analyses of social structure yield interesting results, the knowledge of social behaviour at an individual level is central to the understanding of the dynamics of social relationships. To collect behavioural data on individuals, the present study makes use of two focal follow sampling techniques on bottlenose dolphins for the first time in Ireland. This provides the basis for investigating dyadic associations and sex-specific differences in activity budgets at an individual level using focal follow data (Chapter 5 (Manuscript IV)). Preferred nearest neighbours and sex differences in activity budgets and exhibited behaviours are investigated in an in-depth analysis of focal follow data. Male alliance formation is an important component of many bottlenose dolphin societies and this study seeks to provide potential evidence for or against the formation of male alliances in the Shannon Estuary population.

1.7.2 Hypotheses and theoretical assumptions

As indicated above, the main objectives of this project were to establish a much better knowledge of some of the central social and behavioural features of the Shannon Estuary dolphins. For this reason, most of the results in this thesis are primarily descriptive in character: they provide a much more accurate description of the behaviour and social structure of this population than previous research.

This is not to say that this research proceeded without hypotheses. On the contrary, many of the analyses in Chapters 2-5 test straightforward hypotheses of the sort that are typical of social and behavioural research. For example, the sex difference in activity budgets (Chapter 5 (Manuscript IV)) is tested against the null hypothesis that there are no such differences. In some cases, a guiding hypothesis was drawn from studies of other populations. For example, the hypothesis that the social structure would exhibit a clear pattern of single-sex groups and strong within-sex-class associations (Chapter 4 (Manuscript III)) was based on research in Shark Bay and Sarasota Bay demonstrating the existence of male dolphin alliances. These hypotheses are informed by the generally-shared theoretical assumptions common to cetacean social and behavioural research, such as the assumption that the primary units of social analysis are interactions among individuals, that bottlenose dolphins live in complex fission-fusion societies, and that their behaviour and social structure are often patterned by sex, age class and location (Connor *et al.* 2000b, Whitehead 2008).

Some of the discussions of Chapters 4-6 suggest hypotheses about the reasons for similarities and differences between the behaviour and social structure of this population and that of others. For example, I suggest that increased probability of reproductive success may be important in explaining female-male associations in the Shannon Estuary (Chapter 6). These hypotheses are generally drawn from the received theoretical framework of evolutionary biology which seeks to explain behaviour through its effect on individual or inclusive fitness.

1.7.3 Overall contribution

Overall, this thesis provides the first baseline information on reproductive parameters and behaviour for bottlenose dolphins in Ireland, along with a detailed analysis of the population's social structure and individual sociality measures. This work is important in an international context because it provides information on a bottlenose dolphin population of high conservation importance in Ireland to the global scientific community. It extends the knowledge available on complex societies of intelligent species and informs the management of small resident communities for extrapolation globally. By bringing new data for this population into the international discussion, this work contributes to a deeper understanding of cetacean life history and behaviour. To achieve this understanding of the biology and ecology of complex organisms, it is necessary to study a species in all of the environments it inhabits. In addition, studying bottlenose dolphins in varying social systems contributes to an increase in knowledge of social structure and the evolutionary drivers that may have affected differences among them. These results could have a strong influence on conservation and management priorities. Evidence-based advice for conservation comes from an overall consideration of how species live, behave and interact with conspecifics.

1.8 List of manuscripts

All the data chapters in this thesis were written and formatted as journal manuscripts and have either been published or will be submitted as peer-reviewed papers:

Manuscript I (Appendix A)

Baker, I., J. O'Brien, K. McHugh and S. Berrow. 2018. Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Marine Biology 165:15.

Manuscript II (Appendix B)

Baker, I., J. O’Brien, K. McHugh and S. Berrow. 2017. An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Aquatic Mammals 43:594-613.

Manuscript III (Appendix C)

Baker, I., J. O’Brien, K. McHugh, S. N. Ingram and S. Berrow. 2017. Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations. Marine Mammal Science.

Manuscript IV

Baker, I., J. O’Brien, K. McHugh and S. Berrow. *To be submitted.* Fine-scale sociality reveals female-male affiliations and absence of male alliances in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland.

I also co-authored two other published peer-reviewed articles over the course of my PhD:

Appendix D

Levesque, S., K. Reusch, I. Baker, J. O'Brien and S. Berrow. 2016. Photo-identification of bottlenose dolphins (*Tursiops truncatus*) in Tralee Bay and Brandon Bay, Co. Kerry: A case for SAC boundary extension. Biology and Environment: Proceedings of the Royal Irish Academy 116B:1-10.

Appendix E

O'Brien, J., I. Baker, J. Barker, S. Berrow, C. Ryan, M. O'Connell and B. O'Donoghue. 2014. The first confirmed successful refloat of a stranded bottlenose dolphin (*Tursiops truncatus*) in Ireland and subsequent resighting with a neonate. Aquatic Mammals 40:191-194.

I also presented posters at four international conferences:

Appendix F

Poster 1. Bottlenose dolphin life history and population demographics in the Shannon Estuary, Ireland. Society for Marine Mammalogy (SMM) Conference, Halifax, Nova Scotia, Canada, 2017.

Poster 2. Longitudinal study of a live-stranded female bottlenose dolphin in the Shannon Estuary, Ireland. European Cetacean Society (ECS) Conference, Funchal, Madeira, 2016.

Poster 3. Exploring the social structure of the resident bottlenose dolphin population in the Shannon Estuary, Ireland. SMM Conference, San Francisco, USA, 2015.

Poster 4. Long-term boat-based monitoring of bottlenose dolphins (*T. truncatus*) in the Shannon Estuary, Ireland. ECS Conference, Setúbal, Portugal, 2013.

In addition, I designed and wrote a volunteer information document (not included in this thesis) and a protocols handbook, discovered a number of additional findings over the course of my work, and conducted a Population Viability Analysis:

Appendix G

Baker, I. 2015. Researcher's Guide to Protocols for Fieldwork and Data Entry. Third edition. Shannon Dolphin and Wildlife Foundation. 32 pp.

Appendix H

Notes on additional research findings.

Appendix I

A Population Viability Analysis for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland.

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Chapter 2

Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

This chapter is a reproduction of the following published paper (published version can be found in Appendix A).

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2 Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

This study investigates the female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, using long-term relational sightings and photographic databases. Data were collected between 2008 and 2016, during 654 boat-based surveys, from two dolphin-watching vessels and a research vessel. During 1,018 sightings, 4,231 identifications of 184 individual dolphins were recorded. The population size was charted through direct counts of known dolphins from 2011 to 2015 (mean = 142, range = 131-150), with 145 extant individuals in 2015: 80 adults, 25 juveniles and 40 calves. Excluding dependent calves, 121 individuals were sighted, of whom 98% (*n* = 119) were sighted in multiple years, with 64% (*n* = 77) sighted in all four years (2012-2015). Between 2008 and 2016, 37 reproductive females and 69 dependent calves were recorded. Overall, 35% (*n* = 13) of these females were sighted with one calf, 43% (*n* = 16) with two calves, and 22% (*n* = 8) with three calves. An average of seven (range = 3-10) calves were born each year. Parturition peaked in July. Weaning ages ranged from 2.0-4.1 (mean = 2.9) years. The mean inter-birth interval ranged between 2.7±0.6 to 3.5±1.3 years, depending on method used. Mean annual calving rate was 0.29 young-of-year/reproductive female/year. Average crude birth rate was 0.07±0.01. Fecundity was 0.26±0.03. An average 11% of newborn calves were lost before age 1. These results are generally within the lower range of values reported for similar populations and provide essential data for conservation management and global bottlenose dolphin research.

Key words bottlenose dolphin; reproductive rates; calving; inter-birth interval; weaning; *Tursiops truncatus*; photo-identification

2.1 Introduction

Bottlenose dolphins (*Tursiops* spp.) are found across the globe in temperate and tropical waters and in a range of habitats (Wells and Scott 1999). As a result, different populations are subject to different ecological and environmental conditions and pressures. Marked variations in population dynamics, behavior and social structure have also been reported, perhaps due to the high level of intelligence of the species (Connor et al. 2000). In light of these socio-environmental differences between demographically different populations, it is to be expected that the life history parameters of populations may also vary considerably. This makes it essential to establish baseline life history parameters for specific populations to explore species ecology and inform management.

The production of reliable life history parameters is dependent on longitudinal studies with consistent continuous data collection (Wells 1991; Mann and Karniski 2017). Repeated sightings of identifiable individuals over a long time period allows for the aggregation of individual reproductive histories and thus, the estimation of reproductive parameters such as birth rates, calf mortality and inter-birth intervals (Fruet et al. 2015; Tezanos-Pinto et al. 2015). For long-lived, slow-reproducing mammals like bottlenose dolphins, these long-term datasets are essential for producing both individual- and population-level parameters for demographics, patterns of reproduction and a better understanding of the basic biology of the species across its global range (Fruet et al. 2015).

Female reproductive parameters such as inter-birth intervals (Connor et al. 2000) and reproductive success (Fruet et al. 2015) play a crucial role in determining long-term population viability. For example, in a study of two Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations, in Shark Bay and Bunbury, Australia, Manlik et al. (2016) used a Population Viability Analysis (PVA) to demonstrate that reproductive rates had a stronger influence on long-term viability than adult survival rates. Thus, population-specific life history data are essential for the production and interpretation of reliable PVA results and the investigation of long-term population trends. Studies of population dynamics have often used life history parameters from other study populations because baseline data were not available for the population in question, but this may be misleading (Arso Civil et al. 2017).

Understanding the life history characteristics of a specific population is also essential for conservation and management, since the results can have significant effects on management plans. For example, Manlik et al. (2016) concluded that focusing management on calf survival was the best way to improve the viability of the Bunbury bottlenose dolphin population that is forecast to decline.

While there have been many studies of bottlenose dolphin reproductive parameters worldwide, there are few from Europe and none from Ireland. The bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland are a study population with a high dolphin encounter rate, year-round presence and long-term site fidelity (Berrow 2009; Levesque et al. 2016 (Appendix D)). The population has been shown to be genetically discrete (Mirimin et al. 2011). The development of a dolphin-watching tourism industry has enabled systematic long-term data collection on this population, with two dolphin-watching boats providing opportunistic platforms for research (Berrow and Holmes 1999). Photo-identification studies have been conducted since the early 1990s, resulting in the identification of many recognizable individuals (Berrow et al. 1996; Ingram 2000; Berrow et al. 2012).

Population estimates from previous studies of bottlenose dolphins in the Shannon Estuary using mark-recapture statistical models (with limited numbers of surveys) have estimated the extant population size to be 113 ± 14 (Ingram 2000), 121 ± 14 (Ingram and Rogan 2003), 140 ± 12 (Englund et al. 2007), 114 ± 17 (Englund et al. 2008), 107 ± 12 (Berrow et al. 2012), and 114 ± 14 (Rogan et al. 2015). These studies made use of mark-recapture techniques to derive abundance estimates and results from six surveys over a 20-year period suggest the population is stable. The Lower River Shannon was designated as a Special Area of Conservation (SAC) in 2000 under the EU Habitats Directive with bottlenose dolphins as a qualifying interest (NPWS 2012). The demographics (age and sex composition) of this population have not yet been described.

Annual sightings of newborn calves in the Shannon Estuary indicate that the population is reproducing; however, no reproductive parameters have been produced for this population. Previous work on population viability (*e.g.*, the population viability analysis carried out by Englund *et al.* (2008)) made use of parameters from very dissimilar populations and study sites, which may not be representative of the population.

In this study, we used a long-term database of photo-id and related sightings data, based on surveys conducted between 2008 and 2016, to describe the demographics and estimate critical life history parameters for the Shannon Estuary bottlenose dolphin population. This provided similar data to that collected for populations elsewhere, enabling comparisons across populations. In contrast to previous work, the detailed analysis of high-quality digital photographs has allowed us to track every individual in the population over five years, including those that were previously regarded as “unmarked”. Thus, we used a novel “headcount” technique to produce an updated population estimate for this population. Our two main aims were (i) to describe the Shannon Estuary bottlenose dolphin population’s size and demography (age and sex class) and (ii) to calculate baseline reproductive parameters for the Shannon Estuary bottlenose dolphin population. Similar to the study of New Zealand bottlenose dolphins by Tezanos-Pinto et al. (2015), we expected to obtain similar values to those reported for other populations using similar methodologies, and for our values to be most similar to those found in other temperate-water European populations such as around the British Isles.

2.2 Methods

2.2.1 Study site

The study site was the Lower River Shannon Special Area of Conservation (Site Code: 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland’s west coast between Co. Clare, Co. Kerry and Co. Limerick (52°36'N, 9°38'W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 2.1).

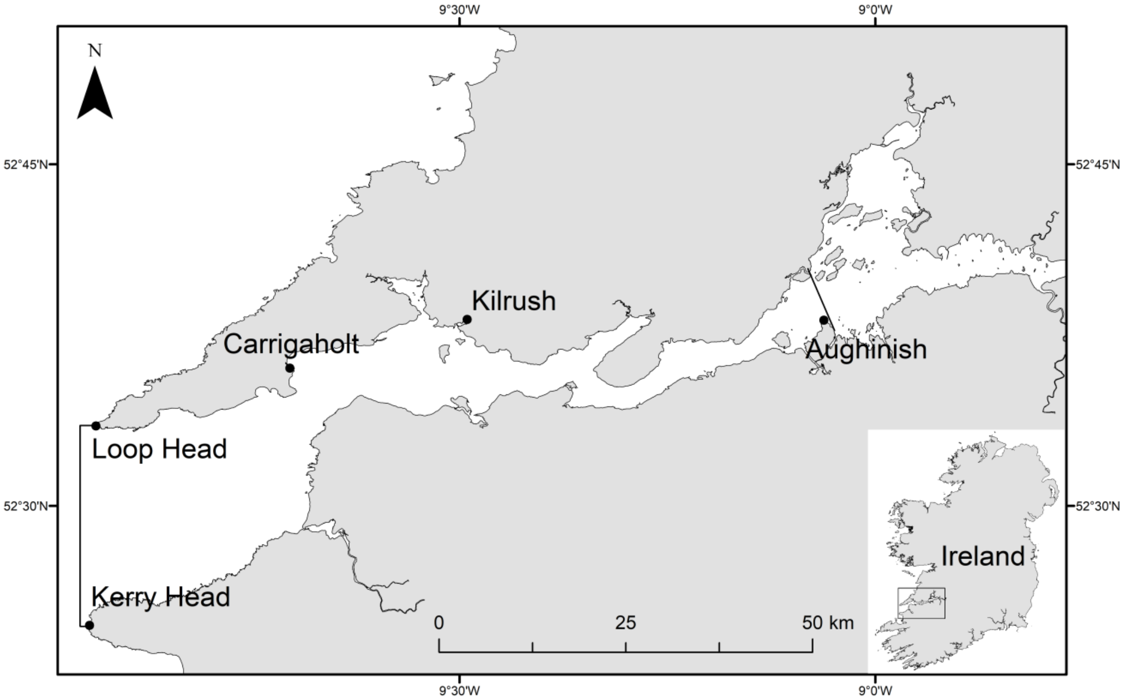

Figure 2.1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area surveyed during this study

2.2.2 Data collection

Boat-based surveys were conducted between March and November each year from 2008 to 2016 on board three vessels – two commercial dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats provided opportunistic platforms for research, operating independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 2.1). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor. Trained onboard observers located dolphins visually by eye and with the use of binoculars (Minox 7x50 or 8x42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~5 m, while observers on the Kilrush tour boat and research vessel were positioned on the bow of the boats at <2 m above sea level.

During surveys, a dolphin encounter or “sighting” began when at least one dolphin was within 100 m of the vessel and ended after ≤30 minutes due to national regulations, designed to minimise the potential impact of dolphin-watching on the dolphin population (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and at a distance of approximately 100 m unless the dolphins approached the boat. Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin identifications (IDs), mother-calf pair presence, group size and composition, environmental measures (including swell and sea state), location (using a Garmin 72H GPS), activity states (*e.g.*, travel) and behavioral events (*e.g.*, leap, see Baker et al. 2017a (Chapter 3)). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al. 2011).

Attempts were made to photograph each individual in each group (regardless of their degree of marking or individual differences in behavior) for the photo-identification of individual dolphins using unique markings on their dorsal fins and bodies (Würsig and Würsig 1977; Würsig and Jefferson 1990). Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70-300 mm lenses).

2.2.3 Data management

Following Shannon Dolphin and Wildlife Foundation (SDWF) protocols (Baker 2015 (Appendix G)), images from all surveys and sightings were maintained in a database using the photographic software environment *IMatch 5.6* (https://photools.com). A digital photo-id catalogue housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities and persistent skin lesions, by using the filter function in *IMatch* to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then re-matched. The final identifications of every individual dolphin in every sighting were verified by the lead researcher who had the most photo-id experience, as recommended by Pearson et al. (2016). These methods are similar to standardized protocols used by the Sarasota Dolphin Research Program (SDRP 2006).

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of *FinBase* (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams et al. 2006). The *FinBase* Catalog Browser shows the best left and right side image of the dorsal fin for each unique individual in the photo-id catalogue. It also contains the best dorsal fin photo for each individual for every sighting of that individual in the database.

All dorsal fin photographs in *FinBase* were graded for Photographic Quality by the lead researcher exclusively (Urian et al. 2015), before each being assigned to their specific sighting and survey using the *FinBase* Match/Catalog form (Adams et al. 2006). Each photograph was graded according to focus, contrast, angle, visibility and distance. Each of these fields was limited to a set of fixed scoring options which the user could choose from (Adams 2013). When a dorsal fin image was added to a sighting in *FinBase*, the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program.

Population demographics and adult/juvenile mortality were estimated using data collected during 2011-2015 exclusively, when dolphin monitoring surveys were consistent and protocols were clearly defined (Baker 2015 (Appendix G)), whereas reproductive parameters were determined using data collected between 2008-2016 to allow a more longitudinal investigation. Sighting data for reproductive females and their calves were produced through a *FinBase* query of individual and shared sightings within the database. In some cases, including all cases in which mother-calf pairs were sighted <3 times, these data were supplemented with further photographic evidence from the *IMatch* database.

A separate matrilineal database was maintained to keep specific records of estimated birth and “weaning” dates from the first and last sightings of mothers with calves. Here, we define weaning date/age as the date/age of separation (*i.e.*, independence) of a calf from its mother (rather than weaning in terms of nutritional independence). A mother had to have been seen at least three times (mean = 22 sightings) without her calf before weaning was confirmed. Additionally, information on deaths of calves <1 yr old and sightings of known weaned juveniles was also recorded. Calf mortality was estimated only for calves <1 yr old, whose mothers were frequently seen following the birth and subsequent disappearance of the dependent calf. Subsets of data from *FinBase* and the matrilineal database were used to calculate some reproductive parameters, such as age at weaning.

The large dataset and specialized long-term databases maintained on this relatively small population, coupled with the high encounter rate and in-depth knowledge of individual IDs, provided a unique and robust dataset for investigating the demographics and life history parameters of this dolphin population.

2.2.4 Data classification

(i) Age determination

Individuals were assigned to one of four relative age classes on the basis of observations of individual estimated size and body length (Smith et al. 2013), reproductive state and/or knowledge of long-term life history. Adults were larger and darker in color than juveniles, and sometimes with a dependent calf (Bearzi et al. 1997; Wilson et al. 1999). Juveniles were less than two-thirds the size of adults and were not themselves dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years prior to weaning. Calves were those dolphins >1 yr of age that were consistently in association with their adult mothers. Young-of-year (YOY) were <1 yr old, often with visible prominent fetal folds (dark vertical lines on the body) and swimming in a characteristic infant position with their mothers (Mann and Smuts 1999).

(ii) Sex determination

The sex of individual dolphins was determined through (1) genetic evidence from tissue samples collected through biopsy sampling (n = 37; collected under NPWS permits; Berrow et al. 2002; Mirimin et al. 2011); (2) photographs of the genital area (n = 1); and, (3) in the case of adult females, observations of the mother swimming in close association with a dependent calf (n = 25). For females identified through association with a calf, numbers of shared mother-calf sightings were determined using a specially developed query in *FinBase* and ranged from 1 to 72 (mean = 10). Following Tezanos-Pinto's (2009) definitions, reproductive females (*i.e.*, sexually mature females) were those individuals who had given birth to viable calves during the study period, whereas non-reproductive females were adults positively sexed as females that were never sighted in close association with a calf.

2.2.5 Data analysis

(i) Population size, demography and adult/juvenile mortality

In order to estimate population size, we used our extensive knowledge of catalogued individuals from five recent data-rich years (2011-2015) to produce an estimate of the number of individuals extant in the population. First, we examined the number of sightings of individual dolphins in each year, incorporating age class, and including a discovery curve which reached a clear plateau by 2015. Then, using sighting histories and age class determination, we calculated the number of individuals known to be extant in the population per year. The assumption was made that if an adult/juvenile was alive in a subsequent year, it was alive in all previous years.

Presumed deaths of well-known individuals were also incorporated based on their previous annual sighting rates and their absence during the 2015 and 2016 field seasons. Individuals not recorded since 2013 or earlier all had additional sightings in the database from previous years (2008-2012) but no sightings in 2014, 2015 or 2016. Individuals not recorded since 2014 each had at least one sighting (range = 1-22 sightings y^{-1}) in each of at least two (range = 2-6 y) of the previous six years (2008-2013), but no sightings in 2015 or 2016. Using these disappearances of adult/juvenile individuals from the population between 2012 and 2015, we calculated the mean annual maximum mortality rate as “$l/(n\text{-}b)$” where l = number of individual disappearances, n = extant population count and b = number of calves born (Wells and Scott 1990).

We calculated the mean extant population size by directly counting the number of catalogued individuals known to be alive in each year and averaging it (Wells and Scott 1990). To visualize how the size and demography of the population changed over time, we constructed a stacked bar chart of population size in each year and incorporated age class demography, adult/juvenile and calf deaths. To investigate population coverage, we plotted the frequency of resightings of individual dolphins in the Shannon Estuary and constructed a histogram of counts of individual sightings.

(ii) Female reproductive rates

The entire 2008-2016 dataset was used to document associations between mothers and calves in the study population. The number of annual births was a count of individual calves born in the population during each study year. To test if differences in numbers of surveys each year had an effect on the number of recorded births, a linear regression analysis was carried out in *R* (*R* Core Team 2016). The number of calves born to each female individually was also calculated.

In addition, the number of annual calf deaths was counted. If a mother had been sighted ≥2 times with a newborn calf, but then sighted on multiple occasions (≥2 sightings) without it, less than one year later, we assumed the calf had died. Minimum weaning age in bottlenose dolphins has been estimated to be 18-20 months (Smolker et al. 1992; Wells and Scott 1999), so all calves under this age and that were no longer with their mothers were believed to be dead. Although minimum weaning age is likely to differ among populations, there was no evidence of bottlenose dolphin calves weaning before they were one year old, so we used a minimum of 1 y to infer calf death as a conservative measure. Consistent with Tezanos-Pinto et al. (2015), a calf that was associated with an individually identifiable reproductive female during its first year was assumed to be the same calf, providing it looked older over consecutive sightings. Additionally, in some cases, it was possible to identify calves even as young as <1 yr due to distinctive markings and/or lesions on their bodies and dorsal fins, and, in three cases, deformities such as scoliosis.

There were some cases where the first sighting of newborns occurred at the beginning of the field season (usually May) but it was clear that they were not recently born. Thus, estimated date of birth (DOB) was calculated as the mid-point between the date of the last sighting of the mother without a newborn calf and the date of her first sighting with a newborn calf (Wells et al. 1987; Urian et al. 1996). We primarily used the mid-point rather than the date of the first sighting (of the mother-calf pair) because the first sighting method of DOB estimation would have suggested that older calves were much younger than their actual age. Even so, the use of imprecise (>60 d) DOBs was restricted for analyses in which date was an important factor.

To investigate temporal patterns in reproduction, DOB estimates were used to plot births across the four main months for which data were available (Jun-Sep), using the ordinal date (*i.e.*, day-of-year) of the last sighting of mother without calf and the date of the first sighting of mother with newborn calf. We then overlaid a plot of number of births per month using the mid-point between dates (to estimate month of birth) to illustrate patterns of parturition for this population.

Calving interval or inter-birth interval (IBI) was estimated as the time elapsed between subsequent births (Mitcheson 2008; Arso Civil 2015). We used three approaches to calculate IBIs. The first two approaches, based on dates, used (a) the estimated date of birth (DOB) for each calf and (b) the first sighting of a female with her initial calf and then the first sighting of the same female with her subsequent calf; (c) the third approach used year of birth. In the first method, IBIs were calculated for individual mothers with two consecutive births where the estimated DOB was available for both calves. The IBI was calculated as the difference between these two dates divided by 365.25 (*i.e.*, IBI in years). Using the second method, each IBI was estimated as the time elapsed between when a female was first sighted with her initial newborn calf to the date of the first sighting of that female with her subsequent newborn calf (Tezanos-Pinto et al. 2015). These methods were restricted to reproductive females who had consecutive calves and where the fate of the calf was known in all cases.

To estimate IBIs using the larger dataset of sighting histories for all reproductive females in this study, we calculated the inter-birth interval based on annual calving (*i.e.*, year of birth rather than date of birth). IBIs were calculated as the number of years between births and charted for all female dolphins with consecutive births (*i.e.*, those who had 2 or more calves) and known years of calf birth during the study period.

Weaning ages were determined for individuals with known birth and weaning dates, including those who had been observed as independent juveniles post-weaning, and a mean weaning age was calculated. A calf was presumed to have weaned if it was >1 yr old and it and/or its mother had been observed independently in at least three subsequent dolphin group sightings.

Annual calving rate was estimated as the total number of young-of-year (YOY) divided by the total number of reproductive females sighted during that year (Baker et al. 1987; Tezanos-Pinto et al. 2015). We used a weighted average to calculate mean annual calving rate and a binomial variance to calculate the confidence interval for calving rates across the years with 95% limits (Baker et al. 1987; Wells and Scott 1990; Tezanos-Pinto 2009).

The annual crude birth rate was calculated as the total number of documented births divided by the total abundance estimate for the dolphin population in each year

(Fruet et al. 2015). We used the catalogue-based abundance estimates from 2012-2015 to calculate crude birth rates. The same years were used to calculate fecundity – the ratio between the number of surviving calves and the number of reproductive females in the population (Wells and Scott 1990) – because we knew the number of known births surviving to one year with certainty for these years. Overall mean fecundity is a measure of the potential reproductive capacity of the population (Fruet et al. 2015). Additionally, using Arso Civil *et al.*'s (2017) definition (which takes into account all births and not only surviving calves), where fecundity rate is defined as 'the annual probability of a mature female having a calf', we also estimated fecundity rate as the reciprocal of the expected IBI, using the average IBI from the three methods used to calculate IBIs.

Calf mortality was estimated as the number of YOYs (<1 yr old calves) that were inferred to have died, divided by the total number of YOYs assigned to individual reproductive females (Wells and Scott 1990) for 2012-2015.

Mean female reproductive success of the Shannon Estuary bottlenose dolphin population was quantified by calculating how many calves each female had to the minimum age at weaning and the mean and standard deviation for them (Fruet et al. 2015). It was assumed that a female reproduced successfully if her calf survived from birth to the minimum age at weaning estimated for Shannon Estuary bottlenose dolphins (this study; Mann et al. 2000; Fruet et al. 2015).

Mother-calf association longevity was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any situation- or sex-related patterns associated with these pairings.

2.3 Results

2.3.1 Survey effort and photo-identification

Between 2008 and 2016, 654 surveys (1,018 sightings) were carried out, during which 213,056 photographs were taken; 83,527 of these were used for the photographic analysis of individually identifiable bottlenose dolphins. Surveys were conducted between March and November but the majority (84%) of surveys took place during June, July and August. In total, 4,231 identifications were made of 184 distinct individual dolphins over the nine study years.

2.3.2 Population size, demography and adult/juvenile mortality

The number of sightings of dolphin groups varied in each year, from 34 sightings (34 surveys) in 2011, 95 sightings (61 surveys) in 2012, 119 sightings (86 surveys) in 2013, 180 sightings (111 surveys) in 2014 to 128 sightings (95 surveys) in 2015, with similar proportions of adults, juveniles and calves sighted in each year (Fig. 2.2). The number of unique individual dolphins sighted per annum varied from 79 in 2011 to 140 in 2014, with 135 individuals sighted in the most recent study year (2015). A discovery curve showed a clear plateau had been reached with only two new individuals added to the catalogue during 2014 and no new individuals added during 2015 (excluding additions of newborn calves to the population).

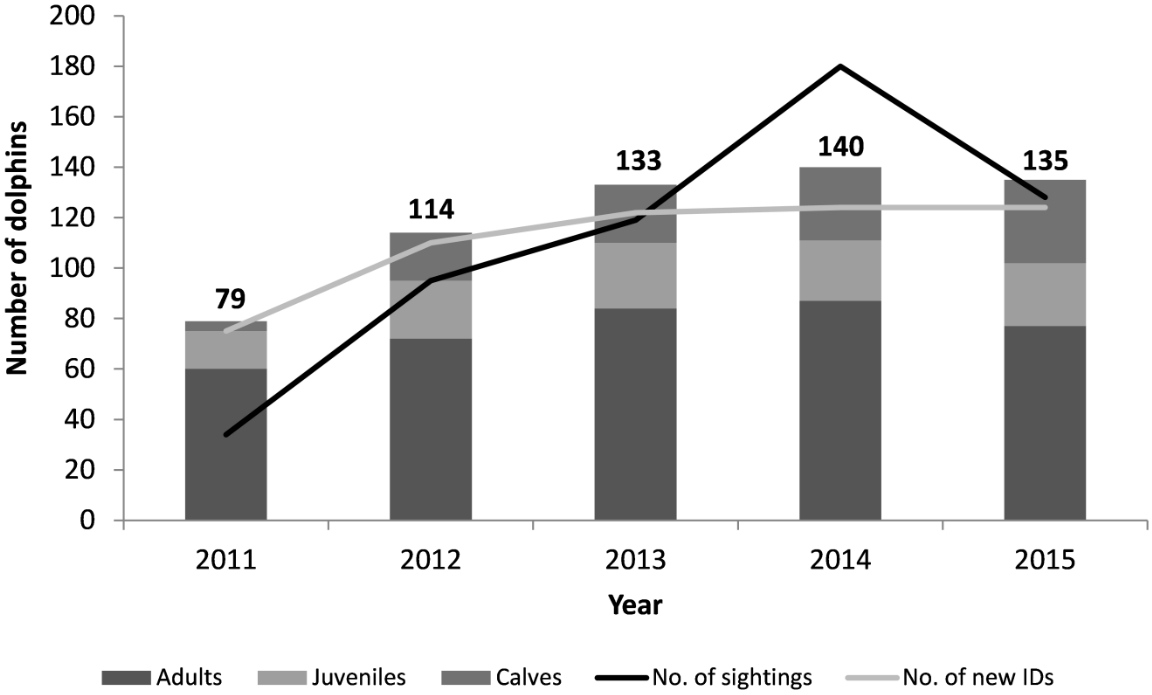

Figure 2.2 The number of individual bottlenose dolphins identified each year (bars), the number of sightings (*i.e.*, dolphin group encounters) with photo-id records (black line) and the number of new (non-calf) IDs recorded (*i.e.*, discovery curve; grey line) in the Shannon Estuary between 2011 and 2015, with individual dolphins categorized into age classes (adults, juveniles, calves)

The mean extant population size was estimated to be 142 bottlenose dolphins. Population size estimates in each year (2011-2015), incorporating age class demography and the presumed deaths of well-known individuals varied from 131 in 2011 to 150 in 2014 (Fig. 2.3). Individual records of estimated adult/juvenile dolphin deaths correspond to counts of five, one, two and 10 individuals having not been sighted since 2011, 2012, 2013 and 2014 respectively, despite multiple sightings of these individuals in previous years and 325 subsequent sightings of dolphin groups (during 212 surveys) in 2015 and 2016 (Fig. 2.3). Therefore, a total of 18 individual adult/juvenile dolphins were not sighted during population surveys between 2012 and 2015. Thus, the mean annual maximum mortality rate was 0.038±0.0286.

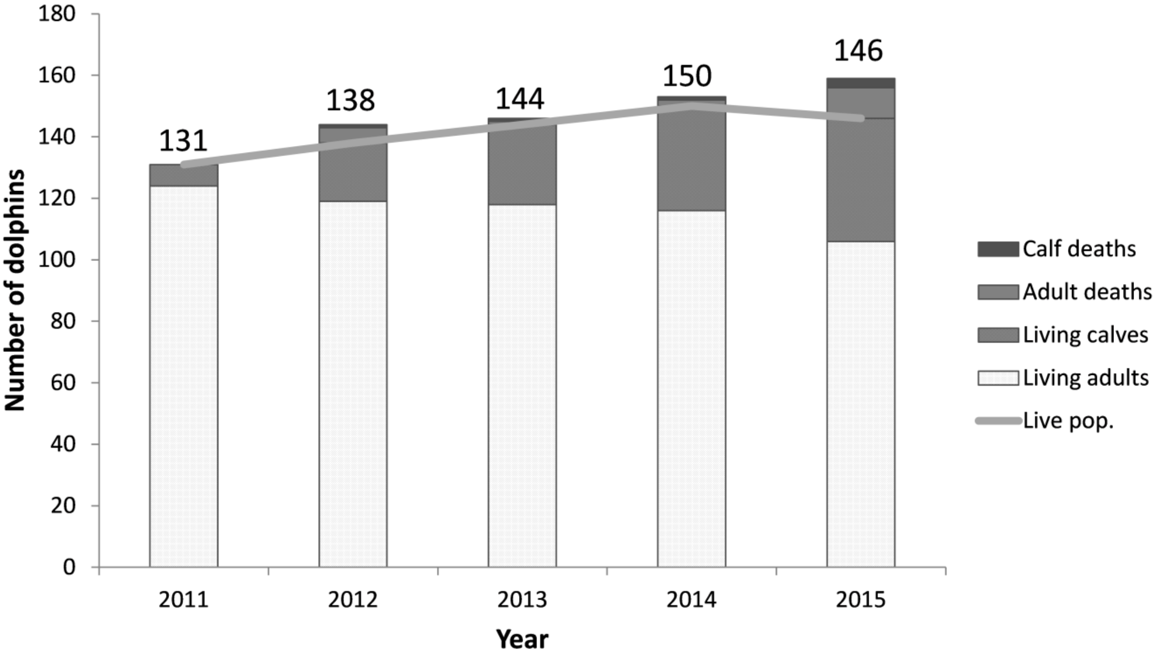

Figure 2.3 Estimates of the extant population size of bottlenose dolphins in the Shannon Estuary from 2011 to 2015, incorporating age class (“adults” includes adults and juveniles, “calves” includes all dependent individuals) and possible deaths of well-known individuals. The population size figures are slightly larger than the number of sightings of known individual dolphins per year (Fig. 2.2) because some individuals were not seen in years when they were still alive

Excluding 2011, a year with fewer (<50%) surveys than in other years, and comparing sighting numbers to extant population estimates, an average 92% (*n* = 130) of the population was recorded each year (2012-2015). In 2015, an estimated 93% (*n* = 135) of the population was recorded during dolphin surveys. Between 2012 and 2015, excluding dependent calves, 121 individuals were identified, of which an average of 106 individuals (88%) were sighted each year. Ninety-eight percent of these individuals (*n* = 119) were sighted in multiple years, with 64% (*n* = 77) seen in all four years from 2012 to 2015 (Fig. 2.4A). The mean number of sightings per individual was 24.4±21.7 (*n* = 121, range = 1-101; Fig. 2.4B).

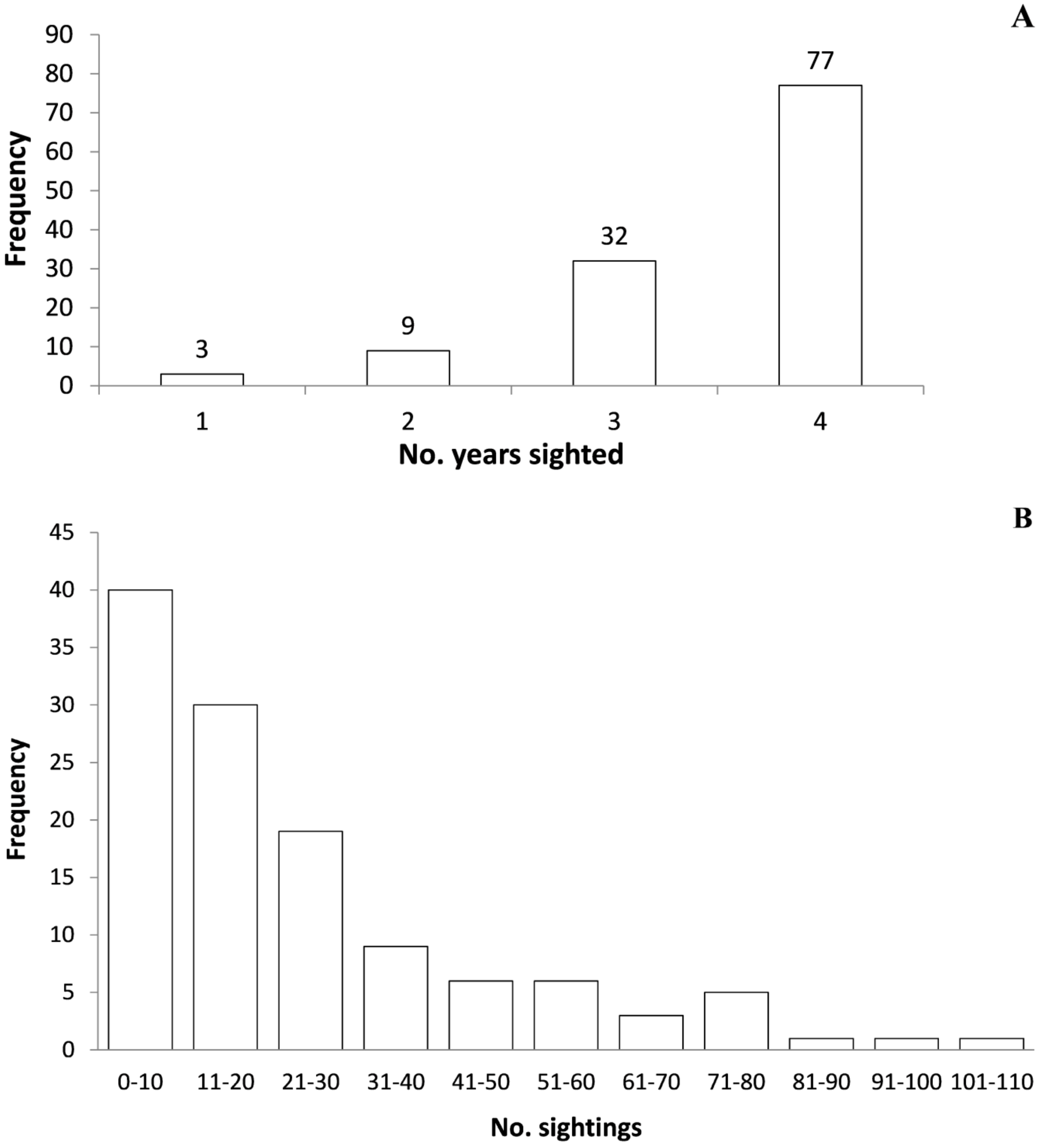

Figure 2.4 Histograms of juvenile/adult bottlenose dolphin sightings (*n* = 121) by number of (A) years sighted and (B) sightings (2012-2015)

Of all 167 individuals sighted between 2012 and 2015, 63 were of known sex (49 female, 14 male) and 104 were of unknown sex. Age class, based on first assignation, was divided into 91 adults, 30 juveniles, 13 calves and 33 YOYs. In 2015, the population consisted of 145 unique individuals – 55% adults (*n* = 80), 17% juveniles (*n* = 25) and 28% calves/YOYs (*n* = 40). Thus, the adult:calf ratio of the population was 2:1. Of the 105 adults and juveniles, sex was known for 49% (*n* = 51) of individuals – 42 females and 9 males.

2.3.3 Female reproductive parameters

(i) Mothers and calves

Between 2008 and 2016, 1,254 individual identifications of 37 reproductive females were made. Of these, 57% (*n* = 719) were identifications of reproductive females with a calf (Table 2.1). The sex of these reproductive females was determined using associations with calves (*n* = 24), a combination of biopsy tissue samples and calves (*n* = 12) and observation of the genital slit during a live-stranding and subsequent calves (*n* = 1; O'Brien et al. 2014 (Appendix E); Appendix F, Poster 2). Of these 37 females, all (100%) were sighted in more than one year and 13 (35%) were sighted in all nine of the study years, with an average of 34 sightings per female (range = 6-108; Table 2.1).

Of the 37 reproductive females, 35% (*n* = 13) were sighted with only one calf, 43% (*n* = 16) with two successive calves, and 22% (*n* = 8) with three successive calves. The maximum number of documented births per female in the 9-yr study was three calves. The mean number of reproductive females in the population per year from 2008 to 2016 was 26 (range = 8-35; Table 2.1). A total of 69 dependent calves were recorded during the study period with year of birth determined for 67 of these calves. There were 831 sightings of these 69 calves with an average of 12 sightings per calf (range = 1-88; Table 2.1).

Table 2.1 Sightings of reproductive females (ID# = individual photo-id catalogue number) and their calves from 2008 to 2016 in the Shannon Estuary, including sightings of females without a calf (marked with a "•") and with their first (1), second (2), or third (3) calves (different numbers indicate a different calf for each female). Calf ages were categorized as young-of-year (<1 yr old; YC), calves (1-3 yr old; C) and juveniles (>3 yr old; J). The total number of sightings of each female (NF), total number of sightings of each female with each of her calves (WC1, WC2, WC3; *i.e.*, WC1 = number of sightings with first calf), and total number of sightings of each calf (NC1 = first calf, NC2 = second calf, NC3 = third calf) are given. The total number of calves born to each female (#C), the number of reproductive females in each year (#F) and the number of calves born in each year (#YOY) are also shown. Underlined female IDs are those that were also genetically confirmed as female. Year of birth could not be determined for the first calves of ID#s 225 and 280 and they are therefore not included in the total of number of calves born per year (#YOY). ID# 242 was first identified as a female through observations of the genital slit during her live-stranding (O'Brien et al. 2014 (Appendix E); Appendix F, Poster 2). Blank cells indicate no sighting of the female in that year. Dark grey cells indicate years with no sighting where year of birth was inferred for the calf (after Arso Civil 2015; Tezanos-Pinto et al. 2015)

	Years									**Sightings 2008-2016**							
ID#	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**NF**	**WC1**	**WC2**	**WC3**	**NC1**	**NC2**	**NC3**	**#C**
006	•	•	•	•	YC1	C1	C1	YC2		108	72	2		88	2		2
011	•	•	YC1	C1	C1	J1	J1	J1	J1	29	19			19			1
019	•		YC1			•	•	•	•	26	1			1			1
027	YC1		•		•	•	•	•		10	1			1			1
042	YC1		C1	J1	J1	YC2	C1	C1	J1	18	4	12		6	12		2
044	•	•	•	•	•	•	YC1	C1	YC2	64	36	1		37	1		2
045	•	•	•	•	YC1	C1	C1	YC2	C2	44	18	4		19	4		2

	Years									**Sightings 2008-2016**							
ID#	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**NF**	**WC1**	**WC2**	**WC3**	**NC1**	**NC2**	**NC3**	**#C**
052	•	YC1		•	J1	J1	•	YC2	•	30	3	3		3	3		2
070	•	YC1	C1		YC2	•	YC3		•	15	5	3	1	5	3	1	3
071	YC1	C1	C1	J1	J1	J1	YC2	C2	C2	79	28	23		32	27		2
085	•	•	•	•	•	YC1	•	•	YC2	43	4	1		4	1		2
092	YC1	C1								6	2			2			1
096	•	YC1	C1	C1	J1	YC2	C2	C2	J2	40	4	16		4	20		2
100		•	•	•	•	•	YC1	C1		20	2			2			1
114	YC1	C1	C1	•	•	•	•			31	5			17			1
118	YC1	C1	C1	J1	J1	•	•	YC2	C2	77	10	19		20	20		2
121		•	•		•		•	YC1		6	2			2			1
151	•	•	•	•		YC1	C1	C1	J1	12	7			8			1
171	•	YC1	C1	•	YC2	C2	C2	J2	•	56	8	41		8	42		2
204		YC1	C1	C1	YC2		C2	YC3	C3	10	3	2	4	3	2	4	3
205	YC1	C1	C1	•	YC2	C2	C2	YC3	C3	24	3	9	4	3	10	4	3
209		YC1	C1	C1	J1	YC2	C2	C2	J2	38	3	23		12	28		2
210		YC1				YC2	C2	C2	J2	11	1	7		1	7		2
216	•	•	•	YC1	•	YC2	C2	YC3	C3	82	2	37	8	2	43	8	3
218	YC1	C1	C1	J1	•	YC2	C2	C2	YC3	33	4	20	2	4	22	2	3
220			YC1		C1	J1	J1	•		6	5			9			1

	Years									**Sightings 2008-2016**							
ID#	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**NF**	**WC1**	**WC2**	**WC3**	**NC1**	**NC2**	**NC3**	**#C**
223	•	YC1	C1			•	YC2	•	YC3	31	2	2	14	2	2	14	3
225							J1	YC2	C2	9	7	2		7	2		2
228	•		•		YC1	•	C1	J1	J1	12	8			9			1
231	•	YC1	C1	YC2		•	YC3		•	17	9	1	2	9	1	2	3
232		•	YC1		C1	J1	YC2	C2	C2	26	4	10		7	10		2
233		•	•	•		•	YC1	C1	C1	21	6			6			1
242	•	•	•	•	YC1	C1	C1	J1	YC2	98	65	7		70	7		2
246					•	•	YC1	C1		22	3			3			1
250	•	•		YC1	C1	C1	J1			43	33			35			1
280	C1	C1	J1	J1	YC2	C2	C2	J2	J2	27	6	18		19	22		2
285		YC1	C1		YC2	C2	C2	YC3	C3	30	2	15	9	2	15	9	3
#F	**8**	**19**	**23**	**25**	**29**	**31**	**35**	**34**	**29**								
#YOY	**8**	**10**	**4**	**3**	**10**	**8**	**9**	**10**	**5**								**69**

(ii) Births

An average of seven (mean = 7.4, SD = 2.6, range = 3-10) calves was born each year (2008-2016), with one recorded calf death each year between 2011 and 2015 (Fig. 2.5). There was no correlation between number of surveys and number of births recorded annually (linear regression, $r^2 = 0.02$, $P = 0.73$), thus the variation in the number of births could not be explained by the variation in number of surveys.

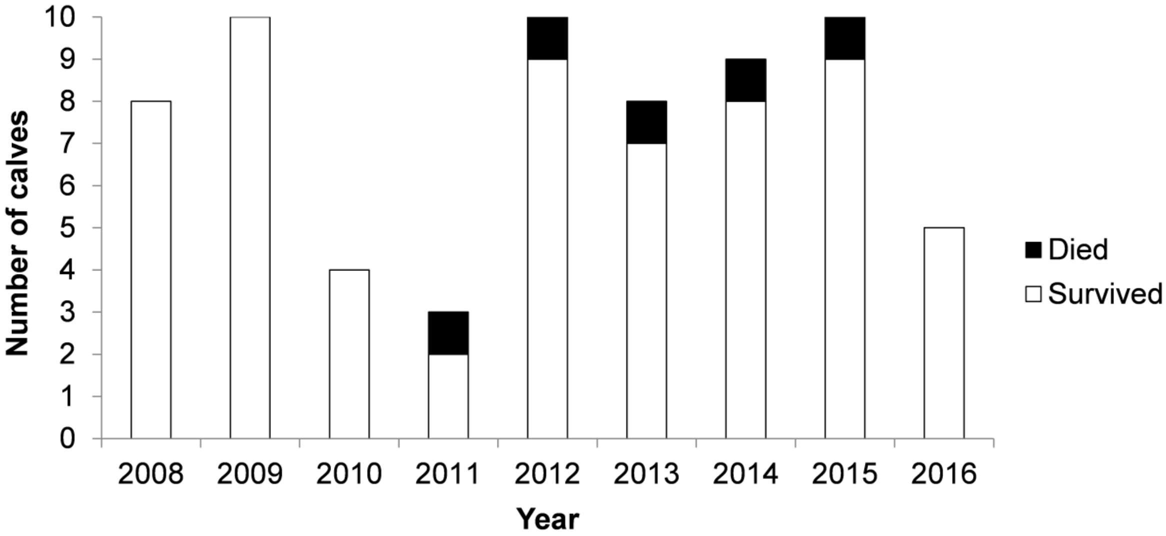

Figure 2.5 Number of bottlenose dolphin calves born in the Shannon Estuary from 2008 to 2016, with those that subsequently died in black (no mortality data for 2016)

(iii) Temporal patterns in reproduction

Parturition peaked in July with 45% (*n* = 14) of 31 calves with moderately precise (within 60 d) birthdates estimated to be born in this month (Fig. 2.6). In the other main study months, 16% (*n* = 5) of these calves were estimated to be born in June, 32% (*n* = 10) in August and 6% (*n* = 2) in September.

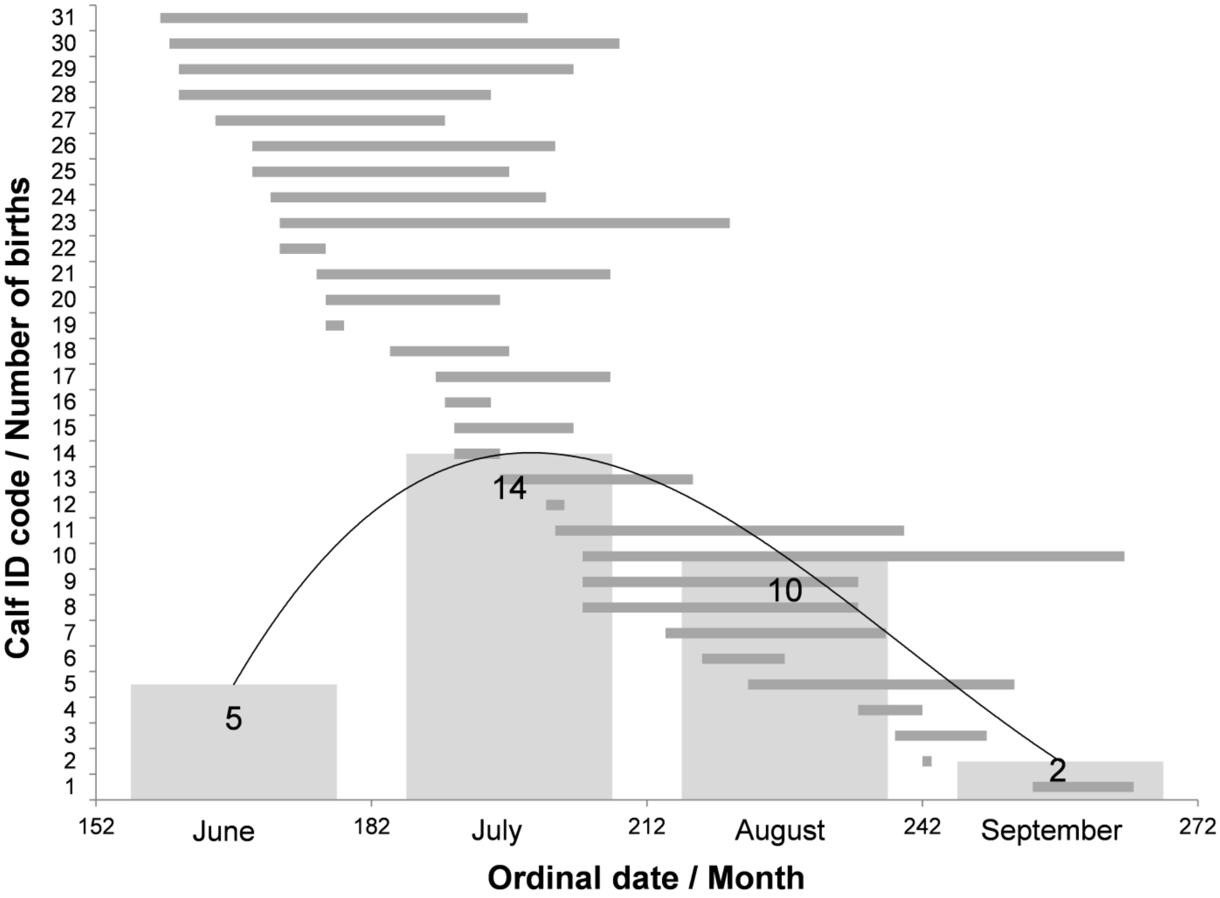

Figure 2.6 The number of births per month estimated using calves with within 60d-precision birthdate estimates (*n* = 31), with a polynomial regression line fitted. Thick grey lines indicate the window of time between ordinal dates (*i.e.*, days-of-year) when each of the 31 calves could have been born (*i.e.*, dates from the last sighting of the mother without her calf to the first sighting of the mother with her newborn calf)

(iv) Inter-birth intervals

(a) Using date of birth

There were 13 reproductive females with two consecutive births and for whom the estimated date of birth (DOB) and fate of the calf was available for both calves (*n* = 26; Table 2.2). Using estimated DOBs to calculate inter-birth intervals (IBIs) by the time elapsed between successive births, the mean IBI was 2.9±0.7 years (95% CL = 2.6-3.3, SD = 0.67, median = 3.02, range = 1.4-4.0).

Table 2.2 Inter-birth intervals (in years) for reproductive females with consecutive calves of known fate, using two approaches: (i) calculated from an estimated date of birth (DOB) derived from the mid-point of the dates between when the mother was last seen before the birth of her calf and the first sighting of the mother with her newborn calf; and (ii) calculated from the time-lapse between the first sighting of the mother with her initial calf and the first sighting of the mother with her subsequent calf. Underlined calf codes are those known to have died

Female ID#	Calf code	DOB estimate	DOB accuracy (d)	Mother last seen before birth of calf	First sighting of mother with calf	IBI (DOB)	IBI (sightings)
006	YC2	01/09/2015	10	27/08/2015	06/09/2015		
	YC1	10/01/2012	337	26/07/2011	27/06/2012	3.64	3.19
044	YC2	29/08/2016	1	29/08/2016	30/08/2016		
	YC1	09/01/2014	307	09/08/2013	12/06/2014	2.64	2.22
045	YC2	11/07/2015	5	09/07/2015	14/07/2015		
	YC1	04/07/2012	30	19/06/2012	19/07/2012	3.02	2.98
070	YC3	01/07/2014	43	10/06/2014	23/07/2014		
	YC2	22/06/2012	5	20/06/2012	25/06/2012	2.02	2.08
085	YC2	02/07/2016	49	08/06/2016	27/07/2016		
	YC1	09/07/2013	13	03/07/2013	16/07/2013	2.98	3.03
204	YC3	27/06/2015	34	10/06/2015	14/07/2015		
	YC2	20/06/2012	377	09/06/2011	20/06/2012	3.02	3.06
205	YC3	12/07/2015	5	10/07/2015	15/07/2015		
	YC2	12/01/2012	343	25/07/2011	02/07/2012	3.50	3.03
216	YC3	25/07/2015	21	15/07/2015	05/08/2015		
	YC2	19/12/2012	266	08/08/2012	01/05/2013	2.60	2.26
218	YC3	27/06/2016	40	07/06/2016	17/07/2016		
	YC2	02/01/2013	313	30/07/2012	08/06/2013	3.48	3.11
223	YC3	13/12/2015	232	19/08/2015	07/04/2016		
	YC2	08/08/2014	30	24/07/2014	23/08/2014	1.35	1.62
232	YC2	16/07/2014	13	10/07/2014	23/07/2014		
	YC1	20/06/2011	746	12/06/2010	27/06/2012	3.07	2.07
242	YC2	09/08/2016	9	05/08/2016	14/08/2016		
	YC1	24/08/2012	29	10/08/2012	08/09/2012	3.96	3.93
285	YC3	26/06/2015	25	14/06/2015	09/07/2015		
	YC2	20/07/2012	2	19/07/2012	21/07/2012	2.93	2.97
					Median	3.02	2.98
					Average	2.94	2.74
					Range	1.35-3.96	1.62-3.93
					95% CL	2.58-3.30	2.41-3.07
					SD	0.67	0.61

(b) Using sightings of calves

When the difference in time elapsed between the first sighting of a female with her initial calf and the first sighting of the same female with her subsequent calf was used, the mean inter-birth interval was 2.7±0.6 years (95% CL = 2.4-3.1, SD = 0.61, median = 2.98, range = 1.6-3.9; Table 2.2).

Excluding the three females whose calves died (underlined calf codes; Table 2.2), the mean IBI for the other 10 females whose calves survived to weaning age was 3.2±0.4 years (95% CL = 2.9-3.5, SD = 0.42, median = 3.05, range = 2.6-4.0). Of these 10 females, eight IBIs were of approximately 3 years and two of 4 years. For the three females whose calves died, the mean IBI was 2.1±0.7 years (95% CL = 1.4-2.9, SD = 0.67, median = 2.02, range = 1.4-3.0).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, female ID#s 044 and 216 had the lowest IBIs at 2.22 and 2.26 years respectively, while female ID#s 242 and 006 had the highest IBIs at 3.93 and 3.19 years respectively (Table 2.2).

(c) Using year of birth

Of all the reproductive females and their full sighting histories across the 9-yr study period, the inter-birth interval (based on year of birth) ranged from 2 to 7 years. Using this larger dataset of sighting histories for all reproductive females in the study (22 females with more than one calf of known year of birth; 50 calves), the mean inter-birth interval (based on annual consecutive births) was 3.5±1.3 years (median = 3, mode = 3; Fig. 2.7). In two cases where the calf was lost (ID#s 070 and 223, both YC2) the mothers went on to have subsequent calves around two years later. Results were similar when the four cases where a birth was possibly missed in the timeline were excluded; the mean inter-birth interval was 3.2±1.0 (median = 3, mode = 3).

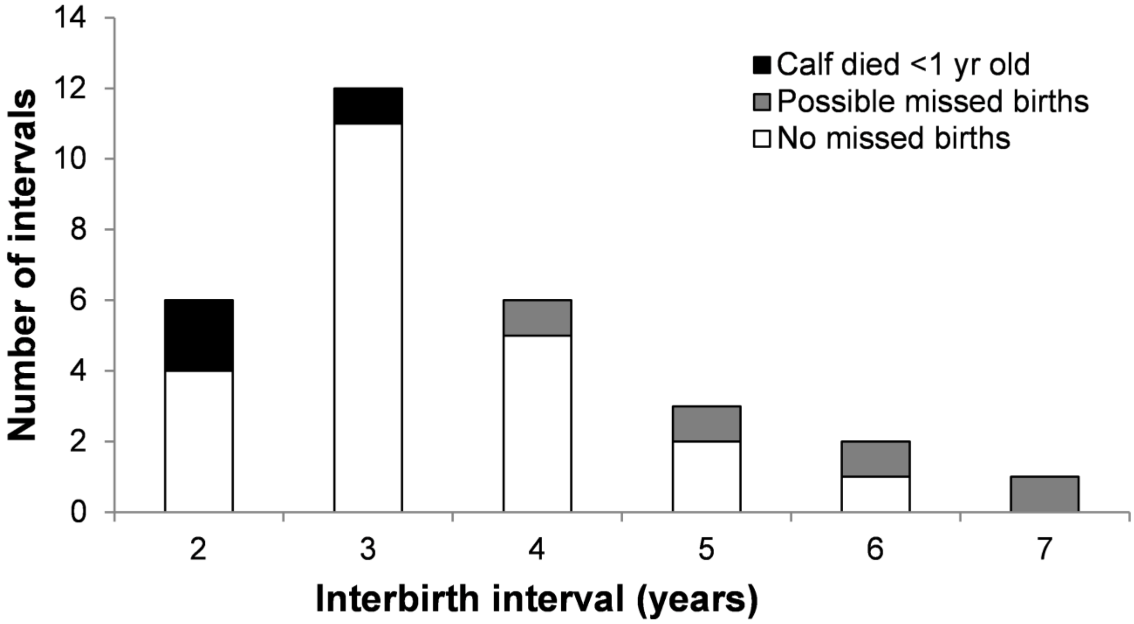

Figure 2.7 Inter-birth intervals for females whose calves survived to weaning (white bars) and whose calves died <1 yr old (black bars), and for those where a birth may have been missed in the interim (grey bars) (*n* = 30). Mean inter-birth interval was 3.53 (SD = 1.28, median = 3) (after Mann et al. 2000; Fruet et al. 2015)

(v) Calving rate, birth rate and fecundity

Annual calving rates for the population between 2008 and 2016 ranged from 0.13 to 1.00 (mean = 0.29) young-of-year/reproductive female/year (95% binomial CL = 0.12-0.46). Annual crude birth rates for the years 2012 to 2016 ranged from 0.06 to 0.09 with an average annual crude birth rate of 0.07±0.01 (or mean crude birth rate of 7.2%). The estimated fecundity of the population, accounting for calf mortality, was 0.26±0.03, while the estimated fecundity rate, not accounting for calf mortality, was 0.33.

(vi) Calf mortality and reproductive success

Between 2012 and 2015, an average 11% of recorded newborn calves (*n* = 4) were lost before age 1. Reproductive success rates for female bottlenose dolphins in the Shannon Estuary with >1 documented births, where the calf survived to the minimum known weaning age for Shannon dolphins (2.0 yr) and/or the fate of the calf could be determined, varied from 0.5 to 1.0 (*n* = 17). Three females had calves that died before they weaned, two of whom raised another calf successfully, and the third of whom raised two more calves successfully within the study period. The mean individual reproductive success was 0.9 (SD = 0.17).

(vii) Non-reproductive females

There were 12 adult dolphins sexed as female that were never observed with calves during the 9-yr study period, despite some individuals having a large number of sightings (*e.g.,* ID# 093 with 81 sightings and seen during each of all nine years; Table 2.3). All 12 individuals were sexed by genetic determination from biopsy tissue samples.

Table 2.3 Sighting frequency of non-reproductive female bottlenose dolphins in the Shannon Estuary from 2008-2016, including total number of sightings (*n*) and total number of years sighted (#yrs). The sex of all 12 individuals was determined through genetic analysis of tissue samples from biopsies

ID#	2008	2009	2010	2011	2012	2013	2014	2015	2016	*n*	#yrs
051	1	2								3	2
066				3	3	10	9	3	1	28	6
080		1		6	2	2	12	7	1	30	7
081	1	2			2	5	2	1	1	13	7
093	1	4	1	11	7	9	31	17	1	81	9
094	1									1	1
126					7	6	4	6	1	23	5
168		3	1	1	1	5	5	1	1	17	8
200	3	6	1	9	3	12	20	9	1	63	9
227					2	1	4			7	3
247		2		4	7	18		11	1	42	6
260		1				5	16	2	1	25	5

(viii) Weaning and mother-calf associations

Weaning ages, calculated for 11 individuals with known birth and weaning dates, ranged from 2.0 to 4.1 yr (mean = 2.9 yr). Of 22 calves known to have reached weaning age, eight (30%) were not sighted after their weaning date and 14 were sighted at least once following weaning. Four of these individuals were never seen with their mothers, but the other 10 had between one and 14 shared sightings with their mothers post-weaning. Interestingly, two cases of shared sightings involved the weaned calf's presence in a group during the first sighting of its mother with her subsequent newborn calf.

The calf who had the most shared sightings with her mother (*n* = 14) was a female, and one of the individuals present during the first sighting of a newborn, surfacing <1 m next to it in a group of seven dolphins. The only other weaned calf of known sex was a male who shared two sightings with his mother, but was seen in groups with other juveniles (and without his mother) during seven other encounters.

2.4 Discussion

This study has presented female reproductive parameters for bottlenose dolphins in the Shannon Estuary, Ireland, for the first time. Additionally, new information on the demographics of this population has been revealed through the analysis of a detailed long-term dataset collected through observations of live animals.

2.4.1 Population size and composition

Of the 145 extant individual dolphins recorded in 2015, over half were adults, with about one quarter dependent calves, and the others independent juveniles. Notably, the adult:calf ratio of the population was 2:1. Wells (2014b) reports the Sarasota Bay dolphin community as comprising 58% adult and 42% subadult individuals (which presumably includes juveniles, calves and YOYs). This age class ratio is comparable to the 55% adult, 17% juvenile and 28% calf contingents found in the Shannon Estuary population. Manlik et al. (2016) report a similar proportion of 55% adults for dolphins in Shark Bay, but the proportions of younger age classes are reversed, with 30% juveniles and 15% dependent calves. Similarly, Manlik et al. (2016) also report proportions of 58% adults, 25% juveniles and 17% calves for the Bunbury bottlenose dolphin population.

In contrast, Bearzi et al. (1997) found the percentages of adults, juveniles and calves (140 individuals) in the Adriatic Sea to be 85.2%, 8.2% and 6.6% respectively, Chabanne et al. (2012) found that the Swan Canning Estuary population (55 individuals) contained 78.2% adults/sub-adults and 21.8% calves, while Augusto et al.

(2011) reported the Sado Estuary bottlenose dolphin population (24 individuals) to be 79.2% adults, 12.5% juveniles and 8.3% calves. As the Sado Estuary population appears to be critically declining with a community composed primarily of adults and few young animals, the contrast of adult and calf proportions between that and the Shannon Estuary population points towards the apparent “good health” of the Shannon Estuary population and a comparatively higher percentage of calves.

The sex of most adult/juvenile individuals in the Shannon Estuary bottlenose dolphin population is still unknown (51%) with 49% animals of known sex (comprising 40% females and 9% males). Since consistent close association with a calf is a reliable way to determine the sex (female) of individual adult bottlenose dolphins, it is likely that most if not all females in the current population who were reproductively mature during our study were identified as such. However, it would be very valuable to gain more information on adult males in the population, as well as the sexes of calves. In particular, information on the age of individuals reaching reproductive maturity would be useful for population viability analyses and management scenarios.

2.4.2 Adult/juvenile mortality rate

The mean annual maximum adult/juvenile mortality rate was 0.038. Interestingly, this is the same value calculated by Wells and Scott (1990) for the Sarasota Bay bottlenose dolphin community. This is a maximum value because it includes all individuals who have ceased to be sighted; unfortunately, it was not possible to confirm any certain deaths because no known dead individuals were ever recovered from strandings, nor was it possible to identify any individuals as emigrants outside the population’s known home range. In Sarasota Bay, an adult male dolphin returned to the community after an 8-yr absence suggesting that at least a small number of individuals may leave their core home range for extended periods of time (Wells and Scott 1990). Since it is possible that some individuals temporarily emigrated or were not recorded in the Shannon Estuary study area in the most recent two years, and are still alive, the mortality rate for the Shannon Estuary population is likely lower than the maximum value given.

2.4.3 Female reproductive parameters

(i) Births

In the Shannon Estuary, seven calves were born on average each year, but this number fluctuated from a minimum of three to a maximum of ten during the nine years of our study. Interestingly, the three years (2009, 2012 and 2015) where the number of calves born was ten were each three years apart. Maybe this is a potential cyclical characteristic of reproduction in this population, or perhaps a cohort of females reproducing together at regular intervals. In an estuarine resident population of 74 Indo-Pacific bottlenose dolphins in the Port River Estuary, Australia, Steiner and Bossley (2008) calculated that an average of 2.6 calves were born each year; much lower than the mean of 7.4 births per year in the present study. However, in Cardigan Bay, an average of 10 calves were born each year to a population of 103 individuals (Veneruso and Evans 2012). The number of calves born in a population can be related to many socio-environmental parameters including population size and habitat ecology, and different study sites have reported varying reproductive parameters (see Table 2.4 for comparative summary of studies).

The reproductive female dolphins in this 9-yr study had between one and three calves each. In some cases, for those that had only one calf during the study period, it was not that they had long periods without a dependent calf, but that their dependent calf was with them for a longer duration. For example, ID# 011 gave birth to a calf in 2010 and was still with that calf in 2016. However, the majority of reproductive females (65%) had more than one calf throughout the study period.

(ii) Temporal patterns in reproduction

The dataset from the Shannon Estuary was seasonally biased because most data were collected during summer months, so it was not possible to get an annual estimate of seasonal peaks in birth. However, of the four main months for which data were available (Jun-Sep), births peaked in July. Similarly, 76% of all bottlenose dolphin births in Cardigan Bay, Wales occurred between July and September (Norrman et al. 2015). With further research, it is possible that a predictable summer calving season might be uncovered such as in other populations (*e.g.*, Steiner and Bossley 2008; Smith et al. 2016). It is well-documented that in many bottlenose dolphin populations, births tend to peak in spring and summer months, possibly due to an increase in water temperature and food supply (Steiner and Bossley 2008; Veneruso and Evans 2012; McFee et al. 2014; Fruet et al. 2015; Tezanos-Pinto et al. 2015). Additional winter data collection and information on sea surface temperature, dolphin prey abundance, distribution and variability would be valuable for exploring fluctuations in the reproductive biology of the Shannon Estuary dolphin population.

(iii) Inter-birth intervals

We used three methods to calculate mean inter-birth interval (IBI) – difference between estimated dates of birth (DOBs), difference between sighting dates of mothers with initial and subsequent newborns, and difference between annual births based on year of birth – and found that the mean IBI for the Shannon Estuary bottlenose dolphin population was 2.9 yr, 2.7 yr and 3.5 yr for each method respectively. Average IBI (in years) has been reported for many other bottlenose dolphin populations including estimates from 5.4 in Sarasota Bay, USA (Wells and Scott 1999) to 3.0 in the Adriatic Sea (Bearzi et al. 1997) (Table 2.4). Thus, our estimate of 3.5 yr (based on year of birth) falls within the lower values from these examples, including, interestingly, the values obtained from studies of resident bottlenose dolphin populations in Scotland (4.5 yr, Arso Civil et al. 2017; 3.8 yr, Robinson et al. 2017) and Wales (3.3 yr, Norrman et al. 2015) – the two closest study sites to the Shannon Estuary. However, the IBIs estimated from more detailed dates in our study of 2.9 yr and 2.7 yr suggest that the Shannon Estuary bottlenose dolphin population has some of the lowest inter-birth intervals documented for populations worldwide, most similar to values of 3.0 yr reported for dolphins in the Adriatic Sea (Bearzi et al. 1997) and the Patos Lagoon Estuary, Brazil (Fruet et al. 2015). Of course, every population manifests individual variability and ranges of IBIs for individual reproductive females, but our results do suggest relatively frequent births for the reproductive females of this population.

Of the 13 reproductive females where estimated DOBs could be used to calculate IBIs between each of their two consecutive calves, results were noticeably different when comparing those whose initial calf died (IBI = 2.1±0.7 yr) to those whose initial calf survived to weaning (IBI = 3.2±0.4 yr). Although the sample size for calves that died was small (*n* = 3), this suggests that there could be a marked difference between IBIs in this population for females who lose a calf in its first year (and thus mate again shortly afterwards).

Table 2.4 Summary of reproductive parameters for bottlenose dolphins

Study area	Species	No. dolphins	Annual births	(SD)	Study length (yrs)	% of pop.			Crude birth rate (SD)	Mean IBI (yrs)	IBI range	Fecundity	1st yr mortality	References
						Adults	Juveniles	Calves						
Shannon Estuary, Ireland	*T. truncatus*	142	7.4	(2.6)	9	55	17	28	0.072 (0.01)	2.7-3.5	2-7	0.26 (0.03)	0.11	This study
Cardigan Bay, Wales	*T. truncatus*	103	10	(4.1)	13				0.075	3.3	2-7		0.15	Norrman et al. 2015
Moray Firth, Scotland	*T. truncatus*	192	6.2	(5.2)[a]	24[a]				0.060[b]	4.5[a]	2-9[a]	0.22[a]	0.38[b]	Arso Civil et al. 2017[a]; Sanders-Reed et al. 1999[b]
North Sea, Scotland	*T. truncatus*	108[c]	9	(4.0)[d]	20[d]				0.12 (0.05)[d]	3.8[d]	2-9[d]	0.16 (0.04)[d]	0.45[d]	Culloch 2004[c]; Robinson et al. 2017[d]
Sado Estuary, Portugal	*T. truncatus*	24			4[e]; 16[f]	79.2[e]	12.5[e]	8.3[e]	0.054[f]		3-11[f]			Augusto et al. 2011[e]; Gaspar 2003[f]
Adriatic Sea, Croatia	*T. truncatus*	106	4.2	(1.2)[h]	5[g]; 9[h]	85.2[g]	8.2[g]	6.6[g]	0.049 (0.034)[g]	3[g]		0.17 (0.05)[h]	0.18[h]	Bearzi et al. 1997[g]; Fortuna 2007[h]
Sarasota Bay, USA	*T. truncatus*	163	7			58[i]			0.055 (0.009)[j]	5.4[k]	2-11[k]	0.14 (0.24)[i]	0.19[j]	Wells 2014[i]; Wells and Scott 1990[j]; Wells and Scott (1999)[k]
Patos Lagoon Estuary, Brazil	*T. truncatus*	83	7.4	(1.6)					0.090 (0.01)	3		0.11 (0.02)	0.16	Fruet et al. 2015
Bay of Islands, New Zealand	*T. truncatus*	408	4.1	(2.7)	13				0.0625	4.3		0.25	0.42	Tezanos-Pinto et al. 2015
Doubtful Sound, New Zealand	*T. truncatus*	66	4.1		17				0.040 (0.04)	5.3	2-5		0.33	Henderson et al. 2014
Port River Estuary, Australia	*T. aduncus*	74	2.6		17				0.064	3.8	1.1-6		0.30	Steiner and Bossley 2008
Shark Bay, Australia	*T. aduncus*	83	10		11					4.6	3-6.2		0.29	Mann et al. 2000
Mikura Island, Japan	*T. aduncus*	169	7						0.071 (0.024)	3.4		0.136 (0.04)	0.13	Kogi et al. 2004

Two of the females in our study who lost their calves had subsequent calves just two years later and the third female who lost a calf had her subsequent calf three years later. This has also been reported in other populations. For example, Kogi et al. (2004) reported that the shortest IBIs of 1 and 2 yr in Indo-Pacific bottlenose dolphins at Mikura Island, Japan, involved females who had lost their calves and then became pregnant the same or following year. Similarly, Bearzi et al. (1997) reported two females with 2 yr and 3 yr IBIs when calves disappeared before weaning. In Scotland, a female dolphin conceived again in the breeding season immediately following the death of each of her two calves (Mitcheson 2008). Steiner and Bossley (2008) report an example of one female with a 1.9 yr IBI between surviving calves (*i.e.*, the short IBI was not the result of the death of the previous calf). Although there are some calves in the Shannon Estuary population who weaned around age 2, the only example from our dataset of an IBI of less than two years was from a mother (ID# 223) whose initial calf died. Similarly, female dolphins in the Moray Firth, Scotland, are capable of reproducing on a two-year cycle after the death of a newborn calf but have never been observed producing a subsequent calf in less than 2 years (Grellier 2000; Robinson et al. 2017).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, females ID# 044 and ID# 216 had the lowest IBIs at 2.22 and 2.26 years respectively. However, because, in both cases, the mothers had not been sighted since the previous autumn, these IBIs could be closer to 3 years. For example, if ID# 044's calf had been born the day after her last sighting in 2013, the IBI would have been 3.06 years.

The quantification of IBIs for the 13 reproductive females with two consecutive births and known calf fate may have shown bias in the results of IBIs of only 3 and 4 years' length. This might be a result of the length of the study period as there are no examples of female dolphins with IBIs of greater than 4 years in this subset of data. From the analysis based on year of birth, we know examples exist of longer (>6 yr) IBIs. For example, individual ID# 011 has had the same dependent calf for the last six years. If the calf had weaned by the end of our study period, her data would have increased the results of the IBI analysis based on date of birth and weaning date considerably. The relatively short 9-yr length of our study period when compared to the life span for bottlenose dolphins may have biased our results towards more frequently reproducing females and thus seemingly shorter IBIs and younger weaning ages (Arso Civil et al. 2017).

(iv) Crude birth rate, calving rate and fecundity

The mean annual crude birth rate for Shannon dolphins of 7.2% was consistent with the values calculated for other populations, which range from 4.0% in Doubtful Sound, New Zealand (Henderson et al. 2014) to 12.0% in the North Sea, Scotland (Robinson et al. 2017) (Table 2.4). Some of these studies noted that their crude birth rates were probably underestimated as some calves could have been born and died before being recorded (*e.g.*, Steiner and Bossley 2008) – this might explain why the birth rates calculated for Shannon Estuary dolphins are among the highest; the population was well-studied with multiple sightings of the reproductive females. However, it is always possible to miss births, particularly for young primiparous females where calves could have been born and lost before observations were made of the mother-calf pair (Kogi et al. 2004).

The mean annual calving rate of 0.29 for bottlenose dolphins in the Shannon Estuary was comparable to that for the same species in the Bay of Islands, New Zealand where average annual calving rate was 0.25 young-of-year/reproductive female/year (95% binomial CL = 0.16–0.35; Tezanos-Pinto 2009; Tezanos-Pinto et al. 2013; Tezanos-Pinto et al. 2015). The fecundity of the Shannon Estuary population, calculated differently to calving rate in that it takes into account only the births surviving to >1 yr, was estimated to be 0.26, which appears relatively high when compared to other populations. In the Patos Lagoon Estuary, Brazil and Sarasota Bay, Florida, fecundity rates were reported as 0.11 and 0.14 respectively (Wells and Scott 1990; Fruet et al. 2015). This suggests that the reproductive capacity of the Shannon Estuary dolphin population is potentially relatively good. Arso Civil et al. (2017) estimated a similar fecundity rate of 0.22 for bottlenose dolphins in the Moray Firth, Scotland. Using their method, where fecundity rate is ‘the annual probability of a reproductive female having a calf’, irrespective of its survival, the estimated fecundity rate for the Shannon Estuary population was even higher at 0.33. Estimating fecundity rate using the ratio of the number of calves surviving to the first year and the number of reproductive females in that year yields a lower estimate than the fecundity rate when not accounting for calf survival (Wells and Scott 1990; Arso Civil 2015).

(v) Calf mortality

The 11% mortality rate calculated for YOYs in the Shannon dolphin population seems to be quite low in comparison with other study populations, where first-year calf mortality rates of between 13% and 45% have been reported (Robinson et al. 2017; Kogi et al. 2004) (Table 2.4). However, our sample size of four calf deaths is very small, and mortality rates are most likely higher in cases where the sighting frequency of mother-calf pairs is low. Our study contained no known occurrences of calf deaths in the second year of life.

The causes of calf mortality in the Shannon Estuary remain largely unknown. There are no known predators of bottlenose dolphins in Ireland; dolphins are not subjected to predation by sharks as they are in other populations such as in Shark Bay, Australia (Heithaus 2001). Therefore, predation does not seem to account for any calf deaths in the Shannon Estuary. Naturally occurring biological causes might be responsible for calf mortality, such as genetic birth defects, which might make calves more susceptible to disease or illness. Interestingly, two calves born to one of the reproductive females (ID# 280) in the Shannon population were both observed to have visible morphological deformities, which may have been the result of a genetic mutation; however, neither has died to date. Several other calves in the Shannon Estuary population such as ID# 118’s calf (YC2, born in 2015) have been observed with deformities, which could also be the result of scoliosis (Berrow and O'Brien 2006) or physical trauma (Robinson 2014).

Additionally, there is no evidence in the Shannon Estuary of the direct anthropogenic threats that occur at other study sites, such as entanglement and boat strikes (*e.g.,* Port River Estuary, Australia; Steiner and Bossley 2008). However, it is possible that there are less obvious human impacts affecting the survival of the population; for example, dolphins in the Shannon Estuary have been shown to have high levels of PCB contamination which could affect their ability to reproduce adequately (although their levels are relatively low compared to other European populations; Jepson et al. 2016). Thus, this type of pollution could be causing observed or unobserved calf deaths, particularly for firstborn calves; bottlenose dolphin mothers off-load contaminant burdens into their firstborn calves (Schwacke et al. 2002). One female in the current study (ID# 027; Table 2.1) was found to have contaminant loads that were high enough that they could potentially have affected her reproductive success (Jepson et al. 2016); she was observed with only one calf in 2008 despite being sighted during five of the following years of this study. Other potential indirect anthropogenic threats to calf survival in the Shannon Estuary include acoustic disturbance from shipping. The Shannon Estuary is Ireland's second-largest waterway and a large shipping route. As acoustic communication between mothers and calves is essential to their associations, shipping noise could have a negative impact on a calf's ability to keep in contact with its mother (O'Brien et al. 2016). Overall, it is likely that a combination of factors influences calf mortality in the Shannon Estuary.

(vi) Reproductive success and non-reproductive females

Generally, reproductive success appeared to be quite high for reproductive female dolphins in the Shannon Estuary (mean individual reproductive success was 0.9 (SD = 0.17)), with only three of the 17 females examined having success rates of less than 100% - two of these females had one calf die and one survive, while the third had one calf die and two survive (to the minimum weaning age). Studies have shown that factors such as birth timing, maternal size and age, and birth order may be causes for variability in female dolphin reproductive success (Wells et al. 2014; Brough et al. 2016). Fruet et al. (2015) noted an age-related decrease in reproductive fitness in bottlenose dolphins in Brazil, with older females reproducing at lower rates. Differences in maternal experience and behavior appear to be crucially important to calf survival in some populations (Henderson et al. 2014; Fruet et al. 2015). Further behavioral research on the Shannon Estuary dolphin population could highlight individual differences in the maternal care of young.

Tezanos-Pinto et al. (2015) report what they inferred to be a “high proportion”, 14%, of non-reproductive females in their study population in the Bay of Islands, New Zealand. However, an even higher proportion of 25% of the known females in the Shannon Estuary population were found to be non-reproductive in this study. The large proportion of non-reproductive females in the population is curious. Clearly, the survival of calves of known reproductive females is high, but it is possible that additional calves of “non-reproductive” females have gone undocumented; it is impossible to know how many newborn (especially firstborn) calf deaths are not recorded, and how many stillbirths or miscarriages occur. Such occurrences might explain the apparently high proportion of non-reproductive females in the population.

