Plaice on Irish and Scottish coasts:

Contributions to the ecosystem-based management approach for *Pleuronectes platessa* fisheries

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Declaration

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: Melanie Zotl Candidate

ID No.: 600255153

Date: 18/09/2013

"In essence, science sees the world as it was; reflects the world as it is; and imagines the world as it could be"

“Oh Lord, thy sea is so great and my boat so small”
Breton Fisherman’s Prayer

Für meine Eltern die immer für mich da waren; in guten und in schlechten Zeiten und nie aufgehört haben an mich zu glauben

To my parents for being there for me through it all; the highs and the lows and never stopped believing

Plaice on Irish and Scottish coasts: Contributions to the ecosystem-based management approach for *Pleuronectes platessa* fisheries

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Abstract

This study examines aspects of the early life history, growth and condition of plaice (*Pleuronectes platessa*) populations in Irish and Scottish waters, using innovative modelling approaches, among other techniques, to inform management and conservation efforts. Growth rate is an important determinant of a young fish's survival and recruitment probability. A state space growth stanza/phase model was used to describe and quantify spatial variation in early life history traits and growth patterns of Irish and Scottish plaice at a regional scale and investigate possible drivers. Generally, these traits varied significantly at a regional level and although temperature accounted for some of the variation present, it was not the sole driver. Western Irish Sea fish had shorter larval durations, fewer cumulative degree days to settlement, higher larval and juvenile growth rates, post settlement acceleration and reached stable growth rates faster than west Irish or Scottish fish. A region independent positive correlation between larval and juvenile increment widths indicated that juvenile growth rates were somewhat pre-determined by larval growth. The feasibility of using variation in otolith microchemistry to discriminate between plaice from western Irish and Scottish nurseries was assessed. Sufficient variation was found to successfully classify fish on a regional and local scale, a tool for assessing population structure and connectivity. The dispersal of plaice larvae on the west coast of Ireland was modelled and the likely spawning ground identified. Larval behaviour, temperature mediated growth and hydrodynamic variability were found to greatly influence rates of larval delivery to nursery grounds. The impact of bottom trawling on fish condition was investigated. Condition effects appeared to be size and mobility related, with diet as a possible driver, although results were not conclusive. The study results are discussed in terms of their use to fisheries management.

Acknowledgements

"...you didn't build that"
President Barack H. Obama, July 13th 2012

Why begin my acknowledgements with a much maligned and misinterpreted quote made by the President of the United States, during a campaign event? Well, for one U.S. politics has always fascinated me but more importantly, its the bigger point that the President was trying to make, that makes quoting him appropriate here.

What he was getting at was, that no matter who you are, what you do or what you've achieved in your life, you didn't get there by yourself. There were people along the way who helped you get there, played a part in making you the person you are today and ultimately contributed to your success. This is a thank you to all the people in my life, without whom I wouldn't have made it this far.

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My parents once described the process of doing a PhD, as similar to being lost out in the wide open ocean, with no land in sight. Well guess what, with all your help I made it to the beach and there's even a bar serving cocktails with those tiny umbrellas in them! Thank you to all of you for making it possible.

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Chapter 1

General Introduction

1.1 Plaice life cycle and ecology

European plaice (*Pleuronectes platessa* Linnaeus, 1758) are widely distributed, ranging from the Mediterranean, throughout European waters, to Iceland and the White Sea (UN Food and Agriculture Organization, `http://www.fao.org`; Gibson, 2005, 1999). The species is characterised by a complex life cycle, encompassing both pelagic and demersal environments.

Plaice spawn on offshore spawning grounds, in water depths of more than 50 metres (Gibson, 1999), from approximately December to May, depending on latitude (Ellis and Nash, 1997b; Solmundsson et al., 2003; Rijnsdorp, 1989). The spawning season is thought to be limited, to ensure that hatching occurs before peak planktonic production to provide sufficient food supply for larvae (Cushing, 1990), although this is not universally true (Ellis and Nash, 1997b). Plaice spawning grounds usually occur in areas where residual and wind driven currents are strong, normally upstream from any potential nursery habitat (Gibson, 1999), to facilitate transport and dispersal of the eggs and larvae.

The planktonic eggs, of which female plaice produce around ten to four hundred thousand (Horwood, 1990), are released in batches related to an ovulatory periodicity of 1-4 days for approximately five weeks, during which the female is in spawning condition (Rijnsdorp, 1989; Rijnsdorp and Witthames, 2005). These pelagic eggs are positively buoyant, drifting passively, with their distribution in the water column depending on the prevalent hydrodynamic conditions (Nielsen et al., 1998; Van der Veer et al., 1998). Mortality during the egg stage is high, with the major cause thought to be predation by other fish, such as sprat and herring (Ellis and Nash, 1997a). Egg development and the timing of larval hatching is inversely related to temperature (Fox et al., 2003b) and can range from 13 to 118 days (Apstein, 1909 in Hyder and Nash, 1998; Ryland and Nichols, 1975).

Developing plaice larvae are transported to inshore shallow coastal areas via a combination of passive and active transport. Larvae, in contrast to the pelagic eggs, are capable of influencing their dispersal and transport, as they display size dependent behaviours, such as active vertical, horizontal and tidally synchronised swimming (selective tidal stream transport) (De Veen, 1978; Rijnsdorp et al., 1985; Jager, 1999), which allow them to counteract the prevailing currents. They are capable of speeds of up to three body lengths per second for horizontal swimming (Arnold, 1969) and move up and down in the water column to facilitate ingress into the nursery areas with the tide (Bolle et al., 2009; Fox et al., 2006; Rijnsdorp et al., 1985). Such behaviours have been shown to be very important for successful settlement in plaice (Fox et al., 2006). The time the larvae spend in the plankton prior to settlement is termed Pelagic Larval Duration (PLD), which has been established to correlate negatively with temperature (Van der Veer et al., 2009; Green and Fisher, 2004; McCormick and Molony, 1995), but can also be influenced by other factors, such as food availability (Van der Veer and Witte, 1993; Fiksen and Jørgensen, 2011) or genetics (Watts et al., 2004).

The transport of eggs and larvae from spawning to nursery grounds has direct impacts on their settlement distributions (Van der Molen et al., 2007) and thereby stock dynamics (Wegner et al., 2003). Connectivity between these stages and subsequent recruitment to the population can be influenced by various factors (Anderson, 1988). Larval concentrations near nursery areas can show large interannual variability, due to changes in circulation patterns and wind conditions (Nielsen et al., 1998; Van der Veer et al., 1998; Oshima et al., 2010). Larval concentrations can further be affected by egg production (Nash and Geffen, 1999; Gibson, 1994), subsequent pelagic stage mortality (Fox et al., 2000; Van der Veer et al., 2000) due to predation (Ellis and Nash, 1997b), a mismatch between hatching and peak plankton production (Anderson, 1988; Leggett and DeBlois, 1994) and temperature (Van der Veer et al., 1990; Van der Veer and Witte, 1999; Fox et al., 2000).

As they approach metamorphosis, the process whereby larvae transform from the pelagic to the demersal/benthic form, plaice spend increasing amounts of time on the seabed and need to actively swim to change their position in the water column (Rijnsdorp et al., 1985; Arnold, 1969; Wennhage and Gibson, 1998), ensuring retention in the nursery habitat. Metamorphosis involves significant physiological changes, such as eye migration, posture rotation and asymmetrical pigmentation. During this time, activity levels decrease, feeding patterns change and growth decreases, with individuals switching from planktonic to benthic and epibenthic prey (Geffen et al., 2007). Juvenile plaice settle onto shallow inshore coastal areas (nursery grounds), usually comprised of muddy or sandy substrate (Gibson, 1997, 1999), although substrate type alone is not the only indicator of suitable habitat. Vegetation, macroalgal cover, organic content, presence of suitable prey and absence of predators, are also important determinants of suitability (Gibson, 1994; Wennhage and Pihl, 1994; Wennhage and Gibson, 1998; Modin et al., 1996; De Raedemaecker et al., 2012).

Variability in growth of flatfish during the early life stages is primarily driven by the quality and quantity (Van der Veer et al., 2010) of the food supply, except during the first summer of life (Amara et al., 2001). The main factors which influence growth and survival include presence or absence of predators and temperature (Ryer and Hurst, 2008; Gibson et al., 2002; Wennhage and Gibson, 1998), while salinity, oxygen (Augley et al., 2008; Yamashita et al., 2001), habitat structure (Wennhage and Pihl, 1994), water depth and hydrodynamics (Gibson, 1994), are thought to be secondary. Habitats that maximise growth and survival will be preferred and are therefore usually those with sandy or muddy substrates, with low vegetative cover, low organic content, abundant food supply and low predation risk (Gibson, 1994, 1999; De Raedemaecker et al., 2012).

The settled juveniles will remain on the nursery grounds at depths of less than 7-10 metres, migrating to deeper waters during the day to feed and returning to shallow waters at night. The extent and depth of this migration will depend on prey distribution and the size of the plaice juveniles, with larger individuals moving into deeper water (Gibson, 1999; Modin et al., 1996). This onshore/offshore movement is also seasonal in nature; during the summer fish will move offshore into deeper, cooler, water and remain there until spring, when the fish return inshore (Gibson, 1999). These offshore migrations also have the purpose of preparing the juveniles for the migration to the spawning grounds, once they have matured, gradually bringing them into adult habitat (Gibson, 1999). Spawning migrations can be over large distances (250km in the North Sea), taking advantage of tidal stream transport, and allow for plaice from segregated feeding grounds to mix on the spawning ground, as they show spawning site fidelity (Hunter et al., 2003, 2004).

1.2 Plaice in Europe: Commercial importance, stock status and the knowledge gap

Plaice (*Pleuronectes platessa* L.) is among the most widely researched flatfish species in the Northeast Atlantic, in part due to its value as a commercially exploited species, having been caught as a food fish for many centuries (Gibson, 1999). Of all commercially exploited flatfish, it accounts for the highest landings by weight in Europe. 17,000 tonnes of plaice were landed by the UK fleet in 2011, with a value of £22.4 million (Elliott et al., 2012). This represents over 10% of the total demersal landings by weight and over 7% by value. The most important fishing ground for the UK fleet in 2011 was the North

Sea, followed by Scotland and the English Channel (Elliott et al., 2012). The Netherlands (29,272 tonnes), the UK (15,169 tonnes) and Denmark (11,634 tonnes), caught the majority of North Sea plaice by landings in 2011 (ICES, 2012b,d).

Considering its commercial importance and value, it is perhaps not surprising that the plaice populations in the North Sea are also the best documented and therefore a considerable amount of the information we have, regarding the species, has been obtained from studies conducted there (Hufnagl et al., 2012). There have also been important studies of the species in the Irish Sea (Nash and Geffen, 2000; Nash et al., 2000). Research conducted on the species has revealed the developmental cycle of eggs and larvae (Fox et al., 2003a; Ryland and Nichols, 1975), information on growth (Alhossaini and Pitcher, 1988; Hovenkamp and Witte, 1991; Rijnsdorp and Van Beek, 1991) and variability therein (Bolle et al., 2004; Geffen et al., 2011; Nash and Geffen, 2000) the location of spawning and nursery areas and the transport mechanisms that connect them (Bolle et al., 2009; Nielsen et al., 1998; Rijnsdorp et al., 1985; Van der Veer et al., 1998, 2009), feeding, biology and life history (Amara et al., 2001; Hinz et al., 2005; Jager, 1999; Modin et al., 1996), as well as the processes affecting plaice once on nursery grounds, including the impact of climate change (Bergman et al., 1988; Hufnagl et al., 2012; Teal et al., 2008).

In other regions however, plaice populations have not been as well documented and we only have limited information on their biology and ecology, such as in the case of the west of Ireland or the west of Scotland. Relatively recently, nursery ground studies have provided information on early life history (Allard, 2006; Allen et al., 2008; Haynes et al., 2012; De Raedemaecker et al., 2012; Comerford et al., 2013). However, spawning ground locations are currently unknown for both the west of Ireland and the west of Scotland, although their locations have been inferred from the limited information available (Gerritsen, 2010; Coull et al., 1998).

As a consequence, while management plans (EU Council Regulation No. 676/2007) are currently in place for areas where there is abundant information available, such as the North Sea (ICES, 2012b), this is not the case in other areas, such as the west of Ireland (Marine Institute Stock Book 2012, `http://hdl.handle.net/10793/841`) or the west of Scotland (ICES, 2012a). These stocks are considered to be data limited by ICES, partly because catches from the area (VIIb, c; Figure 1.1) are too low to justify collection of the necessary information needed to assess stock status (ICES, 2012c). In their advice

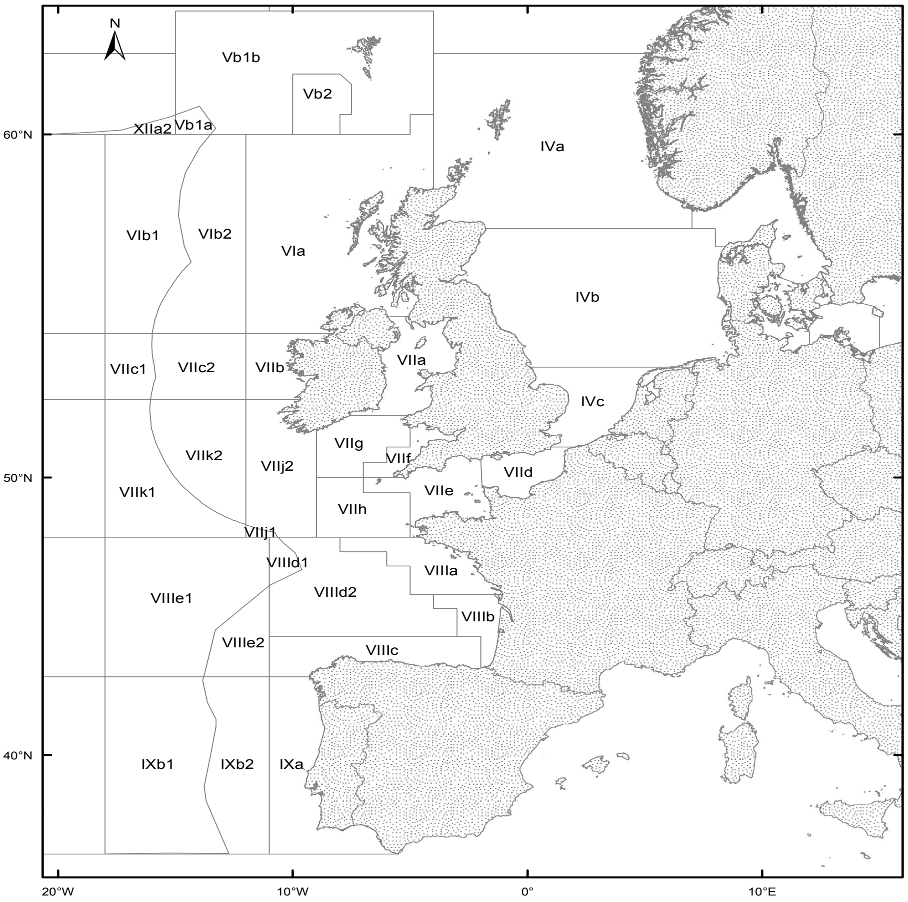

Figure 1.1: Map of ICES statistical areas in western European waters (`http://www.ices.dk/marine-data/maps/Pages/default.aspx`)

for 2012 and recommendations for 2013, ICES considers only the North Sea plaice stock in Subarea IV to be within precautionary boundaries. This stock has reached its highest levels in recorded history, with recruitment maintained at the long term average since 2007 and estimated fishing mortality at historic lows (ICES, 2012b,d). The stock status of the other plaice populations in European waters assessed by ICES, is either unknown, due to lack of data or reference points, or above target, with regards to fishing mortality at Maximum Sustainable Yield (F_{MSY}).

When there is a lack of reliable information and uncertainty regarding stock status, ICES advises a precautionary reduction in catches, unless there is additional information to indicate that the current level of exploitation is sustainable for the population in question. Currently, no assessment is made for the plaice populations in western Scotland and in the west of Ireland. Plaice in these waters are caught as bycatch in a mixed demersal fishery, mainly by Ireland, France and the UK and a 20% reduction in total allowable catches (TAC's) has been recommended by ICES for the areas (ICES, 2012c). However, TAC's limit only landings, not actual fish catches. In a mixed fishery this is problematic because fishing continues even if the TAC for one by-catch species has been exhausted (and the fish are discarded), as mortality is not addressed. Due the data limited nature of these stocks, it is impossible to know if this reduction will be effective to ensure the sustainable exploitation of the population.

1.3 Sustainable fisheries management and the ecosystem based approach

Fisheries make an important contribution both to global food security and economic growth, providing almost three billion people with 20% of their animal protein (FAO, 2012). However, the sector is still beset by problems relating to poor governance, natural resource use conflicts, poor fisheries practices and weak fisheries management regimes, leading to fisheries overexploitation and ecosystem degradation (FAO, 2012). While all of these problems have a political, as well as a socio-economic context, the weakness of fisheries management regimes can also be viewed in the context of a lack of reliable information on a number of fish populations and the ecosystems they live in. This lack of information makes it very difficult and even impossible for assessments to be conducted, in order to provide a foundation on which fisheries managers can base management regimes, that will allow for the sustainable, long term exploitation of the resource.

Until recently, fisheries management focused on single species, an approach by which the the catch of one species was maximised, while effects on predator, prey and competitor species, the habitat, the mixed nature of fisheries and ecosystem interactions, are not taken into account (Pikitch et al., 2004; Sainsbury et al., 2000). Increasingly however, it has become clear that many commercially exploited fish species and associated ecosystems are coming under increased pressure from fishing. This has resulted in marked declines in abundance (Callaway et al., 2007; Hutchings et al., 2010), restructuring of exploited communities, leading to regime shifts (Choi et al., 2004; Collie et al., 2000), indirect declines in growth and condition of several fish species (Hiddink et al., 2011; Lloret et al., 2007; Shephard et al., 2010) and even in some cases, such as northwest Atlantic cod, in population collapse. These unintended consequences of fishing (Pikitch et al., 2004), have lead to the realisation that fisheries management needs to become more sustainable, precautionary and ecosystem-based in nature.

Ecosystem Based Fishery Management (EBFM) is a management regime in which ecosystem considerations, including the impact of climate change (McGoodwin, 2007; Hannesson, 2007; Stenevik and Sundby, 2007), are taken into account and included in any management decisions, essentially reversing the priorities of traditional management, with the overall objective of sustaining healthy marine ecosystems and the fisheries therein (Pikitch et al., 2004; Sainsbury et al., 2000; Crowder and Norse, 2008). Therefore it is necessary for any EBFM plan to: avoid habitat degradation, minimize the risks of causing irreversible changes to species composition, ecosystem structure and function and maintain socio-economic benefits, without harming the ecosystem. This requires a sufficient understanding of ecosystem processes so as to assess consequences of human impacts (Pikitch et al., 2004; Link, 2002). When knowledge and understanding of ecosystem processes is insufficient, such as is the case for data limited stocks, a precautionary and robust management regime is to be implemented to favour the ecosystem (ICES, 2012c).

The concepts of EBFM and the precautionary approach, as well as multi-species considerations have been incorporated into European fishery management plans (EU Council Regulation No. 676/2007) and the Common Fisheries Policy (CFP) (Stokke and Coffey, 2004). These agreements and policies are international in nature, involve the input and interests of many different stakeholders and interest groups (Varjopuro et al., 2008), but also need to be implemented on a national level. Therefore, the objectives are very broadly defined and difficult to implement or convert into fishery management plans (Sainsbury et al., 2000). The scientific advice that is given to managers and policy makers, with its inherent uncertainty, needs to pass along a chain of political institutions prior to being incorporated into policy, which can often lead to recommendations being reduced down to the lowest common acceptable level (Daw and Gray, 2005). This is in part why the Common Fisheries Policy (CFP) has not been able to achieve sustainable European fisheries for the most part and is considered a failure by some (Daw and Gray, 2005; Khalilian et al., 2010).

Since the inception of the CFP in 2002, recovery plans and long term management plans have been implemented, technical measures revised and data collection systems improved, to provide the basis for ecosystem-based management. Although there is widespread recognition of the need to reverse fish stock declines, ecosystem degradation and to avert the parallel socio-economic impacts, the decision making process under which the CFP operates, continues to compromise fisheries sustainability and the ecosystems upon which they depend (Daw and Gray, 2005; Lutchman et al., 2009). It is therefore not surprising, that in 2012 the CFP underwent its third review since 2002 (Symes, 2005, 2009). The review is being conducted with the goal of providing a fully ecosystem based management framework. Such a management system is expected to lead to long term sustainability and management of target species, in a multispecies context. The level of fishing mortality is to be maintained below that at Maximum Sustainable Yield (F_{MSY}) and reference points will be established to monitor biomass (B_{MSY}), so as to avoid a decline below that required for sustainable recruitment (Mace, 2001; Lutchman et al., 2009; Symes, 2009).

Implementing EBFM in a multi-species or ecosystem context is difficult, as species interactions are sometimes poorly understood, especially when data on the species of interest are limited (Mace, 2001). Providing information for data limited populations on growth, larval and juvenile origin, connectivity and dispersal, as well as identifying the location of spawning grounds will directly assist management efforts, as it will allow us to more precisely delineate stocks and model recruitment variability. In the context of EBFM, it will also allow us to gain insight into the entire life cycle, linking larval, juvenile and adult stages and assess environmental impacts, prior to recruitment to the fishery. However, while stock assessments will allow us to quantify the effects of fishing on population age structure and biomass, they will not highlight more subtle and indirect effects. Trawling induced reduction in biomass and production of the benthos, is speculated to indirectly drive declines in condition and growth rate of several fish species that prey on this community (Hiddink et al., 2011; Lloret et al., 2007; Shephard et al., 2010). Thus it is important to understand the interactions between commercially exploited fish and other ecosystem components and the mechanisms driving them.

1.4 Techniques used to study plaice growth, origin, dispersal and connectivity

Information on fish age and growth is of paramount importance for fisheries management. Otoliths (ear stones) have proven invaluable in this regard (Panfili et al., 2002), ever since the discovery that otolith material is deposited incrementally on a regular basis (Pannella, 1971).

Otoliths play a role in hearing and balance and are made up of calcium carbonate (aragonite), which is precipitated onto a protein matrix and once the material is deposited, it is not reabsorbed (Mugiya, 1987). Otolith material is deposited incrementally, on a daily basis (Pannella, 1971; Mugiya, 1987), resulting in the formation of one light and one dark increment, except under conditions of stress (Campana, 1983; Morales-Nin, 2000). Increment counts can be used to determine the daily age of fish during their first year (Campana, 1990) and age in years can be determined by counting annual increments thereafter, allowing assessment of population age structure. The rate of increment formation is influenced both by biotic and abiotic factors (Alhossaini and Pitcher, 1988) and is proportional to somatic growth rate. Otolith size and increment width measurements can be used to draw inferences about the effects of environmental conditions, such as temperature and food availability on the growth and indirectly, survival of individuals (Folkvord et al., 1997; Sponaugle, 2010; Aguilera et al., 2009; Godiksen et al., 2012; Takasuka et al., 2007).