(vii) Weaning and mother-calf associations

Although the sample size was small (*n* = 11), the range of weaning ages from 2.0 to 4.1 yr in the Shannon population suggested variability in the age of independence for young bottlenose dolphins.

The longevity of mother-calf associations was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any patterns (perhaps related to sex class) associated with these pairings. Wells (2014b) observed that older calves, especially females, sometimes associated closely with their mothers and new siblings for months or more, and Steiner and Bossley (2008) reported a previous calf seen with its mother and her subsequent calf on a number of occasions. In the current study, 10 calves were observed in close association with their mothers post-weaning. Of these 10 mother-calf pairs, eight are considered members of the "inner estuary community", shown to have stronger associations and longer lasting bonds than other individuals in the population (Baker et al. 2017b (Chapter 4)).

The female calf that had the most shared sightings with her mother was sighted in a group with her mother and her subsequently newborn sibling. Associations such as this after weaning could be important for maintaining social bonds and learning about motherhood, and perhaps also serve to provide relief to the mother in the sharing of calf rearing responsibilities (Wells 2014).

2.5 Conclusion

The purpose of this study was to derive baseline data on the population demographics and female reproductive parameters of bottlenose dolphins in the Shannon Estuary, Ireland. Using a detailed dataset to count the number of individuals in the population led to a population estimate of 142 which is just above the higher limits of previous estimates calculated through mark-recapture analysis. Results revealed that although the Shannon Estuary bottlenose dolphin population's life history parameters include some of the shortest inter-birth intervals and youngest weaning ages reported for bottlenose dolphins worldwide, they are within the ranges reported in other studies. Interestingly, they are similar to those reported for nearby populations in the Moray Firth, Scotland and Cardigan Bay, Wales.

This study increases our knowledge of bottlenose dolphin reproductive rates and population demographics. The results will allow for comparative studies of the Shannon Estuary dolphin population, exploring similarities and differences with other populations of well-studied resident dolphins in temperate and tropical waters. Given the variability between populations, it is imperative to report regionally specific demographics (Arso Civil et al. 2017). This study complements other longitudinal research studies in offering essential guidance for the development of sustainable practices in population conservation (Mann and Karniski 2017). The population and life history parameters presented here make an important contribution to the global conservation of the species. They also serve to show how variable the demographics of different populations can be, reinforcing the importance of extending research to a wide geographical range.

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Compliance with ethical standards

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Chapter 3

An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

This chapter is a reproduction of the following published paper (published version can be found in Appendix B).

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3 An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

Ethograms, or categorized lists of behavioral descriptors, are fundamental research tools in the study of animal behavior, essential to the overall understanding of the behavioral ecology of a species. With specific definitions of activity state categories and behavioral event types, the behavior of a species can be described, quantified and compared across populations. We present the first ethogram for bottlenose dolphins (*Tursiops truncatus*) in Ireland based on sighting records collected during 256 surveys (2014-2016) in the Shannon Estuary. The ethogram consists of 11 activity states and 45 behavioral events. The most frequently recorded activity state was travel (52%) while the most frequently recorded behavioral events were slow travel (40% of sightings), surface rush (28%), and leap (28%). The 10 least frequently recorded behaviors were seen in only 10% of total sightings with <8 records each. A video test for multiple researchers to assess inter-observer reliability in behavioral data recording demonstrated the validity of this study's behavioral data and the efficacy of the ethogram in its applicability to other studies. Validity (percentage agreement = 88.1 ± 7.0) and reliability (Fleiss' Kappa = 0.81) scores were high across 24 test participants (12 trained, 12 untrained), but results indicated that those with prior training scored significantly higher. Furthermore, we investigate the presence/absence of behaviors recorded in other studies of bottlenose dolphins. This ethogram and behavioral discussion serve to describe and compare quantitative data on the behavior of bottlenose dolphins in Ireland for the first time and provide a strong basis for further research.

Key words: behavior, bottlenose dolphin, ethogram, repertoire, Shannon Estuary, Special Area of Conservation, *Tursiops truncatus*

3.1 Introduction

Understanding the repertoire of behaviors exhibited by a species, particularly when a population is composed of individually recognizable animals, is crucial to providing baseline scientific data for many avenues of study. To allow for accurate comparison between study sites, it is important to standardize terms and categories used in behavioral research (Masatomi, 2004). Precise descriptions, definitions and quantification of behaviors provide a valuable standard that can be used for the systematic and quantitative study of bottlenose dolphin (*Tursiops truncatus*) behavior, especially in understudied wild populations (Martin & Bateson, 1986; Lichtenberg & Hallager, 2007). Baseline data on the behavioral repertoire of a species must be collected before more complex analytical procedures can be introduced (Lehner, 1996). A systematic presentation of categorical definitions and of the specific behaviors within each category, known as an ethogram, is a fundamental research tool in the study of behavior (Mann et al., 2000). Ethograms aim to describe the full behavioral repertoire of a species (in the habitat under study) and can be the foundation(s) of research contributing to knowledge and conservation of the species as a whole (Hill et al., 2015). They are essential for collecting and analyzing sound scientific data, and thus for understanding the behavioral repertoire of a species. In particular, when multiple observers are used to collect behavioral data, the preparation and use of an ethogram can facilitate consistency in recording (Margulis, 2010).

Ethograms have been developed for a wide range of taxa in the field of animal behavior including chimpanzees (*Pan troglodytes*) (e.g., Nishida et al., 1999; Hobaiter & Byrne, 2011), elephants (e.g., Esposito, 2008; Riyas Ahamed, 2015), birds (e.g., Masatomi, 2004; Lichtenberg & Hallager, 2007), river otters (*Lontra canadensis*) (e.g., Green et al., 2015) and fish (e.g., Bolgan et al., 2016), and have also been developed for some cetacean species (e.g., humpback whales (*Megaptera novaeangliae*, Kavanagh et al., 2016), pilot whales (*Globicephala* sp., Scheer et al., 2004), and belugas (*Delphinapteras leucas*, Howe et al., 2015)).

As one of the most extensively studied cetaceans, information on bottlenose dolphins (*Tursiops* spp.) and accounts of their surface behavior have been widely published (Shane et al., 1986; Connor et al., 2000b). There are some general surface behavior ethograms for specific populations (e.g., USA: Shane, 1990; Croatia: Bearzi et al., 1999; New Zealand: Lusseau, 2006b; Australia: Steiner, 2011), but many published studies place specific emphasis on particular associations, such as mother-infant relationships (e.g., Gubbins et al., 1999; Mann & Smuts, 1999), or behaviors, such as foraging (e.g., Nowacek, 2002; Sargeant et al., 2006; Sargeant & Mann, 2009), or human interactions (e.g., Jaiteh et al., 2013). In many cases, ethograms come from research on captive dolphins (e.g., von Streit, 2011) or are limited to describing only the broad activity state categories (e.g., Mann & Watson-Capps, 2005; Genov et al., 2008; Baş et al., 2015; Karniski et al., 2015).

In the study of animal behavior, it is important to distinguish between “states” (long-duration behaviors) and “events” (short-duration behaviors) (Altmann, 1974; Connor et al., 2000b). For example, “eyes open” is a behavioral state of some duration, whereas “blinking” is an essentially instantaneous behavioral event (Nowacek, 2002). Herein, we use the terms “activity state” and “behavioral event” to distinguish between these two types of behavior.

A table of behavioral definitions was published by Bearzi et al. (1999) for bottlenose dolphins in the Adriatic Sea, largely based on work carried out in the U.S. (Weaver, 1987; Shane, 1990). Bottlenose dolphin surface behavior has also been studied to varying degrees in other European study sites (e.g., Italy: Díaz López & Shirai, 2008; Slovenia: Genov et al., 2008; Portugal: Augusto et al., 2011). No ethograms currently exist for any of the three discrete populations of bottlenose dolphins in Ireland (including the resident population in the Shannon Estuary) or for the two geographically closest resident populations in the Moray Firth, Scotland and Cardigan Bay, Wales.

There have been few detailed behavioral studies of dolphins in the temperate waters of the Northeast Atlantic. A number of studies in Ireland have included behavioral components, mainly as part of impact assessments focusing on cause and effect (e.g., behavioral responses to acoustic pingers, Leeney et al., 2007). Some studies of behavior in common dolphins (*Delphinus delphis*, Berrow et al., 2008) and killer whales (*Orcinus orca*, Ryan & Wilson, 2003) have also been conducted. In the Moray Firth, Scotland and Cardigan Bay, Wales, researchers have used broad categories to record bottlenose dolphin behavior (e.g., Pierpoint et al., 2009; Pirotta et al., 2015), but information on specific behavioral events within activity state categories for these populations is lacking.

Few published papers present basic activity budget data on the frequency of activity states in cetacean populations (Mann & Wursig, 2014), even though these are important data for understanding the life history of a species and informing conservation management (Karniski et al., 2015). Even fewer studies present behavioral event data, in which the distinct surface behaviors of wild bottlenose dolphins are described and their occurrence quantified, with only a handful of studies attempting to then explain the context and purpose of these surface behaviors (e.g., Lusseau, 2006a; Furuichi et al., 2014). However, the collection of behavioral data is integral to the overall understanding of animal populations (Lehner, 1996).

When sighting data on activity states and behavioral events are collected by multiple independent observers, tests are required to assess the reliability and validity of these data (Martin & Bateson, 1986; Kaufman & Rosenthal, 2009). The literature on the collection and analysis of data on cetacean surface behavior contains few examples of such tests (Mann, 1999). Kavanagh et al. (2016) carried out inter-observer reliability tests using video data during a study of humpback whales to examine the effects of observers' experience and native language on data reliability and validity. Using video data incorporating 16 behavioral event types, they found that neither factor had a significant effect on behavioral data recording by observers. However, their test results did highlight specific behavioral event types that were more accurately and consistently recorded than others, and they suggested that future studies could use similar tests to assess the suitability of specific behavioral event types for analysis (Kavanagh et al., 2016).

The bottlenose dolphin population in the Shannon Estuary, Ireland, is composed of about 120 individuals (Berrow et al., 2012) and is genetically discrete (Mirimin et al., 2011). Dolphins are present in the estuary year-round (Berrow et al., 1996; Ingram, 2000; Berrow, 2009) and have been observed exclusively in the Shannon Estuary and adjacent Tralee and Brandon Bays (Ryan & Berrow, 2013; Levesque et al., 2016 (Appendix D)). This species also occurs around the entire Irish coast (O'Brien et al., 2009) and in offshore waters (Louis et al., 2014), but these are thought to constitute distinct populations (Oudejans et al., 2015). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (NPWS, 2012), which are listed in Annex II of the EU Habitats Directive. Given the level of protection assigned to this population, information on the behavior of dolphins in the estuary is vital for their long-term conservation and the development of specifically tailored management plans.

This article aims to describe a detailed ethogram for wild bottlenose dolphins in the Shannon Estuary, to provide some quantitative data on the frequency of different activity states and behavioral events, and to report the presence or absence of behaviors recorded in other studies. Its more general aim is to provide a tool for future bottlenose dolphin behavioral research, that will give an insight into the behavioral repertoire and activity budget of bottlenose dolphins in the estuary and highlight common and rare behaviors. A greater understanding of bottlenose dolphin behavior will contribute towards the management and conservation of bottlenose dolphin stocks in Ireland (especially those in SACs (NPWS, 2012)) and of the species throughout its geographical range.

3.2 Methods

3.2.1 Study site and vessels

The study site was within the Lower River Shannon Special Area of Conservation (SAC; Site Code: 002165) for bottlenose dolphins, a 684 km^2 Natura 2000 designated site (NPWS, 2012) on Ireland’s west coast between Co. Clare, Co. Kerry, and Co. Limerick (52°36'N, 9°38'W). Surveys occurred west of Shannon Airport and east of Loop Head and Kerry Head (Fig. 3.1).

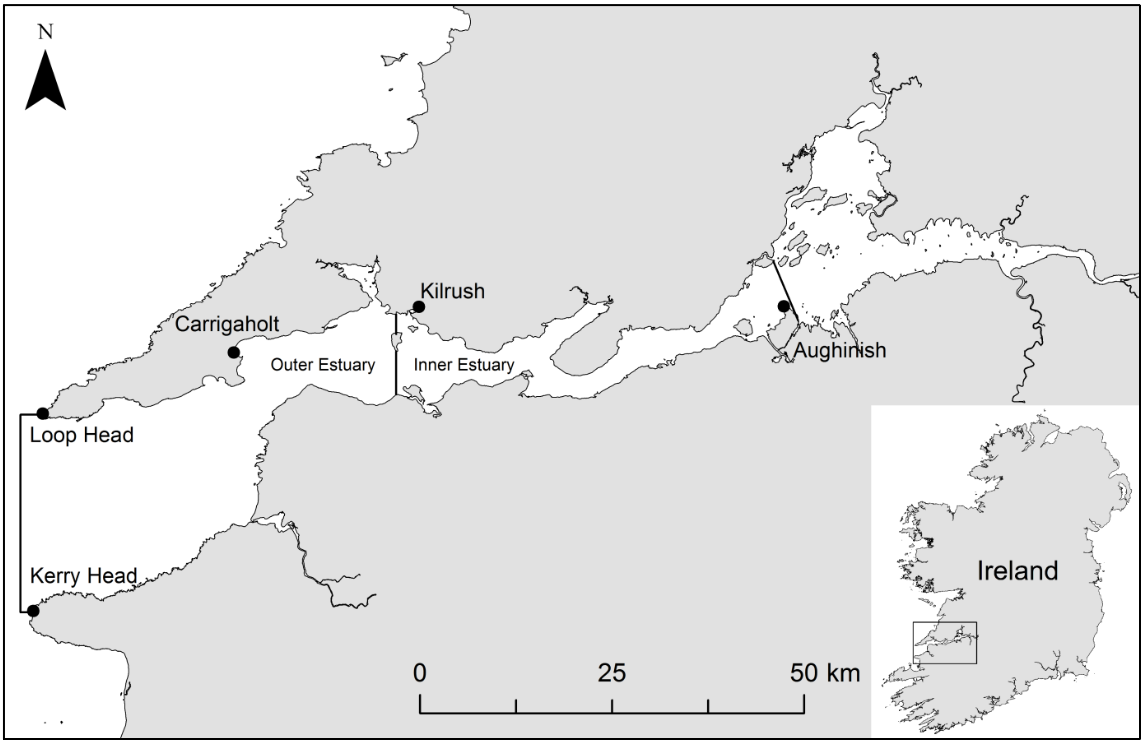

Figure 3.1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush.

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow et al., 2010; Berrow et al., 2012; O'Brien et al., 2014). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow & Holmes, 1999). The dolphin-watching tour boats, *Draíocht* and *Dolphin Discovery*, operated from the ports of Carrigaholt and Kilrush, respectively (Fig. 3.1). *Draíocht* and *Dolphin Discovery* primarily concentrated effort in the outer estuary and inner estuary areas, respectively, with a mean dolphin-watching trip length of 2.3 h (Berrow & Ryan, 2009; Barker & Berrow, 2016). The research vessel, based in Kilrush, was a 6 m XS RIB (Rigid-hulled Inflatable Boat) with which surveys were conducted throughout all areas of the estuary. Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~4 m while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at <1 m above sea level. In general, behavioral observations were made visually, but observers were also equipped with digital SLR cameras (Nikon D300 or Canon EOS 20D with 70-300 mm lenses), binoculars (Minox 7x50 or 8x42), GPS (Garmin 72H), and datasheets.

3.2.2 Data collection

In addition to reviewing published ethograms (e.g., Weaver, 1987; Shane, 1990), eight researchers who manage different bottlenose dolphin research projects worldwide were contacted for expert advice and information on ethograms from the populations they work on, to gain insight for constructing our initial ethogram. These research projects and study sites were chosen based on geographical region, personal contacts, and length of study.

A pilot study was carried out in the Shannon Estuary in 2013, from commercial dolphin-watching tour boats and a dedicated research vessel, to begin collecting behavioral data, refine bottlenose dolphin behavioral event descriptors, and determine if it was necessary to supplement the proposed ethogram with additional behaviors observed in the field.

Activity states and behavioral events were subsequently recorded during three field seasons – March-September 2014, June-September 2015, and May-September 2016. Observers made visual observations from the three different platforms previously described. Sighting datasheets were completed during every survey in which encounters with dolphin groups (sightings) occurred. A sighting began when at least one dolphin was within 100 m of the vessel and ended after ≤30 min. due to national regulations (Maritime Safety Directorate, 2005). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al., 2011a).

Behavioral data collection methods were based on the recommendations of Mann (1999) who defines the two basic sampling decisions as “follow protocol” – the length of observation and the choice of subject(s) – and “sampling method” – the procedure used to sample behavior. The follow protocol used was “survey”, with sightings providing a snapshot of dolphin activity including group estimates, GPS location, and behaviors. The sampling methods used were “predominant group activity sampling”, “one-zero”, and “*ad libitum*” sampling. Predominant group activity sampling involved selecting the activity state that >50% of individuals in a group were engaged in within the first five min. of a sighting. One-zero sampling involved scoring whether or not specific behavioral events occurred within the first five min. of a sighting. *Ad libitum* sampling was used to make additional anecdotal comments throughout the duration of a sighting.

For each sighting, the observer selected one of six options – rest, travel, social, forage, other, unknown – as the predominant (>50% of individuals) group activity state during the first five min. of a sighting. Five minutes was used as the initial period within which to record behavior in an effort to record how the dolphins were most likely to have been behaving before the boat arrived in the vicinity. In addition, the observer circled all behaviors seen within the first five min. from the behavioral events listed on the datasheet and recorded additional activity states and behavioral events (after five min.) in the comments section of the datasheet with the time of occurrence.

3.2.3 Inter-observer validity and reliability testing

During dedicated behavioral surveys from the research RIB, video footage of bottlenose dolphins was recorded. Seventeen segments, each <35 s in duration, were extracted from these videos for three of the ethogram’s major activity states and 14 behavioral event types, and used to assess inter-observer reliability in selecting visually observed behaviors. (The video segments are available on the “Supplementary Materials” page of the Aquatic Mammals website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.) To verify the video test behaviors, an experienced dolphin behavior researcher (KM) completed the test, prior to commencement of trials. The expert’s answers matched those of the test designer and compiler of the overall ethogram (IB) prior to the test going live.

The 17 videos were shown to 24 people – 12 trained research assistants who collected the data and 12 other marine biologists with no previous marine mammal behavior research experience and who had not participated in the fieldwork of this study. Each trained research assistant had at least two weeks of training with the Shannon Dolphin and Wildlife Foundation involving fieldwork methods, equipment usage, and data collection protocols, before independently collecting data. At the end of the final field season, each participant was provided with a copy of the ethogram and was requested to identify the activity state or behavioral event exhibited by the dolphin(s) in each video segment, i.e. to code each clip.

Using similar methodologies to Kavanagh et al. (2016), percentage agreement and Kappa score statistical analyses were employed to measure the validity and reliability of the behaviors recorded by the test participants (Kaufman & Rosenthal, 2009). Percentage agreement was calculated to measure how often observers agreed on the correct classification of a behavior (Martin & Bateson, 1986). Percentage agreement scores were calculated for each of the behaviors and each of the test participants. As validity data were non-normally distributed (Levene’s test), Mann-Whitney U tests were used to compare validity scores between trained and other test participants (Venables & Ripley, 2002).

Kappa scores (which include a correction for chance) were used to examine the reliability of the recording of individual behaviors by each observer (Fleiss, 1971; Conger, 1980), using the designer’s (IB) scores as baseline data within the *R* (*R* Core Team, 2016) package *irr* (Gamer et al., 2012). Category-wise Kappa scores were generated for all behaviors used in the test. These scores compute the probability of a randomly chosen observer assigning a specific behavior to a video given that another randomly chosen observer has also assigned that behavior to that video. Where behaviors were misclassified (i.e., a participant selected a different behavior to the baseline), the behavior most frequently selected in each case was recorded and presented.

The test had two aims: 1) to establish whether trained observers agreed sufficiently well to validate the behavioral data collected and used in the present study, and 2) to validate the broader use of the ethogram by marine biologists to accurately record dolphin behavior (which could reduce significant variability in long-term monitoring projects).

3.2.4 Behavioral analysis

Activity state and behavioral event data were entered into a specially adapted version of *FinBase* (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams et al., 2006). Using one form per sighting, activity states were entered as

Initially Observed (first five min.) and sometimes also Observed (after five min.), if an additional activity state was recorded in the comments. A specifically designed ethogram sub-form within the sighting form in *FinBase* was used to enter all of the behavioral events recorded during each sighting.

Behavioral data from sightings were queried in *FinBase* and summary statistics were calculated using *MS Excel* and *R* (*R* Core Team, 2016). Analyses used predominant group activity data recorded exclusively within the first five minutes of each sighting, while both one-zero and *ad libitum* behavioral event data were used for behavioral events analysis. Percentage occurrence and activity budgets were calculated by summing the records of each behavior from the sightings and dividing by the total number of data points.

In addition to the written data recorded during sightings, photographs were taken simultaneously, primarily for photo-identification of individuals, but with the benefit of obtaining photographic data on behaviors. Photos from all surveys and sightings were maintained in a database using the photographic software environment *IMatch* 5.6 (https://photools.com; Westphal, 2016). The Categories Assignment tool was used to categorize every photo in which a behavioral event from the ethogram was exhibited by one or more dolphins. These photographs were used during the training of multiple observers for collecting behavioral data in the field.

3.2.5 Comparison with other studies

Data from other studies of bottlenose dolphin behavior were gathered to generate tables comparing the activity states of the Shannon Estuary dolphins with those of other populations. The classification of behaviors, terminology, and definitions employed by these studies were compared with those used in the present study. Behavioral events that have been described in other studies but which have not (yet) been observed or recorded in the present study were noted.

3.3 Results

3.3.1 Summary of data collection

Of the 489 sightings (256 surveys), 209 sightings (91 surveys) were made from the tour boat *Draíocht*, 154 sightings (116 surveys) were made from the tour boat *Dolphin*

Discovery, and 126 (49 surveys) were made from the research RIB. Overall, 18 observers contributed sighting records to the database, but the top 10 observers with the most records collectively contributed the data from 81% (395) of the sightings.

In 2014, 2015 and 2016, both activity states and behavioral events were recorded for 193 sightings (100 surveys), 145 sightings (76 surveys) and 151 sightings (80 surveys), respectively. However, no behavioral events were observed in 62 of these sightings (14, 24, and 24 sightings in 2014, 2015, and 2016, respectively). Thus, a total of 489 sighting records with activity states and 427 sighting records with behavioral events were available for analysis. The average length of a sighting was 24 min. representing approximately 200 h of total dolphin observation time. Overall survey effort was approximately 765 h.

3.3.2 Bottlenose dolphin ethogram

Overall, our ethogram contains codes and descriptions for 11 activity states and 45 behavioral event types (Tables 3.1 to 3.4) for bottlenose dolphins in the Shannon Estuary. In the sightings data collected for the present study, information on six activity states and 35 behavioral event types was recorded and quantified (Tables 3.7 and 3.8). The ethogram is divided into four categorized sections, beginning with 11 activity state definitions, adapted from those published by McHugh et al. (2011b), which are based on Waples (1995) (Table 3.1). This section is followed by three separate behavioral event sections detailing surface behaviors, foraging/feeding, and social behaviors (Tables 3.2 to 3.4). Many of these behavioral definitions are adapted from Richard Connor's ethogram (pers. comm., 25 January 2017) for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. The activity states recorded were *travel*, *forage*, *social*, *rest*, *other*, and *unknown*. However, *probable forage*, *feed*, *mill*, *play*, and *with boat* have also been observed as part of the Shannon Estuary bottlenose dolphins' behavioral repertoire and are included in the ethogram. Each of these activity states is mutually exclusive.

Table 3.1 Activity states for bottlenose dolphins in the Shannon Estuary, Ireland, including a description for each activity state. Behaviors in italics were not recorded or quantified separately in this study: *probable forage*, *feed*, and *mill* were recorded as *forage*, while *play* and *with boat* were recorded as *other* during sightings.

UNIT	CODE	NAME	DESCRIPTION
ACTIVITY STATES	FE	*Feed*	Dolphin observed catching a fish or with a fish in its mouth
	FO	Forage	Indications of searching for prey, prey capture or feeding behaviors
	MI	*Mill*	Non-directional movement with no overall spatial progress
	OT	Other	Observed activity is clear but does not fit any other definition
	PL	*Play*	Interactions with objects other than dolphins which serve no obvious purpose
	PFO	*Probable forage*	Indications of foraging but not confirmed
	RE	Rest	Slow, steady activity in absence of other identifiable activities, often with long dive bouts (1-5 minutes)
	SO	Social	All active interactions with conspecifics, including body contact, chasing/following and sexual behaviors
	TR	Travel	Regular directional movement, including zig-zag and meandering movement
	UN	Unknown	Activity cannot be defined
	WB	*With Boat*	All cases where dolphins interact with a boat, including bow- and wake-riding

A total of 27 behavioral event types for observed surface behaviors were defined (Table 3.2), many of which were observed during more than one type of activity state. Twenty of these behavioral events were recorded at least once during sightings. A total of 10 behavioral event definitions for observed feeding/foraging behaviors (Table 3.3) were included in the ethogram. Nine of these behavioral events were recorded at least once during sightings. Eight behavioral event definitions were included for social behaviors (Table 3.4) observed during social activity by bottlenose dolphins in the Shannon Estuary. Six of these behavioral events were recorded at least once during sightings.

Table 3.2 Surface behaviors for bottlenose dolphins in the Shannon Estuary, Ireland, including a description for each behavioral event. *Halfway = to the dolphin’s belly button but genital slit is not visible above water. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

UNIT	CODE	NAME	DESCRIPTION
SURFACE BEHAVIORS	BKS	Backslap	Body exits halfway* out of water and falls against dorsal surface
	BST	Backstroke	Body is horizontal and ventral part of body is visible above surface with both pectoral fins extended
	BEL	Belly roll	Body rotates c. 180 degrees in water so that light ventral underside of the animal becomes visible
	BOW	*Bow-riding*	Dolphins surfacing at the bow of a moving vessel
	BR	Breach	Body exits water over halfway* and vertically and then falls horizontally creating white water
	BB	*Bubble-blow*	Bubble(s) emitted underwater from blowhole
	CNS	Chinslap	Body exits halfway* out of water and falls against ventral surface
	CHF	Chuff	Strong audible exhale from blowhole
	DEF	Defecation	Faeces are emitted from body
	FTR	Fast travel	Directed movement at a speed of over 10 km/h
	HO	Head out	Head and rostrum emerge above water surface and reenter water smoothly
	HD	*Headstand*	Dolphin is vertical with tail-end of body exposed above water surface
	LP	Leap	Body exits water entirely in an arcuate path and reenters water smoothly
	MO	*Motorboating*	Tailslapping repeatedly in forward motion at the water surface
	ONS	On side	Body rotates c. 90 degrees in water
	PEC	Pec out	Pectoral fin is extended above water surface
	PP	Porpoise	Repeated leaps in a straight direction
	SCO	*Scouting*	An individual dolphin leaves its group to approach the boat before returning again to its group
	SHK	*Sharking*	Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water
	SDS	Sideslap	Body exits halfway* out of water and falls against flank
	STR	Slow travel	Directed movement at a speed of under 10 km/h
	SNG	Snag	Body is stationary, horizontal and dorsal part of body is visible at surface
	SQ	*Squeeze breath*	A sound emitted from the blowhole that sounds like air escaping a balloon
	SR	Surface rush	Fast movement breaking the surface causing a flurry of white water at either side of the animal
	TO	Tail out	Tail is exposed above water surface
	TS	Tailslap	Flukes raised above water surface and then lowered making a strong audible impact
	WS	With seaweed	Dolphin interacting with seaweed, in its mouth or draped over its dorsal fin, body or fluke

Table 3.3 Feeding/foraging behaviors for bottlenose dolphins in the Shannon Estuary, Ireland, including a description for each behavioral event. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

UNIT	CODE	NAME	DESCRIPTION
FEEDING/FORAGING	CF	Catch fish	Dolphin catches a fish
	FSW	Fast swim	Dolphin moves quickly through water, apparently chasing fish
	FJ	Fin jerk	Abrupt movement of dorsal fin, indicating possible prey capture
	FS	Fish seen	A fish is seen next to a dolphin, in the water or air, with no evidence of a fish toss
	FT	Fish toss	Dolphin throws fish into the air from its mouth
	HS	*Humping surface*	Dolphin arches its body at surface and moves up and down
	LF	Leap feeding	Many dolphins are leaping, apparently chasing fish
	PD	Peduncle dive	Dolphin dives and peduncle is visible but its tail is not
	TD	Tail dive	Dolphin dives and tail is visible
	WF	With fish in mouth	Dolphin has fish in its mouth

Table 3.4 Social behaviors for bottlenose dolphins in the Shannon Estuary, Ireland, including a description for each behavioral event. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

UNIT	CODE	NAME	DESCRIPTION
SOCIAL	CHA	*Chase*	One dolphin in pursuit of another dolphin
	GEN	Genital slit/Genitals	Pink genital area or erect penis observed
	GS	*Goose*	One dolphin contacts another's genital slit with its rostrum
	PR	Pec rub	One dolphin rubs along another's pectoral fin
	PET	Pet	Gentle contact between pectoral fin of one dolphin and body of another
	RUB	Rub	Gentle to vigorous body-body contact
	SPL	Splash	Water splash caused by movement of dolphin(s) but action cannot be defined
	SPY	Spyhop	Head and rostrum emerge vertically from water and dolphin appears to view its surroundings

3.3.3 Inter-observer validity and reliability testing

The mean percentage agreement score and standard deviation (data validity) across 24 test participants was 88.1 ± 7.0. The scores of trained research assistant (mean = 92.5 ± 3.4) and other marine biologist (mean = 83.8 ± 7.1) test participants differed significantly (Mann-Whitney U test: W = 19.5, p <0.05). Fleiss's Kappa score (data reliability) across all participants was 0.81. The Kappa score of the trained participants was 0.88 and of the other participants was 0.74.

Every test participant correctly assigned the first two activity states (forage and travel) to their respective videos with only one incorrectly assigning the third (rest instead of social). All 24 test participants correctly assigned four of the 14 videos of single behavioral events with the behaviors tail dive, tailslap, fish toss and with seaweed. Of the remaining 10 videos, test participants correctly assigned behaviors to varying degrees. The behaviors tail out (0.95, 95.8%) and slow travel (0.84, 95.8%) had relatively high reliability and validity scores, with only one misclassified behavior each – pec out and fast travel, respectively – out of all 24 test responses (Table 3.5). Snag (0.91, 91.7%) and surface rush (0.91, 91.7%) were misclassified twice, each with the same two incorrect behavior assignations – slow travel and fast swim, respectively. Peduncle dive (0.86, 87.5%) and with fish in mouth (0.86, 87.5%) were both misclassified three times each, but with a different behavior each time – slow travel, head out and leap for peduncle dive and catch fish, fish toss and chuff for with fish in mouth. The scores for chinslap (0.59, 62.5%), spyhop (0.46, 50.0%), and breach (0.12, 20.8%) were the lowest. Breach was the behavior most frequently misclassified with five of the 24 participants correctly assigning the behavior and 16 misclassifying it as sideslap and three as backslap.

Table 3.5 Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors used in the inter-observer video test, with the most common misclassification for each behavior.

Behavior	**Percentage agreement**	**Category-wise Kappa**	**Most common misclassification**
Forage	100.0	1.00	N/A
Travel	100.0	1.00	N/A
Social	95.8	0.95	Rest
Breach	20.8	0.12	Sideslap
Fish toss	100.0	0.96	N/A
Chinslap	62.5	0.59	Head out
Surface rush	91.7	0.91	Fast swim
Slow travel	95.8	0.84	Fast travel
Tail dive	100.0	1.00	N/A
Tailslap	100.0	1.00	N/A
With fish in mouth	87.5	0.86	Catch fish/Fish toss/Chuff
Leap	83.3	0.71	Breach
Spyhop	50.0	0.46	Backslap/Backstroke/Head out
With seaweed	100.0	1.00	N/A
Peduncle dive	87.5	0.86	Slow travel/Head out/Leap
Snag	91.7	0.91	Slow travel
Tail out	95.8	0.95	Pec out

When differences between trained research assistant and other marine biologist test participant assignations were investigated, six of the behaviors had both higher validity scores (>10% difference in percentage agreement) and reliability scores (>0.10 difference in Kappa) for the trained participants than the other participants, compared to zero behaviors for the other participants vs. the trained participants (Table 3.6). These behaviors were surface rush, with fish in mouth, leap, spyhop, peduncle dive, and snag. Leap was the only behavior misclassified consistently by both trained and other test participants as a single alternative behavior, breach. Of the 17 behaviors tested, trained participants had three validity scores under 80% and the other participants had six validity scores under 80%.

Table 3.6 Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors assigned by trained research assistant and other marine biologist test participants in the inter-observer video test, with the most common misclassification for each behavior, for each test group.

	Trained Research Assistants			**Other Marine Biologists**		
Behavior	**Percentage agreement**	**Category-wise Kappa**	**Most common misclassification**	**Percentage agreement**	**Category-wise Kappa**	**Most common misclassification**
Forage	100.0	1.00	N/A	100.0	1.00	N/A
Travel	100.0	1.00	N/A	100.0	1.00	N/A
Social	100.0	1.00	N/A	91.7	0.90	Rest
Breach	25.0	0.09	Sideslap	16.7	0.12	Sideslap
Fish toss	100.0	1.00	N/A	100.0	0.92	N/A
Chinslap	66.7	0.62	Head out	58.3	0.53	Head out/Fast travel
Surface rush	100.0	1.00	N/A	83.3	0.81	Fast swim
Slow travel	91.7	0.90	Fast travel	100.0	0.80	N/A
Tail dive	100.0	1.00	N/A	100.0	1.00	N/A
Tailslap	100.0	1.00	N/A	100.0	1.00	N/A
With fish in mouth	100.0	1.00	N/A	75.0	0.72	Catch fish/Fish toss/Chuff
Leap	91.7	0.82	Breach	75.0	0.57	Breach
Spyhop	75.0	0.72	Backstroke	25.0	0.17	Head out
With seaweed	100.0	1.00	N/A	100.0	1.00	N/A
Peduncle dive	100.0	1.00	N/A	75.0	0.72	Leap/Head out/Slow travel
Snag	100.0	1.00	N/A	83.3	0.81	Slow travel
Tail out	100.0	1.00	N/A	91.7	0.90	Pec out

3.3.4 Activity state budgets

Using our ethogram, six of the activity states and 35 of the behavioral events observed in this bottlenose dolphin population were recorded and quantified. Activity states were recorded for 489 sightings during 256 surveys (on 171 d) from 2014 to 2016, and activity state budgets were calculated (Table 3.7). A single predominant group activity state (in the first five min.) was recorded for every sighting. For the sightings in this study, the five additional states listed in the ethogram were not separately recorded, and were pooled under either forage (probable forage, feed, and mill) or other (play and with boat).

Table 3.7 The six recorded activity states during 489 sightings of bottlenose dolphins in the Shannon Estuary, Ireland, including the number (n) and percentage (%) of records for each year and all years pooled together. Note: Percentages are rounded but exact figures add up to 100.

UNIT	**CODE**	**NAME**	**2014**		**2015**		**2016**		**All Years**	
			n	**%**	**n**	**%**	**n**	**%**	**n**	**%**
ACTIVITY STATES	TR	Travel	132	**68**	52	**36**	70	**46**	254	**52**
	FO	Forage	28	**15**	64	**44**	47	**31**	139	**28**
	SO	Social	19	**10**	14	**10**	7	**5**	40	**8**
	RE	Rest	5	**3**	9	**6**	18	**12**	32	**7**
	OT	Other	1	**1**	2	**1**	2	**1**	5	**1**
	UN	Unknown	8	**4**	4	**3**	7	**5**	19	**4**
		Total	**193**	**100**	**145**	**100**	**151**	**100**	**489**	**100**

Travelling was the predominant group activity state in over half (52%) of all sightings, while foraging was recorded in over one quarter (28%) of sightings. Socializing was the predominant group activity state for 8% of sightings while resting was recorded during 7% of sightings. Together, other and unknown activity states were recorded during 5% of sightings. A significant difference was found between annual activity budgets (χ^2 = 60.499, df = 10, $p<0.0001$). Of all three years, the highest proportion for travelling (68%) was recorded in 2014, the highest for foraging (44%) in 2015, and the highest for resting (12%) in 2016. The lowest proportion for socializing (5%) was recorded in 2016 (Table 3.7).

3.3.5 Behavioral events

Behavioral events were recorded for 427 sightings during 250 surveys (on 169 d) between 2014 and 2016. Of the 35 behavioral events used for analysis, each was observed at least once. In total, 1,452 behavioral events were recorded; of these, 198 were recorded in *ab libitum* data and excluded in further analysis. Thus, 1,254 behavioral event records were used for analysis. The average number of behavioral events recorded during the first five min. of a sighting was three (0.59 behaviors/min; range: 0-14) behavioral events (Table 3.8).

The most frequently observed behaviors in the surface behaviors, feeding/foraging, and social ethogram categories were slow travel (14% of records), tail dive (8%), and splash (2%), respectively (Table 3.8). Of all behavioral events, the five most frequently observed behaviors were slow travel (seen in 40% of all sightings), leap (28%), surface rush (28%), tail dive (23%), and tailslap (22%). These five behaviors accounted for 48% of the overall records. The 10 least frequently recorded behaviors were pet, spyhop, porpoise, catch fish, genital slit/genitals, fin jerk, snag, pec rub, defecation, and backstroke. These 10 behavioral events were seen in only 10% of total sightings, with <8 records each.

Table 3.8 The 35 recorded behavioral events in the ethogram, recorded during the first five minutes of sightings of bottlenose dolphins in the Shannon Estuary, Ireland, including the number of records made from each platform, the total number of records (n), percentage (%) of records and sightings for each behavioral event.

Behavior	**RIB**	**Draíocht**	**Dolphin Discovery**	**n**	**% of records**	**% of sightings**
Slow travel	43	57	72	172	14%	40%
Leap	31	44	46	121	10%	28%
Surface rush	37	45	38	120	10%	28%
Tail dive	31	43	26	100	8%	23%
Tailslap	25	32	36	93	7%	22%
Peduncle dive	23	45	21	89	7%	21%
Head out	10	33	26	69	6%	16%
Fast travel	11	24	24	59	5%	14%
Breach	8	21	24	53	4%	12%
Belly roll	14	18	19	51	4%	12%
Tail out	13	19	18	50	4%	12%
Fish seen	8	11	7	26	2%	6%
Fast swim	4	11	10	25	2%	6%
Splash	1	12	11	24	2%	6%
Sideslap	7	7	9	23	2%	5%
Fish toss	5	8	5	18	1%	4%
Pec out	7	4	6	17	1%	4%
On side	8	2	6	16	1%	4%
Rub	2	9	5	16	1%	4%
Chinslap	6	6	3	15	1%	4%
Leap feeding	2	6	6	14	1%	3%
Backslap	1	8	3	12	1%	3%
With fish	4	2	4	10	1%	2%
Chuff	0	7	3	10	1%	2%
With seaweed	1	3	5	9	1%	2%
Pet	1	3	3	7	1%	2%
Spyhop	1	2	4	7	1%	2%
Porpoise	2	3	1	6	0.5%	1%
Catch fish	2	1	3	6	0.5%	1%

Behavior	RIB	Draíocht	Dolphin Discovery	n	% of records	% of sightings
Genital slits/Genitals	4	0	0	4	0.3%	1%
Fin jerk	1	2	0	3	0.2%	1%
Snag	0	3	0	3	0.2%	1%
Pec rub	0	0	3	3	0.2%	1%
Defecation	1	1	0	2	0.2%	0.5%
Backstroke	0	0	1	1	0.1%	0.2%
Total Behaviors	314	492	448	1254		
Total Surveys	49	85	116	250		
Total Sightings	114	169	144	427		
Total Minutes	570	845	720	2135		
Behaviors per min	0.55	0.58	0.62	0.59		

There are 10 additional behavioral events defined in our ethogram that have been observed but not yet quantified for Shannon Estuary bottlenose dolphins. Motorboating (MO) (a series of rapid and repetitive tailslaps during forward progress by a dolphin (Weaver, 1987)) has been observed twice during focal follows. Video footage and photographs of headstand (HD) behavior exist, wherein the dolphin is completely vertical with its tail stock in the air above the surface of the water for a few seconds in a stationary position. It is possible that some headstands were recorded in the present study as tail outs. Dolphins in the Shannon Estuary are regularly observed bow-riding (BOW) the research vessel, tour boats, recreational vessels and large ships, but this behavioral event has not yet been quantified. On two occasions during focal follows, a snagging dolphin emitted a squeaky sound from its blowhole defined as a squeeze breath (SQ). Bubble-blows (BB) (Lusseau, 2006a), equivalent to Weaver's (1987) subsurface exhalation, have also been observed periodically wherein a dolphin underwater emits air from its blowhole creating bubbles at the surface. Sharking (SHK) has been seen at least 10 times during focal follows during which the tip of a dolphin's dorsal fin is visible cutting through the water surface at one level while the rest of the dolphin's body remains underwater. During one encounter, an individual dolphin exhibited scouting (SCO) behavior (Bearzi et al., 1999) in leaving the rest of its group and approaching the research vessel before returning to its group. Humping surface

(HS) behavior has been noted *ab libutum* on a few separate occasions where a dolphin has remained at the water surface moving up and down with its back arched. Goosing (GS), contact between the rostrum of an individual dolphin and the genital slit of another, was recorded twice during focal follows involving only juvenile dolphins on both occasions. During one focal follow, repeated chase (CHA) behavior (two dolphins actively surfacing, one dolphin following another (Lusseau, 2006a; Steiner, 2011)), was observed by an adult following a juvenile, interspersed with intense socializing.

3.3.6 Comparison with other studies

Although studies of bottlenose dolphin behavior elsewhere have reported activity budgets of strikingly different proportions, the daytime activity budgets observed in the Shannon Estuary fall within the ranges observed for this species in other areas (Table 3.9). All of the studies used for comparison included travel, forage, social, and rest activity states except for Sanibel Island (Shane 1990), which did not include rest in its analyses and included two additional activity state definitions for travel/feed and social travel. Other studies also included mill, travel/feed, and play in their activity budget breakdowns.

Table 3.9 Daytime activity budgets (in percentages) of bottlenose dolphins in the Shannon Estuary and from the published literature: Port River Estuary, South Australia (Steiner, 2011, foraging and feeding combined); Patos Lagoon Estuary, Brazil (Mattos et al., 2007); San Diego County, USA (Hanson & Defran, 1993); Sanibel Island, USA (Shane, 1990); Sarasota Bay, USA (Waples, 1995; McHugh et al., 2011b (juveniles only), combined and averaged); Shark Bay, Western Australia (Gero et al., 2005; Karniski et al., 2015 (estimated from Fig. 1, females only), combined and averaged); Moreton Bay, Queensland (Chilvers et al., 2003; non-trawler dolphin community only); Cardigan Bay, Wales (Veneruso & Evans, 2012)

Study Area:	**Shannon Estuary**	**Port River**	**Patos Lagoon**	**San Diego**	**Sanibel Island**	**Sarasota Bay**	**Shark Bay**	**Moreton Bay**	**Cardigan Bay**
Study Method:	Survey	Individual Follow	Group Follow	Group Follow	Group Follow	Individual Follow	Survey	Survey	Survey
Travel	52	23	29	63	46	61	23	55	43
Forage	28	48	38	19	17	16	30	34	50
Social	8	14	6	12	7	5	10	8	6
Rest	7	11	1	3		1	37	3	0
Other	1	4				1			
Unknown	4								
Mill			4			16			
Travel/feed			22		21				
Social travel					10				
Play				3					

While 52% of the Shannon Estuary bottlenose dolphins’ activity budget during this study was allocated to travelling, dolphins in the Port River Estuary, South Australia (Steiner, 2011) and the Patos Lagoon Estuary, Brazil (Mattos et al., 2007) had much lower travelling proportions (23% and 29%, respectively). The highest travelling proportion in the investigated studies was recorded for bottlenose dolphins in San Diego County, USA (Hanson & Defran, 1993), at 63%. Foraging proportions ranged from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012), with similar proportions of 28%, 30% and 34% in the Shannon Estuary, Shark Bay (Gero et al., 2005; Karniski et al., 2015) and Moreton Bay (Chilvers et al., 2003), respectively. Social behavior proportions ranged from 5% in Sarasota Bay to 14% in the Port River Estuary while rest behavior proportions ranged from 1% in Sarasota Bay and the Patos Lagoon Estuary to a high of 37% in Shark Bay. A systematic review of published studies shows some variation in the classification of behavioral event descriptors (Table 3.10).

Table 3.10 Behaviors described in this study's ethogram and some comparable descriptors for similar behaviors in other studies

Behavior name	**Behavioral descriptor**	**Reference(s)**
Slow travel	Directed movement at a speed of under 10 km/h	This study
Fast travel	Directed movement at a speed of over 10 km/h	This study
Straight travel	Traveling in a general direction with all surfacings in that direction	Waples (1995)
Zigzag travel	Traveling in a general direction by straight segments of different directions	Waples (1995)
Meandering travel	Traveling in a general direction but orientation changes frequently	Waples (1995)
Surface rush	Fast movement breaking the surface causing a flurry of white water at either side of the animal	This study
Active surfacing	Rapid surfacing with spray, a major part of the back is visible during the surfacing	Lusseau (2006a)
Racing	Regular dive performed at high speed with more of dolphin's back exposed and white water forming as animal surfaces	Bearzi et al. (1999)
Feeding rush	A sudden acceleration and splash	Shane (1990)
Rapid surface	A rapid surface in which the dolphin maintains a normal horizontal posture and the dolphin's ventrum does not clear the water surface	R. Connor, pers. comm.
Leap	Body exits water entirely in an arcuate path and reenters water smoothly	This study
Forward leap	Exit and enter head first with venter facing down	Shane (1990)
Backward leap	Exit and enter with dorsum facing down	Shane (1990)
Side leap	Exit and enter with either side facing down	Shane (1990)
Snag	Body is stationary, horizontal and dorsal part of body is visible at surface	This study
Floating	Stationary position at interface exposing foresection of animal in pronounced concave arc	Bearzi et al. (1999)
Lie at surface	Lie stationary with part of body exposed at surface for 5 or more seconds	Shane (1990)
Snaggle	Dolphin floats stationary at the water surface, its body horizontally flexed	Lusseau (2006a)
Chuff	Strong audible exhale from blowhole	This study
Forced blow	Dolphin forcefully exhales above water producing a loud 'chuff' sound	Lusseau (2006a)
Noisy blow	Dolphin made a loud noise with the blowhole at the surface	Steiner (2011)
Cough	A loud, forceful exhalation	Shane (1990)

Behavior name	**Behavioral descriptor**	**Reference(s)**
Tailslap	Flukes raised above water surface and then lowered making a strong audible impact	This study
Upside-down tailslap	Flukes raised above the surface and dorsal side slapped downward	Shane (1990)
Inverted tailslap	The dorsal side of the flukes is brought down flatly on the water surface by an animal in the inverted position	Weaver (1987)
Tail slapping dorsal	Dolphin slapped the surface with the dorsal side of the tail	Steiner (2011)
Head out	Head and rostrum emerge above water surface and reenter water smoothly	This study
Head out	Entire head exposed at surface; rostrum pointed at an angle; dolphin stationary	Shane (1990)
Peek	Head raised out of the water far enough to expose the eyes; rostrum pointed forward; occurs during forward motion	Shane (1990)
Tail out	Tail is exposed above water surface	This study
Tail out	Exposure of the caudal section at the surface in a head-down position. The straight tailstock is elevated by a modulated upward movement and the flukes may be flipped up or moved up-and-down briefly during exposure	Weaver (1987)
Fluke up	Exposure of one fluke at the surface by a moving or stationary animal. The fluke is usually angled and may flex briefly, often with splashing	Weaver (1987)
With seaweed	Dolphin interacting with seaweed, in its mouth or draped over its dorsal fin, body or fluke	This study
Weed rub	A dolphin rubs into a patch of weed while rolling side or belly up. Pectorals and flukes are often lifted out of the water, draped with weed	R. Connor, pers. comm.
Kelp dragging	Strands of kelp are hooked around the front of the dorsal fin and trail off either side of the body as the animal males forward progress at the interface	Weaver (1987)
Carry weed	Dolphin carries algae on its beak, fin, flippers or tail fluke	Lusseau (2006a)
Squeeze breath	A sound emitted from the blowhole that sounds like air escaping a balloon	This study
Squeeze breath	Audible and brief expulsion of air from the blowhole that sounds like air escaping the tightened neck of a balloon	Weaver (1987)
Fart blow	Dolphin exhales above water with its blowhole contracted producing a fart-like sound	Lusseau (2006a)
Sharking	Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water	This study
Sharking	Dolphin swims horizontally at the water surface with its dorsal fin visible above water	Lusseau (2006a)
Surface finning	The dorsal fin is continuously visible and the only exposed part as the animal makes forward progress at the interface at any speed	Weaver (1987)
Humping surface	Dolphin arches its body at surface and moves up and down	This study
Humping surface	A normal speed surface in which the dolphin “humps up” its posterior half to break its forward motion as it descends (when dolphins are pursuing fish)	R. Connor, pers. comm.
Buck	Body bent forward and back hunched and exposed at surface while dolphin bounces vigorously (social)	Shane (1990)

3.4 Discussion

3.4.1 Bottlenose dolphin ethogram

The search for ethograms of surface behavior in the published literature and in research project protocols resulted in a varied set of behavioral terms and descriptions for bottlenose dolphins globally. Some behavioral studies have not used detailed ethograms with behavioral events to date (K. McHugh, pers. comm., 14 April 2017; T. Genov, pers. comm., 14 March 2016; K. Robinson, pers. comm., 14 March 2016; G. Veneruso, pers. comm., 14 March 2016), and others have unpublished ethograms, which they use as a basis for behavioral research (R. Connor, pers. comm., 25 January 2017; E. Krzyszczyk, pers. comm., 08 February 2016; S. Gazda, pers. comm., 09 March 2016; K. Sprogis, pers. comm., 19 March 2016). Some very detailed ethograms have been created as elements of students' Masters theses (e.g., Weaver, 1987; Waples, 1995). Of the ethograms found in the peer-reviewed literature, the terms and definitions are different for every study site; although, many of the descriptions describe the same or similar behaviors. Because many of these published ethograms were used for specific studies, only a small number are appropriate to the general description of adult bottlenose dolphin behaviors within a population.

All of the behaviors that were observed in our study were added to the present ethogram with detailed descriptions and should lend themselves to straightforward comparison with behaviors documented elsewhere. These behaviors have all been described in the literature on bottlenose dolphins, but some are rarely mentioned (e.g., defecation) and, in one case, we have used our own term ("backstroke" – possibly equivalent to inverted motorboating in Weaver's (1987) ethogram).

In some comparable studies, behavioral events have been described which have not (yet) been observed or recorded in the present study of Shannon Estuary bottlenose dolphins. Surface behaviors such as stretching (Weaver, 1987; Steiner, 2011) where a dolphin stretches its back with its head, and sometimes tail flukes, lifting above the surface, and swell-riding (a stationary animal faces land until a swell passes and then moves forward with it, exposing the dorsal fin and tailstock (Weaver, 1987)), have not been observed in the Shannon Estuary.

Many foraging behaviors in the literature have not been observed in the Shannon Estuary population. These include sponging (carrying a sponge on the rostrum (Smolker et al., 1997)), strand-feeding (surging out of the water in unison onto mud banks to feed on small fish (Duffy-Echevarria et al., 2008; Jiménez & Alava, 2015)) and kerplunking (fluke-slapping that produces a high splash of water and an audible sound (Connor et al., 2000a)). Pinwheels (flip-turns performed by a dolphin in side-swim orientation (Nowacek, 2002)), benthic-feeding methods (e.g., Rossbach & Herzing, 1997), fish whacking (propelling a fish into the air with a forceful thrust of the flukes (Nowacek, 2002)) and belly up behavior (a dolphin upside-down chasing a fish at the surface (R. Connor, pers. comm., 25 January 2017)) have also not yet been observed.

Social behaviors described in the literature that have not been recorded in the Shannon Estuary include jaw clap (dolphin clapping its mouth at the surface, without anything in it (Waples, 1995; Steiner, 2011)), bite (one dolphin bites another (Lusseau, 2006a)) and headbutt (two dolphins jump simultaneously and hit their heads together (Lusseau, 2006a; K. Robinson, pers. comm., 14 March 2016)). Neither bonding (two dolphins swimming next to one another with prolonged pectoral fin contact) nor head-to-head (two or more dolphins facing one another rostrum-to-rostrum for a prolonged period) behaviors described by R. Connor (pers. comm., 25 January 2017) have been observed in the Shannon Estuary. No clear displays such as the elaborate synchronous ones by male bottlenose dolphins, described by Connor et al. (2006), have been observed in the Shannon Estuary to date.

There are various reasons why some of the behaviors recorded in other studies may not yet have been recorded in ours. One very obvious constraint is that water visibility in the Shannon Estuary is poor (<1 m) compared to other study sites (e.g., Shark Bay, where visibility into the water from the boat is 2-8 m (Mann & Smuts, 1999)). In this study, we focused exclusively on surface behaviors. Occasional days of good water visibility may present opportunities for documenting underwater dolphin behavior in the Shannon Estuary in the future, but these opportunities are limited. Many clear-water sites have *Tursiops aduncus* rather than *T. truncatus* and it may be that subtle differences exist between the overall behavioral repertoires of these two different species. In addition, observations were restricted seasonally, and further behaviors might be documented if behavioral observations were made in winter months. As with any catalog of behaviors, the ethogram we developed should be interpreted as an evolving document and not a full list of Shannon Estuary bottlenose dolphin behavior.

There is no evidence to suggest that the presence of either our research vessel or the tour boats had an effect on the behavior of the dolphins. However, land-based research using our ethogram could help to reinforce that the sighting records from boats illustrate the true behavioral repertoire and budgets of the dolphins (although the different perspectives of observing from land vs water might also affect this).

3.4.2 Inter-observer validity and reliability testing

The high validity and reliability scores obtained in the inter-observer video test by trained research assistants suggest that errors in behavioral data collected for this study did not have a significant impact on our results. The higher results for trained research assistants compared to the other participants indicate that training in the field will remain an important component of good behavioral research. The fact that some behaviors, such as breaches, were misclassified more often than others points to the need for specific attention to such behaviors in the training process. Nevertheless, the relatively high validity and reliability of the test even for other marine biologist participants suggest that our ethogram is well suited for being used as a research tool by other research groups, and for facilitating behavioral comparison between different populations.

3.4.3 Activity state budgets

Our results suggest that bottlenose dolphins in the Shannon Estuary spend over half (52%) of their time travelling, a quarter (28%) of their time foraging, and the rest of their time (20%) engaged in all other activities. These results are somewhat similar to results from Ingram’s (2000) study of Shannon Estuary bottlenose dolphins: 64% travel, 26% forage, 8% social, and 2% rest, calculated from land-based observational data. A comparison of our results with activity budgets in the literature leads to interesting parallels and some differences: time spent travelling for this population is relatively high (52%) maybe because the habitat is a geographically narrow but long estuary. However, in contrast, another estuarial population (the Port River Estuary, South Australia; Steiner, 2011), had a much lower proportion of travelling (23%), although the estuary shape was quite different. Comparison with the Patos Lagoon Estuary, Brazil (Mattos et al., 2007) is more difficult because of that study’s distinction between travel (29%) and travel/feed (22%). Foraging proportions vary substantially across populations ranging from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012). The Shannon dolphins’ foraging budget (28%) is similar to Shark Bay (30%) (Gero et al., 2005; Karniski et al., 2015) and Moreton Bay (34%) (Chilvers et al., 2003). What accounts for such a wide variation in foraging proportions? Presumably it is partly explained by differences in the availability of prey, habitat geography, different nutritional requirements and foraging strategies, hand-in-hand with changing environmental effects. In addition, it is also possible that differences in the vessels used as research platforms might have an effect on dolphin behavior. Christiansen et al. (2010) reported that dolphins (*T. aduncus*) around tour boats were more likely to be travelling or foraging than resting or socializing. A further explanation for behavioral differences is habitat use; depending on where surveys were conducted in a study site, dolphins could be found to be engaging in behaviors related to that part of the survey area.

Social behavior proportions range from 5% in Sarasota Bay to 14% in the Port River Estuary (Waples, 1995; McHugh et al., 2011b; Steiner, 2011). The Shannon dolphins spent 8% of their time engaged in social activity, a similar proportion to Shark Bay dolphins (Gero et al., 2005; Karniski et al., 2015). Interestingly, Shark Bay dolphins have much higher resting rates (37%) than those of other populations used for comparison. Dolphins in the Shannon Estuary spent 7% of their time resting while bottlenose dolphins in the Patos Lagoon Estuary and Sarasota Bay allocated only 1% of their daytime activity budgets to resting (Waples, 1995; Mattos et al., 2007; McHugh et al., 2011b). Further research should investigate if differences in activity state budgets could help to explain differences found in behavioral event occurrence. For example, dolphins snag much more in Shark Bay than the Shannon Estuary, and snagging behavior is associated with resting (R. Connor, pers. comm., 25 January 2017). Thus, the fact that the social activity budget is similar in both of these populations may be very important in the further study of the social behavior of Shannon Estuary bottlenose dolphins, especially in comparing the societal complexity of these two populations.

The study population’s activity budget was considerably different in different survey years, particularly for foraging and travelling activity. Dolphins spent less time foraging and more time traveling in 2014, and vice versa in 2015 (with values for 2016 between the values of these two years), and this inter-annual variation in foraging activity is likely to be related to changing environmental conditions in the Shannon Estuary in turn affecting prey distribution and abundance. The differences in activity budget proportions allocated to socializing and resting may be explained by reproduction with inter-annual calving rates also playing a role in changing activity budgets. There is no clear explanation for the differences between years but this certainly warrants further attention and the addition of further years of data may help to explain fluctuations in the activity budget proportions over different years for this population.

3.4.4 Limitations and further study

The data used in this paper do not distinguish among classes of animals or individuals. It was therefore not possible to examine whether there were significant behavior differences between, for example, males and females or adults and juveniles. Anecdotal observations suggest that head out behavior is displayed more frequently by dependent calves in their first two years of life, but this hypothesis needs to be investigated further. In other studies (e.g., Nowacek, 2002), individual dolphins within the same community displayed different, though overlapping, repertoires of foraging behavior. In this study, our observations suggest that one individual, a dolphin with scoliosis, often displayed a head out and tail out in quick succession during a surfacing bout, which was probably related to its deformity. Some individuals seem to leap or tailslap more than others. These and other individual differences need further investigation.

The data used in this paper are based on observations of less than 30 minutes, made primarily from the opportunistic platform of tour boats adhering to marine regulations (Maritime Safety Directorate, 2005). The data therefore provide little information about potentially rare behaviors. In addition, the tour boats often target the same areas leading to a sampling bias in survey effort. In other studies, longer observations from dedicated research vessels have identified behaviors that seem unique to particular populations, such as sponging (Smolker et al., 1997) and beach hunting (Sargeant et al., 2005). Lusseau (2006a) identified some behaviors in the Doubtful Sound bottlenose dolphin population which relate to cues for the start and end of certain activity states. Longer observations, using focal follows and dedicated survey transects, may provide greater insights into the role of specific, and rare, behaviors and perhaps of behaviors unique to this population.

The data used in this paper were collected over a limited period, primarily during the summers of three years. Therefore, a comparison of behaviors between seasons was not applicable, nor was year-to-year variation discoverable over the long-term. Future research over more consecutive years, as well as throughout each year, is necessary to answer questions about how this population's behavior varies over time.

Our ethogram is an extremely useful tool because it likely covers all age classes, sexes, group sizes and survey areas within the Shannon Estuary. The sampling of different areas provides good coverage of different individuals in the population. On some occasions, both tour boats and the research vessel sampled at the same time on the same day simultaneously (in different areas of the estuary), providing a widespread snapshot of bottlenose dolphin sightings across the study site.

3.5 Conclusions

The purpose of this article was to provide the first ethogram for bottlenose dolphins in the Shannon Estuary, to describe and quantify these behaviors, and to compare behaviors documented in this study with those of other studies of bottlenose dolphins in different geographical locations. The ethogram presented contains 11 activity state and 45 behavioral event definitions. The results presented are based on observational records from three years of study and the ethogram behaviors quantified were each recorded at least once for dolphins in the Shannon Estuary, with 10 additional behaviors included from anecdotal records. We expect our ethogram to develop over time, adding some of the behaviors reported for bottlenose dolphins elsewhere, as and if they are observed in the Shannon Estuary. The behaviors reported here are some of the most frequently observed and documented for bottlenose dolphins in other wild environments; however, this ethogram is the first for temperate European waters and will provide a fundamental tool for future behavioral research.

Activity states and behavioral events recorded in the Shannon Estuary were quantified and an activity state budget for this bottlenose dolphin population was presented. Bottlenose dolphins in the Shannon Estuary allocated relatively more time to travelling and less to resting, compared to other populations. These results make an important contribution to global dolphin research by adding to a remarkably varied set of activity budgets reported for other populations, where some similarities and some differences are apparent. Overall, this study establishes a foundation for investigating the behavior of the Shannon Estuary bottlenose dolphin population and for engaging in the systematic comparison with other populations necessary for understanding the complex lives of these social mammals.

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Chapter 4

Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations

This chapter is a reproduction of the following published paper (published version can be found in Appendix C).

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4 Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations

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ABSTRACT

Social and network analyses that incorporate information on individuals within a population enhance our knowledge of complex species. In this study, the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, was analyzed by examining the dynamics of the whole population and then of individuals classed by sex, age, and area. 121 dolphins were identified during 522 sightings between 2012 and 2015. The mean half-weight association index (HWI) of the population was 0.07±0.02. The highest HWIs for individuals of known sex were for female-male pairs. Mean within-class HWI was significantly higher than mean between-class HWI for both age and area classes. Ordinations and sociograms were used to visualize social networks. Permutation tests revealed nonrandom associations for the population overall and both between and within classes. Temporal analyses showed associations persisting for >1,000 d. The whole population's best fit model was for two levels of casual acquaintances. Movement analyses demonstrated the use of the inner estuary by only 25% of the population revealing a potential community division by area. The difference between mean HWI when socializing (0.09±0.03) compared to foraging (0.06±0.03) was significant. These results highlight the importance of localized research, reflecting the complexity found in bottlenose dolphin societies globally.

Key words: bottlenose dolphin, social structure, photo-identification, associations, networks, *Tursiops truncatus*, individual classification

4.1 Introduction

Social structure, a concept that integrates the ethological interactions and ecological relationships between conspecifics, is a fundamental component of the biology of an animal population (Lusseau *et al.* 2006). For intelligent mammals with complex societies, the social structures of populations are integral to our overall knowledge of the species. Social structure can affect population growth, genetics, and animal movements, and represents an important factor in management and conservation (Whitehead 2008, 2009). Because not all individuals of a species are the same, it is important to explore population demographics and examine the interactions of different members within the social structure of a population. For example, sociality can be driven by individual classes such as sex (Connor *et al.* 2000) or age (Lusseau and Newman 2004, McHugh 2010), or other factors such as habitat use (Wiszniewski *et al.* 2009, Titcomb *et al.* 2015). It is therefore important to take such variables into account during the investigation of a population's social structure.

If nonrandom patterns of association are found in a population, this can suggest the patterning of social relationships that characterizes that society as a whole (Smolker *et al.* 1992). Because of the many spatiotemporal changes in associations in a society, assessing its structure can be difficult, but available quantitative techniques, such as association and network analyses (Whitehead 2008), help to define social structure more precisely and explain observed association patterns (Lusseau *et al.* 2006). Additionally, sophisticated studies of social structure based on identifiable individuals can provide detailed measures and examples of these social systems (Whitehead 2008).

Bottlenose dolphins (*Tursiops* spp.) are highly intelligent marine mammals known to live in extremely dynamic complex social systems referred to as fission-fusion societies (Connor *et al.* 2000). This is one of the most complex social organization systems seen in the animal kingdom (Smolker *et al.* 1992), where large numbers of individuals associate in small groups that change size and composition frequently, at different spatial and temporal scales (Connor *et al.* 2000). Social relationships exhibited by individual dolphins are maintained within a constantly changing social environment where individuals are drawn from a large social network (where they may be present in a wide range of different groups) but associate consistently with just a few other individuals (Smolker *et al.* 1992).

Well-studied bottlenose dolphin societies in Shark Bay, Australia, and Sarasota Bay, USA, exhibit strong long-term associations between adult individuals of the same sex (Smolker *et al.* 1992, Connor *et al.* 2000, Owen *et al.* 2002, Wells 2014, Connor and Krützen 2015). These associations are characterized by dramatic sex differences in association patterns comprising long-term bonds between males in alliances and looser network associations among female dolphins. In Doubtful Sound, New Zealand, sex-specific alliances were not observed amongst bottlenose dolphins, but some male-female associations were stable over the course of several years (Lusseau *et al.* 2003). However, in well-studied bottlenose dolphin populations in the Moray Firth, Scotland and Sado Estuary, Portugal, no strong sex-specific associations have been found (Wilson 1995, Augusto *et al.* 2011). In the Sado Estuary, associations are similar between all individuals, with no patterning according to sex or age class (Augusto *et al.* 2011). Thus, it would appear that the sex class of individuals plays a varying role in bottlenose dolphin societies globally.

For long-lived, slow-developing species like bottlenose dolphins, there is a prolonged juvenile period. Typically, most studies tend to focus only on adults because they are more easily identifiable; however, an understanding of juvenile association patterns and social structure is necessary to achieve a full understanding of the social dynamics of a population (McHugh 2010). In some studies that explored age effects, differences in patterns of association have been discovered in relation to age class (Samuels 1996). Exclusively juvenile groups are found in some populations (Wells 2014) and age-related homophily has been found in dolphin social networks (Lusseau and Newman 2004). In other studies where bottlenose dolphin groups do not seem to be segregated by sex or age class, some of these demographically mixed groups have formed socially distinct communities within populations (Lusseau *et al.* 2006).

The study of association patterns with respect to area use is important because differences in area use do not necessarily lead to differences in association patterns and *vice versa*. However, if the social structure of a population *is* related to area use, this has important implications for population management (Lusseau *et al.* 2006, Cantor *et al.* 2012). To answer these questions, sightings of individual dolphins may be classified by area within the study site. Then, association analyses can be used with classifiers to interrogate the data set for potential preferences or avoidances between the classes.

The bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland, is stable and composed of *ca*. 120 individuals (Berrow *et al.* 2012) and is genetically discrete (Mirimin *et al.* 2011). Dolphins are present in the estuary year-round (Berrow *et al.* 1996, Ingram 2000, Berrow 2009) and have been observed exclusively in the Shannon Estuary and adjacent (<25 km) Tralee and Brandon Bays (Ryan and Berrow 2013, Levesque *et al.* 2016 (Appendix D)). This species also occurs around the entire Irish coast (O'Brien *et al.* 2009) and in offshore waters (Louis *et al.* 2014) but these are thought to constitute distinct populations (Mirimin *et al.* 2011). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (NPWS 2012), which are listed on Annex II of the EU Habitats Directive. Given the level of protection assigned to this population, information on the social structure of dolphins in the estuary is important for their long-term conservation and the development of a local management plan.

Only two studies to date have investigated the social structure of bottlenose dolphins in the Shannon Estuary (Ingram 2000, Foley *et al.* 2010); however, neither had access to data on individual sex or age, and although Ingram (2000) identified some spatial patterns, these were not based on classifying individuals by area of sighting locations. Our study marks a significant advance on previous work by operating with a much larger set of data and by considering within-population structure based on sex, age, and area.

In describing and analyzing the social structure of a unique population of bottlenose dolphins in Ireland, this paper makes data available for comparisons with similar studies. Studying bottlenose dolphins in varying social systems contributes to current knowledge of social structure and the evolutionary mechanisms that may have affected differences among populations. Knowledge of the social structure of a bottlenose dolphin population contributes to the conservation of the species, especially to population management within SACs and Marine Protected Areas, and helps to understand trends in long-term monitoring.

This paper aims to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland using a 4-year data set. We begin by (1) examining the social attributes of the population as a whole, and then explore the social dynamics of the population further by classifying individual dolphins by (2) sex, (3) age, and (4) area. We hypothesized that the structure of the population would be similar to that of many other populations described worldwide in several ways, specifically that there would be (1) preferred and avoided associations between individuals; (2) a pattern of single-sex groups and strong within-sex-class associations;

(3) a pattern of single-age-class groups and strong within-age-class associations; and (4) area-based social clustering of the population within the study area as a whole.

4.2 Methods

4.2.1 Study site

The study site is located in the Lower River Shannon Special Area of Conservation (SAC; Site Code 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland's west coast between Co. Clare, Co. Kerry, and Co. Limerick (52°36'N, 9°38'W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 4.1).

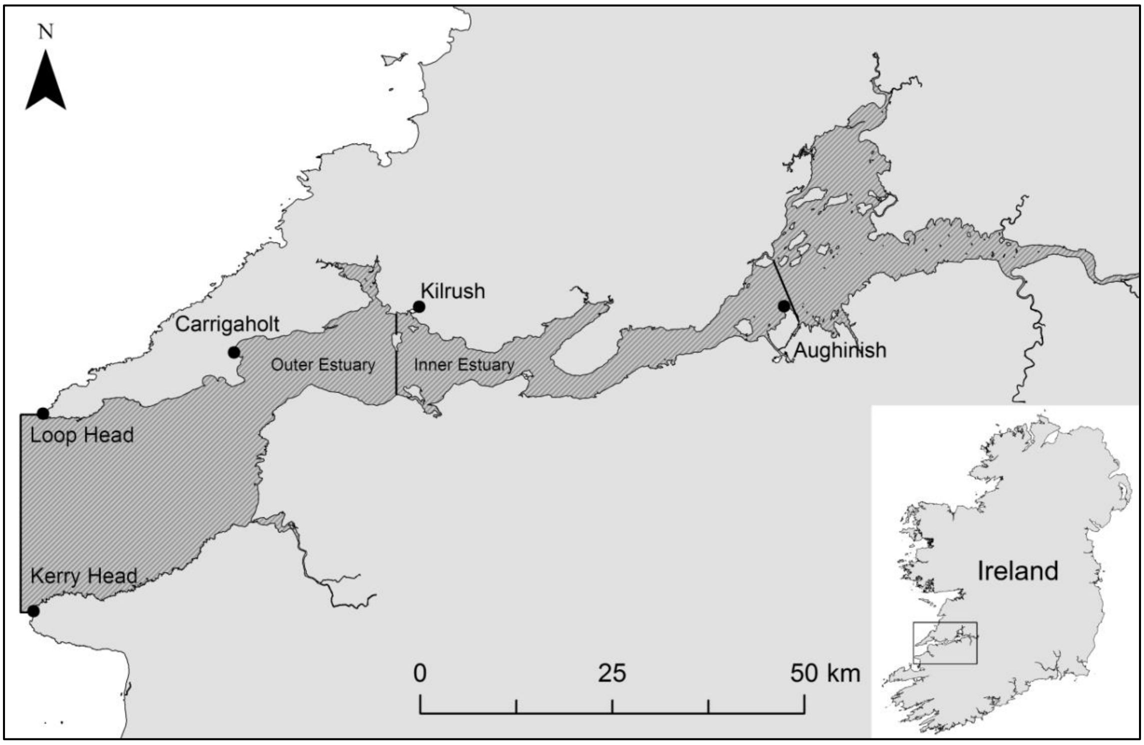

Figure 4.1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC; shaded dark gray area) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush.

4.2.2 Data collection

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow *et al.* 1996, 2012; Ingram 2000; O'Brien *et al.* 2014 (Appendix E); Appendix F, Poster 4). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow and Holmes 1999).

In this study, surveys were conducted between March and November each year from 2012 to 2015 on board three vessels – the two dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats operated independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 4.1). The Carrigaholt tour boat concentrated effort in the outer estuary exclusively while the Kilrush tour boat primarily concentrated effort in the inner estuary area with some outer estuary trips. Overall, the mean length of dolphin-watching trips was 2.3 h (Barker and Berrow 2016). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor, with which surveys were conducted throughout all areas of the estuary between Loop Head and Aughinish. Trained onboard observers (n = 19 over 4 yr) located dolphins visually by eye and with the use of binoculars (Minox 7x50 or 8x42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~5 m, while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at <2 m above sea level. The tour boats had a minimum of one observer and a maximum of six observers per survey while the research vessel had between three and five crew per survey.

A sighting began when at least one dolphin was within 100 m of the vessel and ended after ≤30 minutes due to national regulations (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and approximately 100 m from them unless the dolphins approached the boat themselves.

Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin IDs, group estimates, environmental measures (including water temperature, depth, and sea state), location (Latitude and Longitude; Garmin GPS 72H), activity states (travel, social, forage, rest, other, or unknown) and behavioral events (*e.g.*, leap; see definitions in Baker *et al.* 2017 (Chapter 3)). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh *et al.* 2011).

Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70-300 mm lenses) in an attempt to photograph each individual in each group for individual recognition through the photo-identification of dorsal fins (Würsig and Würsig 1977, Würsig and Jefferson 1990).

4.2.3 Data management

Photos from all surveys and sightings were maintained in a database using the photographic software environment IMatch 5.6 (https://photools.com/). A digital photo-id catalogue housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, based on the nicks and notches along the edge of the dorsal fin, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities, and persistent skin lesions, by using the filter function in IMatch to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then rematched. The final identifications of each individual dolphin in each sighting were verified by the lead researcher who had the most photo-id experience, as recommended by Pearson *et al.* (2016). The long-term monitoring of this relatively small population, coupled with the high encounter rate, knowledge of life history and well-maintained photo-id catalogue of 204 known individuals (recorded between 2008 and 2016) greatly enhanced the process and efficiency of individual dolphin identification.

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of FinBase (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams *et al.* 2006). Each dorsal fin photo's quality was graded using the FinBase Photographic Quality form and assigned to its specific sighting and survey using the FinBase Match/Catalog form, wherein the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program. Activity state data originated from the FinBase database, where each sighting was assigned a single predominant activity state (travel, social, forage, rest, other, or unknown) by the observer during data collection.

4.2.4 Data classification

(i) Sex classification

Information on the sex of individual dolphins was obtained in three ways, using (1) genetic sex determination from biopsy tissue samples (*n* = 27), collected under NPWS permits (Berrow *et al.* 2002, Mirimin *et al.* 2011); (2) photographs of the genital area (*n* = 1); and (3) consistent observations with a dependent calf multiple times over multiple years (*n* = 30; Smith *et al.* 2016). As a result, 47% of known sexes were determined through biopsy sampling and 53% from observational data. For females identified through association with a calf, the number of mother-calf pair sightings ranged from 6 to 92. Overall, 48% of individuals available for analysis were of known sex.

(ii) Age classification

Age class was determined by observations of individual size, reproductive state and/or knowledge of long-term life history (unpublished data). Adults were larger and darker in color than juveniles, and sometimes with a dependent calf. Juveniles were less than two-thirds the size of adults and were not observed to be dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years before weaning.

(iii) Area classification

The study site was divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush. This line divided the estuary roughly in half, was a reference point for the center of the study area and divided research surveys east and west of the port of Kilrush. A classifier for area was created based on the sighting records of individuals by location, because preliminary evidence suggested differences in the use of the inner and outer survey areas by individuals in the population. If an individual had *ever* been observed in the inner estuary, it was classified as 'inner'. If an individual had *never* been observed in the inner estuary, it was classified as 'outer' (Table S1). This provided a basic classification from which individual area use within the study site could be explored (see map in Fig. 4.1; Fig. S1).

4.2.5 Data analysis

4.2.5.1 Analytical definitions

Data were queried in FinBase and input into SOCPROG 2.7 (compiled version), a dedicated software package that uses data on the associations of identified individual animals for the analysis of their social structure (Whitehead 2009), in group mode, with a supplemental file detailing individual sex, age, and area classifiers. The sampling period was defined as one day, based on the natural break between daylight sampling sessions and because the proportion of individuals sampled within a one day timeframe was appropriate for data analysis. Associations between individuals were defined by shared group membership, with each record/sighting constituting one group. The half-weight association index (HWI) was used as the coefficient of association. This measure represents the strength of social bonds among individuals (with a range of possible values between 0 (never seen together) and 1 (always seen together)), while also accounting for the possibility of missing individuals during sighting encounters (which is a possibility when opportunistic research platforms like dolphin-watching tour boats are used). The HWI is defined as $\mathrm{HWI} = 2N_T/(N_a+N_b)$ where N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns and Schwager 1987). Thus, this association index indicates the proportion of time that each pair of individuals is seen in a group together. For all analyses other than the temporal analyses and movement analyses (where all data were used), restrictions were set within SOCPROG to include only individuals with >5 sighting records.

Dependent calves were excluded from analyses because their presence was a result of their mothers' presence in groups. Excluding dependent calves from the dataset left adults and juveniles, but for analyses using sex class, only adults were available as sex had not been determined for any of the juveniles. Both adults and juveniles were included in the analyses using area class.

SOCPROG was used to generate basic population data, quantify the number of individuals in defined classes, produce descriptive statistics and examine association patterns between individuals in the population. A discovery curve was plotted to assess photographic coverage of identified population members using cumulative number of identifications and year of sampling.

4.2.5.2 Group composition, associations and clusters

Group composition was explored by examining the identities of individuals in every group, classifying them by sex and age and calculating overall proportions. Associations between and within sex classes were quantified and compared using a Mantel test and a histogram of proportional HWIs (Whitehead 2009).

Average linkage hierarchical cluster analysis was used to investigate relationships within the inner area class wherein individuals were assigned to clusters (clusters may be semipermanent social units, communities, or other social entities). A Cophenetic Correlation Coefficient (CCC) value greater than 0.8 (where 1.0 = perfect fit and 0.0 = no relationship) and a modularity greater than 0.30 indicate that a dendrogram is an acceptable representation of input distances and its division into clusters is appropriate (Whitehead 2009).

4.2.5.3 Social networks

Association matrices were visualized as social networks (or sociograms) for all associations with HWI ≥0.20 with individual nodes shaded, first by age and then by area class, and weighted links representing strength of association between individuals at three levels. A further sociogram was constructed using cluster analysis results to visualize the clustering of individuals in the inner estuary network.

Weighted social network measures were calculated for all individuals and for age, area, and sex classes separately using the network analysis statistics module in SOCPROG and standard errors were calculated using the bootstrap method with 1,000 replicates. ‘Strength’ was calculated as the sum of association indices of any individual with all other individuals; thus, high strength values indicate strong associations with other individuals in the population. ‘Reach’ was measured as the overall strength of network neighbors.

4.2.5.4 *Behaviorally specific associations and preferences*

We used methods similar to Gero *et al.* (2005) to determine whether behaviorally specific preferred associations existed within the population, as it is important to assess the effect of activity state on associations in fission-fusion networks (Gazda *et al.* 2015, Moreno and Acevedo-Gutiérrez 2016). Restrictions were implemented in SOCPROG for each of four main activity states – rest, travel, social, and forage. The data were restricted by each activity state in turn and the HWI matrix was saved as a SOCPROG association measure. Then, SOCPROG’s analyses of multiple association measures module was used to view dyadic plots and different dyadic outputs of the association measures. A Mantel test was run to test for correlation between social and foraging HWIs.

4.2.5.5 *Association preferences/avoidances*

Permutation tests (Bejder *et al.* 1998, Whitehead *et al.* 2005) were used to test for preferred/avoided associations across the whole population, the null hypothesis being that there were no bottlenose dolphin dyads in the Shannon Estuary population that preferred or avoided to associate. Then, permutations were run to test for preferred/avoided associations within and between classes (age, area, and sex) as well as for each year of data separately (and sex-specific associations within each year) and for activity states (social, forage, rest, and travel). The null hypothesis in each case was that individuals would associate randomly with one another. The real HWI matrix was permuted 40,000 times with 100 trials per permutation for each analysis. Associations were permuted within sampling periods (*i.e.*, days). The test calculates a statistic for the real data and for many permutations of random data (with constraints). The null hypothesis that only random associations exist is rejected if the statistic for real data is greater than the statistic for 95% of the random data ($P < 0.05$) (Bejder *et al.* 1998).

4.2.5.6 Stability of associations over time

Temporal analyses were used to determine the stability and persistence of associations over time. The lagged association rates were standardized as we could not be certain that all individuals had been identified in every sighting. These standardized lagged association rates (SLARs) were plotted against time lag with moving averages and standard errors calculated using the temporal jackknife method. The null association rate was added to the plots; this represents the theoretical SLAR if individuals associated randomly (Whitehead 2008). Four exponential models were fitted and the model with the lowest Quasi Akaike Information Criterion (QAIC) was determined the best fit, with the ΔQAIC (difference between QAIC and that of the best model) indicating the degree of support for the other models (>10 difference = no support; Whitehead 2008). To determine if sex-specific patterns of association persisted over time, SLARs were plotted for female-male associations using the same methods.

4.2.5.7 Movements throughout study area

To investigate movements between the two defined areas of the study site, sighting records were filtered and categorized as either Area 1 (inner estuary) or Area 2 (outer estuary). We used movement analyses in SOCPROG to examine how individuals moved among the inner and outer estuary areas of the study site. The lagged identification rate (LIR), the probability that if an individual is identified in the area at any time it is identified during any single identification made in the area some time lag later (Whitehead 2001), was used to assess movements among the two areas. LIRs were calculated for each single area and then between the two areas. We then used overall LIRs to assess movements within and between areas which indicated the general probabilities that individuals would be in the same study area or in a different one after particular time lags (Whitehead 2009). The number of bootstrap replications was set to 1,000 to calculate bootstrap-estimated standard errors of the LIRs. Again, selection of the best fitting models was determined using the lowest Quasi Akaike Information Criterion (QAIC) value. The QAIC was used (rather than the AIC) to compensate for overdispersed data (Whitehead 2007).