The effect of differential temperature regimes on otolith microstructure has even been used in sockeye salmon, to determine that these fish home to their natal incubation sites (Quinn et al., 1999). Growth information stored in otoliths can also be used to reconstruct individual growth trajectories. Other than determining fish growth rates and trajectories, we can also calculate length at age, as well as determine hatch and settlement time distributions, enabling us to assess differential growth and mortality among cohorts of fish (Al-Hossaini et al., 1989). In some species, including many flatfishes, the timing of life history events can also be determined from visible marks in the otolith microstructure. For example, the hatch check (HC) marks the transition from the egg to the larval phase, while accessory primordia (AP) are associated with metamorphosis of pelagic larvae into benthic juveniles and settlement onto nursery grounds (Modin and Pihl, 1996). These marks (Figure 1.2) allow us to determine the duration of the pelagic larval phase, termed Pelagic Larval Duration (PLD). Otolith microstructure therefore can provide us with insights into flatfish early life histories and adult life. Variations in growth, hatch and settlement timing, as well as in PLD are useful indicators of differential larval and juvenile origin of adult fish and can be used to differentiate between possible distinct populations present in an area (Arai et al., 1999; Brophy and King, 2007; Gunnarsson et al., 2010).

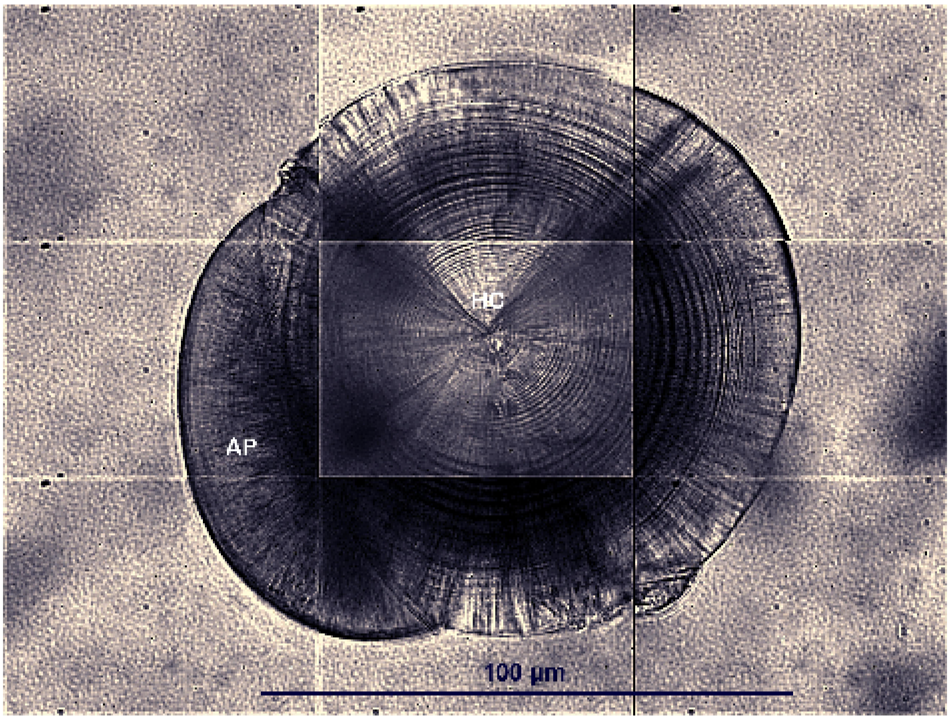

Figure 1.2: Plaice otolith showing location the hatch check (HC) and accessory primordium (AP) or settlement mark

Although otolith microstructural analysis can provide useful insights into the origin of adult fish and distinguish between populations, it can only serve as an indicator of such differences. For more definite differentiation, higher resolution methods are needed. Otolith elemental analysis, or otolith microchemistry, is one such technique and involves using the trace and ultra-trace elements that are incorporated from the endolymph surrounding the otolith during deposition (Campana, 1999; Payan et al., 2004) and may be used to assess origin, population structure and connectivity. The incorporated trace and ultra trace elements stem from the marine environment in which the fish lives (Lin et al., 2007). While otolith composition is not a direct reflection of the environment (Weiner and Dove, 2003), due to differences in biology, diet, physiology, genetics and environmental conditions, it is useful to distinguish between fish, because the differences in conditions and habitats in which fish live, causes differences in elemental composition, which can be population and region specific (Clarke et al., 2011; Chang and Geffen, 2012). Otolith elemental composition can be used as natural tag to track individuals from their larval stage, through the pelagic phase and recruitment, to benthic populations (Campana et al., 2000; Campana, 2005; Thorrold et al., 2002). This makes it possible to assess individual larval and juvenile origin (tracing adult fish back to their spawning and nursery grounds), with higher resolution than microstructural analysis alone. This allows us to assess population structure and connectivity in more detail and may even be useful to track small scale movements of fish (Fodrie and Herzka, 2008).

For any fish population, especially those with complex life cycles such as flatfish, it is essential to have knowledge of the location of their spawning and nursery grounds, the paths eggs and larvae take to get there, how they disperse and what influences their success in reaching their destination, as this has direct impacts on stock dynamics (Wegner et al., 2003). While physical tagging has been useful in larger fish, this is not an option for the eggs or larvae (Gawarkiewicz et al., 2007; Cowen and Sponaugle, 2009). In recent years, biophysical oceanographic models have been used to simulate eggs and larval dispersal and assess the probable location of spawning and nursery grounds (Savina et al., 2010; Werner et al., 2007; Van der Molen et al., 2007; Lacroix et al., 2012). Regional oceanographic models are used to simulate the oceanography (including wind, currents, temperature, tides, topography etc.) of the area of interest and may incorporate biological information, such as growth, PLD, hatch and settlement timing, physical and behavioural characteristics of eggs and larvae, to provide realistic dispersal pathways (Gawarkiewicz et al., 2007; Gallego et al., 2007). These pathways allow us to then identify the probable spawning and nursery ground locations and also make inferences on the influence of biotic and abiotic factors on successful dispersal (Fox et al., 2006, 2009; Leis, 2007; Fiksen et al., 2007; North et al., 2009; Lacroix et al., 2012).

1.5 Thesis overview and objectives

The overall objective of the work presented in this thesis was to provide basic information on larval and juvenile plaice growth and regional variability therein, as well as their origin, connectivity and dispersal, for the data limited stocks in the west of Ireland, west of Scotland and the western Irish Sea. Such information will allow us to more accurately define and delineate stocks, so that appropriate management units can be defined. These can then be used in the stock assessments that form the scientific basis upon which management plans for the region are formulated. Effective ecosystem based management also needs to take into account the direct and indirect effects human activities have, not only on the target species, but also on the habitats they occur in. Therefore, investigating the ecosystem wide effects on target and non-target species and habitats, is another important component for management, so as to incorporate mitigating measures. Plaice are part of the benthic fish community and are therefore likely to be affected by bottom trawling. Thus, the effects of fishing on the condition and diet of plaice and other fish species, with which it interacts, are investigated.

This thesis is divided into a general introduction followed by the four chapters detailed below, as well as a general discussion section, in which the application of data, such as that provided by this study, to fisheries management is discussed:

Chapter 2 *Spatial variation in early life history traits and growth patterns of Irish and Scottish plaice described using a state space growth stanza model*

In this chapter the relative influence of temperature at the regional (1000km) scale on larval and juvenile growth of plaice *Pleuronectes platessa* from Irish and Scottish nursery grounds is investigated. Spatial variation in otolith growth and pelagic larval duration (PLD) is examined using otolith microstructure data. A state space growth stanza model is used to describe changes in otolith growth rates in relation to time (increment number).

Chapter 3 *Otolith microchemistry of plaice (Pleuronectes platessa L.) from the western Irish Sea and western Scotland: a potential marker of juvenile* *origin and connectivity*

In this chapter spatial and temporal variation in whole otolith chemistry of juvenile plaice (*Pleuronectes platessa*), is examined over two years (2009/11) at regional and local (nursery ground) scales in the western Irish Sea and western Scotland. This spatial and temporal variation in otolith chemical composition is used to classify fish at regional and nursery ground scales.

Chapter 4 *Elucidating probable plaice spawning grounds and the influence of behaviour and growth on successful settlement in western Ireland*

In this chapter the first Individually Based Coupled Physical Biological Model (ICPBM) for plaice in W. Ireland is presented. The main aim is to identify probable plaice spawning ground locations by reconstructing the dispersal pathways of 0–group juveniles collected from nursery grounds in Galway Bay. The relative importance of passive transport, behaviour and individual growth rates on the successful delivery of larvae by the model, from putative spawning grounds to suitable nursery areas and interannual variability therein, is investigated.

Chapter 5 *Indirect effects of bottom trawling on fish condition and diet: influence of fish size and mobility*

In this chapter the indirect effects of bottom trawling on diet and body condition of three flatfish (*Microstomus kitt*, *Pleuronectes platessa*, *Lepidorhombus whiffiagonis*) and one gadoid species (*Merlangius merlangus*), are investigated. These species represent a range of feeding and migratory strategies, from a sedentary obligate benthivore (*M. kitt*) to a mobile piscivore (*M. merlangus*), which fishing may affect differentially.

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Chapter 2

Spatial variation in early life history traits and growth patterns of Irish and Scottish plaice described using a state space growth stanza model

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This chapter is in preparation for publication as Zölck, M., Minto, C., Brophy, D., Fox, C.J., McGrath, D. Spatial variation in early life history traits and growth patterns of Irish and Scottish plaice described using a state space growth stanza model

Abstract

Growth rate is thought to be an important determinant of a fish's survival, particularly during the larval and juvenile phases. This study investigates the relative influence of temperature at the regional (1000km) scale on larval and juvenile growth of plaice (*Pleuronectes platessa*) from Irish and Scottish nursery grounds. Spatial variation in otolith growth, as a proxy for somatic growth and pelagic larval duration (PLD) was examined using otolith microstructure data. A state space growth stanza (phase) model was used to describe changes in otolith growth rates in relation to time (increment number). These traits varied significantly at a regional level. Although temperature was an important determinant of PLD and growth, it was not the sole driver of the observed spatial variability. Regional differences were detected in both PLD (PLD: E. Ireland < W. Scotland and < W. Ireland, $p < 0.04$) and the number of cumulative degree days, CDD's, needed to complete the larval phase (CDD: E. Ireland < W. Scotland and < W. Ireland, $p < 0.02$). This perhaps reflected a greater spatial separation of spawning and nursery grounds in W. Scotland and W. Ireland compared to E. Ireland. Larval (otolith increment widths) and juvenile growth rates (as indicated by otolith radius 30 days after settlement was completed), were greater in plaice from E. Ireland than W. Scotland ($p \leq 0.03$), while the rate at which growth rate accelerated during the period after settlement was lower in W. Scotland than E. Ireland or W. Ireland. Growth rates of fish from Scottish nursery grounds also reached a plateau later than Irish fish after settlement. A region independent positive correlation between larval and juvenile increment widths ($p < 0.001$), indicated that juvenile growth rates were somewhat pre–determined by larval growth, although temperature effects may play a role. These geographic differences could be a marker of juvenile origin to assess connectivity between nursery and spawning grounds, valuable information for fisheries management.

Keywords: State space growth modelling; western Irish Sea; West of Scotland; West of Ireland; Larval/juvenile origin; Otolith microstructure; Plaice (*Pleuronectes platessa*); Temperature mediation

2.1 Introduction

Flatfish are of great commercial importance (Bels and Davenport, 1996; Munk et al., 2002) with plaice being one of the main species caught. European catches of plaice reached a high of 202,510 tonnes in 1990 and have since steadily declined, reaching 78,433 tonnes in 2009 (UN Food and Agriculture Organization, `http://www.fao.org`). In Europe, the Netherlands and Denmark have the highest reported share of the total catch. A considerable amount of information is available on plaice biology and life history for certain important fishing grounds, such as the North Sea (Amara et al., 2001; Hinz et al., 2005; Jager, 1999; Modin et al., 1996). While there is considerable information available on plaice in the Irish Sea (Nash and Geffen, 2000; Nash et al., 2000), and management plans are in place there, less is known about their populations in the west of Scotland or the west of Ireland (Haynes et al., 2012). In these regions plaice are landed as by-catch, and there are no formal stock assessments or explicit management plans at the present time (Marine Institute Stock Book 2011, `http://hdl.handle.net/10793/669`). Within Europe there is however increasing emphasis on improving the management of data poor stocks and knowledge regarding life history can aid this.

Plaice are characterised by a life cycle with pelagic egg and larval stages and benthic juvenile and adult stages. Pelagic eggs and larvae are transported from offshore spawning grounds towards inshore coastal areas where they metamorphose and settle into shallow nursery areas (Gibson, 1997, 1999). Recruitment following settlement is subject to interannual variability in year class strength (Van der Veer et al., 2000), the majority of which is thought to be generated during the planktonic egg and larval stages. This is attributable to variations in quantity and quality of egg production (Nash and Geffen, 1999; Gibson, 1994), as well as differences in larval growth and survival which appear to be linked to temperature (Van der Veer et al., 1990; Van der Veer and Witte, 1999; Fox et al., 2000). Although the mechanisms behind this link are unclear they may include changes in spawning ground to nursery ground transport (Van der Veer et al., 1998; Oshima et al., 2010), as well as effects on mortality due to predation (Fox et al., 2000; Van der Veer et al., 2000; Ellis and Nash, 1997) and food availability (Anderson, 1988; Leggett and DeBlois, 1994). Variability generated in the egg and larval phase tends to be dampened in the juvenile phase due to the limited area of suitable nursery habitat (Amara et al., 2001; Beggs and Nash, 2007; Gibson, 1994; Nash and Geffen, 2000), as well as inter– and intraspecific competition (Van der Veer et al., 2000; Beverton, 1995). However, there may be regional variation in the life cycle phase at which year class strength is determined. In the Irish Sea year class strength is thought to be determined at the juvenile stage on the nursery ground (via density dependent processes) in contrast to the North Sea, where year class strength appears to be set during the pelagic stage (Nash and Geffen, 2000; Bannister et al., 1974). Regardless of when year class strength is determined, individual larval and juvenile growth is thought to be an important influence on a fish's probability of survival (Anderson, 1988). Since faster growing larvae spend less time in the plankton compared to than slower growing fish they should experience lower overall predation mortality ("stage duration hypothesis", Houde 1989). Faster growth also ensures that size refuges from predation are reached more quickly ("Bigger is better", Miller et al. 1988), allowing them to successfully transition to the next phase in their life cycle. Evidence has been found to support these hypotheses (Houde, 2008), although there have been experimentally based exceptions (Litvak and Leggett, 1992). Gaining a better understanding of the controls on larval and juvenile growth is thus important in terms of early life history ecology. Variability in the growth of the early life stages of flatfish is primarily driven by the quantity and quality of available food (Van der Veer et al., 2010) and temperature (Ryer and Hurst, 2008; Gibson et al., 2002; Wennhage and Gibson, 1998; Comerford et al., 2013), with salinity, oxygen (Augley et al., 2008; Yamashita et al., 2001), habitat structure (Wennhage and Pihl, 1994), water depth and hydrodynamics (Gibson, 1994), also thought to play a role.

Growth information stored in otoliths has been widely used to reconstruct individual growth trajectories. Otolith material is deposited incrementally, on a daily basis (Mugiya, 1987), generally resulting in the formation of one light and one dark increment per day, although this can be disrupted under conditions of stress (Campana, 1983, 1990; Morales-Nin, 2000). Increment formation is influenced both by biotic and abiotic factors (Alhossaini and Pitcher, 1988) and so otolith size and increment width measurements can be used to draw inferences about the effects of environmental conditions, such as temperature and food availability on the growth and indirectly, survival of individuals (Folkvord et al., 1997; Sponaugle, 2010; Aguilera et al., 2009; Godiksen et al., 2012; Takasuka et al., 2007). In some species, including many flatfishes, the timing of life history events can be determined from visible marks in the otolith microstructure. Accessory primordia (AP) are associated with metamorphosis of pelagic larvae into benthic juveniles and settlement onto nursery grounds (Modin and Pihl, 1996), allowing the timing of metamorphosis and the length of the pelagic larval phase (Pelagic Larval Duration: PLD) to be estimated. As well as providing insight into drivers of growth variability, regional variation in growth, timing of hatching and settlement and PLD, can provide a useful marker of larval and juvenile origin and can be used to differentiate between putative stocks present in an area and to evaluate population connectivity (Arai et al., 1999; Brophy and Danilowicz, 2002; Brophy and King, 2007; Gunnarsson et al., 2010), an important prerequisite for effective fisheries management.

In organisms with complex life cycles, variation in individual traits associated with survival during one life history stage can affect survival during the next stage (Gagliano et al., 2007; Rankin and Sponaugle, 2011). For example, larval growth rates do not only influence larval survival, but can carry over and affect the survival of juveniles (Sponaugle and Grorud-Colvert, 2006; Grorud-Colvert and Sponaugle, 2006), possibly due to differential condition of larvae at settlement (McCormick, 2006). While otoliths contain information of the growth of an individual thoughout its life, it is a challenge to link the information from different life stages. By linking growth phases through the fitting of a single model, this potential source of auto-correlation can be accounted for.

In order to assess the possibility of regional links between plaice in Irish and Scottish waters and carry over effects between the larval and juvenile phase, variation in larval and juvenile growth, pelagic larval duration, hatch and settlement timing of *Pleuronectes platessa* from Irish and Scottish nursery grounds was examined over the regional scale in the present study. Growth through the larval and juvenile phases is described by fitting a single state space growth stanza model across both phases. The aims were fourfold: a) to characterize spatial variation in growth of plaice between regions b) to assess the extent to which this variability is attributable to temperature c) to assess possible carry over effects between the larval and juvenile phase and d) to assess the potential for using microstructure as a marker of larval/juvenile origin in plaice.

2.2 Materials and Methods

2.2.1 Sampling Sites and Collection

0–group plaice were collected from beaches on the west coast of Scotland, west coast of Ireland and east coast of Ireland (Figure 2.1). Sampling was carried out using a beach seine (5mm mesh) on the east coast of Ireland and Riley push net (2mm mesh) on the west coast of Ireland and a 1.5m beam trawl fitted with a single tickler chain and 10mm meash in Scotland. Five sites were sampled on the west coast of Scotland, four sites on the east coast of Ireland and two sites on the west coast of Ireland in August 2009. The sites on the west coast of Ireland were also sampled in August 2008, due to the low number of fish available in 2009. Fish were frozen or stored in ethanol on collection. All fish selected for analysis were between 30 and 70mm in standard length.

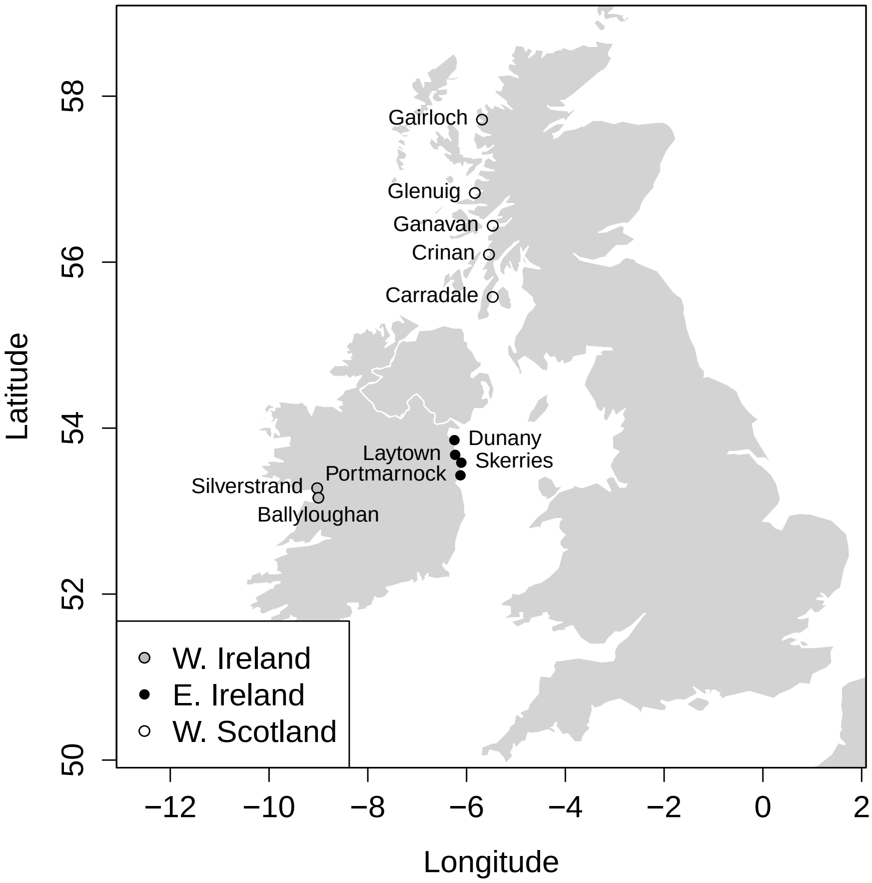


Figure 2.1: Map of sampling sites in W. Ireland, E. Ireland and W. Scotland. All sites were sampled in August 2009, sites in W. Ireland were also sampled in August 2008

2.2.2 Sample Preparation and Processing

All fish were measured (standard length) using digital callipers. Fish for analysis were randomly selected from the catch on each nursery ground. Otolith extraction was carried out under an Olympus SX16 dissection microscope with an Olympus SDF Plapo 0.5x PF parafocal objective and a polarization filter attachment (Olympus UK Ltd.). The otoliths were cleaned manually with dissection needles and distilled water and mounted onto round, 16mm cover slips and embedded in Crystal Bond™509 (Buehler, 41 Waukegan Rd., Lake Bluff, IL 60044, USA).

Otoliths were ground to expose daily increments using dissolved 15 and 3 micron calcinated Aluminium Oxide powder (Logitech Ltd., Materials Technologists and Engineers Scotland) and polished using a Jewellers Rouge bar.

2.2.3 Microstructural Analysis

Otoliths (n = 87; 19 east coast of Ireland, 29 west coast of Ireland, 39 west coast of Scotland) were viewed using an Olympus BX15 binocular microscope (Olympus UK Ltd.) with a motorized stage attached to an image analysis system running Image Pro Plus 6.3 (Media Cybernetics Inc., Bethesda, MD, USA). Measurements were taken under 200x or 400x magnification, depending on the size of the otolith.