4.3 Results

4.3.1 Survey effort and photo-identification

Of the 353 surveys (607 sightings) carried out between 2012 and 2015, 312 (522 sightings) contained photos of individually identifiable adult and/or juvenile bottlenose dolphins (Table 4.1). A total of 136,486 photographs were taken and 45,371 of these were used for photographic analysis of dolphin sightings. A total of 2,948 identifications were made of 121 distinct individual dolphins. On average, 106 individuals (88%) of the 121 identified were sighted each year. Ninety-eight percent of individuals (*n* = 119) were sighted in multiple years, with 64% of individuals (*n* = 77) seen in all four study years from 2012 to 2015.

Table 4.1 Summary of survey effort by sampling variable, for sightings containing photos of individually identifiable bottlenose dolphins, in the Shannon Estuary, Ireland. Named vessels are *Muc Mhara* (the research RIB), *Draíocht* (the Carrigaholt tour boat), and *DD (Dolphin Discovery*, the Kilrush tour boat).

Survey Effort		2012	2013	2014	2015	Total
No. days		29	50	65	53	197
No. surveys		57	78	100	77	312
No. sightings		95	119	180	128	522
No. sightings by vessel	*Muc Mhara*	1	7	59	15	82
	Draíocht	66	78	52	70	266
	DD	28	30	65	39	162
No. sightings by survey area	Outer estuary	76	96	89	95	356
	Inner estuary	13	17	66	29	125
	Whole estuary	6	6	25	4	41

On average, surveys (from all boats collectively) yielded 2.7 sightings of bottlenose dolphins per day, with a mean of 12.2 individual dolphins identified per day (*n* = 121, range = 1-60), thus about 10% of the adult/juvenile population in this study was identified each day. The mean number of sightings per individual was 24.4±21.7 (*n* = 121, range = 1-101).

A discovery curve plotting number of individuals identified against cumulative number of identifications reached a clear plateau suggesting good coverage of the population after about 1,000 identifications and that almost all the individuals recorded in 2014 and 2015 were resighted from records in 2012 and/or 2013 (Fig. 4.2). In fact, no new (adult/juvenile) individuals were recorded during the 2015 field season.

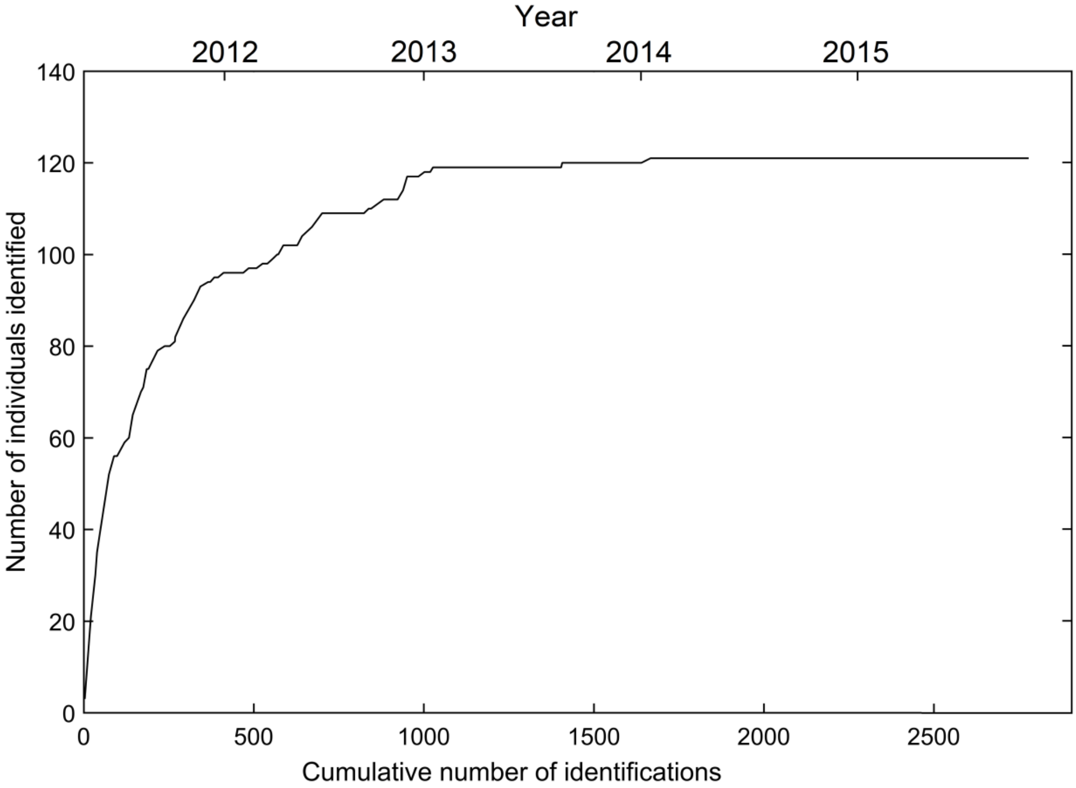

Figure 4.2 Discovery curve of number of individual bottlenose dolphins identified *vs.* cumulative number of identifications, with year of sampling between 2012 and 2015 (*n* = 121).

Of the 121 individuals sighted, 58 were of known sex (46 female, 12 male) and 63 were of unknown sex. Age class was divided into 93 adults and 28 juveniles. The area classifier consisted of 33 'inner' and 88 'outer' estuary individuals. Within this, the inner class consisted of 27 adults and 6 juveniles; the outer class of 66 adults and 22 juveniles.

4.3.2 Group composition, associations and clusters

Of 268 group sightings in which at least one individual was identified as male, 241 (90%) had females present. While, of 450 group sightings in which at least one individual was identified as female, 241 (54%) had known males present. Of the 522 sightings analyzed, 225 groups contained juveniles; only 7% (16) of these groups contained no other age class. The overall proportion of single sex groups *vs.* mixed sex groups could not be determined because 80% of the sightings analyzed contained at least one individual of unknown sex. When restrictions were set within SOCPROG to include only individuals with >5 sighting records, 106 distinct individual dolphins and 519 sightings were available for association and network analyses.

The overall mean HWI of the Shannon Estuary population was 0.07±0.02. The maximum HWI that any individual had with any other individual ranged from 0.16 to 0.72 (mean = 0.41, SD = 0.11; *n* = 106).

When sex was selected as the class variable, and analyses included only individuals of known sex, the HWIs over 0.4 were for female-female and female-male pairs only, with female-male association indices higher than all others (>0.6; Fig. 4.3). The mean HWI for male-male associations was the highest (mean = 0.1191, SD = 0.0313), and mean female-female (mean = 0.0872, SD = 0.0259) and female-male (mean = 0.0913, SD = 0.0427) association indices were almost equal. However, this may have been due to the much larger sample size for females (*n* = 45) compared to males (*n* = 10). Overall, associations between different sex classes were roughly the same (mean = 0.0913, SD = 0.0402) as those within same sex classes (mean = 0.0930, SD = 0.0294) and the difference between them was not statistically significant (two-sided Mantel test, *t* = -0.30, *r* = -0.01, *P* = 0.81).

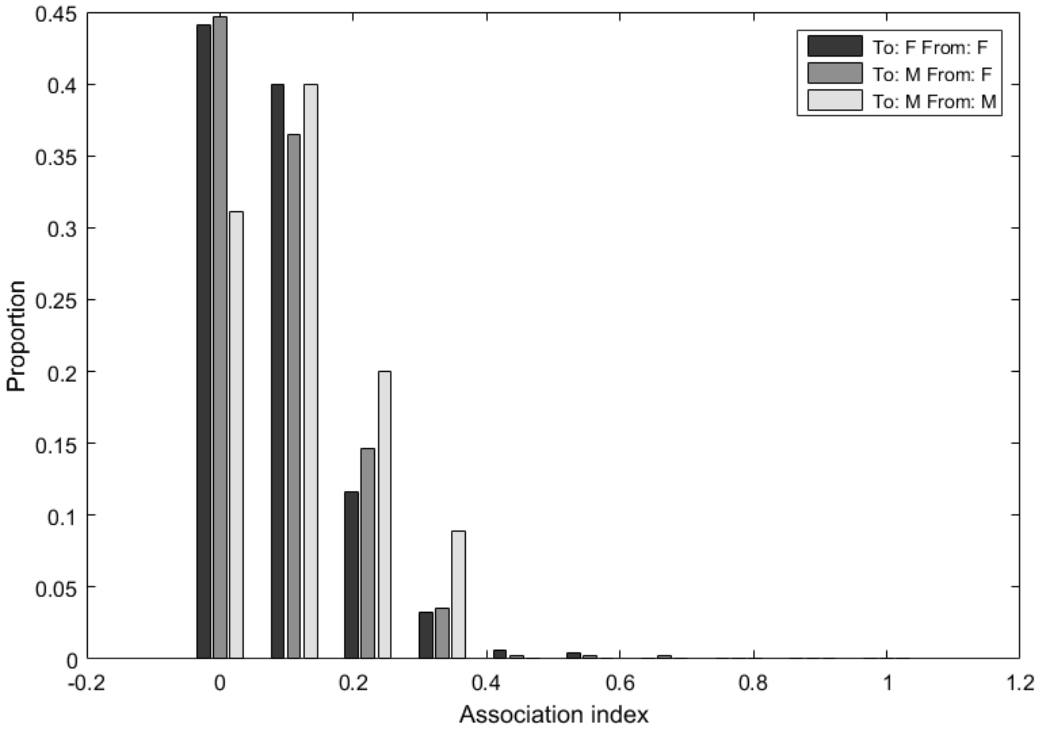

Figure 4.3 Histogram of half-weight association indices (HWIs) between female-female, female-male and male-male pairs in the Shannon Estuary (*n* = 55).

In age classes, juvenile-juvenile associations were the strongest (mean = 0.13, SD = 0.04), followed by adult-adult associations (mean = 0.09, SD = 0.02). Adult-juvenile associations were the weakest (mean = 0.05, SD = 0.02). The strongest association recorded in the population was between two juveniles (HWI = 0.72). Generally, associations within same age classes (mean = 0.10, SD = 0.03) were stronger than those between different age classes (mean = 0.05, SD = 0.02) and this difference was statistically significant (two-sided Mantel test, t = 10.72, r = 0.22, P = 0.00).

Similarly, associations within same area classes (mean = 0.11, SD = 0.05) were much stronger than those between different area classes (mean = 0.04, SD = 0.03) and this difference was also statistically significant (two-sided Mantel test, t = 16.75, r = 0.30, P = 0.00). Inner-outer class associations were the weakest (mean = 0.04, SD = 0.02), outer-outer associations were relatively stronger (mean = 0.08, SD = 0.02), but inner-inner associations were by far the strongest (mean = 0.17, SD = 0.06).

Average-linkage cluster analysis of the matrix of HWIs of individuals classified as inner in the bottlenose dolphin population resulted in three clusters, with a maximum modularity (Type 1; controlling for gregariousness) of 0.13 at a HWI of 0.10. IDs 244 and 150 were the most associated individuals with a HWI of 0.72 (Fig. 4.4). Although the modularity was low (indicating that the division into clusters may not be appropriate), the Cophenetic Correlation Coefficient (CCC) value of 0.88 indicates that the dendrogram is an acceptable representation of input distances. Thus, inner estuary individuals appear to be clustered into two major groups consisting of 21 individuals and 11 individuals, and a third 'cluster' with a single individual (ID 34). A similar cluster analysis of outer class individuals resulted in ten clusters but the CCC value of 0.67 was not high enough to accept the dendrogram as a true representation of individual clustering.

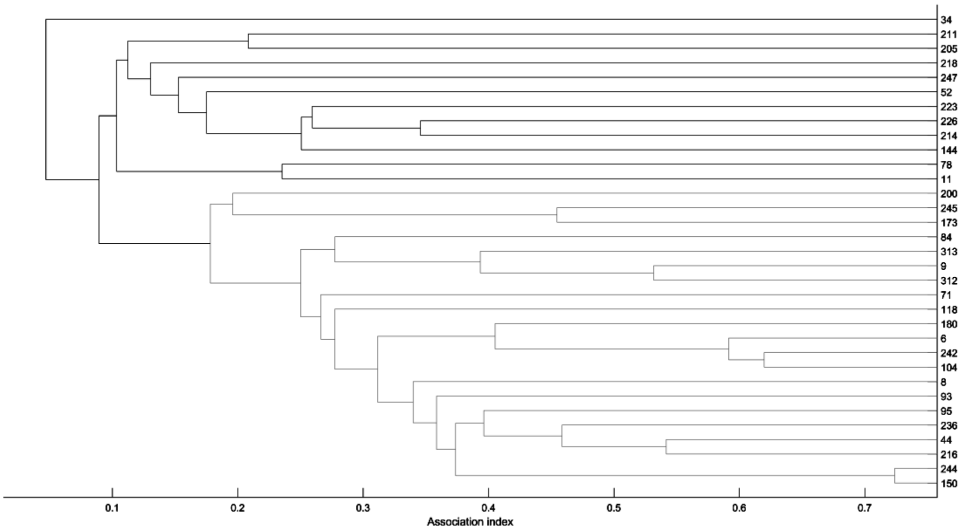

Figure 4.4 Average-linkage cluster analysis (CCC = 0.88) of the matrix of HWIs of individual bottlenose dolphins classified as inner (*n* = 33).

4.3.3 Social networks

A sociogram was constructed for all individuals analyzed (*n* = 106) with age classifiers (adult, juvenile), illustrating the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50 and 0.75).

The population appears to be somewhat aggregated according to associations by age class, with a major mass of adults associating with adults and two smaller collections of juveniles associating closely with other juveniles (Fig. 4.5).

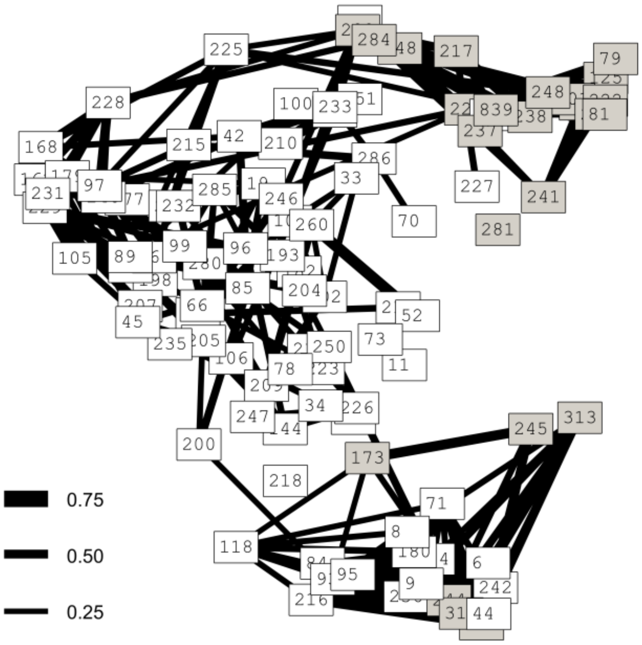

Figure 4.5 Sociogram of all individual bottlenose dolphins (*n* = 106) with node color for age (adult = white, juvenile = gray), illustrating the social connections between individuals with HWI ≥0.25. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

Next, a sociogram was constructed for all individuals analyzed (*n* = 106) with area classifiers for outer (*n* = 73) and inner (*n* = 33), with the inner class further divided (using the results of the previous cluster analysis) into three clusters (Fig. 4.6A). This diagram illustrates the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50, and 0.75). Overall, the population appears to be roughly assembled by association into two groups or communities with a third group of key individuals forming connections between the two major groups, although their associations are weaker than those among the major group members themselves.

The strong associations between individuals within the inner class (n = 33) are apparent in a sociogram of only inner individuals (Fig. 4.6B) where the clustering of individuals from the cluster analysis is clearly depicted. The major inner cluster of 21 individuals and the other 12 individuals who sit between this major cluster and the outer estuary individuals are apparent.

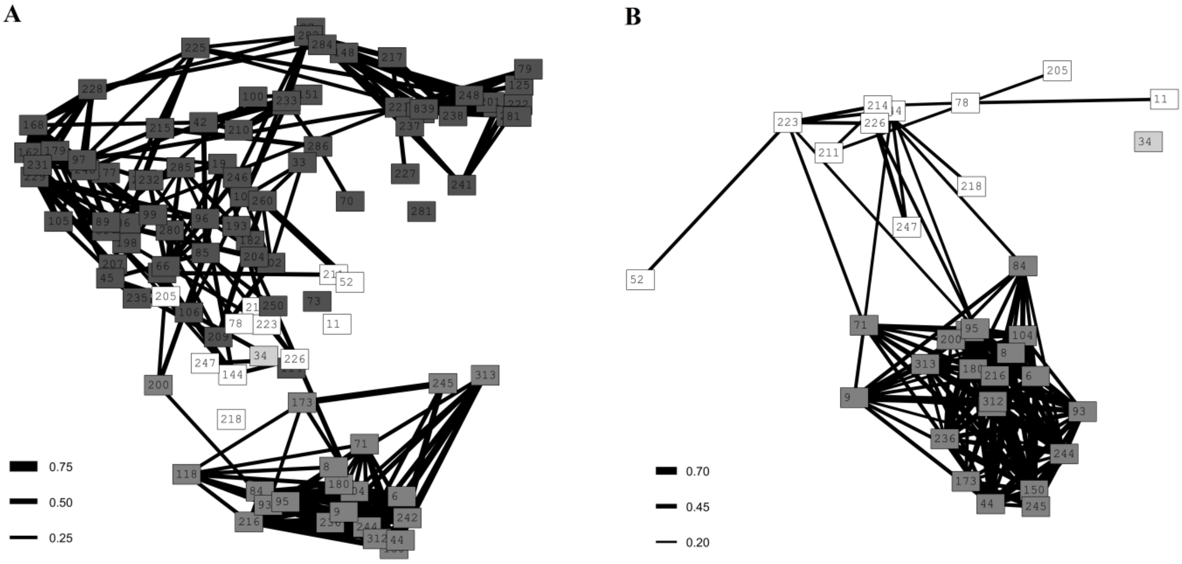

Figure 4.6 Sociograms of (A) all individual bottlenose dolphins (n = 106) with node color for area (outer = dark gray, inner = gray, light gray and white) and (B) individuals assigned to the inner class (n = 33) clustered using the hierarchical cluster analysis results into three clusters (gray, light gray and white). The diagrams illustrate the social connections between individuals with (A) HWI ≥0.25 and (B) HWI ≥0.20. Different scales were used to most clearly illustrate the structure of each network. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

With further exploration of age class division in the social network, not only do juveniles and adults have closer associations within classes than between, but if each age class is further classed by area, there are clear dissimilarities in association between inner and outer adults and inner and outer juveniles. Thus, individuals of each age group are divided from each other and are further divided within their age groups by their area class.

Social network metrics were calculated for the population overall and for each identified class (age, area and sex) separately (Table 4.2). For both direct (strength) and indirect (reach) connectedness, the average measures for adults were significantly higher than for juveniles ($P < 0.05$; determined because the difference in mean values between classes was greater than twice the sum of the bootstrapped standard errors). Similarly, the average measures of strength and reach for females (and unknown sex individuals) were significantly higher than for males ($P < 0.05$), although the small sample size for males may have affected the measures for that class.

Table 4.2 Social network measures calculated for the Shannon Estuary bottlenose dolphin population overall and by age, area and sex classes separately. Values are presented as Mean ± SD [bootstrapped standard error].

	n	**Strength**	**Reach**
Overall	106	7.77 ± 1.91 [0.52]	64.04 ± 17.30 [8.46]
Age			
Juveniles	25	3.21 ± 0.93 [0.37]	11.12 ± 4.06 [2.64]
Adults	81	6.83 ± 1.84 [0.43]	49.94 ± 14.09 [6.39]
Area			
Inner	33	5.28 ± 1.91 [0.31]	31.45 ± 12.97 [3.71]
Outer	73	6.08 ± 1.63 [0.55]	39.60 ± 11.36 [7.40]
Sex			
Female	45	3.84 ± 1.14 [0.30]	15.99 ± 4.95 [2.46]
Male	10	1.07 ± 0.28 [0.11]	1.22 ± 0.27 [0.26]
Unknown	51	3.65 ± 0.91 [0.30]	14.14 ± 4.12 [2.48]

4.3.4 Behaviorally specific associations and preferences

Restrictions on sightings based on predominant activity state produced four separate association matrices. The mean HWI for socializing groups was higher (0.09±0.03) than for foraging groups (0.06±0.03). HWIs for pairs of individuals in sightings where the activity state was foraging were significantly different to those in sightings where the activity state was socializing (n = 77, two-sided Mantel Z-test, matrix correlation of association matrices = 0.28, $P < 0.05$). Permutation tests were carried out for sightings of the four main activity states (travel, forage, social, rest). The coefficients of variation (CVs) of the real HWIs were significantly larger than those of the random data for travel ($P < 0.0001$), social ($P < 0.0001$) and foraging ($P < 0.05$) behavioral associations (Table 4.3). No significance was found for associations calculated for the activity state rest, although this may have been due to the small sample size in this case (only 13 sightings compared to more for other activity states, unpublished data). The significance found for the first three activity states indicated that behaviorally specific preferred associations exist in this population.

4.3.5 Association preferences/avoidances

The overall significance for preferred/avoided associations in the population, using the coefficient of variation (CV) of association indices as a test statistic, was $P < 0.0001$ (CV = 1.24 for real data, compared with CV = 1.11 for mean of randomly permuted data). Thus, the null hypothesis that only random associations exist could be rejected.

When the HWIs within and between classes (age, sex and area) and years were investigated, the CVs of the real HWIs were significantly larger than those of the random data ($P < 0.0001$, Table 4.3) in most cases, although the strength of significance varied for juvenile-juvenile ($P < 0.01$) and male-male ($P < 0.05$) associations. The persistence of significant results for most variables provides further evidence for rejecting the null hypothesis that there are no bottlenose dolphin dyads in the Shannon Estuary population that prefer or avoid association.

Table 4.3 Real and random coefficients of variation (CV) of half-weight association indices (HWIs) across age, area and sex class, year (and within year female-male HWIs) and activity state, and pooled for all sightings.

Variable	***n***	**CV of real HWI mean**	**CV of random HWI mean**	***P***	**Variable**	***n***	**CV of real HWI mean**	**CV of random HWI mean**	***P***
Age class					***Year***				
Adult	81	1.08	0.97	<0.0001	2012	88	1.88	1.80	<0.0001
Juvenile	25	1.04	1.01	<0.01	Female-male	37-9	1.55	1.51	<0.05
Adult-juvenile		1.53	1.49	<0.0001	2013	103	1.71	1.65	<0.0001
Area class					Female-male	43-10	1.32	1.31	<0.05
Inner	33	0.74	0.68	<0.0001	2014	101	1.75	1.63	<0.0001
Outer	73	1.14	1.07	<0.0001	Female-male	44-10	1.33	1.27	<0.0001
Inner-outer		1.31	1.27	<0.0001	2015	95	2.10	2.02	<0.0001
Sex class					Female-male	40-8	1.68	1.67	0.31
Female	45	1.06	0.95	<0.0001	***Activity State***				
Male	10	0.84	0.80	<0.05	Social	88	2.22	2.21	<0.0001
Female-male		1.03	0.98	<0.0001	Foraging	93	2.21	2.19	<0.05
					Rest	47	1.88	0.00005	1.00
					Travel	95	2.03	1.95	<0.0001
					Overall	106	1.24	1.11	<0.0001

4.3.6 Stability of associations over time

Standardized lagged association rates (SLARs) and null association rates were plotted against time lag (with moving averages and standard errors estimated using the temporal jackknife method) for all 121 bottlenose dolphins (Fig. 4.7A) and four exponential models for SLARs were fitted. The SLARs remain consistently higher than the null association rate; after 1,000 d, the stabilization is still well above the standardized null association rate. The fourth model – "two levels of casual acquaintances" – had the lowest QAIC and so fit best (Fig. 4.7A). There was no support for the other three models (ΔQAIC > 15).

Interestingly, when female-male association rates were plotted, the best fit model was for "preferred companions and casual acquaintances" (Fig. 4.7B). This indicates that sex-specific patterns of association may persist over time between females and males at two levels of association – one of "preferred companions" and one of "casual acquaintances".

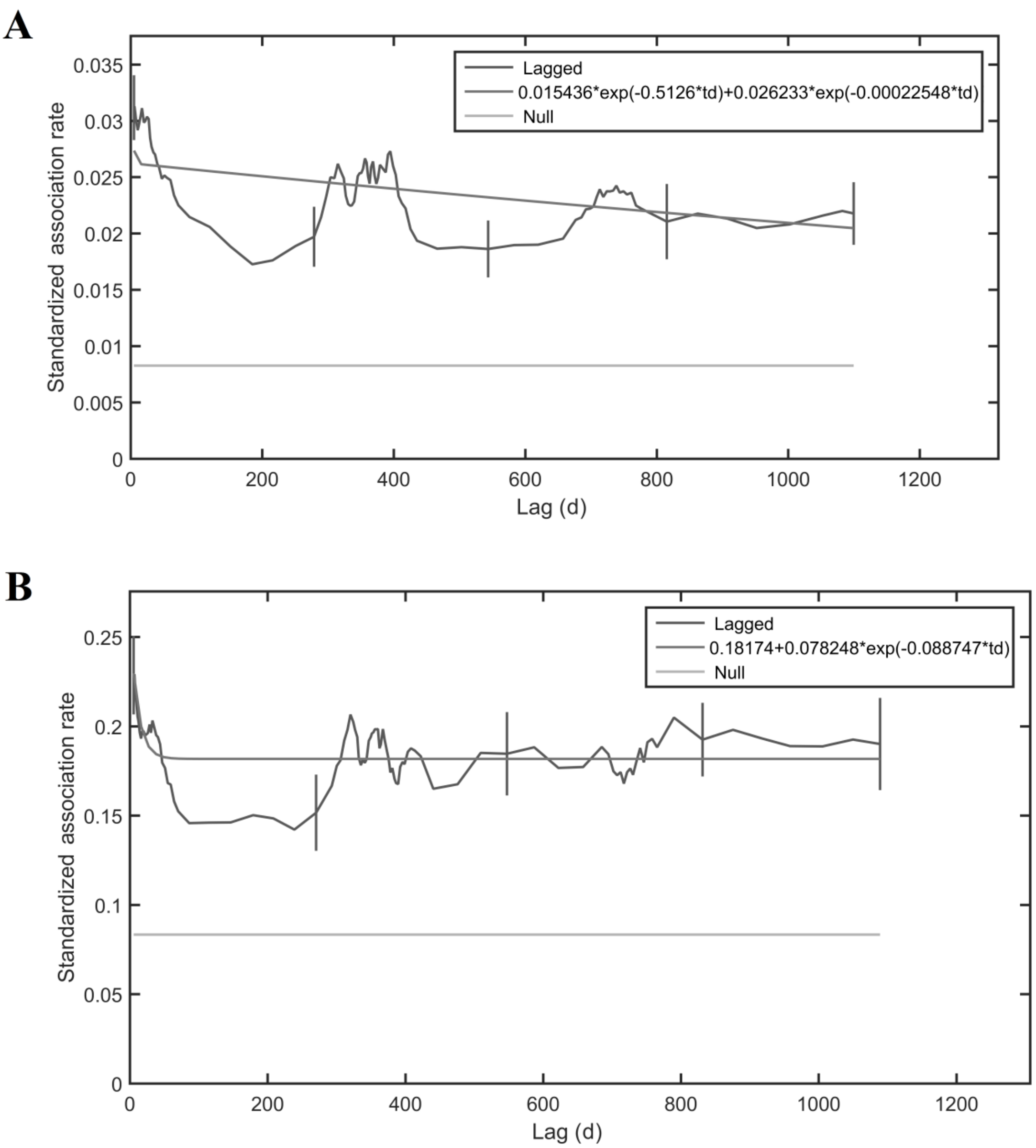

Figure 4.7 Standardized lagged association rates (SLARs) and null association rate plotted against time lag with best fit exponential model for (A) whole population (*n* = 121) and (B) female-male (*n* = 55) associations. Standard error bars (vertical lines) estimated using temporal jackknife method. SLAR curves were smoothed with moving averages of (A) 160,000 and (B) 2,000 associations.

4.3.7 Movements throughout study area

Lagged identification rates (LIRs) plotted against time lag, among the two areas of the study site, suggest that the probability of an individual being identified in either the inner or outer estuary and then being identified in either area some time later remains almost the same over time (LIRs for inner estuary to inner estuary were higher than all others, at ~0.045). The best fitting models for the probabilities of movements from one area to the other (either Area 1 to 2, or Area 2 to 1) were different for the two cases; for LIRs of individuals moving from the inner to the outer estuary, the first two models indicating a “fully mixed” population fit best, whereas for LIRs of individuals moving from the outer to the inner estuary, the last two models indicating a “migration/interchange” population fit best. The goodness of fit chi-squared value was significant (*P* = 0.00) for all models.

Overall LIRs plotted to assess movements within and between areas suggest that after 200 d, the probability that an individual is in the same study area is higher than the probability that an individual is in a different study area, but after 360 d (and up to 1,100 d) the probabilities are virtually the same for either scenario (Fig. 4.8).

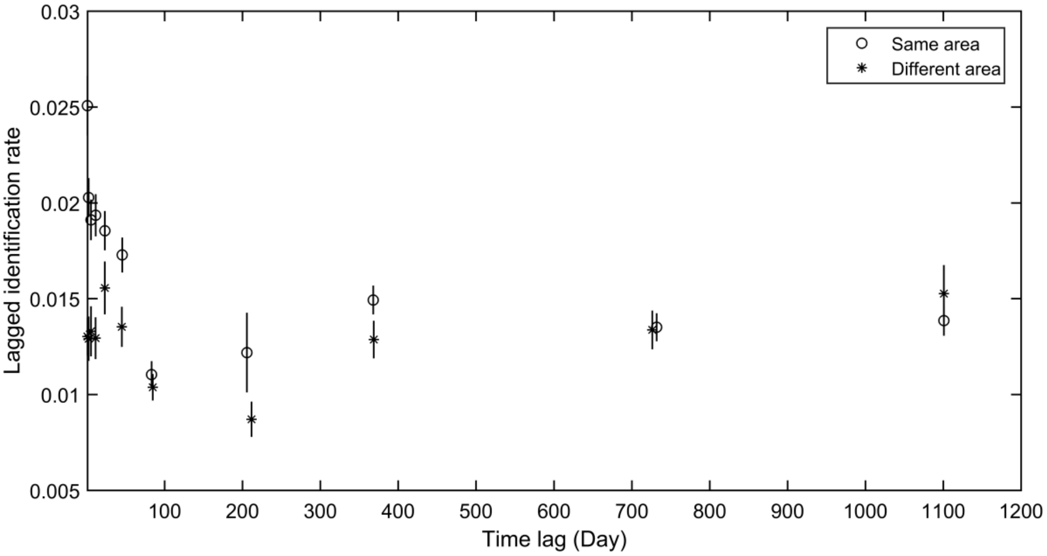

Figure 4.8 Plot of lagged identification rates against time lag (day) for individual movements within (circles) and between (asterisks) areas of the study site (bootstrap-estimated standard errors (bars) from 1,000 bootstrap replications) of individual bottlenose dolphins sighted in the Shannon Estuary.

4.4 Discussion

Research on bottlenose dolphin social structure began in the 1980s (*e.g.*, Wells *et al.* 1987, Wells *et al.* 1991, Smolker *et al.* 1992) and continues today (*e.g.*, Wells 2014, Connor and Krützen 2015, Louis *et al.* 2015). The structure of many resident populations has been described including in Sarasota Bay, USA (Wells 2014), Shark Bay, Australia (Connor *et al.* 2001), the St John's River, USA (Ermak 2014), the Aeolian Archipelago, Italy (Blasi and Boitani 2014), Laguna, Brazil (Daura-Jorge *et al.* 2012), Port Stephens, Australia (Wiszniewski *et al.* 2010) and the Sado Estuary, Portugal (Augusto *et al.* 2011). Recently, studies have illuminated the importance of social structure in relation to cetacean culture (Krutzen *et al.* 2005, Mann *et al.* 2012, Cantor and Whitehead 2013) and activity patterns (Gazda *et al.* 2015).

Studies of bottlenose dolphins have shown that the species generally lives in a fission-fusion social system (Connor *et al.* 2000) in which societies encompass both extremely fluid *and* stable associations between individuals (Smolker *et al.* 1992). Individuals within a population associate in temporary groups of variable size and composition, but there can be long-term associations among identified individuals within these fluid groups (Wells *et al.* 1991, Lusseau *et al.* 2003).

This study shows that bottlenose dolphins in the Shannon Estuary fit the general pattern of a fission-fusion society structured by age and area class, but perhaps also characterized by unusual female-male associations. Although individuals in the population associate with many others in a complex social network, significantly strong, persistent and preferred associations exist between individual dolphins. In Sarasota Bay, Florida, dolphin group composition is generally based on within-age and -sex class associations, including groups of females and calves, exclusively juvenile groups, and adult males, typically as strongly bonded pairs (Wells 2014). Our initial hypothesis was that the Shannon Estuary population would contain similar groups; however, this does not appear to be the case. In contrast, groups of dolphins in the Shannon Estuary appear to be composed of mixed sex and age classes although the associations between specific individuals indicate certain between- and within-class social preferences. Similarly, in Shark Bay, although Smolker *et al.* (1992) found groups often contained both sexes, there were consistent long-term associations between individuals of the same sex. This illustrates the difference between group composition and individual association preferences. Additionally, there is little evidence in the Shannon Estuary population for adult male groups, female-calf groups or exclusively juvenile groups.

The mean HWI of the Shannon Estuary population was 0.07±0.02. Several other bottlenose dolphin populations have reported mean HWIs including the Indian River Lagoon (0.010±0.006; Titcomb *et al.* 2015), Cedar Key (0.03±0.08; Gazda *et al.* 2015), St John's River, Florida (0.05±0.02; Ermak 2014), Sicily, Italy (0.06±0.02; Papale *et al.* 2017) and the Sado Estuary, Portugal (0.45±0.15; Augusto *et al.* 2011). The lowest of these mean HWIs is reported from the Indian River Lagoon where the dolphin population is spatially segregated into six distinct communities in which members of the furthest apart communities have the lowest association indices (Titcomb *et al.* 2015). By contrast, the highest example given here of mean HWI is reported for a very small (n = 24) bottlenose dolphin population in the Sado Estuary with strong stable community-wide associations (Augusto *et al.* 2011). These examples show that there is much variation in the observed mean HWI of a dolphin population. The presence of male alliances (with high HWIs) has been linked to population density (Ermak 2014) and this could be a possible factor in the differences found between the mean HWI values of different populations. The insular nature of small, localized or isolated populations may also lead to overall high mean HWIs regardless of within-population social structure.

Associations were not random in the Shannon Estuary dolphin population and this result was significant when applied to sex, age and area classes tested separately. The preference/avoidance of particular associates was also apparent for each year of data tested separately which further indicates the strength of this result as a representation of nonrandom population level associations.

The temporal stability of bottlenose dolphin social structure globally varies drastically, from being driven by constant companionship (Lusseau *et al.* 2003) to featuring casual acquaintances that last just a few days (Lusseau *et al.* 2006). Preferred associations in the Shannon Estuary dolphin population persisted over 1,000 days. The peaks in associations for all individuals after approximately 365 d and 730 d are most likely an effect of cyclical summer sampling periods. The best fitting model was for "two levels of casual acquaintances" associating and dissociating at two different time scales. The two time scales may simply be explained by the periods within and between field seasons. However, the two different levels of disassociation might also relate to the associating and dissociating of individuals within two separate classes; for example, age class and area class. Whitehead (2008) also similarly suggests that this type of SLAR might indicate the fission/fusion of nearly permanent social units into and out of subgroups on the short time scale and transfers between units on the longer one.

Although, as explained above, the line between the inner and outer estuary was based simply on dividing the study area into two roughly equal parts and reflecting operational issues, it turned out to be a useful reference point for tracking the movement and associations of individuals. The probability of identifying an individual in the inner estuary and then identifying it again in the inner estuary sometime later remained high over time. The same was true of outer estuary to outer estuary, although to a lesser extent. These results may represent some long-term site fidelity of individuals to certain parts of the estuary. The best fitting models for individuals moving from the inner to the outer estuary were for a “fully mixed” population. As all individuals who have been sighted in the inner estuary have also been sighted in the outer estuary, it follows that the population mixes in this area. The opposite was true of the best fitting models for individuals moving from the outer to the inner estuary which were for a “migration/interchange” population. Perhaps this can be explained by the fact that only a small number of individuals (~25% of the population) use the inner estuary, and thus would be returning to that area from the outer estuary over time. Overall rates suggest that individuals are more likely to be identified in the same study area after 200 d, but either the same or a different study area after longer periods. Perhaps this is suggestive of within-season site fidelity to either the inner or outer estuary. The use of the inner estuary by only a small percentage of the population seasonally has strong implications for management of the population as a whole, especially if other individuals are likely to go from the inner to outer but not likely to enter the inner area from the outer area during one season. For example, the degree of exposure to anthropogenic threats would be different for individuals of the inner and outer area classes.

There was good evidence for behaviorally specific preferred associations in the population with the mean HWI for socializing groups significantly higher than for foraging groups. The presence of preferred/avoided associations in sightings where individuals were engaged in either social or traveling behavior was highly significant, compared to slightly less significance during foraging activity. The low sample size for sightings of resting behavior may have had an effect on the lack of significance for this activity state. The difference in the level of significance for associations during foraging behavior *vs.* social or traveling behavior is interesting as Gero *et al.* (2005) similarly found that bottlenose dolphins have lower level "acquaintance"-type HWIs when foraging compared to socializing. This evidence for behaviorally specific preferred associations points to the behavioral flexibility of these dolphins and their ability to adjust their social patterns to optimally fit each of various behavioral situations.

4.4.1 Sex class associations

For adult individuals of known sex, the highest HWIs were for female-male pairs. Contrastingly, Smolker *et al.* (1992) found that female-male associations were generally inconsistent and primarily within the lowest HWI class in their study. In our study, the mean HWI of male-male associations was higher than the others; however, the much larger sample size for females may have affected this due to the incorporation of some female-female associations with low HWIs into the calculation of the overall mean for that sex class. Similarly, the very small sample size for males may have obscured association patterns for that sex class. Associations between different sex classes were similar to same-sex associations, and their difference was not statistically significant. Even so, the high mean HWI for male-male associations provides a good justification for further research with an increase in sample size of known males in the population. In the reporting of the societal attributes of cetacean social structure, one of the most frequently assessed aspects is sex-specific differences in patterns of association, and contrastingly, in other bottlenose dolphin studies, these associations are often stronger between members of the same sex (*i.e.*, within-class; *e.g.*, in Shark Bay, Smolker *et al.* 1992). In Sarasota Bay, adult females interact extensively with other females and adult males typically form strong male associations or alliances (Wells *et al.* 1987, Owen 2003) – features that do not seem to be present in the social characteristics of the Shannon Estuary bottlenose dolphin population.

When permutation tests were used to test for preferred/avoided associations between females and males, significance for nonrandom associations was apparent in the overall analysis. Thus, female and male bottlenose dolphins in the Shannon Estuary do not associate at random. However, when each year of data was tested separately, one year (2015, with 48 individuals of known sex) did not result in significant preferred/avoided female-male associations ($P = 0.31$). This year had the lowest number of males at eight individuals and it may be that significance could not be found within the small sample size.

Stable long-term female-male associations have been recorded in bottlenose dolphin populations in Doubtful Sound, New Zealand (Lusseau *et al.* 2003) and in Port Stephens, Australia, where constant companionships occur between females and males (Wiszniewski *et al.* 2010). Associations between female and male dolphins in the Shannon Estuary continued steadily over long time scales (>1,000 d), indicating that female-male associations are more long-lasting than the general associations of individuals in the population as a whole. The best fit model was, again, for two levels of disassociation, but this time for “preferred companions and casual acquaintances”, indicating that sex-specific patterns of association may persist over time between females and males at both strong and weaker levels of association. As with the general lagged association rates, this result may simply reflect the gaps between field seasons, but it is possible that the stronger associations (the “preferred companions” level) might hold interesting information with respect to the mating system of this population.

Although only 52% of individuals in the current study were of known sex, there were no apparent divisions in the social network explained by the sex of individuals. In the Shark Bay social network, females tended to form longer chains of associates than males and almost every female was connected to all other females by a chain of consistent associates (Smolker *et al.* 1992). The significantly higher measures of strength (direct connectedness) and reach (indirect connectedness) found in our study substantiate the idea that female dolphins in the Shannon Estuary are also better connected than males.

More information on the life history of the Shannon Estuary bottlenose dolphin population will provide necessary data to assess the influence of female reproductive state on female-male relationships which has been shown to have a strong effect on differences in the consistency of female-male associations in other populations (Smolker *et al.* 1992). In Sarasota Bay, sexual segregation of males and females is common outside of the breeding season (McHugh 2010). It would be pertinent to gather more winter data on the Shannon dolphins to assess potential differences in their social structure, particularly with this in mind, as it is known that dolphins are present in the estuary during winter months (Berrow 2009). If additional winter data could be collected, analyses of year-round social associations could point to seasonality-related changes in the social structure of the population.

When combining the social analysis and group composition investigations, there was no evidence of all-male groups or the presence of male alliances that occur in other populations such as Shark Bay (Connor and Krützen 2015), Sarasota Bay (Owen *et al.* 2002), the Bahamas (Parsons *et al.* 2003, Rogers *et al.* 2004), and Port Stephens, Australia (Moller *et al.* 2001). There was similarly no evidence for long-term male-male associations such as those in Bunbury, Australia (Smith 2012), or the Moray Firth and Cardigan Bay (Sim 2015). Additionally, it is unusual to find relatively strong female-male associations in bottlenose dolphins, such as we have in this present study, so this warrants further research. There are various reasons why significant female-male associations might exist in a population, such as increased reproductive success (through increased mating opportunities, female mate choice, mate guarding, or increased access to food resources), reduced risk of infanticide or reduced harassment by other group members (Owen *et al.* 2002, Haunhorst *et al.* 2017).

4.4.2 Associations by age

Juveniles and adults had stronger within-class associations than those between age classes. The strongest association recorded in the population was between two juveniles, suggesting that the formation of strong associations early in life may be important in this population or might perhaps be related to maturing in the same age cohort, similarities in habitat use or kinship. Some other bottlenose dolphin populations typically contain exclusively juvenile groups (*e.g.*, Shark Bay, Smolker *et al.* 1992; Sarasota Bay, Wells 2014). Gero *et al.* (2005) observed a higher frequency of behavioral associations between juveniles than among any other relative age category in Shark Bay, while Smolker *et al.* (1992) noted that the most consistent preferential associations tended to be between subadults. In Sarasota Bay, young animals typically socialized at higher rates than adults, and juveniles preferred to interact with other juveniles and calves, and avoided adults (relative to their availability in the Sarasota Bay community) (McHugh 2010).

Samuels (1996) found that female juvenile dolphins in Shark Bay had stronger associations with adult females (their mothers) and other juvenile females than with male juveniles, while the top-ranked associates of juvenile males were other juvenile males and not adults or juvenile females. Similarly, juveniles in Sarasota Bay showed a marked preference for associating with other juveniles, especially of their own sex (McHugh 2010) – juvenile females interacted with more adult females and calves than males, while males interacted with more juvenile males than females did. McHugh (2010) suggested that differences between the association patterns of male *vs.* female juvenile dolphins might relate to their future reproductive roles in relation to calf-rearing and male mating strategies. Unfortunately, it was not possible to test sex-based differences in juvenile associations in the current study due to lack of data on the sexes of juvenile animals.

There are various potentially beneficial reasons why juveniles might form preferential groups with other juveniles. While the formation of groups is often to reduce predation risk in other populations, the lack of any known predators of bottlenose dolphins in the Shannon Estuary suggests this is an unlikely cause. It is possible that juvenile dolphins might benefit from associating in groups to increase foraging efficiency, perhaps via increased efficiency of prey detection or capture (McHugh 2010). A third potential reason for juvenile-juvenile associations is socialization, wherein social interactions may be particularly important for young bottlenose dolphins due to the complex nature and fluidity of fission-fusion social systems and the long time period over which many relationships may develop (Kaplan and Connor 2007, McHugh 2010). Indeed, Stanton and Mann (2012) found that the survival of juvenile male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, could be predicted by the social bonds they formed as calves earlier in their lives.

In Doubtful Sound, New Zealand, evidence suggests that age-related homophily in bottlenose dolphin networks can influence the formation of clusters of preferred companionship (Lusseau and Newman 2004). Although somewhat mixed, there were clusters in the social network of the population for juveniles and adults. Adults had stronger social network measures for strength and reach than juveniles, meaning they had more direct and indirect connections to the rest of the network. Lusseau (2003) found that the social network of bottlenose dolphins in Doubtful Sound was held together by key individuals creating hubs for associations between other individuals and that these individuals were often older adults. In our network diagrams, the 12 inner estuary individuals who are not part of the core inner estuary cluster were located between that core group and the rest of the individuals in the overall population network diagram and were all adults, suggesting that they might play a similar role in linking the connections of associated individuals in this population.

4.4.3 Associations by area

The classification of individuals by sighting area revealed an interesting social division in the population. Inner individuals, that is, individuals who had been observed at least once in the inner estuary, had strong associations with inner individuals and, overall, within-area-class associations were stronger than between-area-class associations. Inner and outer estuary individuals had the lowest association indices; a similar result was found by Titcomb *et al.* (2015), where the lowest association indices were among individuals at the study site's northern and southern boundaries.

Dolphins in different habitats experience different environmental pressures which may influence individual association patterns (Smolker *et al.* 1992). Ecological factors, such as resource availability and distribution, might cause a population to split into two social units related to differences in habitat use or foraging specializations. If there were two key foraging areas, as suggested by the differences in habitat utilization described by Ingram and Rogan (2002), this could lead to niche partitioning in the Shannon Estuary. In some populations, bottlenose dolphins have formed communities defined as "associated individuals with long-term site fidelity to a specific area" (Wells 1986, Urian *et al.* 2009). Chabanne *et al.* (2017) suggest that a dolphin community might constitute a relevant local population comprising a total number of animals that could be affected by a proposed development and representing a population unit of some biological significance. Although all of the bottlenose dolphins in the Shannon Estuary use the outer estuary area of the study site, the differences in association between and within individuals in the inner and outer classes fits Croft *et al.*'s (2008) definition of a community as a group of individuals that are more associated amongst each other than with the rest of the society, and it might be appropriate to employ the term 'community' to describe these two social units.

The cluster analysis of inner individuals divided them into two main clusters. The largest cluster was a core group of 21 individuals who most frequently used the inner estuary area. Twelve other inner estuary individuals in the other major cluster appear to form a connection between this core inner group and the outer estuary individuals. These 12 individuals were all adults and had some of the highest betweenness centrality measures (*i.e.*, the number of shortest paths between other nodes/individuals that pass through that node/individual; Whitehead 2008) of the population further indicating the importance of their place in the overall network as individuals connecting other individuals. (A third ‘cluster’ was assigned to a single individual who did not have any HWIs > 0.2 with any other individual in the inner estuary network.) Similarly, Lusseau and Newman (2004) found some individuals that they described as “playing the role of broker” in their dolphins’ social network and highlighted the importance of individuals that have preferred companionships in two communities, thus linking them together in a larger social context.

Additionally, when the age of individuals classified by area was taken into account, the social network divisions between inner and outer adults were apparent but especially clear were the divisions between inner and outer estuary juvenile dolphins. These six inner estuary juveniles (21% of all juveniles and 18% of inner estuary individuals) represented a key cohort within the inner estuary social unit.

It is important to emphasize that the clustering of these groups does not follow from the classification of the population by area: there is no reason in principle why the associations between individuals only observed in the outer estuary should be higher than those between these individuals and individuals who are sometimes observed in the inner estuary. The data presented here are necessary to substantiate the connection between area class and association. Similarly, Lusseau *et al.* (2006) found that their identification of two separate social units which mainly used two different areas was the result of genuine social affiliation and not an artefact of spatial distribution. Cantor’s (2012) work on spatiotemporal dynamics in a dolphin society found that spatial distribution did not influence the probability of individuals associating with one another.

‘Spatiosocial’ divisions in bottlenose dolphin networks can be related to many factors, including the geography of the study site (Wells 2014, Titcomb *et al.* 2015), individual ranging patterns (Lusseau *et al.* 2006), habitat preferences (Wiszniewski *et al.* 2009) or differences in cultural behavior (Mann *et al.* 2012). Overall, this apparent division of the population into two social units which correspond to area use within the study site is an important finding for management of the population as a whole.

4.5 Conclusions

The purpose of this study was to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, with the inclusion of additional data on sex, age, and area class for individual dolphins. Social analysis of the whole population revealed groups of mixed composition and variation in association measures across individuals. There is strong evidence that associations between bottlenose dolphins in the Shannon Estuary are not random and that they persist over time. There is also evidence that association measures are related to behavioral state.

Through the classification of individuals by sex, age, and area, important class-determined associations that were somewhat apparent between sex classes were found, but especially strong for within-age and within-area class relationships. Although the strength of female-male associations could not be absolutely determined, the results suggest that female-male associations persist without decline over periods of more than three years. Social network analyses illustrated the preferences of juveniles to associate with juveniles and adults with adults.

Movements between the inner and outer estuary areas of the study site were quite stable over time but use of the inner estuary was limited to a quarter of the population's individuals exclusively. This inner estuary social unit was further divided into a core group of individuals and another group with associations linking core group members and outer estuary individuals. This division in the social structure with respect to area use has important implications for management. This dolphin population has traditionally been managed as one unit, however this study, mirroring others such as in the Moray Firth, Scotland (Wilson *et al.* 2004, Lusseau *et al.* 2006), shows that it may be appropriate to consider the dynamics of the population's social structure in terms of area use when defining management guidelines, especially when the inner estuary is used by such a small (and therefore potentially vulnerable) number of individuals.

This study increases our knowledge of bottlenose dolphin social structure and could be used for comparative studies, to explore similarities and differences in bottlenose dolphin population dynamics. It is unique in its coverage of a moderately sized bottlenose dolphin population in Europe with considerable data on individual sex and age. The results presented have demonstrated the importance of investigating local social behavior in a species known to show a high degree of behavioral plasticity, and provide additional material for cetacean scientists to better understand bottlenose dolphin societies in all their variety. Furthermore, an understanding of the social structure of this population, especially because of its presence within a Special Area of Conservation designated for the species (NPWS 2012), is critical. The findings of this research will contribute to the management and conservation of this important dolphin population in Irish waters.

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Conflicts of Interest

The authors wish to declare that there are no conflicts of interest.

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Table S1 The number of sightings in the inner estuary and outer estuary survey areas for each individual dolphin (3-digit ID code) and the area class assigned to each individual for analysis.

	No. of sightings		
ID	Inner estuary	Outer estuary	Assigned class
001		2	Outer
006	41	46	Inner
008	36	13	Inner
009	19	20	Inner
011	6	13	Inner
016		15	Outer
019		16	Outer
027		6	Outer
033		26	Outer
034	6	10	Inner
042		14	Outer
044	41	9	Inner
045		33	Outer
052	5	13	Inner
066		21	Outer
070		12	Outer
071	19	45	Inner
073		9	Outer
078	3	32	Inner
079		7	Outer
080		19	Outer
081		10	Outer
084	20	36	Inner
085		28	Outer
086		16	Outer
089		10	Outer
093	34	23	Inner
095	34	40	Inner
096		29	Outer
097		5	Outer
099		26	Outer
100		11	Outer
102		21	Outer
104	34	62	Inner
105		8	Outer
106		28	Outer
114		21	Outer
118	27	39	Inner

	No. of sightings		
ID	Inner estuary	Outer estuary	Assigned class
121		4	Outer
123		10	Outer
125		11	Outer
126		20	Outer
144	2	41	Inner
148		20	Outer
150	49	16	Inner
151		8	Outer
162		5	Outer
168		9	Outer
171		42	Outer
173	10	8	Inner
177		12	Outer
179		10	Outer
180	25	44	Inner
182		9	Outer
184		5	Outer
185		16	Outer
193		12	Outer
196		4	Outer
198		9	Outer
200	13	29	Inner
201		11	Outer
202		17	Outer
203		3	Outer
204		7	Outer
205	1	18	Inner
207		9	Outer
208		5	Outer
209		34	Outer
210		10	Outer
211	2	32	Inner
213		4	Outer
214	4	45	Inner
215		6	Outer
216	36	28	Inner
217		6	Outer
218	9	16	Inner
219		3	Outer
220		5	Outer
221		14	Outer
222		6	Outer
223	3	23	Inner
224		10	Outer

	No. of sightings		
ID	Inner estuary	Outer estuary	Assigned class
225		7	Outer
226	6	35	Inner
227		4	Outer
228		8	Outer
229		13	Outer
231		6	Outer
232		18	Outer
233		10	Outer
234		5	Outer
235		17	Outer
236	33	23	Inner
237		11	Outer
238		8	Outer
239		2	Outer
240		16	Outer
241		14	Outer
242	32	48	Inner
243		3	Outer
244	43	15	Inner
245	11	17	Inner
246		21	Outer
247	5	28	Inner
248		6	Outer
249		1	Outer
250		39	Outer
255		4	Outer
260		17	Outer
280		21	Outer
281		10	Outer
282		5	Outer
283		9	Outer
284		11	Outer
285		26	Outer
286		11	Outer
300		1	Outer
312	35	16	Inner
313	24	26	Inner
813		5	Outer
839		10	Outer

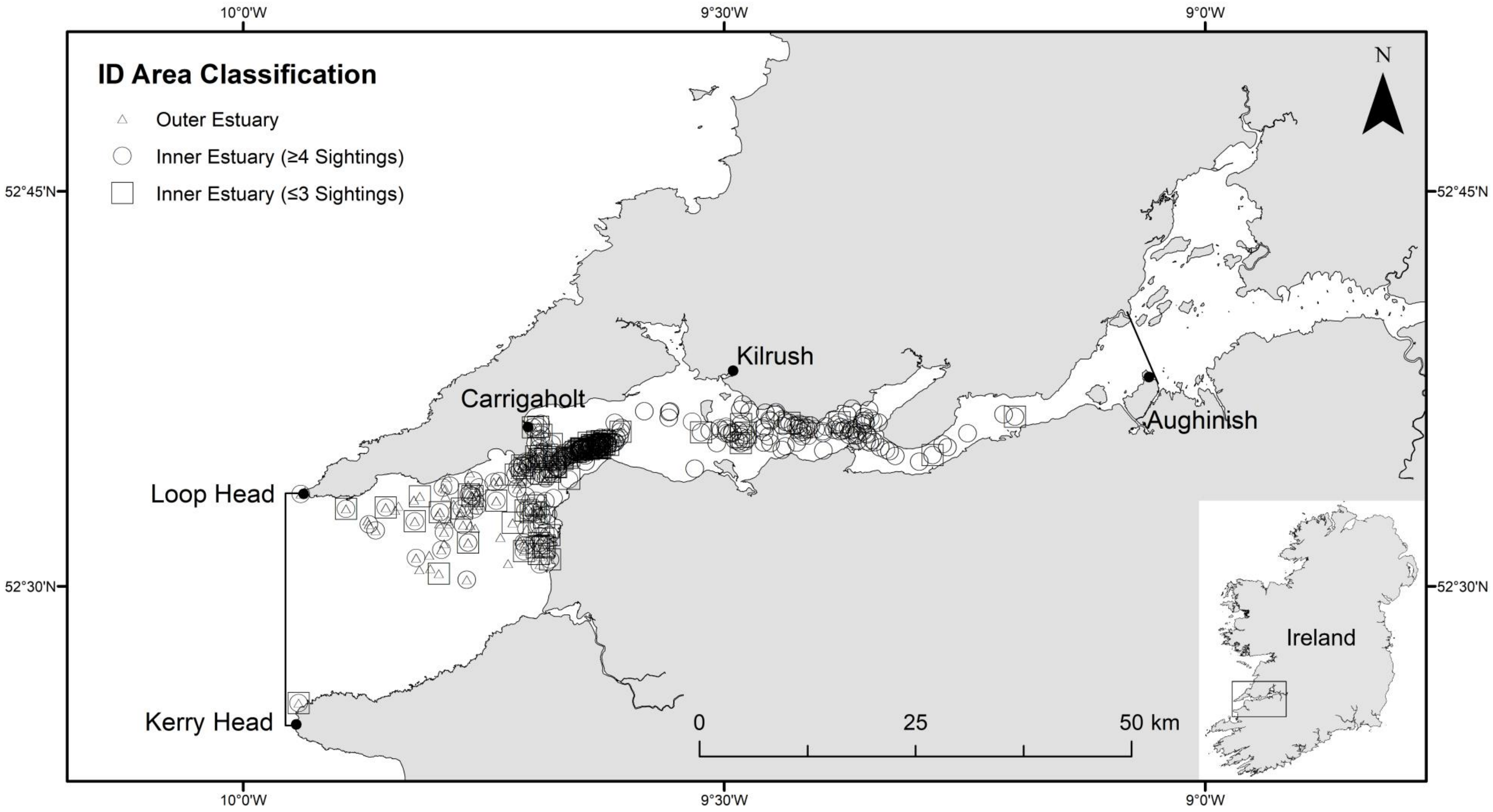

Figure S1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. Sightings of individual dolphin IDs are classified by area as “Outer Estuary” (triangles), “Inner Estuary (≥4 sightings)” (circles), and “Inner Estuary (≤3 sightings)” (squares), and correspond to area classifications for each individual in Table S1.

Chapter 5

Fine-scale sociality reveals female-male affiliations and absence of male alliances in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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5 Fine-scale sociality reveals female-male affiliations and absence of male alliances in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

Knowledge of social behavior at an individual level is central to the understanding of complex mammalian societies. In this study, the fine-scale sociality of wild bottlenose dolphins in the Shannon Estuary, Ireland, was analyzed by examining the dynamics of associations between members of the whole population and between specific female and male dolphins. Fifty-one boat-based individual focal follows were carried out on 18 identifiable bottlenose dolphins over 90.8 h (39 d) between 2014 and 2016. Additionally, 353 boat-based surveys (with 607 sightings) of the dolphin population between 2012 and 2015 were conducted, and 121 distinct individual adult/juvenile dolphins were identified. The mean group size of focal dolphin groups was 7.2 ± 4.1 (range = 1-20) and the mean fission-fusion rate was 3.06 ± 1.35 changes/h. Dolphins were rarely solitary (< 5 h of follows) and females and males had an average of 67 ± 11.63 (range = 37-82) and 75 ± 11.86 (range = 53-86) associates, respectively. The most frequent composition of within-group affiliate pairs was female-male. Whilst the proportions of time that a focal female had either a female or male nearest-neighbor were similar, focal males were much more likely to spend time with female nearest-neighbors than male nearest-neighbors ($P = 0.013$). Activity state means suggested that female dolphins spent more time traveling and resting than males, and less time foraging, socializing and milling. However, a randomization test of activity budgets by sex class indicated that female and male dolphin activity budgets were not significantly different ($P = 0.13$). There was no evidence for male alliance formation in the Shannon Estuary population, and all of the known-sex top-ranked associates ($n = 7$) of known males ($n = 10$) were females. The results of this detailed behavioral research make an important contribution to the knowledge of complex and diverse bottlenose dolphin societies globally.

Key words: bottlenose dolphin, *Tursiops truncatus*, sociality, interval sampling, continuous sampling, activity budget, photo-identification, associations, Shannon Estuary

5.1 Introduction

Knowledge of social behavior at an individual level is central to the understanding of the dynamics of social relationships (Mann 1999, Karniski *et al.* 2015). Coupled with network analyses of social structure at the population level (*e.g.*, Lusseau *et al.* 2006, Baker *et al.* 2017b (Chapter 4)), individual-specific data provide a deeper understanding of overall population dynamics by uncovering behavioral patterns among and between individual animals. To collect behavioral data on individuals, commonly used survey techniques can be supplemented with continuous behavioral observation sessions termed “focal follows” (McHugh *et al.* 2011b, Karniski *et al.* 2015). During focal follows, fine-scale behavioral data are collected on individual focal animals and the groups of conspecifics in which they are found, including information on group size, activity states and positions of other individuals relative to the focal individual. While surveys are essential for gathering basic population information, focal follows allow researchers to gain much more detailed behavioral data (Altmann 1974, Mann 1999). For example, two individual animals might always be recorded as being in a group together, but if the group is not investigated further, it may never be known that they are always (or never) observed side by side.

Nearest-neighbor relationships provide a way of defining associations between two individuals that is distinct from that of basic group membership (Whitehead 2008). These distinct measurements may then be used together to assess whether two individuals have a particularly strong association (a “bond”; Whitehead 2008). Nearest-neighbor associations may have important biological significance; for example, they have been used to assess the behavioral effect on western gorillas (*Gorilla gorilla*) of the introduction of hand-reared infants into an established group (McCann & Rothman 1999), and are clearly of potential relevance to the analysis of mating strategies, dominance hierarchies and social learning. In an analysis of within-group affiliations in juvenile bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, USA, McHugh (2010) found that individuals showed a marked preference for associating with other juveniles as nearest-neighbors, especially those of their own sex, further demonstrating the value of data collected through detailed within-group behavioural observations.

Noteworthy sex-specific behavioral differences may also be found when animals are studied at the individual level (Samuels 1996). Sex differences in behavior are likely to be most pronounced in the most dimorphic species (Magurran & Maciás Garcia 2000; *e.g.*, black howler monkeys (*Alouatta caraya*), Bicca-Marques & Calegaro-Marques 1994); but even in monomorphic species, behavioral differences may result from differences in parental care (Clutton-Brock 1991), particularly reflecting the different nutritional needs of lactating females (Clutton-Brock 1977). Among primates, females of many species feed for longer periods than males, and in some species, females rest for longer periods too (Hemingway 1999). Using focal follow techniques, Waples (1995) found that male bottlenose dolphins in Sarasota Bay engaged in more summertime traveling behavior than female dolphins, while females foraged, socialized and rested more than males during the same period. In an analysis of the activity budgets of focal juvenile dolphins, McHugh (2010) found that males spent more than twice as much time socializing as females. In their study of survey *vs.* focal follow techniques, Karniski *et al.* (2015) determined that the sampling methods of focal follows better captured the sequence and transition of dolphin behaviors and thus produced a more complete picture of an individual's activity budget.

The examination of male-male and female-male associations can provide potential evidence for or against the formation of male alliances in a population. Previous studies have shown preferences for females to associate with females and males with males in some bottlenose dolphin societies (*e.g.*, Smolker *et al.* 1992, Samuels 1996, McHugh 2010). Complex sex-specific strategies exist, such as the formation of male dolphin alliances whereby males associate in long-term bonds in nested alliances and compete for access to receptive females (*e.g.*, in Shark Bay, Western Australia, Connor *et al.* 2000, St John's River, Florida, Ermak *et al.* 2017). The formation of these alliances is therefore an important component of the mating systems in these populations (Connor & Krützen 2015).

Photo-identification studies of bottlenose dolphins (*T. truncatus*) in the Shannon Estuary, Ireland, have been ongoing since 1993, resulting in the identification of many recognizable individuals (Berrow *et al.* 1996, Ingram 2000) who show year-round presence (Berrow 2009) and long-term site fidelity to the area (Berrow *et al.* 2012, Levesque *et al.* 2016 (Appendix D)). The population has been shown to be genetically discrete (Mirimin *et al.* 2011) and the Lower River Shannon was designated as a Special Area of Conservation (SAC) in 2000 under the EU Habitats Directive with bottlenose dolphins as a qualifying interest (National Parks and Wildlife Service (NPWS) 2012). Recent research based on detailed records of catalogued individuals has estimated the extant population size to be 142 dolphins (Baker *et al.* 2018 (Chapter 2)), with a fission-fusion social structure related to age class and area use (Baker *et al.* 2017b (Chapter 4)).

In this study, we report findings from the first focal follows of bottlenose dolphins in Ireland. We used an individual-follow protocol and two focal follow sampling techniques (interval and continuous sampling; Altmann 1974, Mann 1999) to collect behavioral data. We conducted these focal follows over three summers (May-September) from 2014 to 2016 and coupled them with a larger database of photo-id and related sightings data, based on surveys conducted between 2012 and 2015. The key aims of this study were: (i) to calculate the baseline measures of sociality for this population; (ii) to examine individual-level affiliation patterns (*i.e.*, potential nearest-neighbor preferences) within groups; (iii) to test for sex-specific differences in activity budgets; and (iv) to determine if any evidence existed for male alliance formation in the Shannon Estuary population. By addressing these questions, this work expands on previous research on the overall social structure and behavior of the population and illuminates interesting individual- and site-specific differences between the Shannon Estuary and other bottlenose dolphin populations.

5.2 Methods

5.2.1 Study site

This study was conducted within the Lower River Shannon Special Area of Conservation (SAC; site code: 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland’s west coast between Co. Clare, Co. Kerry and Co. Limerick (52°36'N, 9°38'W), in which bottlenose dolphins are a qualifying interest (Fig. 5.1).

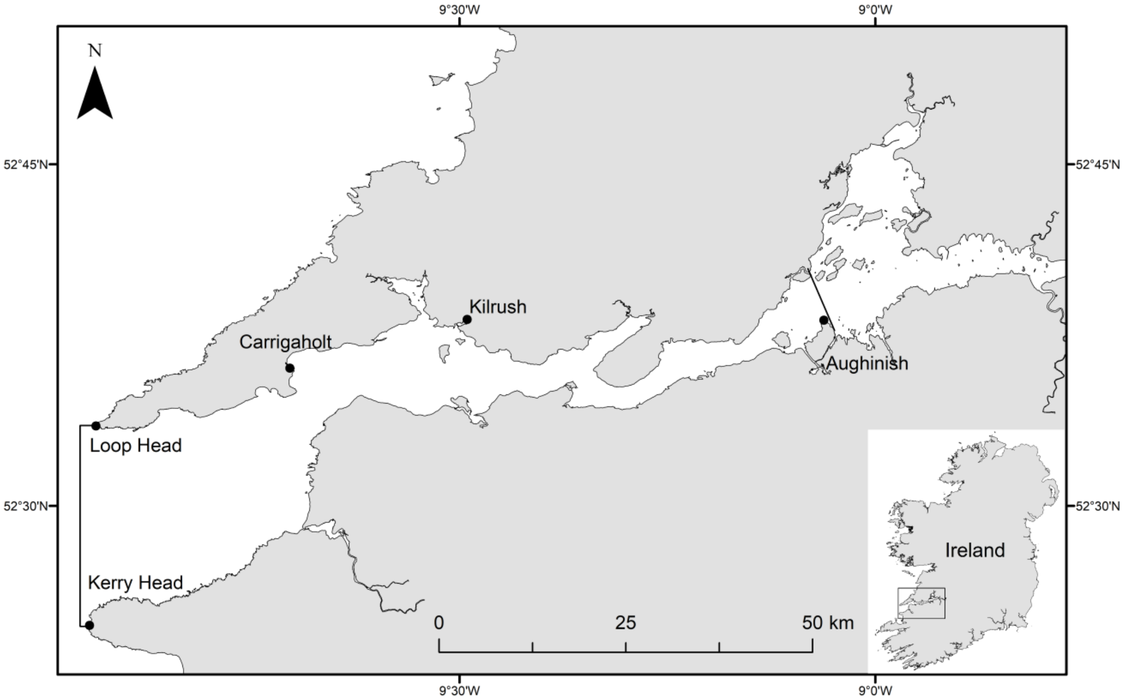

Figure 5.1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area surveyed during this study.

5.2.2 Data collection

Boat-based surveys were conducted during daylight hours between March and November each year from 2012 to 2016 on board a dedicated research vessel, *Muc Mhara*, based in Kilrush, and two dolphin-watching tour boats – *Draíocht* and *Dolphin Discovery* – based in Carrigaholt and Kilrush (Berrow & Holmes 1999), respectively (Fig. 5.1). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor. Trained observers on each vessel located dolphins visually by eye and with the use of binoculars (Minox 7x50 or 8x42).

Data collection methods were based on the recommendations of Mann (1999) who defines the two basic sampling decisions as “follow protocol” – the length of observation and the choice of subject(s) – and “sampling method” – the procedure used to sample behavior. Dedicated data collection comprised two different follow protocols – survey and individual-follow.

(i) Surveys and sightings

During surveys, a dolphin encounter or “sighting” began when at least one dolphin was within 100 m of the vessel and ended after ≤30 minutes due to national regulations (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and at a distance of approximately 100 m unless the dolphins approached the boat. Mann’s (1999) survey protocol was used to collect data during sightings, including records of individual dolphin identifications, group size and composition, changes in group membership, environmental measures (*e.g.*, water temperature, depth and sea state), location (Latitude and Longitude; using a Garmin 72H GPS), activity states (travel, social, forage, rest, other or unknown) and behavioral events (*e.g.*, leap; see Baker *et al.* 2017a (Chapter 3)). A group was defined as all animals sighted together and moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh *et al.* 2011a). Thus, survey sightings provided a snapshot of dolphin group activity, location, and behaviors. The sampling methods used during surveys were “predominant group activity sampling”, “one-zero”, and “*ad libitum*” sampling (see Baker *et al.* 2017a (Chapter 3) for definitions).

(ii) Individual focal follows

Focal follows were initiated following the collection of survey data, if three necessary conditions were met: (1) all members of a dolphin group had been identified, (2) all were individually recognizable by eye to the lead researcher, and (3) sea conditions were calm.

Focal follows (carried out under NPWS permits) were conducted from the research RIB (previously described) during May-September 2014, 2015 and 2016. Standardized techniques for focal follows were developed based upon Sarasota Dolphin Research Program protocols for bottlenose dolphin focal follows (SDRP 2006), which were built upon Altmann’s (1974) guidelines. The follow protocol was “individual-follow” wherein a single individual is chosen as the focal animal in a group, *i.e.*, behavioral observations (“focal follows” or “follows”) conducted on specific individuals (“focal animals”) (Mann 1999, McHugh *et al.* 2011b). Two sampling methods were used during individual-follows – continuous sampling to gather data on group dynamics and behavioral events, and point sampling at 3-minute intervals to determine activity budgets, identify nearest-neighbors and gain information on individual associations. Generally, the first adult dolphin of known sex encountered during the day was selected as a focal animal, and if two or more potential focal individuals were present in a group, we chose the individual that had been followed less often or less recently, as recommended by McHugh *et al.* (2011a). The sex of individual dolphins was determined through (1) genetic evidence from tissue samples collected through biopsy sampling (*n* = 37; collected under NPWS permits; Berrow *et al.* 2002, Mirimin *et al.* 2011); (2) photographs of the genital area (*n* = 1); and, (3) in the case of adult females, observations of the mother swimming in close association with a dependent calf (*n* = 25). Overall, 48% of individuals available for analysis were of known sex; 47 of 51 follows were of focal individuals of known sex.

Focal follows were conducted up to four days a month, focal dolphins were followed for up to 2 h per day, and a maximum of two focal follows a day were carried out. During a follow, the research vessel maintained a position parallel to the animals and at a distance of approximately 20 m unless the dolphins approached the boat. Boat speed and direction were kept gradual and consistent in an effort to minimize any disturbance to the dolphins (Mann *et al.* 2000). Pre-follow sightings lasted at least 15 min to provide time for the habituation of dolphins to the research vessel before beginning focal follows.

Follows were confined to adults (and one juvenile), as the behavior of dependent calves could not be considered independent of their mothers' behavior. Age class was determined by observations of individual size and body length (Smith *et al.* 2013), reproductive state and/or knowledge of long-term life history (Baker *et al.* 2018 (Chapter 2)). Adults were fully grown animals (about 4 m in length) and well-known from long-term photo-identification studies in the Shannon Estuary (*e.g.*, Berrow *et al.* 1996, Ingram 2000, Berrow *et al.* 2012, O'Brien *et al.* 2014 (Appendix E)). Juveniles were less than two-thirds the size of adults and were not themselves dependent calves. Calves were dolphins that were consistently in association with their adult mothers, often with visible fetal folds (dark vertical lines on the body) and swimming in a characteristic infant position alongside their mothers (Mann & Smuts 1999).

During focal follows, fine-scale behavioral data (instantaneous point samples) were collected every 3 min on: (1) GPS location of the research boat, (2) focal animal and group activity state (travel, forage, probable forage, feed, social, rest, play, or with boat; see Baker *et al.* 2017a (Chapter 3) for definitions), (3) group size and number of calves, (4) group composition (including the identities of all individuals in the group), (5) group spread (in meters), (6) nearest-neighbor distance (from the focal individual) and identification, and (7) focal animal position (*i.e.*, the location of the focal individual relative to the rest of the group – ahead, center, behind, side-by-side, in a lateral line, infant position or peripheral). The countdown timer of a phone app (*Impetus*) set to beep at 3-min intervals for 2 h was used to mark each sample point for data collection. If the focal individual was below the surface of the water at the 3-min time point, the data were recorded at the first surfacing of the focal individual and the rest of their group. Concurrent continuous data sampling allowed changes in group membership to be noted as fusion or fission events when dolphins joined or left the group. Additionally, all behavioral events (*e.g.*, fish toss; see Baker *et al.* 2017a (Chapter 3)) were recorded as they occurred, with information on the individuals engaged in the behavior where possible.

Upon each surfacing, the lead researcher (IB) identified each individual dolphin in real time using distinctive markings on their dorsal fins to recognize them by eye. The number of individuals identified was used to record group size and number of calves. Group activity state was recorded as the predominant group activity state, *i.e.*, the activity state that over 50% of the group was engaged in at the time. To eliminate any potential inter-observer variability in distance estimates, the same observer (IB) estimated group spread and nearest-neighbor distance for each point sample during every focal follow.

(iii) Photo-identification

Photographs were taken throughout sightings and focal follows using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70-300 mm lenses). Initially, attempts were made to photograph each individual in each group (regardless of their degree of marking or individual differences in behavior) for individual recognition through the photo-identification of dorsal fins (Würsig & Würsig 1977, Würsig & Jefferson 1990). Then, once a focal follow was initiated, photographs were taken throughout the follow to continuously record the identity of group members, and with particular attention to recording changes of group composition. These photos could then also be used to cross-validate the field IDs determined by the lead researcher throughout the follow. Each focal individual was well-known from the photo-id catalogue and identifiable by the lead researcher in the field (see Appendix 1 of this paper for all focal dolphin dorsal fins).

5.2.3 Data management

Database design and management is described in Baker *et al.* 2018 (Chapter 2) and followed Shannon Dolphin and Wildlife Foundation (SDWF) protocols (Baker 2015 (Appendix G)). Briefly, two databases were maintained in (1) *IMatch 5.6* (https://photools.com), a photographic software environment where all photos from surveys and sightings were stored and processed, and (2) *FinBase* (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams *et al.* 2006) where both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered and where the related data could be queried for specific analytical purposes. A digital photo-id catalogue housing the best images of each individual in the population was used for initial dorsal fin comparisons.

5.2.4 Data analysis

5.2.4.1 Analytical setup

Focal follow data were analyzed in *R* (*R* Core Team 2016) and *MATLAB* (version 9.2). All data (51 follows) were analyzed together for overall population results. For sex-specific analyses, adult female and male focal follow data were split for separate calculations (26 follows of 10 known adult females and 20 follows of five known adult males).

Survey and sighting data (2012-2015) were queried in *FinBase* and input into *SOCPROG 2.7* (compiled version), a dedicated software package that uses data on the associations of identified individual animals for the analysis of their social structure (Whitehead 2009), in group mode, with a supplemental file detailing individual sex and age class. The sampling period was defined as one day, based on the natural break between daylight sampling sessions and because the proportion of individuals sampled within a one-day timeframe was appropriate for data analysis. Associations between individuals were defined by shared group membership, with each record/sighting constituting one group. The half-weight association index (HWI) was used as the coefficient of association. This measure represents the strength of social bonds among individuals (with a range of possible values between 0 (never seen together) and 1 (always seen together)), while also accounting for the possibility of missing individuals during sighting encounters (which is a possibility when opportunistic research platforms like dolphin-watching tour boats are used). The HWI is defined as HWI = $2N_T/(N_a+N_b)$ where N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns & Schwager 1987). Thus, this association index indicates the proportion of time that each pair of individuals is seen in a group together. Restrictions were set to include in the analysis only individuals with > 5 sighting records in the database.

5.2.4.2 Group composition and sociality metrics

The range, mean, median and mode of group sizes within follows were obtained from the overall follow dataset. Additionally, the range, mean, median and mode were calculated for the number of calves in groups, group spread in meters, and nearest-neighbor distance in meters. The most common focal animal position was also determined. Group composition was described by using the IDs (with individual age and sex classes) of all individuals in each group follow at any point in time.

To examine fine-scale group stability and how group composition changed over time, the fission-fusion rate for each focal individual was calculated by dividing the number of group composition changes (individual dolphins either joining or leaving the focal individual’s group) during focal follows by the number of hours each focal animal was followed (McHugh *et al.* 2011b). The average fission-fusion rate was then calculated for females and males separately and for all focal individuals combined. A linear regression was used to test if females and males had significantly different fission-fusion rates. The fission-fusion rate for each focal animal was entered as the outcome variable into a linear regression with sex entered as a fixed effect.

Three measures of sociality were calculated for each focal individual: (1) proportion of time spent alone (including with dependent calf, if mother), (2) mean group size, and (3) number of associates (Gibson & Mann 2008, McHugh *et al.* 2011b). Proportion of time spent alone was calculated by summing the time that each individual was solitary (*i.e.*, without any other group members within 100 m (excluding dependent calves)) during behavioral observation sessions, standardizing for observation time (McHugh *et al.* 2011b). The mean group size was calculated from follows for all individuals overall and for each individual separately, and then averaged across females and males to generate means for each sex class (46 follows, of 10 known adult females (26 follows) and five known adult males (20 follows)). A Shapiro-Wilk normality test indicated that the data were normally distributed (P = 0.12). A linear mixed-effects model (LMM) was used to test if focal females and males had significantly different mean group sizes during focal follows. Mean group size was entered as the outcome variable into the LMM. Sex was entered as a fixed effect and ID as a random effect.

Using the association matrix generated in *SOCPROG* (for all individuals with > 5 sighting records; n = 106), the raw number of associates of each focal individual was calculated from survey data by summing the total number of unique individuals observed interacting with each focal individual in those years (2012-2015). The raw number of associates was also calculated for females and males separately. Each individual value was then standardized by the number of sighting records of each individual to account for differences in sighting frequency among individuals. A generalized linear mixed-effects model (GLMM) was used to test if females and males had significantly different numbers of associates. Total number of associates per focal animal was entered as the outcome variable into a GLMM with Poisson error structure. Sex was entered as a fixed effect and ID as a random intercept.

5.2.4.3 Nearest-neighbor preferences/Within-group affiliation

To better understand within-group affiliation patterns, nearest-neighbor point sample data from focal follows were investigated. The "nearest-neighbor" was defined as the closest individual that overlapped in surfacing with the focal dolphin (McHugh 2010), with the proviso that a dependent calf was recorded as a female's nearest-neighbor only at times when it was the only individual with her. The number of distinct individuals observed with each focal adult individual was counted. Then, the identities of each focal individual's nearest-neighbors were classed by sex and age to determine if differences existed in the nearest-neighbor preferences of focal individuals, relative to the set of distinct individuals observed in all of each focal individual's groups. To account for the relative availability of different age classes of individual in the population, these results were then adjusted using the age class ratio reported by Baker *et al.* (2018 (Chapter 2); 80:25:40 adult:juvenile:calf) to provide the ratio-adjusted preferential associations of focal individuals with nearest-neighbors of each age class.

To examine which individuals were the most common nearest-neighbors to each focal individual in each of 50 focal follows (one follow was eliminated because there were no nearest-neighbor data), the individual with the highest proportion of observations as nearest-neighbor to the focal individual was extracted from each follow dataset, and then each pairing was classified by sex of both the focal individual and the nearest-neighbor. The frequency of sex-related pairings was then calculated. Consistency in the identity of nearest-neighbors was also assessed for all focal individuals with more than one follow. A GLMM was used to test if focal individual sex (female or male) had an effect on the sex of the nearest-neighbor (for all focal follow point samples for which the sexes of both the focal individual and its nearest-neighbor were known). Nearest-neighbor sex was entered as the outcome variable into a GLMM with binomial error structure. Sex of the focal individual was entered as a fixed effect and ID as a random intercept.

To further investigate individuals' preferred nearest-neighbors, the adult female and male with the largest datasets (*i.e.*, greatest number of hours followed) were chosen as examples. Their 3-min point samples where nearest-neighbor data were available were input into *SOCPROG* to generate results regarding age and sex preferences for within-group affiliates. The proportion of time observed with their most common nearest-neighbor during each follow was calculated to discern if a large portion of time was spent with a specific individual within follows and to get a clearer picture of patterns of affiliation.

We then investigated if a focal individual's most frequent nearest-neighbor in each of its focal follows was the same as its highest ranking associate based on HWIs from the population's sightings data. Associations in the population were generally considered to be important and strong if they were greater than twice the population's mean HWI (Whitehead 2008), determined from previous research to be 0.07 (Baker *et al.* 2017b (Chapter 4)). If the nearest-neighbors (from follows) were among the focal individual's top associates (from sightings), this might be indicative of a "bond" between the animals, *i.e.*, a pair of individuals with strong relationships across two "independent" interaction/association measures (Whitehead 2008).

5.2.4.4 Sex-specific differences in activity budgets

To investigate if the proportion of time spent in different activity states differed between males and females, focal follow data from the five adult males (20 follows, 28.7 h) and the 10 adult females (26 follows, 57.5 h) were used. Individual differences in behavior and/or follow duration can influence results so activity budgets were calculated by weighting for differences in follow durations to avoid bias towards particular activity states (Steiner 2011). Thus, for each individual follow, the percentage of time the dolphin spent engaging in an activity was calculated, *i.e.*, one value for each activity state per follow for each focal individual. Then, values for each activity state were averaged over all follows for each individual dolphin separately to arrive at values specific to that individual (Powell & Wells 2011). The individual means for each sex class were then averaged to determine the overall activity means for female and male individuals. Pie charts were created in *R* (*R* Core Team 2016) to illustrate the activity budgets of female and male focal dolphins.