Otolith images were analysed using Image Pro Analyser 6.2 (Media Cybernetics Inc., Bethesda, MD, USA). Otolith increment counts were made starting from the hatch check (approximately 10 micrometers from the nucleus of the otolith) along the longest axis of the otolith to the edge of the specimen. The position of the first accessory primordium (AP) was noted and the number of increments up to this point was taken as the larval duration of the specimen. The AP was also used to estimate the date of settlement, as the first AP has been shown to form during this period (Al-Hossaini et al., 1989). The total number of increments from the hatch check to the edge of the otolith was used to back–calculate hatch date. Each otolith image was read a second time 1–2 months later, without prior knowledge of the first reading in order to quantify intra—reader variability.

2.2.4 Data Analysis

2.2.4.1 Early Life History Traits

Data were first examined graphically in order to identify any outliers (8 identified using boxplots and excluded from the analysis). As there were fish collected in 2008 and 2009 in the data set, variation in response variables (Hatching and settlement dates, pelagic larval duration and increment widths) between years was examined and none was found ($p > 0.1$), allowing for data from the two years to be pooled together for analysis. The statistical analysis was carried out using Linear Mixed Effect (LME) models (Bolker et al., 2009), employing R packages nlme (Pinheiro et al., 2011) and gdata (Warnes et al., 2011).

Linear mixed effect models were chosen for their ability to handle unbalanced and highly variable data sets, that show some degree of interdependence, where the response variable is to some extent auto–correlated (Bolker et al., 2009; Zuur et al., 2009).

Table 2.1: Summary table of AIC values for the different model configurations tested for each response variable. The model with the lowest AIC value is considered to be the best (shown in bold). HD = Hatch Date, SD = Settlement Date, PLD = Pelagic Larval Duration, LIW = Larval increment width, SAP = otolith radius at settlement, SAP30 = otolith radius 30 days after settlement, RG = Region, S = Site, ID = Fish and RD = Reading.

Model	Fixed	Random	HD	SD	PLD	LIW	SAP	SAP30
1	Intercept	-	1448	1440	885	10236	1179	1537
2	RG	-	1437	1430	866	10173	1181	1527
3	Intercept	S/ID/RD	1071	1083	758	9501	1147	1502
4	RG	S/ID/RD	1060	1073	748	**9499**	1150	1500
5	RG	S/ID	**1058**	**1071**	746	9625	1148	1498
6	RG	ID	1064	1076	**744**	9623	**1146**	**1497**

Hatching and settlement dates, pelagic larval duration and increment widths were compared between regions. For each of these response variables, different LME models with distinct fixed and random effect structures were compared using Relative Maximum Likelihood and Maximum Likelihood methods. In order to assess the effect of intra–reader precision, an additional variable "Reading" (repeated measurements from the same otolith), was included as a random effect. The best random effects structure was then determined by comparing the variance of the random effects in the models (all with the same fixed effects) using a likelihood ratio test. The model with the lowest AIC value was considered to be the most appropriate for the response variable under consideration. In the event that two models were not significantly different from each other (in their random effects structure) and had AIC values that differed by 2 or less, the model with the simplest fixed and random effect structure was chosen as the most appropriate and used for analysis (Table 2.1).

2.2.4.2 Temperature history reconstruction

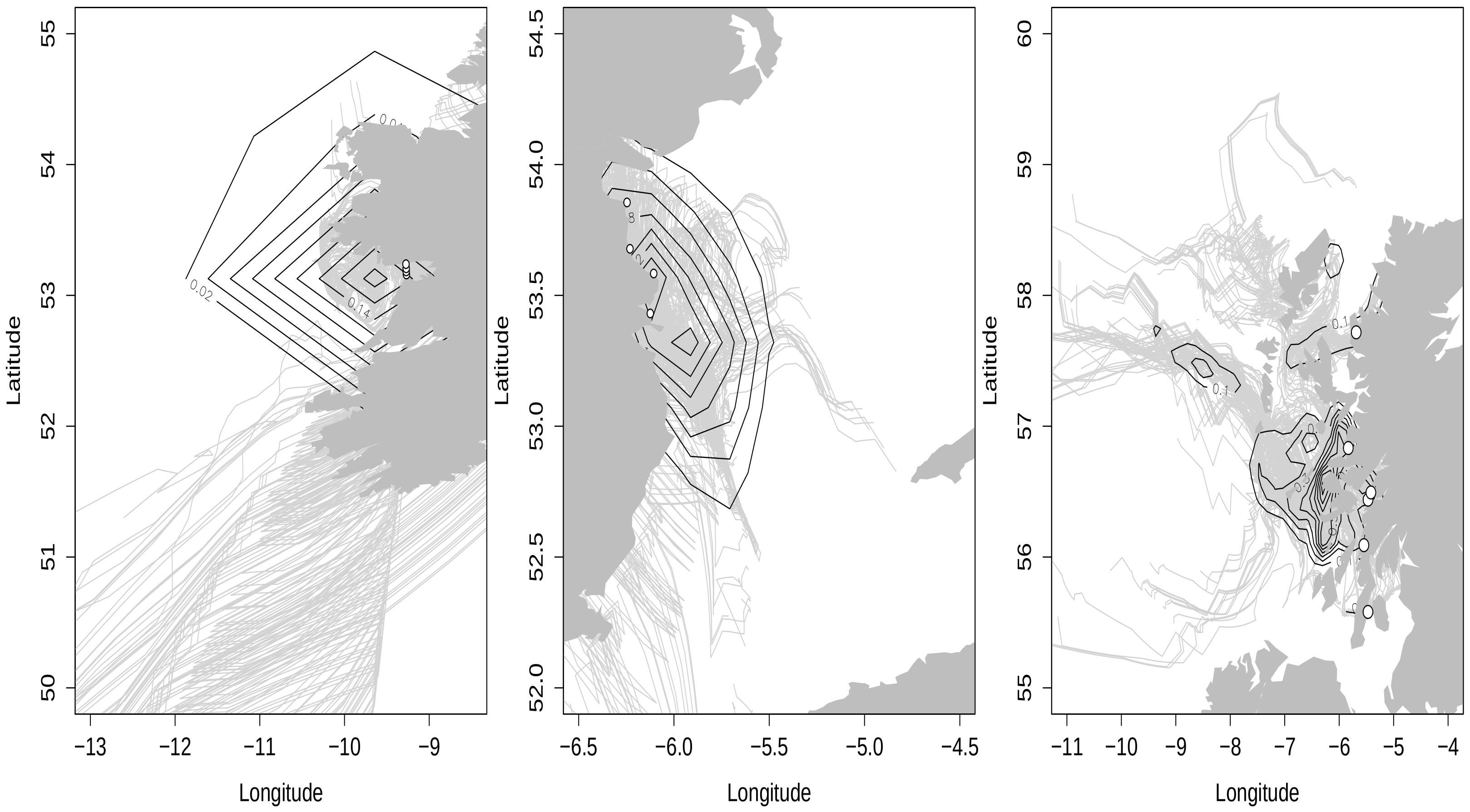
The likely individual temperature histories were reconstructed in order to examine the effect of temperature on growth.

Temperature data was obtained from the GHRSST L4 grided optimally interpolated data set of daily sea surface temperatures (SST), obtained using OPeNDAP at the Physical Oceanography Distributed Active Archive Center (PO.DAAC), NASA Jet Propulsion Laboratory, Pasadena, CA (`http://data.nodc.noaa.gov/opendap/ghrsst/L4/GLOB/JPL/MUR/`). SST could be used because during the early part of the year, the water column in the areas considered is predominantly mixed.

In order to identify the regions of interest (polygons) for the extraction of temperature data, egg and larval dispersal pathways were approximated by modelling in reverse, passive trajectories for particles released from the sampling site locations, using current speed and direction data for 2009 and 2008 (dataset PSY3V3R1 from `http://www.mercator-ocean.fr`). Particle release timing and length of the run was determined using the hatch and settlement distributions obtained for each area from the microstructural analysis. A thin-plate spline was then applied to the current data to determine the predicted trajectories of the particles. The trajectories obtained were approximate only, since individual behaviour was not included. The pathways were used to define the likely maximum geographical origins of the sampled fish during their planktonic phase.

The trajectories obtained were used to generate contour plots of particle densities. The outer edges of these contours plus the natural land barrier, provided the boundaries for the polygons plotted for each area of interest (Figure 2.2). Temperature data were extracted from within the polygon delineated for each region, using the point in polygon function in R.

Extracted temperature data were combined with otolith increment data to calculate cumulative degree day (CDD) for each individual increment measurement, by adding daily SST at each increment to the next. Cumulative



(a) (b) (c)

Figure 2.2: Contour plots for estimation of maximum geographic range of particle trajectories (grey lines) for SST extraction for (a) W. Ireland (b) E. Ireland and (c) W. Scotland

degree day , combines both temperature and time, and was used rather than daily SST as a descriptor of the fish's temperature history, as it provides a better indicator of temperature exposure over time and because the effects of temperature on growth from one day to the next are not independent of each other and may be cumulative (Neuheimer and Taggart, 2007; Comerford et al., 2013).

2.2.4.3 State Space Growth Stanza Model

In fish, individual growth patterns over time are not constant, but display distinct phases or "stanzas", which can be accounted for by fitting separate models for each phase (Buckley et al., 2006; Günther et al., 2012; Quiñonez-Velázquez, 1999). This approach has the advantage that the models fitted to each phase are simple (linear or power functions) and require relatively little parametrization. However, growth trajectories for each period are fitted independently and the potential influence of a given stanza on subsequent growth are not accounted for. The state space model presented here is very flexible, allowing for the stochastic nature of otolith data to be accounted for. The present model links the larval and juvenile growth phases in a single model comprised of three stages or stanzas, the larval phase up to settlement (as indicated by the first accessory primordia represented by the first changepoint, see below), the post larval phase up to the point where juvenile growth levels off (as indicated by the second changepoint, see below) and the post settlement phase where growth has stabilized. Thus the model allows us to describe and quantify individual growth during larval and juvenile phases, linking the different stages, such that not only can regional differences be detected but the influence of larval on juvenile growth assessed.

The state space growth stanza model is a stochastic model of the underlying relationship between true increment width as a function of time and their relationship to the observed measurements. The parameterization using time was chosen to account for time and resource restraints. While measurement error only growth stanza models have previously been used in early life history studies (Buckley et al., 2006; Günther et al., 2012; Quiñonez-Velázquez, 1999; Dortel et al., 2013), the model presented here extends these by implementing a three stage process error time series growth model. The variables of the model are

W True increment width (μm)

w Measured increment width (μm)

t Increment number (days)

j Reading number (two readings: $j \in \{1, 2\}$)

The growth model is given by the process error equation

$$W_{t+1} = W_t + b_1 I_{t,1} + b_2 I_{t,2} + \eta_t, \text{ for t>1} \tag{2.1}$$

where b_1 and b_2 are the second and third stage increment widths; $I_{1,t}$ and $I_{2,t}$ are indicator variables such that

$$I_{1,t} = \begin{cases} 1 & \text{if } c_1 \leq t < c_2, \\ 0 & \text{otherwise,} \end{cases} \tag{2.2}$$

and

$$I_{2,t} = \begin{cases} 1 & \text{if } c_2 \leq t, \\ 0 & \text{otherwise,} \end{cases} \tag{2.3}$$

where c_1 and c_2 are the first and second changepoints respectively. Persistent variability in growth caused by environmental factors is captured by the process error variance ηt in Equation (2.1), such that $\eta t \sim N(0, \sigma_\eta^2)$. The increment width at the first time step is assumed to be $W_1 = a$ and in the model growth varies around an average value of a during the first stage, then changes at rate b_1 during the second stage and at rate b_2 during the third stage. Constant growth during a stage is indicated by either b_1 or b_2 being equal to 0. Increment width measurements (by reading) are assumed to be normally distributed around the true increment width such that

$$w_{t,j} \sim N(W_t, \sigma_\in^2) \tag{2.4}$$

where $\sigma_\in^2$ is the measurement error variance, assumed to be constant across readings. While this term is interpreted as the measurement error, its is likely a combination of measurement error and high frequency variability in increment widths caused by non-persistent random short term variation in environmental factors such as temperature and food availability, among others. The state space growth model combines Equations (2.1) and (2.4), illustrated graphically in Figure 2.3.

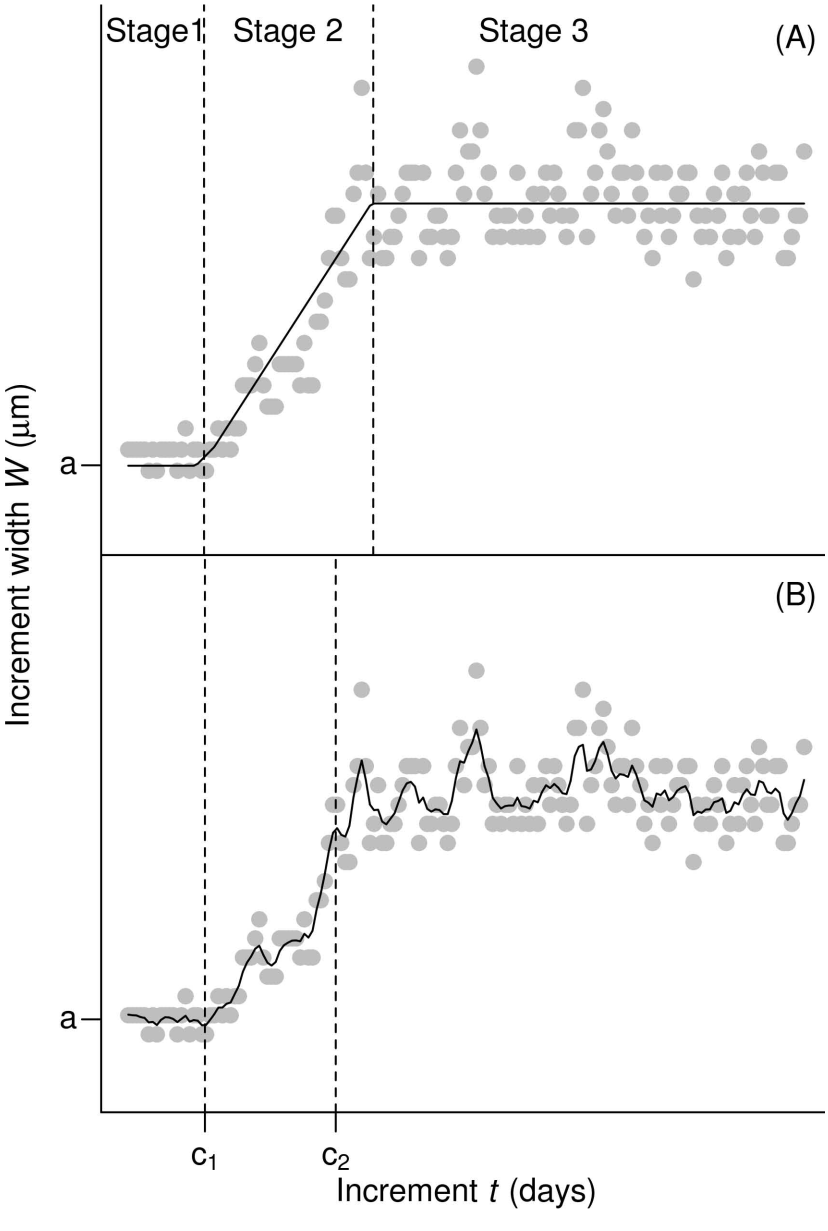


Figure 2.3: Schematic of the state space growth model. Underlying growth pattern is shown as a black solid line and increment measurements are shown as grey points. (A) no process error variance; (B) with process error variance. Changepoints c_1 and c_2 mark the transition between the first and second and second and third stages, respectively. The first underlying increment width is given by a

The growth model provides three different growth rates: pre-settlement growth rate a (from hatch to the point of settlement, indicated by the first accessory primordia); post settlement growth rate acceleration b (from settlement to the second changepoint c_2); and b_2, indicating the average change in growth rate after the second changepoint.

2.3 Results

2.3.1 Early Life History Traits

Results of the microstructure analysis are summarised in Table 2.2.

The timing of hatching and settlement showed no significant variation between regions.

Table 2.2: Results of regional comparisons of early life history traits(HD = Hatch date, SD = Settlement date, PLD = Larval duration, LIW = Larval increment width, SAP = otolith radius at settlement, SAP30 = otolith radius 30 days after settlement)

Comparison	HD	SD	PLD	LIW	SAP	SAP30
E. Ireland/W.Scotland	ns	ns	0.008**	0.03*	ns	0.01*
E. Ireland/W. Ireland	ns	ns	0.03*	ns	ns	ns
W. Ireland/W. Scotland	ns	ns	ns	ns	ns	ns

Signif. levels: ***0.001 **0.01 *0.05 ns (non–significant)

Mean PLD was significantly shorter for plaice collected on the east coast of Ireland compared to the west coast of Scotland (p = 0.008) and the west coast of Ireland (p = 0.03), indicating that the surviving juveniles on Scottish and west Irish beaches have spent longer in the plankton than those on east Irish nursery grounds.

Mean larval increment width was also significantly greater in plaice collected from the east coast of Ireland compared to the west of Scotland (p = 0.03), suggesting that juvenile plaice on Scottish nursery grounds had grown more slowly as larvae. Otolith size at settlement, as indicated by cumulative increment width up to the first AP, was not significantly different between regions, but 30 days later, the size of east Irish fish was significantly greater than that of Scottish fish (p = 0.01), suggesting that juvenile plaice on nursery grounds in western Scotland also grew more slowly as juveniles (Figure 2.4).

There was a significantly positive regionally independent correlation between larval increment width and juvenile increment width (up to 30 days after

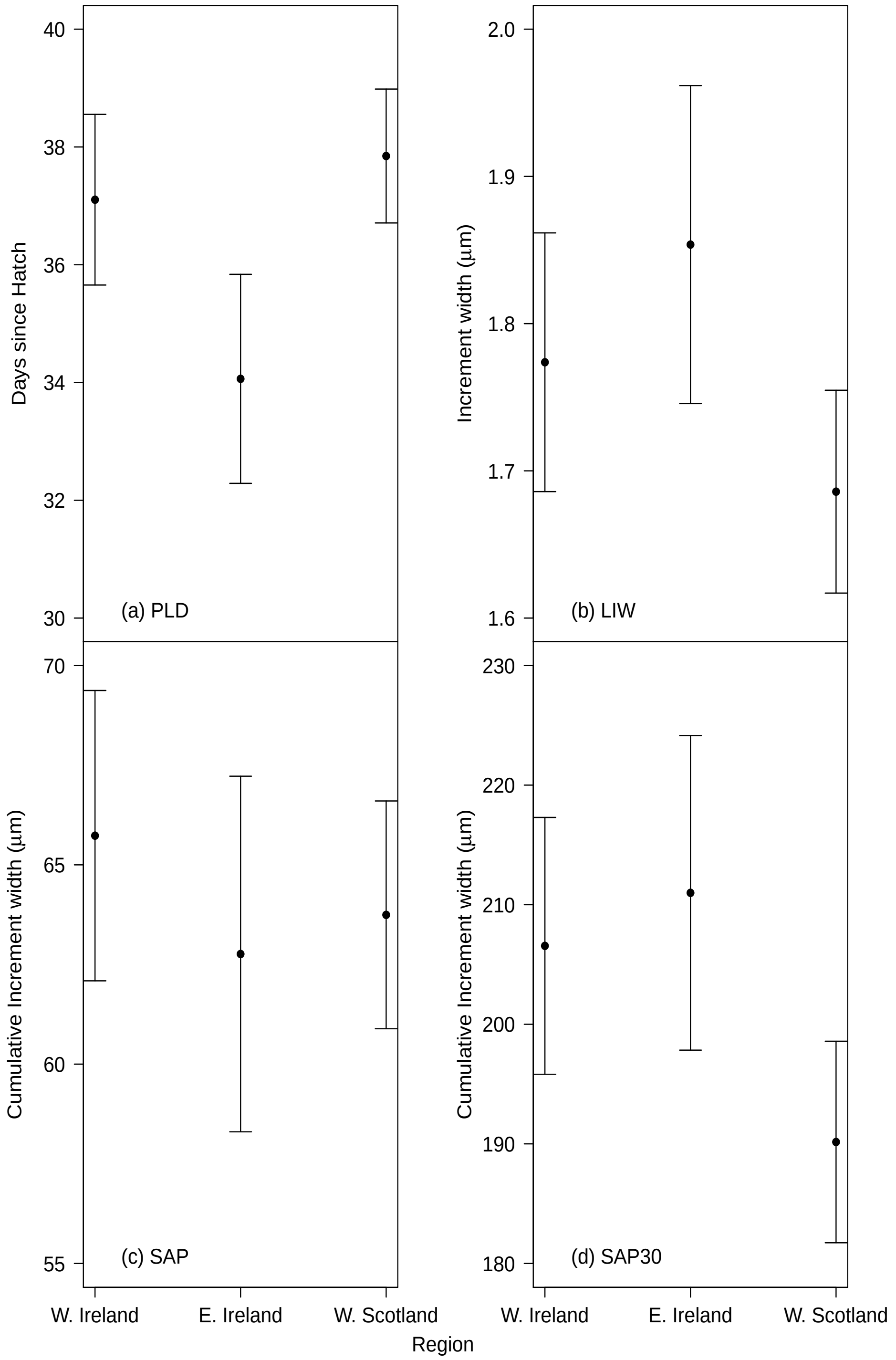


Figure 2.4: Variation in early life history traits between regions: (a) Pelagic Larval Duration (PLD) (b) Larval increment width (LIW) (c) Otolith radius (cumulative increment width) at settlement (SAP) and (d) Otolith radius (cumulative increment width) 30 days after settlement (SAP30)

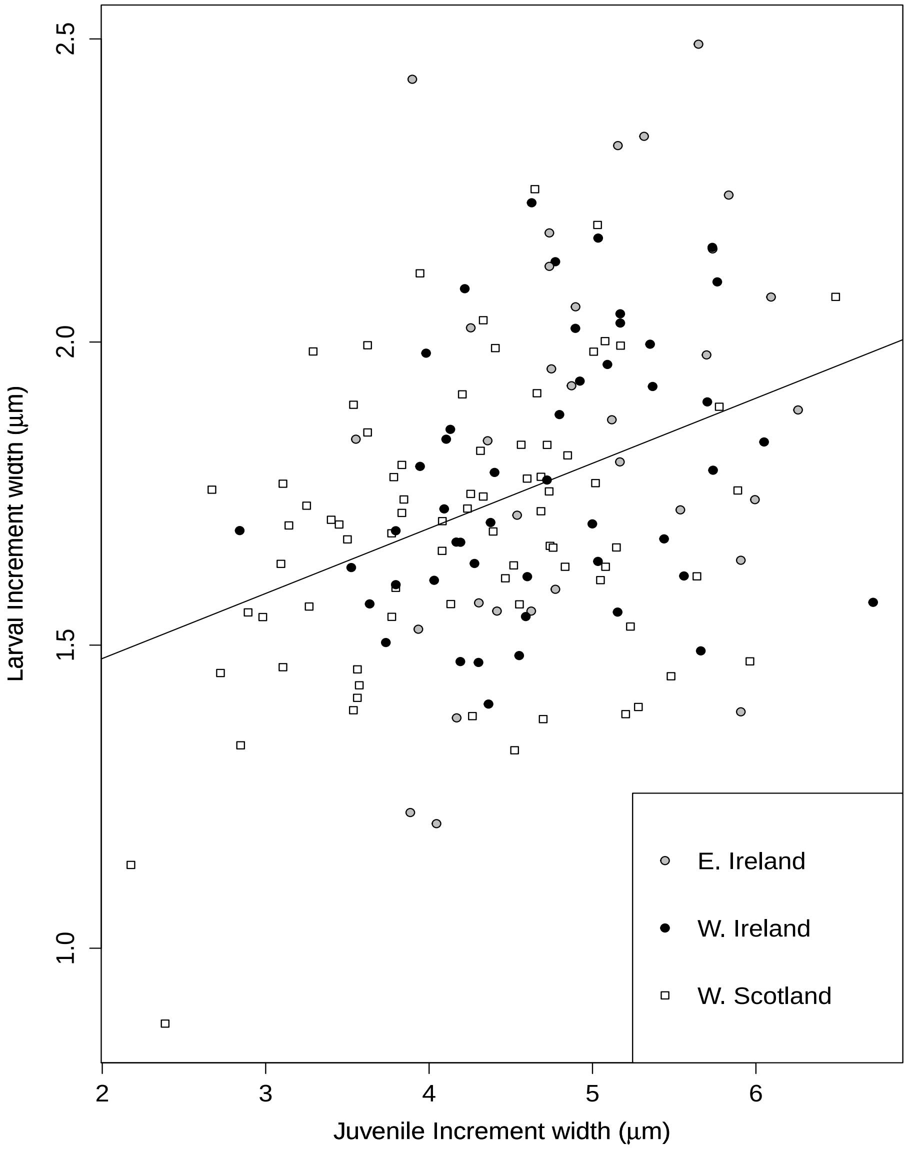


Figure 2.5: Correlation between mean larval and post settlement increment width (average of 30 days after settlement) within individuals for all regions.

settlement), when all the data were pooled (r^2:0.36, t = 4.816, p < 0.001). This suggests that individuals which grew faster during the planktonic stages also grew faster post–settlement (Figure 2.5). However, the observed correlation, although significant, was weak and it may also be a result of differences in temperature between regions.

2.3.2 Temperature reconstruction and Growth

Regional variation in average sea surface temperature was evident from the reconstructed temperature histories. Plaice collected from sites on the west coast of Ireland had experienced the highest temperatures and plaice from the west coast of Scotland the lowest, with plaice from the east coast of Ireland experiencing intermediate temperatures (Figure 2.6).

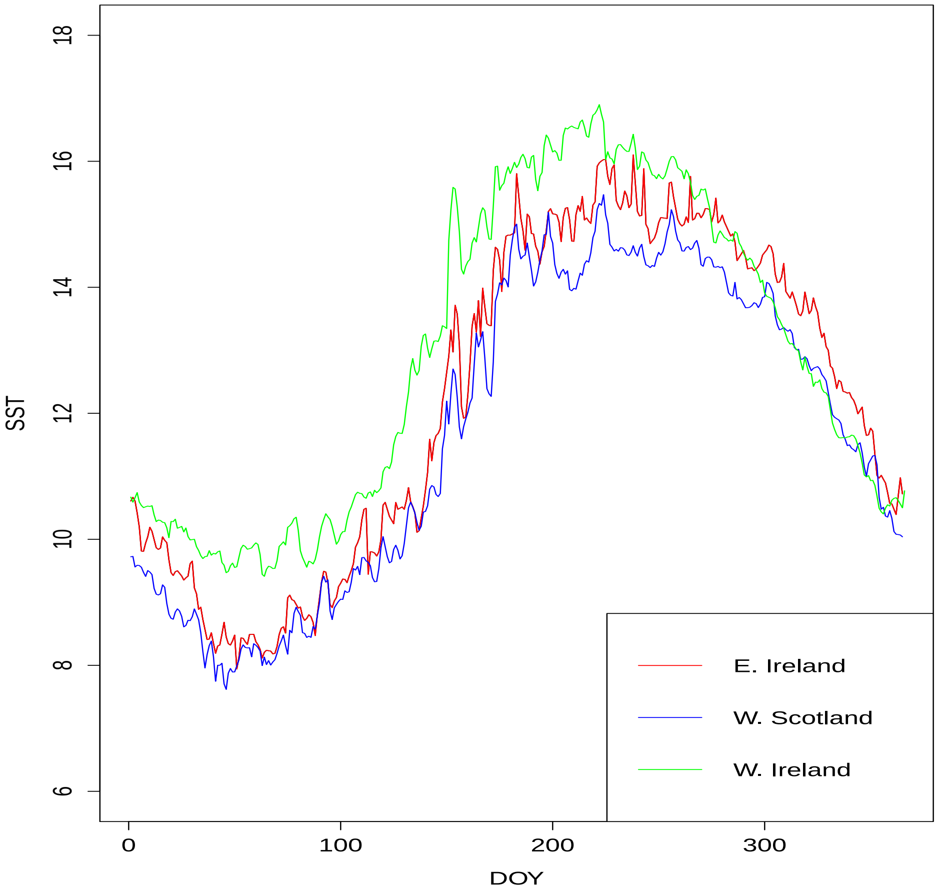


Figure 2.6: Average Sea Surface Temperature (SST) by Day of the Year (DOY) for all three regions

If temperature were the sole driver of the length of pelagic larval duration, regional measurements of cumulative degree day (CDD) would be expected to overlap and larval duration on the west coast of Ireland would be expected to be shorter than in the other two regions. However, CDD over the larval period was significantly lower on the east coast of Ireland than the west coast of Scotland ($p = 0.01$) or the west of Ireland ($p < 0.001$) (Figure 2.7) and larval duration on the west coast of Ireland was longer than could be expected from temperature alone.

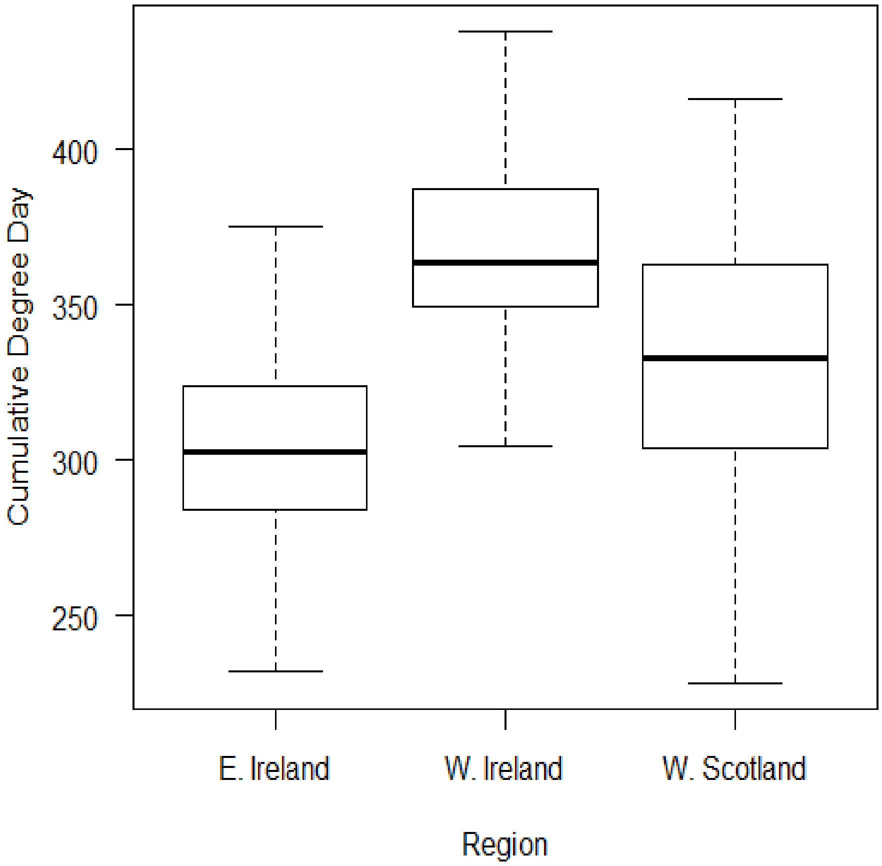


Figure 2.7: Cumulative degree day by region over the larval period

2.3.3 State Space Growth Stanza Model

Posterior hierarchical parameter distributions from the growth model fits by region are shown in Figure 2.8 and summarized in Table 2.3. As can be seen in Figure 2.9 fish on nursery grounds on the west coast of Ireland show higher growth than their counterparts on the east coast or the west of Scotland, possibly owing to the significantly higher temperature on the west coast of Ireland than the other two regions.

Their growth trajectory also seems similar to their west Scottish counterparts, although their post larval trajectory is steeper. The growth trajectory

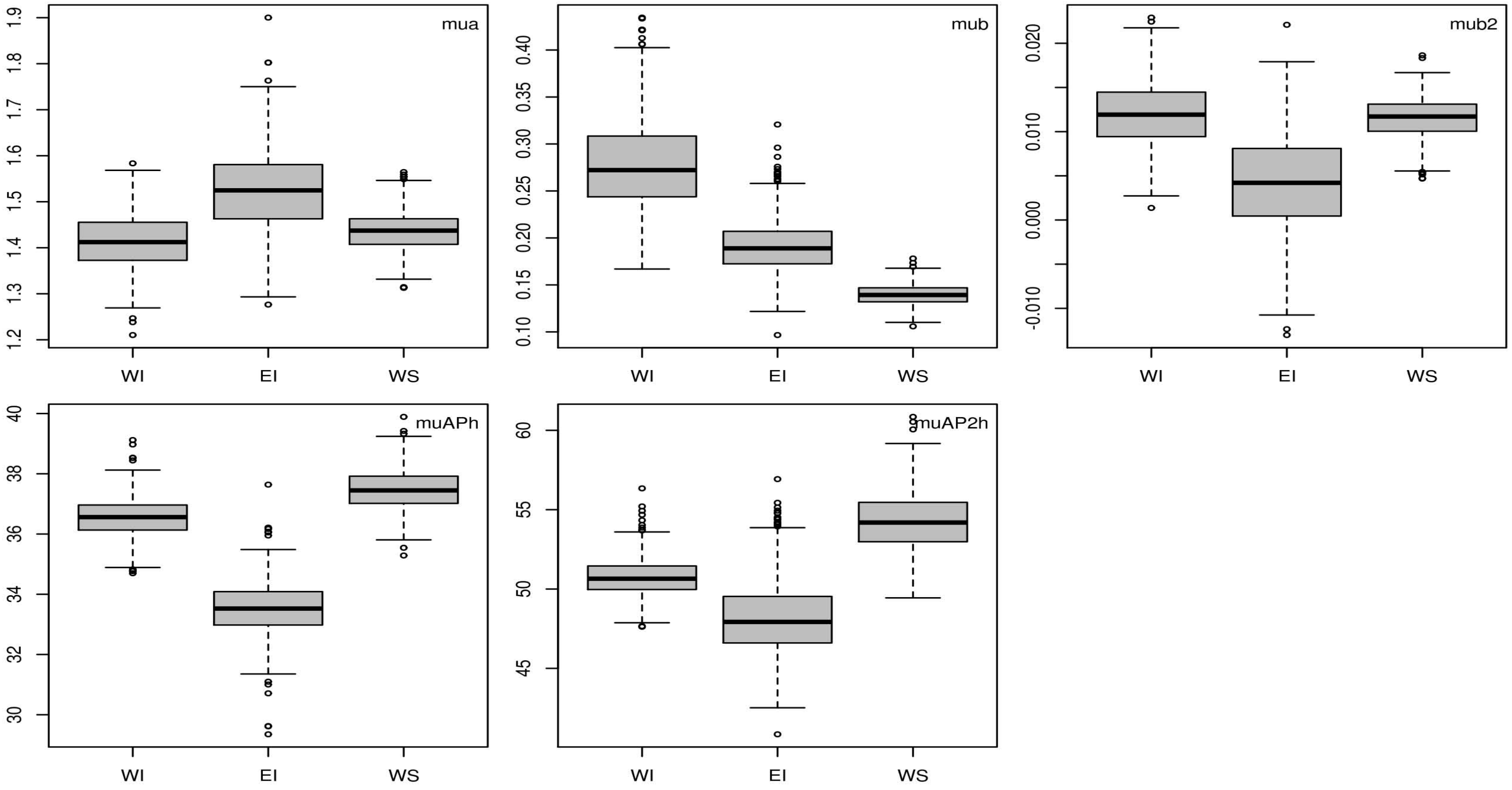


Figure 2.8: Posterior hierarchical parameter distributions from the hierarchical state space growth stanza model fit to the west coast of Ireland (WI); east coast of Ireland (EI); and west coast of Scotland (WS). Distributions are based on MCMC samples from the posterior mean. mua - pre-settlement growth rate; mub - post-settlement growth rate acceleration; mub2 - average change in growth rate after changepoint c_2; muAPh - first accessory primordia (AP); muAP2h - changepoint c_2

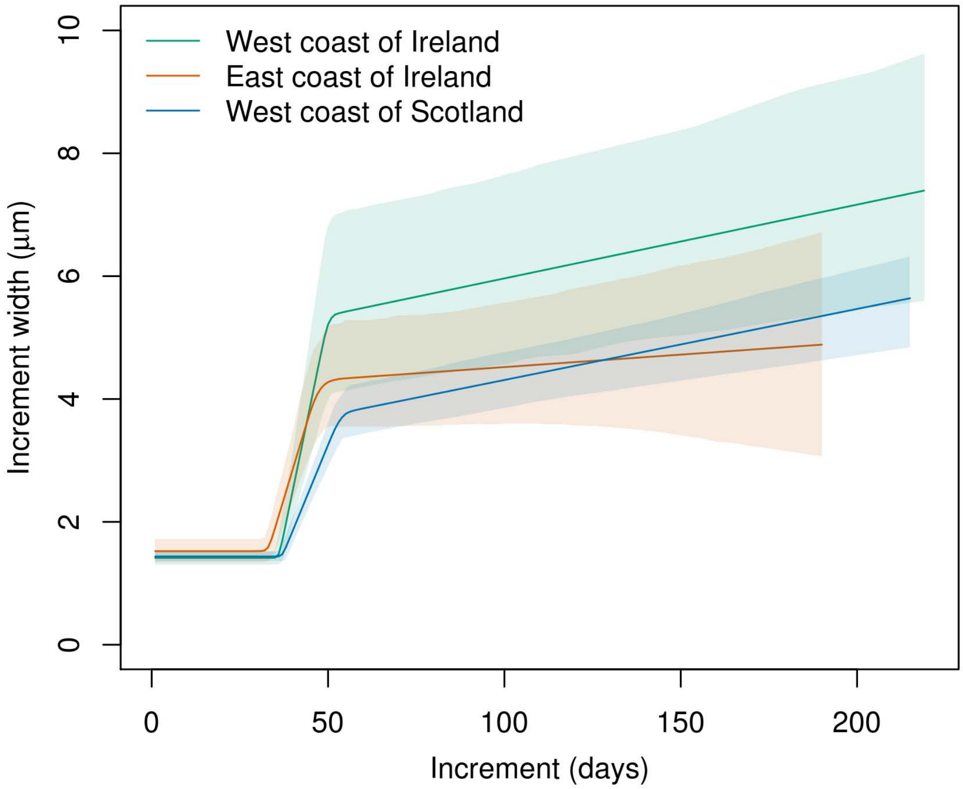


Figure 2.9: Mean regional growth trajectories obtained from state space model hierarchical means. Coloured areas indicate the associated 95% Credibility Interval

Table 2.3: Hierarchical growth model parameter summaries by region. The hierarchical mean (mu), standard error (S.E.) and 95% Credibility Interval (Bayesian equivalent to 95% Confidence Interval) are shown. WI - West of Ireland, EI - East of Ireland, WS - West of Scotland

Parameter	Region	Mean	S.E.	95% Credible Interval
mua	WI	1.415	0.059	1.307, 1.524
mua	EI	1.523	0.09	1.346, 1.717
mua	WS	1.436	0.041	1.36, 1.516
mub	WI	0.278	0.051	0.194, 0.394
mub	EI	0.191	0.028	0.143, 0.258
mub	WS	0.139	0.011	0.118, 0.162
mub2	WI	0.012	0.004	0.005, 0.019
mub2	EI	0.004	0.006	-0.008, 0.015
mub2	WS	0.012	0.002	0.007, 0.016
muAPh	WI	36.554	0.671	35.194, 37.882
muAPh	EI	33.522	0.913	31.716, 35.162
muAPh	WS	37.465	0.683	36.116, 38.814
muAP2h	WI	50.765	1.186	48.802, 53.284
muAP2h	EI	48.202	2.351	44.365, 53.868
muAP2h	WS	54.29	1.758	51.325, 58.091

of east Irish fish is less steep than the other two and although they grow faster than their Scottish counterparts in the early juvenile phase, the Scottish fish catch up with them later in the juvenile phase, when they show higher growth.

Posterior probability tests on the parameters (Table 2.4) showed that pre-settlement growth rates (mua) did not differ significantly between regions, while post-settlement growth rate acceleration (mub) did. Post-settlement growth rate acceleration was greater on the east and west coast of Ireland than the west coast of Scotland, but acceleration on the west coast of Ireland was not greater than that on the east coast. Fish on the west coast of Scotland also took longer to reach c_2, the point at which post-settlement growth rates begin to level off, than fish from both Irish coasts. Larval duration (APh) was also significantly shorter on the east coast of Ireland than both the west coasts of Ireland and Scotland, which did not differ significantly from each other in this regard. Regression analysis of pre-settlement growth rate a and post-settlement growth rate acceleration b by region did not show a significant relationship, indicating that they are independent of each other.

Table 2.4: Posterior hypothesis test results. Each cell denotes the probability of that hypothesis being true. Probabilities >0.95 indicates the hypothesis to be true. Conversely, probabilities <0.05 indicate the reverse of the hypothesis to be true

Parameter	**P(WI>EI)**	**P(WI>WS)**	**P(EI>WS)**
mua	0.147	0.373	0.838
mub	0.94	1	0.97
mub2	0.897	0.535	0.113
muAPh	0.997	0.177	0.002
muAP2h	0.838	0.038	0.027

2.4 Discussion/Conclusions

It is well established that temperature correlates negatively with PLD and positively with growth (Van der Veer et al., 2009; Green and Fisher, 2004; McCormick and Molony, 1995; Comerford et al., 2013). This study found regional variation in pelagic larval duration (PLD) and individual larval growth rates that were partially consistent with observed differences in reconstructed temperature histories. In general, PLD in plaice decreased and growth rates increased as temperature increased. However, temperature was not the sole driver of the observed spatial variation, as larval duration on the west coast of Ireland was higher than expected and CDD's overlapped. This suggests that the influence of temperature on the rate of larval development and timing of settlement is region specific. It also lends further support to the hypothesis that the length of the larval duration and growth are dependent on other factors such as food availability and genetic predisposition, acting in concert with temperature. This is consistent with the work of Comerford et al. (2013), who found that larval duration and growth could be estimated using a pan regional model of temperature experienced during the larval phase, temperature accounting for 73% of the variability in the model. However, in contrast to the findings reported by Comerford et al. (2013), in the present study there was no significant difference between regions in hatching and settlement times. This may be because the fish in the Comerford et al. (2013) study were collected earlier in the year (around March) than the ones in the present study and so different cohorts of fish may have been present at the time of collection. Other unmeasured factors which vary regionally such as food availability (Van der Veer and Witte, 1993; Fiksen and Jørgensen, 2011) or genetics (Watts et al., 2004) may underlie the unexplained variation in growth in this and previous work.

The reconstruction of temperature histories in the present study employed reverse passive particle tracking, which did not take into account changes in the physical characteristics of eggs (buoyancy) and subsequent larval behaviour (active swimming). It is therefore possible that the methodology did not accurately capture the geographical regions and thus the temperatures regimes that the fish were exposed to. In certain areas, the onset of tidally synchronized vertical movements can lead to rapid transport of larvae over large distances (Fox et al., 2006). It is therefore possible that the planktonic envelopes (Figure 2.2) underestimated total transport distances. However, vertical swimming behaviour (selective tidal stream transport) is probably most important in the final stages of immigration into the shallow inshore nurseries, with passive drift through wind–driven currents being the predominant transport mechanism prior to this (de Graaf et al., 2004; Fox et al., 2006). In addition, the estimated planktonic envelopes show broad agreement with the plaice spawning grounds illustrated in Coull et al. (1998), suggesting that the technique employed in this study is adequate for broadly estimating thermal history. Temperature data were also based on sea surface measurements which might vary from temperature at depth. However, during the early part of the year, the water column in the areas considered is predominantly mixed so this should not have lead to any substantial bias.

As the fish sampled in this study represent the survivors of the planktonic and early settled phase (Geffen et al., 2011), the observed region specific effects of temperature could be the result of selective mortality. Selective mortality occurs when particular behavioural, morphological (such as size) or physiological traits (such as growth rate) enhance the survival probabilities of a subset of individuals in a population (Sogard, 1997). Selective mortality can be directional, removing either the lower or upper tail in a trait distribution, stabilizing, by removing both tails, or disruptive by removing intermediate individuals from the trait distribution (Sogard, 1997). Mechanisms through which selective mortality can occur include predation via size biased consumption (gape limitation) (Ellis and Gibson, 1995), behavioural selection by predators (Meekan et al., 2010), differential condition (Hamilton, 2008) and variation in escape capacity with size (Johnson and Hixon, 2010). Refuges from predation attained through size, are more reliable than those attained through behavioural predator preferences (Sogard, 1997) and thus morphological or physiological traits are more likely to come under selection. It is difficult to ascertain if mortality acts selectively directly on growth rate rather than size, but Takasuka et al. (2003) reported that larvae can experience selective mortality on growth rate, independent on size or stage duration, termed ”growth-selective predation", via differences in potential for anti-predator behaviours, such as escape activity and responsiveness in encountering predators. The degree to which mortality is selective depends on not only the life stage (Gagliano et al., 2007), variation in prey traits (Sogard, 1997) and prey availability, but also on the environment the individual is in (Rankin and Sponaugle, 2011; Grorud-Colvert and Sponaugle, 2011) as well as the characteristics of the predator (Takasuka et al., 2007). Variation in growth between regions (Gagliano et al., 2007), such as observed in the present study may be maintained by spatial and temporal differences in the shape of the selective mortality (Meekan et al., 2010) and possibly mediated by differential temperature regimes (Rankin and Sponaugle, 2011), making it difficult to disentangle the two.