Sex differences in activity means were compared statistically in *MATLAB* (version 9.2) using a custom randomization program built in *MATLAB* (version 7.4) by Powell and Wells (2011). To estimate the probability of differences in activity state proportions between female and male dolphins, the one-tailed test uses a test statistic (ratio between female and male dolphins) determined by randomizing a matrix 10,000 times. The values were permuted (excluding information on individual sex) to detect if there was an apparent difference between female and male individual activity state budgets with *P* values indicating the level of significance in any differences found.

5.2.4.5 Male alliances

To investigate the potential presence of male alliances in the Shannon Estuary bottlenose dolphin population, a matrix of half-weight association indices (HWIs) was produced using *SOCPROG* for all individual associations of known males with > 5 sighting records (n = 10). As in previous studies, male alliances were defined as pairs of dolphins with high levels of association (very high HWIs) and where each member of the male pair ranks as each other's closest associate (Wells *et al.* 1987, Connor *et al.* 1992). Dyads were considered to be important "friends" if their HWIs were twice the mean for all male dyads; these are pairs of individuals that are associated at least twice as much as the expected value of a dyad chosen randomly from the population

(Whitehead 2008). The matrix of HWIs produced in *SOCPROG* for all individual associations in the population was then used to examine each male dolphin's maximum association index (max HWI) with any other individual in the population, to determine the strength of their strongest association, as well as whether they were also the strongest associate of that individual (*i.e.*, reciprocal closest associates). The sex of each male's strongest associate was also noted.

We ran a two-sided dyadic significance test (Monte Carlo test) in *SOCPROG* and used the results to determine the significant dyads with HWIs greater than two times the mean HWI of all males. The two-sided test for dyadic association simultaneously tests for preferred companionship (a significantly high value of the association index) or avoided companionship (a significantly low value of the association index) (Whitehead 2008). Associations were permuted within sampling periods (20,000 permutations with 100 flips per permutation) and the coefficient of variation (CV) of association indices was used as the test statistic. If any pairs were identified as male alliances, the follow data would be interrogated to discover if these alliances were reflected in nearest-neighbor relationships.

5.3 Results

5.3.1 Surveys and focal follows

Between 2012 and 2015, 353 surveys (with 607 sightings) were carried out, during which 136,486 photographs were taken; 45,371 of these were used for the photographic analysis of individually identifiable bottlenose dolphins. In total, 2,948 identifications were made of 121 distinct individual adult/juvenile dolphins. Dependent calves were excluded from analyses because their presence was a result of their mothers' presence in groups. When restrictions were set within *SOCPROG* to include only individuals with > 5 sighting records, 106 distinct individual dolphins and 519 sightings were available for association analyses.

In total, 51 focal follows were carried out (over 39 d, during 39 surveys) on 18 unique individual dolphins: five adult males (20 follows), 10 adult females (26 follows), one juvenile female (1 follow), and two adults of unknown sex (4 follows). The total duration of focal follows conducted was 90.8 h. All groups combined, 60 individuals were observed in follow groups comprising 23 females, 8 males and 29 individuals of unknown sex; age classes consisted of 37 adults, 10 juveniles and 13 calves. Given the current population estimate of 142 (Baker *et al.* 2018 (Chapter 2)), these individuals represent about 42% of the Shannon Estuary bottlenose dolphin population.

5.3.2 Group composition and sociality

The number of individuals recorded in a focal group ranged from one to 20 animals (mean group size = 7.2 ± 4.1; Table 5.1). The mean number of calves found in focal groups was 1.8 ± 1.3 (range = 0-6). Group spread varied from 1 to 400 m but was most often 10 m. The closest nearest-neighbor distance recorded was 0 m (*i.e.*, the individuals' bodies were touching) while the farthest nearest-neighbor distance was 300 m. The focal animals were recorded in all possible positions (*i.e.*, ahead, center, behind, side-by-side, in a lateral line, infant position or peripheral) but the most common position recorded was "center", meaning the focal animal was positioned in the center of the focal group.

Table 5.1 Group composition data summary from 51 focal follows of bottlenose dolphins in the Shannon Estuary (NN = nearest-neighbor).

	Group size	No. of calves	Group spread (m)	NN distance (m)
Min	1	0	1	0
Max	20	6	400	300
Mean ± SD	7.2 ± 4.1	1.8 ± 1.3	38.8 ± 35.5	9.0 ± 20.3
Median	6	2	30	2
Mode	2	2	10	1

Group composition varied from follow to follow, but often contained a combination of adults, juveniles and calves, and both females and males; of the 51 focal follows, 53% contained all three age classes, while 84% of the groups followed contained both sexes. Only 18% of followed groups contained adults exclusively. No followed groups contained solely juveniles and all of the 25 followed groups which included juveniles also contained both adults and calves. Of 44 focal follows with at least one identified known male in them, 39 (89%) had calves in them. In fact, 70% (*n* =

31) of these follows had multiple calves in them. Of the 39 follow groups containing both adult males and calves, 59% (*n* = 23) contained at least one young-of-year (YOY) calf while the other 41% (*n* = 16) contained older (> 1 yr old) calves. These results indicate the presence of groups with both male and calf members in this study population. Of the 44 focal follows containing at least one identified known adult male, all but one also contained adult females; the remaining follow consisted of a known adult male and one other individual of unknown sex. Seventeen (33%) of the follow groups contained more than one known adult male.

Group composition during follows changed frequently. The average fission-fusion rate of focal female dolphins' (*n* = 11) groups was 3.22 ± 1.57 changes/h, while the average fission-fusion rate of focal male dolphins' (*n* = 5) groups was 2.79 ± 0.89 changes/h (Fig. 5.2A). The linear regression indicated that focal individual sex did not have a significant effect on average fission-fusion rate (estimate = -0.62[0.82], z = -0.75, *P* = 0.47). The overall fission-fusion rate for all focal individuals' (*n* = 18) groups was 3.06 ± 1.35 changes/h (Table 5.2).

Bottlenose dolphins in the Shannon Estuary were rarely solitary; of 90.8 h of focal follows, less than 5 h included observations of focal animals on their own (or with only their dependent calf). Seven of the 18 focal individuals were observed in groups 100% of the time they were followed, and the other 11 dolphins were observed spending between 1% and 41% of their time on their own (mean = 6.6%, SD = 10.2). The two individuals with the highest proportions of time spent alone were females ID#s 011 (25%) and 118 (41%) (Table 5.2). In both cases, these values were derived from a single follow of the focal individual wherein the females were initially sighted alone with their dependent calves, but were joined by other dolphins as the follow progressed. On average, focal dolphins in the Shannon Estuary spent 93.4% (SD = 10.2) of their time in groups with other individuals (Table 5.2).

Table 5.2 The sex class and ID# of focal dolphins followed during behavioral observations in the Shannon Estuary. The number of hours observed (hrs obs), 3-min instantaneous behavioral observations per individual (obs (3-min)) and changes in focal individual's group composition are given, as are the fission-fusion rate, mean group size (*i.e.*, the average size of groups each focal individual spent time in), proportion of time spent alone and proportion of time spent in groups.

Sex class	ID#	Hrs obs	Obs (3-min)	# of changes	Fission-fusion rate	Mean group size	% time alone	% time in groups
Females (*n* = 11)	006	3.9	77	12	3.12	6.0	5	95
	011	1.6	32	9	5.63	5.5	25	75
	019	0.7	13	0	0.00	2.0	0	100
	044	8.3	166	23	2.77	6.6	9	91
	052	5.3	105	13	2.48	4.9	9	91
	071	7.1	141	25	3.55	9.9	5	95
	093	3.5	69	9	2.61	7.8	6	94
	118	2.7	54	16	5.93	2.8	41	59
	216	8.8	175	36	4.11	8.6	0	100
	242	15.9	317	52	3.28	6.2	2	98
	801	1.1	21	2	1.90	6.7	0	100
Males (*n* = 5)	008	9.2	183	17	1.86	12.1	0	100
	009	6.8	136	20	2.94	2.9	1	99
	078	0.9	18	4	4.44	7.0	0	100
	104	7.4	148	19	2.57	7.3	6	94
	313	4.5	89	8	1.80	7.8	9	91
Unknown (*n* = 2)	095	1.9	38	6	3.16	8.6	0	100
	211	1.7	34	5	2.94	6.4	0	100
Total (*n* = 18)		90.8	1816	276				
Mean ± SD					3.06 ± 1.35	6.6 ± 2.4	6.6 ± 10.2	93.4 ± 10.2

When mean group size was calculated for each individual separately, the overall average group size ranged from 2.0 to 12.1 dolphins/group (mean = 6.6 ± 2.4 dolphins/group; Table 5.2). The average group size for all focal males was 7.4 ± 2.9 while the average group size for all focal females was 6.1 ± 2.2 (Fig. 5.2B). Focal individual sex did not have a significant effect on group size (LMM, estimate = 1.57[1.41], z = 1.12, *P* = 0.29).

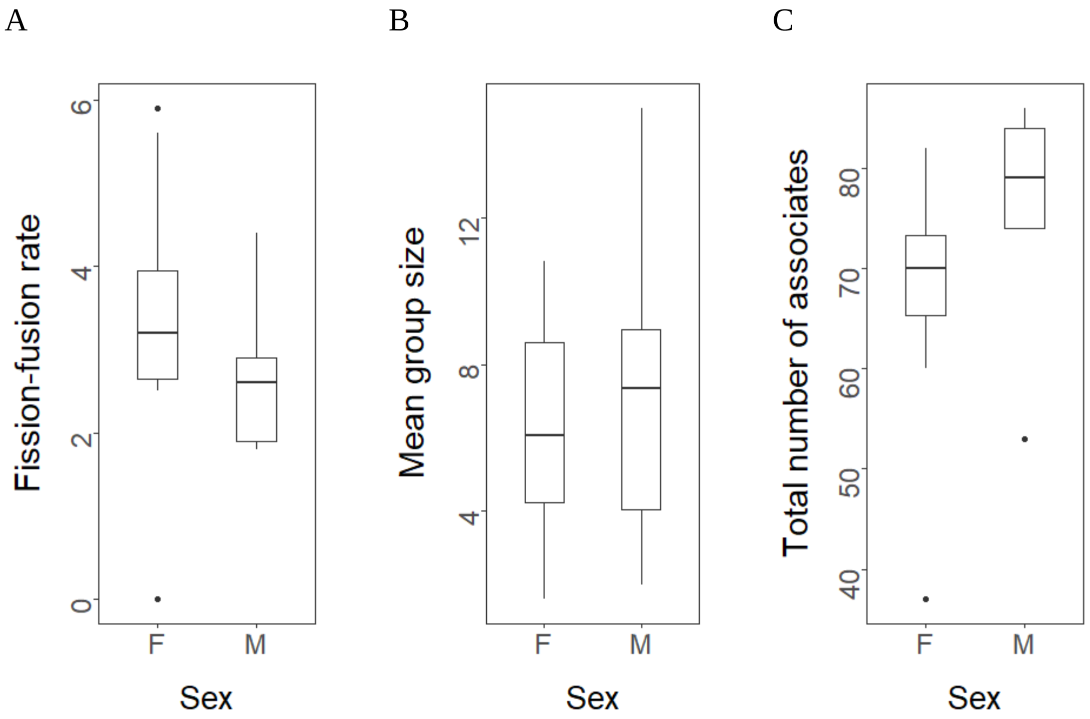

Figure 5.2 Boxplots of adult female (F) and male (M) bottlenose dolphin (A) fission-fusion rate, (B) mean group size and (C) total number of associates (*n* = 15). A linear regression, LMM and GLMM indicated that there was no significant effect of sex on fission-fusion rate (*P* = 0.47), mean group size (*P* = 0.29) or total number of associates (*P* = 0.24), respectively.

Results from the sightings data revealed that focal males had more unique associates than focal females (over 4 yr; 2012-2015). Focal males had an average of 75 associates each (range = 53-86, SD = 11.86) compared to focal females who had an average of 67 associates each (excluding calves; range = 37-82, SD = 11.63; Fig. 5.2C). However, focal individual sex did not have a significant effect on total number of associates (GLMM, estimate = 0.11[0.09], z = 1.18, *P* = 0.24). When standardized for number of sightings per individual (range = 21-92 sightings each), focal males had 1.46 associates per sighting compared to 1.58 for focal females. The average number of associates per individual was 71 (range = 37-86, SD = 11.85) which corresponded to an average 1.56 ± 0.85 associates per sighting.

5.3.3 Nearest-neighbor preferences

The average number of distinct individuals observed interacting as nearest-neighbor with each focal adult individual of known sex was 10 ± 4.87 (range = 1-19). There was no difference in the average number of distinct nearest-neighbors (*i.e.*, different individual dolphin IDs who took the place of nearest-neighbor during a follow) by focal individual sex (focal females = 10 ± 5.14 (range = 1-19); focal males = 10 ± 4.26 (range = 3-15)).

For adult focal females (excluding their own dependent calves), the majority (65%) of distinct nearest-neighbors were other adults (32% females, 11% males, 22% unknown sex), followed by calves (22%) and juveniles (14%). For adult focal males, the majority (72%) of distinct nearest-neighbors were also other adults (42% females, 11% males, 19% unknown sex), followed by juveniles (19%) and calves (8%). Adjusting for the proportions of adults, juveniles and calves in the population as a whole, the focal females' nearest-neighbors were 43% adults, 29% calves and 29% juveniles. For focal males, distinct nearest-neighbors were 48% adults, 41% juveniles and 11% calves. So, all adult dolphins associated preferentially with other adults, and both females and males had a higher proportion of female nearest-neighbor affiliates than males or individuals of unknown sex. Adult females and males differed in their affiliation patterns in terms of age class, in that females were equally likely to associate with calves and juvenile nearest-neighbors, but males were more likely to associate with juveniles than with calf nearest-neighbors.

Excluding six follows where nearest-neighbor data were not available or the most common nearest-neighbor to the focal individual was a dependent calf, the most frequent type of nearest-neighbor pairings between two individuals of known sex was female-male, followed by female-female pairings (Table 5.3). During the 45 focal follows available for this analysis, there were no cases where an adult male spent the majority of his time with another known adult male (*i.e.*, no male-male pairings).

Table 5.3 Nearest-neighbor pairings by sex class for the majority of time of each of 45 individual focal follows

Sex classes of focal individual-nearest-neighbor pair	Frequency
Female-Male	17
Female-Female	7
Male-Male	0
Female-Unknown	12
Male-Unknown	8
Unknown-Unknown	1

Focal individual sex had a significant effect on the sex of nearest-neighbor individuals (GLMM, estimate = -2.85[1.15], z = -2.48, *P* = 0.013). Whilst the proportions of time that a focal female had either a female or male nearest-neighbor were fairly similar, focal males were much more likely to have female nearest-neighbors (Fig. 5.3).

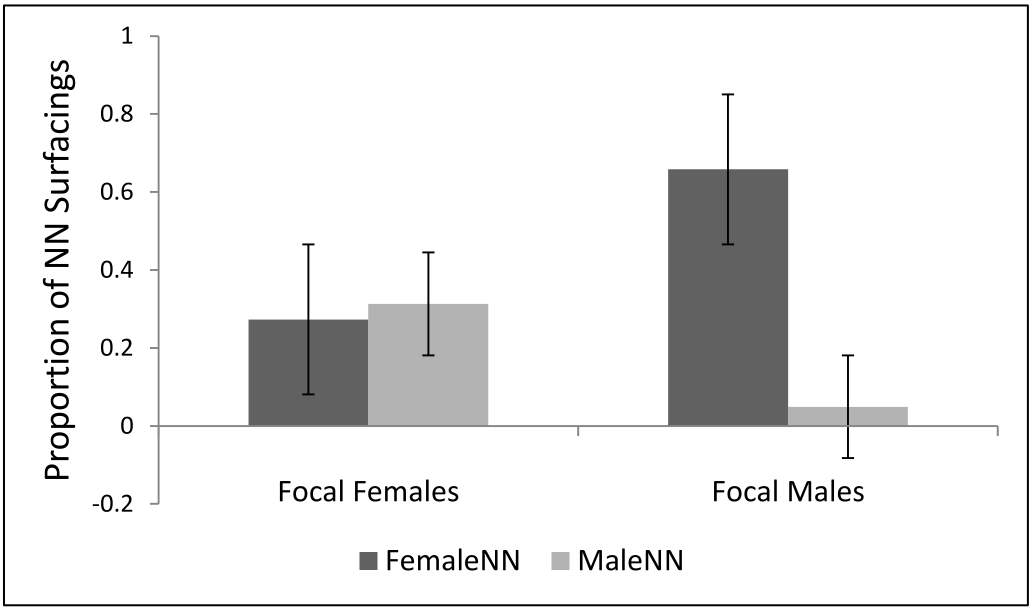

Figure 5.3 A comparison of the proportion of time (3-min point samples) a female or male was a nearest-neighbor (NN) for all focal animal follows (for adult individuals of known sex; focal female follows on the left, focal male follows on the right). Standard error bars are shown. Focal individual sex had a significant effect on the sex of nearest-neighbor individuals (*P* = 0.013).

The adult female and male with the largest datasets were ID#s 242 and 008, respectively. ID# 242 had 19 distinct nearest-neighbors during her 15.9 h of focal follows. Of those, three were adult females, five were adult males and 11 were of unknown sex (four adults, three juveniles and four calves). Of the four calves that ID# 242 was affiliated with, two were her own dependent calves (each recorded as her nearest-neighbor only at times when they were the only individual with her and otherwise excluded as candidates for her nearest-neighbor). Of the five focal follows conducted on ID# 242, her most frequently recorded nearest-neighbor during each follow was: (1) female ID# 093 (65% of the observation time in that follow); (2) male ID# 104 (21%); (3) male ID# 104 (64%); (4) ID# 244 (unknown sex; 20%); and (5) female ID# 118 (35%). In the two follows with male ID# 104 as her nearest-neighbor, the pair was observed in a “trio” with her calf.

The male ID# 008 was observed associating with 24 individuals during focal follows and had 15 distinct nearest-neighbors during his 9.4 h of behavioral observations. Of those, four were adult females, one was an adult male and 10 were of unknown sex (three adults, four juveniles and three calves). Of the five focal follows conducted on ID# 008, his most common nearest-neighbor during each follow was: (1) female ID# 118 (62% of the observation time in that follow); (2) female ID# 118 (84%); (3) ID# 236 (unknown sex; 31%); (4) female ID# 044 (68%); and (5) female ID# 044 (62%). The consecutive follows involving the same female nearest-neighbor occurred on 05 Jul 2016 and 18 Jul 2016 (with female ID# 118) and on 06 Sep 2016 and 12 Sep 2016 (with female ID# 044). In both cases, ID# 008 consistently surfaced in a trio with the female and her calf – ID# 118’s calf was >1 yr old (born in 2015) while ID# 044’s calf was a neonate born 29 Aug 2016. (For a discussion of male-female-calf trios, see Chapter 6, section 6.7).

Bottlenose dolphins in the Shannon Estuary tended to have different nearest-neighbors each time they were followed. The proportion of time a pair spent together as nearest-neighbors within a follow was high (often > 50% of the time) but the identity of focal individuals’ nearest-neighbors often changed between follows. When only focal animals with > 1 follow were analyzed (n = 12), their subsequent follows rarely had the same most frequent nearest-neighbor; in 72% of cases, the most frequent nearest-neighbor was a different individual.

Of each focal individual’s pairings with its most frequent nearest-neighbor, 86% consisted of dyadic associations with individuals with whom they had an important and strong (> twice the population mean) HWI from sightings. However, although these dyads had generally high HWIs relative to other dyadic associations in the population, the specific individuals in each pair tended to have higher overall HWIs with a different dolphin and not their nearest-neighbor from focal follows. Thus, the nearest-neighbors (from follows) were among the strongest associates (from sightings), but almost never *the* top associate from sightings. In fact, of the 51 follows, only seven follows (four distinct pairs of individuals) presented situations where the focal animal's nearest-neighbor for the majority of the follow was also its strongest associate (greatest HWI) from sightings. These pairs were ID#s 242-104 (female-male; HWI = 0.62), 216-008 (female-male; HWI = 0.48), 095-216 (unknown sex-female; HWI = 0.5), and 313-312 (male-unknown sex; HWI = 0.44).

5.3.4 Sex-specific differences in activity budgets

Activity budgets were constructed for the five adult males (20 follows, 28.7 h) and the 10 adult females (26 follows, 57.5 h). Both female and male focal dolphins spent the majority of their time traveling (78% and 69%, respectively) with less time spent foraging, socializing, resting, milling and with boats. Females spent more time traveling and resting than males; males spent more time foraging, socializing and milling (Fig. 5.4). However, the difference between female and male activity budgets was not statistically significant (randomization test, 10,000 permutations; $P = 0.13$).

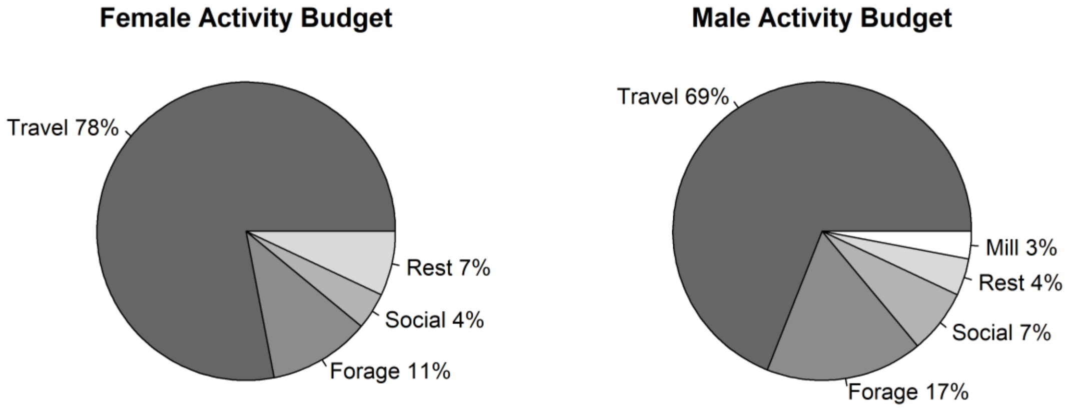

Figure 5.4 Overall mean activity budgets for adult female (*n* = 10) and male (*n* = 5) focal dolphins compiled from summer 2014-2016 individual focal follows. No milling behavior was recorded for females and with boat activity was recorded for < 1% of both the female and male activity budgets.

5.3.5 No evidence of male alliances

Wells *et al.* (1987) and Connor *et al.* (1992) proposed two criteria to define a male alliance: (1) a pair of dolphins with very high HWIs, and (2) each member of the pair ranks as each other's closest associate. In our dataset, there were 263 sightings that included 10 known male dolphins (each individual had 16-101 sightings in the database). The mean male HWI, using sampling periods of days and association defined by group membership, was 0.119. Of the 45 potential dyads in the matrix of association indices for male dolphins, seven pairs of dolphins had high levels of association (where the dyads' HWIs were at least twice the mean; Table 5.4).

The results of the two-sided dyadic association test (Monte Carlo test) revealed only one significant dyad (preferred companions) with HWI greater than two times the mean HWI for all males and with a significantly high value of the association index – these were male ID#s 009 and 313 (HWI = 0.35; dyadic P > 0.95 for test for preferred association using permutation of associations within sampling periods (20,000 permutations with 100 flips per permutation)). The overall significance for preferred/avoided associations in the matrix, using the coefficient of variation (CV) of association indices as a test statistic, was $P = 0.02$ with a CV of 0.84 for the real data, compared with a CV of 0.79 for the mean of the random data.

However, it was not the case for any of these pairs that each member ranked as the other’s closest associate. Thus, the second criterion in the definition of male alliances was not met. In fact, each of the 10 males’ maximum HWI was higher than any HWI they shared with another of the males, except for ID# 033 whose maximum HWI was 0.28 with two other dolphins – ID# 102 (a male, whose highest HWI (0.34) was with female ID# 019) and ID# 260 (a female). The other nine males’ maximum HWI associates were either female ($n = 6$) or individuals of unknown sex ($n = 3$) (Table 5.4).

The data in this study, then, while limited to that of 10 known males, provide no evidence for the existence of male alliances in this population. On the contrary, it is noteworthy that the top associate of known sex for every male in the study was a female. The lack of sightings evidence for male alliances made it inapplicable to see if the members of these alliances were reflected within follows in nearest-neighbor relationships. However, this lack of evidence does seem consistent with the follow data presented above showing the high level of female-male nearest-neighbor pairs and the absence of any (known) male-male pairs.

Table 5.4 Association indices among 10 adult male bottlenose dolphins, their max HWI and the corresponding individual associate with whom the max HWI was shared. The mean male HWI, using sampling periods of days and association defined by group membership, was 0.119. Dyads with association indices at least twice the mean are shown in bold. Asterisk indicates dyadic $P > 0.95$ for test for preferred association using permutation of associations within sampling periods (20,000 permutations with 100 flips per permutation). The overall significance for preferred/avoided associations in this matrix, using the coefficient of variation (CV) of association indices as a test statistic, was $P = 0.02$ (CV = 0.84 for real data, compared with CV = 0.79 for mean of random permutations) (after Whitehead 2008). Note: ID# 033's max HWI was 0.28 with two individuals – ID# 102 (male) and ID# 260 (female).

Male ID#	Half-weight association indices (HWIs)										Max HWI	Associate ID#	Associate Sex
102											0.34	019	Female
104	0.06										0.62	242	Female
144	0.22	0.16									0.45	106	Unknown
016	**0.33**	0.00	0.14								0.36	027	Female
202	**0.26**	0.09	0.21	0.20							0.35	209	Female
313	0.15	**0.27**	0.12	0.07	0.10						0.44	312	Unknown
033	**0.28**	0.02	0.10	0.06	**0.27**	0.06					0.28	260/102	Female/Male
034	0.06	0.05	0.11	0.07	0.00	0.00	0.00				0.16	096	Female
008	0.06	0.18	0.14	0.04	0.00	**0.28**	0.00	0.15			0.48	216	Female
009	0.03	0.22	0.13	0.00	0.00	**0.35***	0.00	0.12	0.21		0.53	312	Unknown
	102	104	144	016	202	313	033	034	008	009			

5.4 Discussion

The fine-scale analysis of individual female and male focal dolphin data from the Shannon Estuary has provided new information on the sociality, behavior and association patterns of individual bottlenose dolphins. Variability in group composition, marked preferences for female-male within-group affiliations and the varied activity budgets of female and male dolphins have been presented. Furthermore, our analysis has uncovered no evidence of male alliance formation in this population.

5.4.1 Group size, composition and sociality

Bottlenose dolphin group size during focal follows averaged around seven animals, ranging from groups of one to 20 dolphins. Using sightings data from 2005 to 2011, Barker and Berrow (2016) previously estimated average dolphin group size in the Shannon Estuary to be around nine individuals (range = 1-50). The slightly smaller mean group size in the present study could be due to a difference in sampling methods, as focal follow data may be biased towards smaller groups (as follows are not initiated on large disorderly groups and may be terminated if groups become so large that not all individuals can be accounted for upon every surfacing). Nevertheless, this study supports Barker and Berrow's (2016) conclusion that the mean dolphin group size in the Shannon Estuary is larger than those found in the closest resident bottlenose dolphin populations in Cardigan Bay, Wales (4.59; Bristow & Rees 2001) and the Moray Firth, Scotland (4.5; Wilson 1995). Our mean group size of 7.2 dolphins is very similar to those reported for bottlenose dolphin populations in the Northern Adriatic Sea (7.4; Bearzi *et al.* 1997), Sado Estuary, Portugal (7.8; Augusto *et al.* 2011) and Sarasota Bay, USA (7; Scott *et al.* 1990).

The composition of dolphin groups during focal follows was generally mixed in terms of both sex and age of individuals. Unlike predictable group compositions from other studies, such as the female-calf nursery groups and all-male groups found in Sarasota Bay (Wells 2014), groups of bottlenose dolphins in the Shannon Estuary often had both males and calves in them, and a mixture of other adults and juveniles. However, this high proportion of mixed groups may have been an effect of surveying almost exclusively during the breeding and calving season. Although individuals in this population often form mixed age groups, previous research has indicated that consistent long-term associations between individuals of the same age class do exist within the social structure of the population (Baker *et al.* 2017b (Chapter 4)).

The overall fission-fusion rate for Shannon Estuary bottlenose dolphin groups was about three changes every hour, *i.e.*, once every 20 minutes. In Shark Bay, bottlenose dolphin group composition can change four to 10 times per hour (Mann & Karniski 2017). The highest fission-fusion rate recorded for any focal individual in the Shannon Estuary was 5.93 changes in group composition per hour. Interestingly, the individual with the highest fission-fusion rate (female ID# 118) was also the individual with the highest proportion of time spent alone; whereas previous work suggests that individuals with high fission-fusion rates would be those who spend the most time in groups rather than alone (Stanton & Mann 2014). Pearson (2008) found that, during focal group follows of dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand, group composition changed every five minutes. In comparison, bottlenose dolphins groups in the Shannon Estuary exhibited much less fission and fusion, perhaps indicating a higher degree of group stability.

All of the focal dolphins in this study spent more of their time in groups than alone. In fact, although measures of sociality for bottlenose dolphins in the Shannon Estuary varied, most individual dolphins were quite sociable, with seven individuals observed in groups 100% of the time they were followed. However, these results could be biased as groups might be more likely to be spotted in the field compared to solitary animals. Overall, the average size of bottlenose dolphin groups that focal individuals spent time in was 6.6 individuals. While the range of mean group sizes per focal individual recorded in this population of 2.0 to 12.1 dolphins/group was similar to the range of group sizes recorded in Sarasota Bay, from 1.9 to 9.8 dolphins/group, the overall mean group size for Shannon Estuary focal dolphins was almost twice the mean group size of 3.8 individuals per group recorded for focal animals in Sarasota Bay (McHugh 2010). However, the focal individuals in the Sarasota Bay study were all juveniles, while those in the present study were primarily adults, so this may have affected the average size of the groups individuals spent time in.

Shannon Estuary focal dolphins had a larger average number of identifiable associates per individual than reported for bottlenose dolphins in the Cedar Keys, Florida, with 71 associates *vs.* 55 associates per individual, respectively (Quintana-Rizzo & Wells 2001). While the number of associates recorded for individuals in the Cedar Keys ranged from 10 to 85 (Quintana-Rizzo & Wells 2001), Shannon Estuary dolphins had a similar upper limit of 86 associates but a much higher minimum number of 37 associates. This might point to Shannon Estuary dolphins having a larger or more fluid social network overall than Cedar Keys dolphins.

Measures of the number of associates an individual has can be biased by sampling effort and the sighting frequencies of different individuals. It is important to take this into account and provide additional measures such as number of associates per sighting. Still, this may not be truly representative of the actual number of individual associates each individual has because presumably those with a low number of sightings are likely to have smaller associate counts than those with a larger number of sightings, at least to some threshold number of sightings where the number of associates could potentially plateau. Nevertheless, it is worthwhile to report these results as number of associates is a valid and interesting measure of sociality. Unfortunately the standardization of this measure remains a challenge.

When standardized by number of sightings, female dolphins in the Shannon Estuary had more associates per sighting than males, suggesting that they have larger social networks. Similarly, Quintana-Rizzo and Wells (2001) found that females had an average 10 more associates than males (64 *vs.* 54 associates). The generally larger social networks of female dolphins have been widely reported in other populations (*e.g.*, Shark Bay, Smolker *et al.* 1992, Doubtful Sound, New Zealand, Lusseau *et al.* 2003, Sarasota Bay, Wells 2014) and the social network metrics of Shannon Estuary dolphins also indicate that females are more socially connected than males (Baker *et al.* 2017b (Chapter 4)).

5.4.2 Nearest-neighbor affiliations

Mann (1999) states that ‘observing the continuous stream of individual behavior in different contexts is central to the understanding of the dynamics of social relationships’ and this emphasizes the importance of using focal follow techniques to examine close associations in detail. While previous research defined associations between individuals simply as group membership (*i.e.*, two individuals were considered associated if they were in the same group), the nearest-neighbor data in the present study has allowed for a more detailed investigation into within-group affiliations. The finding of nearest-neighbor associations and sex-specific differences at an individual level supports the findings on individual preferences and differences found at a population level in previous studies (Baker *et al.* 2017b (Chapter 4)).

Bottlenose dolphins in the Shannon Estuary, whether female or male, interacted with an average of 10 distinct nearest-neighbors. This is much less than the average number of 37 distinct individuals observed interacting as nearest-neighbor with focal juvenile individuals in Sarasota Bay (McHugh 2010). Juveniles may socialize more and have more connections as they grow up and develop, so these values may not be directly comparable.

Among adults of known sex, both adult females and adult males associated with more distinct adult females as within-group nearest-neighbor affiliates. While the genetic relatedness of individual dolphins in the Shannon Estuary is currently unknown, Wiszniewski *et al.* (2010) found that both female and male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) seemed to target kin interactions with other females. In terms of distinct individuals that dolphins spent time with as their nearest-neighbor, both adult females and adult males had the same proportion (11%) of within-group affiliations with known adult males. This low proportion could partly be due to the lower number of known males in the population. If, for example, it turned out that all the remaining adult individuals of unknown sex in the population were male, the results would indicate that adult females had 32% female and 38% male nearest-neighbors and that adult males had 42% female and 30% male nearest-neighbors. In this case, there would still be a clear preference for adult males to affiliate closely with adult females, but a closer to equal preference for adult females to affiliate closely with either female or male nearest-neighbors. As it is unlikely that *all* individuals of unknown sex will turn out to be males, the preference of both females and males to associate closely with female nearest-neighbors seems to hold true. Contrastingly, in Sarasota Bay, juvenile dolphins preferred surfacing with members of the same sex (McHugh 2010), whereas in the Shannon Estuary, both sexes of adults preferred their nearest-neighbor to be female.

There is some evidence to suggest variable sex ratios among bottlenose dolphin populations; for example, Manlik *et al.* (2016) report sex ratios of 50:50 and 45:55 male:female for the Shark Bay and Bunbury bottlenose dolphin populations, respectively. As the sex ratio of the Shannon Estuary bottlenose dolphin population is not yet known, it is possible that the preference calculations for female *vs* male nearest-neighbors might be affected by an unequal sex ratio and this could alter the results of our findings.

When the type of pairing between each focal individual and her or his nearest-neighbor was categorized by sex class, the most frequent of nearest-neighbor affiliations were between adult female and adult male dolphins. There were no cases where an adult focal male spent the majority of his time with one of the other nine known adult males during a focal follow. Additionally, the proportion of time focal adult males spent with known adult female nearest-neighbors was significantly greater than time spent with known adult male nearest-neighbors. Again, these results may be affected by the lower number of known males in the population, but it remains likely that female-male pairings were more prevalent than either female-female or male-male pairings.

Although individuals usually showed strong preferences for a specific nearest-neighbor during each follow, the identity of their most frequent nearest-neighbor was prone to change from follow to follow. A "bond" or a pair of individuals with strong relationships across two "independent" interaction/association measures (Whitehead 2008) was potentially found between four pairs of individuals, including two female-male pairs (the other two pairs contained individuals of unknown sex).

5.4.3 Sex-specific activity patterns

Female and male bottlenose dolphins in the Shannon Estuary had broadly similar activity budgets. Both female and male focal individuals engaged in traveling activity for more than half of the time they were under behavioral observation. Each of the two sexes also engaged in foraging, social and resting behavior, although only males were observed milling. Females allocated more time to traveling and resting, while males allocated more time to socializing and foraging.

The fact that these differences were not statistically significant means that any discussion of the effects of sex on activity budget must proceed with caution; however, in some cases effect size should take precedence over P values (Whitehead 2008). For example, the observation that female dolphins spend more time traveling and resting than male dolphins may reflect a real biological difference. It is possible that female dolphins in the Shannon Estuary spend more time resting and traveling due to the presence of their dependent calves, who often surface alongside them in infant position. Indeed, on more than one occasion, the focal female had a newborn calf; Mann and Smuts (1999) showed that mother-calf pairs tend to swim synchronously and slowly (< 2 mph) during the first eight weeks of life. Additional focal follow data on a wider range of individuals would provide a better test of whether real sex differences in activity budgets exist in this population.

While it is important to consider that consecutively sampled activity state data from focal follows are inherently autocorrelated, the small size of our dataset precluded any potential subsampling of the data, because if subsampling is to occur, a large initial dataset is required (Karniski *et al.* 2015). Additionally, there is some evidence to suggest that eliminating autocorrelation can reduce the biological relevance of results (de Solla *et al.* 1999). In their thorough study of autocorrelation in survey and focal follow data collected on bottlenose dolphins, Karniski *et al.* (2015) concluded that complete focal follow datasets retain relevant behavioral autocorrelation that is otherwise not revealed in subsampled follow data. Nevertheless, future research on the activity budgets of Shannon Estuary dolphins should be carried out in order to collect more data; this would allow for a similar analysis to investigate the appropriate sample interval for studying the behavior of Shannon Estuary bottlenose dolphins, as suggested by Steiner (2011) in her study of bottlenose dolphins in the Port River Estuary, Australia.

5.4.4 Male alliances

Male alliance formation occurs in several resident bottlenose dolphin populations including in Shark Bay, Australia (Connor *et al.* 1992, Connor & Krützen 2015), Sarasota Bay, USA (Wells 1991, Owen *et al.* 2002), the Moray Firth, Scotland and Cardigan Bay, Wales (Sim 2015), and St John’s River, USA (Ermak *et al.* 2017) and is an important component of the societal structure in these populations. It might be expected that the dolphin society of the Shannon Estuary would be most similar to those of the Moray Firth or Cardigan Bay because of their geographic proximity and the fact that they involve similarly sized populations in similar temperate environments (Sim 2015). However, previous studies reporting on the social structure of the Shannon Estuary dolphin population found no evidence of sex segregation or single sex alliances in the population (Ingram 2000, Foley *et al.* 2010). The only study that investigated dyads in the Shannon Estuary (Ingram 2000) did not find sex-specific association patterns, but mentioned that most preferred pairings (*i.e.*, those with the highest association index between two individuals) were between probable females and probable males.

In our study, there were preferred/avoided associations among male dolphins, but there was no evidence for male alliance formation in the Shannon Estuary population. That is to say, there were no pairs of male dolphins that had high levels of association and where each member of the male pair ranked as each other’s closest associate. However, our results must be taken with caution, due to the low sample size

(10 males), as it is possible that alliance-forming males could exist outside the pool of known sampled individuals. Interestingly, when looking at the associate of each male with whom he shared his maximum HWI, seven of the 10 associate individuals were female (and the other three of unknown sex). In his study of Shannon Estuary bottlenose dolphins, Ingram (2000) also noted that in 13 maximum associated dyads (in which the probable sex of both individuals was assigned), 12 were female-male pairs. Contrastingly, in Shark Bay, females were never the top ranked associates of males (Smolker *et al.* 1992). In the present study, over half of the 10 known males' strongest associates were females. The fact that we could find no examples of male-male pairings among most frequent nearest-neighbors adds further support to the suggestion that male alliances are not a feature of this population.

Additionally, during observations of dolphin behavior, there were no groups of dolphins that appeared to behave in any ways typical of male alliances recorded in other study sites. For example, we did not observe chasing, bolting, displays or aggression (*e.g.*, charging or biting) that are often typical components of the behaviors exhibited by male alliances and the females they are herding during consortship behavior in Shark Bay (Baker *et al.* 2017a, Connor *et al.* 1992, Connor & Krützen 2015). Similarly, no popping vocalizations were ever recorded to be produced by dolphins in the Shannon Estuary, nor did the dolphins exhibit 'formation swimming' typical of that shown by male alliances during herding behavior (males traveling just behind and to either side of the herded female; Connor *et al.* 1992). This lack of behavioral evidence coupled with the reported results from data analysis support the idea that the Shannon Estuary bottlenose dolphins may not form male alliances.

5.4.5 Effect of vessel presence

There was no evidence to suggest that the presence of either our research vessel or the tour boats had a negative effect on the behavior of the dolphins; we did not observe any evasive behavior, nor did we observe any obvious changes in group size or composition in relation to vessel presence. However, it is important to consider that the presence of a boat could have had an impact on the behavior of the dolphins. For example, Christiansen *et al.* (2010) found that the activity state of Indo-Pacific bottlenose dolphins (*T. aduncus*) was influenced by the differences in the vessels used as research platforms; dolphins around tour boats were more likely to be travelling or foraging than resting or socializing. Similarly, Bejder *et al.* (2006a) found that boat presence had an impact on group spread, fission-fusion rates, speed and changes in the direction of travel for Indo-Pacific bottlenose dolphins in Shark Bay. Another study in the same region showed that increased dolphin-watching tourism from boats caused local declines in dolphin abundance (Bejder *et al.* 2006b).

Karniski *et al.* (2015) examined the effect of research vessel presence on the activity state of bottlenose dolphins for both survey and focal follow methods. For surveys, they compared dolphin behavior before the research vessel approached to within 100 m to behavior after approach and found that dolphin behavior before and after the research vessel approached did not differ for any activity states. For follows, they compared individual female activity budgets in the first 5 min of a focal follow to a 5 min period 1 h into the focal follow and found that there were no significant differences for any activity states. Thus, Karniski *et al.*'s (2015) results indicated that the approach and continued presence of their research vessel, which was a similar type and size (a small motor boat <5.7 m) to the research vessel used in this study, were not associated with any changes in dolphin behavior. Although we encountered no apparent avoidance behavior during observations of bottlenose dolphins in the Shannon Estuary, it would be pertinent to conduct a similar study in the future to assess the potential impact of our research vessel on dolphin behavior during surveys and focal follows.

5.5 Conclusions

This study complements previous research on the overall behavior and social structure of this bottlenose dolphin population and reveals interesting individual- and site-specific differences between the Shannon Estuary population and other dolphin populations. Bottlenose dolphins in the Shannon Estuary formed relatively stable fission-fusion groups of around seven individuals changing composition roughly three times an hour. They were rarely solitary and both females and males had many associates in the population. Both females and males had more adult females as distinct nearest-neighbors but the most frequent composition of within-group affiliate pairs was female-male, and focal males spent a significantly greater proportion of their time with female nearest-neighbors than with male nearest-neighbors. Although the activity budgets of female dolphins showed that female dolphins spent more time traveling and resting, and less time socializing, foraging and milling, than male dolphins, these differences were not statistically significant. There was no evidence for male alliance formation in the Shannon Estuary population and over half of the 10 known males' top-ranked associates were females.

Research on the fine-scale sociality of bottlenose dolphin populations is challenging and requires detailed data collection and analysis coupled with long-term datasets. This study contributes to current knowledge of bottlenose dolphin sociality, association patterns and mating systems, and especially to an increase in the information available for populations in temperate coastal waters. The presence of a potentially different societal structure to those known thus far in bottlenose dolphin societies globally emphasizes the value of continuing to monitor and protect this population. A better understanding of the behavior and sociality of bottlenose dolphins in Irish waters will also help to support future conservation and management efforts of this important and unique population.

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Conflicts of Interest

The authors wish to declare that there are no conflicts of interest.

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Appendix 1 – Focal individual dolphin catalogue photos and ID codes


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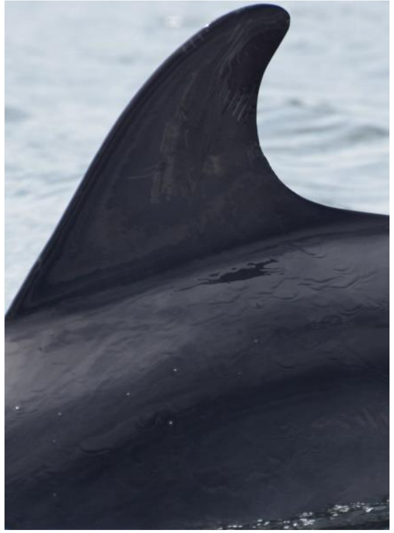
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Appendix 1 – Focal individual dolphin catalogue photos and ID codes


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Appendix 1 – Focal individual dolphin catalogue photos and ID codes


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Appendix 1 – Focal individual dolphin catalogue photos and ID codes

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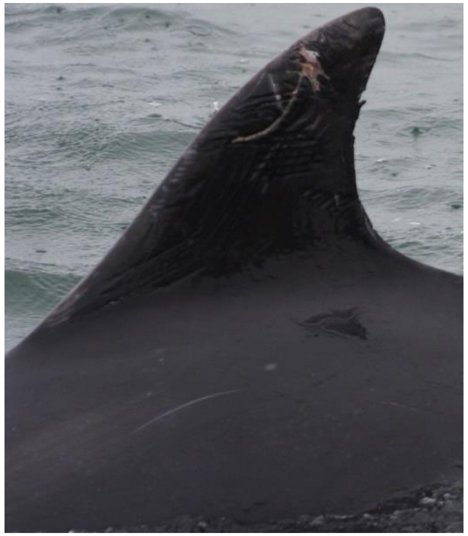

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Chapter 6

General discussion


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6 General discussion

6.1 Overview

The research conducted for this thesis aimed to provide the first baseline data on reproductive parameters, behaviour and social structure for bottlenose dolphins in Ireland, using the most extensive and detailed databases to date, together with novel (to Irish research) data collection techniques, to produce new findings. These initial objectives have been accomplished and are presented in the research studies constituting Chapters 2 to 5 (Manuscripts I to IV). These studies reveal new detailed knowledge about the Shannon Estuary bottlenose dolphin population.

Overall, this research has provided an essential first step into the investigation of reproductive parameters, behaviour and social structure of bottlenose dolphins in Ireland. Importantly, these findings have introduced results for dolphins in Ireland to the global bottlenose dolphin research community. A new estimate of the total size of the Shannon Estuary bottlenose dolphin population, 142 individual dolphins, was produced, using a different calculation method to all previous estimates. The current population consists of about 55% adults, 17% juveniles and 28% calves. Perhaps not surprisingly, bottlenose dolphins in the Shannon Estuary appear to exhibit similar reproductive traits and demographics to those of some of the bottlenose dolphin populations found in other study sites, with most values obtained falling within or just outside the range of values found for populations elsewhere. In global terms, this population seems to have a high fecundity rate, a low calf mortality rate, and a relatively low mean inter-birth interval. Similarly, the Shannon Estuary bottlenose dolphins' full behavioural repertoire did not depart substantially from that found in other populations, although it is likely to grow as more behavioural research is undertaken. Its overall range of behaviour was similar to that of other populations, although some specific behaviours observed elsewhere have not so far been recorded here. In relation to activity budgets, the Shannon Estuary bottlenose dolphins seem to spend rather more time travelling than most populations; and females seem to allocate more of their activity budget to resting than males. Significant social associations between bottlenose dolphins in the estuary were found according to age and area use. Perhaps one of the most interesting findings of this research was that only about 25% of the population used the inner estuary study area, and had stronger associations with each other than with those using only the outer estuary. Preferred associations existed between some individuals in the population for at least three years, and were somewhat unusually exhibited by female-male pairs too. This presence of female-male dyads in the population was further revealed in the within-group preferences for female-male nearest-neighbour pairs. In contrast to other studies, there was no evidence for the existence of male alliances in the Shannon Estuary bottlenose dolphin population.

This study was the first to gather and analyse enough detailed longitudinal data to calculate life history values for this population and the first to use individual focal follow behavioural observation techniques on cetaceans in Ireland. The methods employed could be replicated for other cetacean population studies in Ireland, especially on those containing identifiable individuals with well-managed catalogues (*e.g.*, humpback whales (*Megaptera novaeangliae*)). Additionally, with the growth of these datasets on the Shannon Estuary bottlenose dolphin population, further research questions could be investigated with more fine-scale data and a longer term dataset. The results of this work will also be useful for global comparisons using available parameters from other behavioural studies of resident bottlenose dolphin populations.

In what follows, some of the key findings of this research are discussed, along with some comparisons with other studies and a critical evaluation of two alternative methodologies used in similar research. Rather than reproducing the discussions of Chapters 2 to 5, I focus on aspects of the study that raise additional issues and knowledge gaps. Recommendations for future research are also proposed. The topics addressed in this general discussion are:

(6.2) Population size and demography
(6.3) Reproductive parameters and population viability
(6.4) Behavioural repertoire
(6.5) Age- and area-related social structure
(6.6) Absence of male alliances
(6.7) Female-male associations and affiliations
(6.8) Implications for conservation and management and recommendations for future research

6.2 Population size and demography

Interestingly, this study’s estimate of mean extant population size (142 animals) derived from direct counts of known catalogued individuals was higher than those previously derived from mark-recapture studies (Baker *et al.* 2018 (Chapter 2)). However, it was similar to Englund *et al.*'s (2007) estimate of 140 ± 12 (SE) (CV = 0.08, 95% CI 125-174) and within the 95% Confidence Intervals for most other surveys carried out to date, including the most recent mark-recapture population estimate of 114 ± 14 (SE) (CV = 0.12, 95% CI 90-143) (Rogan *et al.* 2015).

As my work for this study involved a detailed investigation into every individual catalogued in the population, I thought it would be interesting to provide a direct count of all the individuals as an alternative to producing an estimate based on mark-recapture analysis. Additionally, there had already been six previous mark-recapture studies of this population, and the data collection protocols in the current study were not designed to meet the assumptions of a mark-recapture analysis. For example, this study used opportunistic platforms and the research vessel was specifically used for finding focal groups rather than conducting whole population line transect surveys, and thus the assumption of equal probability of capture could not be met. It would also be difficult to meet the assumptions of a closed population mark-recapture model with these data as these would imply that there was no immigration or emigration of individuals inside and outside the study area. Recent evidence suggests that individuals regularly use Tralee Bay and Brandon Bay, areas southwest of the border of the study site (Levesque *et al.* 2016 (Appendix D)) and there is some evidence of "Shannon" dolphins found along the Irish coast north and south of the estuary mouth (unpublished data; IWDG 2017).

Despite the use of an alternative technique, far from underestimating the population, the direct-count method generated a population estimate of 142, exceeding the estimates derived from the mark-recapture studies. While it would not have been possible to conduct a mark-recapture abundance estimate using the data on which this thesis is based, it is interesting to reflect on possible reasons why these data have resulted in a larger population estimate using direct counts of known individuals.

One possibility is that the proportion of distinctive "marked" individuals input into mark-recapture analyses might have affected the results. Looking closely at the two most recent studies (Berrow *et al.* 2012, Rogan *et al.* 2015), it appears that previous population estimates of bottlenose dolphins in the Shannon Estuary using mark-recapture statistical models have, in comparison to this study, underestimated the actual extant population size by about 22%. Comparing Berrow *et al.*'s (2012) 2010 estimate of 107 dolphins to my closest (annual) extant population count in 2011 of 138 dolphins, and comparing Rogan *et al.*'s (2015) 2015 estimate of 114 dolphins to my extant population count in 2015 of 145 dolphins, the same difference in number of animals results from both comparisons – 31 dolphins. So, in both cases, I counted that there were 31 more dolphins in the population than these studies estimated there to be. Because mark-recapture studies rely heavily on the values used to indicate the proportion of “marked”/”unmarked” animals in the population, it seemed pertinent to investigate this further. I found that Berrow *et al.* (2012) estimated 60-63% of individuals to be “marked” (Severity Grade 1) whereas Rogan *et al.* (2015) estimated 71-74% of individuals to be “marked” (Severity Grades 1 and 2). In order to shift the mark-recapture calculations of these studies to match the population counts of mine, Berrow *et al.* (2012) would have needed to use 47% (to generate an estimate of 138 dolphins) while Rogan *et al.* (2015) would have needed to use 57% (to generate an estimate of 145 dolphins). Thus, if both studies had dropped their proportion of “marked” animals by about 13%, they would have generated estimates more similar to mine for the population count of those years. So, one explanation of the difference in population estimates is that each of these studies overestimated the proportion of “marked” animals in their dataset by about 13%.

Read *et al.* (2003) cautioned that population estimates based on only the best-marked individuals in a population can be imprecise because they are calculated from relatively few data. Similarly, recent research into capture-mark-recapture modelling has shown that the inclusion of only very distinct individuals can result in severe underestimates of population size (regardless of the quality of images included in the analysis) (Tyson *et al.* 2017). This could provide an alternative explanation for the previously lower estimates of population size in the Shannon Estuary, as they might have relied too heavily on highly distinctive fins. By contrast, the present study relied on direct counts of all of the individuals in the population irrespective of their degree of marking. However, this is only one possibility; ultimately, a variety of factors are likely to affect the outcome of mark-recapture analyses and the different results obtained from alternative methods for estimating population size.

6.3 Reproductive parameters and population viability

Female reproductive parameters for bottlenose dolphins in the Shannon Estuary were presented. Overall, most of the parameters fell within the range of values reported from other studies used for comparison (Baker *et al.* 2018 (Chapter 2, Table 2.4)).

Interestingly, Shannon Estuary bottlenose dolphins had a slightly higher fecundity rate (0.26 ± 0.03) than the other populations examined, with the closest being that of bottlenose dolphins in the Bay of Islands, New Zealand (0.25; Tezanos-Pinto *et al.* 2015). Furthermore, first-year calf mortality in the Shannon Estuary population (11%) was the lowest of all compared populations, with the next lowest calculated for bottlenose dolphins in Mikura Island, Japan (13%; Kogi *et al.* 2004). These values suggest that the Shannon Estuary population is in relatively good reproductive condition, and appear promising for the long-term viability of the population (if they remain consistent over time). The comparatively high proportion of calves (28%) in the Shannon Estuary population may also provide a promising outlook for the population in terms of viability and growth.

This research has shown that the reproductive females in the Shannon Estuary bottlenose dolphin population exhibit a range of inter-birth intervals (IBIs) between 2 and 7 years. If more IBIs are calculated with more accurate date-of-birth estimates in the future, additional IBIs of less than 2 years may be discovered. Similarly, if IBIs are calculated using year-of-birth with a longer term dataset in the future, additional IBIs of more than 7 years may be found. However, this will depend on the maintenance of rigorous data collection protocols and frequent encounters with reproductive females to minimise the occurrence of possible missed births in the dataset.

An interesting result of this study was the detection of shorter IBIs for females whose newborn calves had died prior to weaning. These IBIs of 2 (n = 2) and 3 (n = 1) years were shorter than they might have been had these females' calves survived to weaning age. The comparison of these data with results available from other populations strengthens the idea that shorter IBIs following the death of a calf may be a general trait of bottlenose dolphins as a species, given the evidence from other studies of this also occurring in other bottlenose dolphin populations globally (*e.g.*, Bearzi *et al.* 1997, Kogi *et al.* 2004, Steiner & Bossley 2008).

Population Viability Analysis (PVA) techniques use population data to determine the stability (or growth/decline) of animal populations, predicting the future status of a population by quantifying its probability of extinction (Boyce 1992). Englund *et al.* (2008) conducted the only PVA available on dolphins in the Shannon Estuary; however, they used no data from the dolphins in the estuary besides the population estimate they had generated (using mark-recapture analysis in 2008). All other data values that they input into the PVA were derived from various other international studies, including life expectancy estimates (Read *et al.* 1993) and mortality rates (Wells & Scott 1990) from Sarasota Bay, and reproductive maturity estimates from northeast Florida (Sergeant *et al.* 1973). Using these values, they concluded that the bottlenose dolphin population in the Shannon Estuary would likely increase from 114 to 160 individuals in 250 years. However, this result seems to be of little scientific value given that it is based on population parameters derived from other populations and not the Shannon dolphin population.

Given this previous study, I conducted a similar PVA (Appendix I) on the Shannon dolphin population using reproductive parameters from my research (Baker *et al.* 2018 (Chapter 2)); however the only values it was possible to change were fecundity rate (from 14.4% to 26%), first-year calf mortality (from 20% to 11%) and population size (from 114 to 142). In both PVAs, carrying capacity was estimated as twice the highest estimate of population size (280 in Englund *et al.* (2008) and 300 in this study).

Obviously, using the same exact data as Englund *et al.* (2008) but replacing their values for initial population size (114) and fecundity (14.4%) with our higher values (142 and 26%, respectively), and replacing their value of 20% for first-year calf mortality with our lower value of 11%, was bound to result in a higher predicted population size and lower chance of population extinction after 250 years.

Unfortunately, the results again appear to have little scientific interest, as too many factors of the PVA still rely on surrogate data, such as life expectancy and female-male ratios, not yet available from the current population data for dolphins in the Shannon Estuary. I hope that we will gain more population data in years to come that may allow us to carry out a scientifically meaningful PVA for this population.

In a similar discussion, Arso Civil (2015) suggests that new reproductive parameters for bottlenose dolphins in Scotland derived from her PhD research would allow for the production of a PVA using the same procedure as that carried out by Sanders-Reed *et al.* (1999) but with more accurate population-specific data. Like Englund *et al.* (2008), the Sanders-Reed *et al.* (1999) PVA had only three values from the study population (bottlenose dolphins in the Moray Firth), with the rest of the model parameters input from other studies. Here again, it is hard to attribute great scientific interest to an analysis relying on so many surrogate parameters (Arso Civil *et al.* 2017). Additional population data gained from the growing longitudinal Shannon dolphin dataset will be important in helping to produce more meaningful results for PVAs in the future.

6.4 Behavioural repertoire

The compilation of large amounts of data from behavioural observations resulted in a detailed ethogram for bottlenose dolphins in the Shannon Estuary (Baker *et al.* 2017a (Chapter 3)). The 11 activity states and 45 behavioural events defined have all been recorded during behavioural observations of bottlenose dolphins in other study sites, but the data presented provide the first record of these behaviours for Irish dolphins along with the first behavioural analysis of this kind for the Shannon Estuary study site. The ethogram is an evolving research tool; there were 10 additional behaviours that were not analysed in the present study (as they were recorded as anecdotal data during focal follows), but if more data were to become available, these could be included in future analyses. As many bottlenose dolphin populations exhibit site-specific behaviours, it seems likely that further study of the Shannon Estuary bottlenose dolphins could reveal the presence of interesting behaviours unique to this site.

In addition, the activity budgets calculated for Shannon Estuary dolphins provide essential information for this population and for comparisons with other study sites. The fact that Shannon Estuary dolphins spent a similar proportion of their time engaged in social activity to dolphins in Shark Bay, where evolutionarily significant social behaviours have been documented, is promising for future behavioural research on this population. The inter-annual variation in activity budgets, particularly in relation to foraging activity, could be due to a number of factors, such as resource availability. Further research on prey distribution and abundance could help to explain changes in foraging behaviour from one year to the next. It would also be interesting to investigate differences in activity state budgets spatially within the estuary. An important next step for behavioural research on dolphins in the Shannon Estuary will be to begin trying to put these behaviours into context. For example, Lusseau (2006) and Pearson (2017) demonstrated that aerial behaviours exhibited by dolphins played a number of different roles/functions including communicating changes in group behaviour and affecting fission-fusion dynamics. Preliminary analysis of the proportion of behavioural events in different activity state categories suggests that this could be an interesting area for future research.

6.5 Age- and area-related social structure

The social structure of the Shannon Estuary bottlenose dolphin population fits the general pattern of a fission-fusion society characterised by a large social network of interconnected individuals with different strengths of association over both spatial and temporal scales. The most outstanding feature was the structuring of these associations by age and area class, but the presence of relatively unusual female-male associations was also of interest (Baker *et al.* 2017b (Chapter 4)).

Associations between juveniles were strong, as were the associations between adult individuals. Similar preferential associations between juveniles have been observed in Shark Bay and Sarasota Bay (Smolker *et al.* 1992, Gero *et al.* 2005). Given that bottlenose dolphins in the Shannon Estuary wean at around 2.9 years of age (Baker *et al.* 2018 (Chapter 2)) and become independent of their mothers at that stage, it is predictable that they would form groups with other juveniles rather than remain solitary; the benefits of associating in groups can include increased foraging efficiency as well as socialisation (McHugh 2010).

Perhaps one of the most interesting findings of this research was that only about 25% of the population were using the inner estuary study area, that is the area of the study site (and SAC) east of the north-south line through Scattery Island, Co. Clare (Baker *et al.* 2017b (Chapter 4)). The social analysis of these “inner” class individuals *vs.* “outer” class individuals (those dolphins using only the outer estuary area) revealed strong within-area-class associations, particularly within the “inner estuary community”. Further analysis of the “inner” class associations highlighted 12 individuals who may serve as important social connectors between inner and outer estuary individuals, perhaps maintaining an important level of social cohesion in the population as a whole. Further research into the effect that the loss of one or more of these socially important individuals might have on the social makeup of the population would be interesting. These results also raise questions about and may have implications for the management of this dolphin population, if a relatively small and socially distinct community unit is using an area of the estuary more affected by anthropogenic disturbance. Additionally, the social mixing occurring within the entire population from year to year may be useful information for management in order to deliver and maintain protective measures for these dolphins in the future.

6.6 Absence of male alliances

There was no evidence of all-male groups or the formation of stable long-term male alliances in the Shannon Estuary bottlenose dolphin population (Chapter 5). The proportion of time adult males spent with adult female nearest-neighbours was significantly greater than the time they spent with adult male nearest-neighbours and over half of the known males' strongest associates were females (see section 6.7 below).

Various factors have been suggested to explain the presence of male alliances in other populations, such as habitat use, population density (and thus the extent of individual interactions and mating opportunities) and reproductive rates (Owen 2003, Connor *et al.* 2017, Ermak *et al.* 2017). Thus, it seems likely that the ecological, social and/or environmental pressures at play in the Shannon Estuary have an opposite influence that explains the lack of male alliance formation. In her research on the mating strategies of bottlenose dolphins (*T. truncatus*) in the St Johns River, USA, Ermak (2014) compared the population density of her study population with that of 11 others, including the Shannon Estuary, and noted the tendency of male alliances to be reported from the study sites with the greatest population densities (between 0.60 and 6.76 dolphins/km^2). Ermak (2014) also compared inter-birth intervals between nine study sites and found that only the two with the highest IBIs (Shark Bay, Australia and Sarasota Bay, USA) reported having male alliances. More recently, Ermak *et al.* (2017) concluded that increased male-male competition, perhaps due to long inter-birth intervals and high population density, seemed to best predict alliance formation in the St Johns River dolphin population.

In the longest-running study of alliance formation in bottlenose dolphins (*T. cf. aduncus*) in Shark Bay (where dolphins exhibit the most complex alliance formation known outside of humans), Connor and Krützen (2015) have proposed various demographic and ecological suggestions for male alliance formation. For instance, predator and prey abundance may impact alliance formation, along with habitat use. Connor and Krützen (2015) caution against reaching conclusions based on any strict single-factor relationships between cause and effect of alliance formation, suggesting it more likely that a range of contributing factors are at play; for example, although habitat use may influence alliance formation, they have recorded variation in the size of second-order alliances in all habitats, so it cannot be a sole determining factor. By the same token as Ermak (2014), Connor and Krützen (2015) believe that the rate at which males encounter rivals (*i.e.*, encounter rate), especially in competition over females, will influence selection for alliance formation and thus may explain differences among populations of bottlenose dolphins in alliance formation. Population density, home range and communication range (with sound traveling further in open water relative to shallow/subdivided habitats), may work together to impact encounter rates, and thus alliance formation (Connor and Krützen 2015).

The potential impacts of different demographic and ecological factors on the formation of male alliances may be correspondingly responsible for the lack of male alliance formation in the Shannon Estuary bottlenose dolphin population. For example, this population appears to have a relatively low IBI (2.7-3.5 y; Chapter 2) and a relatively low population density (0.21 dolphins/km^2; Chapter 2), consistent with Ermak's (2014) observations. Examining the other factors discussed by Connor and Krützen (2015) requires further research. In the absence of male alliances, alternative mating strategies must exist, and future research should focus on distinguishing and empirically investigating the possible mating systems of this population.

6.7 Female-male associations and affiliations

Some of the strongest associations in the Shannon Estuary bottlenose dolphin population were between female-male pairs, and associations between female and male dolphins included preferred companionships that persisted over multiple years (> 1000 d; Baker *et al.* 2017b (Chapter 4)). The fact that the strength of these between-sex-class associations was not significantly different to that of within-sex-class associations warrants further attention. Stable long-term female-male associations have been documented in bottlenose dolphin populations in Doubtful Sound, New Zealand (Lusseau *et al.* 2003) and in Port Stephens, Australia (Wiszniewski *et al.* 2010), so it could be that similar associations occur in the Shannon Estuary, with these associations likely to be linked to the reproductive characteristics of the population. However, a caveat of this research study is that data collection was largely limited to summer months (probably the breeding season). In Sarasota Bay, females and males are often seen associating in groups during the breeding season, while sexual segregation of males and females is common outside of the breeding season (McHugh 2010). If it were possible to collect winter data on female-male associations in the Shannon Estuary, this would help to shed light on the potential seasonality and longevity of these associations.

Nevertheless, the finding of within-group affiliations between adult females and adult males (Chapter 5) suggests there may be more to discover about these female-male relationships. The results presented show that focal adult males preferentially associated with adult females as their nearest-neighbours and that the proportion of time females and males spent together as nearest-neighbours was significantly more than they spent with individuals of their own sex. Of course, nearest-neighbour associations in tight groups could be misinterpreted; if, for example, a male alliance pair was consorting a female, and thus flanking her on either side, this could be documented as a female-male nearest-neighbour pairing, but in fact involve a male consorting/herding/escorting a female in close proximity (McHugh, pers. comm.). For this reason, it is important to outline the context in which many of these nearest-neighbour pairs were observed – in many cases, they were observed as male-female-calf "trios" which were tight (< 1 m apart) groups consisting of an adult male, adult female and her calf, often separated by 10-75 m from the rest of the dolphin group.

These female-male associations, particularly in male-female-calf trios, appeared to occur quite frequently. Unfortunately, however, efforts to explain their occurrence with the current dataset did not produce statistically significant results and so they were not incorporated into the four main analyses included in this thesis. Nonetheless, I will discuss them briefly here.

Observations of male-female-calf trios were often made, particularly during focal follows where behavioural observations were longer in duration and groups could be followed more closely. These trios consisted of a known adult male, an adult female and her calf, with calf age ranging from newborn (one-day-old) to over 3 years old. The trio often persisted in a tight group formation for the entire duration of the follow (typically 2 h) and some groups contained multiple trios along with other individuals. The membership of some trios was consistent across multiple weeks or within the 4-month summer season, while others changed membership slightly throughout a field season, *i.e.*, a different male with the same mother-calf pair. In one case, the same trio was observed across years, once in 2012 and once in 2015; in some cases, including this one, the same male accompanied the same female but with different calves, from one that weaned to the next newborn she gave birth to.

To investigate how these associations between female and male dolphins in male-female-calf trios might change between years, I inputted annual female-male HWIs into SOCPROG's multiple measures analysis tool, to produce a dyadic output.

Because males seemed to preferentially associate with females when they had calves with them, my initial hypothesis was that associations would be stronger between males and females in the year their calves were born compared to the year of gestation or the pre-gestation/cycling year. However, the potential increase in female-male dyadic associations following the birth of a calf was not significant, even when the data were filtered to analyse only those individuals specifically observed in male-female-calf trios.

I also investigated the possibility of designating “escorts” by comparing the HWI of the top male associate of each reproductive female with that of her next strongest male associate (Grellier *et al.* 2003, Whitehead 2008). Examining the six reproductive females observed in trios during follows, the top male associates of each female did have significantly greater HWIs with them (mean = 0.49 ± 0.13) than each of the females’ next male associates (mean = 0.34 ± 0.09; $t = 2.06$, $P < 0.05$), thus, potentially allowing these male dolphins to be designated as the females’ escorts (Grellier *et al.* 2003, Whitehead 2008). However, the sample size was really too small to state anything conclusively.

Nevertheless, it appears that some mature males in the Shannon Estuary bottlenose dolphin population form bonds, possibly seasonally, with mother-calf pairs. While it has been difficult to determine the prevalence and meaning of these associations, they certainly warrant further investigation. In other populations, female reproductive state has a strong effect on differences in the consistency of female-male associations from year to year (Connor *et al.* 2000). For example, Smolker *et al.* (1992) found that female-male associations were generally inconsistent and depended in part on female reproductive state – females had more consistent associations with males in the years when they were cycling than with the same males in the years when they were pregnant. The observations in the Shannon Estuary suggest that female-male associations might be strongest during the years when females are nursing a dependent calf, but this requires further investigation.

Lusseau *et al.* (2003) suggested that significant associations between female and male bottlenose dolphins in Doubtful Sound, New Zealand, might represent an increased involvement of both sexes in reproductive strategies, and that long-term relationships between females and males might then influence these strategies. Additionally, the increased probability of reproductive success (through increased mating opportunities, female mate choice, mate guarding, or increased access to food resources) could also influence female and male dolphins to associate with one another

(Owen *et al.* 2002). Female dolphins might also benefit from associations with male dolphins through reduced risk of infanticide (Dunn *et al.* 2002, Owen *et al.* 2002) or support against harassment by other male dolphins (Scott *et al.* 2005).

While sightings of groups with only one male are very rare in Shark Bay (Smolker *et al.* 1992), Quintana-Rizzo and Wells (2001) observed an association of this type between a female-calf pair and a male in the Cedar Keys, USA, and some large single males in Sarasota Bay are known to form associations with females solitarily (*i.e.*, not in a paired male alliance; Wells *et al.* 1987). Behavioural studies of the franciscana dolphin (*Pontoporia blainvillei*) have revealed a single male mating system (Wells *et al.* 2013) and it may be that such a mating strategy is being employed by male dolphins in the Shannon Estuary, although more data are needed to validate this hypothesis.

A single male might preferentially associate with a mother-calf pair for various reasons. For example, mother-son associations (between the female and adult male) could increase inclusive fitness. However, if this were the case then males would have only one permanent female associate (Lusseau *et al.* 2003) – in the present study some males associated preferentially with more than one mother-calf pair. Wiszniewski *et al.* (2010) found that genetic relatedness influenced associations between females and males and played a role in maintaining the cohesiveness of dolphin social networks and the social relationships between female and male dolphins in Port Stephens, Australia. In some other cetacean species, such as long-finned pilot whales (*Globicephala melas*; Amos *et al.* 1993) and killer whales (*Orcinus orca*; Baird 2000), female and male relatives form strong, long-term social bonds. Male dolphins may also gain inclusive fitness benefits if increased association with their kin results in the increased survival of their siblings (Wells 1991, Connor *et al.* 2000).

A male might also benefit by associating with female relatives if it were to increase his familiarity with potential mating partners (Wiszniewski *et al.* 2010). However, if this were the case, it seems unlikely that males would stay in tight trios with one particular female, as was observed in our study, and instead would be expected to move around members of the group more often. McHugh (2010) observed alloparental (*i.e.*, babysitting) behaviour in juvenile male bottlenose dolphins and suggested that the adult females for whom they were babysitting might look favourably upon them in years to come, as potential mating partners, if they had helped to care for their young in the past. Synergistically, the males in this case might consider adult females with older, non-related calves to be ideal mates – likely to be both sexually receptive and successful at raising their calves (McHugh 2010). It is possible that the multiple adult male dolphins “escorting” female dolphins in the Shannon Estuary might similarly use their attentiveness to the female’s current calf as a means to increase their chances of future mating opportunities. Overall, this presents a topic of great interest and potential scientific value for further research within this dolphin population.

6.8 Implications for conservation and management and recommendations for future research

Although it was not the objective of this research project, the knowledge and information it provides could be helpful in setting conservation and management priorities in the Lower River Shannon Special Area of Conservation (SAC). Most importantly, future analyses conducted with a view to protect and conserve this population will now be able to use the baseline parameters and behavioural information from this study instead of values derived from population studies of bottlenose dolphins elsewhere. Additionally, the difference in the use of the inner and outer estuary areas by individual dolphins in the population and their corresponding social connectivity may have important implications for management. Furthermore, the potential cyclical aspect of reproduction in the estuary and the range of individual female dolphin reproductive rates may highlight priorities for population conservation.

In addition to the topics discussed above, this study implies a number of recommendations for future research.

(i) More biopsy sampling of individual dolphins of unknown sex should be conducted. This would make it possible to identify the sex of a larger proportion of the population (particularly males), thus facilitating sex-related social analyses and an accurate estimate of the sex ratio of the Shannon dolphin population. It would also provide data for genetic relatedness studies.

(ii) If future mark-recapture analyses are to be conducted, the “marked” proportion value used should be reassessed. Preferably, researchers should continue to use detailed long-term datasets to track every individual dolphin (although this method relies heavily on dedicated teams of researchers conducting 100+ surveys per year and maintaining large databases).

(iii) There is little published evidence about the range of the Shannon Estuary bottlenose dolphins outside the estuary. They have been observed in Tralee Bay and Brandon Bay, Co. Kerry (Levesque *et al.* 2016 (Appendix D)), and north of Loop Head (unpublished data). I have matched a number of dolphins sighted outside the research area with individuals in the Shannon photo-id catalogue, had sightings within the research area of dolphins included in the IWDG coastal bottlenose dolphin photo-id catalogue, and made connections between the two catalogues (see Appendix H). More photo-id surveys should be conducted to establish a better knowledge of the true extent of Shannon Estuary bottlenose dolphin movements and to get a more accurate indication of the extent to which the population is open to immigration and emigration.

(iv) Research using tagging techniques should be conducted to complement the methods used in this study. (a) Tagging with cetacean-borne video camera and integrated sensor system (C-VISS) tags developed for dusky dolphins by Pearson *et al.* (2017) would enable the identification of social and environmental parameters including conspecific body condition, mother-calf spatial positioning, affiliative behaviour, sexual behaviour, minimum social index, prey species and habitat types. However, underwater visibility in the Shannon Estuary could be a limiting factor. (b) Tagging with the long-term satellite-linked time and depth recording tags used in the study of bottlenose dolphins in the Sargasso Sea by the SDRP (Wells *et al.* 2017) would enable the study of lung function, diving and ranging patterns.

(v) Researchers should systematically collect data on pollutant and contaminant levels to build upon previous studies (Berrow *et al.* 2002, Jepson *et al.* 2016) in order to monitor the health status of cetaceans in Irish waters (O'Brien *et al.* 2009) and provide a greater insight into the mortality rates provided in this study (Baker *et al.* 2018 (Chapter 2)). It would be particularly interesting to closely monitor, and sample if possible, the calves found in this study with deformities (including scoliosis and a deformed rostrum) to see if there is a link to contaminant burdens.

(vi) Skin lesions may indicate poor health or exposure to harmful environmental factors. The databases constructed for this study could provide the basis for an analysis of the prevalence of skin lesions in the Shannon Estuary dolphin population and for comparing the results with those of other study sites (*e.g.*, in the Northwest Atlantic; Hart *et al.* 2012).

(vii) Detailed research into bottlenose dolphin diet, foraging techniques, and prey distribution and abundance would make an important contribution to understanding foraging behaviour, as well as the associations and reproductive patterns set out in this study. There are few studies from Ireland of bottlenose dolphin diet. Recently, Hernandez-Milian *et al.* (2015) reported information from 12 bottlenose dolphins stranded on the west/southwest coast of Ireland, indicating that they had a varied diet of pelagic and demersal fishes, predominantly Gadiformes species, such as pollack (*Pollachius pollachius*), saithe (*P. virens*) and haddock (*Melanogrammus aeglefinus*). During my research, I observed and photographed bottlenose dolphins in the Shannon Estuary with a range of prey species including salmon (*Salmo salar*), garfish (*Belone belone*), mackerel (*Scomber scombrus*), some undefined fish species that resembled flatfish, and a possible ray species. Ingram (2000) also reported observations of bottlenose dolphins chasing and catching salmon, garfish and eels (*Anguilla anguilla*) in the Shannon Estuary. Further work should build upon this anecdotal knowledge by analysing these observational data, quantifying prey types observed and investigating foraging behaviour in relation to habitat use in the estuary. Additionally, it would be of great interest to carry out studies similar to those conducted by Berens McCabe *et al.* (2010) in Sarasota Bay where purse seine surveys were used to assess prey availability; similar fishing techniques could be used in areas of the estuary where dolphins engage in foraging activity, to assess prey abundance and distribution, and prey selection.

6.9 Conclusions

The findings in this thesis form a knowledge base that can be used as a scientific foundation for life history and behavioural measures of the Shannon Estuary bottlenose dolphin population in future studies. Continuous long-term photo-identification and behavioural data collection is highly recommended and would benefit from a dedicated funding source.

In conclusion, I hope that the results of this work have made a valuable contribution by establishing baseline scientific data on reproductive rates, behaviour and social structure of dolphins in Ireland, contributing to global knowledge of bottlenose dolphins, enhancing public awareness of cetaceans and providing material that will be of use for future research and for the management and conservation of this unique bottlenose dolphin population.

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Appendices

Appendix A – Published version Manuscript I

Appendix B – Published version Manuscript II

Appendix C – Published version Manuscript III

Appendix D – Co-authored published article – Levesque *et al.* 2016

Appendix E – Co-authored published article – O'Brien *et al.* 2014

Appendix F – Conference posters

Poster 1: Bottlenose dolphin life history and population demographics in the Shannon Estuary, Ireland (SMM Conference, 2017)

Poster 2: Longitudinal study of a live-stranded female bottlenose dolphin in the Shannon Estuary, Ireland (ECS Conference, 2016)

Poster 3: Exploring the social structure of the resident bottlenose dolphin population in the Shannon Estuary, Ireland (SMM Conference, 2015)

*Poster 4: Long-term boat-based monitoring of bottlenose dolphins (*T. truncatus*) in the Shannon Estuary, Ireland (ECS Conference, 2013)*

Appendix G – Protocols document: Researcher's Guide to Protocols for Fieldwork and Data Entry (3rd edition; 2015)

Appendix H – Notes on additional research findings

Appendix I – A Population Viability Analysis for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Appendix A

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ORIGINAL PAPER

Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

This study investigates the female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, using long-term relational sightings and photographic databases. Data were collected between 2008 and 2016, during 654 boat-based surveys, from two dolphin-watching vessels and a research vessel. During 1018 sightings, 4231 identifications of 184 individual dolphins were recorded. The population size was charted through direct counts of known dolphins from 2011 to 2015 (mean 142, range 131–150), with 145 extant individuals in 2015: 80 adults, 25 juveniles, and 40 calves. Excluding dependent calves, 121 individuals were sighted, of whom 98% ($n = 119$) were sighted in multiple years, with 64% ($n = 77$) sighted in all 4 years (2012–2015). Between 2008 and 2016, 37 reproductive females and 69 dependent calves were recorded. Overall, 35% ($n = 13$) of these females were sighted with one calf, 43% ($n = 16$) with two calves and 22% ($n = 8$) with three calves. An average of seven (range 3–10) calves were born each year. Parturition peaked in July. Weaning ages ranged from 2.0 to 4.1 (mean 2.9) years. The mean inter-birth interval ranged between 2.7 ± 0.6 and 3.5 ± 1.3 years, depending on the method used. Mean annual calving rate was 0.29 young-of-year/reproductive female/year. Average crude birth rate was 0.07 ± 0.01. Fecundity was 0.26 ± 0.03. An average 11% of newborn calves were lost before age 1. These results are generally within the lower range of values reported for similar populations and provide essential data for conservation management and global bottlenose dolphin research.

Introduction

Bottlenose dolphins (*Tursiops* spp.) are found across the globe in temperate and tropical waters and in a range of habitats (Wells and Scott 1999). As a result, different populations are subject to different ecological and environmental conditions and pressures. Marked variations in population dynamics, behaviour and social structure have also been reported, perhaps due to the high level of intelligence of the species (Connor et al. 2000). In light of these socio-environmental differences between demographically different populations, it is to be expected that the life history parameters of populations may also vary considerably. This makes it essential to establish baseline life history parameters for specific populations to explore species ecology and inform management.

The production of reliable life history parameters is dependent on longitudinal studies with consistent continuous data collection (Wells 1991; Mann and Karniski 2017). Repeated sightings of identifiable individuals over a long time period allows for the aggregation of individual reproductive histories and thus, the estimation of reproductive parameters such as birth rates, calf mortality and inter-birth intervals (Fruet et al. 2015; Tezanos-Pinto et al. 2015). For long-lived, slow-reproducing mammals like bottlenose dolphins, these long-term datasets are essential for producing both individual- and population-level parameters for demographics, patterns of reproduction and a better understanding

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of the basic biology of the species across its global range (Fruet et al. 2015).

Female reproductive parameters such as inter-birth intervals (Connor et al. 2000) and reproductive success (Fruet et al. 2015) play a crucial role in determining long-term population viability. For example, in a study of two Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations, in Shark Bay and Bunbury, Australia, Manlik et al. (2016) used a population viability analysis (PVA) to demonstrate that reproductive rates had a stronger influence on long-term viability than adult survival rates. Thus, population-specific life history data are essential for the production and interpretation of reliable PVA results and the investigation of long-term population trends. Studies of population dynamics have often used life history parameters from other study populations because baseline data were not available for the population in question, but this may be misleading (Arso Civil et al. 2017).

Understanding the life history characteristics of a specific population is also essential for conservation and management, since the results can have significant effects on management plans. For example, Manlik et al. (2016) concluded that focusing management on calf survival was the best way to improve the viability of the Bunbury bottlenose dolphin population that is forecast to decline.

While there have been many studies of bottlenose dolphin reproductive parameters worldwide, there are few from Europe and none from Ireland. The bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, are a study population with a high dolphin encounter rate, year-round presence and long-term site fidelity (Berrow 2009; Levesque et al. 2016). The population has been shown to be genetically discrete (Mirimin et al. 2011). The development of a dolphin-watching tourism industry has enabled systematic long-term data collection on this population, with two dolphin-watching boats providing opportunistic platforms for research (Berrow and Holmes 1999). Photo-identification studies have been conducted since the early 1990s, resulting in the identification of many recognizable individuals (Berrow et al. 1996; Ingram 2000; Berrow et al. 2012).