The relatively high number of growing degree days required to complete the larval phase in plaice settling on west Irish and Scottish nursery grounds may reflect not just the effects of selective mortality but adaptations to regional differences in oceanographic conditions, the availability of nursery habitat and the distance between spawning and settlement sites, which have been found to be in relative proximity to each other in the Irish Sea (Fox et al., 2006, 2009). Successful survival of the larval phase and recruitment to the juvenile phase depends on larvae taking advantage of prevalent transport and retention mechnisms (Cushing, 1990) to ensure their delivery to habitats that are suitable for juvenile development. Extension of the pelagic larval duration by delaying metamorphosis, even though the individual is capable given the right cues (Victor, 1986), may be advantageous in situations where suitable habitat is sparse, as this will increase the probability of finding a suitable nursery ground (Cowen, 1991), by increasing dispersal (Sponaugle et al., 2005). The increased chance of finding habitat of suitable quality may even outweigh the increased risk of predation and starvation (Pankhurst and Munday, 2011), associated with spending more time in the plankton (Cowen, 1991). Slower growth, extended larval development and delayed metamorphosis has been shown to occur in fish that do not encounter a suitable environment for settlement (McCormick, 1999) and delayed settlement has been observed in plaice that have reached a suitable size for metamorphosis, in response to food supply and predator presence (Wennhage and Gibson, 1998).

Larval traits have been hypothesised to carry over into juvenile and adult life (Sponaugle et al., 2006; Sponaugle and Grorud-Colvert, 2006; Grorud-Colvert and Sponaugle, 2006), as larval experiences, such as starvation (McCormick and Molony, 1992) may be exhibited in juveniles and adults (Pechenik et al., 1998; Pechenik, 2006), since these traits are maintained throughout life (Pepin et al., 1999). Our results lend support to this hypothesis, as there was a significant positive correlation between larval growth and juvenile growth 30 days after settlement, as indicated by increment width. There was no correlation between pre-settlement growth rate and post-settlement growth acceleration, which illustrates the importance of linking larval and juvenile growth when trying to assess variability in juvenile growth. However, the observed correlation may partially be driven by temperature differences. Thus, it may be worthy of further investigation to establish if plaice in from these regions show true carry over effects, by transferring recently settled fish between nursery grounds and seeing if growth rates remain unchanged.

Although fish in the present study showed no regional difference in size at settlement (as indicated by otolith radius), possibly due to size related metamorphosis in plaice (Gibson, 2005; Geffen et al., 2007), 30 days after settlement, fish from the east coast of Ireland were significantly larger than fish from the west coast of Scotland. In addition, Scottish fish took significantly longer to reach a plateau in growth rates (as indicated by changepoint c_2) than fish from Irish coasts, while post-settlement growth acceleration also differed significantly between regions. While reaching this growth rate plateau took longer for Scottish fish, they make up for this later in the juvenile phase, when their growth trajectory catches up to their east Irish counterparts and subsequently surpasses them. These findings suggest regional variation in nursery ground quality. Various habitat characteristics have been shown to promote faster growth and higher condition in juvenile plaice, including shallow water and high polychaete and shrimp densities, low macroalgal cover and low organic content (De Raedemaecker et al., 2012). Juvenile plaice also grow faster in warmer, less saline water, possibly due to the costs of osmoregulation and higher food requirements at higher salinities (Augley et al., 2008). Habitat specific rates of mortality have been shown in Atlantic cod (*Gadus morhua*) and cunner (*Tautogolabrus aalspensus*) in the north-west Atlantic (Juanes, 2007), while the condition, feeding and reproductive potential of white seabream (*Diplodus sargus*) was found to be affected by habitat type in the Mediterranean (Lloret and Planes, 2003). Growth has also been found to be significantly influenced by physical habitat characteristics (Ciotti et al., 2013) in plaice and was also found to be a better indicator of habitat quality, in combination with other factors, than condition indices for sole (Gilliers et al., 2006). Improving our understanding of the habitats that serve as nursery areas for marine fish and the factors that affect site-specific variability in nursery quality and productivity will assist in the conservation and management of these areas (Beck et al., 2001). Models such as the one presented here can assist in this task, as it allows us to look at differences in growth at different stages but also links them, giving us a more complete picture of the factors affecting growth.

Regardless of the underlying cause, the observed regional differences in early life history traits could be used as markers of larval and juvenile origin (Brophy and Danilowicz, 2002; Brophy and King, 2007) in order to assist in describing connectivity between nursery and spawning grounds. Previous studies on plaice in the Irish Sea have come to the conclusion that sub populations may exist in the area, although they are currently managed as one stock. Similarities in growth and maturation in plaice in the north–east and south–east Irish Sea and differences in these measures when compared to western Irish Sea plaice found by Nash et al. (2000) may be evidence of such populations. Differences can indicate a lack of mixing between them (Begg et al., 1999), which may be due, in the case of the western and eastern Irish Sea, to the existence of a deep water channel, separating the main spawning grounds although a certain degree of mixing was probable (Fox et al., 2009). Differences in growth between regions found in the present study, may indicate that there is little or no mixing between regions. However, growth variability alone is not a clear separator for larval and juvenile origin, but can be used with other methods such as otolith microchemical analysis (Geffen et al., 2003; Vasconcelos et al., 2008; Gillanders, 2002; Gillanders et al., 2003) of juveniles, tagging of adults (Dunn and Pawson, 2002) and dispersal modelling (Fox et al., 2006, 2009) or a combination thereof (Ashford et al., 2010) to provide a clearer picture of larval/juvenile origin and connectivity to nursery areas. Models, such as the state space model used in the present study, also greatly assist in this task because they allow us to capture aspects of growth trajectories that are lost when increment width alone is used, thus giving much more detailed insight into the growth patterns used to characterise fish from different regions.

While temperature alone was not found to be the sole driver of variations in early life history traits and growth in this study, modification of the state space growth stanza model for cumulative degree day may be a further avenue of research, as models using CDD have been used previously (Comerford et al., 2013). This would be of particular interest as temperature specific growth models could be used to better inform dispersal models and thus further elucidate the impact on growth on dispersal, connectivity, and recruitment, in view of changing sea surface temperatures and ocean circulation due to climate change (Harley et al., 2006). Even though species level effects are difficult to predict and regional and seasonal projections are uncertain, shorter larval durations will likely mean that individuals may no longer be able to extend their competent phases so as to ensure wide enough dispersal to find suitable nursery habitat (O'Connor et al., 2007). Changes in dispersal may have negative impacts on population connectivity, with less exchange occurring between populations and replenishment through self–recruitment and influx from other populations declining, endangering population regulation and persistence (Cowen and Sponaugle, 2009). Population connectivity and effective population size should, in general, be inversely related to ocean temperature (O'Connor et al., 2007). So not only may connectivity and population size be affected, but growth rate of 0–group plaice may be negatively affected if temperatures go above the optimal temperature for growth and benthic food production cannot meet their increased energy requirements (Teal et al., 2008), negatively impacting survival and condition of subsequent life stages, due to carry over effects (Smith and Shima, 2011). Such changes in habitat quality will likely lead to changes in plaice distribution, moving into deeper and colder waters (Van Keeken et al., 2007), but also more importantly to weaker (poorer condition) less abundant year classes recruiting to the adult population. Such possible impacts of climate change, due to region specific effects of temperature need to be taken into account when designing future management plans for plaice.

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Chapter 3

Otolith microchemistry of plaice (*Pleuronectes platessa* L.) from the western Irish Sea and western Scotland: a potential marker of juvenile origin and connectivity

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Abstract

Spatial and temporal variation in whole otolith chemistry of juvenile plaice (*Pleuronectes platessa*) was examined over two years (2009 and 2011), to assess the feasibility of using this technique to determine juvenile origin of plaice from the western Irish Sea and western Scotland. Composition was analysed using Inductively Coupled Plasma Mass Spectrometry (ICP–MS). Significant regional variation was found in Titanium (Ti), Manganese (Mn), Cadmium (Cd), Barium (Ba), Copper (Cu), Magnesium (Mg) and Strontium (Sr). Local (within region) variation was found in Ti, Mn, Chromium (Cr), Mg and Sr. At both regional and local scales, Mg and Sr exhibited temporal stability, showing no interannual variability, which was not the case for other elements. Discriminant function analysis of otolith elemental composition showed that fish could be classified to their region of origin with an accuracy of 88-90% (average 89%) and to individual nursery grounds with an accuracy of 53–89% (average 76%). Although some Irish fish were misclassified to Scottish nursery grounds, likely due to insufficient environmental variation, overall sufficient elemental variation was found for successful regional and local classification. Regional differences in Sr and Mg are likely linked to differences in salinity/temperature, as well as growth and metabolism. Local and regional differences in Ti, Cr, Cd and Cu possibly reflect variation in pollution levels, while differences in Ba possibly reflect differential freshwater input. Local signatures may be useful to trace small scale juvenile movements on and between nursery grounds. The present study suggests that otolith elemental composition can be a useful tool in the future to provide further insight into plaice population connectivity in the western Irish Sea and the west of Scotland.

Keywords: Plaice (*Pleuronectes platessa*); Otolith chemistry; juvenile origin; Elemental signatures; Connectivity; Stock delineation; Western Irish Sea; West Scotland

3.1 Introduction

Formulation of effective fisheries management plans requires knowledge of population stock structure and connectivity, as not accounting for these features may increase the risk of overexploitation or depletion (Fogarty and Botsford, 2007; Ying et al., 2011). Techniques that allow discrimination between stocks, identification of juvenile origin of adults and quantification of the extent of larval retention and population connectivity, are essential for the development of realistic spatially explicit population models for marine systems (Thorrold et al., 2002). For the management of flatfish stocks, identifying and protecting those nursery grounds which contribute most to the adult populations, can help to maintain flatfish recruitment (Gibson, 1994; Van der Veer et al., 2010; De Raedemaecker et al., 2012).

Otoliths, or ear stones, located in the inner ear of teleost fish are biomineralised structures made up of calcium carbonate (aragonite), precipitated onto a protein matrix. They play a role in hearing and balance and grow continuously throughout a fish's life (Mugiya, 1987). New layers are normally deposited on a diel cycle and once incorporated into the matrix, the constituents of the otolith are not reabsorbed. Trace elements, pass through the gill membranes or intestine wall of the fish into the blood plasma, from which they are carried to the endolymph fluid in which the otoliths sit, available to be incorporated during otolith deposition (Campana, 1999; Payan et al., 2004).

The interplay of differences in physiology, genetics, diet (Weiner and Dove, 2003; Freitas et al., 2006) and environmental conditions fish are exposed to, will lead to differences in otolith elemental composition, which can be population and region specific (Clarke et al., 2011; Chang and Geffen, 2012). This makes it possible to use otolith elemental composition as a natural tag to track fish through the early life stages to their eventual recruitment to adult populations (Campana et al., 2000; Campana, 2005; Thorrold et al., 2002). Otolith microchemistry has been used successfully in a variety of species, including cod, chum salmon and several flatfish species to discriminate between marine and freshwater populations (or life stages) (Arai and Hirata, 2006; Kennedy et al., 2000; Secor et al., 1992), assess the degree of connectivity between spawning and nursery areas and to estimate the contributions of different reproductive units to adult stocks (Gillanders, 2005; Thorisson et al., 2011; Vasconcelos et al., 2008; Yamashita et al., 2000) and to assess population structure (Wright et al., 2006; Campana, 2005; Correia et al., 2012;

Geffen et al., 2011b). Most published otolith chemistry studies have focused on estuarine and coastal populations, possibly reflecting the greater variability in ambient elemental composition compared to the open ocean (Gillanders and Kingsford, 2000; Gillanders, 2005). The nursery grounds for many commercially important fish species are also found in inshore locations, including plaice (Gibson, 1997).

Otolith microchemical analysis can complement genetic techniques as a method for assessing population structure (Hoarau et al., 2002) and connectivity. Detectable genetic heterogeneity is lost with even low levels of reproductive mixing between populations (Thorrold et al., 2001). Using genetic techniques, populations or stocks with low levels of connectivity or mixing between them will be considered as one, even if the level of connectivity is insufficient to ensure replenishment or population resilience in the event of overexploitation (Cowen and Sponaugle, 2009). Phenotypic markers, such as otolith elemental composition, are useful for distinguishing between populations with limited connectivity, that for management purposes should be assessed separately and can provide greater resolution of the spatial extent of population mixing (Campana et al., 1999).

Although the genetic structuring of plaice in the eastern Irish Sea has been studied (Watts et al., 1999), less is known about plaice stock and population structure in the western Irish Sea (E. Ireland) and the west of Scotland (Nash and Geffen, 2000; Nash et al., 2000). For fisheries assessment purposes, these populations are grouped into larger ICES areas, which may not reflect plaice stock structure in the region (Dunn and Pawson, 2002). Assessments indicate that the Irish Sea is the most important in terms of plaice biomass and landings, whilst plaice on the west coast of Scotland are not formally assessed at this time (Fox et al., 2009). Spawning grounds in the Irish Sea are relatively well defined (Fox et al., 2000), occurring off the west coast of England and Wales and the east coast of Ireland, with a deep water channel separating the two locations (Fox et al., 2009). In western Scotland the location of the spawning grounds is largely unknown at present (Fox et al., 2014).

Spatial variation in growth and maturation (Nash et al., 2000), as well as the movements of tagged plaice (Dunn and Pawson, 2002) and simulated larval dispersal trajectories (Fox et al., 2006, 2009), indicate that sub populations may exist in the Irish Sea. In the event that sufficient region specific differences in elemental composition exist (Chang and Geffen, 2012) in the Irish Sea and the west of Scotland, otolith microchemistry could potentially be used to elucidate plaice population structure and assess connectivity between nursery and spawning grounds (Gillanders et al., 2003; Vasconcelos et al., 2008; Cuveliers et al., 2010).

In the present study the elemental composition of 0–group plaice (*Pleuronectes platessa*) otoliths from west Irish Sea and west Scottish nursery grounds was analysed using solution based Inductively Coupled Plasma Mass Spectrometry (ICP–MS). The objectives were: a) to examine spatial and temporal variation in elemental composition of plaice otoliths at both local (nursery ground) and broader (regional) scales and b) assess the potential for using elemental composition to discriminate between plaice from different nursery grounds and regions and for identifying the juvenile origin of older life stages.

3.2 Materials and Methods

3.2.1 Sampling

Juvenile 0–group plaice were collected from two sites on the east coast of Ireland (using a 5mm beach seine) and from two sites on the west coast of Scotland (using a 2mm Riley pushnet) in August 2009 and 2011 (Figure 3.1). Fish were frozen immediately and stored until further processing. Fish were subsequently thawed, measured (Standard Length – SL) using digital callipers and their otoliths extracted using ceramic forceps. A total of 107 otoliths were analysed (Carradale: 27, Ganavan: 29, Total W. Scotland: 56; Laytown: 23, Portmarnock: 28, Total E. Ireland: 51).

3.2.2 Elemental Analysis (SB-ICP-MS)

All work described below, except weighing, was carried out in a class 100 clean room using Aristar grade chemicals. All equipment and consumables were cleaned with a 10% nitric acid solution before use. Otoliths to be used for analysis were transferred to 2 ml Eppendorf microcentrifuge tubes filled with 18.2 MΩ cm deionised water (DIW) (Elga LabWater, High Wycombe, UK). Samples were sonicated for 3 minutes, in order to loosen any remaining adhering tissue and cleaned following the methods of Swan et al. (2003). The deionised was then siphoned off and replaced by 1 ml of 3% high purity hydrogen peroxide in which the otoliths remained for 10 minutes, before being washed in DI water three times. The hydrogen peroxide step was employed

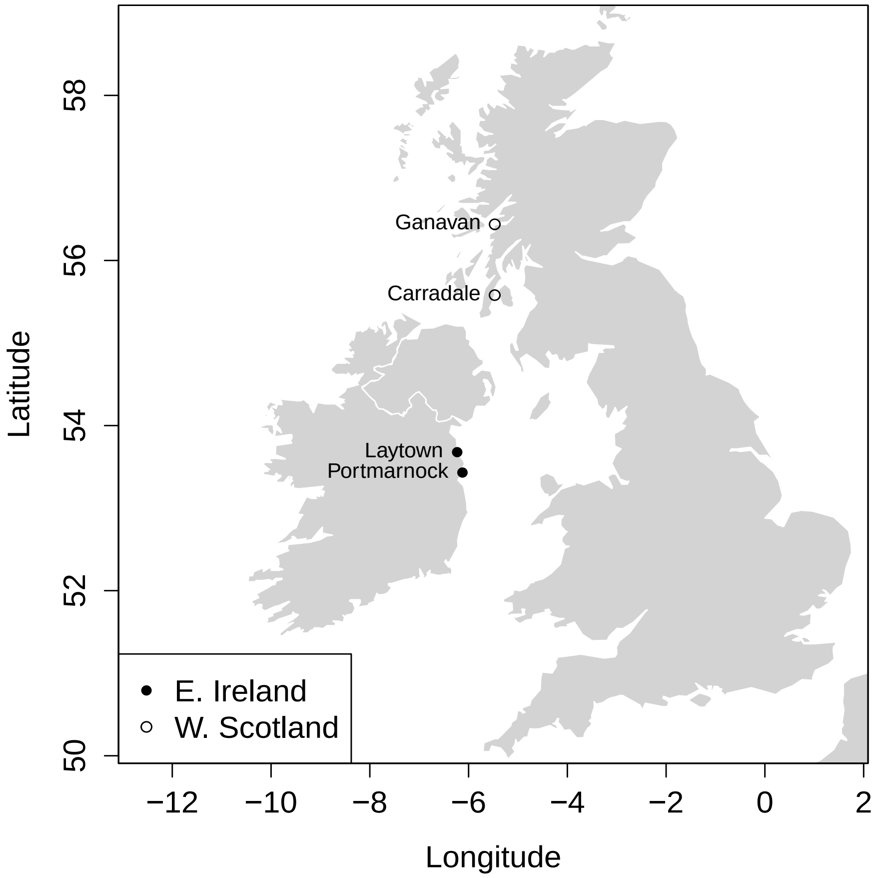

Figure 3.1: Map of sampling sites in E. Ireland and W. Scotland. All sites were sampled in August 2009 and 2011

to ensure that any remaining tissue was completely removed. Finally, the otoliths were acid cleaned in 200 μl 1% high purity nitric acid for 10 seconds before being washed in MilliQ three times. The samples were then dried overnight. Otoliths were subsequently weighed on a glass cover slip using a Mettler Toledo UMX2 microbalance to the nearest 0.1μg. After weighing, the samples were again rinsed in deionised water to remove any surface contamination that may have occurred during the weighing process.

Samples were air dried before being digested overnight with 25% nitric acid in covered Teflon beakers (previously cleaned in Aqua Regia) at 75°C. The certified reference materials (CRM) National Institute for Environmental Studies (NIES) no. 22 Fish Otolith (Yoshinaga et al., 2000) and JCp-1 (Okai et al., 2002) were digested in tandem with otolith samples. Digestion was carried out in batches of up to 36 (30 samples, 2 acid blanks, 100 mg NIES, 2 x 1 mg NIES, 100 mg JCp-1).

Any remaining acid was evaporated off the following day and the samples were subsequently taken up in a previously determined quantity of 2% high purity nitric acid (calculated using sample weight) to matrix match Ca concentrations (± 10 %) with the standard addition added to the calibration standards. All samples were spiked with 5 ppb Rhodium, Bithmuth and Indium (except batch 4 which was only spiked with Rhodium) to serve as internal standards with which to correct for instrument drift and matrix effects. The analytical methodologies of Swan et al. (2003) were followed whereby 5 calibration solutions were prepared using a standard addition technique. Multi element solutions (SPEX CertiPrep Inc. New Jersey, USA), and the internal standards above were spiked to a gravimetrically prepared NIES CRM solution.

3.2.2.1 Instrumentation

All trace elemental analysis was performed on a Thermo Scientific X-Series (II) quadrupole Inductively Coupled Plasma Mass Spectrometer (ICP-MS), equipped with Collision Cell Technology (CCT hexapole mass analyser) and Cetac autosampler. The ICP-MS operating conditions are listed in Table 3.1.

For acid digested otolith samples abundances of ^{7}Li, ^{9}Be, ^{24}Mg, ^{26}Mg, ^{48}Ca, ^{47}Ti, ^{52}Cr, ^{55}Mn, ^{56}Fe, ^{59}Co, ^{64}Zn, ^{66}Zn, ^{65}Cu, ^{63}Cu, ^{85}Rb, ^{86}Sr, ^{88}Sr, ^{111}Cd, ^{138}Ba, ^{137}Ba, ^{208}Pb, ^{206}Pb and ^{238}U were monitored in pulse counting and analogue mode. To account for variation in analyte abundances, an internal cross calibration was carried out to ensure collected data was correctly

Table 3.1: ICP-MS Operating Conditions

ICP-MS Component	Settings
Mass Analyser	Simultaneous Quadrupole Hexapole Collision Cell
RF Power	1388W
Acquisition Mode	Continuous
Mass Range	7 - 240amu
Auxiliary Flow rate	0.70 L min^{-1}
Nebuliser Flow rate	0.86 L min^{-1}
Coolant Flow Rate	13.00 L min^{-1}
Collision Cell Gas Flow rate	3.50 ml min^{-1}

converted between detector modes. The ICP-MS was tuned for 1 hour prior to analysis. Performance checks in Standard Mode (Argon only) were then carried out to check mass calibration, peak widths, peak positions, optimise lens/gas/torch conditions for maximum count rate at ^{7}Li, ^{115}In and ^{238}U and to achieve CeO and BaO oxide ratios of <0.02. A performance check was also carried out in CCT mode (using the 93% He: 7% H_2 gas mixture) to monitor count rates and ensure optimal performance prior to analysis of unknown samples.

Calibration equations were applied to samples using PlasmaLab software. The instrument was re–calibrated every 15 samples. In addition to calibration standards, 'check' standards were run for every analysis batch. These standards were run as unknown samples to monitor any possible instrument calibration drift.

3.2.3 Data Analysis

Inspection of the residuals from the raw data showed that they did not meet the normality or homogeneity of variance requirements. A log transformation was applied and the data was checked for outliers using diagnostic plots, which were removed to normalise the residuals (5-29, depending on element see Table 3.2). Subsequent Shapiro and Levene's tests showed that the concentrations of all elements, except Ca, U, met the normality and homogeneity of variance assumptions. Thus Ca and U elements were excluded from further analysis. A nested ANOVA was performed on each element, in which sites were nested within region and sampling year was included as the interaction term. The discriminatory power of combinations of elements to distinguish between regions and locations was tested using Robust Quadratic Discriminate Function Analysis (RQDFA) in Systat 11 (Systat Software Inc., Chicago, Illinois, USA, `http://www.systat.com`). RQDFA is both robust to violations of multivariate normality as well as violations of equal covariance between discriminant elements, as were found in the present data (Box's M: $p < 0.05$).

3.3 Results

Table 3.2: Summary table of mean concentrations and associated standard deviations (S.D.), standard errors (S.E.) of elements analysed in otolith samples

Element	Mean Conc.	Units	S.D.	S.E.	LOD	Outliers
Li	498.79	ppb	101.50	10.05	0.006	5
Be	29.17	ppb	28.48	2.92	0.009	12
Mg	74.82	ppm	47.83	4.76	0.081	6
Ti	3050.51	ppb	1041.51	105.21	0.095	9
Cr	1621.16	ppb	1223.16	128.22	0.051	16
Mn	5204.90	ppb	1508.25	153.93	0.052	11
Fe	23.71	ppm	15.18	1.53	0.001	9
Co	486.49	ppb	472.73	47.04	0.012	6
Cu	2759.13	ppb	1920.08	212.04	0.130	25
Zn	896.85	ppm	848.70	84.45	0.042	6
Rb	182.63	ppb	74.00	7.84	0.032	18
Sr	1686.75	ppm	286.90	31.12	0.014	22
Cd	72.85	ppb	22.84	2.31	0.008	9
Ba	4023.40	ppb	939.40	106.37	0.091	29
Pb	398.11	ppb	192.85	19.48	0.012	9

Elemental concentrations, associated standard deviations, standard errors, outliers and limits of detection (LOD) for each element are summarized in Table 3.2. Measured average precision and recovery values for the certified reference materials (CRM's) are summarized in Table 3.3. Precision was good for most elements, with the exception of Cr, Mg, Ca and Cu, while recovery rates were good for all elements, except Ti and Cu and Cd, in part likely due to the low sample size used.

Table 3.3: Measured average precision and recovery values of certified reference materials (CRM's)

Element	NIES no. 22 Certified Value	Coral JCp-1 Certified Value	Mean Precision (%)	Mean Recovery (%)
Mg	21±1 mg/kg	1.21 mg/kg	48.8	107.3
Ca	38.8±0.05 %	38.8 (%)	31.9	109
Ti	N/A	15.0 mg/kg	23.0	12.4
Cr	N/A	N/A	44.7	-
Mn	N/A	N/A	14.2	-
Cu	0.74 mg/kg	N/A	28.8	236.1
Sr	0.236±0.005 %	7275 mg/kg	6.8	96.3
Cd	0.0028 mg/kg	0.095 mg/kg	12.7	1071.4
Ba	2.89±0.08 mg/kg	10.0 mg/kg	6.6	99.1

3.3.1 Spatial and temporal variation between and within regions (Nested ANOVA)

The results of the nested ANOVA analysis are summarized in Table 3.4. Significant regional variation in otolith elemental concentrations were found for Ti, Mn, Cd, Ba, Cu, Mg and Sr. Cd, Cu and Mg occurred at significantly higher concentrations in otoliths from the east coast of Ireland compared to the west coast of Scotland, while Ti, Mn, Ba and Sr occurred at higher concentrations in otoliths from W. Scotland. Of the elements that showed regional variation, all except Mg and Sr, also showed significant temporal variation, as indicated by the significance of the main effect (year) or a significant interaction term (region/year; region/location/year).

Table 3.4: Results of single element analyses using nested ANOVA for spatial and temporal differences between and within region

Element	Region	Year	Region/Location	Region/Year	Region/Location/Year
Li	ns	<0.001***	0.098	<0.001***	0.002**
Be	ns	<0.001***	ns	0.013*	0.0037**
Mg	0.0014**	ns	0.046*	0.061.	ns
Ti	0.028*	<0.001***	0.025*	0.059	ns
Cr	ns	<0.001***	0.012*	<0.001***	ns
Mn	<0.001***	<0.001***	0.014*	0.0027**	ns
Fe	ns	0.012*	0.058	0.0019**	ns
Co	ns	ns	ns	<0.001***	ns
Cu	0.024*	0.0064**	ns	<0.001***	ns
Zn	ns	ns	ns	0.014*	ns
Rb	ns	ns	ns	0.0067**	0.025*
Sr	<0.001***	ns	<0.001***	ns	ns
Cd	0.0071**	ns	0.067	0.0032**	ns
Ba	0.034*	ns	ns	ns	<0.001***
Pb	0.078.	0.0018**	0.073	ns	ns

Signif. levels: ***0.001 **0.01 *0.05 ns (non–significant)

Differences between sites within a region were apparent for Ti, Cr Mn, Mg and Sr. Ti, Mn and Cr concentration was highest in Carradale, followed by Laytown, Portmarnock and Ganavan. Cr also exhibited temporal variation between years and between regions (Figure 3.2 and Figure 3.3).

3.3.2 Discriminatory Power of Local and Regional Elemental Signatures

The results of the single element analyses were used to select the combination of elements used in two Robust Quadratic Discriminant Function Analyses (RQDFA). To test the discriminatory power of elemental signatures to classify samples to region, Ti, Mn, Cd, Ba, Cu, Mg and Sr were used.

Table 3.5: Classification success of Robust Quadratic Discriminant Function Analysis using elemental signatures with (*sow*) and without (*nsow*) including standardized otolith weight to discriminate between regions. Correct classification success by chance alone 50%

	E. Ireland	W. Scotland	% Correct^{sow}	% Correct^{nsow}
E. Ireland	18	2	90	90
W. Scotland	2	14	88	69
Total	20	16	89	81

Discriminatory power to correctly assign samples to sites was tested using Ti, Mn, Cr, Mg and Sr. Otolith weight, standardized for fish length by using the residuals of the regression of otolith weight against standard length, was also included in both discriminatory analyses, as a proxy for otolith growth.

Table 3.6: Classification success of Robust Quadratic Discriminant Function Analysis using elemental signatures with (*sow*) and without (*nsow*) including standardized otolith weight to discriminate between sampling sites. Correct classification success by chance alone 25%

	Carradale	Ganavan	Laytown	Portmarnock	% Correct^{sow}	% Correct^{nsow}
Carradale	16	2	0	0	89	83
Ganavan	2	10	1	0	77	62
Laytown	1	1	13	0	87	80
Portmarnock	3	5	0	9	53	59
Total	22	18	14	9	76	71

By chance alone, fish would be correctly assigned to region of origin 50% of the time and to site of origin 25% of the time. Therefore, the discriminatory power of elemental signatures is effectively higher when classifying fish to sites (76% average classification success rate) than to regions (89% average

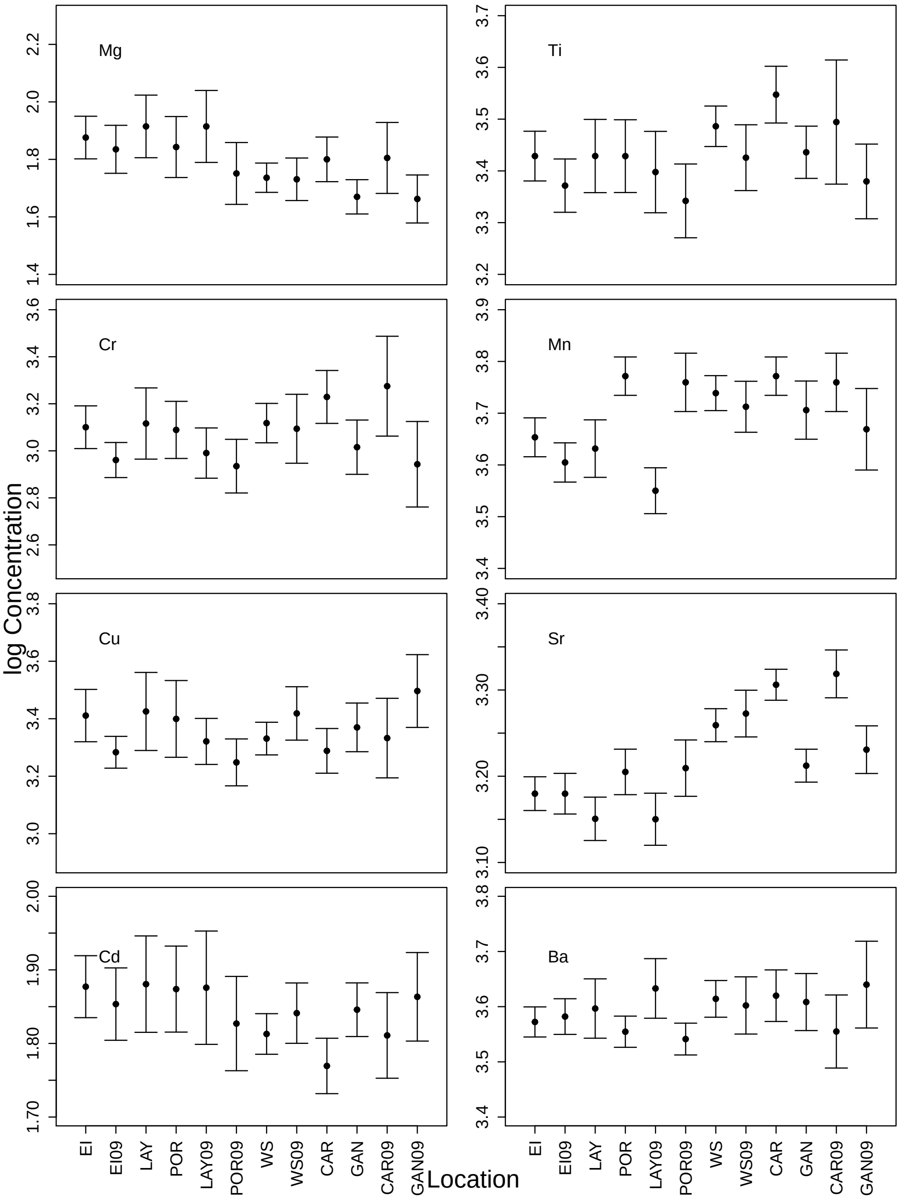

Figure 3.2: Summary plot of regional and site elemental concentration differences in 2009. The 95% upper and lower C.I.'s are shown. Elemental concentrations are the log of the elemental concentration. EI - Eastern Ireland, WS - Western Scotland, LAY - Laytown, POR - Portmarnock, CAR - Carrdale, GAN - Ganavan

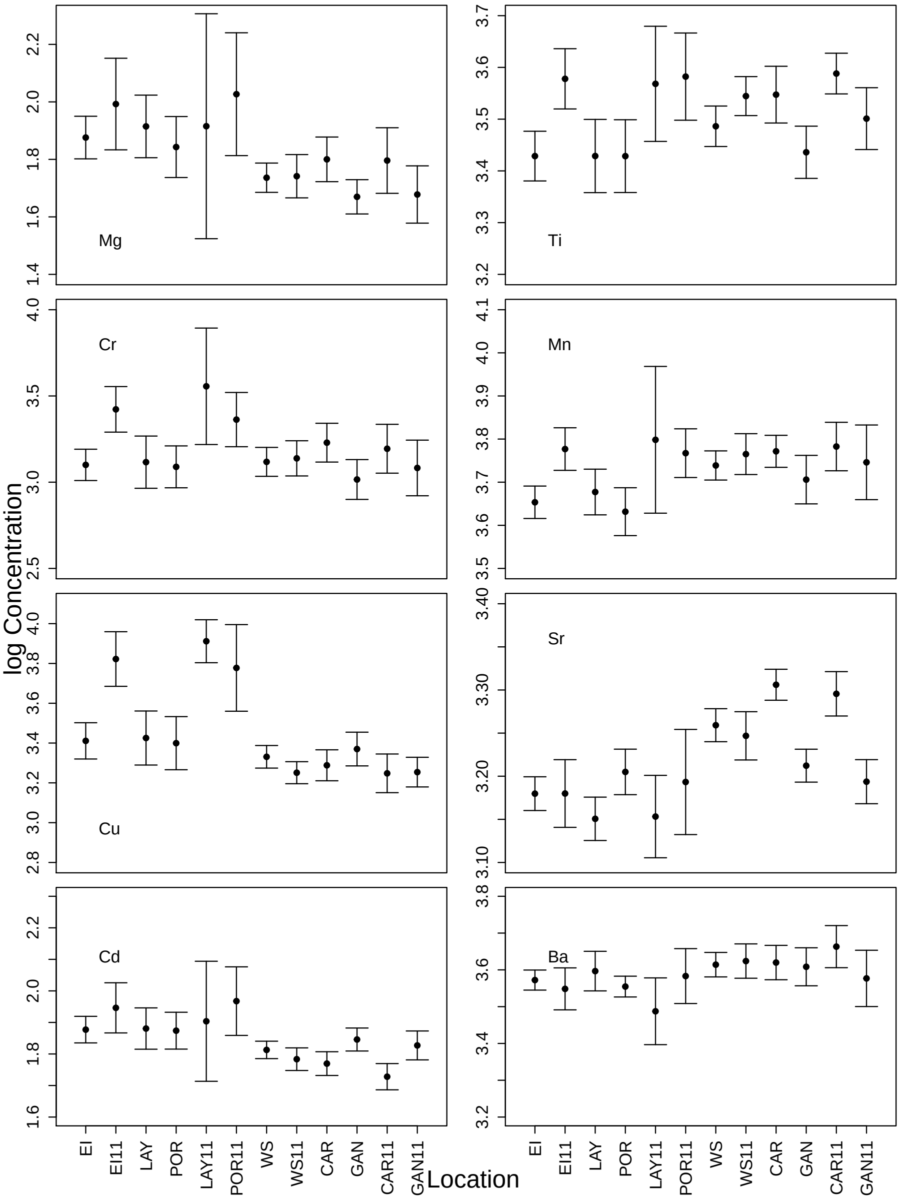

Figure 3.3: Summary plot of regional and site elemental concentration differences in 2011. The 95% upper and lower C.I.'s are shown. Elemental concentrations are the log of the elemental concentration. EI - Eastern Ireland, WS - Western Scotland, LAY - Laytown, POR - Portmarnock, CAR - Carrdale, GAN - Ganavan

classification success rate) (Table 3.5 and Table 3.6). As is apparent from the tables, classification rates varied between sites within both regions.

The inclusion of standardized otolith weight, improved classification success rates (Table 3.5 and Table 3.6). Sr and Mg appear to be the best candidates for tracing the origins of juvenile fish on a regional scale across multiple years. Within regions, Ti, Mn, Cr, Mg and Sr may be useful for characterising nursery grounds, with the caveat that due to temporal variation in some of these elements they should only be used to classify fish of the same year class.

3.4 Discussion/Conclusions

This study found that certain elements present in otoliths showed sufficient variation between and within regions to be useful, in combination, as natural tags to classify plaice successfully on a regional and/or nursery ground scale, although some misclassification did occur. When accounting for classification success by chance alone, classification at the nursery ground scale was more successful than at the overall regional scale. In accordance with previous studies (Chang and Geffen, 2012), Sr and Mg proved to be the most powerful discriminators over regional scales and showed no temporal variation over the two years of the study. In order for the method to be applied to plaice from different years, temporal stability would need to be reconfirmed. Precision and recovery may also be improved using a larger sample size, but this was not possible due to resource restrictions in the present study. Classification success was improved by including a measure of otolith growth, which is consistent with other studies incorporating additional biological information (Geffen et al., 2011a). On a nursery ground scale, Ti, Mn, Cr, Mg and Sr were the suite of elements with the highest discriminatory power, but some of these elements were not temporally stable.

Otolith chemistry has been successfully used to identify the juvenile origin of adult fish (Vasconcelos et al., 2008; Rooker et al., 2001; Cuveliers et al., 2010). To do this the elemental composition of the juvenile core of the adult fish is compared to previously collected juvenile otolith material (Gillanders et al., 2003; Gillanders, 2002a, 2005). If the chemical composition of the otolith varies temporally, so that the juvenile signature is not identical from year to year, such signatures will only be useful for adults from the same year class (Thorisson et al., 2011; Gillanders, 2002b). The method has limited success in areas where fish from many different areas mix (Thorisson et al., 2011), because in this case all possible contributing groups must be characterised (Campana et al., 2000; Gillanders, 2002a; Wright et al., 2006). For resolving juvenile origin in plaice otolith elemental signatures that vary on a larger regional scale (Sr and Mg in the present study), are more useful than those that vary over a smaller local (nursery ground) scale, as it is highly impractical to sample every possible nursery ground.

Incorporation pathways of elements will differ, depending on whether they are associated with precipitation of the mineral or protein matrix (Campana, 1999; Chang and Geffen, 2012). The marine environment in which the fish lives is the main source of these trace (Lin et al., 2007). However, the elemental concentration found in the otolith is not a direct reflection of the ambient water chemistry, because of the variety of pathways and biochemical and physiological controls of biomineralization, which may have a genetic component (Clarke et al., 2011). In addition, diet (Buckel et al., 2004) and other factors such as geological composition (Friedrich and Halden, 2008) can have an effect on the rates at which different elements are incorporated into the otolith. The prey fish consume has been found to account for 25% of calcium(Farrell and Campana, 1996), 10-34% of strontium and 5% of barium found in otoliths (Gibson-Reinemer et al., 2009; Walther and Thorrold, 2006), depending on predator species and habitat (Elsdon et al., 2008). Variations in environmental conditions (Elsdon and Gillanders, 2004), such as salinity and temperature, have also been found to significantly affect otolith elemental composition and can also lead to temporal variability in their concentration in the otolith (Gillanders, 2002a; Cook, 2011). Elemental composition can also be affected by physiological events such as metamorphosis (de Pontual et al., 2003; Chen et al., 2008) and reproduction (Kalish, 1989, 1991), as well as age (Campana, 1999; Kalish, 1989), possibly because of their effects on growth and metabolic rate (Fowler et al., 1995; DiMaria et al., 2010). Thus these physiological influences have been found to outweigh the environmental signal for some elements (Sturrock et al., 2014).

Differences in otolith Sr have been linked to differences in ambient salinity and therefore it is one of the most commonly used elements for discrimination (Kennedy et al., 2000), particularly in areas where there are large differences in salinity (Kraus and Secor, 2004; Macdonald and Crook, 2010). Otolith Sr concentrations have also been linked to temperature (Elsdon and Gillanders, 2004; DiMaria et al., 2010) and are negatively correlated with fish growth rates (Lin et al., 2007; Chen et al., 2008), possibly due to the elements affinity for protein in the blood and endolyph (Borelli et al., 2001; Payan et al., 2004). Due to the low availability of protein in these fluids during periods of slow growth, more Sr is incorporated into the otolith (Sadovy and Severin, 1992, 1994; Brown and Severin, 2009). Because of the interactions between temperature, salinity and growth, the effects on otolith Sr levels of these different factors are difficult to separate (Elsdon and Gillanders, 2004; DiMaria et al., 2010). As with other elements, otolith Sr levels may have a genetic component (Clarke et al., 2011).

Given the multiple influences on Sr concentrations in otoliths, it is difficult to identify the underlying cause of the regional differences observed in the present study. Scottish waters are more saline than Irish Sea waters (OSPAR Commission, 2000), at least offshore, so this may be linked to the higher Sr concentrations in otoliths of plaice from the west coast of Scotland nursery grounds compared to those from eastern Ireland, since the fish did spend considerable time offshore prior to settlement. Differences in ambient water chemistry (Farrell and Campana, 1996; Walther and Thorrold, 2006) and to a lesser extent diet (Gallahar and Kingsford, 1996; Buckel et al., 2004; Chen et al., 2008) have also previously been shown to affect otolith composition and may explain the regional variability seen in this study. Otolith microstructure analysis of fish from the same nursery grounds showed that Scottish fish exhibited significantly slower growth (as indicated by increment widths) than fish from the east coast of Ireland (Chapter 2). These growth differences are consistent with the higher Sr concentrations and lower Mg concentrations in the otoliths of plaice from the Scottish nursery grounds, compared to the east of Ireland nursery grounds, although no correlation was found between the otolith growth measurement (residuals from the regression of otolith weight on length) and Sr or Mg concentrations. An investigation of the chemical composition of the mineral and protein component of the otoliths of fish from the two regions may be worthwhile to elucidate growth effects on otolith elemental composition. The protein component of the otolith is thought to reflect growth (moderated by temperature and feeding), while the mineral component is thought to reflect mainly temperature effects, although this is still to be demonstrated (Dr Steve E. Campana, personal communication).

At the nursery ground scale, the differences in Ti and Cr concentration may indicate spatial variability in these heavy metals, arising both from natural variability and anthropomorphic inputs (Geffen et al., 1998). Significantly higher concentrations of these elements were found in otoliths from Carradale, in the Firth of Clyde and in otoliths from the Irish Sea (Laytown and Portmarnock close to Dublin), compared to Ganavan in the Atlantic. On the regional scale, higher concentrations of Cd and Cu were found in otoliths from the east coast of Ireland. This is in accordance with previous studies, reporting elevated heavy metal levels in the Irish Sea close to sources of anthropomorphic contamination, such as the Dublin Bay, the North Channel and Liverpool Bay (Laslett, 1995; Service et al., 1996) and the occurrence of such heavy metals in the surficial sediments of the north-west Irish Sea (Charlesworth et al., 1999). The significant differences in Ba concentration in juvenile plaice otoliths from nursery grounds on the east coast of Ireland and the west coast of Scotland, may be an indication of geological differences between these areas (Friedrich and Halden, 2008). Areas of high primary production and significant freshwater input also tend to exhibit high Barium concentrations (Chang and Geffen, 2012) and incorporation into the otolith also affected by salinity (De Vries et al., 2005; Martin and Thorrold, 2005). Consistently, Carradale exhibited the highest Ba concentrations of all sites, possibly due to the presence of numerous fresh water inputs into the Firth of Clyde.

This study demonstrates that regional differences in otolith elemental composition could be used together with other markers, such as otolith increment widths, to identify the juvenile origin of adult plaice, and assist in establishing the extent of connectivity between plaice populations in the western Irish Sea and the west of Scotland. The temporal stability of such signatures must however be taken into account, requiring validation for each year class. Smaller scale movements, within regions and between nursery grounds, will also need to be taken into account when assessing connectivity. Differences in elemental composition between the nursery grounds in each region, found in the present study, may be useful to trace small scale movements of fish of the same year class during their time on the nursery grounds or even assess movements of fish between nursery grounds in each region, during that time period (Fodrie and Herzka, 2008). Because of the large number of plaice nursery grounds which could supply recruits to the adult populations, it remains challenging to use otolith element chemistry to apportion adults to their nursery ground origins, as not all have been characterised or are known. However, a large number of nursery grounds have been identified on the west coast of Scotland and the east and west coasts of Ireland (Fox et al., 2007; Haynes et al., 2012; Fox et al., 2014). Among these sites, those with the highest average abundances of juvenile plaice have also been identified. While this metric does not necessarily correlate with the greatest contribution to the adult stock, sites of low abundance are less likely to be major contributors. Thus future work should aim to microchemically characterise the major nursery grounds identified to date. In the meantime however, passive dispersal pathways used to reconstruct temperature histories in a previous study (Chapter 2, Figure 2.2b and Figure 2.2c), suggest that juveniles from the western Irish Sea and western Scotland probably originate from different spawning grounds. This may in future be confirmed by using laser ablation ICP-MS on juvenile plaice otoliths, as previously done for herring (Geffen et al., 2011a). While the misclassification pattern found, has previously been indicative of exchange between populations (Tanner et al., 2012) and this would be consistent with the results of Fox et al. (2009), which suggested a small degree of mixing between otherwise separate populations, this is unlikely the case here. Rather, the present misclassification pattern is more likely to result from similar environmental conditions experienced once on the nursery ground, reflected in similar otolith composition.