Population estimates from previous studies of bottlenose dolphins in the Shannon Estuary using mark-recapture statistical models (with limited numbers of surveys) have estimated the extant population size to be 113 ± 14 (Ingram 2000), 121 ± 14 (Ingram and Rogan 2003), 140 ± 12 (Englund et al. 2007), 114 ± 17 (Englund et al. 2008), 107 ± 12 (Berrow et al. 2012), and 114 ± 14 (Rogan et al. 2015). These studies made use of mark-recapture techniques to derive abundance estimates and results from six surveys over a 20-year period suggest the population is stable. The Lower River Shannon was designated as a Special Area of Conservation (SAC) in 2000 under the EU Habitats Directive with bottlenose dolphins as a qualifying interest (NPWS 2012). The demographics (age and sex composition) of this population have not yet been described.

Annual sightings of newborn calves in the Shannon Estuary indicate that the population is reproducing; however, no reproductive parameters have been produced for this population. Previous work on population viability [e.g., the population viability analysis carried out by Englund et al. (2008)] made use of parameters from very dissimilar populations and study sites, which may not be representative of the population.

In this study, we used a long-term database of photo-id and related sightings data, based on surveys conducted between 2008 and 2016, to describe the demographics and estimate critical life history parameters for the Shannon Estuary bottlenose dolphin population. This provided similar data to that collected for populations elsewhere, enabling comparisons across populations. In contrast to previous work, the detailed analysis of high-quality digital photographs has allowed us to track every individual in the population over 5 years, including those that were previously regarded as “unmarked”. Thus, we used a novel “head-count” technique to produce an updated population estimate for this population. Our two main aims were (1) to describe the Shannon Estuary bottlenose dolphin population’s size and demography (age and sex class) and (2) to calculate baseline reproductive parameters for the Shannon Estuary bottlenose dolphin population. Similar to the study of New Zealand bottlenose dolphins by Tezanos-Pinto et al. (2015), we expected to obtain similar values to those reported for other populations using similar methodologies, and for our values to be most similar to those found in other temperate-water European populations such as around the British Isles.

Methods

Study site

The study site was the Lower River Shannon Special Area of Conservation (site code: 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland’s west coast between Co. Clare, Co. Kerry and Co. Limerick (52°36′N, 9°38′W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 1).

Data collection

Boat-based surveys were conducted between March and November each year from 2008 to 2016 on board three vessels—two commercial dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats provided opportunistic platforms for research, operating

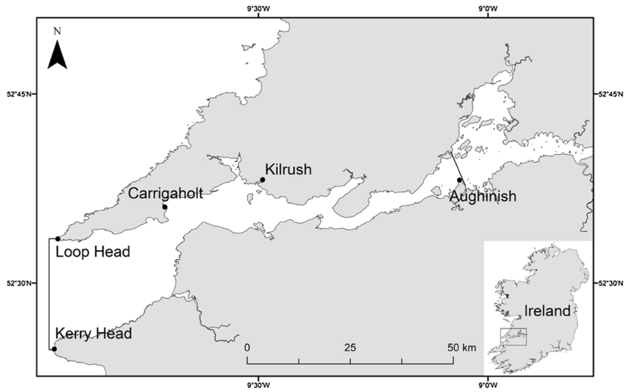

Fig. 1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area surveyed during this study

independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 1). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor. Trained onboard observers located dolphins visually by eye and with the use of binoculars (Minox 7 × 50 or 8 × 42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~ 5 m, while observers on the Kilrush tour boat and research vessel were positioned on the bow of the boats at < 2 m above sea level.

During surveys, a dolphin encounter or "sighting" began when at least one dolphin was within 100 m of the vessel and ended after ≤ 30 min due to national regulations, designed to minimise the potential impact of dolphin-watching on the dolphin population (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and at a distance of approximately 100 m unless the dolphins approached the boat. Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin identifications (IDs), mother–calf pair presence, group size and composition, environmental measures (including swell and sea state), location (using a Garmin 72H GPS), activity states (e.g., travel) and behavioural events (e.g., leap, see Baker et al. 2017a). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al. 2011).

Attempts were made to photograph each individual in each group (regardless of their degree of marking or individual differences in behaviour) for the photo-identification of individual dolphins using unique markings on their dorsal fins and bodies (Würsig and Würsig 1977; Würsig and Jefferson 1990). Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70–300 mm lenses).

Data management

Following Shannon Dolphin and Wildlife Foundation (SDWF) protocols (Baker 2015), images from all surveys and sightings were maintained in a database using the photographic software environment IMatch 5.6 (https://photools.com). A digital photo-id catalogue housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities and persistent skin lesions, by using the filter function in IMatch to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then re-matched. The final identifications of every individual dolphin in every sighting were verified by the lead researcher who had the most photo-id experience, as recommended by Pearson et al. (2016). These methods are similar to standardized protocols used by the Sarasota Dolphin Research Program (SDRP 2006).

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of FinBase (MS Access), a relational sightings database for bottlenose dolphin research (Adams et al. 2006). The FinBase Catalog Browser shows the best left- and right-side image of the dorsal fin for each unique individual in the photo-id catalogue. It also contains the best dorsal fin photo for each individual for every sighting of that individual in the database.

All dorsal fin photographs in FinBase were graded for photographic quality by the lead researcher exclusively (Urian et al. 2015), before each being assigned to their specific sighting and survey using the FinBase Match/Catalog form (Adams et al. 2006). Each photograph was graded according to focus, contrast, angle, visibility and distance. Each of these fields was limited to a set of fixed scoring options which the user could choose from (Adams 2013). When a dorsal fin image was added to a sighting in FinBase, the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program.

Population demographics and adult/juvenile mortality were estimated using data collected during 2011–2015 exclusively, when dolphin monitoring surveys were consistent and protocols were clearly defined (Baker 2015), whereas reproductive parameters were determined using data collected between 2008 and 2016 to allow a more longitudinal investigation. Sighting data for reproductive females and their calves were produced through a FinBase query of individual and shared sightings within the database. In some cases, including all cases in which mother–calf pairs were sighted < 3 times, these data were supplemented with further photographic evidence from the IMatch database.

A separate matrilineal database was maintained to keep specific records of estimated birth and "weaning" dates from the first and last sightings of mothers with calves. Here, we define weaning date/age as the date/age of separation (i.e., independence) of a calf from its mother (rather than weaning in terms of nutritional independence). A mother had to have been seen at least three times (mean 22 sightings) without her calf before weaning was confirmed. Additionally, information on deaths of calves < 1 year old and sightings of known weaned juveniles was also recorded. Calf mortality was estimated only for calves < 1 year old, whose mothers were frequently seen following the birth and subsequent disappearance of the dependent calf. Subsets of data from FinBase and the matrilineal database were used to calculate some reproductive parameters, such as age at weaning.

The large dataset and specialized long-term databases maintained on this relatively small population, coupled with the high encounter rate and in-depth knowledge of individual IDs, provided a unique and robust dataset for investigating the demographics and life history parameters of this dolphin population.

Data classification

Age determination

Individuals were assigned to one of four relative age classes on the basis of observations of individual estimated size and body length (Smith et al. 2013), reproductive state and/or knowledge of long-term life history. Adults were larger and darker in colour than juveniles, and sometimes with a dependent calf (Bearzi et al. 1997; Wilson et al. 1999). Juveniles were less than two-thirds the size of adults and were not themselves dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years prior to weaning. Calves were those dolphins > 1 year of age that were consistently in association with their adult mothers. Young-of-year (YOY) were < 1 year old, often with visible prominent foetal folds (dark vertical lines on the body) and swimming in a characteristic infant position with their mothers (Mann and Smuts 1999).

Sex determination

The sex of individual dolphins was determined through (1) genetic evidence from tissue samples collected through biopsy sampling ($n = 37$; collected under NPWS permits; Berrow et al. 2002; Mirimin et al. 2011); (2) photographs of the genital area ($n = 1$); and, (3) in the case of adult females, observations of the mother swimming in close association with a dependent calf ($n = 25$). For females identified through association with a calf, numbers of shared mother–calf sightings were determined using a specially developed query in FinBase and ranged from 1 to 72 (mean 10). Following Tezanos-Pinto's (2009) definitions, reproductive females (i.e., sexually mature females) were those individuals who had given birth to viable calves during the study period, whereas non-reproductive females were adults positively sexed as females that were never sighted in close association with a calf.

Data analysis

Population size, demography and adult/juvenile mortality

In order to estimate population size, we used our extensive knowledge of catalogued individuals from five recent data-rich years (2011–2015) to produce an estimate of the number of individuals extant in the population. First, we examined the number of sightings of individual dolphins in each year, incorporating age class, and including a discovery curve which reached a clear plateau by 2015. Then, using sighting histories and age class determination, we calculated the number of individuals known to be extant in the population per year. The assumption was made that if an adult/juvenile was alive in a subsequent year, it was alive in all previous years.

Presumed deaths of well-known individuals were also incorporated based on their previous annual sighting rates and their absence during the 2015 and 2016 field seasons. Individuals not recorded since 2013 or earlier all had additional sightings in the database from previous years (2008–2012) but no sightings in 2014, 2015 or 2016. Individuals not recorded since 2014 each had at least one sighting (range 1–22 sightings/year) in each of at least two (range 2–6 years) of the previous 6 years (2008–2013), but no sightings in 2015 or 2016. Using these disappearances of adult/juvenile individuals from the population between 2012 and 2015, we calculated the mean annual maximum mortality rate as "$l/(n - b)$" where l = number of individual disappearances, n = extant population count and b = number of calves born (Wells and Scott 1990).

We calculated the mean extant population size by directly counting the number of catalogued individuals known to be alive in each year and averaging it (Wells and Scott 1990). To visualize how the size and demography of the population changed over time, we constructed a stacked bar chart of population size in each year and incorporated age class demography, adult/juvenile and calf deaths. To investigate population coverage, we plotted the frequency of resightings of individual dolphins in the Shannon Estuary and constructed a histogram of counts of individual sightings.

Female reproductive rates

The entire 2008–2016 dataset was used to document associations between mothers and calves in the study population. The number of annual births was a count of individual calves born in the population during each study year. To test if differences in numbers of surveys each year had an effect on the number of recorded births, a linear regression analysis was carried out in R (R Core Team 2016). The number of calves born to each female individually was also calculated.

In addition, the number of annual calf deaths was counted. If a mother had been sighted ≥ 2 times with a newborn calf, but then sighted on multiple occasions (≥ 2 sightings) without it, less than 1 year later, we assumed the calf had died. Minimum weaning age in bottlenose dolphins has been estimated to be 18–20 months (Smolker et al. 1992; Wells and Scott 1999), so all calves under this age and that were no longer with their mothers were believed to be dead. Although minimum weaning age is likely to differ among populations, there was no evidence of bottlenose dolphin calves weaning before they were 1 year old, so we used a minimum of 1 year to infer calf death as a conservative measure. Consistent with Tezanos-Pinto et al. (2015), a calf that was associated with an individually identifiable reproductive female during its first year was assumed to be the same calf, providing it looked older over consecutive sightings. Additionally, in some cases, it was possible to identify calves even as young as < 1 year due to distinctive markings and/or lesions on their bodies and dorsal fins, and, in three cases, deformities such as scoliosis.

There were some cases where the first sighting of newborns occurred at the beginning of the field season (usually May), but it was clear that they were not recently born. Thus, estimated date of birth (DOB) was calculated as the mid-point between the date of the last sighting of the mother without a newborn calf and the date of her first sighting with a newborn calf (Wells et al. 1987; Urian et al. 1996). We primarily used the mid-point rather than the date of the first sighting (of the mother–calf pair) because the first sighting method of DOB estimation would have suggested that older calves were much younger than their actual age. Even so, the use of imprecise (> 60 days) DOBs was restricted for analyses in which date was an important factor.

To investigate temporal patterns in reproduction, DOB estimates were used to plot births across the four main months for which data were available (June–September), using the ordinal date (i.e., day-of-year) of the last sighting of mother without calf and the date of the first sighting of mother with newborn calf. We then overlaid a plot of number of births per month using the mid-point between dates (to estimate month of birth) to illustrate patterns of parturition for this population.

Calving interval or inter-birth interval (IBI) was estimated as the time elapsed between subsequent births (Mitcheson 2008; Arso Civil 2015). We used three approaches to calculate IBIs. The first two approaches, based on dates, used (a) the estimated date of birth (DOB) for each calf and (b) the first sighting of a female with her initial calf and then the first sighting of the same female with her subsequent calf; (c) the third approach used year of birth. In the first method, IBIs were calculated for individual mothers with two consecutive births where the estimated DOB was available for both calves. The IBI was calculated as the difference between these two dates divided by 365.25 (i.e., IBI in years). Using the second method, each IBI was estimated as the time elapsed between when a female was first sighted with her initial newborn calf to the date of the first sighting of that female with her subsequent newborn calf (Tezanos-Pinto et al. 2015). These methods were restricted to reproductive females who had consecutive calves and where the fate of the calf was known in all cases.

To estimate IBIs using the larger dataset of sighting histories for all reproductive females in this study, we calculated the inter-birth interval based on annual calving (i.e., year of birth rather than date of birth). IBIs were calculated as the number of years between births and charted for all female dolphins with consecutive births (i.e., those who had two or more calves) and known years of calf birth during the study period.

Weaning ages were determined for individuals with known birth and weaning dates, including those who had been observed as independent juveniles post-weaning, and a mean weaning age was calculated. A calf was presumed to have weaned if it was > 1 year old and it and/or its mother had been observed independently in at least three subsequent dolphin group sightings.

Annual calving rate was estimated as the total number of young-of-year (YOY) divided by the total number of reproductive females sighted during that year (Baker et al. 1987; Tezanos-Pinto et al. 2015). We used a weighted average to calculate mean annual calving rate and a binomial variance to calculate the confidence interval for calving rates across the years with 95% limits (Baker et al. 1987; Wells and Scott 1990; Tezanos-Pinto 2009).

The annual crude birth rate was calculated as the total number of documented births divided by the total abundance estimate for the dolphin population in each year (Fruet et al. 2015). We used the catalogue-based abundance estimates from 2012 to 2015 to calculate crude birth rates. The same years were used to calculate fecundity—the ratio between the number of surviving calves and the number of reproductive females in the population (Wells and Scott 1990)—because we knew the number of known births surviving to 1 year with certainty for these years. Overall mean fecundity is a measure of the potential reproductive capacity of the population (Fruet et al. 2015). Additionally, using Arso Civil et al.'s (2017) definition (which takes into account all births and not only surviving calves), where fecundity rate is defined as 'the annual probability of a mature female having a calf', we also estimated fecundity rate as the reciprocal of the expected IBI, using the average IBI from the three methods used to calculate IBIs.

Calf mortality was estimated as the number of YOYs (< 1 year old calves) that were inferred to have died, divided by the total number of YOYs assigned to individual reproductive females (Wells and Scott 1990) for 2012–2015.

Mean female reproductive success of the Shannon Estuary bottlenose dolphin population was quantified by calculating how many calves each female had to the minimum age at weaning and the mean and standard deviation for them (Fruet et al. 2015). It was assumed that a female reproduced successfully if her calf survived from birth to the minimum age at weaning estimated for Shannon Estuary bottlenose dolphins (this study; Mann et al. 2000; Fruet et al. 2015).

Mother–calf association longevity was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any situation- or sex-related patterns associated with these pairings.

Results

Survey effort and photo-identification

Between 2008 and 2016, 654 surveys (1018 sightings) were carried out, during which 213,056 photographs were taken; 83,527 of these were used for the photographic analysis of individually identifiable bottlenose dolphins. Surveys were conducted between March and November but the majority (84%) of surveys took place during June, July and August. In total, 4231 identifications were made of 184 distinct individual dolphins over the nine study years.

Population size, demography and adult/juvenile mortality

The number of sightings of dolphin groups varied in each year, from 34 sightings (34 surveys) in 2011, 95 sightings (61 surveys) in 2012, 119 sightings (86 surveys) in 2013, 180 sightings (111 surveys) in 2014 to 128 sightings (95 surveys) in 2015, with similar proportions of adults, juveniles and calves sighted in each year (Fig. 2). The number of unique individual dolphins sighted per annum varied from 79 in 2011 to 140 in 2014, with 135 individuals sighted in the most recent study year (2015). A discovery curve showed a clear plateau had been reached with only two new individuals added to the catalogue during 2014 and no new individuals added during 2015 (excluding additions of newborn calves to the population).

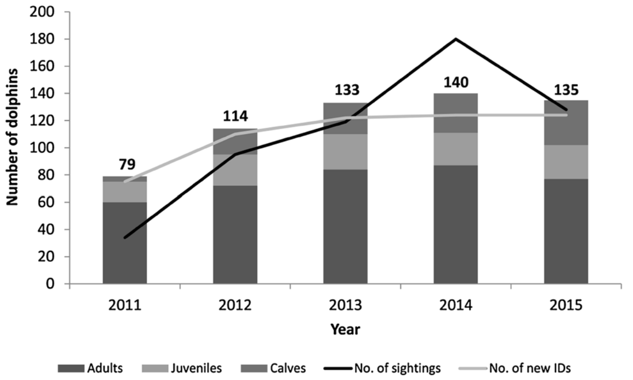

Fig. 2 The number of individual bottlenose dolphins identified each year (bars), the number of sightings (i.e., dolphin group encounters) with photo-id records (black line) and the number of new (non-calf) IDs recorded (i.e., discovery curve; grey line) in the Shannon Estuary between 2011 and 2015, with individual dolphins categorized into age classes (adults, juveniles, calves)

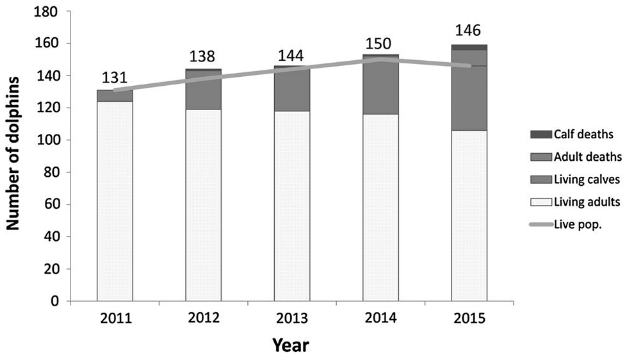

Fig. 3 Estimates of the extant population size of bottlenose dolphins in the Shannon Estuary from 2011 to 2015, incorporating age class ("adults" includes adults and juveniles, "calves" includes all dependent individuals) and possible deaths of well-known individuals. The population size figures are slightly larger than the number of sightings of known individual dolphins per year (Fig. 2) because some individuals were not seen in years when they were still alive

The mean extant population size was estimated to be 142 bottlenose dolphins. Population size estimates in each year (2011–2015), incorporating age class demography and the presumed deaths of well-known individuals varied from 131 in 2011 to 150 in 2014 (Fig. 3). Individual records of estimated adult/juvenile dolphin deaths correspond to counts of five, one, two and ten individuals having not been sighted since 2011, 2012, 2013 and 2014, respectively, despite multiple sightings of these individuals in previous years and 325 subsequent sightings of dolphin groups (during 212 surveys) in 2015 and 2016 (Fig. 3). Therefore, a total of 18 individual adult/juvenile dolphins were not sighted during population surveys between 2012 and 2015. Thus, the mean annual maximum mortality rate was 0.038 ± 0.0286.

Excluding 2011, a year with fewer (< 50%) surveys than in other years, and comparing sighting numbers to extant population estimates, an average 92% ($n = 130$) of the population was recorded each year (2012–2015). In 2015, an estimated 93% ($n = 135$) of the population was recorded during dolphin surveys. Between 2012 and 2015, excluding dependent calves, 121 individuals were identified, of which an average of 106 individuals (88%) were sighted each year. Ninety-eight percent of these individuals ($n = 119$) were sighted in multiple years, with 64% ($n = 77$) seen in all 4 years from 2012 to 2015 (Fig. 4a). The mean number of sightings per individual was 24.4 ± 21.7 ($n = 121$, range 1–101; Fig. 4b).

Of all 167 individuals sighted between 2012 and 2015, 63 were of known sex (49 female, 14 male) and 104 were of unknown sex. Age class, based on first assignation, was divided into 91 adults, 30 juveniles, 13 calves and 33 YOYs. In 2015, the population consisted of 145 unique individuals—55% adults ($n = 80$), 17% juveniles ($n = 25$) and 28% calves/YOYs ($n = 40$). Thus, the adult:calf ratio of the population was 2:1. Of the 105 adults and juveniles, sex was known for 49% ($n = 51$) of individuals—42 females and 9 males.

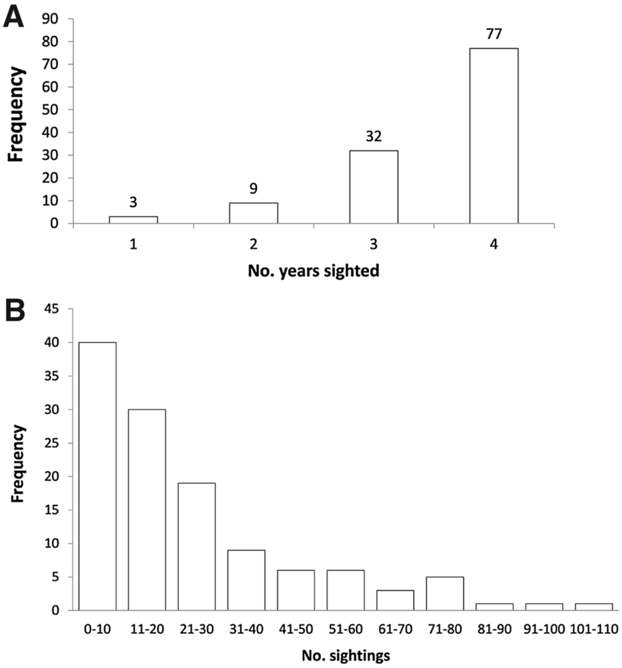

Fig. 4 Histograms of juvenile/adult bottlenose dolphin sightings ($n = 121$) by number of **a** years sighted and **b** sightings (2012–2015)

Female reproductive parameters

Mothers and calves

Between 2008 and 2016, 1254 individual identifications of 37 reproductive females were made. Of these, 57% ($n = 719$) were identifications of reproductive females with a calf (Table 1). The sex of these reproductive females was determined using associations with calves ($n = 24$), a combination of biopsy tissue samples and calves ($n = 12$) and observation of the genital slit during a live-stranding and subsequent calves ($n = 1$; O'Brien et al. 2014). Of these 37 females, all (100%) were sighted in more than 1 year and 13 (35%) were sighted in all nine of the study years, with an average of 34 sightings per female (range 6–108; Table 1).

Of the 37 reproductive females, 35% ($n = 13$) were sighted with only one calf, 43% ($n = 16$) with two successive calves, and 22% ($n = 8$) with three successive calves. The maximum number of documented births per female in the 9-year study was three calves. The mean number of reproductive females in the population per year from 2008 to 2016 was 26 (range 8–35; Table 1). A total of 69 dependent calves were recorded during the study period with year of birth determined for 67 of these calves. There were 831 sightings of these 69 calves with an average of 12 sightings per calf (range 1–88; Table 1).

Births

An average of seven (mean 7.4, SD 2.6, range 3–10) calves was born each year (2008–2016), with one recorded calf death each year between 2011 and 2015 (Fig. 5). There was no correlation between number of surveys and number of births recorded annually (linear regression, $r^2 = 0.02$, $P = 0.73$), thus the variation in the number of births could not be explained by the variation in number of surveys.

Temporal patterns in reproduction

Parturition peaked in July with 45% ($n = 14$) of 31 calves with moderately precise (within 60 days) birthdates estimated to be born in this month (Fig. 6). In the other main study months, 16% ($n = 5$) of these calves were estimated to be born in June, 32% ($n = 10$) in August and 6% ($n = 2$) in September.

Inter-birth intervals

Using date of birth There were 13 reproductive females with two consecutive births and for whom the estimated date of birth (DOB) and fate of the calf was available for both calves ($n = 26$; Table 2). Using estimated DOBs to calculate inter-birth intervals (IBIs) by the time elapsed between suc-

Table 1 Sightings of reproductive females (ID# = individual photo-id catalogue number) and their calves from 2008 to 2016 in the Shannon Estuary, including sightings of females without a calf (marked with a "•") and with their first (1), second (2), or third (3) calves (different numbers indicate a different calf for each female)

Years										Sightings 2008–2016							
ID#	2008	2009	2010	2011	2012	2013	2014	2015	2016	NF	WC1	WC2	WC3	NC1	NC2	NC3	#C
006	•	•	•	•	YC1	C1	C1	YC2		108	72	2		88	2		2
011	•	•	YC1	C1	C1	J1	J1	J1	J1	29	19			19			1
019	•		YC1			•	•	•	•	26	1			1			1
027	YC1		•		•	•	•	•		10	1			1			1
042	*YC1*		C1	J1	J1	YC2	C1	C1	J1	18	4	12		6	12		2
044	•	•	•	•	•	•	YC1	C1	YC2	64	36	1		37	1		2
045	•	•	•	•	YC1	C1	C1	YC2	C2	44	18	4		19	4		2
052	•	YC1		•	J1	J1	•	YC2	•	30	3	3		3	3		2
070	•	YC1	C1		YC2	•	YC3		•	15	5	3	1	5	3	1	3
071	YC1	C1	C1	J1	J1	J1	YC2	C2	C2	79	28	23		32	27		2
085	•	•	•	•	•	YC1	•	•	YC2	43	4	1		4	1		2
092	YC1	C1								6	2			2			1
096	•	YC1	C1	C1	J1	YC2	C2	C2	J2	40	4	16		4	20		2
100		•	•	•	•	•	YC1	C1		20	2			2			1
114	*YC1*	C1	C1	•	•	•	•			31	5			17			1
118	YC1	C1	C1	J1	J1	•	•	YC2	C2	77	10	19		20	20		2
121		•	•		•		•	YC1		6	2			2			1
151	•	•	•	•		YC1	C1	C1	J1	12	7			8			1
171	•	YC1	C1	•	YC2	C2	C2	J2	•	56	8	41		8	42		2
204		YC1	C1	C1	YC2		C2	YC3	C3	10	3	2	4	3	2	4	3
205	YC1	C1	C1	•	YC2	C2	C2	YC3	C3	24	3	9	4	3	10	4	3
209		*YC1*	C1	C1	J1	YC2	C2	C2	J2	38	3	23		12	28		2
210		YC1				YC2	C2	C2	J2	11	1	7		1	7		2
216	•	•	•	YC1	•	YC2	C2	YC3	C3	82	2	37	8	2	43	8	3
218	YC1	C1	C1	J1	•	YC2	C2	C2	YC3	33	4	20	2	4	22	2	3
220			*YC1*		C1	J1	J1	•		6	5			9			1
223	•	YC1	C1			•	YC2	•	YC3	31	2	2	14	2	2	14	3
225							J1	YC2	C2	9	7	2		7	2		2
228	•		•		YC1	•	C1	J1	J1	12	8			9			1
231	•	YC1	C1	YC2		•	YC3		•	17	9	1	2	9	1	2	3
232		•	YC1		C1	J1	YC2	C2	C2	26	4	10		7	10		2
233		•	•	•		•	YC1	C1	C1	21	6			6			1
242	•	•	•	•	YC1	C1	C1	J1	YC2	98	65	7		70	7		2
246					•	•	YC1	C1		22	3			3			1
250	•	•		YC1	C1	C1	J1			43	33			35			1
280	C1	C1	J1	J1	YC2	C2	C2	J2	J2	27	6	18		19	22		2
285		YC1	C1		YC2	C2	C2	YC3	C3	30	2	15	9	2	15	9	3
#F	8	19	23	25	29	31	35	34	29								
#YOY	8	10	4	3	10	8	9	10	5								69

Calf ages were categorized as young-of-year (< 1 year old; YC), calves (1–3 year old; C) and juveniles (> 3 year old; J). The total number of sightings of each female (NF), total number of sightings of each female with each of her calves (WC1, WC2, WC3; i.e., WC1 = number of sightings with first calf), and total number of sightings of each calf (NC1 = first calf, NC2 = second calf, NC3 = third calf) are given. The total number of calves born to each female (#C), the number of reproductive females in each year (#F) and the number of calves born in each year (#YOY) are also shown. Underlined female IDs are those that were also genetically confirmed as female. Year of birth could not be determined for the first calves of ID#s 225 and 280 and they are, therefore, not included in the total of number of calves born per year (#YOY). ID# 242 was first identified as a female through observations of the genital slit during her live-stranding (O'Brien et al. 2014). Blank cells indicate no sighting of the female in that year. Italicized cells indicate years with no sighting where year of birth was inferred for the calf (after Arso Civil 2015; Tezanos-Pinto et al. 2015)

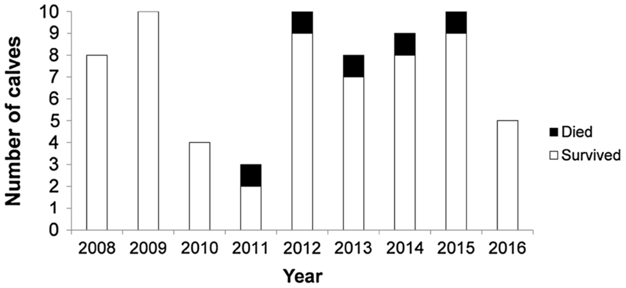

Fig. 5 Number of bottlenose dolphin calves born in the Shannon Estuary from 2008 to 2016, with those that subsequently died in black (no mortality data for 2016)

cessive births, the mean IBI was 2.9 ± 0.7 years (95% CL 2.6–3.3, SD 0.67, median 3.02, range 1.4–4.0).

Using sightings of calves When the difference in time elapsed between the first sighting of a female with her initial calf and the first sighting of the same female with her subsequent calf was used, the mean inter-birth interval was 2.7 ± 0.6 years (95% CL 2.4–3.1, SD 0.61, median 2.98, range 1.6–3.9; Table 2).

Excluding the three females whose calves died (underlined calf codes; Table 2), the mean IBI for the other ten females whose calves survived to weaning age was 3.2 ± 0.4 years (95% CL 2.9–3.5, SD 0.42, median 3.05, range 2.6–4.0). Of these ten females, eight IBIs were of approximately 3 years and two of 4 years. For the three females whose calves died, the mean IBI was 2.1 ± 0.7 years (95% CL 1.4–2.9, SD 0.67, median 2.02, range 1.4–3.0).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, female ID#s 044 and 216 had the lowest IBIs at 2.22 and 2.26 years, respectively, while female ID#s 242 and 006 had the highest IBIs at 3.93 and 3.19 years, respectively (Table 2).

Using year of birth Of all the reproductive females and their full sighting histories across the 9-year study period, the inter-birth interval (based on year of birth) ranged from 2 to 7 years. Using this larger dataset of sighting histories for all reproductive females in the study (22 females with more than one calf of known year of birth; 50 calves), the mean inter-birth interval (based on annual consecutive births) was 3.5 ± 1.3 years (median 3, mode 3; Fig. 7). In two cases where the calf was lost (ID#s 070 and 223, both YC2) the mothers went on to have subsequent calves around 2 years later. Results were similar when the four cases where a birth was possibly missed in the timeline were excluded; the mean inter-birth interval was 3.2 ± 1.0 (median 3, mode 3).

Calving rate, birth rate and fecundity Annual calving rates for the population between 2008 and 2016 ranged from 0.13 to 1.00 (mean 0.29) young-of-year/reproductive female/year (95% binomial CL 0.12–0.46). Annual crude birth rates for the years 2012–2016 ranged from 0.06 to 0.09 with an average annual crude birth rate of 0.07 ± 0.01 (or mean crude birth rate of 7.2%). The estimated fecundity of the population, accounting for calf mortality, was 0.26 ± 0.03, while the estimated fecundity rate, not accounting for calf mortality, was 0.33.

Fig. 6 The number of births per month estimated using calves with within 60 days-precision birthdate estimates ($n = 31$), with a polynomial regression line fitted. Thick grey lines indicate the window of time between ordinal dates (i.e., days-of-year) when each of the 31 calves could have been born (i.e., dates from the last sighting of the mother without her calf to the first sighting of the mother with her newborn calf)

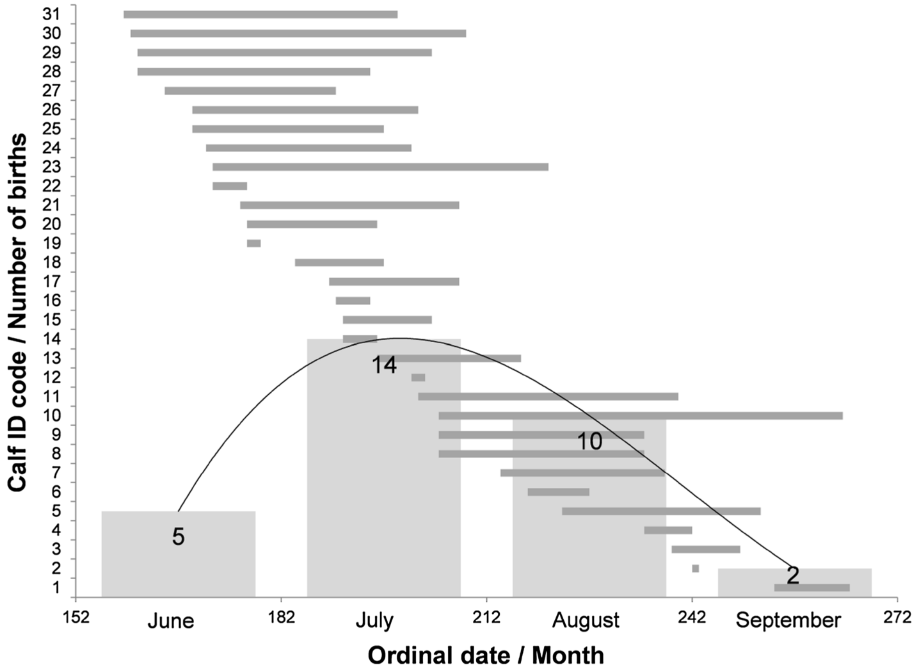

Table 2 Inter-birth intervals (in years) for reproductive females with consecutive calves of known fate, using two approaches: (1) calculated from an estimated date of birth (DOB) derived from the midpoint of the dates between when the mother was last seen before the birth of her calf and the first sighting of the mother with her newborn calf; and (2) calculated from the time-lapse between the first sighting of the mother with her initial calf and the first sighting of the mother with her subsequent calf

Female ID#	Calf code	DOB estimate	DOB accuracy (days)	Mother last seen before birth of calf	First sighting of mother with calf	IBI (DOB)	IBI (sightings)
006	YC2	01/09/2015	10	27/08/2015	06/09/2015		
	YC1	10/01/2012	337	26/07/2011	27/06/2012	3.64	3.19
044	YC2	29/08/2016	1	29/08/2016	30/08/2016		
	YC1	09/01/2014	307	09/08/2013	12/06/2014	2.64	2.22
045	YC2	11/07/2015	5	09/07/2015	14/07/2015		
	YC1	04/07/2012	30	19/06/2012	19/07/2012	3.02	2.98
070	YC3	01/07/2014	43	10/06/2014	23/07/2014		
	YC2	22/06/2012	5	20/06/2012	25/06/2012	2.02	2.08
085	YC2	02/07/2016	49	08/06/2016	27/07/2016		
	YC1	09/07/2013	13	03/07/2013	16/07/2013	2.98	3.03
204	YC3	27/06/2015	34	10/06/2015	14/07/2015		
	YC2	20/06/2012	377	09/06/2011	20/06/2012	3.02	3.06
205	YC3	12/07/2015	5	10/07/2015	15/07/2015		
	YC2	12/01/2012	343	25/07/2011	02/07/2012	3.50	3.03
216	YC3	25/07/2015	21	15/07/2015	05/08/2015		
	YC2	19/12/2012	266	08/08/2012	01/05/2013	2.60	2.26
218	YC3	27/06/2016	40	07/06/2016	17/07/2016		
	YC2	02/01/2013	313	30/07/2012	08/06/2013	3.48	3.11
223	YC3	13/12/2015	232	19/08/2015	07/04/2016		
	YC2	08/08/2014	30	24/07/2014	23/08/2014	1.35	1.62
232	YC2	16/07/2014	13	10/07/2014	23/07/2014		
	YC1	20/06/2011	746	12/06/2010	27/06/2012	3.07	2.07
242	YC2	09/08/2016	9	05/08/2016	14/08/2016		
	YC1	24/08/2012	29	10/08/2012	08/09/2012	3.96	3.93
285	YC3	26/06/2015	25	14/06/2015	09/07/2015		
	YC2	20/07/2012	2	19/07/2012	21/07/2012	2.93	2.97
					Median	3.02	2.98
					Average	2.94	2.74
					Range	1.35–3.96	1.62–3.93
					95% CL	2.58–3.30	2.41–3.07
					SD	0.67	0.61

Underlined calf codes are those known to have died

Calf mortality and reproductive success

Between 2012 and 2015, an average 11% of recorded newborn calves ($n = 4$) were lost before age 1. Reproductive success rates for female bottlenose dolphins in the Shannon Estuary with > 1 documented births, where the calf survived to the minimum known weaning age for Shannon dolphins (2.0 year) and/or the fate of the calf could be determined, varied from 0.5 to 1.0 ($n = 17$). Three females had calves that died before they weaned, two of whom raised another calf successfully, and the third of whom raised two more calves successfully within the study period. The mean individual reproductive success was 0.9 (SD 0.17).

Non-reproductive females

There were 12 adult dolphins sexed as female that were never observed with calves during the 9-year study period, despite some individuals having a large number of sightings (e.g., ID# 093 with 81 sightings and seen during each of all 9 years; Table 3). All 12 individuals were sexed by genetic determination from biopsy tissue samples.

Weaning and mother–calf associations

Weaning ages, calculated for 11 individuals with known birth and weaning dates, ranged from 2.0 to 4.1 year (mean

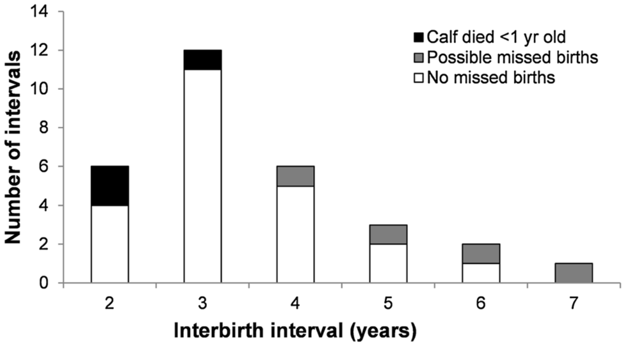

Fig. 7 Inter-birth intervals for females whose calves survived to weaning (white bars) and whose calves died < 1 year old (black bars), and for those where a birth may have been missed in the interim (grey bars) (n = 30). Mean inter-birth interval was 3.53 (SD 1.28, median 3) (after Mann et al. 2000; Fruet et al. 2015)

2.9 year). Of 22 calves known to have reached weaning age, eight (30%) were not sighted after their weaning date and 14 were sighted at least once following weaning. Four of these individuals were never seen with their mothers, but the other 10 had between one and 14 shared sightings with their mothers post-weaning. Interestingly, two cases of shared sightings involved the weaned calf's presence in a group during the first sighting of its mother with her subsequent newborn calf.

The calf who had the most shared sightings with her mother (n = 14) was a female, and one of the individuals present during the first sighting of a newborn, surfacing < 1 m next to it in a group of seven dolphins. The only other weaned calf of known sex was a male who shared two sightings with his mother, but was seen in groups with other juveniles (and without his mother) during seven other encounters.

Discussion

This study has presented female reproductive parameters for bottlenose dolphins in the Shannon Estuary, Ireland, for the first time. Additionally, new information on the demographics of this population has been revealed through the analysis of a detailed long-term dataset collected through observations of live animals.

Population size and composition

Of the 145 extant individual dolphins recorded in 2015, over half were adults, with about one quarter dependent calves, and the others independent juveniles. Notably, the adult:calf ratio of the population was 2:1. Wells (2014) reports the Sarasota Bay dolphin community as comprising 58% adult and 42% subadult individuals (which presumably includes juveniles, calves and YOYs). This age class ratio is comparable to the 55% adult, 17% juvenile and 28% calf contingents found in the Shannon Estuary population. Manlik et al. (2016) report a similar proportion of 55% adults for dolphins in Shark Bay, but the proportions of younger age classes are reversed, with 30% juveniles and 15% dependent calves. Similarly, Manlik et al. (2016) also report proportions of 58% adults, 25% juveniles and 17% calves for the Bunbury bottlenose dolphin population.

In contrast, Bearzi et al. (1997) found the percentages of adults, juveniles and calves (140 individuals) in the Adriatic Sea to be 85.2, 8.2 and 6.6%, respectively, Chabanne et al. (2012) found that the Swan Canning Estuary population (55 individuals) contained 78.2% adults/sub-adults and 21.8% calves, while Augusto et al. (2011) reported the Sado Estuary bottlenose dolphin population (24 individuals) to be 79.2% adults, 12.5% juveniles and 8.3% calves. As the Sado Estuary population appears to be critically declining with

Table 3 Sighting frequency of non-reproductive female bottlenose dolphins in the Shannon Estuary from 2008 to 2016, including total number of sightings (n) and total number of years sighted (#years)

ID#	2008	2009	2010	2011	2012	2013	2014	2015	2016	n	#Years
051	1	2								3	2
066				3	3	10	9	3	1	28	6
080		1		6	2	2	12	7	1	30	7
081	1	2			2	5	2	1	1	13	7
093	1	4	1	11	7	9	31	17	1	81	9
094	1									1	1
126					7	6	4	6	1	23	5
168		3	1	1	1	5	5	1	1	17	8
200	3	6	1	9	3	12	20	9	1	63	9
227					2	1	4			7	3
247		2		4	7	18		11	1	42	6
260		1				5	16	2	1	25	5

The sex of all 12 individuals was determined through genetic analysis of tissue samples from biopsies a community composed primarily of adults and few young animals, the contrast of adult and calf proportions between that and the Shannon Estuary population points towards the apparent "good health" of the Shannon Estuary population and a comparatively higher percentage of calves.

The sex of most adult/juvenile individuals in the Shannon Estuary bottlenose dolphin population is still unknown (51%) with 49% animals of known sex (comprising 40% females and 9% males). Since consistent close association with a calf is a reliable way to determine the sex (female) of individual adult bottlenose dolphins, it is likely that most if not all females in the current population who were reproductively mature during our study were identified as such. However, it would be very valuable to gain more information on adult males in the population, as well as the sexes of calves. In particular, information on the age of individuals reaching reproductive maturity would be useful for population viability analyses and management scenarios.

Adult/juvenile mortality rate

The mean annual maximum adult/juvenile mortality rate was 0.038. Interestingly, this is the same value calculated by Wells and Scott (1990) for the Sarasota Bay bottlenose dolphin community. This is a maximum value because it includes all individuals who have ceased to be sighted; unfortunately, it was not possible to confirm any certain deaths because no known dead individuals were ever recovered from strandings, nor was it possible to identify any individuals as emigrants outside the population's known home range. In Sarasota Bay, an adult male dolphin returned to the community after an 8-year absence suggesting that at least a small number of individuals may leave their core home range for extended periods of time (Wells and Scott 1990). Since it is possible that some individuals temporarily emigrated or were not recorded in the Shannon Estuary study area in the most recent 2 years, and are still alive, the mortality rate for the Shannon Estuary population is likely lower than the maximum value given.

Female reproductive parameters

Births

In the Shannon Estuary, seven calves were born on average each year, but this number fluctuated from a minimum of three to a maximum of ten during the 9 years of our study. Interestingly, the 3 years (2009, 2012 and 2015) where the number of calves born was ten were each 3 years apart. Maybe this is a potential cyclical characteristic of reproduction in this population, or perhaps a cohort of females reproducing together at regular intervals. In an estuarine resident population of 74 Indo-Pacific bottlenose dolphins in the Port River Estuary, Australia, Steiner and Bossley (2008) calculated that an average of 2.6 calves were born each year; much lower than the mean of 7.4 births per year in the present study. However, in Cardigan Bay, an average of 10 calves were born each year to a population of 103 individuals (Veneruso and Evans 2012). The number of calves born in a population can be related to many socio-environmental parameters including population size and habitat ecology, and different study sites have reported varying reproductive parameters (see Table 4 for comparative summary of studies).

The reproductive female dolphins in this 9-year study had between one and three calves each. In some cases, for those that had only one calf during the study period, it was not that they had long periods without a dependent calf, but that their dependent calf was with them for a longer duration. For example, ID# 011 gave birth to a calf in 2010 and was still with that calf in 2016. However, the majority of reproductive females (65%) had more than one calf throughout the study period.

Temporal patterns in reproduction

The dataset from the Shannon Estuary was seasonally biased because most data were collected during summer months, so it was not possible to get an annual estimate of seasonal peaks in birth. However, of the four main months for which data were available (June–September), births peaked in July. Similarly, 76% of all bottlenose dolphin births in Cardigan Bay, Wales occurred between July and September (Norrman et al. 2015). With further research, it is possible that a predictable summer calving season might be uncovered such as in other populations (e.g., Steiner and Bossley 2008; Smith et al. 2016). It is well-documented that in many bottlenose dolphin populations, births tend to peak in spring and summer months, possibly due to an increase in water temperature and food supply (Steiner and Bossley 2008; Veneruso and Evans 2012; McFee et al. 2014; Fruet et al. 2015; Tezanos-Pinto et al. 2015). Additional winter data collection and information on sea surface temperature, dolphin prey abundance, distribution and variability would be valuable for exploring fluctuations in the reproductive biology of the Shannon Estuary dolphin population.

Inter-birth intervals

We used three methods to calculate mean inter-birth interval (IBI)—difference between estimated dates of birth (DOBs), difference between sighting dates of mothers with initial and subsequent newborns, and difference between annual births based on year of birth—and found that the mean IBI for the Shannon Estuary bottlenose dolphin population was 2.9, 2.7 and 3.5 years for each

Table 4 Summary of reproductive parameters for bottlenose dolphins

Study area	Species	No. dolphins	Annual births	(SD)	Study length	% of pop.			Crude birth rate (SD)	Mean IBI (years)	IBI range	Fecundity	1st year mortality	References
						Adults	Juveniles	Calves						
Shannon Estuary, Ireland	*T. truncatus*	142	7.4	(2.6)	9	55	17	28	0.072 (0.01)	2.7–3.5	2–7	0.26 (0.03)	0.11	This study
Cardigan Bay, Wales	*T. truncatus*	103	10	(4.1)	13				0.075	3.3	2–7		0.15	Norrman et al. (2015)
Moray Firth, Scotland	*T. truncatus*	192	6.2	(5.2)^{a}	24^{a}				0.060^{b}	4.5^{a}	2–9^{a}	0.22^{a}	0.38^{b}	Arso Civil et al. (2017)^{a} and Sanders-Reed et al. (1999)^{b}
North Sea, Scotland	*T. truncatus*	108^{c}	9	(4.0)^{d}	20^{d}				0.12 (0.05)^{d}	3.8^{d}	2–9^{d}	0.16 (0.04)^{d}	0.45^{d}	Culloch (2004)^{c} and Robinson et al. (2017)^{d}
Sado Estuary, Portugal	*T. truncatus*	24			4^{e}; 16^{f}	79.2^{e}	12.5^{e}	8.3^{e}	0.054^{f}		3–11^{f}			Augusto et al. (2011)^{e} and Gaspar (2003)^{f}
Adriatic Sea, Croatia	*T. truncatus*	106	4.2	(1.2)^{h}	5^{g}; 9^{h}	85.2^{g}	8.2^{g}	6.6^{g}	0.049 (0.034)^{g}	3^{g}		0.17 (0.05)^{h}	0.18^{h}	Bearzi et al. (1997)^{g} and Fortuna (2007)^{h}
Sarasota Bay, USA	*T. truncatus*	163	7			58^{i}			0.055 (0.009)^{j}	5.4^{k}	2–11^{k}	0.14 (0.24)^{i}	0.19^{j}	Wells (2014)^{i}, Wells and Scott (1990)^{j} and Wells and Scott (1999)^{k}
Patos Lagoon Estuary, Brazil	*T. truncatus*	83	7.4	(1.6)					0.090 (0.01)	3		0.11 (0.02)	0.16	Fruet et al. (2015)
Bay of Islands, New Zealand	*T. truncatus*	408	4.1	(2.7)	13				0.0625	4.3		0.25	0.42	Tezanos-Pinto et al. (2015)
Doubtful Sound, New Zealand	*T. truncatus*	66	4.1		17				0.040 (0.04)	5.3	2–5		0.33	Henderson et al. (2014)

Table 4 (continued)

Study area	Species	No. dolphins	Annual births (SD)	Study length	% of pop.			Crude birth rate (SD)	Mean IBI (years)	IBI range	Fecundity	1st year mortality	References
					Adults	Juveniles	Calves						
Port River Estuary, Australia	*T. aduncus*	74	2.6	17				0.064	3.8	1.1–6		0.30	Steiner and Bossley (2008)
Shark Bay, Australia	*T. aduncus*	83	10	11					4.6	3–6.2		0.29	Mann et al. (2000)
Mikura Island, Japan	*T. aduncus*	169	7					0.071 (0.024)	3.4		0.136 (0.04)	0.13	Kogi et al. (2004)

Superscript letters refer to references cited in the last column

method, respectively. Average IBI (in years) has been reported for many other bottlenose dolphin populations including estimates from 5.4 in Sarasota Bay, USA (Wells and Scott 1999) to 3.0 in the Adriatic Sea (Bearzi et al. 1997) (Table 4). Thus, our estimate of 3.5 years (based on year of birth) falls within the lower values from these examples, including, interestingly, the values obtained from studies of resident bottlenose dolphin populations in Scotland (4.5 years, Arso Civil et al. 2017; 3.8 years, Robinson et al. 2017) and Wales (3.3 years, Norrman et al. 2015)—the two closest study sites to the Shannon Estuary. However, the IBIs estimated from more detailed dates in our study of 2.9 and 2.7 years suggest that the Shannon Estuary bottlenose dolphin population has some of the lowest inter-birth intervals documented for populations worldwide, most similar to values of 3.0 years reported for dolphins in the Adriatic Sea (Bearzi et al. 1997) and the Patos Lagoon Estuary, Brazil (Fruet et al. 2015). Of course, every population manifests individual variability and ranges of IBIs for individual reproductive females, but our results do suggest relatively frequent births for the reproductive females of this population.

Of the 13 reproductive females where estimated DOBs could be used to calculate IBIs between each of their two consecutive calves, results were noticeably different when comparing those whose initial calf died (IBI 2.1 ± 0.7 years) to those whose initial calf survived to weaning (IBI 3.2 ± 0.4 years). Although the sample size for calves that died was small ($n = 3$), this suggests that there could be a marked difference between IBIs in this population for females who lose a calf in its first year (and thus mate again shortly afterwards).

Two of the females in our study who lost their calves had subsequent calves just 2 years later and the third female who lost a calf had her subsequent calf 3 years later. This has also been reported in other populations. For example, Kogi et al. (2004) reported that the shortest IBIs of 1 year and 2 years in Indo-Pacific bottlenose dolphins at Mikura Island, Japan, involved females who had lost their calves and then became pregnant the same or following year. Similarly, Bearzi et al. (1997) reported two females with 2 and 3 year IBIs when calves disappeared before weaning. In Scotland, a female dolphin conceived again in the breeding season immediately following the death of each of her two calves (Mitcheson 2008). Steiner and Bossley (2008) report an example of one female with a 1.9 year IBI between surviving calves (i.e., the short IBI was not the result of the death of the previous calf). Although there are some calves in the Shannon Estuary population who weaned around age 2, the only example from our dataset of an IBI of less than 2 years was from a mother (ID# 223) whose initial calf died. Similarly, female dolphins in the Moray Firth, Scotland, are capable of reproducing on a 2-year cycle after the death of a newborn calf but have never been observed producing a subsequent calf in less than 2 years (Grellier 2000; Robinson et al. 2017).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, females ID# 044 and ID# 216 had the lowest IBIs at 2.22 and 2.26 years, respectively. However, because, in both cases, the mothers had not been sighted since the previous autumn, these IBIs could be closer to 3 years. For example, if ID# 044's calf had been born the day after her last sighting in 2013, the IBI would have been 3.06 years.

The quantification of IBIs for the 13 reproductive females with two consecutive births and known calf fate may have shown bias in the results of IBIs of only 3 and 4 years' length. This might be a result of the length of the study period as there are no examples of female dolphins with IBIs of greater than 4 years in this subset of data. From the analysis based on year of birth, we know examples exist of longer (> 6 year) IBIs. For example, individual ID# 011 has had the same dependent calf for the past 6 years. If the calf had weaned by the end of our study period, her data would have increased the results of the IBI analysis based on date of birth and weaning date considerably. The relatively short 9-year length of our study period when compared to the life span for bottlenose dolphins may have biased our results towards more frequently reproducing females and thus seemingly shorter IBIs and younger weaning ages (Arso Civil et al. 2017).

Crude birth rate, calving rate and fecundity

The mean annual crude birth rate for Shannon dolphins of 7.2% was consistent with the values calculated for other populations, which range from 4.0% in Doubtful Sound, New Zealand (Henderson et al. 2014) to 12.0% in the North Sea, Scotland (Robinson et al. 2017) (Table 4). Some of these studies noted that their crude birth rates were probably underestimated as some calves could have been born and died before being recorded (e.g., Steiner and Bossley 2008)—this might explain why the birth rates calculated for Shannon Estuary dolphins are among the highest; the population was well-studied with multiple sightings of the reproductive females. However, it is always possible to miss births, particularly for young primiparous females where calves could have been born and lost before observations were made of the mother–calf pair (Kogi et al. 2004).

The mean annual calving rate of 0.29 for bottlenose dolphins in the Shannon Estuary was comparable to that for the same species in the Bay of Islands, New Zealand where average annual calving rate was 0.25 young-of-year/reproductive female/year (95% binomial CL 0.16–0.35; Tezanos-Pinto 2009; Tezanos-Pinto et al. 2013, 2015). The fecundity of the Shannon Estuary population, calculated differently to calving rate in that it takes into account only the births surviving to > 1 year, was estimated to be 0.26, which appears relatively high when compared to other populations. In the Patos Lagoon Estuary, Brazil and Sarasota Bay, Florida, fecundity rates were reported as 0.11 and 0.14, respectively (Wells and Scott 1990; Fruet et al. 2015). This suggests that the reproductive capacity of the Shannon Estuary dolphin population is potentially relatively good. Arso Civil et al. (2017) estimated a similar fecundity rate of 0.22 for bottlenose dolphins in the Moray Firth, Scotland. Using their method, where fecundity rate is 'the annual probability of a reproductive female having a calf', irrespective of its survival, the estimated fecundity rate for the Shannon Estuary population was even higher at 0.33. Estimating fecundity rate using the ratio of the number of calves surviving to the first year and the number of reproductive females in that year yields a lower estimate than the fecundity rate when not accounting for calf survival (Wells and Scott 1990; Arso Civil 2015).

Calf mortality

The 11% mortality rate calculated for YOYs in the Shannon dolphin population seems to be quite low in comparison with other study populations, where first-year calf mortality rates of between 13 and 45% have been reported (Robinson et al. 2017; Kogi et al. 2004) (Table 4). However, our sample size of four calf deaths is very small, and mortality rates are most likely higher in cases where the sighting frequency of mother–calf pairs is low. Our study contained no known occurrences of calf deaths in the second year of life.

The causes of calf mortality in the Shannon Estuary remain largely unknown. There are no known predators of bottlenose dolphins in Ireland; dolphins are not subjected to predation by sharks as they are in other populations such as in Shark Bay, Australia (Heithaus 2001). Therefore, predation does not seem to account for any calf deaths in the Shannon Estuary. Naturally occurring biological causes might be responsible for calf mortality, such as genetic birth defects, which might make calves more susceptible to disease or illness. Interestingly, two calves born to one of the reproductive females (ID# 280) in the Shannon population were both observed to have visible morphological deformities, which may have been the result of a genetic mutation; however, neither has died to date. Several other calves in the Shannon Estuary population such as ID# 118's calf (YC2, born in 2015) have been observed with deformities, which could also be the result of scoliosis (Berrow and O'Brien 2006) or physical trauma (Robinson 2014).

Additionally, there is no evidence in the Shannon Estuary of the direct anthropogenic threats that occur at other study sites, such as entanglement and boat strikes (e.g., Port River Estuary, Australia; Steiner and Bossley 2008).

However, it is possible that there are less obvious human impacts affecting the survival of the population; for example, dolphins in the Shannon Estuary have been shown to have high levels of PCB contamination which could affect their ability to reproduce adequately (although their levels are relatively low compared to other European populations; Jepson et al. 2016). Thus, this type of pollution could be causing observed or unobserved calf deaths, particularly for firstborn calves; bottlenose dolphin mothers off-load contaminant burdens into their firstborn calves (Schwacke et al. 2002). One female in the current study (ID# 027; Table 1) was found to have contaminant loads that were high enough that they could potentially have affected her reproductive success (Jepson et al. 2016); she was observed with only one calf in 2008 despite being sighted during five of the following years of this study. Other potential indirect anthropogenic threats to calf survival in the Shannon Estuary include acoustic disturbance from shipping. The Shannon Estuary is Ireland's second-largest waterway and a large shipping route. As acoustic communication between mothers and calves is essential to their associations, shipping noise could have a negative impact on a calf's ability to keep in contact with its mother (O'Brien et al. 2016). Overall, it is likely that a combination of factors influences calf mortality in the Shannon Estuary.

Reproductive success and non-reproductive females

Generally, reproductive success appeared to be quite high for reproductive female dolphins in the Shannon Estuary, with only three of the 17 females examined having success rates of less than 100%—two of these females had one calf die and one survive, while the third had one calf die and two survive (to the minimum weaning age). Studies have shown that factors such as birth timing, maternal size and age, and birth order may be causes for variability in female dolphin reproductive success (Wells et al. 2014; Brough et al. 2016). Fruet et al. (2015) noted an age-related decrease in reproductive fitness in bottlenose dolphins in Brazil, with older females reproducing at lower rates. Differences in maternal experience and behaviour appear to be crucially important to calf survival in some populations (Henderson et al. 2014; Fruet et al. 2015). Further behavioural research on the Shannon Estuary dolphin population could highlight individual differences in the maternal care of young.

Tezanos-Pinto et al. (2015) report what they inferred to be a "high proportion", 14%, of non-reproductive females in their study population in the Bay of Islands, New Zealand. However, an even higher proportion of 25% of the known females in the Shannon Estuary population were found to be non-reproductive in this study. The large proportion of non-reproductive females in the population is curious. Clearly, the survival of calves of known reproductive females is high, but it is possible that additional calves of "non-reproductive" females have gone undocumented; it is impossible to know how many newborn (especially firstborn) calf deaths are not recorded, and how many stillbirths or miscarriages occur. Such occurrences might explain the apparently high proportion of non-reproductive females in the population.

Weaning and mother–calf associations

Although the sample size was small ($n = 11$), the range of weaning ages from 2.0 to 4.1 years in the Shannon population suggested variability in the age of independence for young bottlenose dolphins.

The longevity of mother–calf associations was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any patterns (perhaps related to sex class) associated with these pairings. Wells (2014) observed that older calves, especially females, sometimes associated closely with their mothers and new siblings for months or more, and Steiner and Bossley (2008) reported a previous calf seen with its mother and her subsequent calf on a number of occasions. In the current study, ten calves were observed in close association with their mothers post-weaning. Of these ten mother–calf pairs, eight are considered members of the "inner estuary community", shown to have stronger associations and longer lasting bonds than other individuals in the population (Baker et al. 2017b, in press).

The female calf that had the most shared sightings with her mother was sighted in a group with her mother and her subsequently newborn sibling. Associations such as this after weaning could be important for maintaining social bonds and learning about motherhood, and perhaps also serve to provide relief to the mother in the sharing of calf rearing responsibilities (Wells 2014).

Conclusion

The purpose of this study was to derive baseline data on the population demographics and female reproductive parameters of bottlenose dolphins in the Shannon Estuary, Ireland. Using a detailed dataset to count the number of individuals in the population led to a population estimate of 142 which is just above the higher limits of previous estimates calculated through mark-recapture analysis. Results revealed that although the Shannon Estuary bottlenose dolphin population's life history parameters include some of the shortest inter-birth intervals and youngest weaning ages reported for bottlenose dolphins worldwide, they are within the ranges reported in other studies. Interestingly, they are similar to those reported for nearby populations in the Moray Firth, Scotland and Cardigan Bay, Wales.

This study increases our knowledge of bottlenose dolphin reproductive rates and population demographics. The results will allow for comparative studies of the Shannon Estuary dolphin population, exploring similarities and differences with other populations of well-studied resident dolphins in temperate and tropical waters. Given the variability between populations, it is imperative to report regionally specific demographics (Arso Civil et al. 2017). This study complements other longitudinal research studies in offering essential guidance for the development of sustainable practices in population conservation (Mann and Karniski 2017). The population and life history parameters presented here make an important contribution to the global conservation of the species. They also serve to show how variable the demographics of different populations can be, reinforcing the importance of extending research to a wide geographical range.

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Compliance with ethical standards

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Appendix B

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An Ethogram for Bottlenose Dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

Ethograms, or categorized lists of behavioral descriptors, are fundamental research tools in the study of animal behavior and are essential to the overall understanding of the behavioral ecology of a species. With specific definitions of activity state categories and behavioral event types, the behavior of a species can be described, quantified, and compared across populations. We present the first ethogram for bottlenose dolphins (*Tursiops truncatus*) in Ireland based on sighting records collected during 256 surveys (2014-2016) in the Shannon Estuary. The ethogram consists of 11 activity states and 45 behavioral events. The most frequently recorded activity state was *Travel* (52%), while the most frequently recorded behavioral events were *Slow travel* (40% of sightings), *Surface rush* (28% of sightings), and *Leap* (28% of sightings). The ten least frequently recorded behaviors were seen in only 10% of total sightings with < 8 records each. A video test for multiple researchers to assess inter-observer reliability in behavioral data recording demonstrated the validity of this study's behavioral data and the efficacy of the ethogram in its applicability to other studies. Validity (percentage agreement = 88.1 ± 7.0) and reliability (Fleiss' Kappa = 0.81) scores were high across 24 test participants (12 trained and 12 untrained), but results indicated that those with prior training scored significantly higher. Furthermore, we investigate the presence/absence of behaviors recorded in other studies of bottlenose dolphins. This ethogram and behavioral discussion serve to describe and compare quantitative data on the behavior of bottlenose dolphins in Ireland for the first time and provide a strong basis for further research.

Key Words: ethogram, repertoire, bottlenose dolphin, *Tursiops truncatus*, Shannon Estuary, Special Area of Conservation

Introduction

Understanding the repertoire of behaviors exhibited by a species, particularly when a population is composed of individually recognizable animals, is crucial to providing baseline scientific data for many avenues of study. To allow for accurate comparison between study sites, it is important to standardize terms and categories used in behavioral research (Masatomi, 2004). Precise descriptions, definitions, and quantification of behaviors provide a valuable standard that can be used for the systematic and quantitative study of bottlenose dolphin (*Tursiops truncatus*) behavior, especially in understudied wild populations (Martin & Bateson, 1986; Lichtenberg & Hallager, 2007). Baseline data on the behavioral repertoire of a species must be collected before more complex analytical procedures can be introduced (Lehner, 1996). A systematic presentation of categorical definitions and of the specific behaviors within each category, known as an ethogram, is a fundamental research tool in the study of behavior (Mann et al., 2000). Ethograms aim to describe the full behavioral repertoire of a species (in the habitat under study) and can be the foundation(s) of research contributing to knowledge and conservation of the species as a whole (Hill et al., 2015). They are essential for collecting and analyzing sound scientific data and, thus, for understanding the behavioral repertoire of a species. In particular, when multiple observers are used to collect behavioral data, the preparation and use of an ethogram can facilitate consistency in recording (Margulis, 2010).

Ethograms have been developed for a wide range of taxa in the field of animal behavior, including chimpanzees (*Pan troglodytes*) (e.g., Nishida et al., 1999; Hobaiter & Byrne, 2011), elephants (e.g., Esposito, 2008; Riyas Ahamed, 2015), birds (e.g., Masatomi, 2004; Lichtenberg & Hallager, 2007), river otters (*Lontra canadensis*; e.g., Green et al., 2015), and fish (e.g., Bolgan et al., 2016), and have also been developed for some cetacean species (e.g., humpback whales [*Megaptera novaeangliae*], Kavanagh et al., 2016; pilot whales [*Globicephala* sp.], Scheer et al., 2004; and belugas [*Delphinapterus leucas*], Howe et al., 2015).

As one of the most extensively studied cetaceans, information on bottlenose dolphins (*Tursiops* spp.) and accounts of their surface behavior have been widely published (Shane et al., 1986; Connor et al., 2000b). There are some general surface behavior ethograms for specific populations (e.g., USA: Shane, 1990; Croatia: Bearzi et al., 1999; New Zealand: Lusseau, 2006b; Australia: Steiner, 2011), but many published studies place specific emphasis on particular associations such as mother–infant relationships (e.g., Gubbins et al., 1999; Mann & Smuts, 1999), behaviors such as foraging (e.g., Nowacek, 2002; Sargeant et al., 2006; Sargeant & Mann, 2009), or human interactions (e.g., Jaiteh et al., 2013). In many cases, ethograms come from research on captive dolphins (e.g., von Streit, 2011) or are limited to describing only the broad activity state categories (e.g., Mann & Watson-Capps, 2005; Genov et al., 2008; Baş et al., 2015; Karniski et al., 2015).

In the study of animal behavior, it is important to distinguish between *states* (long-duration behaviors) and *events* (short-duration behaviors) (Altmann, 1974; Connor et al., 2000b). For example, *eyes open* is a behavioral state of some duration, whereas *blinking* is an essentially instantaneous behavioral event (Nowacek, 2002). Herein, we use the terms *activity state* and *behavioral event* to distinguish between these two types of behavior.

A table of behavioral definitions was published by Bearzi et al. (1999) for bottlenose dolphins in the Adriatic Sea, largely based on work carried out in the United States (Weaver, 1987; Shane, 1990). Bottlenose dolphin surface behavior has also been studied to varying degrees in other European study sites (e.g., Italy: Díaz López & Shirai, 2008; Slovenia: Genov et al., 2008; Portugal: Augusto et al., 2011). No ethograms currently exist for any of the three discrete populations of bottlenose dolphins in Ireland (including the resident population in the Shannon Estuary) or for the two geographically closest resident populations in the Moray Firth, Scotland, and Cardigan Bay, Wales.

There have been few detailed behavioral studies of dolphins in the temperate waters of the northeast Atlantic. A number of studies in Ireland have included behavioral components, mainly as part of impact assessments focusing on cause and effect (e.g., behavioral responses to acoustic pingers; Leeney et al., 2007). Some studies of behavior in common dolphins (*Delphinus delphis*; Berrow et al., 2008) and killer whales (*Orcinus orca*; Ryan & Wilson, 2003) have also been conducted. In the Moray Firth and Cardigan Bay, researchers have used broad categories to record bottlenose dolphin behavior (e.g., Pierpoint et al., 2009; Pirotta et al., 2015), but information on specific behavioral events within activity state categories for these populations is lacking.

Few published papers present basic activity budget data on the frequency of activity states in cetacean populations (Mann & Würsig, 2014), even though these are important data for understanding the life history of a species and informing conservation management (Karniski et al., 2015). Even fewer studies present behavioral event data in which the distinct surface behaviors of wild bottlenose dolphins are described and their occurrence quantified, with only a handful of studies attempting to then explain the context and purpose of these surface behaviors (e.g., Lusseau, 2006a; Furuichi et al., 2014). However, the collection of behavioral data is integral to the overall understanding of animal populations (Lehner, 1996).

When sighting data on activity states and behavioral events are collected by multiple independent observers, tests are required to assess the reliability and validity of these data (Martin & Bateson, 1986; Kaufman & Rosenthal, 2009). The literature on the collection and analysis of data on cetacean surface behavior contains few examples of such tests (Mann, 1999). Kavanagh et al. (2016) carried out inter-observer reliability tests using video data during a study of humpback whales to examine the effects of observers' experience and native language on data reliability and validity. Using video data incorporating 16 behavioral event types, they found that neither factor had a significant effect on behavioral data recording by observers. However, their test results did highlight specific behavioral event types that were more accurately and consistently recorded than others, and they suggested that future studies could use similar tests to assess the suitability of specific behavioral event types for analysis.

The bottlenose dolphin population in the Shannon Estuary, Ireland, is composed of about 120 individuals (Berrow et al., 2012) and is genetically discrete (Mirimin et al., 2011). Dolphins are present in the estuary year-round (Berrow et al., 1996; Ingram, 2000; Berrow, 2009) and have been observed exclusively in the Shannon Estuary and adjacent Tralee and Brandon Bays (Ryan &

Berrow, 2013; Levesque et al., 2016). This species also occurs around the entire Irish coast (O'Brien et al., 2009) and in offshore waters (Louis et al., 2014), but these are thought to constitute distinct populations (Oudejans et al., 2015). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (National Parks and Wildlife Service [NPWS], 2012), which are listed in Annex II of the European Union Habitats Directive. Given the level of protection assigned to this population, information on the behavior of dolphins in the estuary is vital for their long-term conservation and the development of specifically tailored management plans.

This article aims to describe a detailed ethogram for wild bottlenose dolphins in the Shannon Estuary, to provide some quantitative data on the frequency of different activity states and behavioral events, and to report the presence or absence of behaviors recorded in other studies. Its more general aim is to provide a tool for future bottlenose dolphin behavioral research that will give insight into the behavioral repertoire and activity budget of bottlenose dolphins in the estuary and highlight common and rare behaviors. A greater understanding of bottlenose dolphin behavior will contribute towards the management and conservation of bottlenose dolphin stocks in Ireland (especially those in SACs) (NPWS, 2012) and of the species throughout its geographical range.

Methods

Study Site and Vessels

The study site was within the Lower River Shannon SAC (Site Code: 002165) for bottlenose dolphins, a 684 km^2 Natura 2000 designated site (NPWS, 2012) on Ireland's west coast between Co. Clare, Co. Kerry, and Co. Limerick (52° 36' N, 9° 38' W). Surveys occurred west of Shannon Airport and east of Loop Head and Kerry Head (Figure 1).

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow et al., 2010, 2012; O'Brien et al., 2014). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow & Holmes, 1999). The dolphin-watching tour boats, *Draíocht* and *Dolphin Discovery*, operated from the ports of Carrigaholt and Kilrush, respectively

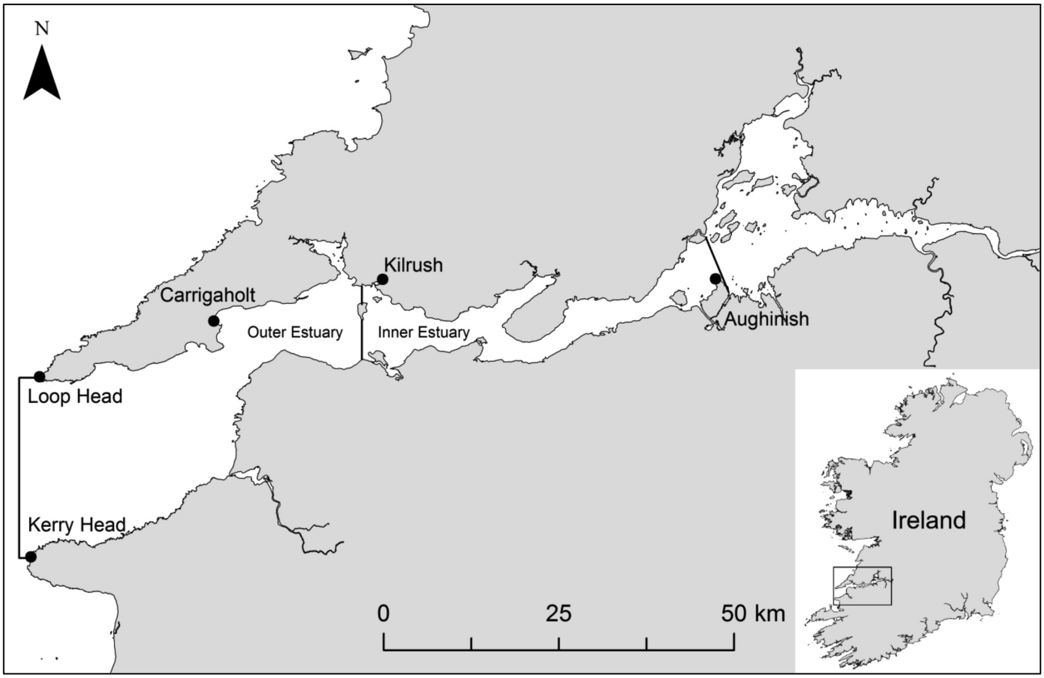

Figure 1. Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC), while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the outer and inner estuary areas by a north-south line drawn through Scattery Island near Kilrush.

(Figure 1). *Draíocht* and *Dolphin Discovery* primarily concentrated effort in the outer and inner estuary areas, respectively, with a mean dolphin-watching trip length of 2.3 h (Berrow & Ryan, 2009; Barker & Berrow, 2016). The research vessel based in Kilrush was a 6-m XS RIB (rigid-hulled inflatable boat) with which surveys were conducted throughout all areas of the estuary. Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~4 m, while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at < 1 m above sea level. In general, behavioral observations were made visually, but observers were also equipped with digital SLR cameras (Nikon D300 or Canon EOS 20D with 70 to 300 mm lenses), binoculars (Minox 7 × 50 or 8 × 42), GPS (Garmin 72H), and datasheets.

Data Collection

In addition to reviewing published ethograms (e.g., Weaver, 1987; Shane, 1990), eight researchers who manage different bottlenose dolphin research projects worldwide were contacted for expert advice and information on ethograms from the populations with which they work to gain insight for constructing our initial ethogram. These research projects and study sites were chosen based on geographical region, personal contacts, and length of study.

A pilot study was carried out in the Shannon Estuary in 2013 from commercial dolphin-watching tour boats and a dedicated research vessel to collect behavioral data, refine bottlenose dolphin behavioral event descriptors, and determine if it was necessary to supplement the proposed ethogram with additional behaviors observed in the field.

Activity states and behavioral events were subsequently recorded during three field seasons: (1) March-September 2014, (2) June-September 2015, and (3) May-September 2016. Observers made visual observations from the three different platforms previously described. Sighting datasheets were completed during every survey in which encounters with dolphin groups (sightings) occurred. A sighting began when at least one dolphin was within 100 m of the vessel and ended after ≤ 30 min due to national regulations (Maritime Safety Directorate, 2005). A *group* was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al., 2011a).

Behavioral data collection methods were based on the recommendations of Mann (1999) who defines the two basic sampling decisions as (1) *follow protocol*—the length of observation and the choice of subject(s)—and (2) *sampling method*—the procedure used to sample behavior. The follow protocol used was *survey*, with sightings providing a snapshot of dolphin activity, including group estimates, GPS location, and behaviors. The sampling methods used were predominant group activity sampling, one-zero sampling, and *ad libitum* sampling. *Predominant group activity sampling* involved selecting the activity state that > 50% of individuals in a group were engaged in within the first 5 min of a sighting; *one-zero sampling* involved scoring whether or not specific behavioral events occurred within the first 5 min of a sighting; and ad libitum *sampling* was used to make additional anecdotal comments throughout the duration of a sighting.

For each sighting, the observer selected one of six options—(1) Rest, (2) Travel, (3) Social, (4) Forage, (5) Other, and (6) Unknown—as the predominant (> 50% of individuals) group activity state during the first 5 min of a sighting. Five minutes was used as the initial period within which to record behavior in an effort to record how the dolphins were most likely to have been behaving before the boat arrived in the vicinity. In addition, the observer circled all behaviors seen within the first 5 min from the behavioral events listed on the datasheet and recorded additional activity states and behavioral events (after 5 min) in the Comments section of the datasheet with the time of occurrence.

Inter-Observer Validity and Reliability Testing

During dedicated behavioral surveys from the research RIB, video footage of bottlenose dolphins was recorded. Seventeen segments, each < 35 s in duration, were extracted from these videos for three of the ethogram's major activity states and 14 behavioral event types and used to assess inter-observer reliability in selecting visually observed behaviors. (The video segments are available on the "Supplementary Material" page of the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.) To verify the video test behaviors, an experienced dolphin behavior researcher (KM) completed the test prior to commencement of trials. The expert's answers matched those of the test designer and compiler of the overall ethogram (IB) prior to the test going live.

The 17 videos were shown to 24 people—12 trained research assistants who collected the data and 12 other marine biologists with no previous marine mammal behavior research experience and who had not participated in the fieldwork of this study. Each trained research assistant had at least 2 wks of training in fieldwork methods, equipment usage, and data collection protocols with the Shannon Dolphin and Wildlife Foundation before independently collecting data. At the end of the final field season, each participant was provided with a copy of the ethogram and was requested to identify the activity state or behavioral event exhibited by the dolphin(s) in each video segment—that is, to code each clip.

Using similar methodologies to Kavanagh et al. (2016), percentage agreement and Kappa score statistical analyses were employed to measure the validity and reliability of the behaviors recorded by the test participants (Kaufman & Rosenthal, 2009). Percentage agreement was calculated to measure how often observers agreed on the correct classification of a behavior (Martin & Bateson, 1986). Percentage agreement scores were calculated for each of the behaviors and each of the test participants. As validity data were non-normally distributed (Levene's test), Mann-Whitney U tests were used to compare validity scores between trained and other test participants (Venables & Ripley, 2002).

Kappa scores (which include a correction for chance) were used to examine the reliability of the recording of individual behaviors by each observer (Fleiss, 1971; Conger, 1980), using the designer's (IB) scores as baseline data within the *R* (R Core Team, 2016) package *irr* (Gamer et al., 2012). Category-wise Kappa scores were generated for all behaviors used in the test. These scores compute the probability of a randomly chosen observer assigning a specific behavior to a video given that another randomly chosen observer has also assigned that behavior to that video. Where behaviors were misclassified (i.e., a participant selected a different behavior to the baseline), the behavior most frequently selected in each case was recorded and presented.

The test had two aims: (1) to establish whether trained observers agreed sufficiently well to validate the behavioral data collected and used in the present study, and (2) to validate the broader use of the ethogram by marine biologists to accurately record dolphin behavior (which could reduce significant variability in long-term monitoring projects).

Behavioral Analysis

Activity state and behavioral event data were entered into a specially adapted version of *FinBase* (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams et al., 2006). Using one form per sighting, activity states were entered as Initially Observed (first 5 min) and sometimes as Observed (after 5 min) if an additional activity state was recorded in the Comments section. A specifically designed ethogram subform within the sighting form in *FinBase* was used to enter all of the behavioral events recorded during each sighting.

Behavioral data from sightings were queried in *FinBase*, and summary statistics were calculated using *MS Excel* and *R* (R Core Team, 2016). Analyses used predominant group activity data recorded exclusively within the first 5 min of each sighting, while both one-zero and *ad libitum* behavioral event data were used for behavioral events analysis. Percentage occurrence and activity budgets were calculated by summing the records of each behavior from the sightings and dividing by the total number of data points.

In addition to the written data recorded during sightings, photographs were taken simultaneously, primarily for photo-identification of individuals but with the benefit of obtaining photographic data on behaviors. Photos from all surveys and sightings were maintained in a database using the photographic software environment *IMatch*, Version 5.6 (https://photools.com; Westphal, 2016). The Categories Assignment tool was used to categorize every photo in which a behavioral event from the ethogram was exhibited by one or more dolphins. These photographs were used during the training of multiple observers for collecting behavioral data in the field.

Comparison with Other Studies

Data from other studies of bottlenose dolphin behavior were gathered to generate tables comparing the activity states of the Shannon Estuary dolphins with those of other populations. The classification of behaviors, terminology, and definitions employed by these studies were compared with those used in the present study. Behavioral events that have been described in other studies but which have not (yet) been observed or recorded in the present study were noted.

Results

Summary of Data Collection

Of the 489 sightings (256 surveys), 209 sightings (91 surveys) were made from the tour boat *Draíocht*, 154 sightings (116 surveys) were made from the tour boat *Dolphin Discovery*, and 126 sightings (49 surveys) were made from the research RIB. Overall, 18 observers contributed sighting records to the database, but the top ten observers with the most records collectively contributed the data from 81% (395) of the sightings.

In 2014, 2015, and 2016, both activity states and behavioral events were recorded for 193 sightings (100 surveys), 145 sightings (76 surveys), and 151 sightings (80 surveys), respectively. However, no behavioral events were observed in 62 of these sightings (14, 24, and 24 sightings in 2014, 2015, and 2016, respectively). Thus, a total of 489 sighting records with activity states and 427 sighting records with behavioral events were available for analysis. The average length of a sighting was 24 min, representing approximately 200 h of total dolphin observation time. Overall survey effort was approximately 765 h.

Bottlenose Dolphin Ethogram

Overall, our ethogram contains codes and descriptions for 11 activity states and 45 behavioral event types (Tables 1 to 4) for bottlenose dolphins in the Shannon Estuary. In the sightings data collected for the present study, information on six activity states and 35 behavioral event types was recorded and quantified (Tables 7 & 8). The ethogram is divided into four categorized sections, beginning with 11 activity state definitions adapted from those published by McHugh et al. (2011b), which are based on Waples (1995) (Table 1). This section is followed by three separate behavioral event sections detailing surface behaviors, foraging/feeding, and social behaviors (Tables 2-4). Many of these behavioral definitions are adapted from Richard Connor's ethogram (pers. comm., 25 January 2017) for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. The activity states recorded were *Travel*, *Forage*, *Social*, *Rest*, *Other*, and *Unknown*. However, *Probable forage*, *Feed*, *Mill*, *Play*, and *With boat* have also been observed as part of the Shannon Estuary bottlenose dolphins' behavioral repertoire and are included in the ethogram. Each of these activity states is mutually exclusive.

A total of 27 behavioral event types for observed surface behaviors were defined (Table 2), many of which were observed during more than one type of activity state. Twenty of these behavioral events were recorded at least once during sightings. A total of ten behavioral event definitions for observed feeding/foraging behaviors (Table 3) were included in the ethogram. Nine of these behavioral events were recorded at least once during sightings. Eight behavioral event definitions were included for social behaviors (Table 4) observed during social activity by bottlenose dolphins in the Shannon Estuary. Six of these behavioral events were recorded at least once during sightings.