Regardless, elemental signatures may be useful to find the missing link, tracing the adult fish back to their respective juvenile origins. The present study suggests that otolith elemental composition can be a useful tool in the future to provide further insight into plaice population connectivity in the western Irish Sea and the west of Scotland. Such information is useful to fisheries management, as it provides unique information on the spatial distribution at the population and life stage level, improving our understanding of the integrity of these populations (Campana, 1999), allowing for assessment and management of fisheries to be adjusted accordingly.

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Chapter 4

Elucidating probable plaice spawning grounds and the influence of behaviour and growth on successful settlement in western Ireland

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This chapter is under review for publication as Zölck, M., Brophy, D., Mohn, C., Minto, C., McGrath, D. Bio-physical model provides insight into dispersal of plaice (*Pleuronectes platessa* L.) from putative spawning grounds to nursery areas on the west coast of Ireland. *Journal of Sea Research*

Abstract

In this study an individual-based coupled physical biological model (ICPBM) is used to reconstruct the dispersal pathways of 0–group juveniles collected from nursery grounds in Galway Bay and to identify probable spawning ground locations for plaice on the west coast of Ireland. The relative importance of passive transport, behaviour and individual growth rates on successful larval delivery, from three putative spawning grounds to suitable nursery areas, was also investigated. Using a hydrodynamic Regional Ocean Modelling System (ROMS), combined with a particle tracking model, three model scenarios were tested: a passive tracer scenario (PTS), a linear growth scenario (LGS) and a temperature-dependent growth scenario (TDS). Hydrodynamic conditions were modelled and biological information (pelagic larval durations and size at settlement) incorporated. The LGS and TDS included vertical migration and tidally synchronised behaviour. Generalized Linear Model (GLM) comparisons showed that incorporation of behaviour and temperature-dependent growth, resulted in approximately two to three times more particles being delivered to sites of suitable depth for settlement ($\leq$10m), compared to passive transport alone ($p < 0.001$, LGS 19–78%; TDS 40–81%). The probability of successful delivery also varied significantly depending on the location, year and week of release ($p < 0.05$). A comparison of temperature histories between particles that were delivered to shallow inshore areas and those that failed to reach depths suitable for settlement indicated that dispersal to coastal nursery areas is facilitated by entrainment into a cool coastal current system. This study identified a probable plaice spawning area in western Ireland and reconfirms the importance of including behaviour and growth in dispersal simulations. The model results suggest that differences in growth can influence larval delivery to potentially suitable nursery areas.

Keywords: Individual-based physically coupled biological model (ICPBM); *Pleuronectes platessa*; Dispersal; Temperature effects; Growth; Behaviour

4.1 Introduction

For plaice stocks that support major commercial fisheries, such as those in the North Sea, a considerable amount of information is available on their biology, life history, location of spawning and nursery grounds and the extent of connectivity between them (Amara et al., 2001; Hinz et al., 2005; Jager, 1999; Modin et al., 1996; Hunter et al., 2003; Bolle et al., 2009). Plaice populations on the west coast of Ireland are less well understood; although nursery ground studies have provided information on early life history (Allard, 2006; Allen et al., 2008; Haynes et al., 2012; De Raedemaecker et al., 2012; Comerford et al., 2013), spawning ground locations are currently unknown. Inferences on their location have been derived from spawner surveys carried out by the Irish Marine Institute (Gerritsen, 2010). As a consequence, no explicit management plan or objectives are in place for the region at the present time (Marine Institute Stock Book 2011, `http://hdl.handle.net/10793/669`). Plaice on the west coast of Ireland (ICES Divisions VIIb, c) are caught as by-catch in the mixed demersal fishery, mainly by Ireland, France and the UK. According to ICES advice, plaice in this area are considered a data limited stock, as catches from the area are currently to low too justify collection of the necessary information needed to assess stock status, with no qualitative evaluation of fishing mortality or Spawning Stock Biomass (SSB) (ICES, 2012). Therefore, landings are to be reduced by 20% from the last three years to 30 tonnes, as a precaution (ICES, 2012). Due to the lack of information on stock size or rate of exploitation, it is impossible to know if this reduction will be effective to ensure the sustainable exploitation of the population. Identifying spawning ground locations in the region, evaluating their connectivity to known nursery grounds and elucidating factors influencing variability in larval delivery and thereby recruitment, are an important piece of information required to eventually allow assessment and management decisions to be made.

The life cycle of plaice is characterised by pelagic egg and larval stages and demersal juvenile and adult stages (Gibson, 1994, 1997). Pelagic eggs and larvae are transported from offshore spawning grounds to inshore coastal areas via a combination of passive, active and selective tidal stream transport (De Veen, 1978; Rijnsdorp et al., 1985; Jager, 1999), where they metamorphose from the pelagic to the demersal form and settle onto shallow nursery areas (Gibson, 1997, 1999). While passive transport, whereby eggs and larvae drift with the residual and wind induced currents, has been shown to play a major role in transport over large distances from the offshore spawning grounds to inshore areas (Nielsen et al., 1998; de Graaf et al., 2004), retention there and immigration into nursery grounds requires the larvae to actively facilitate this process (Fox et al., 2006). The larvae accomplish this by exhibiting active swimming behaviours, both horizontal and vertical, which are tidally synchronised (selective tidal stream transport), allowing them to swim faster than or against the prevailing currents (up to three body length per second for horizontal swimming; Arnold (1969)) and move up and down in the water column and ingress into the nursery areas with the tide (Bolle et al., 2009; Fox et al., 2006; Rijnsdorp et al., 1985).

Variation in circulation patterns and wind conditions (Nielsen et al., 1998) can lead to large interannual changes in the transport of larvae and their concentrations near nursery areas; this variability increases with distance from the spawning grounds (Van der Veer et al., 1998). The quality and quantity of egg production (Nash and Geffen, 1999; Gibson, 1994), mortality during the pelagic stage (Fox et al., 2000; Van der Veer et al., 2000) due to predation (Ellis and Nash, 1997) or lack of food availability (Anderson, 1988; Leggett and DeBlois, 1994), as well as the influence of temperature (Van der Veer et al., 1990; Van der Veer and Witte, 1999; Fox et al., 2000) and hydrodynamic conditions (Van der Veer et al., 1998; Oshima et al., 2010), can further increase variability in larval concentrations reaching nursery areas. Interannual variability in hydrodynamic conditions can affect the survival of pelagic larvae and juveniles of many flatfish species, including plaice, and has been shown to account for some of the variability observed in year class strength and thus recruitment (Van der Veer et al., 2000).

Elucidating population connectivity for species with such complex life cycles, requires knowledge of the origin of eggs and larvae and their dispersal trajectories (Pineda et al., 2007). Due to the difficulty of directly following the small pelagic stages, a substantial amount of our present knowledge on population connectivity, dynamics and larval dispersal has been obtained indirectly, through inference from differences between populations identified using genetic, molecular or microchemical techniques (Taylor and Hellberg, 2003; Hedgecock et al., 2007; Bradbury et al., 2008; Gillanders, 2005; Thorrold et al., 2007). Tagging studies have also been useful in assessing fish movements and connectivity between populations (Jennings et al., 1993; Hunter et al., 2003, 2004; Metcalfe, 2006), as they provide a more direct measurement. However, not only is this technique very labour intensive and expensive, requiring a large number of individuals to be tagged to achieve a sufficient recapture rate (Thorrold et al., 2002; Cowen and Sponaugle, 2009), but it is also limited in its usefulness due to the size of the tags, making the marking of the early life stages of marine organisms difficult or impossible (Gawarkiewicz et al., 2007; Cowen and Sponaugle, 2009).

Individually Based Coupled Physical Biological Models (ICPBM) bridge the gap between indirect and direct methods of measuring connectivity between populations, life stages and spawning and nursery grounds (Savina et al., 2010; Werner et al., 2007). These models are particularly suited to quantifying population connectivity, because larval dispersal is an inherently bio–physical process, involving physical oceanographic transport and biological processes. Larval behaviour, mortality and timing of reproduction (Gawarkiewicz et al., 2007; Gallego et al., 2007) have all been shown to influence transport and dispersal patterns (Fox et al., 2006, 2009; Leis, 2007; Fiksen et al., 2007; North et al., 2009).

Using ICPBM to understand population connectivity is of particular value, because they allow us to identify the scales over which populations or different life stages are connected to each other (Palumbi, 2004; Cowen et al., 2006). At the same time they can assist in the identification of population sources (spawning grounds) and nursery areas, quantify their connectivity (Le Quesne and Codling, 2009) and provide estimates of their contribution to the population (Jones et al., 2007; Fogarty and Botsford, 2007; Fox et al., 2009; Bergman et al., 1988). This is of particular importance to fisheries management, as in order for any management plans to be effective, they need to be scaled to take into account spatial and temporal connectivity (Cowen et al., 2006; Treml et al., 2008; Botsford et al., 2009). Only then is it possible for protective measures, such as Marine Protected Areas (MPA's) to be effective (Palumbi, 2003; Cudney-Bueno et al., 2009). Spatial fisheries management through MPA's requires knowledge of the scale of connectivity, taking account of dispersal distances (Botsford et al., 2009), to enable sufficient exchange between populations to ensure resilience and persistence (Kinlan et al., 2005; Cowen and Sponaugle, 2009).

ICPBM's have proved useful for simulating larval dispersal pathways for plaice and other species in the North Sea (Van der Veer et al., 1998, 2009; Savina et al., 2010; Lacroix et al., 2012) and the Irish Sea (Van der Molen et al., 2007; Fox et al., 2006, 2009). In the present study, the method was applied to plaice on the west coast of Ireland. The objectives of the study were

a) to identify probable plaice spawning ground locations by reconstructing the dispersal pathways of 0–group juveniles collected from nursery grounds in Galway Bay and b) to investigate the relative importance of passive transport, behaviour and individual growth rates on the successful delivery of larvae, from putative spawning grounds to suitable nursery areas.

4.2 Materials and Methods

4.2.1 Biological information

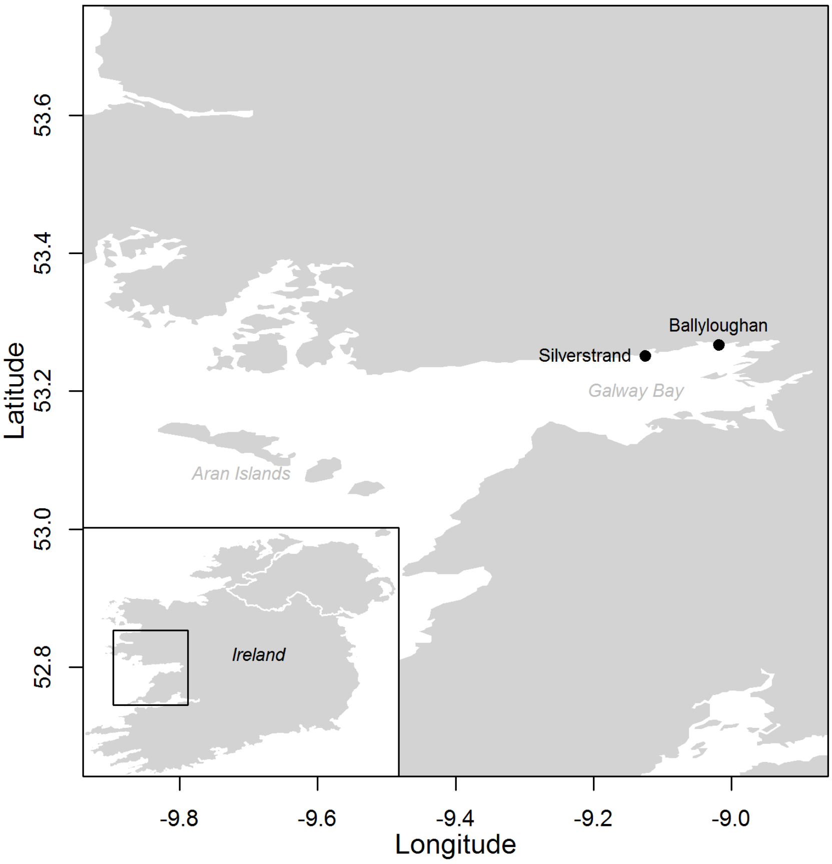


Figure 4.1: Location of sampled nursery grounds where plaice juveniles were collected in 2003 and 2005, providing the biological information incorporated into the models

Early life history information (Pelagic larval duration (PLD), hatch dates, size at settlement, see Table 4.1), was obtained from previous otolith microstructure investigations (Allen, 2004; Allen et al., 2008; Allard, 2006) of juvenile plaice collected from two nursery grounds in Galway Bay (Silverstrand and Ballyloughan), in 2003 and 2005 (Figure 4.1).

As the spawning the ground locations that supply larvae to Galway Bay nursery areas were unknown, three potential spawning areas - termed release areas (Figure 4.2; RA1, RA2 and RA3), were selected based on the locations where spawning female plaice were collected during surveys carried out by the Irish Marine Institute from 2004–2009 (Hans Gerritsen unpublished data; Gerritsen, 2010). These areas spanned an overlapping east-west range associated with the estuary of Galway Bay.

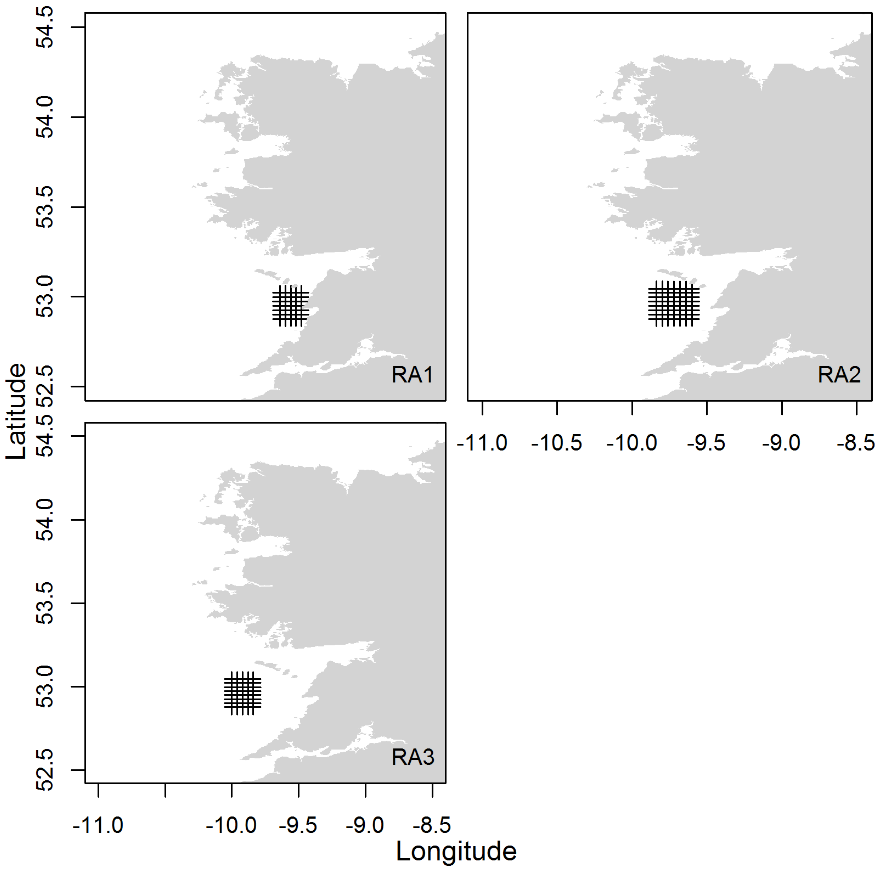


Figure 4.2: Location of proposed spawning/release areas for particle tracking experiments. RA1–Release Area 1, RA2–Release Area 2, RA3–Release Area 3

4.2.2 Model system set–up

Physical forcing fields of currents and temperature for the particle drift simulations were produced using the hydrodynamic circulation model ROMS (Regional Ocean Modelling System; Shchepetkin and McWilliams, 2005).

Table 4.1: Summary table of average values for mean pelagic larval durations (PLD), settlement size (SS) and linear growth scenario (LGS) and temperature-dependent scenario (TDS) mean growth rates (mgr) for the years 2003 and 2005 (Allen, 2004; Allen et al., 2008 and Allard, 2006)

Year	**Mean PLD (days)**	**Mean SS (mm)**	**LGS mgr (mm/day)**	**TDS mgr (mm/day)**
2003	32.58	12.13	0.16	0.14
2005	30.13	16.26	0.31	0.15

The model domain covered Galway Bay and the western Irish shelf from -13 to -9°W and 51 to 55 °N respectively. The model horizontal resolution was 2.5km and included 20 terrain following vertical levels. ROMS was spun up for a full climatological year to ensure a quasi-steady state prior to simulations of physical conditions during the specific target years 2003 and 2005. Forcing and initialisation were based on climatologies for atmospheric forcing (COADS, Comprehensive Ocean-Atmosphere Data Set, `http://icoads.noaa.gov/`) and temperature and salinity initialization (WOCE Ocean Atlas 2005, NOAA National Oceanographic Data Center, `http://www.nodc.noaa.gov/OC5/WOA05/woa05data.html`;Locarnini et al., 2006; Antonov et al., 2006) and the spin up did not include tidal forcing. Results for the years 2003 and 2005 were obtained by restarting the ROMS model from the climatological spin-up run and adding tidal forcing from the TPX0-6.2 OSU inverse tidal model (Egbert and Erofeeva, 2002).

The physical model was then run for five months (January—May) for each study year under 2003 and 2005 tidal and wind conditions. This time period was chosen because it encompasses the reported hatch dates, PLD and settlement times for Galway Bay (Allen et al., 2008), including average egg development time. Hourly averages of modelled physical fields (currents, temperature, sea surface height and salinity) were saved for the full simulation period in each year, serving as input for the particle tracking experiments.

LTRANS (Larval TRANSport Lagrangian Model v1; Schlag et al., 2008), a 3D off–line particle tracking model was used to simulate egg and larval dispersal patterns of plaice with the saved predictions of the hydrodynamic model. The LTRANS code was adapted to simulate different planktonic stages of plaice eggs and larvae. LTRANS included a 4th order Runge-Kutta scheme for particle advection and a random displacement model for vertical turbulent particle motion (Schlag et al., 2008). The model also included different species specific formulations of larval behaviour. These formulations were extended by implementing behavioural characteristics for plaice eggs and larvae, as described in the particle tracking experiments section.

4.2.3 Physical model validation

Daily, gap-free composites of sea surface temperature (SST) were extracted from the global OSTIA reanalysis product (Stark et al., 2007), available from the MyOcean data catalogue (`http://www.myocean.eu`). The OSTIA SST reanalysis incorporates both remote sensing and in-situ data at a spatial resolution of 0.05° in longitude and latitude. Daily OSTIA SST data were compared with corresponding SST data from the model for the period 1st January to 31st March 2005. The modelled SST's were interpolated to match the horizontal OSTIA grid. 90 day averages for OSTIA and modelled SST's are presented in Figure 4.3a and b respectively. Both data sets indicated a sharp offshore SST increase west of Ireland constituting a frontal system known as the Irish Shelf Front (ISF). The ISF separates tidally and wind mixed shelf waters from the oceanic waters of the NE Atlantic (Huang et al., 1991; McMahon et al., 1995; Raine and McMahon, 1998). The ISF exists year-round and is centred at 11°W between the 100 and 150 m depth contours, but frontal gradients associated with the ISF may experience considerable short-term and inter-annual variability (Huang et al., 1991; Nolan and Lyons, 2006). Thus, a more systematic model-data comparison was carried out by calculating two established model skill parameters, i.e. the root mean square (RMS) error and the cost function CF. The RMS error was defined as:

$$RMS = \sqrt{\sum \frac{(D-M)^2}{N}} \tag{4.1}$$

where D and M represent observed and model data, respectively and N is the number of data values (N = 90, corresponding to 90 daily composites at every grid point). CF is the mean absolute error relative to the standard deviation σ_D of the observed data and was defined as:

$$CF = \frac{\sum |M-D|}{N \times \sigma_D} \tag{4.2}$$

CF is a score-based measure of the goodness of fit between model and observed data and indicates very good (CF < 1), good (CF = 1 - 2), reasonable (CF = 2 - 3) or poor (CF > 3) model performance (Radach and Moll, 2006; Wan et al., 2012). The model tended to generally underestimate observed SST values, but RMS errors varied considerably between coastal (1.5 - 2.0 °C) and offshore shelf waters (0.2 - 0.8 °C). However, the RMS error mostly lay within the OSTIA SST error range indicating that the OSTIA SST uncertainty estimates significantly contribute to the model-data differences (Figure 4.3c, d). The goodness of fit between model and observations was very good to reasonable over most of the domain (Figure 4.3e). The high CF values in some coastal areas could be partly explained by limitations of the model setup (e.g. freshwater discharge through major rivers was not explicitly included). In these areas the modelled SST averages were in the range

7 - 8°C, whereas OSTIA SST values never fell below 8.2 °C. In-situ winter SST values of 6 - 8 °C have been measured regularly at individual locations along the west coast of Ireland (e.g. O'Donohoe et al., 2000) indicating that the modelled SST values in near-coastal areas are not entirely unrealistic.