Inter-Observer Validity and Reliability Testing

The mean percentage agreement score and standard deviation (data validity) across 24 test participants was 88.1 ± 7.0. The scores of trained research assistant (mean = 92.5 ± 3.4) and other marine biologist (mean = 83.8 ± 7.1) test participants differed significantly (Mann-Whitney U test: $W = 19.5$, $p < 0.05$). Fleiss's Kappa score (data reliability) across all participants was 0.81. The Kappa score of the trained participants was 0.88 and of the other participants was 0.74.

Every test participant correctly assigned the first two activity states (*Forage* and *Travel*) to their respective videos with only one incorrectly assigning the third (*Rest* instead of *Social*). All 24 test participants correctly assigned four of

Table 1. Activity states for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, including a description for each activity state. Behaviors in italics were not recorded or quantified separately in this study: *Feed*, *Mill*, and *Probable forage* were recorded as *Forage*, while *Play* and *With boat* were recorded as *Other* during sightings.

Unit	Code	Name	Description
Activity states	FE	*Feed*	Dolphin observed catching a fish or with a fish in its mouth
	FO	Forage	Indications of searching for prey, prey capture, or feeding behaviors
	MI	*Mill*	Nondirectional movement with no overall spatial progress
	OT	Other	Observed activity is clear but does not fit any other definition
	PL	*Play*	Interactions with objects other than dolphins which serve no obvious purpose
	PFO	*Probable forage*	Indications of foraging but not confirmed
	RE	Rest	Slow, steady activity in absence of other identifiable activities, often with long dive bouts (1 to 5 min)
	SO	Social	All active interactions with conspecifics, including body contact, chasing/following, and sexual behaviors
	TR	Travel	Regular directional movement, including zig-zag and meandering movement
	UN	Unknown	Activity cannot be defined
	WB	*With boat*	All cases during which dolphins interact with a boat, including bow- and wake-riding

Table 2. Surface behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. *Halfway = to the dolphin's belly button but genital slit is not visible above water. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

Unit	Code	Name	Description
Surface behaviors	BKS	Backslap	Body exits halfway* out of water and falls against dorsal surface
	BST	Backstroke	Body is horizontal, and ventral part of body is visible above surface with both pectoral fins extended
	BEL	Belly roll	Body rotates c. 180° in water so that light ventral underside of the animal becomes visible
	BOW	*Bow-riding*	Dolphins surfacing at the bow of a moving vessel
	BR	Breach	Body exits water over halfway* and vertically and then falls horizontally creating white water
	BB	*Bubble-blow*	Bubble(s) emitted underwater from blowhole
	CNS	Chinslap	Body exits halfway* out of water and falls against ventral surface
	CHF	Chuff	Strong, audible exhale from blowhole
	DEF	Defecation	Faeces are emitted from body
	FTR	Fast travel	Directed movement at a speed of over 10 km/h
	HO	Head out	Head and rostrum emerge above water surface and reenter water smoothly
	HD	*Headstand*	Dolphin is vertical with tail-end of body exposed above water surface
	LP	Leap	Body exits water entirely in an arcuate path and reenters water smoothly
	MO	*Motorboating*	Tailslapping repeatedly in forward motion at the water surface
	ONS	On side	Body rotates c. 90° in water
	PEC	Pec out	Pectoral fin is extended above water surface
	PP	Porpoise	Repeated leaps in a straight direction
	SCO	*Scouting*	An individual dolphin leaves its group to approach the boat before returning again to its group
	SHK	*Sharking*	Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water
	SDS	Sideslap	Body exits halfway* out of water and falls against flank
	STR	Slow travel	Directed movement at a speed of under 10 km/h
	SNG	Snag	Body is stationary, horizontal; dorsal part of body is visible at surface
	SQ	*Squeeze breath*	A sound emitted from the blowhole that sounds like air escaping a balloon
	SR	Surface rush	Fast movement breaking the surface causing a flurry of white water at either side of the animal
	TO	Tail out	Tail is exposed above water surface
	TS	Tailslap	Flukes raised above water surface and then lowered making a strong, audible impact
	WS	With seaweed	Dolphin interacting with seaweed—in its mouth or draped over its dorsal fin, body, or fluke

the 14 videos of single behavioral events with the behaviors *Tail dive*, *Tailslap*, *Fish toss*, and *With seaweed*. Of the remaining ten videos, test participants correctly assigned behaviors to varying degrees. The behaviors *Tail out* (0.95, 95.8%) and *Slow travel* (0.84, 95.8%) had relatively high reliability and validity scores, with only one misclassified behavior each—*Pec out* and *Fast travel*, respectively—out of all 24 test responses (Table 5). *Snag* (0.91, 91.7%) and *Surface rush* (0.91, 91.7%) were misclassified twice, each with the same two incorrect behavior assignations—*Slow travel* and *Fast swim*, respectively. *Peduncle dive* (0.86, 87.5%) and *With fish in mouth* (0.86, 87.5%) were both misclassified three times each, but with a different behavior each time—*Slow*

Table 3. Feeding/foraging behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. Behavior in italics was not quantified in this study but has been recorded during focal follows and/or as anecdotal data during sightings.

Unit	Code	Name	Description
Feeding/Foraging	CF	Catch fish	Dolphin catches a fish
	FSW	Fast swim	Dolphin moves quickly through water, apparently chasing fish
	FJ	Fin jerk	Abrupt movement of dorsal fin, indicating possible prey capture
	FS	Fish seen	A fish is seen next to a dolphin, in the water or air, with no evidence of a fish toss
	FT	Fish toss	Dolphin throws fish into the air from its mouth
	HS	*Humping surface*	Dolphin arches its body at surface and moves up and down
	LF	Leap feeding	Many dolphins are leaping, apparently chasing fish
	PD	Peduncle dive	Dolphin dives, and peduncle is visible but its tail is not
	TD	Tail dive	Dolphin dives, and tail is visible
	WF	With fish in mouth	Dolphin has fish in its mouth

Table 4. Social behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

Unit	Code	Name	Description
Social	CHA	*Chase*	One dolphin in pursuit of another dolphin
	GEN	Genital slit/Genitals	Pink genital area or erect penis observed
	GS	*Goose*	One dolphin contacts another's genital slit with its rostrum
	PR	Pec rub	One dolphin rubs along another's pectoral fin
	PET	Pet	Gentle contact between pectoral fin of one dolphin and body of another
	RUB	Rub	Gentle to vigorous body-body contact
	SPL	Splash	Water splash caused by movement of dolphin(s), but action cannot be defined
	SPY	Spyhop	Head and rostrum emerge vertically from water, and dolphin appears to view its surroundings

travel, *Head out*, and *Leap* for *Peduncle dive*; and *Catch fish*, *Fish toss,* and *Chuff* for *With fish in mouth*. The scores for *Chinslap* (0.59, 62.5%), *Spyhop* (0.46, 50.0%), and *Breach* (0.12, 20.8%) were the lowest. *Breach* was the behavior most frequently misclassified, with five of the 24 participants correctly assigning the behavior and 16 misclassifying it as *Sideslap* and three as *Backslap*.

When differences between trained research assistant and other marine biologist test participant assignations were investigated, six of the behaviors had both higher validity scores (> 10% difference in percentage agreement) and reliability scores (> 0.10 difference in Kappa) for the trained participants than the other participants, compared to zero behaviors for the other participants vs the trained participants (Table 6). These behaviors were *Surface rush*, *With fish in mouth*, *Leap*, *Spyhop*, *Peduncle dive*, and *Snag*. *Leap* was the only behavior misclassified consistently by both trained and other test participants as a single alternative behavior, *Breach*. Of the 17 behaviors tested, trained participants had three validity scores under 80%, and the other participants had six validity scores under 80%.

Activity State Budgets

Using our ethogram, six of the activity states and 35 of the behavioral events observed in this bottlenose dolphin population were recorded and quantified. Activity states were recorded for 489 sightings during 256 surveys (on 171 d) from 2014 to 2016, and activity state budgets were calculated (Table 7). A single predominant group activity state (in the first 5 min) was recorded for

Table 5. Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors used in the inter-observer video test, with the most common misclassification for each behavior

Behavior	Percentage agreement	Category-wise Kappa	Most common misclassification
Forage	100.0	1.00	--
Travel	100.0	1.00	--
Social	95.8	0.95	Rest
Breach	20.8	0.12	Sideslap
Fish toss	100.0	0.96	--
Chinslap	62.5	0.59	Head out
Surface rush	91.7	0.91	Fast swim
Slow travel	95.8	0.84	Fast travel
Tail dive	100.0	1.00	--
Tailslap	100.0	1.00	--
With fish in mouth	87.5	0.86	Catch fish/Fish toss/Chuff
Leap	83.3	0.71	Breach
Spyhop	50.0	0.46	Backslap/Backstroke/Head out
With seaweed	100.0	1.00	--
Peduncle dive	87.5	0.86	Slow travel/Head out/Leap
Snag	91.7	0.91	Slow travel
Tail out	95.8	0.95	Pec out

Table 6. Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors assigned by trained research assistant and other marine biologist test participants in the inter-observer video test, with the most common misclassification for each behavior for each test group

	Trained research assistants			Other marine biologists		
Behavior	Percentage agreement	Category-wise Kappa	Most common misclassification	Percentage agreement	Category-wise Kappa	Most common misclassification
Forage	100.0	1.00	--	100.0	1.00	--
Travel	100.0	1.00	--	100.0	1.00	--
Social	100.0	1.00	--	91.7	0.90	Rest
Breach	25.0	0.09	Sideslap	16.7	0.12	Sideslap
Fish toss	100.0	1.00	--	100.0	0.92	--
Chinslap	66.7	0.62	Head out	58.3	0.53	Head out/Fast travel
Surface rush	100.0	1.00	--	83.3	0.81	Fast swim
Slow travel	91.7	0.90	Fast travel	100.0	0.80	--
Tail dive	100.0	1.00	--	100.0	1.00	--
Tailslap	100.0	1.00	--	100.0	1.00	--
With fish in mouth	100.0	1.00	--	75.0	0.72	Catch fish/Fish toss/Chuff
Leap	91.7	0.82	Breach	75.0	0.57	Breach
Spyhop	75.0	0.72	Backstroke	25.0	0.17	Head out
With seaweed	100.0	1.00	--	100.0	1.00	--
Peduncle dive	100.0	1.00	--	75.0	0.72	Leap/Head out/Slow travel
Snag	100.0	1.00	--	83.3	0.81	Slow travel
Tail out	100.0	1.00	--	91.7	0.90	Pec out

Table 7. The six recorded activity states during 489 sightings of bottlenose dolphins in the Shannon Estuary, including the number (*n*) and percentage (%) of records for each year and all years pooled together. **Note:** Percentages are rounded but exact figures add up to 100.

			2014		2015		2016		All years	
Unit	Code	Name	*n*	%	*n*	%	*n*	%	*n*	%
Activity states	TR	Travel	132	68	52	36	70	46	254	52
	FO	Forage	28	15	64	44	47	31	139	28
	SO	Social	19	10	14	10	7	5	40	8
	RE	Rest	5	3	9	6	18	12	32	7
	OT	Other	1	1	2	1	2	1	5	1
	UN	Unknown	8	4	4	3	7	5	19	4
		Total	193	100	145	100	151	100	489	100

every sighting. For the sightings in this study, the five additional states listed in the ethogram were not separately recorded and were pooled under either *Forage* (*Probable forage*, *Feed*, and *Mill*) or *Other* (*Play* and *With boat*).

Travelling was the predominant group activity state in over half (52%) of all sightings, while *Foraging* was recorded in over one quarter (28%) of sightings. *Socializing* was the predominant group activity state for 8% of sightings, while *Resting* was recorded during 7% of sightings. Together, *Other* and *Unknown* activity states were recorded during 5% of sightings. A significant difference was found between annual activity budgets ($\chi^2 = 60.499$, df $= 10$, $p < 0.0001$). Of all 3 y, the highest proportion for *Travelling* (68%) was recorded in 2014, the highest for *Foraging* (44%) was recorded in 2015, and the highest for *Resting* (12%) was recorded in 2016. The lowest proportion for *Socializing* (5%) was recorded in 2016 (Table 7).

Behavioral Events

Behavioral events were recorded for 427 sightings during 250 surveys (on 169 d) between 2014 and 2016. Of the 35 behavioral events used for analysis, each was observed at least once. In total, 1,452 behavioral events were recorded; of these, 198 were recorded in *ad libitum* data and excluded in further analysis. Thus, 1,254 behavioral event records were used for analysis. The average number of behavioral events recorded during the first 5 min of a sighting was three (0.59 behaviors/min; range: 0 to 14) behavioral events (Table 8).

The most frequently observed behaviors in the surface behaviors, feeding/foraging, and social ethogram categories were *Slow travel* (14% of records), *Tail dive* (8% of records), and *Splash* (2% of records), respectively (Table 8). Of all behavioral events, the five most frequently observed behaviors were *Slow travel* (seen in 40% of all sightings), *Leap* (28% of sightings), *Surface rush* (28% of sightings), *Tail dive* (23% of sightings), and *Tailslap* (22% of sightings). These five behaviors accounted for 48% of the overall records. The ten least frequently recorded behaviors were *Pet*, *Spyhop*, *Porpoise*, *Catch fish*, *Genital slits/Genitals*, *Fin jerk*, *Snag*, *Pec rub*, *Defecation*, and *Backstroke*. These ten behavioral events were seen in only 10% of total sightings, with < 8 records each.

There are ten additional behavioral events defined in our ethogram that have been observed but not yet quantified for Shannon Estuary bottlenose dolphins. *Motorboating* (MO) (a series of rapid and repetitive tailslaps during forward progress by a dolphin; Weaver, 1987) has been observed twice during focal follows. Video footage and photographs of *Headstand* (HD) behavior exist wherein the dolphin is completely vertical with its tailstock in the air above the surface of the water for a few seconds in a stationary position. It is possible that some headstands were recorded in the present study as *Tail outs*. Dolphins in the Shannon Estuary are regularly observed *Bow-riding* (BOW) the research vessel, tour boats, recreational vessels, and large ships, but this behavioral event has not yet been quantified. On two occasions during focal follows, a snagging dolphin emitted a squeaky sound from its blowhole defined as a *Squeeze breath* (SQ). *Bubble-blows* (BB) (Lusseau, 2006a), equivalent to Weaver's (1987) subsurface exhalation, have also been observed periodically wherein a dolphin under water emits air from its blowhole creating bubbles at the surface. *Sharking* (SHK) has been seen at least ten times during focal follows wherein the tip of a dolphin's dorsal fin is visible cutting through the water surface at one level, while the rest of the dolphin's body remains under water. During one encounter, an individual dolphin exhibited *Scouting* (SCO) behavior (Bearzi et al.,

Table 8. The 35 recorded behavioral events in the ethogram, recorded during the first 5 min of sightings of bottlenose dolphins in the Shannon Estuary, including the number of records made from each platform, the total number of records (*n*), and the percentage (%) of records and sightings for each behavioral event. RBI = Rigid-hulled inflatable boat.

Behavior	RIB	*Draíocht*	*Dolphin Discovery*	*n*	% of records	% of sightings
Slow travel	43	57	72	172	14	40
Leap	31	44	46	121	10	28
Surface rush	37	45	38	120	10	28
Tail dive	31	43	26	100	8	23
Tailslap	25	32	36	93	7	22
Peduncle dive	23	45	21	89	7	21
Head out	10	33	26	69	6	16
Fast travel	11	24	24	59	5	14
Breach	8	21	24	53	4	12
Belly roll	14	18	19	51	4	12
Tail out	13	19	18	50	4	12
Fish seen	8	11	7	26	2	6
Fast swim	4	11	10	25	2	6
Splash	1	12	11	24	2	6
Sideslap	7	7	9	23	2	5
Fish toss	5	8	5	18	1	4
Pec out	7	4	6	17	1	4
On side	8	2	6	16	1	4
Rub	2	9	5	16	1	4
Chinslap	6	6	3	15	1	4
Leap feeding	2	6	6	14	1	3
Backslap	1	8	3	12	1	3
With fish	4	2	4	10	1	2
Chuff	0	7	3	10	1	2
With seaweed	1	3	5	9	1	2
Pet	1	3	3	7	1	2
Spyhop	1	2	4	7	1	2
Porpoise	2	3	1	6	0.5	1
Catch fish	2	1	3	6	0.5	1
Genital slits/Genitals	4	0	0	4	0.3	1
Fin jerk	1	2	0	3	0.2	1
Snag	0	3	0	3	0.2	1
Pec rub	0	0	3	3	0.2	1
Defecation	1	1	0	2	0.2	0.5
Backstroke	0	0	1	1	0.1	0.2
Total behaviors	314	492	448	1,254		
Total surveys	49	85	116	250		
Total sightings	114	169	144	427		
Total min	570	845	720	2,135		
Behaviors/min	0.55	0.58	0.62	0.59		

1999) in leaving the rest of its group and approaching the research vessel before returning to its group. *Humping surface* (HS) behavior has been noted *ad libitum* on a few separate occasions in which a dolphin has remained at the water surface moving up and down with its back arched. *Goosing* (GS), contact between the rostrum of an individual dolphin and the genital slit of another, was recorded twice during focal follows; on both occasions, these events involved only juvenile dolphins. During one focal follow, repeated *Chase* (CHA) behavior (two dolphins actively surfacing, with one dolphin following another; Lusseau, 2006a; Steiner, 2011) was observed by an adult following a juvenile, interspersed with intense socializing.

Comparison with Other Studies

Although studies of bottlenose dolphin behavior elsewhere have reported activity budgets of strikingly different proportions, the daytime activity budgets observed in the Shannon Estuary fall within the ranges observed for this species in other areas (Table 9). All of the studies used for comparison included *Travel*, *Forage*, *Social*, and *Rest* activity states except for Sanibel Island (Shane 1990), which did not include *Rest* in its analyses and included two additional activity state definitions for *Travel/Feed* and *Social travel*. Other studies also included *Mill*, *Travel/Feed*, and *Play* in their activity budget breakdowns.

While 52% of the Shannon Estuary bottlenose dolphins' activity budget during this study was allocated to travelling, dolphins in the Port River Estuary, South Australia (Steiner, 2011), and the Patos Lagoon Estuary, Brazil (Mattos et al., 2007), had much lower travelling proportions (23 and 29%, respectively). The highest travelling proportion in the investigated studies was

Table 9. Daytime activity budgets (in percentages) of bottlenose dolphins in the Shannon Estuary and from the published literature: Port River Estuary, South Australia (Steiner, 2011; foraging and feeding combined); Patos Lagoon Estuary, Brazil (Mattos et al., 2007); San Diego County, California (Hanson & Defran, 1993); Sanibel Island, Florida (Shane, 1990); Sarasota Bay, Florida (Waples, 1995; McHugh et al., 2011b [juveniles only], combined and averaged); Shark Bay, Western Australia (Gero et al., 2005; Karniski et al., 2015 [estimated from Figure 1; females only], combined and averaged); Moreton Bay, Queensland (Chilvers et al., 2003 [nontrawler dolphin community only]); and Cardigan Bay, Wales (Veneruso & Evans, 2012)

Study area:	Shannon Estuary	Port River	Patos Lagoon	San Diego	Sanibel Island	Sarasota Bay	Shark Bay	Moreton Bay	Cardigan Bay
Study method:	Survey	Individual follow	Group follow	Group follow	Group follow	Individual follow	Survey	Survey	Survey
Travel	52	23	29	63	46	61	23	55	43
Forage	28	48	38	19	17	16	30	34	50
Social	8	14	6	12	7	5	10	8	6
Rest	7	11	1	3		1	37	3	0
Other	1	4				1			
Unknown	4								
Mill			4			16			
Travel/Feed			22		21				
Social travel					10				
Play				3					

Table 10. Behaviors described in this study's ethogram and some comparable descriptors for similar behaviors in other studies

Behavior name	Behavioral descriptor	Reference(s)
Slow travel	Directed movement at a speed of under 10 km/h	This study
Fast travel	Directed movement at a speed of over 10 km/h	This study
Straight travel	Travelling in a general direction with all surfacings in that direction	Waples, 1995
Zig-zag travel	Travelling in a general direction by straight segments of different directions	Waples, 1995
Meandering travel	Travelling in a general direction but orientation changes frequently	Waples, 1995
Surface rush	Fast movement breaking the surface causing a flurry of white water at either side of the animal	This study

Active surfacing	Rapid surfacing with spray; a major part of the back is visible during the surfacing	Lusseau, 2006a
Racing	Regular dive performed at high speed with more of dolphin's back exposed and white water forming as animal surfaces	Bearzi et al., 1999
Feeding rush	A sudden acceleration and splash	Shane, 1990
Rapid surface	A rapid surface in which the dolphin maintains a normal horizontal posture, and the dolphin's ventrum does not clear the water surface	R. Connor, pers. comm.
Leap	Body exits water entirely in an arcuate path and reenters water smoothly	This study
Forward leap	Exit and enter head first with venter facing down	Shane, 1990
Backward leap	Exit and enter with dorsum facing down	Shane, 1990
Side leap	Exit and enter with either side facing down	Shane, 1990
Snag	Body is stationary, horizontal; dorsal part of body is visible at surface	This study
Floating	Stationary position at interface exposing foresection of animal in pronounced concave arc	Bearzi et al., 1999
Lie at surface	Dolphin lies stationary with part of body exposed at surface for 5 s or more	Shane, 1990
Snaggle	Dolphin floats stationary at the water surface, with its body horizontally flexed	Lusseau, 2006a
Chuff	Strong, audible exhale from blowhole	This study
Forced blow	Dolphin forcefully exhales above water producing a loud "chuff" sound	Lusseau, 2006a
Noisy blow	Dolphin made a loud noise with the blowhole at the surface	Steiner, 2011
Cough	A loud, forceful exhalation	Shane, 1990
Tailslap	Flukes raised above water surface and then lowered making a strong, audible impact	This study
Upside-down tailslap	Flukes raised above the surface, and dorsal side slapped downward	Shane, 1990
Inverted tailslap	The dorsal side of the flukes is brought down flatly on the water surface by an animal in the inverted position	Weaver, 1987
Tail slapping dorsal	Dolphin slapped the surface with the dorsal side of the tail	Steiner, 2011
Head out	Head and rostrum emerge above water surface and reenter water smoothly	This study
Head out	Entire head exposed at surface; rostrum pointed at an angle; dolphin stationary	Shane, 1990
Peek	Head raised out of the water far enough to expose the eyes; rostrum pointed forward; occurs during forward motion	Shane, 1990
Tail out	Tail is exposed above water surface	This study
Tail out	Exposure of the caudal section at the surface in a head-down position; the straight tailstock is elevated by a modulated upward movement, and the flukes may be flipped up or moved up and down briefly during exposure	Weaver, 1987
Fluke up	Exposure of one fluke at the surface by a moving or stationary animal; the fluke is usually angled and may flex briefly, often with splashing	Weaver, 1987
With seaweed	Dolphin interacting with seaweed, in its mouth or draped over its dorsal fin, body, or fluke	This study
Weed rub	A dolphin rubs into a patch of weed while rolling side or belly up; pectorals and flukes are often lifted out of the water, draped with weed	R. Connor, pers. comm.
Kelp dragging	Strands of kelp are hooked around the front of the dorsal fin and trail off either side of the body as the animal makes forward progress at the interface	Weaver, 1987
Carry weed	Dolphin carries algae on its beak, fin, flippers, or tail fluke	Lusseau, 2006a
Squeeze breath	A sound emitted from the blowhole that sounds like air escaping a balloon	This study
Squeeze breath	Audible and brief expulsion of air from the blowhole that sounds like air escaping the tightened neck of a balloon	Weaver, 1987
Fart blow	Dolphin exhales above water with its blowhole contracted producing a fart-like sound	Lusseau, 2006a
Sharking	Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water	This study
Sharking	Dolphin swims horizontally at the water surface with its dorsal fin visible above water	Lusseau, 2006a
Surface finning	The dorsal fin is continuously visible and the only exposed part as the animal makes forward progress at the interface at any speed	Weaver, 1987
Humping surface	Dolphin arches its body at surface and moves up and down	This study
Humping surface	A normal speed surface in which the dolphin "humps up" its posterior half to break its forward motion as it descends (when dolphins are pursuing fish)	R. Connor, pers. comm.
Buck	Body bent forward and back hunched and exposed at surface while dolphin bounces vigorously (social)	Shane, 1990

recorded for bottlenose dolphins in San Diego County, California (Hanson & Defran, 1993), at 63%. Foraging proportions ranged from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012), with similar proportions of 28, 30, and 34% in the Shannon Estuary, Shark Bay (Gero et al., 2005; Karniski et al., 2015), and Moreton Bay (Chilvers et al., 2003), respectively. *Social* behavior proportions ranged from 5% in Sarasota Bay to 14% in the Port River Estuary, while *Rest* behavior proportions ranged from 1% in Sarasota Bay and the Patos Lagoon Estuary to a high of 37% in Shark Bay. A systematic review of published studies shows some variation in the classification of behavioral event descriptors (Table 10).

Discussion

Bottlenose Dolphin Ethogram

The search for ethograms of surface behavior in the published literature and in research project protocols resulted in a varied set of behavioral terms and descriptions for bottlenose dolphins globally. Some behavioral studies have not used detailed ethograms with behavioral events to date (T. Genov, pers. comm., 14 March 2016; K. Robinson, pers. comm., 14 March 2016; G. Veneruso, pers. comm., 14 March 2016; K. McHugh, pers. comm., 14 April 2017), and others have unpublished ethograms, which they use as a basis for behavioral research (E. Krzyszczyk, pers. comm., 8 February 2016; S. Gazda, pers. comm., 9 March 2016; K. Sprogis, pers. comm., 19 March 2016; R. Connor, pers. comm., 25 January 2017). Some very detailed ethograms have been created as elements of students' Master's theses (e.g., Weaver, 1987; Waples, 1995). Of the ethograms found in the peer-reviewed literature, the terms and definitions are different for every study site, although many of the descriptions describe the same or similar behaviors. Because many of these published ethograms were used for specific studies, only a small number are appropriate to the general description of adult bottlenose dolphin behaviors within a population.

All of the behaviors that were observed in our study were added to the present ethogram with detailed descriptions and should lend themselves to straightforward comparison with behaviors documented elsewhere. These behaviors have all been described in the literature on bottlenose dolphins, but some are rarely mentioned (e.g., *Defecation*); and in one case, we have used our own term *Backstroke*, which is possibly equivalent to inverted motorboating as described in Weaver's (1987) ethogram.

In some comparable studies, behavioral events have been described which have not (yet) been observed or recorded in the present study of Shannon Estuary bottlenose dolphins. Surface behaviors, such as *Stretching* (Weaver, 1987; Steiner, 2011) wherein a dolphin stretches its back with its head, and sometimes tail flukes, lifting above the surface, and *Swell-riding* wherein a stationary animal faces land until a swell passes and then moves forward with it, exposing the dorsal fin and tailstock (Weaver, 1987), have not been observed in the Shannon Estuary.

Many foraging behaviors in the literature have not been observed in the Shannon Estuary population. These include *Sponging* (carrying a sponge on the rostrum; Smolker et al., 1997), *Strand-feeding* (surging out of the water in unison onto mud banks to feed on small fish; Duffy-Echevarria et al., 2008; Jiménez & Alava, 2015), and *Kerplunking* (fluke-slapping that produces a high splash of water and an audible sound (Connor et al., 2000a). *Pinwheels* (flip-turns performed by a dolphin in side-swim orientation; Nowacek, 2002), *Benthic-feeding methods* (e.g., Rossbach & Herzing, 1997), *Fish whacking* (propelling a fish into the air with a forceful thrust of the flukes; Nowacek, 2002), and *Belly up behavior* (a dolphin upside-down chasing a fish at the surface; R Connor, pers. comm., 25 January 2017) have also not yet been observed.

Social behaviors described in the literature that have not been recorded in the Shannon Estuary include *Jaw clap* (dolphin clapping its mouth at the surface, without anything in it; Waples, 1995; Steiner, 2011), *Bite* (one dolphin bites another; Lusseau, 2006a), and *Headbutt* (two dolphins jump simultaneously and hit their heads together; Lusseau, 2006a; K. Robinson, pers. comm., 14 March 2016). Neither *Bonding* (two dolphins swimming next to one another with prolonged pectoral fin contact) nor *Head-to-head* (two or more dolphins facing one another rostrum-to-rostrum for a prolonged period) behaviors described by Richard Connor (pers. comm., 25 January 2017) have been observed in the Shannon Estuary. No clear displays, such as the elaborate synchronous ones by male bottlenose dolphins, described by Connor et al. (2006), have been observed in the Shannon Estuary to date.

There are various reasons why some of the behaviors recorded in other studies may not yet have been recorded in ours. One very obvious constraint is that water visibility in the Shannon Estuary is poor (< 1 m) compared to other study sites (e.g., Shark Bay, where visibility into the water from the boat is 2 to 8 m; Mann & Smuts, 1999). In this study, we focused exclusively on surface behaviors. Occasional days of good water visibility may present opportunities for documenting underwater dolphin behavior in the Shannon Estuary in the future, but these opportunities are limited. Many clear-water sites have *T. aduncus* rather than *T. truncatus*, and it may be that subtle differences exist between the overall behavioral repertoires of these two different species. In addition, observations were restricted seasonally, and further behaviors might be documented if behavioral observations were made in winter months. As with any catalog of behaviors, the ethogram we developed should be interpreted as an evolving document and not a full list of Shannon Estuary bottlenose dolphin behavior.

There is no evidence to suggest that the presence of either our research vessel or the tour boats had an effect on the behavior of the dolphins. However, land-based research using our ethogram could help to reinforce that the sighting records from boats illustrate the true behavioral repertoire and budgets of the dolphins (although the different perspectives of observing from land vs water might also affect this).

Inter-Observer Validity and Reliability Testing

The high validity and reliability scores obtained in the inter-observer video test by trained research assistants suggest that errors in behavioral data collected for this study did not have a significant impact on our results. The higher results for trained research assistants compared to the other participants indicate that training in the field will remain an important component of good behavioral research. The fact that some behaviors, such as breaches, were misclassified more often than others points to the need for specific attention to such behaviors in the training process. Nevertheless, the relatively high validity and reliability of the test even for other marine biologist participants suggest that our ethogram is well-suited for being used as a research tool by other research groups and for facilitating a behavioral comparison between different populations.

Activity State Budgets

Our results suggest that bottlenose dolphins in the Shannon Estuary spend over half (52%) of their time travelling, a quarter (28%) of their time foraging, and the rest of their time (20%) engaged in all other activities. These results are somewhat similar to Ingram's (2000) for Shannon Estuary bottlenose dolphins: 64% travel, 26% forage, 8% social, and 2% rest, calculated from land-based observational data. A comparison of our results with activity budgets in the literature leads to interesting parallels and some differences: time spent travelling for this population is relatively high (52%), maybe because the habitat is a geographically narrow but long estuary. However, in contrast, another estuarial population (the Port River Estuary, South Australia; Steiner, 2011) had a much lower proportion of travelling (23%), although the estuary shape was quite different. Comparison with the Patos Lagoon Estuary in Brazil (Mattos et al., 2007) is more difficult because of that study's distinction between travel (29%) and travel/feed (22%).

Foraging proportions vary substantially across populations ranging from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012). The Shannon dolphins' foraging budget (28%) is similar to Shark Bay (30%) (Gero et al., 2005; Karniski et al., 2015) and Moreton Bay (34%) (Chilvers et al., 2003). What accounts for such a wide variation in foraging proportions? Presumably it is partly explained by differences in the availability of prey, habitat geography, different nutritional requirements, and foraging strategies hand-in-hand with changing environmental effects. In addition, it is also possible that differences in the vessels used as research platforms might have an effect on dolphin behavior. Christiansen et al. (2010) reported that dolphins (*T. aduncus*) around tour boats were more likely to be travelling or foraging than resting or socializing. A further explanation for behavioral differences is habitat use; depending on where surveys were conducted in a study site, dolphins could be found to be engaging in behaviors related to that part of the survey area.

Social behavior proportions range from 5% in Sarasota Bay to 14% in the Port River Estuary (Waples, 1995; McHugh et al., 2011b; Steiner, 2011). The Shannon dolphins spent 8% of their time engaged in social activity, a similar proportion to Shark Bay dolphins (Gero et al., 2005; Karniski et al., 2015). Interestingly, Shark Bay dolphins have much higher resting rates (37%) than those of other populations used for comparison. Dolphins in the Shannon Estuary spent 7% of their time resting, while bottlenose dolphins in the Patos Lagoon Estuary and Sarasota Bay allocated only 1% of their daytime activity budgets to resting (Waples, 1995; Mattos et al., 2007; McHugh et al., 2011b). Further research should investigate if differences in activity state budgets could help to explain differences found in behavioral event occurrence. For example, dolphins snag much more in Shark Bay than in the Shannon Estuary, and snagging behavior is associated with resting (R. Connor, pers. comm., 25 January 2017). Thus, the fact that the social activity budget is similar in both of these populations may be very important in the further study of the social behavior of Shannon Estuary bottlenose dolphins, especially in comparing the societal complexity of these two populations.

The study population's activity budget was considerably different in different survey years, particularly for foraging and travelling activity.

Dolphins spent less time foraging and more time travelling in 2014, and vice versa in 2015 (with values for 2016 between the values of these two years), and this inter-annual variation in foraging activity is likely to be related to changing environmental conditions in the Shannon Estuary. This, in turn, affects prey distribution and abundance. The differences in activity budget proportions allocated to socializing and resting may be explained by reproduction, with inter-annual calving rates also playing a role in changing activity budgets. There is no clear explanation for the differences between years, but this certainly warrants further attention; and the addition of further years of data may help to explain fluctuations in the activity budget proportions over different years for this population.

Limitations and Further Study

The data used in this article do not distinguish among classes of animals or individuals. It, therefore, was not possible to examine whether there were significant behavioral differences between, for example, males and females or adults and juveniles. Anecdotal observations suggest that head out behavior is displayed more frequently by dependent calves in their first 2 y of life, but this hypothesis needs to be investigated further. In other studies (e.g., Nowacek, 2002), individual dolphins within the same community displayed different, though overlapping, repertoires of foraging behavior. In this study, our observations suggest that one individual, a dolphin with scoliosis, often displayed a head out and tail out in quick succession during a surfacing bout, which was probably related to its deformity. Some individuals seem to leap or tailslap more than others. These and other individual differences need further investigation.

The data used in this article are based on observations of less than 30 min that were made primarily from the opportunistic platform of tour boats adhering to marine regulations (Maritime Safety Directorate, 2005). The data, therefore, provide little information about potentially rare behaviors. In addition, the tour boats often target the same areas, which leads to a sampling bias in survey effort. In other studies, longer observations from dedicated research vessels have identified behaviors that seem unique to particular populations such as sponging (Smolker et al., 1997) and beach hunting (Sargeant et al., 2005). Lusseau (2006a) identified some behaviors in the Doubtful Sound bottlenose dolphin population which relate to cues for the start and end of certain activity states. Longer observations using focal follows and dedicated survey transects may provide greater insights into the role of specific, and rare, behaviors and perhaps of behaviors unique to this population.

The data used in this article were collected over a limited period, primarily during the summers of 3 y. Therefore, a comparison of behaviors between seasons was not applicable, nor was year-to-year variation discoverable over the long-term. Future research over more consecutive years, as well as throughout each year, is necessary to answer questions about how this population's behavior varies over time.

Our ethogram is an extremely useful tool because it likely covers all age classes, sexes, group sizes, and survey areas within the Shannon Estuary. The sampling of different areas provides good coverage of different individuals in the population. On some occasions, both tour boats and the research vessel sampled at the same time on the same day simultaneously (in different areas of the estuary), providing a widespread snapshot of bottlenose dolphin sightings across the study site.

Conclusions

The purpose of this article was to provide the first ethogram for bottlenose dolphins in the Shannon Estuary, to describe and quantify these behaviors, and to compare behaviors documented in this study with those of other studies of bottlenose dolphins in different geographical locations. The ethogram presented contains 11 activity state and 45 behavioral event definitions. The results presented are based on observational records from 3 y of study, and the ethogram behaviors quantified were each recorded at least once for dolphins in the Shannon Estuary, with ten additional behaviors included from anecdotal records. We expect our ethogram to develop over time, adding some of the behaviors reported for bottlenose dolphins elsewhere as, and if, they are observed in the Shannon Estuary. The behaviors reported herein are some of the most frequently observed and documented for bottlenose dolphins in other wild environments; however, this ethogram is the first for temperate European waters and will provide a fundamental tool for future behavioral research.

Activity states and behavioral events recorded in the Shannon Estuary were quantified, and an activity state budget for this bottlenose dolphin population was presented. Bottlenose dolphins in the Shannon Estuary allocated relatively more time to travelling and less to resting compared to other populations. These results make an important contribution to global dolphin research by adding to a remarkably varied set of activity budgets reported for other populations, for which some similarities and some differences are apparent. Overall, this study establishes a foundation for investigating the behavior of the Shannon Estuary bottlenose dolphin population and for engaging in the systematic comparison with other populations necessary for understanding the complex lives of these social mammals.

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Appendix C

Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2017)

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Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations

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Abstract

Social and network analyses that incorporate information on individuals within a population enhance our knowledge of complex species. In this study, the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, was analyzed by examining the dynamics of the whole population and then of individuals classed by sex, age, and area. One hundred and twenty-one dolphins were identified during 522 sightings between 2012 and 2015. The mean half-weight association index (HWI) of the population was 0.07 ± 0.02. The highest HWIs for individuals of known sex were for female-male pairs. Mean within-class HWI was significantly higher than mean between-class HWI for both age and area classes. Ordinations and sociograms were used to visualize social networks. Permutation tests revealed nonrandom associations for the population overall and both between and within classes. Temporal analyses showed associations persisting for >1,000 d. The whole population's best fit model was for two levels of casual acquaintances. Movement analyses demonstrated the use of the inner estuary by only 25% of the population revealing a potential community division by area. The difference between mean HWI when socializing (0.09 ± 0.03) compared to foraging (0.06 ± 0.03) was significant. These results highlight the importance of localized research, reflecting the complexity found in bottlenose dolphin societies globally.

Key words: bottlenose dolphin, social structure, photo-identification, associations, networks, *Tursiops truncatus*, individual classification.

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Social structure, a concept that integrates the ethological interactions and ecological relationships between conspecifics, is a fundamental component of the biology of an animal population (Lusseau *et al.* 2006). For intelligent mammals with complex societies, the social structures of populations are integral to our overall knowledge of the species. Social structure can affect population growth, genetics, and animal movements, and represents an important factor in management and conservation (Whitehead 2008, 2009). Because not all individuals of a species are the same, it is important to explore population demographics and examine the interactions of different members within the social structure of a population. For example, sociality can be driven by individual classes such as sex (Connor *et al.* 2000) or age (Lusseau and Newman 2004, McHugh 2010), or other factors such as habitat use (Wiszniewski *et al.* 2009, Titcomb *et al.* 2015). It is therefore important to take such variables into account during the investigation of a population's social structure.

If nonrandom patterns of association are found in a population, this can suggest the patterning of social relationships that characterizes that society as a whole (Smolker *et al.* 1992). Because of the many spatiotemporal changes in associations in a society, assessing its structure can be difficult, but available quantitative techniques, such as association and network analyses (Whitehead 2008), help to define social structure more precisely and explain observed association patterns (Lusseau *et al.* 2006). Additionally, sophisticated studies of social structure based on identifiable individuals can provide detailed measures and examples of these social systems (Whitehead 2008).

Bottlenose dolphins (*Tursiops* spp.) are highly intelligent marine mammals known to live in extremely dynamic complex social systems referred to as fission-fusion societies (Connor *et al.* 2000). This is one of the most complex social organization systems seen in the animal kingdom (Smolker *et al.* 1992), where large numbers of individuals associate in small groups that change size and composition frequently, at different spatial and temporal scales (Connor *et al.* 2000). Social relationships exhibited by individual dolphins are maintained within a constantly changing social environment where individuals are drawn from a large social network (where they may be present in a wide range of different groups), but associate consistently with just a few other individuals (Smolker *et al.* 1992).

Well-studied bottlenose dolphin societies in Shark Bay, Australia, and Sarasota Bay, Florida, exhibit strong long-term associations between adult individuals of the same sex (Smolker *et al.* 1992, Connor *et al.* 2000, Owen *et al.* 2002, Wells 2014, Connor and Krützen 2015). These associations are characterized by dramatic sex differences in association patterns comprising long-term bonds between males in alliances and looser network associations among female dolphins. In Doubtful Sound, New Zealand, sex-specific alliances were not observed amongst bottlenose dolphins, but some male-female associations were stable over the course of several years (Lusseau *et al.* 2003). However, in well-studied bottlenose dolphin populations in the Moray Firth, Scotland, and Sado Estuary, Portugal, no strong sex-specific associations have been found (Wilson 1995, Augusto *et al.* 2011). In the Sado Estuary, associations are similar between all individuals, with no patterning according to sex or age class (Augusto *et al.* 2011). Thus, it would appear that the sex class of individuals plays a varying role in bottlenose dolphin societies globally.

For long-lived, slow-developing species like bottlenose dolphins, there is a prolonged juvenile period. Typically, most studies tend to focus only on adults because they are more easily identifiable; however, an understanding of juvenile association patterns and social structure is necessary to achieve a full understanding of the social dynamics of a population (McHugh 2010). In some studies that explored age effects, differences in patterns of association have been discovered in relation to age class (Samuels 1996). Exclusively juvenile groups are found in some populations (Wells 2014) and age-related homophily has been found in dolphin social networks (Lusseau and Newman 2004). In other studies where bottlenose dolphin groups do not seem to be segregated by sex or age class, some of these demographically mixed groups have formed socially distinct communities within populations (Lusseau *et al.* 2006).

The study of association patterns with respect to area use is important because differences in area use do not necessarily lead to differences in association patterns and *vice versa*. However, if the social structure of a population *is* related to area use, this has important implications for population management (Lusseau *et al.* 2006, Cantor *et al.* 2012). To answer these questions, sightings of individual dolphins may be classified by area within the study site. Then, association analyses can be used with classifiers to interrogate the data set for potential preferences or avoidances between the classes.

The bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland, is stable and composed of approximately 120 individuals (Berrow *et al.* 2012) and is genetically discrete (Mirimin *et al.* 2011). Dolphins are present in the estuary year-round (Berrow *et al.* 1996, Ingram 2000, Berrow 2009) and have been observed exclusively in the Shannon Estuary and adjacent (<25 km) Tralee and Brandon Bays (Ryan and Berrow 2013, Levesque *et al.* 2016). This species also occurs around the entire Irish coast (O'Brien *et al.* 2009) and in offshore waters (Louis *et al.* 2014) but these are thought to constitute distinct populations (Mirimin *et al.* 2011). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (NPWS 2012), which are listed on Annex II of the EU Habitats Directive. Given the level of protection assigned to this population, information on the social structure of dolphins in the estuary is important for their long-term conservation and the development of a local management plan.

Only two studies to date have investigated the social structure of bottlenose dolphins in the Shannon Estuary (Ingram 2000, Foley *et al.* 2010); however, neither had access to data on individual sex or age, and although Ingram (2000) identified some spatial patterns, these were not based on classifying individuals by area of sighting locations. Our study marks a significant advance on previous work by operating with a much larger set of data and by considering within-population structure based on sex, age, and area.

In describing and analyzing the social structure of a unique population of bottlenose dolphins in Ireland, this paper makes data available for comparisons with similar studies. Studying bottlenose dolphins in varying social systems contributes to current knowledge of social structure and the evolutionary mechanisms that may have affected differences among populations. Knowledge of the social structure of a bottlenose dolphin population contributes to the conservation of the species, especially to population management within SACs and Marine Protected Areas, and helps to understand trends in long-term monitoring.

This paper aims to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland using a 4 yr data set. We begin by (1) examining the social attributes of the population as a whole, and then explore the social dynamics of the population further by classifying individual dolphins by (2) sex, (3) age, and (4) area. We hypothesized that the structure of the population would be similar to that of many other populations described worldwide in several ways, specifically that there would be (1) preferred and avoided associations between individuals,

(2) a pattern of single-sex groups and strong within-sex-class associations, (3) a pattern of single-age-class groups and strong within-age-class associations, and (4) area-based social clustering of the population within the study area as a whole.

METHODS

Study Site

The study site is located in the Lower River Shannon Special Area of Conservation (SAC; Site Code 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland's west coast between County Clare, County Kerry, and County Limerick (52°36′N, 9°38′W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 1).

Data Collection

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow *et al.* 1996, 2012; Ingram 2000; O'Brien *et al.* 2014). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow and Holmes 1999).

Figure 1. Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC; shaded dark gray area) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush.

In this study, surveys were conducted between March and November each year from 2012 to 2015 on board three vessels—the two dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats operated independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 1). The Carrigaholt tour boat concentrated effort in the outer estuary exclusively while the Kilrush tour boat primarily concentrated effort in the inner estuary area with some outer estuary trips. Overall, the mean length of dolphin-watching trips was 2.3 h (Barker and Berrow 2016). The research vessel was a 6 m RIB (rigid-hulled inflatable boat) with a 115 hp outboard motor, with which surveys were conducted throughout all areas of the estuary between Loop Head and Aughinish. Trained onboard observers (n = 19 over 4 yr) located dolphins visually by eye and with the use of binoculars (Minox 7 × 50 or 8 × 42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~5 m, while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at <2 m above sea level. The tour boats had a minimum of one observer and a maximum of six observers per survey while the research vessel had between three and five crew per survey.

A sighting began when at least one dolphin was within 100 m of the vessel and ended after ≤30 min due to national regulations (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and approximately 100 m from them unless the dolphins approached the boat themselves.

Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin IDs, group estimates, environmental measures (including water temperature, depth, and sea state), location (latitude and longitude; Garmin GPS 72H), activity states (travel, social, forage, rest, other, or unknown) and behavioral events (*e.g.*, leap) (see definitions in Baker *et al.* 2017). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh *et al.* 2011).

Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70–300 mm lenses) in an attempt to photograph each individual in each group for individual recognition through the photo-identification of dorsal fins (Würsig and Würsig 1977, Würsig and Jefferson 1990).

Data Management

Photos from all surveys and sightings were maintained in a database using the photographic software environment IMatch 5.6 (https://photools.com/). A digital photo-id catalog housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, based on the nicks and notches along the edge of the dorsal fin, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities, and persistent skin lesions, by using the filter function in IMatch to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then rematched. The final identifications of each individual dolphin in each sighting were verified by the lead researcher, who had the most photo-id experience, as recommended by Pearson *et al.* (2016). The long-term monitoring of this relatively small population, coupled with the high encounter rate, knowledge of life history, and well-maintained photo-id catalog of 204 known individuals (recorded between 2008 and 2016) greatly enhanced the process and efficiency of individual dolphin identification.

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of FinBase (Microsoft Access), a relational sightings database for bottlenose dolphin research (Adams *et al.* 2006). Each dorsal fin photo's quality was graded using the FinBase Photographic Quality form and assigned to its specific sighting and survey using the FinBase Match/Catalog form, wherein the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program. Activity state data originated from the FinBase database, where each sighting was assigned a single predominant activity state (travel, social, forage, rest, other, or unknown) by the observer during data collection.

Data Classification

Sex classification—Information on the sex of individual dolphins was obtained in three ways, using (1) genetic sex determination from biopsy tissue samples (n = 27), collected under NPWS permits (Berrow *et al.* 2002, Mirimin *et al.* 2011); (2) photographs of the genital area (n = 1); and (3) consistent observations with a dependent calf multiple times over multiple years (n = 30; Smith *et al.* 2016). As a result, 47% of known sexes were determined through biopsy sampling and 53% from observational data. For females identified through association with a calf, the number of mother-calf pair sightings ranged from 6 to 92. Overall, 48% of individuals available for analysis were of known sex.

Age classification—Age class was determined by observations of individual size, reproductive state and/or knowledge of long-term life history (unpublished data). Adults were larger and darker in color than juveniles, and sometimes with a dependent calf. Juveniles were less than two-thirds the size of adults and were not observed to be dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years before weaning.

Area classification—The study site was divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush. This line divided the estuary roughly in half, was a reference point for the center of the study area and divided research surveys east and west of the port of Kilrush. A classifier for area was created based on the sighting records of individuals by location, because preliminary evidence suggested differences in the use of the inner and outer survey areas by individuals in the population. If an individual had *ever* been observed in the inner estuary, it was classified as "inner." If an individual had *never* been observed in the inner estuary, it was classified as "outer" (Table S1). This provided a basic classification from which individual area use within the study site could be explored (see map in Fig. 1; Fig. S1).

Data Analysis

Analytical definitions—Data were queried in FinBase and input into SOCPROG 2.7 (compiled version), a dedicated software package that uses data on the associations of identified individual animals for the analysis of their social structure (Whitehead 2009), in group mode, with a supplemental file detailing individual sex, age, and area classifiers. The sampling period was defined as one day, based on the natural break between daylight sampling sessions and because the proportion of individuals sampled within a 1 d time frame was appropriate for data analysis. Associations between individuals were defined by shared group membership, with each record/sighting constituting one group. The half-weight association index (HWI) was used as the coefficient of association. This measure represents the strength of social bonds among individuals (with a range of possible values between 0 [never seen together] and 1 [always seen together]), while also accounting for the possibility of missing individuals during sighting encounters (which is a possibility when opportunistic research platforms like dolphin-watching tour boats are used). The HWI is defined as HWI = $2N_T/(N_a + N_b)$ where N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns and Schwager 1987). Thus, this association index indicates the proportion of time that each pair of individuals is seen in a group together. For all analyses other than the temporal analyses and movement analyses (where all data were used), restrictions were set within SOCPROG to include only individuals with >5 sighting records.

Dependent calves were excluded from analyses because their presence was a result of their mothers' presence in groups. Excluding dependent calves from the data set left adults and juveniles, but for analyses using sex class, only adults were available as sex had not been determined for any of the juveniles. Both adults and juveniles were included in the analyses using area class.

SOCPROG was used to generate basic population data, quantify the number of individuals in defined classes, produce descriptive statistics and examine association patterns between individuals in the population. A discovery curve was plotted to assess photographic coverage of identified population members using cumulative number of identifications and year of sampling.

Group composition, associations and clusters—Group composition was explored by examining the identities of individuals in every group, classifying them by sex and age and calculating overall proportions. Associations between and within sex classes were quantified and compared using a Mantel test and a histogram of proportional HWIs (Whitehead 2009).

Average linkage hierarchical cluster analysis was used to investigate relationships within the inner area class wherein individuals were assigned to clusters (clusters may be semipermanent social units, communities, or other social entities). A cophenetic correlation coefficient (CCC) value >0.8 (where 1.0 = perfect fit and 0.0 = no relationship) and a modularity >0.30 indicate that a dendrogram is an acceptable representation of input distances and its division into clusters is appropriate (Whitehead 2009).

Social networks—Association matrices were visualized as social networks (or sociograms) for all associations with HWI ≥ 0.20 with individual nodes shaded, first by age and then by area class, and weighted links representing strength of association between individuals at three levels. A further sociogram was constructed using cluster analysis results to visualize the clustering of individuals in the inner estuary network.

Weighted social network measures were calculated for all individuals and for age, area, and sex classes separately using the network analysis statistics module in SOCPROG and standard errors were calculated using the bootstrap method with 1,000 replicates. "Strength" was calculated as the sum of association indices of any individual with all other individuals; thus, high strength values indicate strong associations with other individuals in the population. "Reach" was measured as the overall strength of network neighbors.

Behaviorally specific associations and preferences—We used methods similar to Gero *et al.* (2005) to determine whether behaviorally specific preferred associations existed within the population, as it is important to assess the effect of activity state on associations in fission-fusion networks (Gazda *et al.* 2015, Moreno and Acevedo-Gutiérrez 2016). Restrictions were implemented in SOCPROG for each of four main activity states: rest, travel, social, and forage. The data were restricted by each activity state in turn and the HWI matrix was saved as a SOCPROG association measure. Then, SOCPROG's analyses of multiple association measures module was used to view dyadic plots and different dyadic outputs of the association measures. A Mantel test was run to test for correlation between social and foraging HWIs.

Association preferences/avoidances—Permutation tests (Bejder *et al.* 1998, Whitehead *et al.* 2005) were used to test for preferred/avoided associations across the whole population, the null hypothesis being that there were no bottlenose dolphin dyads in the Shannon Estuary population that preferred or avoided to associate. Then, permutations were run to test for preferred/avoided associations within and between classes (age, area, and sex) as well as for each year of data separately (and sex-specific associations within each year) and for activity states (social, forage, rest, and travel). The null hypothesis in each case was that individuals would associate randomly with one another. The real HWI matrix was permuted 40,000 times with 100 trials per permutation for each analysis. Associations were permuted within sampling periods (*i.e.*, days). The test calculates a statistic for the real data and for many permutations of random data (with constraints). The null hypothesis that only random associations exist is rejected if the statistic for real data is greater than the statistic for 95% of the random data ($P < 0.05$) (Bejder *et al.* 1998).

Stability of associations over time—Temporal analyses were used to determine the stability and persistence of associations over time. The lagged association rates were standardized as we could not be certain that all individuals had been identified in every sighting. These standardized lagged association rates (SLARs) were plotted against time lag with moving averages and standard errors calculated using the temporal jackknife method. The null association rate was added to the plots; this represents the theoretical SLAR if individuals associated randomly (Whitehead 2008). Four exponential models were fitted and the model with the lowest Quasi Akaike Information Criterion (QAIC) was determined the best fit, with the ΔQAIC (difference between QAIC and that of the best model) indicating the degree of support for the other models (>10 difference = no support; Whitehead 2008). To determine if sex-specific patterns of association persisted over time, SLARs were plotted for female-male associations using the same methods.

Movements throughout study area—To investigate movements between the two defined areas of the study site, sighting records were filtered and categorized as either Area 1 (inner estuary) or Area 2 (outer estuary). We used movement analyses in SOCPROG to examine how individuals moved among the inner and outer estuary areas of the study site. The lagged identification rate (LIR), the probability that if an individual is identified in the area at any time it is identified during any single identification made in the area some time lag later (Whitehead 2001), was used to assess movements among the two areas. LIRs were calculated for each single area and then between the two areas. We then used overall LIRs to assess movements within and between areas which indicated the general probabilities that individuals would be in the same study area or in a different one after particular time lags (Whitehead 2009).

The number of bootstrap replications was set to 1,000 to calculate bootstrap-estimated standard errors of the LIRs. Again, selection of the best fitting models was determined using the lowest quasi Akaike information criterion (QAIC) value. The QAIC was used (rather than the AIC) to compensate for overdispersed data (Whitehead 2007).

RESULTS

Survey Effort and Photo-identification

Of the 353 surveys (607 sightings) carried out between 2012 and 2015, 312 (522 sightings) contained photos of individually identifiable adult and/or juvenile bottlenose dolphins (Table 1). A total of 136,486 photographs were taken and 45,371 of these were used for photographic analysis of dolphin sightings. A total of 2,948 identifications were made of 121 distinct individual dolphins. On average, 106 individuals (88%) of the 121 identified were sighted each year. Ninety-eight percent of individuals (119) were sighted in multiple years, with 64% of individuals (77) seen in all four study years from 2012 to 2015.

On average, surveys (from all boats collectively) yielded 2.7 sightings of bottlenose dolphins per day, with a mean of 12.2 individual dolphins identified per day (n = 121, range = 1–60), thus about 10% of the adult/juvenile population in this study was identified each day. The mean number of sightings per individual was 24.4 ± 21.7 (n = 121, range = 1–101).

A discovery curve plotting number of individuals identified against cumulative number of identifications reached a clear plateau suggesting good coverage of the population after about 1,000 identifications and that almost all the individuals recorded in 2014 and 2015 were resighted from records in 2012 and/or 2013 (Fig. 2). In fact, no new (adult/juvenile) individuals were recorded during the 2015 field season.

Of the 121 individuals sighted, 58 were of known sex (46 female, 12 male) and 63 were of unknown sex. Age class was divided into 93 adults and 28 juveniles. The area classifier consisted of 33 "inner" and 88 "outer" estuary individuals. Within this, the

Table 1. Summary of survey effort by sampling variable, for sightings containing photos of individually identifiable bottlenose dolphins, in the Shannon Estuary, Ireland. Named vessels are *Muc Mhara* (the research RIB), *Draíocht* (the Carrigaholt tour boat), and *DD (Dolphin Discovery*, the Kilrush tour boat).

Survey effort		2012	2013	2014	2015	Total
No. days		29	50	65	53	197
No. surveys		57	78	100	77	312
No. sightings		95	119	180	128	522
No. sightings by vessel	*Muc Mhara*	1	7	59	15	82
	Draíocht	66	78	52	70	266
	DD	28	30	65	39	162
No. sightings by survey area	Outer estuary	76	96	89	95	356
	Inner estuary	13	17	66	29	125
	Whole estuary	6	6	25	4	41

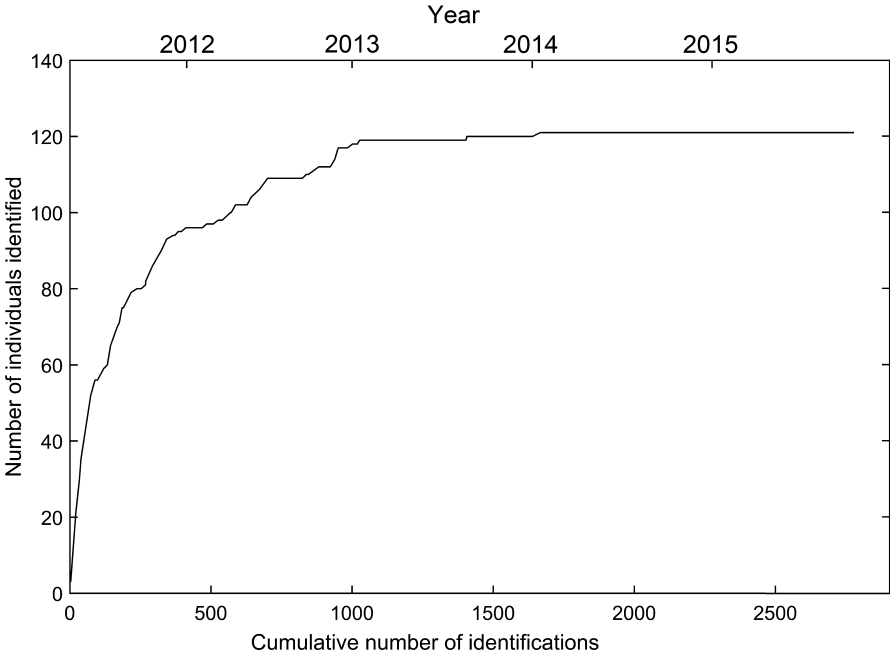


Figure 2. Discovery curve of number of individual bottlenose dolphins identified *vs.* cumulative number of identifications, with year of sampling between 2012 and 2015 (*n* = 121).

inner class consisted of 27 adults and 6 juveniles; the outer class of 66 adults and 22 juveniles.

Group Composition, Associations and Clusters

Of 268 group sightings in which at least one individual was identified as male, 241 (90%) had females present. While, of 450 group sightings in which at least one individual was identified as female, 241 (54%) had known males present. Of the 522 sightings analyzed, 225 groups contained juveniles; only 7% (16) of these groups contained no other age class. The overall proportion of single sex groups *vs.* mixed sex groups could not be determined because 80% of the sightings analyzed contained at least one individual of unknown sex. When restrictions were set within SOCPROG to include only individuals with >5 sighting records, 106 distinct individual dolphins and 519 sightings were available for association and network analyses.

The overall mean HWI of the Shannon Estuary population was 0.07 ± 0.02. The maximum HWI that any individual had with any other individual ranged from 0.16 to 0.72 (mean = 0.41, SD = 0.11, *n* = 106).

When sex was selected as the class variable, and analyses included only individuals of known sex, the HWIs over 0.4 were for female-female and female-male pairs only, with female-male association indices higher than all others (>0.6; Fig. 3). The mean HWI for male-male associations was the highest (mean = 0.1191, SD = 0.0313), and mean female-female (mean = 0.0872, SD = 0.0259) and female-male (mean = 0.0913, SD = 0.0427) association indices were almost equal. However, this may have been due to the much larger sample size for females ($n = 45$) compared to males ($n = 10$). Overall, associations between different sex classes were roughly the same (mean = 0.0913, SD = 0.0402) as those within same sex classes (mean = 0.0930, SD = 0.0294) and the difference between them was not statistically significant (two-sided Mantel test, $t = -0.30$, $r = -0.01$, $P = 0.81$).

In age classes, juvenile-juvenile associations were the strongest (mean = 0.13, SD = 0.04), followed by adult-adult associations (mean = 0.09, SD = 0.02). Adult-juvenile associations were the weakest (mean = 0.05, SD = 0.02). The strongest association recorded in the population was between two juveniles (HWI = 0.72). Generally, associations within same age classes (mean = 0.10, SD = 0.03) were stronger than those between different age classes (mean = 0.05, SD = 0.02) and this difference was statistically significant (two-sided Mantel test, $t = 10.72$, $r = 0.22$, $P = 0.00$).

Similarly, associations within same area classes (mean = 0.11, SD = 0.05) were much stronger than those between different area classes (mean = 0.04, SD = 0.03) and this difference was also statistically significant (two-sided Mantel test, $t = 16.75$, $r = 0.30$, $P = 0.00$). Inner-outer class associations were the weakest (mean = 0.04, SD = 0.02), outer-outer associations were relatively stronger (mean = 0.08, SD = 0.02), but inner-inner associations were by far the strongest (mean = 0.17, SD = 0.06).

Average-linkage cluster analysis of the matrix of HWIs of individuals classified as inner in the bottlenose dolphin population resulted in three clusters, with a maximum modularity (Type 1; controlling for gregariousness) of 0.13 at a HWI of 0.10. IDs 244 and 150 were the most associated individuals with a HWI of 0.72 (Fig. 4). Although the modularity was low (indicating that the division into clusters may not

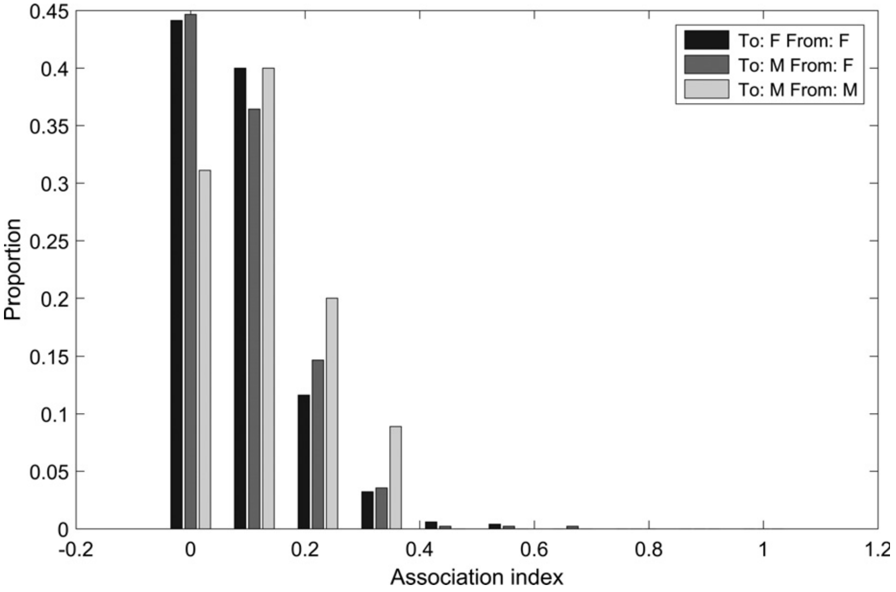


Figure 3. Histogram of half-weight association indices (HWIs) between female-female, female-male and male-male pairs in the Shannon Estuary ($n = 55$).

be appropriate), the cophenetic correlation coefficient (CCC) value of 0.88 indicates that the dendrogram is an acceptable representation of input distances. Thus, inner estuary individuals appear to be clustered into two major groups consisting of 21 individuals and 11 individuals, and a third "cluster" with a single individual (ID 34). A similar cluster analysis of outer class individuals resulted in ten clusters but the CCC value of 0.67 was not high enough to accept the dendrogram as a true representation of individual clustering.

Social Networks

A sociogram was constructed for all individuals analyzed (n = 106) with age classifiers (adult, juvenile), illustrating the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50 and 0.75). The population appears to be somewhat aggregated according to associations by age class, with a major mass of adults associating with adults and two smaller collections of juveniles associating closely with other juveniles (Fig. 5).

Next, a sociogram was constructed for all individuals analyzed (n = 106) with area classifiers for outer (n = 73) and inner (n = 33), with the inner class further divided (using the results of the previous cluster analysis) into three clusters (Fig. 6A). This diagram illustrates the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50, and 0.75). Overall, the population appears to be roughly assembled by association into two groups or communities with a third group of key individuals forming connections between the two major groups, although their associations are weaker than those among the major group members themselves.

The strong associations between individuals within the inner class (n = 33) are apparent in a sociogram of only inner individuals (Fig. 6B) where the clustering of

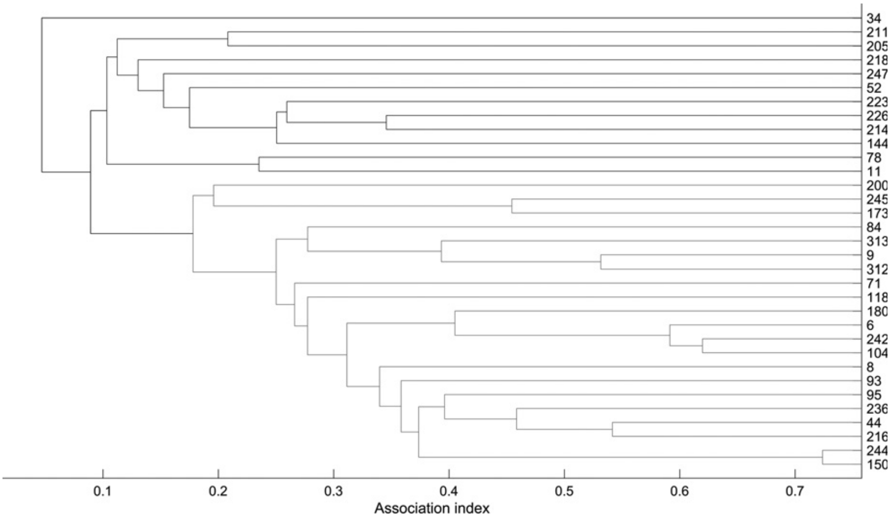


Figure 4. Average-linkage cluster analysis (CCC = 0.88) of the matrix of HWIs of individual bottlenose dolphins classified as inner (n = 33).

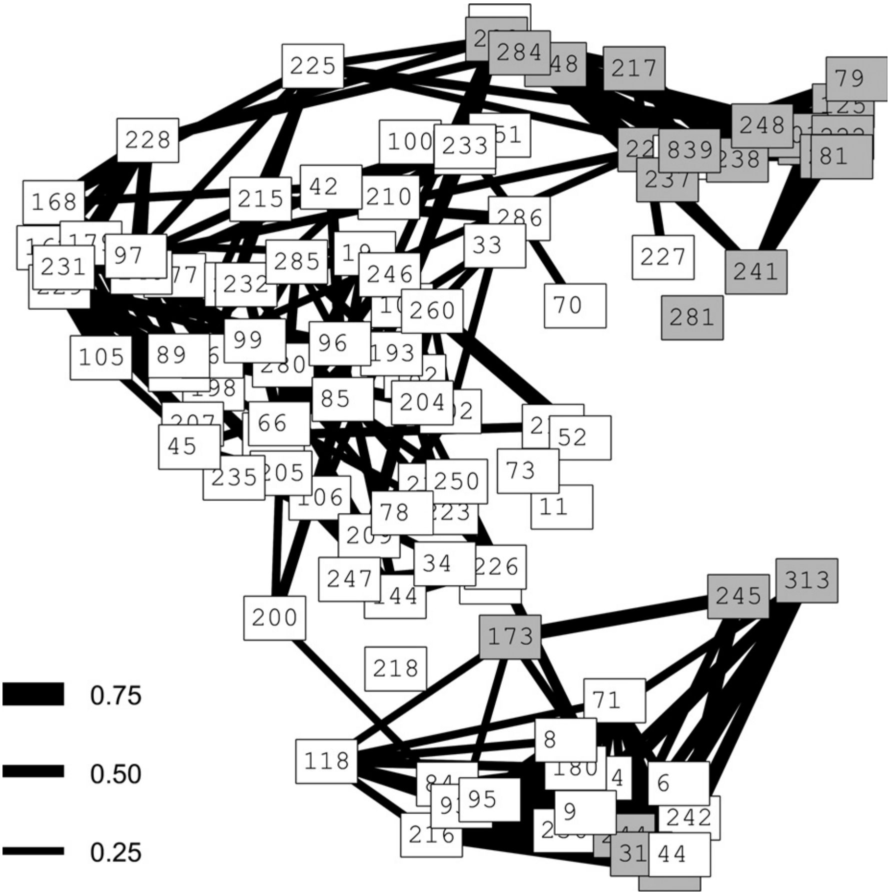
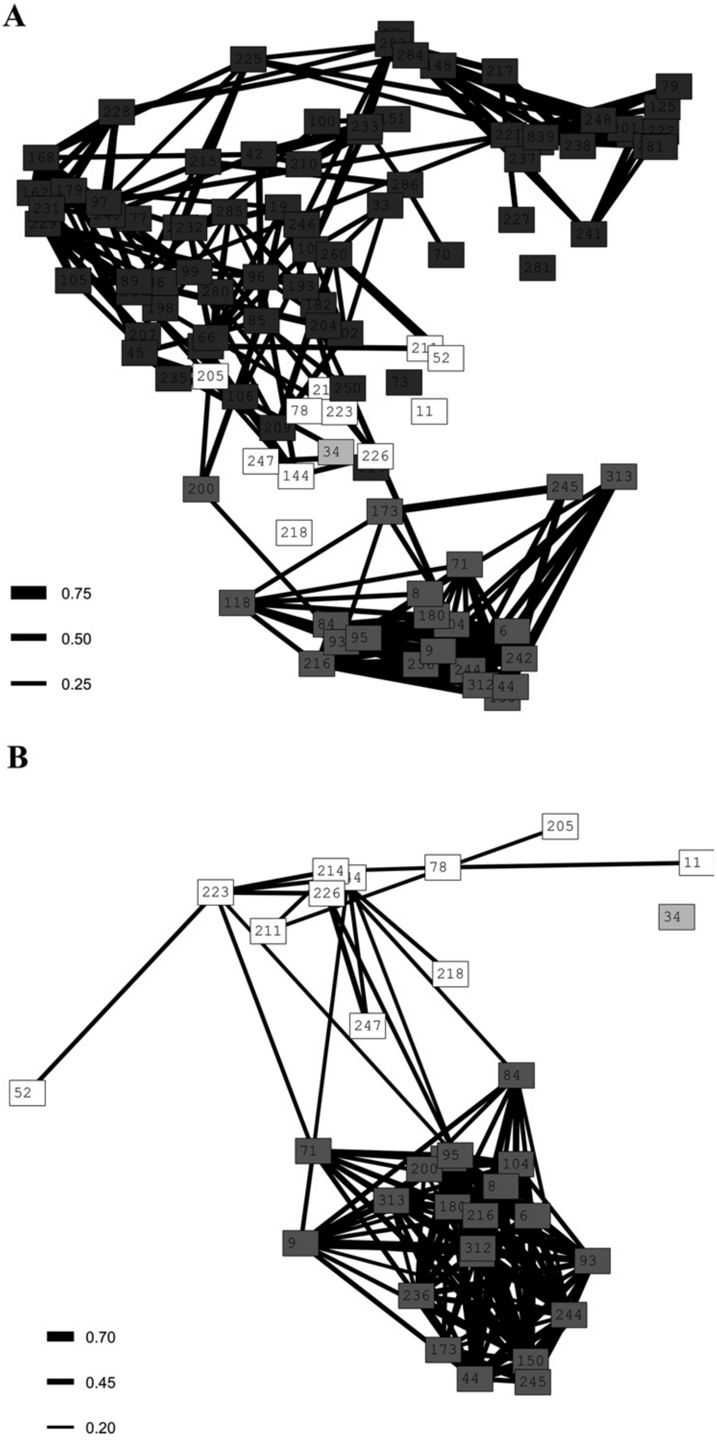


Figure 5. Sociogram of all individual bottlenose dolphins ($n = 106$) with node color for age (adult = white, juvenile = gray), illustrating the social connections between individuals with HWI ≥ 0.25. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

individuals from the cluster analysis is clearly depicted. The major inner cluster of 21 individuals and the other 12 individuals who sit between this major cluster and the outer estuary individuals are apparent.

With further exploration of age class division in the social network, not only do juveniles and adults have closer associations within classes than between, but if each age class is further classed by area, there are clear dissimilarities in association between inner and outer adults and inner and outer juveniles. Thus, individuals of each age group are divided from each other and are further divided within their age groups by their area class.

Social network metrics were calculated for the population overall and for each identified class (age, area and sex) separately (Table 2). For both direct (strength) and indirect (reach) connectedness, the average measures for adults were significantly higher than for juveniles ($P < 0.05$; determined because the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0.20

Figure 6. Sociograms of (A) all individual bottlenose dolphins (n = 106) with node color for area (outer = dark gray, inner = gray, light gray and white) and (B) individuals assigned to the inner class (n = 33) clustered using the hierarchical cluster analysis results into three clusters (gray, light gray and white). The diagrams illustrate the social connections between individuals with (A) HWI ≥ 0.25 and (B) HWI ≥ 0.20. Different scales were used to most clearly illustrate the structure of each network. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

difference in mean values between classes was greater than twice the sum of the bootstrapped standard errors). Similarly, the average measures of strength and reach for females (and unknown sex individuals) were significantly higher than for males ($P < 0.05$), although the small sample size for males may have affected the measures for that class.

Behaviorally Specific Associations and Preferences

Restrictions on sightings based on predominant activity state produced four separate association matrices. The mean HWI for socializing groups was higher (0.09 ± 0.03) than for foraging groups (0.06 ± 0.03). HWIs for pairs of individuals in sightings where the activity state was foraging were significantly different to those in sightings where the activity state was socializing (n = 77, two-sided Mantel Z-test, matrix correlation of association matrices = 0.28, $P < 0.05$). Permutation tests were carried out for sightings of the four main activity states (travel, forage, social, rest). The CVs of the real HWIs were significantly larger than those of the random data for travel ($P < 0.0001$), social ($P < 0.0001$) and foraging ($P < 0.05$) behavioral associations (Table 3). No significance was found for associations calculated for the activity state rest, although this may have been due to the small sample size in this case (only 13 sightings compared to more for other activity states, unpublished data). The significance found for the first three activity states indicated that behaviorally specific preferred associations exist in this population.

Table 2. Social network measures calculated for the Shannon Estuary bottlenose dolphin population overall and by age, area, and sex classes separately. Values are presented as mean ± SD (bootstrapped standard error).

	n	Strength	Reach
Overall	106	7.77 ± 1.91 (0.52)	64.04 ± 17.30 (8.46)
Age			
Juveniles	25	3.21 ± 0.93 (0.37)	11.12 ± 4.06 (2.64)
Adults	81	6.83 ± 1.84 (0.43)	49.94 ± 14.09 (6.39)
Area			
Inner	33	5.28 ± 1.91 (0.31)	31.45 ± 12.97 (3.71)
Outer	73	6.08 ± 1.63 (0.55)	39.60 ± 11.36 (7.40)
Sex			
Female	45	3.84 ± 1.14 (0.30)	15.99 ± 4.95 (2.46)
Male	10	1.07 ± 0.28 (0.11)	1.22 ± 0.27 (0.26)
Unknown	51	3.65 ± 0.91 (0.30)	14.14 ± 4.12 (2.48)

Table 3. Real and random coefficients of variation (CV) of half-weight association indices (HWIs) across age, area and sex class, year (and within year female-male HWIs) and activity state, and pooled for all sightings.

Variable	*n*	CV of real HWI mean	CV of random HWI mean	*P*
Age class				
Adult	81	1.08	0.97	<0.0001
Juvenile	25	1.04	1.01	<0.01
Adult-juvenile		1.53	1.49	<0.0001
Area class				
Inner	33	0.74	0.68	<0.0001
Outer	73	1.14	1.07	<0.0001
Inner-outer		1.31	1.27	<0.0001
Sex class				
Female	45	1.06	0.95	<0.0001
Male	10	0.84	0.80	<0.05
Female-male		1.03	0.98	<0.0001
Year				
2012	88	1.88	1.80	<0.0001
Female-male	37-9	1.55	1.51	<0.05
2013	103	1.71	1.65	<0.0001
Female-male	43-10	1.32	1.31	<0.05
2014	101	1.75	1.63	<0.0001
Female-male	44-10	1.33	1.27	<0.0001
2015	95	2.10	2.02	<0.0001
Female-male	40-8	1.68	1.67	0.31
Activity state				
Social	88	2.22	2.21	<0.0001
Foraging	93	2.21	2.19	<0.05
Rest	47	1.88	0.00005	1.00
Travel	95	2.03	1.95	<0.0001
Overall	106	1.24	1.11	<0.0001

Association Preferences/Avoidances

The overall significance for preferred/avoided associations in the population, using the coefficient of variation (CV) of association indices as a test statistic, was $P < 0.0001$ (CV = 1.24 for real data, compared with CV = 1.11 for mean of randomly permuted data). Thus, the null hypothesis that only random associations exist could be rejected.

When the HWIs within and between classes (age, sex and area) and years were investigated, the CVs of the real HWIs were significantly larger than those of the random data ($P < 0.0001$, Table 3) in most cases, although the strength of significance varied for juvenile-juvenile ($P < 0.01$) and male-male ($P < 0.05$) associations. The persistence of significant results for most variables provides further evidence for rejecting the null hypothesis that there are no bottlenose dolphin dyads in the Shannon Estuary population that prefer or avoid association.

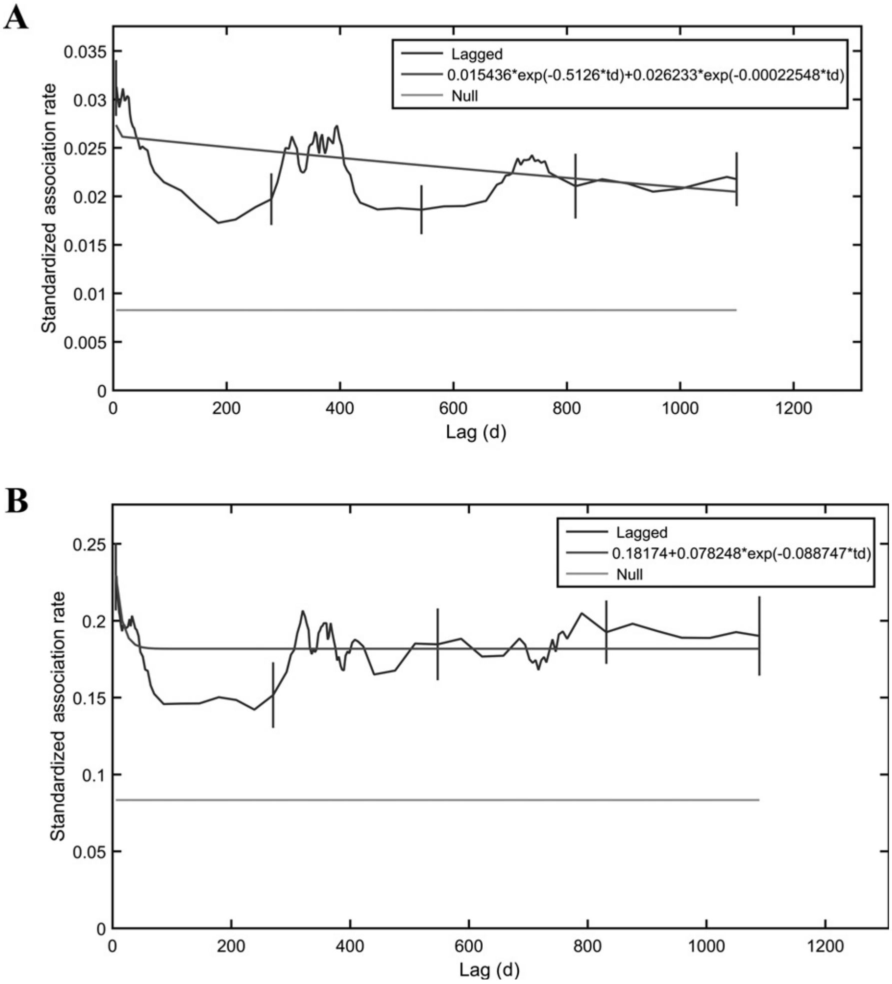

Figure 7. Standardized lagged association rates (SLARs) and null association rate plotted against time lag with best fit exponential model for (A) whole population (n = 121) and (B) female-male (n = 55) associations. Standard error bars (vertical lines) estimated using temporal jackknife method. SLAR curves were smoothed with moving averages of (A) 160,000 and (B) 2,000 associations.

Stability of Associations over Time

Standardized lagged association rates (SLARs) and null association rates were plotted against time lag (with moving averages and standard errors estimated using the temporal jackknife method) for all 121 bottlenose dolphins (Fig. 7A) and four exponential models for SLARs were fitted. The SLARs remain consistently higher than the null association rate; after 1,000 d, the stabilization is still well above the standardized null association rate. The fourth model—"two levels of casual acquaintances"—had the lowest QAIC and so fit best (Fig. 7A). There was no support for the other three models (ΔQAIC > 15).

Interestingly, when female-male association rates were plotted, the best fit model was for "preferred companions and casual acquaintances" (Fig. 7B). This indicates that sex-specific patterns of association may persist over time between females and males at two levels of association—one of "preferred companions" and one of "casual acquaintances."

Movements Throughout Study Area

Lagged identification rates (LIRs) plotted against time lag, among the two areas of the study site, suggest that the probability of an individual being identified in either the inner or outer estuary and then being identified in either area some time later remains almost the same over time (LIRs for inner estuary to inner estuary were higher than all others, at ~0.045). The best fitting models for the probabilities of movements from one area to the other (either Area 1 to 2, or Area 2 to 1) were different for the two cases; for LIRs of individuals moving from the inner to the outer estuary, the first two models indicating a "fully mixed" population fit best, whereas for LIRs of individuals moving from the outer to the inner estuary, the last two models indicating a "migration/interchange" population fit best. The goodness of fit chi-squared value was significant ($P = 0.00$) for all models.

Overall LIRs plotted to assess movements within and between areas suggest that after 200 d, the probability that an individual is in the same study area is higher than the probability that an individual is in a different study area, but after 360 d (and up to 1,100 d) the probabilities are virtually the same for either scenario (Fig. 8).

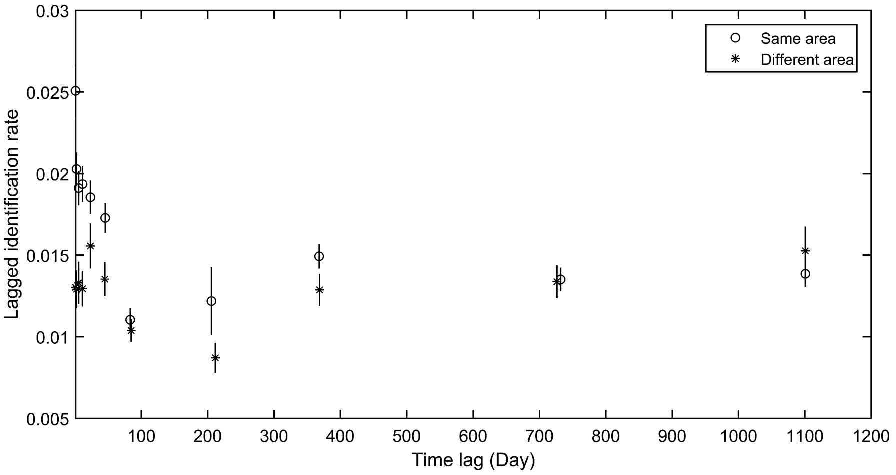

Figure 8. Plot of lagged identification rates against time lag (day) for individual movements within (circles) and between (asterisks) areas of the study site (bootstrap-estimated standard errors (bars) from 1,000 bootstrap replications) of individual bottlenose dolphins sighted in the Shannon Estuary.

Discussion

Research on bottlenose dolphin social structure began in the 1980s (*e.g.*, Wells *et al.* 1987, 1991; Smolker *et al.* 1992) and continues today (*e.g.*, Wells 2014, Connor and Krützen 2015, Louis *et al.* 2015). The structure of many resident populations has been described including in Sarasota Bay, Florida (Wells 2014), Shark Bay, Australia (Connor *et al.* 2001), the St. Johns River, Florida (Ermak 2014), the Aeolian Archipelago, Italy (Blasi and Boitani 2014), Laguna, Brazil (Daura-Jorge *et al.* 2012), Port Stephens, Australia (Wiszniewski *et al.* 2010), and the Sado Estuary, Portugal (Augusto *et al.* 2011). Recently, studies have illuminated the importance of social structure in relation to cetacean culture (Krutzen *et al.* 2005, Mann *et al.* 2012, Cantor and Whitehead 2013) and activity patterns (Gazda *et al.* 2015).

Studies of bottlenose dolphins have shown that the species generally lives in a fission-fusion social system (Connor *et al.* 2000) in which societies encompass both extremely fluid *and* stable associations between individuals (Smolker *et al.* 1992). Individuals within a population associate in temporary groups of variable size and composition, but there can be long-term associations among identified individuals within these fluid groups (Wells *et al.* 1991, Lusseau *et al.* 2003).

This study shows that bottlenose dolphins in the Shannon Estuary fit the general pattern of a fission-fusion society structured by age and area class, but perhaps also characterized by unusual female-male associations. Although individuals in the population associate with many others in a complex social network, significantly strong, persistent and preferred associations exist between individual dolphins. In Sarasota Bay, Florida, dolphin group composition is generally based on within-age and -sex class associations, including groups of females and calves, exclusively juvenile groups, and adult males, typically as strongly bonded pairs (Wells 2014). Our initial hypothesis was that the Shannon Estuary population would contain similar groups; however, this does not appear to be the case. In contrast, groups of dolphins in the Shannon Estuary appear to be composed of mixed sex and age classes although the associations between specific individuals indicate certain between- and within-class social preferences. Similarly, in Shark Bay, although Smolker *et al.* (1992) found groups often contained both sexes, there were consistent long-term associations between individuals of the same sex. This illustrates the difference between group composition and individual association preferences. Additionally, there is little evidence in the Shannon Estuary population for adult male groups, female-calf groups or exclusively juvenile groups.

The mean HWI of the Shannon Estuary population was 0.07 ± 0.02. Several other bottlenose dolphin populations have reported mean HWIs including the Indian River Lagoon (0.010 ± 0.006; Titcomb *et al.* 2015), Cedar Key (0.03 ± 0.08; Gazda *et al.* 2015), St Johns River, Florida (0.05 ± 0.02; Ermak 2014), Sicily, Italy (0.06 ± 0.02; Papale *et al.* 2017), and the Sado Estuary, Portugal (0.45 ± 0.15; Augusto *et al.* 2011). The lowest of these mean HWIs is reported from the Indian River Lagoon where the dolphin population is spatially segregated into six distinct communities in which members of the furthest apart communities have the lowest association indices (Titcomb *et al.* 2015). By contrast, the highest example given here of mean HWI is reported for a very small ($n = 24$) bottlenose dolphin population in the Sado Estuary with strong stable community-wide associations (Augusto *et al.* 2011). These examples show that there is much variation in the observed mean HWI of a dolphin population. The presence of male alliances (with high HWIs) has been linked to population density (Ermak 2014) and this could be a possible factor in the differences found between the mean HWI values of different populations. The insular nature of small, localized or isolated populations may also lead to overall high mean HWIs regardless of within-population social structure.

Associations were not random in the Shannon Estuary dolphin population and this result was significant when applied to sex, age and area classes tested separately. The preference/avoidance of particular associates was also apparent for each year of data tested separately which further indicates the strength of this result as a representation of nonrandom population level associations.

The temporal stability of bottlenose dolphin social structure globally varies drastically, from being driven by constant companionship (Lusseau *et al.* 2003) to featuring casual acquaintances that last just a few days (Lusseau *et al.* 2006). Preferred associations in the Shannon Estuary dolphin population persisted over 1,000 d. The peaks in associations for all individuals after approximately 365 d and 730 d are most likely an effect of cyclical summer sampling periods. The best fitting model was for "two levels of casual acquaintances" associating and dissociating at two different time scales. The two time scales may simply be explained by the periods within and between field seasons. However, the two different levels of disassociation might also relate to the associating and dissociating of individuals within two separate classes; for example, age class and area class. Whitehead (2008) also similarly suggests that this type of SLAR might indicate the fission/fusion of nearly permanent social units into and out of subgroups on the short time scale and transfers between units on the longer one.

Although, as explained above, the line between the inner and outer estuary was based simply on dividing the study area into two roughly equal parts and reflecting operational issues, it turned out to be a useful reference point for tracking the movement and associations of individuals. The probability of identifying an individual in the inner estuary and then identifying it again in the inner estuary sometime later remained high over time. The same was true of outer estuary to outer estuary, although to a lesser extent. These results may represent some long-term site fidelity of individuals to certain parts of the estuary. The best fitting models for individuals moving from the inner to the outer estuary were for a "fully mixed" population. As all individuals who have been sighted in the inner estuary have also been sighted in the outer estuary, it follows that the population mixes in this area. The opposite was true of the best fitting models for individuals moving from the outer to the inner estuary which were for a "migration/interchange" population. Perhaps this can be explained by the fact that only a small number of individuals (~25% of the population) use the inner estuary, and thus would be returning to that area from the outer estuary over time. Overall rates suggest that individuals are more likely to be identified in the same study area after 200 d, but either the same or a different study area after longer periods. Perhaps this is suggestive of within-season site fidelity to either the inner or outer estuary. The use of the inner estuary by only a small percentage of the population seasonally has strong implications for management of the population as a whole, especially if other individuals are likely to go from the inner to outer but not likely to enter the inner area from the outer area during one season. For example, the degree of exposure to anthropogenic threats would be different for individuals of the inner and outer area classes.

There was good evidence for behaviorally specific preferred associations in the population with the mean HWI for socializing groups significantly higher than for foraging groups. The presence of preferred/avoided associations in sightings where individuals were engaged in either social or traveling behavior was highly significant, compared to slightly less significance during foraging activity. The low sample size for sightings of resting behavior may have had an effect on the lack of significance for this activity state. The difference in the level of significance for associations during foraging behavior *vs.* social or traveling behavior is interesting as Gero *et al.* (2005) similarly found that bottlenose dolphins have lower level "acquaintance"-type HWIs when foraging compared to socializing. This evidence for behaviorally specific preferred associations points to the behavioral flexibility of these dolphins and their ability to adjust their social patterns to optimally fit each of various behavioral situations.

Sex Class Associations

For adult individuals of known sex, the highest HWIs were for female-male pairs. Contrastingly, Smolker *et al.* (1992) found that female-male associations were generally inconsistent and primarily within the lowest HWI class in their study. In our study, the mean HWI of male-male associations was higher than the others; however, the much larger sample size for females may have affected this due to the incorporation of some female-female associations with low HWIs into the calculation of the overall mean for that sex class. Similarly, the very small sample size for males may have obscured association patterns for that sex class. Associations between different sex classes were similar to same-sex associations, and their difference was not statistically significant. Even so, the high mean HWI for male-male associations provides a good justification for further research with an increase in sample size of known males in the population. In the reporting of the societal attributes of cetacean social structure, one of the most frequently assessed aspects is sex-specific differences in patterns of association, and contrastingly, in other bottlenose dolphin studies, these associations are often stronger between members of the same sex (*i.e.*, within-class; *e.g.*, in Shark Bay, Smolker *et al.* 1992). In Sarasota Bay, adult females interact extensively with other females and adult males typically form strong male associations or alliances (Wells *et al.* 1987, Owen 2003)—features that do not seem to be present in the social characteristics of the Shannon Estuary bottlenose dolphin population.

When permutation tests were used to test for preferred/avoided associations between females and males, significance for nonrandom associations was apparent in the overall analysis. Thus, female and male bottlenose dolphins in the Shannon Estuary do not associate at random. However, when each year of data was tested separately, one year (2015, with 48 individuals of known sex) did not result in significant preferred/avoided female-male associations ($P = 0.31$). This year had the lowest number of males at eight individuals and it may be that significance could not be found within the small sample size.

Stable long-term female-male associations have been recorded in bottlenose dolphin populations in Doubtful Sound, New Zealand (Lusseau *et al.* 2003) and in Port Stephens, Australia, where constant companionships occur between females and males (Wiszniewski *et al.* 2010). Associations between female and male dolphins in the Shannon Estuary continued steadily over long time scales (>1,000 d), indicating that female-male associations are more long-lasting than the general associations of individuals in the population as a whole. The best fit model was, again, for two levels of disassociation, but this time for "preferred companions and casual acquaintances," indicating that sex-specific patterns of association may persist over time between females and males at both strong and weaker levels of association. As with the general lagged association rates, this result may simply reflect the gaps between field seasons, but it is possible that the stronger associations (the "preferred companions" level) might hold interesting information with respect to the mating system of this population.

Although only 52% of individuals in the current study were of known sex, there were no apparent divisions in the social network explained by the sex of individuals. In the Shark Bay social network, females tended to form longer chains of associates than males and almost every female was connected to all other females by a chain of consistent associates (Smolker *et al.* 1992). The significantly higher measures of strength (direct connectedness) and reach (indirect connectedness) found in our study substantiate the idea that female dolphins in the Shannon Estuary are also better connected than males.

More information on the life history of the Shannon Estuary bottlenose dolphin population will provide necessary data to assess the influence of female reproductive state on female-male relationships which has been shown to have a strong effect on differences in the consistency of female-male associations in other populations (Smolker *et al.* 1992). In Sarasota Bay, sexual segregation of males and females is common outside of the breeding season (McHugh 2010). It would be pertinent to gather more winter data on the Shannon dolphins to assess potential differences in their social structure, particularly with this in mind, as it is known that dolphins are present in the estuary during winter months (Berrow 2009). If additional winter data could be collected, analyses of year-round social associations could point to seasonality-related changes in the social structure of the population.

When combining the social analysis and group composition investigations, there was no evidence of all-male groups or the presence of male alliances that occur in other populations such as Shark Bay (Connor and Krützen 2015), Sarasota Bay (Owen *et al.* 2002), the Bahamas (Parsons *et al.* 2003, Rogers *et al.* 2004), and Port Stephens, Australia (Moller *et al.* 2001). There was similarly no evidence for long-term male-male associations such as those in Bunbury, Australia (Smith 2012), or the Moray Firth and Cardigan Bay (Sim 2015). Additionally, it is unusual to find relatively strong female-male associations in bottlenose dolphins, such as we have in this present study, so this warrants further research. There are various reasons why significant female-male associations might exist in a population, such as increased reproductive success (through increased mating opportunities, female mate choice, mate guarding, or increased access to food resources), reduced risk of infanticide or reduced harassment by other group members (Owen *et al.* 2002, Haunhorst *et al.* 2017).

Associations by Age

Juveniles and adults had stronger within-class associations than those between age classes. The strongest association recorded in the population was between two juveniles, suggesting that the formation of strong associations early in life may be important in this population or might perhaps be related to maturing in the same age cohort, similarities in habitat use or kinship. Some other bottlenose dolphin populations typically contain exclusively juvenile groups (*e.g.*, Shark Bay, Smolker *et al.* 1992; Sarasota Bay, Wells 2014). Gero *et al.* (2005) observed a higher frequency of behavioral associations between juveniles than among any other relative age category in Shark Bay, while Smolker *et al.* (1992) noted that the most consistent preferential associations tended to be between subadults. In Sarasota Bay, young animals typically socialized at higher rates than adults, and juveniles preferred to interact with other juveniles and calves, and avoided adults (relative to their availability in the Sarasota Bay community) (McHugh 2010).

Samuels (1996) found that female juvenile dolphins in Shark Bay had stronger associations with adult females (their mothers) and other juvenile females than with male juveniles, while the top-ranked associates of juvenile males were other juvenile males and not adults or juvenile females. Similarly, juveniles in Sarasota Bay showed a marked preference for associating with other juveniles, especially of their own sex (McHugh 2010)—juvenile females interacted with more adult females and calves than males, while males interacted with more juvenile males than females did. McHugh (2010) suggested that differences between the association patterns of male *vs.* female juvenile dolphins might relate to their future reproductive roles in relation to calf-rearing and male mating strategies. Unfortunately, it was not possible to test sex-based differences in juvenile associations in the current study due to lack of data on the sexes of juvenile animals.

There are various potentially beneficial reasons why juveniles might form preferential groups with other juveniles. While the formation of groups is often to reduce predation risk in other populations, the lack of any known predators of bottlenose dolphins in the Shannon Estuary suggests this is an unlikely cause. It is possible that juvenile dolphins might benefit from associating in groups to increase foraging efficiency, perhaps *via* increased efficiency of prey detection or capture (McHugh 2010). A third potential reason for juvenile-juvenile associations is socialization, wherein social interactions may be particularly important for young bottlenose dolphins due to the complex nature and fluidity of fission-fusion social systems and the long time period over which many relationships may develop (Kaplan and Connor 2007, McHugh 2010). Indeed, Stanton and Mann (2012) found that the survival of juvenile male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, could be predicted by the social bonds they formed as calves earlier in their lives.

In Doubtful Sound, New Zealand, evidence suggests that age-related homophily in bottlenose dolphin networks can influence the formation of clusters of preferred companionship (Lusseau and Newman 2004). Although somewhat mixed, there were clusters in the social network of the population for juveniles and adults. Adults had stronger social network measures for strength and reach than juveniles, meaning they had more direct and indirect connections to the rest of the network. Lusseau (2003) found that the social network of bottlenose dolphins in Doubtful Sound was held together by key individuals creating hubs for associations between other individuals and that these individuals were often older adults. In our network diagrams, the 12 inner estuary individuals who are not part of the core inner estuary cluster were located between that core group and the rest of the individuals in the overall population network diagram and were all adults, suggesting that they might play a similar role in linking the connections of associated individuals in this population.

Associations by Area

The classification of individuals by sighting area revealed an interesting social division in the population. Inner individuals, that is, individuals who had been observed at least once in the inner estuary, had strong associations with inner individuals and, overall, within-area-class associations were stronger than between-area-class associations. Inner and outer estuary individuals had the lowest association indices; a similar result was found by Titcomb *et al.* (2015), where the lowest association indices were among individuals at the study site's northern and southern boundaries.

Dolphins in different habitats experience different environmental pressures which may influence individual association patterns (Smolker *et al.* 1992). Ecological factors, such as resource availability and distribution, might cause a population to split into two social units related to differences in habitat use or foraging specializations. If there were two key foraging areas, as suggested by the differences in habitat utilization described by Ingram and Rogan (2002), this could lead to niche partitioning in the Shannon Estuary. In some populations, bottlenose dolphins have formed communities defined as "associated individuals with long-term site fidelity to a specific area" (Wells 1986, Urian *et al.* 2009). Chabanne *et al.* (2017) suggest that a dolphin community might constitute a relevant local population comprising a total number of animals that could be affected by a proposed development and representing a population unit of some biological significance. Although all of the bottlenose dolphins in the Shannon Estuary use the outer estuary area of the study site, the differences in association between and within individuals in the inner and outer classes fits Croft *et al.*'s (2008) definition of a community as a group of individuals that are more associated amongst each other than with the rest of the society, and it might be appropriate to employ the term "community" to describe these two social units.

The cluster analysis of inner individuals divided them into two main clusters. The largest cluster was a core group of 21 individuals who most frequently used the inner estuary area. Twelve other inner estuary individuals in the other major cluster appear to form a connection between this core inner group and the outer estuary individuals. These 12 individuals were all adults and had some of the highest betweenness centrality measures (*i.e.,* the number of shortest paths between other nodes/individuals that pass through that node/individual; Whitehead 2008) of the population further indicating the importance of their place in the overall network as individuals connecting other individuals. (A third "cluster" was assigned to a single individual who did not have any HWIs > 0.2 with any other individual in the inner estuary network.) Similarly, Lusseau and Newman (2004) found some individuals that they described as "playing the role of broker" in their dolphins' social network and highlighted the importance of individuals that have preferred companionships in two communities, thus linking them together in a larger social context.

Additionally, when the age of individuals classified by area was taken into account, the social network divisions between inner and outer adults were apparent but especially clear were the divisions between inner and outer estuary juvenile dolphins. These six inner estuary juveniles (21% of all juveniles and 18% of inner estuary individuals) represented a key cohort within the inner estuary social unit.

It is important to emphasize that the clustering of these groups does not follow from the classification of the population by area: there is no reason in principle why the associations between individuals only observed in the outer estuary should be higher than those between these individuals and individuals who are sometimes observed in the inner estuary. The data presented here are necessary to substantiate the connection between area class and association. Similarly, Lusseau *et al.* (2006) found that their identification of two separate social units which mainly used two different areas was the result of genuine social affiliation and not an artefact of spatial distribution. Cantor's (2012) work on spatiotemporal dynamics in a dolphin society found that spatial distribution did not influence the probability of individuals associating with one another.

"Spatiosocial" divisions in bottlenose dolphin networks can be related to many factors, including the geography of the study site (Wells 2014, Titcomb *et al.* 2015), individual ranging patterns (Lusseau *et al.* 2006), habitat preferences (Wiszniewski *et al.* 2009) or differences in cultural behavior (Mann *et al.* 2012). Overall, this apparent division of the population into two social units which correspond to area use within the study site is an important finding for management of the population as a whole.

Conclusions

The purpose of this study was to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, with the inclusion of additional data on sex, age, and area class for individual dolphins. Social analysis of the whole population revealed groups of mixed composition and variation in association measures across individuals. There is strong evidence that associations between bottlenose dolphins in the Shannon Estuary are not random and that they persist over time. There is also evidence that association measures are related to behavioral state.

Through the classification of individuals by sex, age, and area, important class-determined associations that were somewhat apparent between sex classes were found, but especially strong for within-age and within-area class relationships. Although the strength of female-male associations could not be absolutely determined, the results suggest that female-male associations persist without decline over periods of more than three years. Social network analyses illustrated the preferences of juveniles to associate with juveniles and adults with adults.

Movements between the inner and outer estuary areas of the study site were quite stable over time but use of the inner estuary was limited to a quarter of the population's individuals exclusively. This inner estuary social unit was further divided into a core group of individuals and another group with associations linking core group members and outer estuary individuals. This division in the social structure with respect to area use has important implications for management. This dolphin population has traditionally been managed as one unit, however this study, mirroring others such as in the Moray Firth, Scotland (Wilson *et al.* 2004, Lusseau *et al.* 2006), shows that it may be appropriate to consider the dynamics of the population's social structure in terms of area use when defining management guidelines, especially when the inner estuary is used by such a small (and therefore potentially vulnerable) number of individuals.

This study increases our knowledge of bottlenose dolphin social structure and could be used for comparative studies, to explore similarities and differences in bottlenose dolphin population dynamics. It is unique in its coverage of a moderately sized bottlenose dolphin population in Europe with considerable data on individual sex and age. The results presented have demonstrated the importance of investigating local social behavior in a species known to show a high degree of behavioral plasticity, and provide additional material for cetacean scientists to better understand bottlenose dolphin societies in all their variety. Furthermore, an understanding of the social structure of this population, especially because of its presence within a Special Area of Conservation designated for the species (NPWS 2012), is critical. The findings of this research will contribute to the management and conservation of this important dolphin population in Irish waters.

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SUPPORTING INFORMATION

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Table S1. The number of sightings in the inner estuary and outer estuary survey areas for each individual dolphin (3-digit ID code) and the area class assigned to each individual for analysis.

Figure S1. Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. Sightings of individual dolphin IDs are classified by area as "Outer Estuary" (triangles), "Inner Estuary (≥4 sightings)" (circles), and "Inner Estuary (≤3 sightings)" (squares), and correspond to area classifications for each individual in Table S1.

Appendix D

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PHOTO-IDENTIFICATION OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN TRALEE BAY AND BRANDON BAY, CO. KERRY: A CASE FOR SAC BOUNDARY EXTENSION

Stephanie Levesque, Katharina Reusch, Isabel Baker, Joanne O'Brien and Simon Berrow

ABSTRACT

The Lower River Shannon is a Special Area of Conservation (SAC) with bottlenose dolphins (*Tursiops truncatus*) as a qualifying interest, and is one of only two SACs for this species in Ireland. Bottlenose dolphins in the Shannon Estuary are present year-round and genetically discrete from other populations in Ireland. They have regularly been reported from Tralee Bay and Brandon Bay, Co. Kerry, adjacent to the Lower River Shannon SAC boundary. In order to determine the provenance of these dolphins, photo-identification data collected between 2008 and 2016 from both bays were used to identify individuals and match them to existing bottlenose dolphin catalogues in Ireland. Bottlenose dolphins were observed on over 90% of the 13 trips carried out, with photo-identification data collected on 11 of these trips. A total of 70 individual dolphins were identified, of which 67 have been regularly recorded within the Lower River Shannon SAC, confirming them to be from this population. Shannon dolphins represented an average of 98% of dolphins photographed during each survey. Of the estimated 108 individual adult dolphins extant in the Shannon population, 62% were identified in Brandon Bay and/or Tralee Bay during the study period. A discovery curve of individuals identified did not reach a plateau, suggesting that not all dolphins occurring in these bays were photographed during the study. Results suggest that these areas are of high importance to the Shannon dolphin population and support the need to extend the current boundary of the Lower River Shannon SAC to include Brandon Bay and Tralee Bay.

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are widespread in Irish coastal waters and are particularly abundant along the western seaboard (Berrow *et al.*, 2010). Three genetically discrete populations have recently been described in Ireland; one resident in the Shannon Estuary, one inshore or coastal population and one offshore population (Mirimin *et al.*, 2011; Louis *et al.*, 2014). The coastal population is highly mobile with resightings of the same individuals reported all around the Irish coast, including Northern Ireland (O'Brien *et al.*, 2009), with some individuals also reported from Scotland and England (Ryan *et al.*, 2010; Robinson *et al.*, 2012).

European member states under the European Union Habitats Directive are required to designate Special Areas of Conservation (SACs) for bottlenose dolphins to protect a representative range of habitats used by this species. The Lower River Shannon SAC (Site Code 002165) was designated in 2000 and includes bottlenose dolphins as a qualifying interest, particularly the Shannon Estuary's resident population. The West Connacht Coast SAC (Site Code 002998) was designated in 2013 solely for bottlenose dolphins and covers an area from North Mayo to West Galway.

SACs, which incorporate marine habitats or species, can be considered as Marine Protected Areas (MPAs). The International Union for Conservation of Nature (IUCN) defines an MPA as 'a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values' (IUCN, 2012). In order for the MPA to be an effective conservation tool, its boundaries must reflect the biological needs of the focal species (Wilson *et al.*, 2004). Managers must have a thorough knowledge of a population's entire distribution in order to allow for the development of successful management and monitoring programmes (Hastie *et al.*, 2003).

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Monitoring programmes may assist in identifying distribution patterns and thus provide vital information to support and advise management decisions (Hastie *et al.*, 2003). Furthermore, they may aid in the identification of critically important habitats, which consist of 'functioning ecological units required for successful breeding and foraging' (Harwood, 2001) whose existence are vital for the species to persist (Jax *et al.*, 1998). In addition to key feeding and breeding sites, critical habitats also include important migration corridors and should be prioritised when considering the placement of MPAs (Hooker and Gerber, 2004). In more recent years, conservation efforts regarding marine species have begun to focus more on the protection of these areas (Agardy, 1994).

MPAs must be large enough to provide suitable protection for the species, yet small enough to allow for effective management of anthropogenic activities within their borders (Ashe *et al.*, 2010). Potential threats to the species within the area must be evaluated in the initial stages of MPA development, and regulations established for how these threats will be managed (Hooker and Gerber, 2004). The management of the Lower River Shannon SAC has been successful in modifying human behaviour through requiring consent for any activity occurring within its boundaries which may have a negative impact on the bottlenose dolphin population (SIFP, 2013).

Current evidence suggests that the population of bottlenose dolphins in the Shannon Estuary is restricted to the estuary and genetically discrete from the inshore population (Mirimin *et al.*, 2011). These Shannon dolphins have rarely been recorded outside of the estuary with the furthest report coming from Sauce Creek, Co. Kerry, *c.* 30km to the west of Kerry Head (Fig. 1) (Montagu, 1821). There are regular reports of bottlenose dolphins to the north of the Shannon Estuary from Kilkee Bay, Doonbeg Bay and Lahinch Bay, Co. Clare and to the south from Tralee Bay and Brandon Bay, Co. Kerry (Fig. 1) (Berrow *et al.*, 2010) although it is not known if these are Shannon dolphins or members of the inshore population. It is essential to determine which population they are from and the range of the Shannon population outside the SAC boundary, which extends between Loop Head and Kerry Head (Fig. 1).

Although it is generally considered that bottlenose dolphins in Tralee Bay and Brandon Bay in North Kerry are most likely from the Shannon population, there have been no studies to validate this hypothesis or to establish their occurrence and use of the bays. The present study used photo-identification

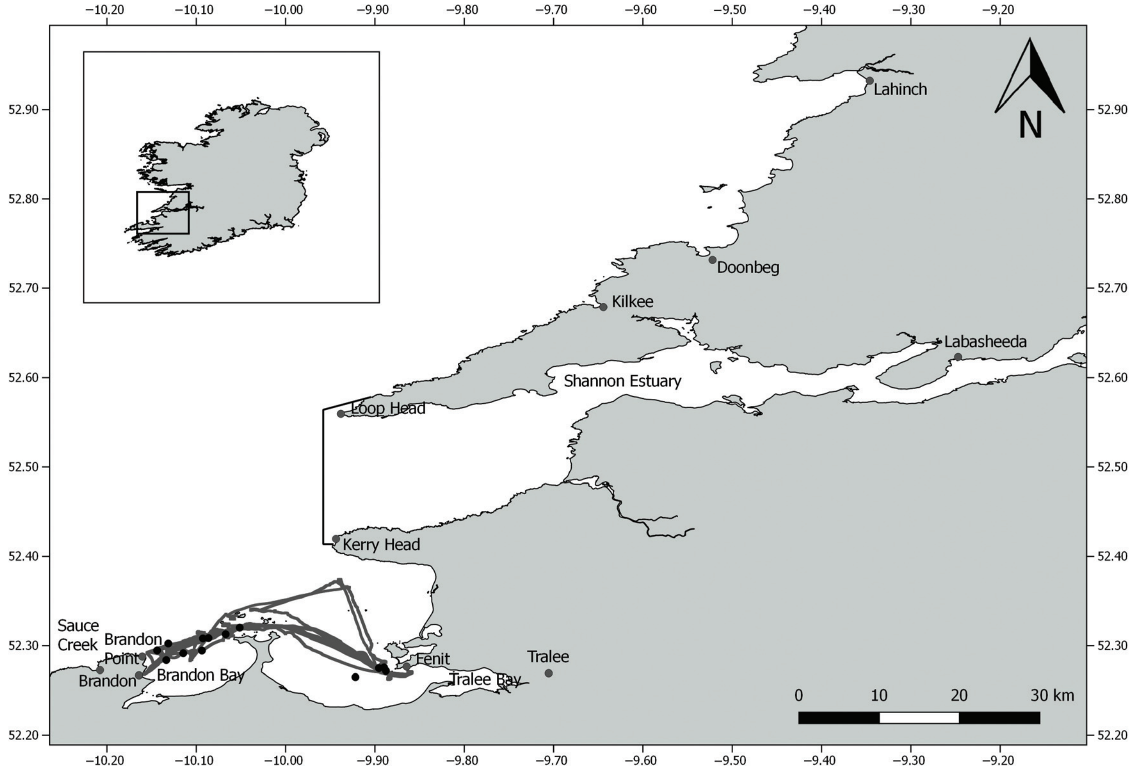

Fig. 1—Bottlenose dolphins are seen regularly from Doonbeg Bay, Kilkee Bay and Lahinch Bay, although no studies have been done to discern which population they are from. Some individuals seen in Brandon/Tralee were also observed as far east as Labasheeda Bay; a distance of 100–120km. Study area is shown with group sightings (black points) and survey tracklines. The black line between Loop Head and Kerry Head represents the boundary of the Lower River Shannon SAC.

(photo-ID) data to discern if dolphins occurring in Brandon Bay and Tralee Bay are indeed part of the Shannon population.

Photo-ID is a non-invasive method of monitoring individuals in a wild population that relies upon the presence of unique markings on the animal (Würsig and Jefferson, 1990). This technique has been widely used in the study of a range of cetacean species worldwide (Berrow *et al.*, 2012) and was first applied to bottlenose dolphins by Würsig and Würsig (1977). Bottlenose dolphins are a suitable species for photo-ID as they frequently acquire markings such as nicks and notches, located primarily on the dorsal fins, allowing them to be identified as unique individuals. This method allows for individual dolphins to be monitored over time and can provide useful information regarding life histories, habitat preferences, distribution, movements, behaviour and associations (Hammond *et al.*, 1990; Kerr *et al.*, 2005).

The Shannon Dolphin and Wildlife Foundation (SDWF) has been collecting images of dolphins in the Shannon Estuary since 1993 (Berrow *et al.*, 1996). Over this period, they have built up a photo-ID catalogue of 204 individual dolphins recognisable by unique markings on their dorsal fins. The best estimate of the current population size according to SDWF records is 136 individuals (108 adults, 28 calves). Due to the availability of long-term data on the population, all individuals in the catalogue can be identified when resighted as any changes in appearance have been tracked over time—a prime example of the value of long-term monitoring. This allows researchers to identify animals that otherwise may be considered too poorly marked for re-identification and result in the loss of data on the population.

The aim of this study was to survey Tralee Bay and Brandon Bay in an attempt to locate and photograph bottlenose dolphins in order to determine if they were from the Shannon population by comparing them to individuals from the SDWF catalogue. In doing so, we hoped to provide evidence that these bays are regularly used by the protected Shannon bottlenose dolphin population and represent important habitats that should be included as part of the Lower River Shannon SAC.

MATERIALS AND METHODS

STUDY AREA

Tralee Bay and Brandon Bay in Co. Kerry are located 20–30km southwest of the mouth of the Shannon Estuary (Fig. 2). Eight dedicated surveys departing from and returning to Fenit, Co. Kerry (Fig. 2) were carried out in the bays onboard Celtic Mist, a

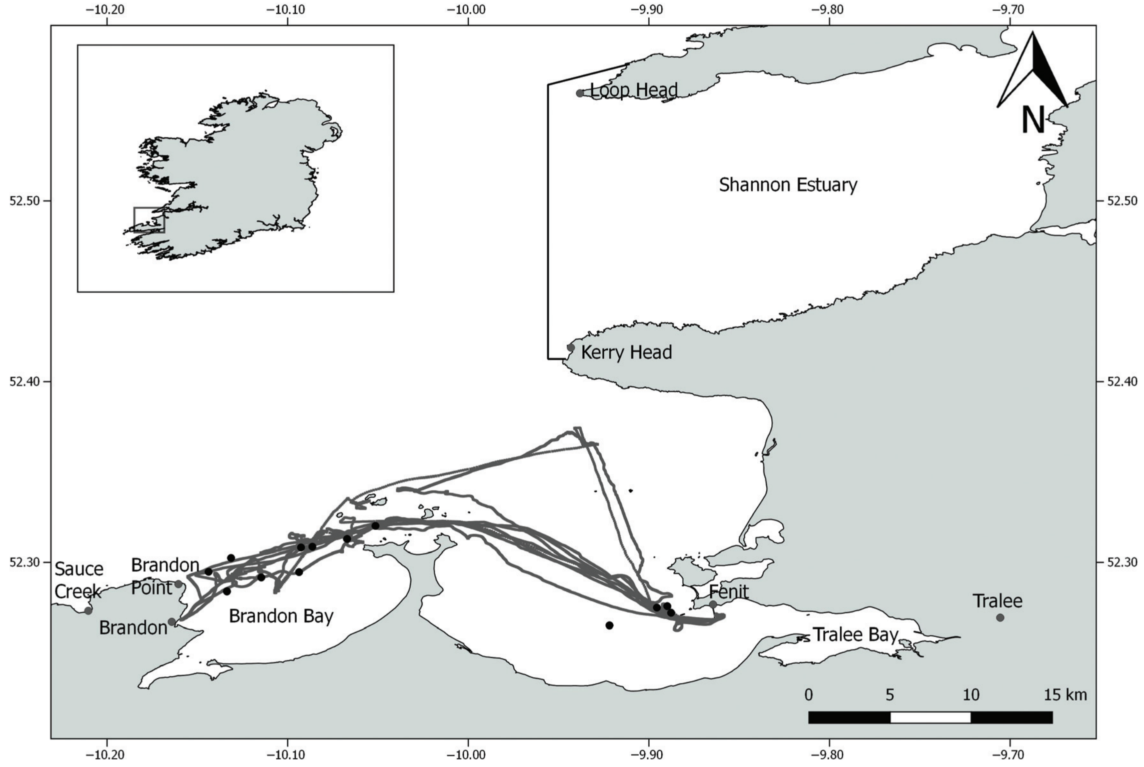

Fig. 2—Brandon Bay/Tralee Bay study area with group sightings (black points) and tracklines from opportunistic and dedicated bottlenose dolphin surveys. The black line between Loop Head and Kerry Head represents the boundary of the Lower River Shannon SAC. See Table 1 for GPS sighting and trackline trip details.

17m sailing yacht with a 360hp caterpillar diesel engine, in search of bottlenose dolphins from 18 May to 25 August 2013 (Berrow and O'Brien, 2013). Efforts were made to conduct surveys on days with favourable sea conditions, i.e. 5km visibility or more and Beaufort Sea State 2 or less. During dolphin encounters, Marine Notice No. 15 of 2005 was adhered to as the vessel remained on a steady course travelling parallel to the animals at a speed of no more than 7 knots (Maritime Safety Directorate, 2005).

Survey tracks were chosen in such a way as to maximise chances of locating dolphins using local knowledge and past experience rather than to provide equal coverage of the area. Most of the survey effort was concentrated in Brandon Bay (Table 1) as the encounter rate with bottlenose dolphins was higher than elsewhere and collection of photo-ID data was a critical aspect of this study. For our purposes this was acceptable as the survey aim was not to estimate abundance but to locate as many dolphins as possible. Upon encountering a group of dolphins, a best estimate of group size was recorded as well as the presence of any calves. Groups were defined using McHugh's (2011) definition: 'All animals sighted at one time moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100m'. Whenever possible, attempts were made to photograph all individuals in the group in order to obtain images suitable for photo-ID.

In addition to these dedicated surveys, images of dolphins collected opportunistically while carrying out other activities in the bays were available to this study and used to identify individual dolphins (Table 1).

PHOTO-IDENTIFICATION

Photo-ID data were collected from a variety of platforms and equipment including Canon EOS D20 and EOS 7D cameras with Canon EF 70–200 F USM lenses. Images obtained from dedicated boat surveys and opportunistic sightings between 2008 and 2016 were processed by the SDWF using their standard protocol (Baker, 2015) in an attempt to recognise individual dolphins.

Two SDWF observers graded images on photo quality using a Q-scale (1–3) based on criteria described by NOAA (2011). Grade 1 images were of excellent quality, Grade 2 images were of average quality and Grade 3 images were of poor quality. Quality was graded by taking into account factors such as image focus/clarity, contrast, angle of the dorsal fin, proportion of the fin visible in the frame and proportion of the frame filled by the fin. Only images of Grades 1–2 were deemed suitable for photo-ID and used for analysis in order to reduce the risk of error. Calves and poorly marked juveniles were excluded from analyses.

Photos were then analysed to determine how many different dolphins were present during each survey and compared to images in the SDWF catalogue to see if individuals could be matched. Photographs were considered a match if the markings on the dorsal fins provided enough evidence to show beyond any doubt that the two were of the same dolphin. Dolphins which could not be matched to the SDWF catalogue were then compared to images in the Irish Whale and Dolphin Group's (IWDG) Coastal Bottlenose Dolphin Catalogue.

One photograph of each unique dorsal fin was then cropped using Microsoft Paint and allocated to one of two categories; A or B. Category A included

Table 1—Summary of trips used in the present study including the date, location of survey, survey type and if photo-ID and GPS data were available.

Date	*Tralee/ Brandon*	*Survey Type*	*Photo ID*	*GPS sighting location*	*GPS trackline*
17 Sept 2008	B	Opportunistic Sea	Yes	No	No
22 Jun 2009	B	Opportunistic Sea	Yes	Yes	No
18 May 2013	T*	Dedicated Sea	No	No	No
19 May 2013	T,B	Dedicated Sea	Yes	Yes	Yes
25 May 2013	T	Dedicated Sea	Yes	Yes	Yes
22 Jul 2013	T,B	Opportunistic Sea	Yes	Yes	Yes
07 Aug 2013	T,B	Dedicated Sea	Yes	Yes	Yes
17 Aug 2013	B	Dedicated Sea	No	No	No
22 Aug 2013	B	Dedicated Sea	Yes	Yes	Yes
24 Aug 2013	T,B	Dedicated Sea	Yes	No	Yes
25 Aug 2013	B	Dedicated Sea	Yes	No	No
07 Sep 2015	B	Dedicated Land	Yes	No	No
05 Aug 2016	B	Opportunistic Land	Yes	Yes	No

*No dolphins were observed on this day

dolphins that were identified as Shannon dolphins after being matched with an individual in the SDWF catalogue. Category B included images of dolphins that were given a Brandon unknown (BRUNK) ID code. These photos were of sufficient quality to be used for photo-ID but were unable to be matched to any dolphin in the SDWF catalogue.

Dorsal fins in categories A and B were then given a score from 1 to 3, reflecting the severity of their markings based upon criteria used by Berrow *et al.* (2012):

- *Grade 1*: Marks consisting of significant fin damage or deep scarring that were considered permanent
- *Grade 2*: Marks consisting of deep tooth rakes and lesions with only minor cuts present
- *Grade 3*: Marks consisting of superficial rakes and lesions

Grade 3 animals were included in the final analysis as the longitudinal data on the Shannon population allowed us to confirm if individuals, although poorly marked, were in the Shannon catalogue.

RESULTS

Bottlenose dolphins were sighted on seven of the eight dedicated surveys from 2013, revealing a very high encounter rate. One survey (18 May 2013) failed to locate dolphins; this was most likely due to unfavourable changes in sea conditions that day (Beaufort Sea State 3–4). Most sightings occurred in Brandon Bay, as that was where the majority of the surveys were carried out, with two sightings of three and four individuals recorded just off Fenit in Tralee Bay.

Photo-ID data were collected during six of the dedicated surveys carried out in 2013 as well as from four additional opportunistic boat-based trips, one each in 2008, 2009, 2013 and 2016, and during a land-based watch in 2015, resulting in photo-ID data available from eleven separate occasions (Table 1). No photo-ID data were collected on 17 August 2013 due to the large minimum distance (> 800m) the dolphins remained from the vessel.

A total of 156 identifiable dolphins were photographically captured throughout the 11 encounters resulting in the identification of 70 unique individual dolphins. The number of individual dolphins captured per trip ranged from one to 34 (M: 14.2, SD: 9.6) (Table 2). Of the 70 individual dolphins photographed, 96% (n = 67) were matched to the SDWF catalogue indicating that they have also been recorded on a regular basis within the boundaries of the Lower River Shannon SAC and are therefore considered Shannon dolphins. Shannon

Table 2—Trip number, group number and estimate, total number of individuals identified per trip, number of animals in category A (identified as Shannon dolphins), percentage of class A dolphins out of total IDs, number of animals in category B (unable to be identified as Shannon dolphins) and percentage of class B dolphins out of total IDs.

Trip no.	*Group no./estimated group size in the field*	*Total no. individuals identified per trip*	*A*	*% of total identified*	*B*	*% of total identified*
1	G1. 20	14	14	100	0	0
2	G1. 30	28	27	96	1	4
3	G1. 2	1	1	100	0	0
4	G1. 15	15	15	100	0	0
5	G1. 2 G2. 12	17	17	100	0	0
6	G1. 4 G2. 60	34	33	97	1	3
7	G1. 6	6	6	100	0	0
8	G1. 15	11	11	100	0	0
9	G1. 10 G2. 10	11	11	100	0	0
10	NA	6	5	83	1	17
11	G1. 20 G2. 7	13	13	100	0	0
Total	213	156	153	98	3	2
Mean	15.2	14.2	13.9	98	0.27	2
STDEV	15.1	9.6	9.3	5	0.46	5

dolphins represented 83 to 100% (M: 98%, SD: 5%) of the individuals identified during each trip (Table 2). Sixty-two percent of the SDWF's current adult dolphin population estimate of 108 was identified in Brandon and Tralee Bay.

Of the 67 Shannon dolphins identified, 37% (n = 25) were seen during more than one survey. Eight individuals, representing 12% of all identified Shannon dolphins, were sighted on five occasions and one individual was resighted six times. The three BRUNK individuals were sighted only once (Fig. 3). Of the 67 Shannon matches, 37 individuals have been sighted 10 or more times in the Shannon Estuary since 1993 and 11 individuals have been sighted more than 5 times—a strong indication that dolphins recorded in Brandon Bay and Tralee Bay are part of the Shannon population.

Interestingly, seven of these individuals have also been observed in the inner Shannon Estuary, suggesting that some individuals have a large home range which extends as far east as Labasheeda Bay, Co. Clare and as far west as Kerry Head/Brandon Bay/Tralee Bay (a distance of 100–120km) (Fig. 1). Two individuals sighted in both Brandon and the Shannon were first sighted in the estuary in 1993. Of the dolphins identified between 18 May and 25 August 2013 in Brandon Bay/Tralee Bay, 56% (n = 27) were also sighted in the Shannon between 1 May and 1 September 2013, indicating a high level of movement between the areas.

We were unable to match 4% (n = 3) of the 70 dolphins identified in this study to dolphins in the SDWF catalogue, which received BRUNK ID codes. None of the dolphins photographed in this study could be matched to the coastal catalogue managed by the IWDG (O'Brien *et al.*, 2009).

When grading the severity of the markings on the dorsal fins, 49% (n = 33) of the Shannon dolphins and 33% (n = 1) of the BRUNKS were considered well marked (Table 3) i.e. significant nicks, notches and other identifiable markings such as unique pigmentation, rake marks, algal staining, skin lesions and deformities (PI. I).

A discovery curve where the cumulative number of new individuals was plotted against the cumulative number of identifications did not reach a plateau, suggesting that not all dolphins which occur in Brandon Bay/Tralee Bay were photographed during this study (Fig 4).

DISCUSSION

Gaining an understanding of a target population's entire range is essential for conservation tools such as MPAs to be effective (Weir *et al.*, 2008), especially for mobile marine species like bottlenose dolphins. This understanding has yet to be achieved with regards to the Shannon bottlenose dolphin population. The use of photo-ID as a technique for studying individual dolphins is a very powerful tool that may be used to further explore their distribution. Using this technique, we were able to match individual dolphins photographed in Tralee Bay and Brandon Bay to individuals from the Shannon Estuary, and provide evidence of their regular presence during the summer months. A monitoring programme may be useful in gathering data which could then help us understand how they are using these habitats.

In the Lower River Shannon SAC, the SDWF's long-term monitoring programme of the resident bottlenose dolphin population has provided large amounts of data regarding the identification of key foraging grounds and prey species. In addition, the frequent presence of neonates during

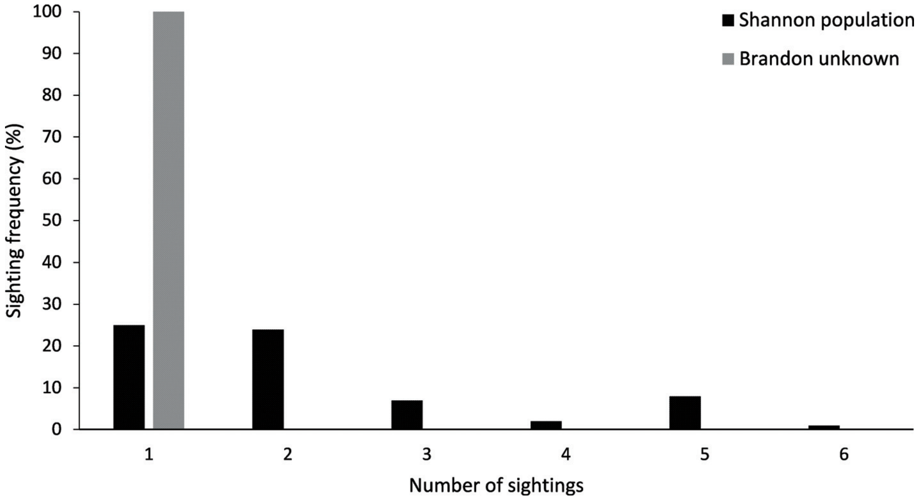

Fig. 3—Sighting frequency (1–6 number of sightings) of individual bottlenose dolphins from the Shannon population (n = 67) and Brandon unknown dolphins (n = 3) during 11 surveys carried out between 2008 and 2016.

Table 3—Severity (percentage in group) of markings assigned to dolphins identified in this study.

	BRUNKs	*Shannon*	*All*
Grade 1	1 (33)	33 (49)	34 (49)
Grade 2	2 (67)	24 (36)	26 (37)
Grade 3	0 (0)	10 (15)	10 (14)
Total	3	67	70

the summer months provides evidence that the Shannon Estuary may also be an important calving area (Baker, unpublished data). Behavioural data were not collected as part of the current study, although 15 different mother-calf pairs from the Shannon population were photographed within Brandon Bay and Tralee Bay, indicating they may also be used as calving or nursing grounds.

Successful long-term management and conservation plans require knowledge of the size, status and spatio-temporal distribution of a population (Evans and Hammond, 2004). An SAC that also includes bottlenose dolphins as a qualifying interest has been designated in the inner Moray Firth, Scotland (Weir *et al.*, 2008). Before its establishment, a number of studies were carried out (Evans, 1992; Mudge *et al.*, 1984; Wilson *et al.*, 1997) to determine where the boundaries of the Moray Firth SAC should be drawn. They were to include the entrances to the firths that were considered important foraging areas. Since designation, Hastie *et al.* (2003) gathered more data on dolphin distribution and habitat use, and confirmed a high level of activity in the small, deep entrances to the firths during the summer months as well as a long-term persistence in the use of these sites (Hastie *et al.*, 2003; MFP, 2001). Incorporating such behavioural data into the development of conservation plans plays a vital role in the protection of a population (Anthony and Blumstein, 2000).

More recent studies have revealed a possible expansion to the Moray Firth population's known range with dolphins spending more time outside the SAC boundary (Wilson *et al.*, 2004; Stockin *et al.*, 2006) and have suggested that the designation of a single protected site, the inner Moray Firth SAC, may not provide as much protection as once believed. Weir *et al.* (2008) investigated site fidelity and movements between dolphins photographed in the Moray Firth SAC and those photographed outside the boundaries of the SAC off Aberdeenshire in Scotland. Opportunistic photo-ID data gathered between 1999 and 2008 recorded an extremely high number of matches with dolphins between Aberdeenshire and the Moray Firth SAC with over half of the known northeast Scotland population occurring off Aberdeenshire, suggesting that the majority of dolphins seen in Aberdeenshire were from the population for which the Moray Firth SAC was designated to protect. Weir *et al.* (2008) stressed the importance of the ongoing assessment of a population throughout its entire range and the need for a dynamic approach to defining SAC boundaries (Hyrenbach *et al.*, 2000) in order to examine their long-term effectiveness.

The only other study of cetaceans in Brandon Bay and Tralee Bay was carried out by Ingram *et al.* (2005) as part of a study to explore the feasibility of marine-based tourism. They conducted three boat-based surveys in Tralee Bay and its surrounding waters in September and November 2004, and 25 land-based watches from three vantage points at Brandon Point, Kerry Head and the Maharees peninsula between July and October 2004. Bottlenose dolphins were seen from Brandon Point and Kerry Head on six occasions in groups ranging from

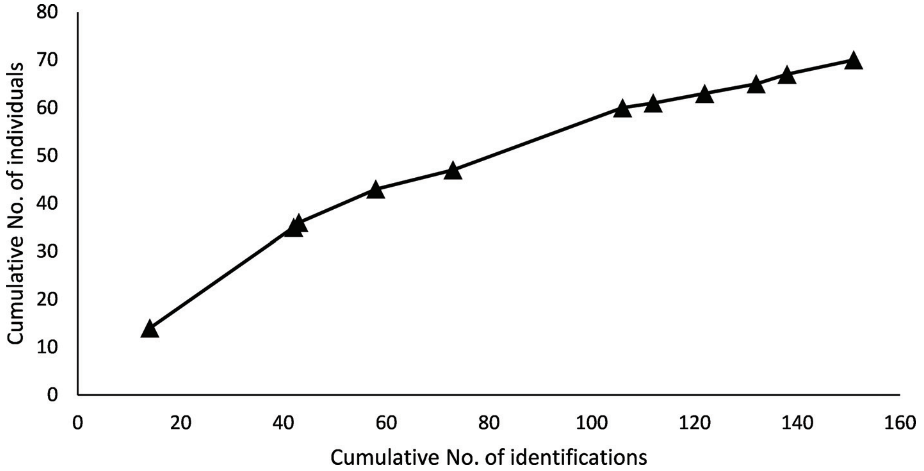

Fig. 4—Discovery curve representing all bottlenose dolphins identified (n = 70) from photo-ID data collected in Brandon Bay/Tralee Bay over the course of 11 trips between 2008 and 2016. The triangles represent the individual trips one to eleven.

PI. I - Images of individual ID 086, a well-marked individual assigned a Grade 1 on the marking severity scale, taken during the 2008 GMIT training course in Brandon Bay (left) and in the Shannon Estuary in 2012 (right).

three to fifteen individuals. Sightings during boat-based surveys were limited to a single bottlenose dolphin that was observed on each survey.

In the summer of 2013, a concurrent study carried out static acoustic monitoring in Tralee Bay and Brandon Bay revealing very high dolphin detection rates, especially in Brandon Bay (Murphy *et al.*, submitted), suggesting the regular presence of bottlenose dolphins in the area. Bottlenose dolphins have also been reported outside the summer period, as demonstrated by Ingram *et al.* (2005). They also noted that the dolphins were frequently sighted within the study area by locals. However, it is unknown if these were Shannon dolphins or individuals from the highly mobile inshore population.

The current study represents the largest dataset collected within Brandon Bay and Tralee Bay to determine the origin of the bottlenose dolphins that regularly occur in these areas and provides important information from an understudied area of the Shannon population's range. Photo-ID from eleven different occasions ranging from 2008 to 2016 yielded extremely high numbers of matches to Shannon dolphins, as well as several resightings throughout the duration of the study. These photo-ID encounters also included data from random opportunistic sightings over the years; all providing evidence supporting the hypothesis that the Shannon dolphins are habitually using Brandon Bay and Tralee Bay.

Over half of the current adult individuals in the Shannon Estuary bottlenose dolphin population were identified within Brandon Bay and Tralee Bay over the course of this study, and over half of those sighted during the dedicated 2013 surveys were also seen within the Shannon Estuary around the same time. This indicates a high level of movement between the two areas, and provides strong evidence that the bottlenose dolphins occurring in Brandon Bay and Tralee Bay are predominantly from the Shannon population.

The Lower River Shannon SAC was designated under the EU Habitats Directive to protect the Shannon dolphin population. Therefore, its boundaries should include areas where these dolphins are known to regularly occur. As the results from this study have shown, the high percentage of Shannon dolphins identified and resighted within the bays over the study period provides evidence that they represent a significant area of the population's distribution. We therefore recommend the boundary of the Lower River Shannon SAC be extended to include both Brandon Bay and Tralee Bay. We also suggest that additional surveys be carried out using a more conventional survey design providing more equal spatio-temporal coverage of the area in order to increase our understanding of the importance and significance of these bays to the Shannon Estuary bottlenose dolphin population.

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Appendix E

Aquatic Mammals 2014, *40*(2), 191-194, DOI 10.1578/AM.40.2.2014.191

Short Note

The First Confirmed Successful Refloat of a Stranded Bottlenose Dolphin (*Tursiops truncatus*) in Ireland and Subsequent Resighting with a Neonate

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Common bottlenose dolphins (*Tursiops truncatus*) are found throughout temperate and tropical waters of the world between 60° N and 50° S of the equator including the Mediterranean Sea (Reynolds et al., 2000). They are widespread and abundant in Irish waters (Ingram et al., 2001), which contain some of the highest concentrations of this species in Europe (Evans, 1992). Photo-identification has greatly advanced studies utilising the identification of individuals for estimating population size (Berrow et al., 2012), site fidelity (Kerr et al., 2005), social structure (Wells et al., 1987), and population dynamics (Wells & Scott, 1990). Photo-identification has been used in Irish waters to track the movements of resident dolphins (Ryan et al., 2010; Berrow et al., 2012) and highly mobile coastal bottlenose dolphins within Ireland (O'Brien et al., 2009), but also between Ireland and the UK (Robinson et al., 2012). In the Shannon Estuary, on the west coast of Ireland, a long-term study of resident individuals has been ongoing since 1993 (Berrow et al., 1996), with a total of 220 individuals identified to date.

The Irish Whale and Dolphin Group (IWDG) coordinate an all Ireland cetacean sighting and stranding scheme that has been in operation since 1991 (www.iwdg.ie). They have established a network of dedicated IWDG observers and volunteers who can respond to stranding events quickly. Live-stranding events occur occasionally in Ireland, with a total of 199 occurring between 1995 and 2012, comprising 8.5% of all stranding events and involving 384 individuals of 16 confirmed species (IWDG Database, accessed November 2012). Two species—common (*Delphinus delphis*) and striped (*Stenella coeruleoalba*) dolphins—account for 50% of all live-stranding events. Refloating attempts were undertaken for 38 (19%) of these live-stranding events, with only two events deemed successful based on the fact that no similar stranding occurred in and around the area after the event (IWDG Database, accessed November 2012). However, the fate of these individuals that were returned remains unknown. The cause of live strandings in each case was not determined, but individuals may have incurred injury during the event, and the rate of survival after refloating remains undetermined. Pelagic or offshore species often strand in good nutritive condition, with no apparent visible traumas such as wounds or lesions; whereas live-stranded coastal species are generally diseased or in poor physical condition (IWDG, 2009).

The Lower River Shannon (Shannon Estuary) on the west of Ireland is one of the most important areas for bottlenose dolphins in Europe and is designated as a Special Area of Conservation (SAC) for the species under the European Union Habitats Directive. They are present in the estuary throughout the year where they calve and nurse their young (Berrow et al., 1996). Herein we describe a successful refloating of a live-stranded bottlenose dolphin and subsequent tracking of the individual and its dependent calf, using photo-identification, over a period of 482 d. This was the first recorded live-stranding event of a bottlenose dolphin in this SAC.

At 0745 h on 1 June 2012, the IWDG and the National Parks and Wildlife Service (NPWS) received a report of a live-stranded bottlenose dolphin at Hannon's Strand, Co. Kerry, located on the southern shore of the Lower River Shannon SAC (Figure 1). Local IWDG and NPWS personnel attended the scene and found an adult female bottlenose dolphin in a shallow (*ca*. 10 cm deep) channel on a sandy beach, facing towards the water, 6 m from

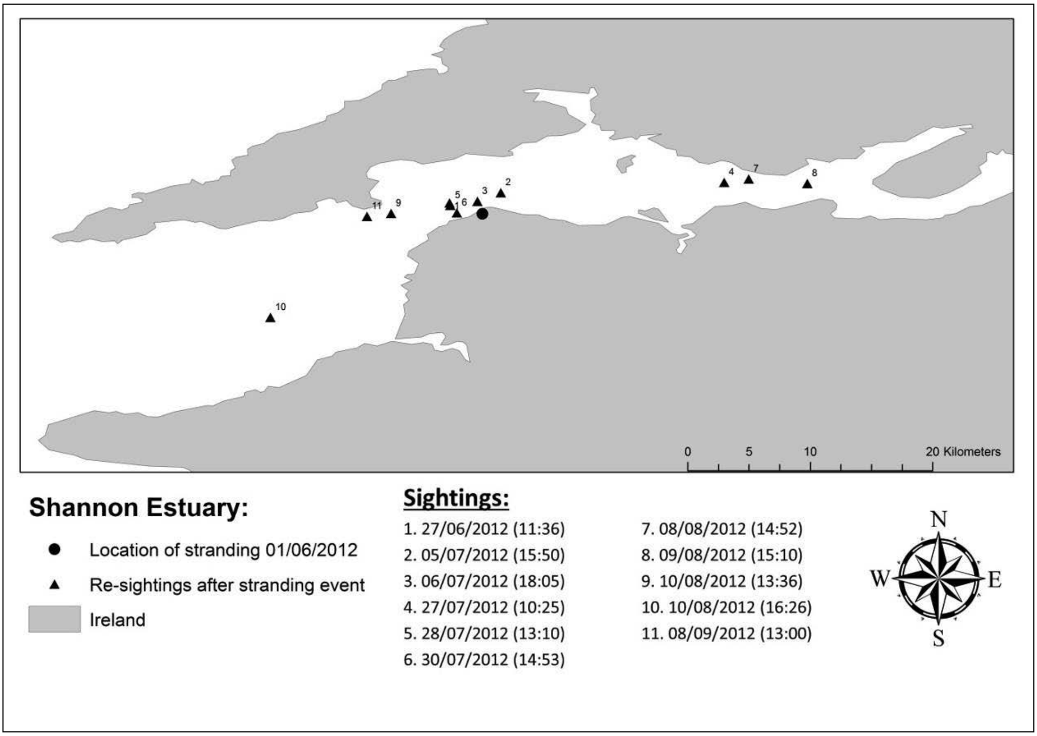

Figure 1. Locations of stranded bottlenose dolphin (*Tursiops truncatus*) (black circle) and subsequent resightings of the same individual from tour boats operating in the Shannon Estuary (black triangles)

the waterline with the tide receding. Given the rate at which the tide was receding and the position of the animal on the beach, it was estimated the individual stranded approximately 45 min prior to discovery. The bottlenose dolphin regurgitated fresh salmon (*Salmo salar*) muscle and bones, indicating it had recently been feeding. Visually, there were no external injuries, and the bottlenose dolphin seemed to be in good physical condition. The breathing rate was initially 8 breaths/min but decreased to 2 breaths/min, 1 h after wet towels were used to cool the animal. The length of the animal was measured (3.5 m) and close-up images of the dorsal fin were recorded to enable future identification of the individual. There were no nicks or notches present on the trailing edge of the dorsal fin. The most prominent identifiable features were four clear tooth rakes down the centre of the right-hand side of her dorsal fin (Figure 3). The IWDG began to mobilize the nearest flotation pontoons to the site, but a farm tractor with an open transport box (box measuring 3 m × 1.3 m × 1 m) was accessed locally and allowed for a faster response (Figure 2). This transport box was attached to the rear of the tractor and could be manoeuvred hydraulically. The transport box was lowered into the sand and pushed beneath the stranded bottlenose dolphin. The bottlenose dolphin was lifted and transported to the water, and then lowered and directed by hand to the open sea. It was observed swimming powerfully and unaided until disappearing from sight approximately 300 m from where researchers had found it stranded 70 min prior.

The Shannon Dolphin and Wildlife Foundation (SDWF) has managed a bottlenose dolphin photo-identification catalogue from the Shannon Estuary since 1993, carrying out surveys between May and October largely from dolphin-watching tour boats. Images of the stranded individual were subsequently matched with an individual in the catalogue, which was first identified from a tour boat in June 2011. As researchers were carrying out daily photo-identification surveys from the tour boats over the summer period, routine comparisons were carried out to determine if the stranded individual had survived.

On 27 June 2012, a group of nine individuals (which included three mother/calf pairs) were encountered 2 km from the stranding site at Beal Point, Co. Kerry. The stranded individual was recorded within this group, identified by the four deep tooth rakes on the right-hand side of its dorsal fin. These marks were new since the 2011 record, but other markings on the dorsal fin and back allowed for a definite identification. Subsequently, the same individual was recorded on 10 occasions between June and September 2012.

Figure 2. Farm tractor with an open transport box measuring 3 m × 1.3 m × 1 m used to transport the bottlenose dolphin back into the sea

Figure 3. Images of the stranded individual's dorsal fin (with four tooth rakes clearly visible on the right-hand side of the fin) from the stranding event on 1 June 2012 and the first resighting on 27 June 2012, 26 d after the stranding event

The furthest distance it was recorded from the stranding site was 14 km upriver in an easterly direction (Figure 1). Additionally, for all encounters, at least one known mother/calf pair was present in the group. On 8 September 2012, the stranded individual showed a very strong association with a newborn calf. This calf had not been previously recorded in images of any mother/calf pairs, despite most calves possessing identifiable features on their dorsal fins and bodies. Although she had previously been recorded in the presence of mother/calf pairs, she never showed strong association with calves as they were always present with their respective mothers. During the 2013 field season, the stranded individual was resighted with the same calf on 18 occasions between May and September, strongly suggesting it was her calf.

To our knowledge, this is the first occasion a successful repatriation attempt of a live-stranded bottlenose dolphin was confirmed using non-invasive methods (i.e., photo-identification) after the event. The bottlenose dolphin was monitored in association with other individuals up to 482 d after the stranding event. This individual may have live-stranded due to navigational error rather than as a result of injury or illness and, as such, was considered to have been a good candidate for a rescue attempt.

This event has a significant and positive impact on a number of levels. First, the stranded female proved to be actively feeding on salmon close to the time of the event as she regurgitated fresh salmon while trapped on the sand. In the absence of dietary records for bottlenose dolphins in the Shannon Estuary SAC, this suggests that salmon is a part of their diet at this time of the year. Second, the use of photo-identification, a non-invasive technique, was again proven to be a valuable method for tracking and monitoring survival of a stranded individual (Visser & Fertl, 2000).

The Shannon Estuary bottlenose dolphins comprise a reproductively isolated population (Mirimin et al., 2011) with an apparently small home range of only 24 km from the boundaries of the SAC as determined through photo-identification (Ryan & Berrow, 2013). Furthermore, none of the Shannon Estuary residents have ever been recorded in association with their coastal more transient counterparts that have been recorded around the Irish coast and as far as UK waters (O'Brien et al., 2009; Robinson et al., 2012). Given this, the loss of a single sexually mature adult female, especially one pregnant with a viable calf, could have a significant negative impact on this population.

A management plan for bottlenose dolphins is not currently in place in the Shannon Estuary SAC, even though it is only one of two SACs in Ireland for this species. The provision of resources for strandings and attempts to refloat live cetaceans are often met with scepticism, but our results show that refloating of live bottlenose dolphins can be successful and, in instances similar to this, should be attempted. The quick response and successful refloat is testament to the widespread distribution of the observer network established by the IWDG stranding scheme.

Acknowledgments

Thank you to Breda Brosnan who reported the stranding to the Irish Whale and Dolphin Group (IWDG) and National Parks and Wildlife Service (NPWS), and to all those who helped with the refloat, especially Conor and Finbar Breen, Mark O'Brien, and Mike-Joe Hennessy. Thanks to the two tour boat operators in the Shannon Estuary for providing a platform from which to carry out photo-identification, namely Dolphinwatch, Carrigaholt (www.dolphinwatch.ie) and Dolphin Discovery, Kilrush (www.discoverdolphins.ie), Co. Clare. Thanks to IWDG members who advised and provided support on the day of the stranding: Dave Wall and Neil Cheape. All stranding data were taken from the IWDG database where all records are validated and available online (www.iwdg.ie).

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Appendix F

Bottlenose dolphin life history and population demographics in the Shannon Estuary, Ireland

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Abstract

This study investigated the female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, using long-term relational sightings and photographic databases.

Data were collected between 2008 and 2016, during 654 boat-based surveys, from two dolphin-watching vessels and a dedicated research vessel. During 1,018 sightings, 4,231 identifications of 184 individual dolphins were recorded.

The population size was charted through direct counts of known dolphins from 2011 to 2015 (range = 131-150), with 145 extant individuals in 2015: 80 adults, 25 juveniles and 40 calves.

Excluding dependent calves, 121 individuals were sighted, of whom 98% (n = 119) were sighted in multiple years, with 64% (n = 77) sighted in all four years (2012-2015). The mean number of sightings per individual was 24.4±21.7 (range = 1-101). Of these 121 dolphins, sex was known for 46 females and 12 males.

Between 2008 and 2016, 37 reproductive females and 69 dependent calves were recorded. Overall, 35% (n = 13) of these females were sighted with one calf, 43% (n = 16) with two calves, and 22% (n = 8) with three calves. An average of seven (range = 3-10) calves were born each year. Parturition peaked in July with 45% (n = 14) of 31 calves with accurate (within 60 d) birthdates born in this month. Weaning ages ranged from 2.0-4.1 (mean = 2.9) years.

The mean inter-birth interval ranged between 2.7±0.6 to 3.5±1.3 years, depending on method used. Mean annual calving rate was 0.29 young-of-year/reproductive female/year. Average crude birth rate was 0.07±0.01. Fecundity was 0.26±0.03. An average 11% of newborn calves were lost before age 1.

These results are generally within the lower range of values reported for similar populations and provide essential data for conservation management and global bottlenose dolphin research.

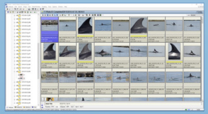
Methods

Surveys were conducted from two dolphin-watching vessels and a dedicated research vessel from 2008 to 2016 (primarily in summer).

Location of the Shannon Estuary study site, a Special Area of Conservation for bottlenose dolphins in Ireland

Surveys	654
Sightings	1018
Identifications	4231
Individuals	184
Reproductive females	37
Calves	69
Non-reproductive females	12

Photo-identification of individual bottlenose dolphins occurred during all sightings. *IMatch* and *FinBase* (Adams *et al.* 2006) were used to enter, store and query photographic, behavioural and related sightings data.



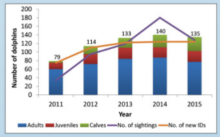
Screenshot of *IMatch* software environment for photographic data entry and processing, which houses 213,000 photos from bottlenose dolphin sightings

Screenshot of the relational sightings database in *FinBase* showing catalogue summary data for reproductive female ID# 006

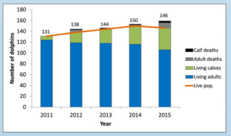
Range of reproductive parameters from other populations		
Individual inter-birth interval (years)	1.1[a]	11[b]
Mean inter-birth interval (years)	3[c]	5.4[b]
Crude birth rate	0.04 ± 0.04[d]	0.12 ± 0.05[e]
Fecundity	0.11 ± 0.02[c]	0.25[f]
1st yr calf mortality	0.13[g]	0.45[e]

[a]Port River Estuary, Australia; Steiner & Bossley 2008
[b]Sarasota Bay, USA; Wells & Scott 1999
[c]Patos Lagoon Estuary, Brazil; Fruet *et al.* 2015
[d]Doubtful Sound, New Zealand; Henderson *et al.* 2014
[e]North Sea, Scotland; Robinson *et al.* 2017
[f]Bay of Islands, New Zealand; Tezanos-Pinto *et al.* 2015
[g]Mikura Island, Japan; Kogi *et al.* 2004

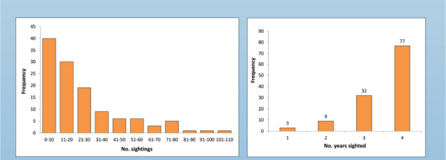
Results



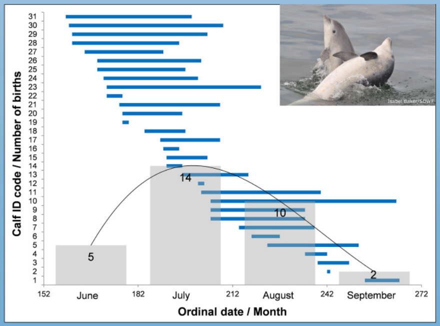
The number of individual bottlenose dolphins identified each year (bars), the number of sightings with photo-id records (purple line) and the number of new (non-calf) IDs recorded (*i.e.,* discovery curve; orange line) with individual dolphins categorized by age (adults, juveniles, calves)



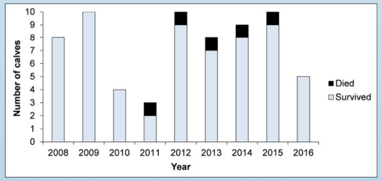
Estimates of the extant population size of bottlenose dolphins in the Shannon Estuary from 2011 to 2015 (mean = 142), incorporating age class ("adults" includes adults and juveniles, "calves" includes all dependent individuals) and presumed deaths of well-known individuals



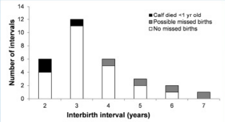
Individual juvenile/adult bottlenose dolphin sightings (n = 121) by number of (left) sightings (2012-2015) and (right) years sighted



The number of births per month estimated using calves with within 60d-precision date of birth (DOB) estimates (n = 31), with a polynomial regression line fitted. Thick blue lines indicate the window of time between ordinal dates when each of the 31 calves could have been born (*i.e.,* dates from the last sighting of the mother without her calf to the first sighting of the mother with her newborn calf)



Number of bottlenose dolphin calves born in the Shannon Estuary from 2008 to 2016, with those that subsequently died in black (no mortality data for 2016)



Inter-birth intervals (IBIs) for females whose calves survived to weaning (white bars) and whose calves died <1 yr old (black bars), and for those where a birth may have been missed in the interim (grey bars) (n = 30)

Reproductive parameter	Mean (± SD)
Annual births	7.4 ± 2.6
Weaning age	2.9
IBI by DOB	2.9 ± 0.7
IBI by sightings	2.7 ± 0.6
IBI by year of birth	3.5 ± 1.3
Annual calving rate	0.29 YOY/ female/year
Crude birth rate	0.07 ± 0.01
Fecundity	0.26 ± 0.03
1st yr calf mortality	0.11

Conclusions

Shannon Estuary bottlenose dolphins

- ⇒ Extant population size of ~142 individuals
- ⇒ 64% of individuals seen 4 years in a row
- ⇒ Give birth to an average of 7 calves a year
- ⇒ 45% of births in July (of 4 study months)
- ⇒ Average inter-birth interval of ~3 years
- ⇒ 11% first-year calf mortality

These results present interesting insights into the **demographics** of this population and provide the **first baseline reproductive parameters** for bottlenose dolphins in Ireland

Acknowledgements This research was carried out with the support of the Marine Institute under the Marine Research Programme with the support of the Irish Government. Thank you to all of the research assistants and tour boat operators who have helped the Shannon Dolphin and Wildlife Foundation to collect long-term monitoring data on the bottlenose dolphins in the Shannon Estuary. Many thanks to Emer Rogan and Simon Ingram who provided data on the sexes of individual dolphins. Thank you to Jeff Adams for ongoing support in using *FinBase* to study the Shannon dolphins. Dedicated behavioural research was carried out under licenses (Nos. 109/2014, 020/2015) issued by the National Parks and Wildlife Service of the Department of Arts, Heritage, Regional, Rural and Gaeltacht Affairs.

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STR03

Longitudinal study of a live-stranded female bottlenose dolphin in the Shannon Estuary, Ireland

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INTRODUCTION

A pregnant female bottlenose dolphin (*Tursiops truncatus*) live-stranded and was refloated in the Shannon Estuary in June 2012 (O'Brien et al. 2014).

She has subsequently been photo-identified during 85 sightings (75 with her calf) for over three years.

Stranding
01 June 2012

First sighting
27 June 2012

Location of the Shannon Estuary study site in Ireland

Stranded female bottlenose dolphin

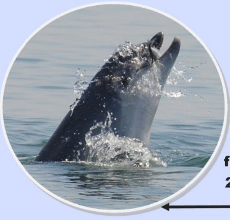
9 months pregnant
Béal Beach, Co. Kerry
01 June 2012

First sighting after stranding
Matched to catalogue #242
27 June 2012

First sighting with newborn calf
08 September 2012

Sighting with calf
Age 1
September 2013

Dolphin-watching vessels and research boat used for surveys 2012-2015



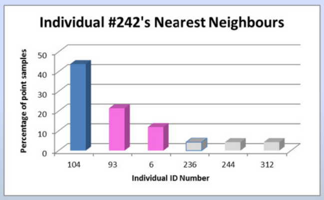
Calf with fish in mouth
25 July 2014

Sighting with calf
Age 2
08 September 2014

Sighting with calf
Age 3
01 September 2015

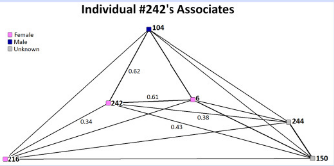
Latest sighting
15 September 2015

RESULTS

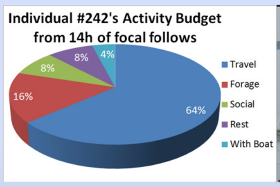


The six most frequently observed nearest neighbours (excluding calves) of #242 during individual focal follows (14h) in 2014 and 2015 using 3-min point sampling.

Seven other juveniles/adults were nearest neighbours for <4% of point samples.



#242 had strong dyadic associations with five other individuals. (Half-weight association indices 0.34 to 0.62; two-sided dyadic significance test within a permutation test for the presence of preferred/avoided companions in SOCPROG, $P < 0.05$. Diagram drawn using NetDraw.) Data from 522 sightings between 2012 and 2015 (197 survey days, 123 individuals).



CONCLUSIONS

This is the first study documenting the long-term survival of a live-stranded pregnant bottlenose dolphin and her calf. It provides insight into the life history and social structure of the Shannon dolphin population.

Acknowledgements Thank you to all of the researchers and tour boat operators who have helped the Shannon Dolphin and Wildlife Foundation to collect long-term monitoring data on the bottlenose dolphins in the Shannon Estuary over the past 23 years. Thank you to Jeff Adams for ongoing support in using FinBase Mapping Tools to study the Shannon dolphins.

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Exploring the social structure of the resident bottlenose dolphin population in the Shannon Estuary, Ireland

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Abstract

This study represents a comprehensive investigation into the social structure of the resident population of wild bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland.

Data were collected between 2012 and 2015, from two dolphin-watching vessels and a dedicated research vessel. Individual dolphins were identified using photo-identification techniques, and locational and environmental data recorded. Data from 493 different sightings on 186 independent survey days were input into FinBase, analyzed using SOCPROG 2.5 and visualized using NetDraw 2.148.

A total of 99 unique adult (≥8 years old) individuals were catalogued, with numbers identified per day ranging from one to 51 individuals. For association analyses, sampling period was defined as one day, association was defined by group membership, with each record/sighting constituting one group, and the half-weight association index (HWI) was used.

Clear plateaus were evident on both discovery curves for number of individuals identified plotted against cumulative number of identifications and sampling period. The social differentiation estimate for the population (using the likelihood method) was 0.884 (SE = 0.024) indicating a well differentiated society. The mean HWI was 0.08 ± 0.02 indicating a very fluid social network, but permutation tests for the presence of preferred/avoided companions rejected the null hypothesis that only random associations exist (p<0.01; 20,000 permutations).

The persistence of preferred associations was confirmed by standardized lagged association rates, which remained consistently higher than the null association rate. Principal coordinates analysis indicated some potential grouping in the population, perhaps related to individual home range. Individuals were divided into clusters (using average-linkage; cophenetic correlation coefficient, CCC = 0.76) and network diagrams were created and visualized at different levels of association.

These results differ in several respects from studies of other resident bottlenose dolphin populations globally.

Methods

Surveys were conducted from two dolphin-watching vessels and a dedicated research vessel from 2012 to 2015 (March-November).

Location of the Shannon Estuary study site in Ireland.

Year	Sightings
2012	93
2013	118
2014	180
2015	102
TOTAL	493

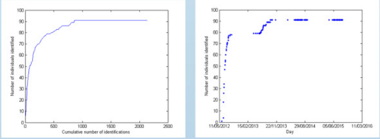
Sex	Individuals
Female	42
Male	11
Unknown	46
TOTAL	99

Photo-identification of individual bottlenose dolphins occurred during all sightings.

FinBase (Adams *et al.* 2006) was used to enter, store and query sighting and related photographic data.

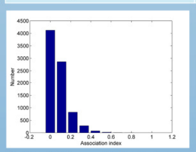
Data input into SOCPROG 2.5 (Whitehead 2009)
Group mode
Supplemental file: Individual sexes
Sampling period: "Day"
Association: Group variable "Record"
Restrictions: 91 individual adults with >5 sightings used for all analyses except SLARs
Analyses excluded animals aged <8 years old

Results

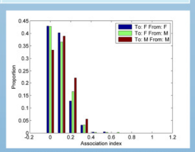


Discovery curves for number of individuals identified plotted against cumulative number of identifications and sampling period. Both reach clear plateaus suggesting good coverage of the population (n = 91).

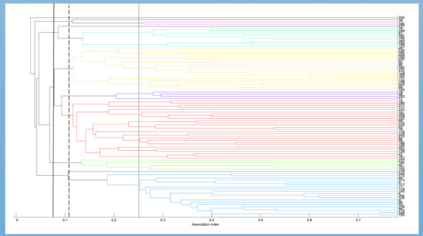
Social differentiation *S*	0.884 (SE = 0.024)
Correlation coefficient *r*	0.746 (SE = 0.025)
Mean HWI	0.08 ± 0.02
Strength	7.21 ± 2.03
Eigenvector centrality	0.10 ± 0.03
Reach	55.97 ± 17.40
Affinity	7.69 ± 0.49
Clustering coefficient	0.17 ± 0.05



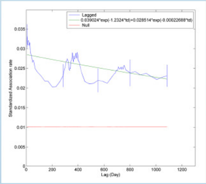
Half-weight association index (HWI) distribution by number of dyads.



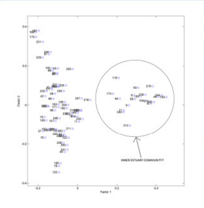
Proportional HWI distribution of female-female (blue), female-male (green) and male-male (red) dyads.



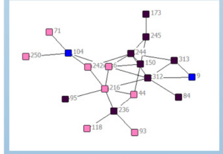
Average-linkage cluster analysis (CCC = 0.76) with modularity controlling for gregariousness (solid line) and permuting associations (dashed line), and suggested AI from knot diagram (dotted line). All modularity measures were below 0.3 — too low to conclude that the population is divided into clusters.



- **Standardized lagged association rates (SLARs) and null association rate plotted against time lag with best-fit exponential model SLAR4.**
- **SE bars (vertical lines) estimated using temporal jackknife method with moving average of 160,000 associations.**
- **The "two levels of casual acquaintances" model (green line) had the lowest QAIC and best fit (Whitehead 2008).**
- **Value at τ=1000 days is still well above the standardized null association rate.**



Principal coordinates analysis (first two coordinates explaining 11.6% of the variance in the matrix of associations) showing some potential grouping of the population, perhaps related to habitat use or individual home range.



Social network diagram (females, *pink squares*; males, *blue squares*; unknown sex, *black squares*) of core group of 19 individual dolphins showing only dyads with significant HWIs >0.3 from permutation analyses, displayed using NetDraw 2.148 (Borgatti 2002).

Conclusions

Shannon Estuary bottlenose dolphins
- ⇒ Exhibit a fluid social network
- ⇒ Have a low mean HWI compared to other populations
- ⇒ But still show some strong associations among particular dyads
- ⇒ And exhibit preferred associations that persist over time

Additional analyses of longitudinal data including 2008-2011 will expand the network analysis and investigate potential effects of home range, individual sex and age class on the social structure of this population

Acknowledgements Attendance at this conference was supported by the Marine Institute under the Marine Research Sub-programme funded by the Irish Government co-financed by the European Union via the European Regional Development Fund. Thank you to all of the researchers and tour boat operators who have helped the Shannon Dolphin and Wildlife Foundation to collect long-term monitoring data on the bottlenose dolphins in the Shannon Estuary over the past 22 years. Thank you to Emer Rogan who provided data on sexes of individual dolphins. Thank you to Jeff Adams for ongoing support in using FinBase to study the Shannon dolphins.

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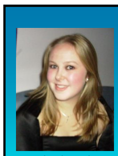
MARINE AND FRESHWATER RESEARCH CENTRE
GMIT INSTITIÚID TEICNEOLAÍOCHTA NA GAILLIMHE-MAIGH EO GALWAY-MAYO INSTITUTE OF TECHNOLOGY
SDWF Shannon Dolphin & Wildlife Foundation
EUROPEAN REGIONAL DEVELOPMENT FUND
Marine Institute Foras na Mara



Isabel Baker

Long-term boat-based monitoring of bottlenose dolphins (*T. truncatus*) in the Shannon Estuary, Ireland

Isabel Baker[1], Simon Berrow[1,2] and Joanne O'Brien[1,2]

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(2) Marine Biodiversity Research Group, Galway-Mayo Institute of Technology, Co. Galway, IRELAND

Introduction A photo-identification study of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland was started 20 years ago, in May 1993. The population is relatively stable with approximately 107 individuals (Berrow *et al*., 2012), genetically discrete (Mirimin *et al*., 2011), and resident in the Shannon Estuary and adjacent Tralee Bay (Ryan and Berrow, in press). The Shannon Estuary is the only candidate Special Area of Conservation (SAC) for bottlenose dolphins in Ireland. It is the second busiest waterway in Ireland with a well-established dolphin-watching industry. Over 45,000 images of bottlenose dolphins have been collected in the last 20 years, along with associated sighting records. Images were taken from commercial dolphin-watching tour boats as well as from research vessels during dedicated surveys. As this is one of the longest-running dolphin studies in Europe, work is being undertaken to construct a complete database, spanning 20 years, of sightings and catalogued photographs. Using dorsal fin photo-identification, this work allows us to begin to examine facts about individual dolphins and research platforms used in data collection.

Aim To summarise the longitudinal datasets of three resident individuals in the Shannon Estuary bottlenose dolphin population and to illustrate the value of tour boats and research vessels in the collection of long-term data.

Methods Photographic and sighting data were collected from tour boats and research vessels. "IMatch" and "FinBase" software were used to manage and investigate the long-term dataset.
Three well-marked individuals were chosen to illustrate the success of long-term monitoring in the Shannon Estuary.

Results 705 surveys comprising 911 sightings of bottlenose dolphins have been carried out from 1993 to 2012. No surveys were carried out in 1995 and 1996 (Fig. 1). Since 2005, the number of surveys per year has been relatively consistent with an average of 49 surveys a year.

81% of surveys were conducted from tour boats and 19% from research vessels.

Longitudinal datasets of the three individual bottlenose dolphins investigated demonstrated the value of long-term monitoring, especially from tour boats. The catalogued individuals 1, 8 and 11 were sighted in 13, 16 and 15 years respectively. Each individual was first seen in 1993 and most recently in 2012. All individuals had sightings recorded from tour boats, research vessels or both (Fig. 2).

Long-term photographic data of the three individuals illustrated changes in both photographic quality and the markings of the dolphins' dorsal fins since 1993 (Fig. 3).

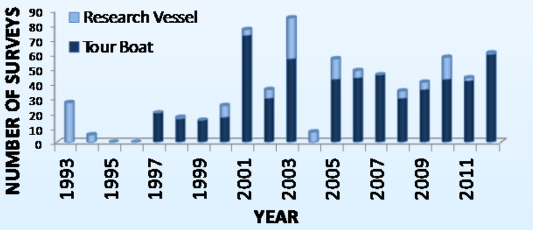

Figure 1. Number of bottlenose dolphin surveys per year from 1993 to 2012 conducted from tour boats (dark blue) and research vessels (light blue).

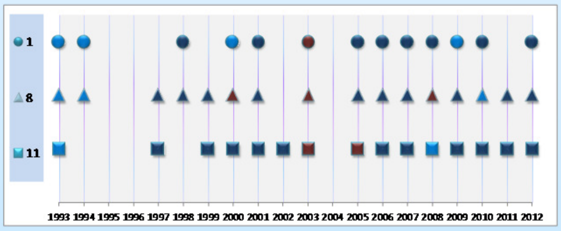

Figure 2. Sightings of catalogued individuals 1, 8 and 11 during survey years 1993-2012, from tour boats (dark blue), research vessels (light blue) or both (dark red).

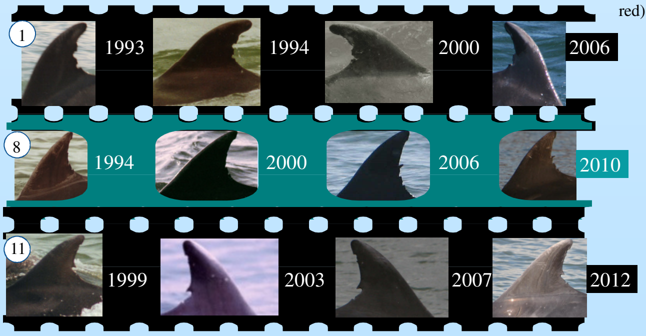

Figure 3. Photographs of catalogued individuals 1, 8 (male) and 11 (female), showing changes in both photographic quality and dorsal fin markings over time.

Conclusions

- Long-term monitoring requires a regular effort over a long period. Funding is often a considerable constraint.
- Dolphin-watching tour boats are especially beneficial for gathering longitudinal baseline data, however limitations include:
  - Seasonal constraints – no tour boat trips in winter
  - Areas visited by tour boats confine data spatially
  - Some research questions cannot be answered
- Work to update this long-term dataset using software to manage and relate photographic data to sighting data is currently underway. We expect to be able to carry out further detailed analyses when the database is fully populated.

Acknowledgements Thank you to all of the researchers and tour boat operators who have helped the Shannon Dolphin and Wildlife Foundation to collect long-term monitoring data on the bottlenose dolphins in the Shannon Estuary over the past 20 years.

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Mirimin, L. *et al*. (2011). Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Animal Conservation 14(4): 342-353.
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Appendix G

Shannon Dolphin and Wildlife Foundation

Researcher's Guide to Protocols for Fieldwork and Data Entry

16 May 2015

www.shannondolphins.ie

www.facebook.com/ShannonDolphinAndWildlifeCentre

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1. Introduction

There are four main objectives for the summer 2015 field season:

1. Monitoring surveys
2. Photo-identification and database entry
3. Dolphin centre education and promotion
4. Behavioural research

Research assistants will carry out dolphin research and education. They will be required to conduct monitoring surveys from dolphin-watching tour boats, spend a considerable amount of time on bottlenose dolphin photo-identification and related office tasks, and assist in the management of the dolphin centre on a daily basis. There may also be opportunities for research assistants to help with research conducted on board the Irish Whale and Dolphin Group's research vessels *Muc Mhara* and *Celtic Mist* and to assist the IWDG with cetacean strandings should the opportunity arise. Research assistants will also assist with PhD research on bottlenose dolphin social and foraging behaviour.

Data collection will usually occur every day when the weather is good (light winds, no rain). Days are long typically starting at 8am or 9am and finishing with data consolidation in the evenings. Days off will be infrequent and mostly during bad weather, though we may carry out a couple of team excursions to nearby places of interest.

Volunteers will rotate responsibilities on a daily basis so that everyone has a chance to take part in all tasks.

1. Monitoring Surveys

Monitoring surveys will be conducted from two dolphin-watching tour boats operating in the Shannon Estuary. One boat (*Dolphin Discovery*) operates from Kilrush Marina, across the road from the dolphin centre, while the other boat (*Draíocht*) operates from Carrigaholt Pier, a 30-min drive from the dolphin centre. While we will try to share research responsibilities evenly, please be aware that there may be restraints on the amount of Carrigaholt trips that those research assistants without their own car can conduct.

Whilst on board the tour boats, research assistants are responsible for collecting photo-id data, recording GPS tracks and waypoints, and collecting data on tour boat encounters with dolphin groups. Surveys involve one to four daily boat trips and are weather dependent – i.e. many days in a row if weather is good.

As the boats are open to environmental conditions, it will be necessary for you to bring a **hat**, **rain jacket**, **fully enclosed shoes, sunscreen, sunglasses, water** etc.

As boat-based research is highly weather dependent, it can vary between weekdays and weekends. Assistants need to be available full-time including weekends and be prepared to work long, consecutive days, in the office during bad weather and in the field during good weather.

If you are conducting boat-based monitoring, the following equipment should be packed and brought with you on the boat:
- Pelican case containing SDWF digital SLR camera with at least one spare (fully charged) battery

- SDWF GPS unit with spare batteries in GPS case

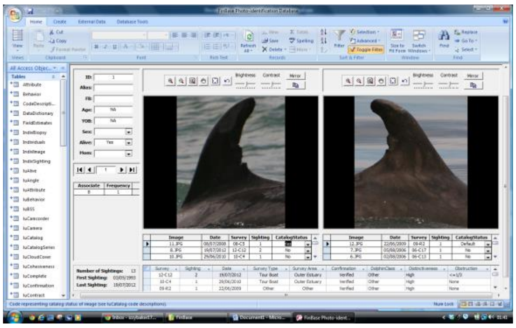
- Clipboard labelled with port name and enough blank datasheets for the day

- Binoculars and binoculars case

- Blue or black pens and large elastic band on clipboard (for windy conditions)

- Lunch or snacks and plenty of water if you are planning to do multiple boat trips

2. Photo-identification and Database Entry



Research assistants should expect to spend over 50% of their time carrying out photo-identification and database entry in the office, including fin identification, fin-matching, photo processing, sighting data entry and maintenance of our long-term photo-id catalogue. Research assistants should be prepared to work long days in the office entering data and analysing and organising photographs, including working with historic archived photographs and related data.

The programs used for database entry and cataloguing are IMatch and FinBase (which operates within MS Access). Assistants will also be responsible for managing and processing scans of old photographs and archived slides from historic research surveys. Detailed instructions on photograph organisation and formatting as well as entering survey, sighting and image data are available throughout this handbook.

There are two computers available in the dolphin centre for dedicated database entry but volunteers are advised to use their own laptops for initial photo-id where possible, to facilitate efficient data entry and processing.

3. Dolphin Centre Education and Promotion

Dolphin centre duties include general administrative tasks, receiving visitors to the dolphin centre, engaging with and educating members of the public, managing merchandise, updating websites and supporting and promoting SDWF, and raising awareness and membership participation. Also, general maintenance of research equipment and facilities. There may also be some school visits to participate in.

4. Behavioural Research

PhD Student: Isabel Baker

PhD Project Title: Life history, social and foraging behaviour of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

PhD Project Abstract

This PhD research project investigates the social and foraging behaviour of bottlenose dolphins in the Shannon Estuary, Ireland for the first time. Bottlenose dolphins have complex societies, and international long-term studies, especially in Florida and Western Australia, have revealed great diversities in their social and foraging behaviours. Detailed behavioural research has never been conducted in Ireland, despite having a resident population of bottlenose dolphins of high conservation status. Using experience from international research, this project aims to answer ground-breaking questions about the social and foraging behaviour of dolphins in Ireland and has the potential to contribute hugely to worldwide scientific knowledge.

The project combines boat-based data collection in the Shannon Estuary with computer-based data processing and analysis. Two different follow protocols, survey and individual-follow, will be employed during dolphin encounters, to gain basic population information as well as much more detailed data. This is the first time focal follows will be used in Irish bottlenose dolphin research. Twenty-three months of boat-based data collection are planned, including eight months of intensive summer fieldwork and 15 months of “off-season” fieldwork during months of the year for which very little information exists.

Previous research in the Shannon Estuary, a candidate Special Area of Conservation for the species, has determined that there are 100-120 resident bottlenose dolphins living there and that this population is genetically discrete. It is known that the dolphins use the estuary for socialising, reproduction and foraging, but there has never been any research focus on these behaviours.

Associated Tasks

Research assistants will be responsible for data collection and photo-id on board the IWDG’s RIB *Muc Mhara*. Both survey and focal follow data will be collected during bottlenose dolphin encounters on day-long surveys of the estuary. Assistants will record data in real-time, including GPS location, photographic and video sampling. Some boat handling may also be involved. Collation and management of the data collected will occur upon return to the dolphin centre.

Data Consolidation

This will occur **every evening** and research assistants are expected to deal with their day's data before going home. Data consolidation for each boat will be handled by the researcher who was on the boat that day.

Monitoring Surveys

Protocols for uploading photographs, downloading GPS tracks and completing datasheets are detailed throughout this handbook. At the very least, details of the trip should be recorded by hand in the blue book; datasheets checked for accuracy and missing entries (to be filled in); and photographs copied onto the computer and backed up. The camera's memory card(s) should be formatted and battery put on to charger. If GPS batteries were replaced, new spares should be put into the GPS case.

Photo-identification and Database Entry

Tasks should not be left unfinished and research assistants should complete the task they have been allocated before going home in the evening. Back-ups should be made for the photo-id and data entry completed that day as per protocols outlined below.

Dolphin Centre

At the end of each day, dolphin centre closing duties should be carried out, including: visitor numbers noted, facilities checked and cleaned if necessary, merchandise replaced, spreadsheet for merchandise sales should be checked for errors and corrected if necessary, cash counted in cash box and amount filled out on cash box spreadsheet. All computers and lights must be switched off before leaving the centre. All doors locked and alarm system armed.

2. Daily Operations

Shift Types

1. Monitoring Surveys (*Dolphin Discovery* and *Draíocht*)
2. Data Processing (Upstairs Office)
3. Centre Duties (Front Desk)
4. PhD Research Assistance (RIB)

Daily Steps for each Shift Type

1. Monitoring Surveys

Before the trip

At the start of the day, you should have an idea of how many boat trips there are likely to be that day from each boat. If you are conducting boat-based monitoring and have been assigned a boat for the day, the following equipment should be packed and brought with you on the boat:

1. CAMERA

- Pelican case containing SDWF digital SLR camera with at least one spare (fully charged) battery
    - Before packing the camera, check that the memory card has been formatted and is empty (if not, you will need to make sure the photos have been copied before you can format it)

2. GPS

- SDWF GPS unit with spare batteries in GPS case

3. SURVEY DATASHEETS

- Clipboard labelled with port name and enough blank datasheets for the day
- Blue or black pens and large elastic band on clipboard (for windy conditions)

4. BINOCULARS

- Binoculars (not essential but very useful for spotting)

5. FOOD and personal effects

- Lunch or snacks and plenty of water if you are planning to do multiple boat trips
- Warm jacket
- Sunglasses (sunscreen, hat)

Be sure to arrive at the boat **at least 10 minutes** before scheduled departure.

On the boat

Place your belongings in a safe place and neatly away from tourists and boat aisles. Start by turning on your GPS so that satellites can locate your position. Press the PAGE button to locate the satellite-finding screen.

Next step, fill out your datasheet for the trip. Time of departure must be the exact GPS time that you left the dock.
Help the crew to look for dolphins and calmly inform them when you have spotted a group.
Upon spotting a group, take a GPS waypoint and write the number down (Boat WPT). Take another waypoint when you are within 100m of the group and write the waypoint number (Start WPT) and coordinates (Lat start, Long start) on your datasheet.
Take your camera out, take a couple of photos to make sure you're on the correct setting, then try to take the most perpendicular and clear shots of the dolphins' dorsal fins that you can get.
Upon leaving a group, note the time and take another GPS waypoint (End WPT) and note it down.
Take a blank of the boat or sky to mark the break in photos between your first sighting and any other dolphin encounters you may have over the course of the trip. Fill out the whole datasheet.

After the trip

Return to the centre. Enter your trip in the blue book with new trip number. If you have not already done so, write the trip number clearly on the top-left corner of your datasheet. Check that there are no omissions on the datasheet, then hole-punch carefully and place it in the trip binder at the front ready for data entry.
Make sure your camera is turned off, then take the memory card out of the camera. Copy your photographs onto a computer and back them up on the SDWF USB stick. When you are sure that all the photos have been copied to both places, place the camera's memory card(s) back into the camera and format them, erasing all data. Put the battery on to the charger if below 50%. If GPS batteries were replaced, new spares should be put into the GPS case.

2. Data Processing (Upstairs Office)

Full protocols for uploading photographs, downloading GPS tracks and completing datasheets are detailed in the following pages of this handbook.

3. Centre Duties (Front Desk)

Start of day

- If you are on "Front Desk 1":
    - **It is your responsibility to open the dolphin centre at 09:30**
    - The following should be looked up and written on the white board:
        1. Dolphin-watching trip times
        2. Tide times
        3. Weather
        4. Wind
- If you are on "Front Desk 2":
    - Your shift begins at 10:00

Managing front desk and general admin

- **Never leave the front desk unattended**
    - If both front desk attendees must be absent (e.g. to continue tours with visitors in the outside area), call someone down from upstairs or lock the doors first

Welcoming visitors

- Be the first to greet visitors to the centre: "You're very welcome to the Shannon Dolphin and Wildlife Centre. Have you been here before? Do you know much about dolphins?" etc.
- Give a tour of the centre with interesting educational information

Managing merchandise

- Black moneybox = SDWF; Blue moneybox = IWDG
    - Always fill in the sales and amounts taken spreadsheet
- Monthly stock take on 1st of every month
- Seek to reorder items low on shelves

Updating websites and supporting and promoting SDWF

- Leaflets dispersed around surrounding towns and local establishments
- Raising awareness and membership participation
    - Facebook page – upload photos, add links, make comments and "Like" other dolphin/wildlife pages, share other pages' photos
    - Ask visitors if they enjoyed visit and to Like Facebook page for info on news and events
    - Ask visitors to sign guestbook

Visitor count

- Fill out a visitor spreadsheet in order to count number of visitors on a daily basis

General maintenance of research equipment and facilities

- Equipment needs to be cleaned regularly
    - Camera bodies should be cleaned gently with a dry/damp cloth (**the cameras are not waterproof**)
    - Take extra care when cleaning camera lenses
        1. Use blower to remove dust
        2. Use brush to further remove smaller dust particles
        3. Gently wipe with soft lens cloth
            - **Do not wipe** with lens cloth **if there is still visible dust** on the lens – this can scratch the lens!
        4. If there are smear marks on the lens, the lens cleaner at the other end of the lens brush can be used to gently wipe in smooth circular motions from inside to outside of lens – however this is not always necessary
- The centre needs to be kept neat and tidy
    - Sweep and hoover, brush/mop stairs
    - Clean toilets – replace toilet roll, bleach, soap, wipe surface
    - Clean kitchen – clean surfaces, dishes, microwave, fridge
    - Tidy up kids play area

End of day

At the end of each day, **dolphin centre closing duties** should be carried out, including:

- Visitor numbers noted
- Facilities checked and cleaned if necessary
- Merchandise replaced
- Spreadsheet for merchandise sales should be checked for errors and corrected if necessary
- Cash counted in cash box and amount filled out on cash box spreadsheet
- **All computers and lights must be switched off** before leaving the centre
- **All doors locked and alarm system armed**

4. PhD Research Assistance (RIB)

The same protocols apply for uploading photographs and downloading GPS tracks. Full protocols for data collection in the field and data processing will be provided during training.

3. Fieldwork Protocols

Survey basics

Bottlenose dolphin population monitoring surveys are conducted from two purpose-built dolphin-watching tour boats in the Shannon Estuary, “Dolphin Discovery” operating from Kilrush and “Draíocht” operating from Carrigaholt. Each boat is equipped with a VHF radio, depth sounder, compass, GPS and EPIRB and meets passenger safety requirements for commercial dolphin-watching vessels.

Research assistants generally survey solo, but occasionally two research assistants will conduct surveys together. The surveys take place on any given day when the weather is good and the boats are running tours. The demand for dolphin-watching tours is at its highest June-July. The times of dolphin-watching tours can be found on the websites for each operator – www.discoverdolphins.ie and www.dolphinwatch.ie the day before. Alternatively, the times for Dolphin Discovery tours are sometimes posted in the window of the Kilrush Marina building, and both tour operators can be phoned to inquire about tour times.

Upon leaving the dock, research assistants will assist in scanning and spotting dolphins from the vessel. Both vessels have a period of down-time for the researcher – Dolphin Discovery exits and enters the marina through a lock and Draíocht incorporates cliff- and wildlife-viewing as part of the tour.

If dolphins are spotted, immediately alert the captain if he is not already aware of them. Take a GPS point of the boat’s location upon spotting dolphins and prepare datasheets and camera. Take another GPS point when the boat is within 100m of the dolphins – this begins the 30-minute survey period with the animals. Note the number of the waypoint you have taken on the datasheet and begin photographing dorsal fins. Try to get an idea of the size of the group throughout your observation. Remember that group size estimates of dolphin groups are often too low because many animals can be submerged during a count – try to account for this in your estimation.

When the survey has reached 30 minutes and the boat is leaving the group, take another waypoint on the GPS and write its number down on the datasheet. Take a blank picture of the sky or boat with the camera to mark the end of the sighting and make it easier to process photos back in the centre.

Survey datasheets

Two survey datasheets should be filled out every time a research assistant goes out on a tour boat trip. When recording data, please use neat and legible handwriting; always write in BLOCK CAPITALS; avoid abbreviations and shorthand that are difficult to interpret during data entry; and try to use blue ink on sighting forms when in the field (this facilitates seeing which blanks remain to be filled in). If specific data cannot be obtained in the field, please fill in ‘999’ instead.

The survey datasheet is designed to enable efficient data collection and input.

Date: The date is entered as DAY-MONTH-YEAR, DD-MMM-YYYY, e.g. 13 JUL 2013.

Platform: This refers to the platform from which the dolphins are sighted. The boat name is entered here. Note correct spelling: DRAÍOCHT; DOLPHIN DISCOVERY; MUC MHARA.

Recorder(s): The first initial and the full last name of the person responsible for filling out the sighting form followed by the names of each extra researcher on the boat.

Trip: The number of the trip for that day (usually between 1-4). If it is your first trip for the day, but the second dolphin-watching trip the boat has done that day, it is Trip 2.

Time: The exact time that the boat left the dock and the exact time it returned.

Group Number: This is the number of the dolphin group encountered during each trip, e. g. the first group encountered is 1.

Time dolphins encountered: The exact time that the dolphin encounter began and the exact time it ended. Get these times from the GPS – they should be the same times as your "within 100m" (i.e. Start WPT) and "end" waypoints are taken.

No Dolphins (No calves): The number of dolphins encountered during the sighting. First the number for *all dolphins* in the group is recorded with best, min and max estimates. Then, the best, min and max estimates for number of calves in the group is recorded in brackets.

Below the cells on the datasheet, record **sighting number and associated waypoints** (e.g. 1. WP 90, 91, 92), **location** (e.g. Béal Bar (ask the skipper)), **animal heading** (e.g. SW) and **notes** about the encounter (e.g. any IDs, fish species sighted, behaviours).

Boat Hours: A reading from the boat odometer should be taken before leaving the boat ramp and a reading should be taken after the outboard has been rinsed during boat cleaning at the end of the day. (applies to RIB only)

Effort: This describes the type of effort under which the sighting was conducted; either Intensive or Opportunistic. (applies to RIB only)

Environmental data

Precipitation: None, Rain

Cloud Cover: Clear, Partly Cloudy or Overcast. Measured on a scale of 0 to 8 as an estimate of how much of the total area of visible sky is covered with clouds. 0 = completely clear, 8 = completely overcast.

Visibility: Clear, Haze or Fog

Sightability: Excellent, Good, Fair, Poor (probably missing dolphins)

Swell: 0-2 ft or 2-4 ft or 4-6 ft or >6 ft (swell in metres can be found on www.windfinder.com, then convert to feet. 1 m is roughly equal to 3 ft)

Tide: Recorded as FLOOD (IN), EBB (OUT), HIGH or LOW. Using the corresponding tide tables for the month, determine the tide state for the start time of **each sighting**. HIGH tide and LOW tide are each recorded as an hour-long period, 30 minutes before and after the predicted time of the tide. E.g. LOW tide at 08:30 would imply that if a sighting started at 08:15 or 08:59, the tide would be recorded as LOW.

Beaufort scale: Standard Beaufort Sea State scale (see last pages of document).

Water temperature and depth: Read from the depth sounder.

Glare: None, Little, Some (could interfere), Much (interfering)

Wind direction: Recorded in km/h, rough estimates made by scribe or find on www.windfinder.com.

Sighting data

Sighting number: The number of the photo identification approach.

Camera: The camera that is being used for the photo identification session. (D300, D300s)

Time: The start and end times of the photo id session.

Initials: The initials of the photographer taking the pictures during the photo id session.

Frames: The start and end frame numbers taken during the photo id session.

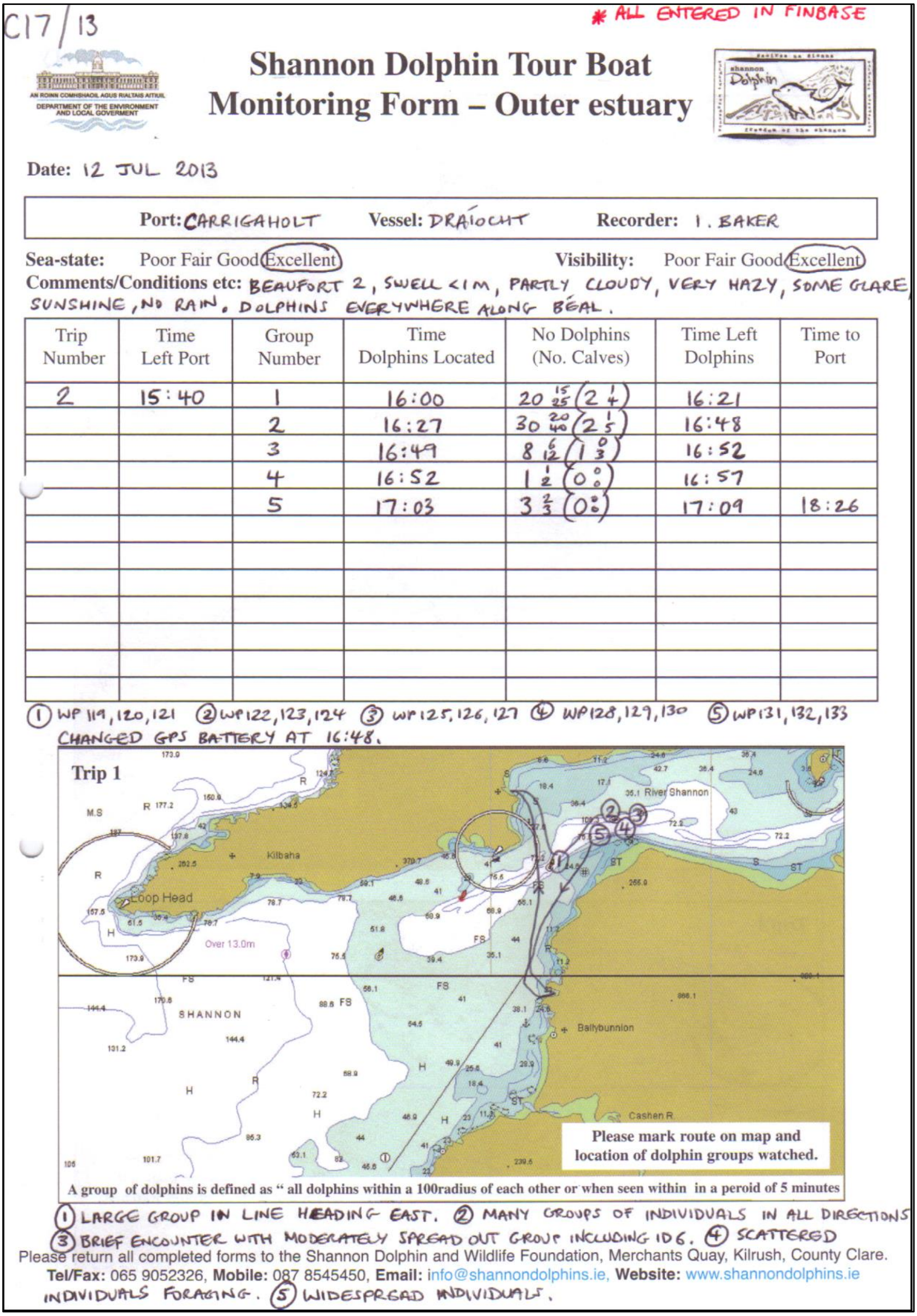
Memory card: The memory card number used during the photo id session.

Comments

Any observations worth noting during the photo id session should be written clearly here. For example if a dolphin was observed with a calf in baby position and a picture taken, the frame number and a brief note should be included here.

Mistakes

Mistakes made on datasheets should be crossed out with a single horizontal line and the correct word written clearly next, e.g. ~~seals~~ dolphins



C17/13

* ALL ENTERED IN FINBASE

AN ROINN COMHSHAOIL AGUS RIALTAIS ÁITIÚIL
DEPARTMENT OF THE ENVIRONMENT AND LOCAL GOVERMENT

Shannon Dolphin Tour Boat Monitoring Form – Outer estuary

Date: 12 JUL 2013

Port: CARRIGAHOLT **Vessel:** DRAÍOCHT **Recorder:** I. BAKER

Sea-state: Poor Fair Good [✓ Excellent] **Visibility:** Poor Fair Good [✓ Excellent]

Comments/Conditions etc: BEAUFORT 2, SWELL <1M, PARTLY CLOUDY, VERY HAZY, SOME GLARE, SUNSHINE, NO RAIN. DOLPHINS EVERYWHERE ALONG BÉAL.

Trip Number	Time Left Port	Group Number	Time Dolphins Located	No Dolphins (No. Calves)	Time Left Dolphins	Time to Port
2	15:40	1	16:00	20 $\genfrac{}{}{0pt}{}{15}{25}$ (2 $\genfrac{}{}{0pt}{}{1}{4}$)	16:21	
		2	16:27	30 $\genfrac{}{}{0pt}{}{20}{40}$ (2 $\genfrac{}{}{0pt}{}{1}{5}$)	16:48	
		3	16:49	8 $\genfrac{}{}{0pt}{}{6}{12}$ (1 $\genfrac{}{}{0pt}{}{0}{3}$)	16:52	
		4	16:52	1 $\genfrac{}{}{0pt}{}{1}{2}$ (0 $\genfrac{}{}{0pt}{}{0}{0}$)	16:57	
		5	17:03	3 $\genfrac{}{}{0pt}{}{2}{3}$ (0 $\genfrac{}{}{0pt}{}{0}{0}$)	17:09	18:26

① WP 119, 120, 121 ② WP 122, 123, 124 ③ WP 125, 126, 127 ④ WP 128, 129, 130 ⑤ WP 131, 132, 133
CHANGED GPS BATTERY AT 16:48.

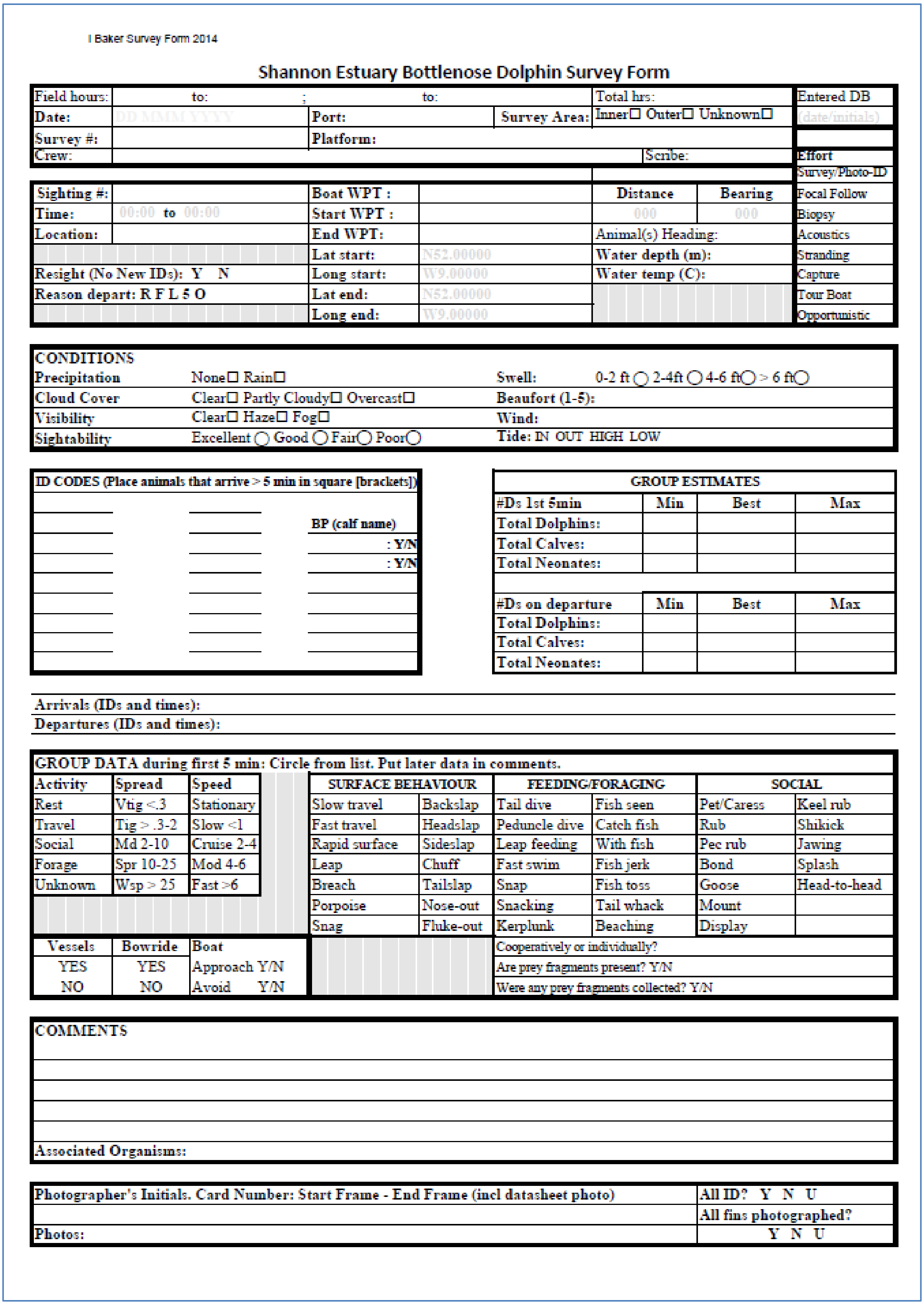
Please mark route on map and location of dolphin groups watched.

A group of dolphins is defined as " all dolphins within a 100radius of each other or when seen within in a peroid of 5 minutes

① LARGE GROUP IN LINE HEADING EAST. ② MANY GROUPS OF INDIVIDUALS IN ALL DIRECTIONS ③ BRIEF ENCOUNTER WITH MODERATELY SPREAD OUT GROUP INCLUDING ID6. ④ SCATTERED INDIVIDUALS FORAGING. ⑤ WIDESPREAD INDIVIDUALS.

Please return all completed forms to the Shannon Dolphin and Wildlife Foundation, Merchants Quay, Kilrush, County Clare.
Tel/Fax: 065 9052326, **Mobile:** 087 8545450, **Email:** info@shannondolphins.ie, **Website:** www.shannondolphins.ie

Sample tour boat datasheet.



I Baker Survey Form 2014

Shannon Estuary Bottlenose Dolphin Survey Form

Field hours:	to:	;	to:	Total hrs:	Entered DB
Date:	DD MMM YYYY	**Port:**	**Survey Area:**	Inner☐ Outer☐ Unknown☐	(date/initials)
Survey #:		**Platform:**			
Crew:			Scribe:		**Effort**
					Survey/Photo-ID

Sighting #:		**Boat WPT :**		**Distance**	**Bearing**	Focal Follow
Time:	00:00 **to** 00:00	**Start WPT :**		000	000	Biopsy
Location:		**End WPT:**		Animal(s) Heading:		Acoustics
		Lat start:	N52.00000	**Water depth (m):**		Stranding
Resight (No New IDs): Y N		**Long start:**	W9.00000	**Water temp (C):**		Capture
Reason depart: R F L 5 O		**Lat end:**	N52.00000			Tour Boat
		Long end:	W9.00000			Opportunistic

CONDITIONS			
Precipitation	None☐ Rain☐	**Swell:**	0-2 ft ○ 2-4ft ○ 4-6 ft○ > 6 ft○
Cloud Cover	Clear☐ Partly Cloudy☐ Overcast☐	**Beaufort (1-5):**	
Visibility	Clear☐ Haze☐ Fog☐	**Wind:**	
Sightability	Excellent ○ Good ○ Fair○ Poor○	**Tide:** IN OUT HIGH LOW	

ID CODES (Place animals that arrive > 5 min in square [brackets])

BP (calf name)

: Y/N

: Y/N

GROUP ESTIMATES			
#Ds 1st 5min	**Min**	**Best**	**Max**
Total Dolphins:			
Total Calves:			
Total Neonates:			
#Ds on departure	**Min**	**Best**	**Max**
Total Dolphins:			
Total Calves:			
Total Neonates:			

Arrivals (IDs and times):

Departures (IDs and times):

GROUP DATA during first 5 min: Circle from list. Put later data in comments.

Activity	Spread	Speed
Rest	Vtig <.3	Stationary
Travel	Tig > .3-2	Slow <1
Social	Md 2-10	Cruise 2-4
Forage	Spr 10-25	Mod 4-6
Unknown	Wsp > 25	Fast >6

SURFACE BEHAVIOUR		FEEDING/FORAGING		SOCIAL	
Slow travel	Backslap	Tail dive	Fish seen	Pet/Caress	Keel rub
Fast travel	Headslap	Peduncle dive	Catch fish	Rub	Shikick
Rapid surface	Sideslap	Leap feeding	With fish	Pec rub	Jawing
Leap	Chuff	Fast swim	Fish jerk	Bond	Splash
Breach	Tailslap	Snap	Fish toss	Goose	Head-to-head
Porpoise	Nose-out	Snacking	Tail whack	Mount	
Snag	Fluke-out	Kerplunk	Beaching	Display	

Vessels	Bowride	Boat
YES	YES	Approach Y/N
NO	NO	Avoid Y/N

Cooperatively or individually?

Are prey fragments present? Y/N

Were any prey fragments collected? Y/N

COMMENTS

Associated Organisms:

Photographer's Initials. Card Number: Start Frame - End Frame (incl datasheet photo)	**All ID? Y N U**
	All fins photographed?
Photos:	**Y N U**

Sample survey datasheet.

Instructions for using the digital SLR cameras

Project cameras

The SDWF uses digital cameras with 200mm-500mm lenses to obtain photos. The cameras are stored in waterproof Pelican cases. In some cases, a lens filter is attached to the front of the lens to protect it from spray and scratching. Each camera starts the day with a memory card in it. There are 6 spare memory cards (2x 8GB, 2x 4GB and 2x 2GB) kept in the camera case. In addition, 2 fully charged backup batteries are kept in the camera case. The camera systems are valued at €2,500 each, and repairs are very expensive – it is imperative that we provide the best possible care for them, especially with regards to shock and exposure to spray and rain. **The cameras are not waterproof.**

Batteries: Important: Turn the camera OFF before inserting or removing batteries. When you turn the camera on, check the battery-level displayed in the control panel to determine whether the battery needs to be replaced/charged. The battery needs to be replaced when the battery-level indicator is below 50%. Keep the two spare batteries fully charged as backups to take out on the boat. On cold days, the capacity of the batteries tends to decrease so make sure it is fully charged before taking photos in cold weather.

Memory cards: Important: Turn the power OFF before inserting or removing the memory cards. Inserting or removing cards with the power on could render them unusable.
Formatting memory cards is the most effective way of deleting all pictures on the card.
To format the card, go to the Setup menu on the display monitor, go to FORMAT and scroll to YES (“Warning! All images will be deleted”), then press the ENTER button to start formatting. Formatting begins immediately.

Date and Time: The date and time of recording is included with all pictures. To ensure that the pictures are stamped with the correct time and date, display the SETUP menu and use the menu button to scroll down to DATE, and scroll through to set the date and time. The time should coincide with GPS time settings. Push the ENTER button at the bottom left of the display to save any changes to the settings. The date and time should be checked daily.

Camera settings (dial on the top of the camera)

When in doubt, use the Sports mode to take photos of dolphins. Always check your initial photos on the display using the play button to ensure that they are coming out correctly. The S mode can also be used to control shutter speed. Shutter speed controls the amount of light allowed to enter your photo. If your images are all overexposed (i.e. too white), try increasing the shutter speed so that less light comes in, e.g. 1/1000. If the images are too dark, you need to decrease the shutter speed to let more light in, e.g. 1/500. The shutter speed generally needs to be between 1/500-1/1250 to take good pictures of dolphins.
Ensure that file names are in a four-digit format, e.g. IMG_0001, not IMG_001, etc.

Taking photos of bottlenose dolphins

Open the Pelican case and carefully take out the camera. Always wear the camera strap around your neck. Remove the lens cap and place it in the Pelican case, then close the lid of the case.
Zooming the lens from 80mm to 400mm decreases the maximum aperture. The best dorsal fin pictures come from photos taken where the camera lens is zoomed out to 400mm, filling the frame with one single dorsal fin. It takes some practice to achieve such photos but it is worth it in the long run! If the dolphins are within 50m of the boat, it is acceptable to zoom out.

Downloading pictures from the day

1) Remove the memory card(s) from the camera and insert into your laptop or the Centre's Desktop Computer. If the computer does not have its own card reader, use the memory card reader with USB cable.

2) Copy the photos to your computer – See "Downloading and initial photo-identification" page **22**

3) Double-check that all the photos have been copied to all three locations – your laptop (Originals and processing folders) and SDWF USB stick

4) Safely remove the memory card(s), replace in the camera and **format** so that the card is ready for the next trip.

5) Recharge the camera batteries if necessary

Replacing datasheets

Remove all the datasheets filled out on the day from their clipboards and check that everything was filled in. If you used multiple datasheets, attach them together using a paperclip on the top-left corner. Place the datasheets in the front of the trip folder ready for data processing.

Check how many forms have been used and replace them with blank forms. It may be necessary to get new forms from the labelled boxes on the bookshelves. Replace other equipment (e.g. elastic bands, pens) when necessary.

Downloading GPS tracks and waypoints

1) Plug the GPS into the GPS cable on the front desk computer

2) Turn the GPS on

3) Open the software “Map Source”

- Go to *File* then *Open from device*
- Click *OK*

4) Go to *waypoints* and *track* tabs

Delete waypoints and tabs which were not part of your trip so that the only ones visible are from your day out on the water. (Note: You can right click on track to show selected track on map).

5) Go to *File* and *Save As*.

- Go to *SDWF* in Dropbox.
- Go to *2015 GPS.*
- Create new folder with date, trip number and underscore GPS. E.g. 2015-07-25_C10_GPS

6) Save Map Source file in this folder with the same name.

7) Repeat steps and save as an Excel file (CSV) too with the same name.

8) Go to *File*; then *Export*.

- Save as *text file* with same name.

9) Close “MapSource”

10) Turn the GPS on again.

11) Open “DNR Garmin”

- Click Waypoints – Download All
    - Delete waypoints which were not part of your trip so that the only ones visible are from your day out on the water.
- Save Waypoints as *text file* (in the same Dropbox folder) with date, trip number, underscore GPS and underscore “Waypoints”. E.g. 2015-07-25_C10_GPS_Waypoints
- Click Tracks – Download All

    - Delete Tracks which were not part of your trip so that the only ones visible are from your day out on the water.

- Save Track as *text file* with date, trip number, underscore GPS and underscore “Track”. E.g. 2015-07-25_C10_GPS_Track

12) Make sure files are in Dropbox.

- If files are saved in Dropbox, delete track and waypoints from GPS.

Deleting tracks and waypoints on the GPS

- Turn on the GPS
- Press the “Menu” button twice
- Go to Tracks- Enter- Clear- Enter- Yes.
- Press Quit.
- Go to Points- Enter- Menu- Delete All- Enter- Yes.
- Press Quit.
- Turn off the GPS

4. Database Entry and Management

On return from the field, the blue book MUST be filled in with trip details and a trip number assigned and written on the **top-left** corner of the datasheet.

Survey and Sighting entry in FinBase

Survey (trip) and sighting (group) data collected during the day is entered into FinBase on IB's laptop. Always enter data into FinBase in pairs to ensure accuracy in data entry.

1) Open FinBase

2) Open switchboard

3) Enter survey/sighting data

Database backup

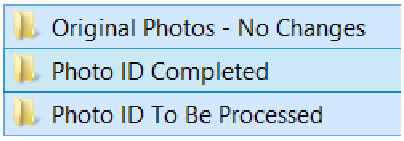
The IMatch database and associated folders should be backed up at least once a week (every Friday)

All the photos and IMatch database are on the red WD My Passport hard drive (case labelled IMATCH)

Everything is backed up on the soft black WD My Passport hard drive (labelled MEDIA/SDWF BACKUP) – plug this hard drive in before backup

- To backup the IMatch database, open IMatch (but have the SDWF IMatch Database closed)
- Click Database – Backup Database
- The database to backup is F:\SDWF IMatch Database
- The target folder for the backup is in the black WD My Passport hard drive: Backup\IMatch DB\1
- Click Start
    - IMatch may ask if you want to replace the existing backup – Yes
- Backup begins and should take 5 mins
- When backup is complete, a dialogue box which says "Backup operation successfully completed" will appear
- Click OK, click Close on the backup dialogue box, and close IMatch

- To backup the photo folders, open both hard drive screens



Original Photos - No Changes
Photo ID Completed
Photo ID To Be Processed

- Select the three folders on the IMATCH drive
- Copy these folders to the My Passport drive – this takes hours so be prepared not to use the computer or IMatch for a while

5. Photo-identification Protocols

Introduction to Photo-identification

Becoming a photo-id expert is like training to become a forensic detective. It takes focus, patience and an eye for detail.

Remember that the same dorsal fins will look different from different angles and in different types of light. Keep the individuals you have already identified in mind as you search through remaining photos. All too often, several photos of the same dolphin are assumed to be different individuals because of picture angle and quality.

Think about the individuals in your sighting. If there is a mother or calf in the sighting, you should be thinking about finding the mother/calf that completes the pairing.

To ensure that you have made a positive match between two dorsal fins, always find at least two pieces of evidence to confirm the match. For example, if you think a notch in the trailing edge of the fin is the same in both photos, find a scar on that side of the fin that also looks the same in both photos.

Get used to checking other people’s matches to make sure they are correct. It is important to check each other’s matches and helps to improve your eye for matching.

Some of the individuals in the catalogue look very similar and are not to be confused. For example:

006 and 106

071 and 173

Look out for these frequently spotted individuals…

001

006

011

071

095

104

Downloading and initial photo-identification

Create a folder on your computer/hard drive where you will save all your SDWF images. For example, in your **Pictures** folder, create a folder called **My SDWF Photos**.

Within this folder, create two folders corresponding to the day's date and trip number: one for all the photos (originals) and one for the photos that you will process (delete and rename), e.g. **2015-06-25_C20_Originals**; **2015-06-25_C20**

Note: DATE IS IN THE FORMAT YYYY-MM-DD

Copy all photos from the memory card(s) to your Originals folder

Then copy all photos again to your second folder – this is the folder where you will manipulate your photos. The Originals folder acts as a backup of all the photos taken during that research trip.

Now, get the SDWF USB stick and copy your Originals folder onto that, as a backup. You should now have the exact same set of photos in three places.

Open the folder for processing photos (e.g. **2015-06-25_C20**) and create a folder for each sighting within your trip named S (for sighting) and the sighting number. E.g. for the first sighting, the folder is named S1, the second sighting is S2, etc.

Then begin looking through your photos

Delete all shots of water or very blurry dolphins – do not delete anything that shows interesting behaviour, e.g. leap sequence

Keep any good photos of people, scenery, boats, other animals, etc.

Matching fins to the catalogue and renaming files

Now start searching for fins and identities

Compare fins in your photos with the photos in the folder "SDWF Photo-ID Catalogues 2015" in the SDWF Dropbox folder. This contains multiple folders of official catalogued adult IDs, intermediate individual IDs and calf IDs. Each of these classes has a folder of all identities together, as well as folders for left and right separately. Bear in mind that not all individuals have photographs in both the left and right catalogues, i.e. if you are looking for the left side of an individual, but don't find it in the left catalogue, it is necessary to check the right catalogue too.

If you find a positive match, rename your photo with the three-unit identity of the individual, the side of the fin (L or R for left or right) and an underscore (_). DO NOT RENAME THE REST OF THE IMAGE. If your original photo filenames are like this: IMG_2093, then your new filename should look like this 009L_IMG_2093

When you have identified all the individuals in a sighting, you need to choose **ONE best** picture of each individual and crop it around the dorsal fin.

Cropping fins

Draw a neat rectangle around the dorsal fin

- This should include the tip of the fin, down to the front, down to the back and the furthest most point of the bottom where the body meets the water
- If part of the fin is in the water, crop as though you are cropping the whole fin
    - COMPENSATE FOR MISSING PARTS OF THE FIN

Bad crop

Good crop

Bad crop

Good crop

"Save As" the image into your processing folder – make sure you save in the correct folder!

Put a "c" at the end of the filename to indicate that the picture was cropped.

E.g. If your original picture was called 009L_IMG_2093, your cropped picture will be called 009L_IMG_2093c

DO NOT "Save" the image thereby replacing it with a cropped version of itself

Make sure the cropped photo is saved as a JPEG

Continue until there is **one** cropped picture for every identified individual in the sighting

When you have finished renaming all the individuals in the sighting, you should have one best dorsal fin picture of each individual next to the pictures it was cropped from, like this:

Well done! Now it is time to import the photos into the IMatch database.

Processing historical photo-id data

Access the folder on your computer/hard drive where you save all your SDWF images. For example, in your **Pictures** folder, a folder called **My SDWF Photos**.

Within this folder, create **one folder** for the photos that you will process (delete and rename), e.g. **2010-06-25_C20**

The Original Photos for the years 2010 and earlier are stored elsewhere.

Open the folder for processing photos (e.g. **2010-06-25_C20**) and create a folder for each sighting within the trip named S (for sighting) and the sighting number. E.g. for the first sighting, the folder is named S1, the second sighting is S2, etc.

Then begin looking through the photos

The photos should be named in a consistent way, i.e. all have the same file name format. For example, all photos from a camera might have filenames that look like this: IMG_0000, IMG_0001, IMG_0002, IMG_0003, and so on.

If the filenames of the photos are not consistent, they must be made so

E.g. If there are three photos in the sighting: IMG_0000, IMG_0001, 77, the file named "77" must be renamed IMG_0003, or **whatever number is free, as long as the format is consistent**

Delete all shots of water or very blurry dolphins – do not delete anything that shows interesting behaviour, e.g. leap sequence

Keep any good photos of people, scenery, boats, other animals, etc.

Matching fins to the catalogue and renaming files

Compare fins in your photos with the photos in the folder "SDWF Photo-ID Catalogues 2015" in the SDWF Dropbox folder. This contains multiple folders of official catalogued adult IDs, intermediate individual IDs and calf IDs. Each of these classes has a folder of all identities together, as well as folders for left and right separately. Bear in mind that not all individuals have photographs in both the left and right catalogues, i.e. if you are looking for the left side of an individual, but don't find it in the left catalogue, it is necessary to check the right catalogue too.

If you find a positive match, rename your photo with the three-unit identity of the individual, the side of the fin (L or R for left or right) and an underscore (_). DO NOT RENAME THE REST OF THE IMAGE. If your original photo filenames are like this: IMG_2093, then your new filename should look like this 009L_IMG_2093

When you have identified all the individuals in a sighting, you need to choose **ONE best** picture of each individual and crop it around the dorsal fin.

Now crop the fin in the same way you crop current data.

Adding photos to the IMatch database

Copy your processed folder onto the SDWF USB stick and take it to the IMatch laptop.

Insert the SDWF USB stick and open it on the computer

Cut and paste your processed folder from the SDWF USB stick onto the IMatch hard drive in the folder **Photo ID To Be Processed – 2015**

Open IMatch from the shortcut on the research assistant laptop. If IMatch tells you that photos have been added and asks you to update, click Yes.

N.B. If IMatch asks you if you want to check for an update online, click NO

If necessary, click the plus sign next to Photo ID To Be Processed, to show all years

Right-click on 2015, click “Rescan”, click Next – Next – Next – Finish

- This will add your newly copied photos into the IMatch database

Smart Rename

Select all (CTRL+A) the photos in your sighting and click Tools on the top toolbar

Select Smart Rename – a dialog box will open

Rename your images so that every file’s name has the date, trip, sighting number and file number

- E.g. 20130622_K01_S1_0103.jpg
- **Note that the file names do not contain hyphens like the folder names do**
- Use a replace sequence in IMatch using */ to replace certain segments, e.g. */IMG/20130622_K01_S1/
- For help, click on the question mark to the right of the field entry box

Scroll down and check that all your “New file names” look correct before clicking OK

Category Assignments

Interesting dolphin photos or scenic pictures taken on the day should be categorised using the Category Assignment Dialog

- To open the Category Assignment Dialog box, either:
    - Click the icon
    - OR hold down **Ctrl+Alt+A**

Select the photos you want to apply the category to by holding down the **Ctrl** key

Click the plus sign for either **Dolphin Pics** or **Scenic Pics**

- Check the squares for which your pictures apply
    - Dolphin Pics include:
        1. Behaviour
            - Backslap
            - Belly roll
            - Bow-riding boats
            - Bow-riding ships
            - Breach
            - Chase
            - Chinslap
            - Defecation
            - Eyes closed
            - Forage
            - Genital slits or genitals
            - Head out
            - Head-to-head
            - Leap
            - Mount
            - On side
            - Pec out
            - Pet
            - Sideslap
            - Snagging
            - Social
            - Spyhop
            - Sunbathing
            - Surface rush
            - Tail out
            - Tailslap
            - Wake-riding
            - With birds
            - With fish
            - With seaweed
        2. Lamprey
        3. Mother-calf Pics
        4. Possible deformities
        5. Skin conditions
        6. Skin wounds
    - Scenic Pics include:
        1. Birds
        2. Boats
        3. Cows
        4. Fish
        5. Industrial
        6. Jellyfish
        7. People
        8. Scenery
        9. Seals
        10. Wild goats

Categorising and copying sighting photos to FinBase

Named Individuals:

In each trip and sighting, select the one cropped photo of each individual by holding down the “Ctrl” key and clicking on each picture.

Open Category Assignment Dialog (Ctrl+Alt+A)

- Click the plus sign for FinBase
- Check box “To be entered into Finbase (Green)”
- Then X out of it

While they are still highlighted, press Ctrl+Shift+**3** to turn **green**

Right click and click “Quick Copy” into shannondolphin/dropbox/SDWF/From IMatch - for FinBase Sightings

When the dialogue box opens, **CLICK NO**

Open Dropbox – SDWF – From IMatch - for FinBase Sightings

Make a new folder with the trip name, e.g. **2014-05-15_C01**

Within that, make a folder for the sighting, e.g. **S1** and then put the photos in

UNK Individuals:

In each trip and sighting, select the one cropped photo of each individual by holding down the “Ctrl” key and clicking on each picture.

Open category assignment dialog (Ctrl+Alt+A)

- Check box for Intermediate Catalogue
- Click the plus sign
- Check box either left or right
- Then X out of it

While they are still highlighted, press Ctrl+Shift+**1** to turn **red**

When all pictures have been entered, and trip is completed, seek IB or KR for checking and submitting trip

Matching and Cataloguing Fins in FinBase

Cut and paste the survey folder from **From IMatch – For FinBase Sightings** to IB's computer folder **OS (C:) – Data – FinBase – SDWF – Sightings**

Go to the desktop and double-click the shortcut icon for **SDWF_FE**

Click Open Switchboard

In the Navigation Pane on the right-hand side of the screen, find the form "PhotographicQuality" and double-click

Click on the "Open Folder" icon and select all of the photos from the sighting of the survey (do one sighting at a time, if there are multiple sightings in the survey)

Click Open

Now, select the photographic quality parameters for each photo in turn

If any of the triangular dorsal fin is covered by water or another obstruction, select Partially Obscured

When finished, click Add/Update and Close the window

Click Match/Catalog Fins

Click on the "Open Folder" icon and select the first photo from the sighting

Further instructions and help from IB

Appendix: The Beaufort scale

Beaufort number	Description	Wind speed	Wave height	Sea conditions	Sea state photo
0	Calm	< 1 km/h < 1 mph < 1 kn < 0.3 m/s	0 m 0 ft	Flat.	
1	Light air	1.1–5.5 km/h 1–3 mph 1–2 kn 0.3–1.5 m/s	0–0.2 m 0–1 ft	Ripples without crests.	
2	Light breeze	5.6–11 km/h 4–7 mph 3–6 kn 1.6–3.4 m/s	0.2–0.5 m 1–2 ft	Small wavelets. Crests of glassy appearance, not breaking	
3	Gentle breeze	12–19 km/h 8–12 mph 7–10 kn 3.4–5.4 m/s	0.5–1 m 2–3.5 ft	Large wavelets. Crests begin to break; scattered whitecaps	

4	Moderate breeze	20–28 km/h 13–17 mph 11–15 kn 5.5–7.9 m/s	1–2 m 3.5–6 ft	Small waves with breaking crests. Fairly frequent white horses.	
5	Fresh breeze	29–38 km/h 18–24 mph 16–20 kn 8.0–10.7 m/s	2–3 m 6–9 ft	Moderate waves of some length. Many white horses. Small amounts of spray.	
6	Strong breeze	39–49 km/h 25–30 mph 21–26 kn 10.8–13.8 m/s	3–4 m 9–13 ft	Long waves begin to form. White foam crests are very frequent. Some airborne spray is present.	
7	High wind, Moderate gale, Near gale	50–61 km/h 31–38 mph 27–33 kn 13.9–17.1 m/s	4–5.5 m 13–19 ft	Sea heaps up. Some foam from breaking waves is blown into streaks along wind direction. Moderate amounts of airborne spray.	
8	Gale, Fresh gale	62–74 km/h 39–46 mph 34–40 kn 17.2–20.7 m/s	5.5–7.5 m 18–25 ft	Moderately high waves with breaking crests forming spindrift. Well-marked streaks of foam are blown along wind direction. Considerable airborne spray.	

9	Strong gale	75–88 km/h 47–54 mph 41–47 kn 20.8–24.4 m/s	7–10 m 23–32 ft	High waves whose crests sometimes roll over. Dense foam is blown along wind direction. Large amounts of airborne spray may begin to reduce visibility.	
10	Storm, Whole gale	89–102 km/h 55–63 mph 48–55 kn 24.5–28.4 m/s	9–12.5 m 29–41 ft	Very high waves with overhanging crests. Large patches of foam from wave crests give the sea a white appearance. Considerable tumbling of waves with heavy impact. Large amounts of airborne spray reduce visibility.	
11	Violent storm	103–117 km/h 64–72 mph 56–63 kn 28.5–32.6 m/s	11.5–16 m 37–52 ft	Exceptionally high waves. Very large patches of foam, driven before the wind, cover much of the sea surface. Very large amounts of airborne spray severely reduce visibility.	
12	Hurricane-force	≥ 118 km/h ≥ 73 mph ≥ 64 kn ≥ 32.7 m/s	≥ 14 m ≥ 46 ft	Huge waves. Sea is completely white with foam and spray. Air is filled with driving spray, greatly reducing visibility.	

Appendix H

Notes on additional research findings

Some of our additional research findings not included in the outputs of this PhD research project include sightings outside the research area of dolphins included in the Shannon dolphin photo-id catalogue, sightings within the research area of dolphins included in the IWDG coastal bottlenose dolphin photo-id catalogue, and connections between them:

1) The Bunratty dolphins. In April 2013, three juvenile dolphins were observed in the Ratty River (a tributary of the Lower River Shannon), next to the mediaeval castle of Bunratty, many miles upriver from where dolphins are usually sighted. They stayed there for two weeks in very shallow water. While there were concerns about their wellbeing, it seemed that they were feeding on an abundance of fish in the river. I matched all three individuals to individuals in the Shannon dolphin photo-id catalogue and on 03 June 2013, photographed them again, alive and well in the estuary. The story was documented by Ireland's national broadcaster RTE and on the Irish Whale and Dolphin Group's website (http://www.iwdg.ie/news/?id=2368).

2) We have made matches between the Shannon dolphin photo-id catalogue and several sightings of bottlenose dolphins in and near Kilkee, on the Atlantic coast of Co. Clare, and a manuscript documenting these sightings is in preparation.

3) In August 2015, I spotted and photographed a group of dolphins traveling in the inner estuary and behaving in an unusual way, who disappeared soon after we approached them in the research vessel. I matched three of these dolphins with individual IDs in the IWDG coastal bottlenose dolphin catalogue and have sighting records of them in various counties around Ireland.

4) In January 2017, video footage and photographs were sent to the IWDG of two bottlenose dolphins apparently attacking a harbour porpoise in Cork Harbour. I was able to identify them as two members of the Shannon dolphin population – ID# 073 and ID# 869. Interestingly, ID# 073 also appears in sightings in the IWDG photo-id catalogue and ID# 869 was an animal that I first recorded as a calf (mother = ID# 220) in the Shannon Estuary but who had weaned by this time. An IWDG news article explains the story further (http://www.iwdg.ie/news/?id=2680).

5) I have noticed several Shannon dolphin IDs in photos posted on Facebook of dolphins visiting the well-known solitary dolphin, "Fungie", in Dingle Harbour, Co. Kerry, including the two individuals mentioned above in the harbour porpoise encounter.

These sightings, and particularly 3-5, raise important questions about the range of the individual dolphins whose behaviour and social structure are analysed in this thesis. Unfortunately there are currently not enough data to provide any systematic answers to these questions. They do, however, illustrate how much more there is to learn about the behaviour and social structure of this population.

Appendix I

A Population Viability Analysis for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

Introduction

Population Viability Analysis (PVA) techniques use population data to determine the stability (or growth/decline) of animal populations, predicting the future status of a population by quantifying its probability of extinction (Boyce 1992). An understanding of the life history characteristics of a specific population coupled with results from PVAs can provide essential information for conservation and management, since the results can have significant effects on management plans. For example, in their study of two Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations, in Shark Bay and Bunbury, Australia, Manlik *et al.* (2016) used a Population Viability Analysis (PVA) to demonstrate that reproductive rates had a stronger influence on long-term viability than adult survival rates. The Bunbury bottlenose dolphin population is forecast to decline by 50% in the next two decades and Manlik *et al.* (2016) concluded that focusing on reproduction would be the best management strategy to improve the viability of the population.

Female reproductive parameters such as inter-birth intervals (Connor *et al.* 2000) and reproductive success (Fruet *et al.* 2015) play a crucial role in determining long-term population viability. However, analyses of population viability have often used life history parameters from other study populations because baseline data were not available for the population in question. This approach may misrepresent the true viability of the population in question (Arso Civil *et al.* 2017). Thus, population-specific life history data are essential for the production and interpretation of reliable PVA results and the investigation of long-term population trends.

The only previous work modelling the population viability of the Shannon Estuary bottlenose dolphin (*Tursiops truncatus*) population, using a PVA carried out in the software program VORTEX (version 9.92), used a population estimate generated from its own mark-recapture study (Englund *et al.* 2008), but otherwise made use of parameters from very dissimilar populations and study sites, including maximum age estimates (Read *et al.* 1993) and mortality rates (Wells & Scott 1990) from Sarasota Bay, and reproductive maturity estimates from northeast Florida (Sergeant *et al.* 1973).

These population parameters may not be truly representative of the Shannon Estuary bottlenose dolphin population. Using these values, Englund *et al.* (2008) concluded that the bottlenose dolphin population in the Shannon Estuary would likely increase from 114 to 160 individuals in 250 years' time. However, the population parameters drawn from other studies may not be representative of the Shannon Estuary bottlenose dolphin population.

In this study, I conduct a similar PVA on the Shannon dolphin population using reproductive parameters from my research (Baker *et al.* 2018 (Chapter 2)), in addition to some of the values used by Englund *et al.* (2008) as well as some values from more recent results of bottlenose dolphin research elsewhere. Specifically, I present information on the analysis and results of three PVAs: i) replicating Englund *et al.*'s (2008) PVA; ii) using Englund *et al.*'s (2008) values but substituting those newly available from Baker *et al.* (2018); and iii) using Englund *et al.*'s (2008) values but both substituting those newly available from Baker *et al.* (2018) and updating first age at reproduction (for males and females) and maximum age with more recent results from wild bottlenose dolphin research reported by Wells (2014). I show that these PVAs generate quite different results.

Methods

VORTEX (version 10.0.7.9, Lacy & Pollak 2014; Lacy 1993) was used to simulate population dynamics and predict population viability outcomes. Multiple simulations were carried out under three discrete scenarios, using (1) exact values input and reported by Englund *et al.* (2008); (2) values input by Englund *et al.* (2008) but substituting those available from Baker *et al.* (2018) and; (3) the values input by Englund *et al.* (2008) but substituting the values from Baker *et al.* (2018) and using updated values from Wells (2014) (Table 1). In agreement with Englund *et al.* (2008), I considered VORTEX to be an appropriate simulation tool because it models the population dynamics by taking both demographic and environmental stochasticity (environmental variation (EV) is modelled using standard deviation) into account.

Table 1. Parameters used in VORTEX simulations, for three discrete scenarios (Scenario 1, 2 and 3), including published sources. Environmental variation (EV) is modelled using standard deviation.

Parameter	***Scenario 1 parameter value***	***Source***	***Scenario 2 parameter value***	***Source***	***Scenario 3 parameter value***	***Source***
First age at reproduction						
Male	11	Sergeant *et al.* 1973	11	Sergeant *et al.* 1973	10	Wells 2014
Female	10	Sergeant *et al.* 1973	10	Sergeant *et al.* 1973	5 to 8	Wells 2014
Maximum age	50	Read *et al.* 1993	50	Read *et al.* 1993	67	Wells 2014
Sex ratio at birth	0.5		0.5		0.5	
Polygynous mating	75% of males in breeding pool		75% of males in breeding pool		75% of males in breeding pool	
Reproduction	14.4% (EV 2.44) of females produce one young not density-dependent	Wells and Scott 1990	25.7% (EV 3.42) of females produce one young not density-dependent	Baker *et al.* 2018	25.7% (EV 3.42) of females produce one young not density-dependent	Baker *et al.* 2018
	Inbreeding depression incorporated (lethal equivalents 3.13)	Ralls *et al.* 1988	Inbreeding depression incorporated (lethal equivalents 3.13)	Ralls *et al.* 1988	Inbreeding depression incorporated (lethal equivalents 3.13)	Ralls *et al.* 1988
	EV (reproduction) not correlated with EV survival		EV (reproduction) not correlated with EV survival		EV (reproduction) not correlated with EV survival	
Mortality (%)						
Age 0 – 1 years	20 (EV = 7.0)	Wells and Scott 1990	11 (EV = 1.0)	Baker *et al.* 2018	11 (EV = 1.0)	Baker *et al.* 2018
Age 1 – 50 years	2.85 (EV = 0.5)	Wells and Scott 1990	2.85 (EV = 0.5)	Wells and Scott 1990	2.85 (EV = 0.5)	Wells and Scott 1990
Initial pop sizes	114	Englund *et al.* 2008	142	Baker *et al.* 2018	142	Baker *et al.* 2018
Carrying capacity	280 (EV 10)	Englund *et al.* 2007	300 (EV 10)	Baker *et al.* 2018	300 (EV 10)	Baker *et al.* 2018

In Scenario 1, a simulation of dolphin population dynamics was carried out by inputting the original parameters used by Englund *et al.* (2008) into VORTEX to replicate the PVA originally carried out by Englund *et al.* (2008). As in Englund *et al.* (2008): a) the model simulated the population for 250 years for 1000 iterations, in increments of one year; b) extinction was defined as occurring when less than 10 individuals remained (*i.e.*, N<10); c) inbreeding depression was included with a genetic load consisting of 3.13 total lethal equivalents per individual, of which 50% are due to recessive lethals, and the remainder are lethal equivalents not subjected to removal by selection; d) the reproductive system was defined as polygynous (75% of adult males in breeding pool), with new selection of mates each year, females breeding from age 10 to age 48 and males breeding from age 11 to age 40; e) maximum age of survival was set at 50; f) sex ratio (percent males) at birth was set to 50; g) percent of adult females breeding each year (producing one young) was 14.4 with EV(SD) of 2.44; h) female and male annual mortality rates were each set at 20% with EV(SD) of 7.0 for "age 0 to 1 years" and at 2.85 with EV(SD) of 0.5 for "age 1 to 50 years"; i) age structure was assumed to be stable; and j) carrying capacity was set as twice the largest population estimate (280 with EV(SD) of 10). Initial population size was set at 114, the population estimate calculated by Englund *et al.* (2008).

In Scenario 2, the dolphin population was simulated in VORTEX by inputting the parameters used by Englund *et al.* (2008), but replacing some with newly available results from Baker *et al.*'s (2018) research. Specifically, the percentage of females reproducing each year was changed from 14.4% to 25.7%, first-year calf mortality was changed from 20% to 11%, and population size changed from 114 to 142 dolphins. As in Scenario 1, carrying capacity was estimated as twice the highest estimate of population size and thus changed from 280 to 300 for Scenario 2. Consequently, for Scenario 2: a) the model simulated the population for 250 years for 1000 iterations, in increments of one year; b) extinction was defined as occurring when less than 10 individuals remained (*i.e.*, N<10); c) inbreeding depression was included with a genetic load consisting of 3.13 total lethal equivalents per individual, of which 50% are due to recessive lethals, and the remainder are lethal equivalents not subjected to removal by selection; d) the reproductive system was defined as polygynous (75% of adult males in breeding pool), with new selection of mates each year, females breeding from age 10 to age 48 and males breeding from age 11 to age 40; e) maximum age of survival was set at 50; f) sex ratio (percent males) at birth was set to 50; g) percent of adult females breeding each year (producing one young) was 25.7 with EV(SD) of 3.42; h) female and male annual mortality rates were each set at 11% with EV(SD) of 1.0 for “age 0 to 1 years” and at 2.85 with EV(SD) of 0.5 for “age 1 to 50 years”; i) age structure was assumed to be stable; and j) carrying capacity was set as twice the largest population estimate (300 with EV(SD) of 10). Initial population size was set at 142, the population estimate calculated by Baker *et al.* (2018).

In Scenario 3, the simulation of dolphin population dynamics was carried out in VORTEX by inputting the parameters used in Scenario 2, but replacing some with more up-to-date results from Wells’ (2014) research. Specifically, first age at reproduction for males was changed from 11 to 10, first age at reproduction for females was changed from 10 to 5 (the youngest wild bottlenose dolphin recorded by Wells (2014) to have had a calf), and maximum age was changed from 50 to 67 years old (the age of the oldest wild bottlenose dolphin recorded to date (Wells 2014)). So, for Scenario 3: a) the model simulated the population for 250 years for 1000 iterations, in increments of one year; b) extinction was defined as occurring when less than 10 individuals remained (*i.e.*, N<10); c) inbreeding depression was included with a genetic load consisting of 3.13 total lethal equivalents per individual, of which 50% are due to recessive lethals, and the remainder are lethal equivalents not subjected to removal by selection; d) the reproductive system was defined as polygynous (75% of adult males in breeding pool), with new selection of mates each year, females breeding from age 5 to age 48 and males breeding from age 10 to age 40; e) maximum age of survival was set at 67; f) sex ratio (percent males) at birth was set to 50; g) percent of adult females breeding each year (producing one young) was 25.7 with EV(SD) of 3.42; h) female and male annual mortality rates were each set at 11% with EV(SD) of 1.0 for “age 0 to 1 years” and at 2.85 with EV(SD) of 0.5 for “age 1 to 50 years”; i) age structure was assumed to be stable; and j) carrying capacity was set as twice the largest population estimate (300 with EV(SD) of 10). Initial population size remained set at 142, the population estimate calculated by Baker *et al.* (2018) for the Shannon Estuary bottlenose dolphin population.

Results

The simulation results from Scenario 1 predicted that the Shannon Estuary bottlenose dolphin population would grow from 114 individuals to a mean size of 120 (1.99 SE; 63.06 SD) individuals after 250 years (Fig. 1). In 1000 simulations of Scenario 1 for 250 years, six predicted extinction and 994 predicted survival, giving a probability of extinction of 0.006 ± 0.002 (SE) or a probability of success of 0.994 ± 0.002 (SE). Of those going extinct, mean time to first extinction was 216.25 ± 8.10 (SE) years.

Results from Scenario 2's simulated population dynamics predicted that the Shannon Estuary bottlenose dolphin population would grow to a mean size of 297 (0.28 SE; 8.97 SD) individuals after 250 years, more than doubling its initial size of 142 individual dolphins (Fig. 1). In 1000 simulations of Scenario 2 over 250 years, zero predicted extinction and 1000 predicted survival, giving a probability of extinction of 0.000 ± 0.000 (SE) or a probability of success of 1.000 ± 0.000 (SE).

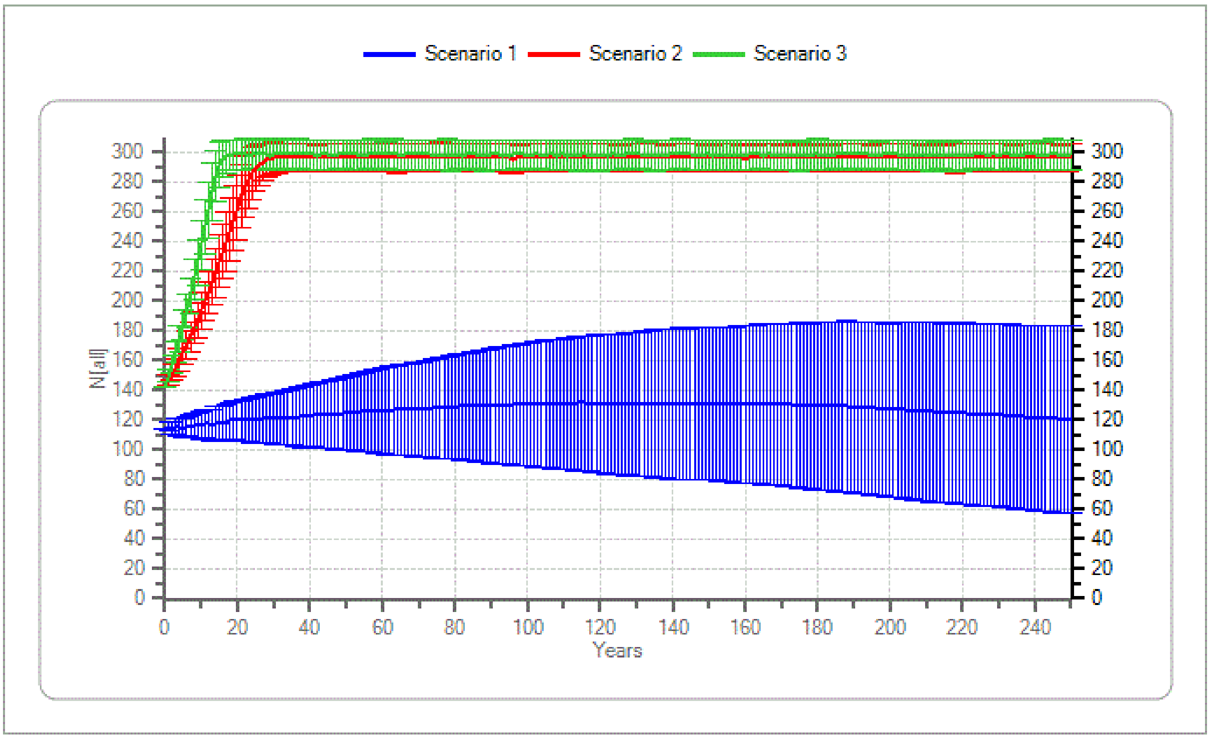


Figure 1. Bottlenose dolphin population size (N [all]) for 250 simulated years, predicting population size in each year for each of three different scenarios. After 250 years, population size is greater than the initial population size for all of the scenarios, with population size rising from 114 to 120 in Scenario 1 (blue), 142 to 297 in Scenario 2 (red) and 142 to 298 in Scenario 3 (green). Error bars represent standard deviation for population size in each simulated year.

The simulation results from Scenario 3 predicted that the Shannon Estuary bottlenose dolphin population would grow from 142 individuals to a mean size of 298 (0.33 SE; 10.41 SD) after 250 years (Fig. 1). In 1000 simulations of Scenario 3 over 250 years, zero predicted extinction and 1000 predicted survival, giving a probability of extinction of 0.000 ± 0.000 (SE) or a probability of success of 1.000 ± 0.000 (SE).

Discussion

PVAs allow us to model the predicted population size using many iterations and variable parameters to effect differences in the simulations for a specific population. In the three PVAs carried out with varying parameters in this study (Scenarios 1 to 3), the Shannon Estuary bottlenose dolphin population experienced growth from its initial population size and all models predicted that the population would likely be extant in 250 years' time.

Englund *et al.*'s (2008) PVA for the Shannon Estuary dolphin population concluded that the population would likely increase from 114 to 160 individuals in 250 years. The replication of Englund *et al.*'s PVA carried out in this study (Scenario 1) predicted a population size of 120 dolphins after 250 years. In both studies, the population increased in size. However, the predicted population sizes were different for each study despite the use of virtually the same dataset. There could be various reasons for this difference. Firstly, the studies used different versions of VORTEX for their PVAs. Englund *et al.* (2008) used version 9.92 while this study used version 10.0.7.9. Unfortunately, the software version (VORTEX, version 9.92) used by Englund *et al.* (2008) is no longer available, so it was impossible to replicate Englund *et al.*'s PVA with the exact same software. However, the replication of their PVA using a newer software version (VORTEX, version 10.0.7.9) was good in some ways as it allowed for an update of their previous PVA with a more sophisticated version of the software and still provided similar results to theirs in that the population was predicted to be stable with little risk of extinction for 250 years. Additionally, some of the data values required by VORTEX to run a PVA were not included in Englund *et al.*'s (2008) research report. For example, it is not clear what 'maximum age at reproduction' Englund *et al.* (2008) used for their PVA. Englund *et al.* (2008) used age 50 for 'maximum age' and VORTEX automatically inputs this as maximum reproductive age if no other age is set. If the value used in Scenario 1 for maximum reproductive age is changed to age 50 for both sexes (instead of 48 for females and 40 for males), then the simulation results from Scenario 1 predict a larger population size increase, with the Shannon Estuary bottlenose dolphin population growing from 114 individuals to a mean size of 155 ± 2.15 (SE) individuals after 250 years. This is a closer result to that reported by Englund *et al.* (2008) of 160 individuals after 250 years, and their inputting a greater maximum reproductive age may be the reason for this.

Regardless of its difference from Englund *et al.*'s (2008) results, the replication of their PVA in Scenario 1 is probably the least reliable of this study's PVAs because it uses outdated data from offsite sources/other populations. Scenarios 2 and 3, on the other hand, both make use of reproductive parameters calculated by Baker *et al.* (2018) specifically for the Shannon dolphin population. Using the same exact data as Englund *et al.* (2008) but replacing their values for initial population size (114) and fecundity (14.4%) with Baker *et al.*'s (2018) higher values (142 and 25.7%, respectively), and replacing their value of 20% for first-year calf mortality with Baker *et al.*'s (2018) lower value of 11%, resulted in a higher predicted population size and lower chance of population extinction after 250 years. The higher fecundity and decreased first-year calf mortality values, in addition to a larger initial population size, could be why the models (Scenario 1 *vs* Scenarios 2 and 3) take on a different shape (Fig. 1). Scenario 1's population size stays almost level with a larger uncertainty (SD) as time goes on, whereas the population sizes for Scenarios 2 and 3 increase rapidly and then level off, staying constant with a smaller degree of uncertainty (SD) from about 30 to 250 years. When Scenario 3 is modelled with Englund *et al.*'s (2008) initial population size instead, it retains the same shape (with a sharp increase followed by the population size plateauing at carrying capacity), suggesting that the initial population size does not have as much of an effect on the model outcome as increased fecundity and decreased mortality rates.

Results of simulations in Scenario 2 and Scenario 3 are so similar that it seems the changes made in Scenario 3 have a very small effect on the overall predicted trend of the population. That is to say, changing the maximum lifespan from 50 to 67 years old and changing 'age at reproduction' for both females (from 10 to 5 years old) and males (11 to 10 years old) seem to have had virtually no effect on the outcome of the simulations. In both of these scenarios, the population grows to be over twice its original size and, in all of the 2000 simulations (1000 for each scenario), the population remains extant and probability of extinction is zero.

Of the three Scenarios, the most reliable would appear to be Scenario 3. Although we do not yet have information on the maximum age, first age at reproduction or maximum age at reproduction for individuals in the Shannon Estuary bottlenose dolphin population, we do have access to new results on the life history of this population, especially regarding female reproductive rates, calf mortality and population size. These results, reported by Baker *et al.* (2018), are the only published life history parameters available specifically for this population, and are thus inevitably the best source of data for PVA input. Additional population data gained from the growing longitudinal Shannon dolphin dataset will be important in helping to produce more site-specific PVA results in the future.

Conclusion

I simulated three different scenarios to model the stability and predict the probability of extinction for the Shannon Estuary bottlenose dolphin population. The most likely scenario simulated, using the most up-to-date values available for wild bottlenose dolphins, including some specific to the dolphins in the Shannon Estuary, was Scenario 3 which predicted population growth with a population size of 298 dolphins after 250 years.

This new PVA for the Shannon Estuary bottlenose dolphins provides an interesting update to the information available on the stability and viability of this population. Fortunately, simulations carried out with the most recent and reliable parameters to date predict population growth and suggest that this dolphin population could potentially double in size in the next 250 years. However, even in the most updated scenario, it was still necessary to use results from research on bottlenose dolphins elsewhere to provide full information for the model. Filling in the missing gaps for data specific to the Shannon dolphin population for input into PVAs should be central to future research, with additional PVAs carried out as more Shannon-specific dolphin life history data become available.

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