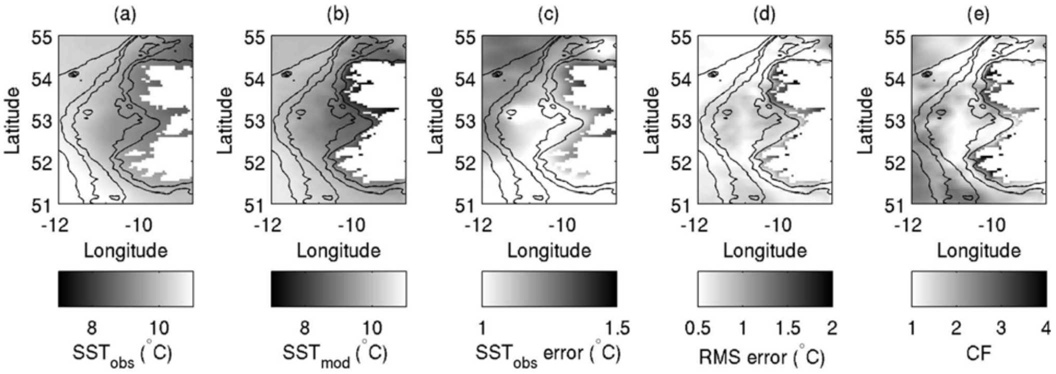


Figure 4.3: Model-data comparison using daily composites of the OSTIA SST reanalysis product (Stark et al., 2007) for the period 1st January – 31st March 2005. (a) 90 day average of OSTIA SST(°C), (b) 90 day average of model SST (°C), (c) Estimated error standard deviation of OSTIA SST (°C), (d) RMS error (°C), (e) cost function CF. The 50 m, 100 m, 150 m, 200 m and 500 m depth contours are indicated

Depth-averaged velocity vectors and current speed for the same period are presented in Figure 4.4. The circulation in coastal waters west of Ireland is dominated by the Irish Coastal Current (ICC). The ICC is a persistent jet-like flow with typical current speeds between 6 and 20 cm s^{-1} (Raine and McMahon, 1998; Fernand et al., 2006). The ICC was well represented in the model following the coastline onshore the 50 m depth contour with current speeds in the range of 5 - 15 cm s^{-1}. The strongest residual currents (20 cm s^{-1}) are found in the narrow channels connecting Galway Bay to the Irish shelf. This area is dominated by tidal dynamics and measurements by White (1996) across the North Sound revealed strong differences in instantaneous current speeds during flood tide (up to 45 cm s^{-1} into the bay) and ebb tide (up to 10 cm s^{-1} out of the bay). The circulation on the shelf was marked by predominantly southward flow between the 100 and 150 m depth contours in the model (Figure 4.4). Corresponding winter observations are sparse, but the results of Fernand et al. (2006) suggest the presence of southward flow in the top 40 m west of the ICC in summer. This was largely confirmed by model results from Holt and Proctor (2008). In contrast, model simulations of spring conditions by Lynch et al. (2004) showed a different situation with weak and predominantly eastward currents on the shelf. Due to limitations of available

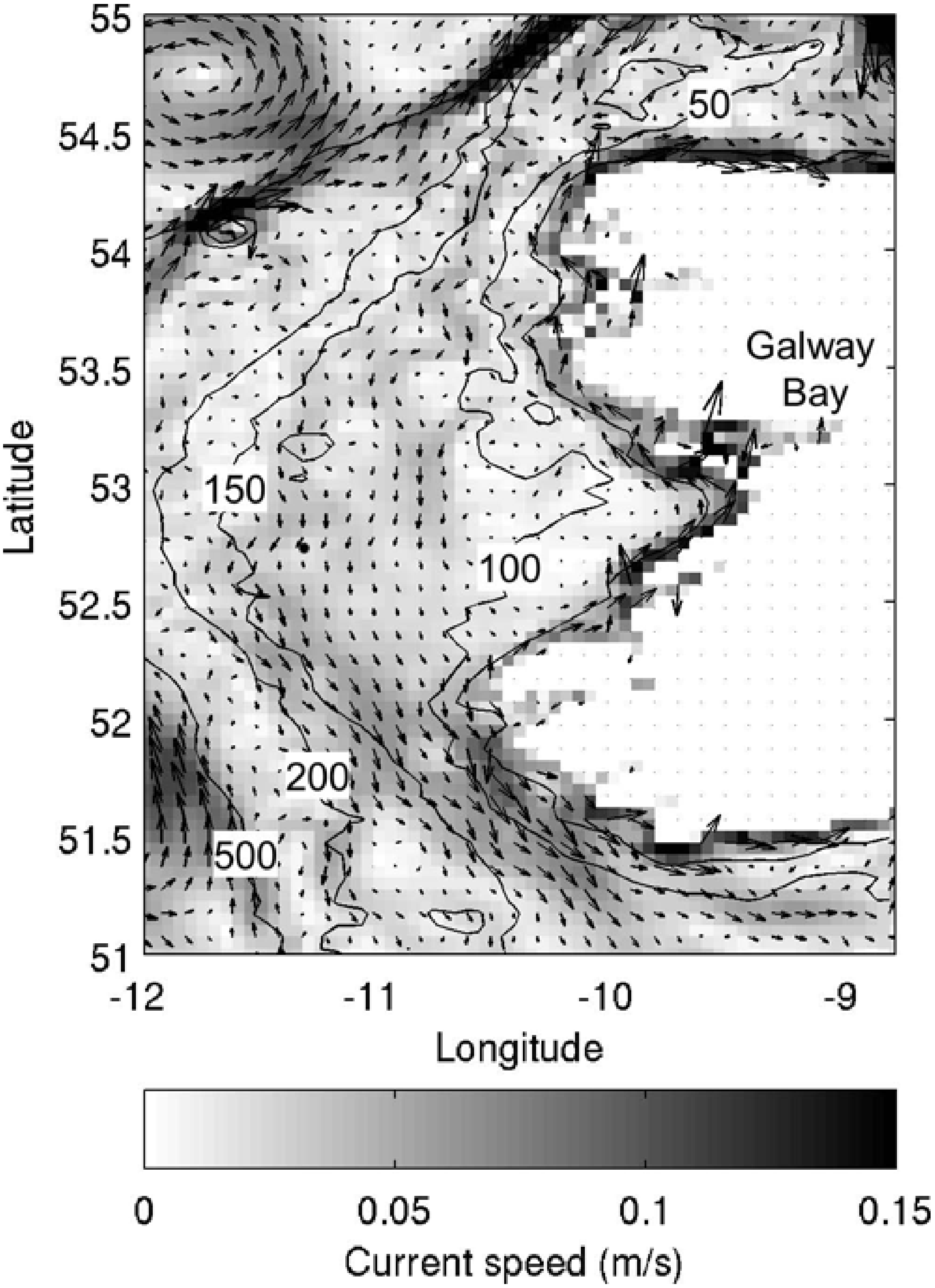


Figure 4.4: Modelled 90 day average of the depth-integrated shelf and coastal circulation west of Ireland. The 50 m, 100 m, 150 m, 200 m and 500 m depth contours are indicated

computational resources we did not consider a coherent simulation covering the full 2003 – 2005 period. Instead, each individual simulation period was started from the same climatological 1 year spin-up using T/S climatologies, monthly averaged wind fields and tidal forcing. Thus, the model was generally capable of reproducing the major circulation features and frontal structures in the study area with sufficient realism, but propagation of mesoscale baroclinic instabilities from the eddying far-field ocean was not represented.

4.2.4 Particle tracking experiments

Three models representing different individual based behaviour scenarios were run for each of the study years. In each of these scenarios, particles were released from our three potential spawning or release areas (Figure 4.2; RA1, RA2 and RA3). The scenarios carried out for each spawning area and year were as follows:

1. Passive tracer scenario (PTS): All particles were assumed to be passive without behavioural or growth characteristics.
2. Linear larval growth scenario (LGS): Larvae were assumed to grow linearly without temperature-dependent growth.
3. Temperature-dependent larval growth scenario (TDS): Larval growth was assumed to be temperature dependent.

The LGS and TDS included behavioural characteristics as described in Fox et al. (2006) and Fox et al. (2009) with minor modifications (Table 4.2; detailed below).

Table 4.2: Summary table of behavioural characteristics included in temperature-dependent (TDS) and linear growth (LGS) model scenario. Diel and tidally synchronized vertical movement indicating vertical movement rates in mm per second, where positive values indicate ascent and negative values indicate descent (from Fox et al., 2006)

Larval length (mm)	**Light + rising tide**	**Dark + rising tide**	**Light + falling tide**	**Dark + falling tide**
7–9	+5	−5	+5	−5
9–10.5	+5	+5	−5	−5
10.5–11	−10	−10	−10	−10

Egg duration (ED) in days was calculated as:

$$ED = \alpha + \beta \times log(T) \tag{4.3}$$

where $\alpha = 43.853$, $\beta = -14.427$ and T is the average temperature on day of hatching. Eggs drift passively with a positive buoyancy of 1 mm s^{-1} (LGS and TDS).

Larvae in the linear growth model: A starting length of 7 mm after hatching was defined (Fox et al., 2006). The larval stage started at the end of the egg stage. Linear larval growth rate (LGR) (mm day^{-1}) was calculated as:

$$LGR = L/t \tag{4.4}$$

where

$$L = LH + (mgr \times (t - t_{egg})) \tag{4.5}$$

where L is larval length, LH is larval length at time of hatching (7 mm), mgr is mean growth rate (mean settlement size − LH / mean larval duration) (Table 4.2), t is model time in decimal days and t_{egg} is egg duration prior to hatching. LGR was updated at every model time step (LGS). In this scenario, larvae increased in size at a fixed rate throughout the larval phase. The growth rate used was based on estimates of larval duration and size at settlement from otolith microstructure analysis of 0–group plaice collected from nursery grounds in the study area in the year of the model run. Growth rates in this scenario therefore reflect approximate early life histories for some portion of the population that survived the larval phase in that year but are not necessarily representative of population mean growth rates.

Larvae in the temperature-dependent growth model had the same starting length and larval stage commencement as in the linear growth model but here larval growth rate was temperature-dependent and was calculated according to:

$$TDGR = 4/12.281e^{(-0.092T)} \tag{4.6}$$

where T is the ambient temperature at each particle location and time step (adapted from Fox et al., 2006, personal communication Richard M. Nash and Clive J. Fox). This value was updated every time step (TDS). In this case, growth rates were allowed to fluctuate according to the temperature experienced along the drift trajectory and so varied between individual particles.

In scenarios 2 and 3, the larvae carried out a daily vertical migration during their early life stages between 7 and 10.5 mm in length, based on light conditions (time of day). Night time was defined to be between 5pm and 8am (winter conditions). During the night particles migrated downwards (5 mm s^{-1}), during the day they migrated upwards (5 mm s^{-1}) (Fox et al., 2006).

Tidally synchronised behaviour (vertical swimming) started at a length of 9mm (Fox et al., 2006). Particles rose in the water column with the rising tide and descended with the falling tide at a rate of 5 mm s^{-1}. At lengths > 10.5 mm, vertical migration was water depth dependent (Fox et al., 2009). Vertical swimming stopped at a size of 10.5mm if the larvae had reached waters of less than 20 meters depth, otherwise it continued (LGS and TDS).

In each scenario, each model cell in each respective spawning area was seeded with a particle (egg). All particles were released at a model depth a 25 m according to Fox et al. (2009). The spawning season was split into 7 separate periods of 5 days. Particle release commenced at midnight of the 1st of January of every year and was repeated every 5 days over a period of 31 days. This release strategy was chosen because plaice are batch spawners (Rijnsdorp, 1989), with the average female in spawning condition for only five weeks, between the end of January and the beginning of March. A spawning peak is reached in mid January, with batch spawning related to an ovulatory periodicity of 1–4 days (Rijnsdorp, 1989; Rijnsdorp and Witthames, 2005). During each of these particle releases, 35 particles were released in RA1, 56 in RA2 and 40 in RA3, depending on the size of the release area, so that one particle per model grid point was released. Thus 1470 were released in RA1, 2352 in RA2 and 1680 in RA3 respectively. These numbers are similar to those used by Fox et al. (2006, 2009). The particle tracking model was integrated forward for a total of 46 days for each spawning area and spawning period with a time step of one hour. An integration period of 46 days was chosen to accommodate both, egg and larval duration period (Table 4.1). This procedure provided at total of 7 data sets for each spawning area and year. Each of these data sets contained hourly values of position (longitude, latitude), depth, temperature and salinity for each particle over the 46 day period.

4.2.5 Data Analysis

The larval dispersal pathways were plotted for each year by model scenario and spawning/release area. As settlement areas for plaice are usually found in shallow waters (Gibson et al., 1993; Beyst et al., 2001), particles that at the end of the model run had reached a water depth of 10m or less, were considered to have successfully settled. To quantify rates of successful delivery for each model/spawning area combination, larval ratios were calculated by dividing the number of particles at the end of the model run by the total number released for each spawning area.

Two Generalized Linear Models (GLM) using a binomial distribution (MacCullagh and Nelder, 1989) were constructed in order to assess the importance of model scenario, spawning/release area and release week on the proportion of particles that were delivered to sites suitably shallow for settlement. The model was parameterized so that y_i is the observed number of successfully settled larvae (particles delivered to water $\leq$ 10m) on release i; n_i is the total number of particles released on release i:

$$y_i \sim \text{Bin}(n_i, p_i), \tag{4.7}$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = \mathbf{x}_i'\boldsymbol{\beta}, \tag{4.8}$$

where Bin is the binomial distribution, p_i is the probability of success for the i^{th} release, which depends on the vector of covariates $\mathbf{x}_i$ and parameters $\boldsymbol{\beta}$ on the logit scale. The covariates included: model scenario, release area and release week.

All possible model combinations of these variables including their interactions were fit and the best model was chosen according to the Akaki Information Criterion (AIC) (Zuur et al., 2009). Potential under or over-dispersion, relative to the binomial assumption, was investigated by testing the residual deviance on a χ^2 distribution with the residual degrees of freedom. In both years the best model included the following terms: model scenario, release area, release week. In 2005 the interactions between model and release area and release area and release week were also included.

In order to assess differences between the LGS and the TDS scenario only in each year, the above model selection process was repeated, excluding the PTS scenario. The GLM models for both years contained the following common covariates: model scenario, release area, week. The 2005 model also contained the model scenario release area interaction.

For each particle, temperatures on each day of release were summed over the trajectory to provide estimates of cumulative degree day (CDD) over the whole model run. For each scenario, temperature histories were compared between particles that reached water sufficiently shallow for settlement (success) and those that remained in deep water (failure) at the end of the model runs. Mean CDD was plotted against day since release for successes and failures from each scenario. ANOVA's were used to compare mean CDD between successes and failures at several points along the trajectories to determine when they showed significant divergence. P-values were adjusted to account for multiple comparisons using Bonferroni correction.

4.3 Results

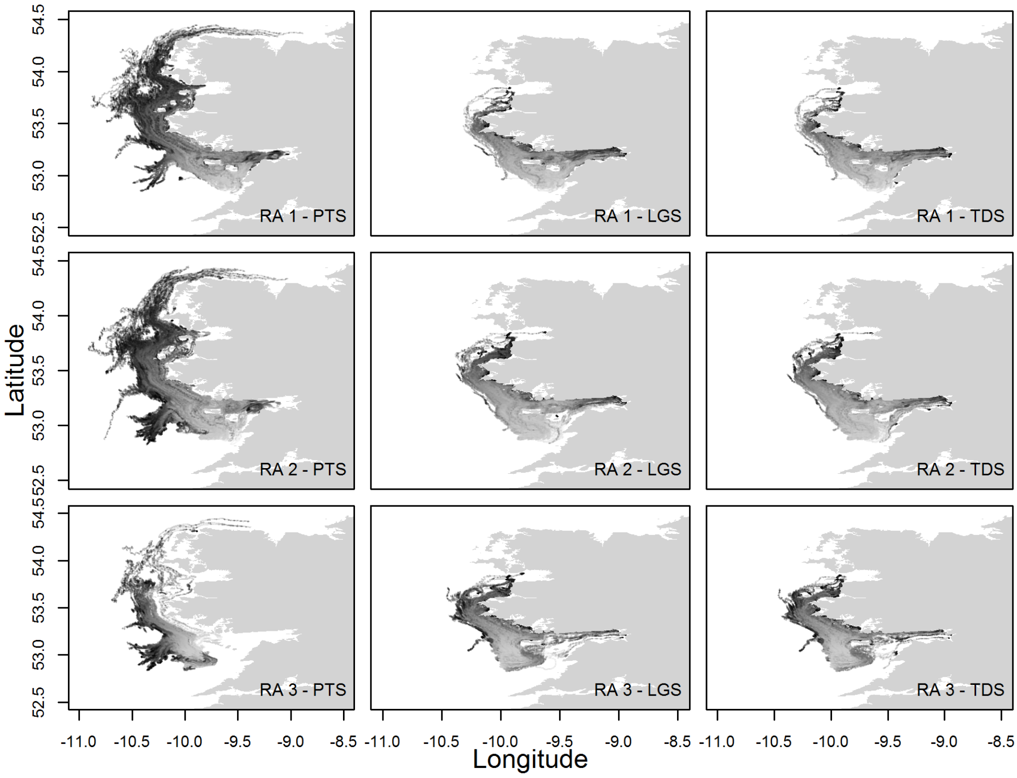


Figure 4.5: Particle dispersal pathways for the 2003 model runs by model scenario and release area. Black areas indicate the end of the larval tracks. PTS–Passive Tracer Scenario, LGS–Linear Growth Scenario, TDS–Temperature-Dependent Growth Scenario

When particle trajectories were modelled using passive transport alone, end points were widely dispersed in offshore areas (Figure 4.5 and Figure 4.6)

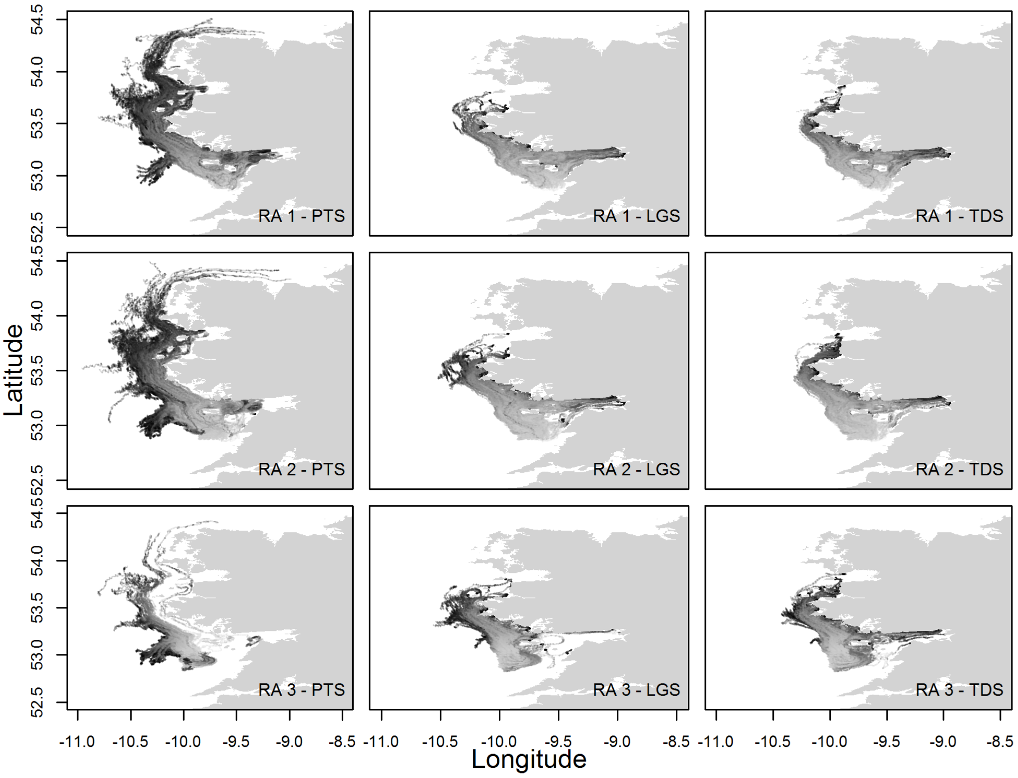


Figure 4.6: Particle dispersal pathways for the 2005 model runs by model scenario and release area. Black areas indicate the end of the larval tracks. PTS–Passive Tracer Scenario, LGS–Linear Growth Scenario, TDS–Temperature-Dependent Growth Scenario

Table 4.3: Percentage larval delivery into suitable settlement depth ($\leq$10m) by scenario, release area (RA), week and year. Passive Tracer Scenario (PTS), Linear Growth Scenario (LGS), Temperature-Dependent Growth Scenario (TDS)

Model	RA	Year	Overall	Wk 1	Wk 6	Wk 11	Wk 16	Wk 21	Wk 26	Wk 31
PTS	1	2003	**24**	31	29	17	26	26	20	20
LGS	1	2003	**78**	86	80	83	77	74	69	80
TDS	1	2003	**81**	83	89	83	77	80	74	80
PTS	2	2003	**15**	11	14	16	16	16	16	18
LGS	2	2003	**71**	80	73	70	80	59	66	68
TDS	2	2003	**70**	80	73	75	68	57	68	71
PTS	3	2003	**7**	5	13	5	3	5	10	8
LGS	3	2003	**43**	33	45	53	43	38	43	45
TDS	3	2003	**40**	38	45	50	38	28	38	43
PTS	1	2005	**26**	20	31	29	29	26	20	29
LGS	1	2005	**69**	66	66	91	57	63	77	66
TDS	1	2005	**78**	74	86	83	91	74	71	66
PTS	2	2005	**14**	11	18	14	14	21	11	7
LGS	2	2005	**53**	57	61	80	45	36	52	41
TDS	2	2005	**68**	64	64	86	68	52	63	80
PTS	3	2005	**7**	10	8	5	8	5	10	5
LGS	3	2005	**19**	20	18	15	15	15	25	25
TDS	3	2005	**43**	30	48	43	45	40	45	53

and across a wide range of depths (Figure 4.7). The inclusion of behaviour in the model delivered particles to shallow inshore areas within Galway Bay and along the west coast with particles accumulating in depths $<$20m (Figure 4.7). Successful delivery rates varied between release areas, weeks and years and ranged from 7–26% for the passive tracer scenario (PTS). The incorporation of behaviour increased successful delivery rates; the linear growth model delivered between 19–78% of particles into $\leq$10m while the most biologically realistic scenario (TDS) in which both behaviour and temperature-dependent growth were incorporated, resulted in 40–81% of particles arriving at depths of $<$10m (Table 4.3).

Table 4.4: GLM comparison results by year (a) including all scenarios and (b) only including the linear and temperature dependent growth scenarios. PTS - Passive Tracer Scenario, LGS - Linear Growth Scenario, TDS - Temperature-Dependent Growth scenario, wk - Release week, "-" indicates a term not included in the model

	Comparison	2003	2005
a)	**PTS/LGS**	<0.001***	<0.001***
	PTS/TDS	<0.001***	<0.001***
	RA1/RA2	<0.001***	<0.001***
	RA1/RA3	<0.001***	<0.001***
	Week	0.008**	0.02*
	Model:RA	-	ns
	Model:wk	-	0.04*
b)	**LGS/TDS**	ns	0.03*
	RA1/RA2	<0.001***	ns
	RA1/RA3	<0.001***	<0.001***
	Week	0.002**	0.02*
	Model:RA	-	0.01*
	Model:wk	-	-

Signif. levels: ***0.001 **0.01 *0.05 ns (non–significant)

Out of the three potential spawning grounds RA1 provided the highest rate of delivery to suitable settlement depth, followed by RA2 and RA3. GLM comparisons (Table 4.4) confirmed that the passive tracer model delivered significantly fewer particles to a depth of 10m or less than the linear growth scenario or the scenario incorporating behaviour and temperature-dependent growth. Delivery rates in the temperature-dependant growth scenario were higher compared to the linear growth scenario in 2005 but not in 2003 (Table 4.3 and Table 4.4b). The rates of successful delivery differed significantly between the three spawning/release areas; most post-hoc comparisons showed that delivery rates from RA1 were higher than those from the other two areas (except for RA2 in 2005). Release week also significantly influenced larval delivery (Table 4.3 and Table 4.4). Significant interaction terms indicated that the effect of release week on larval delivery was not consistent across the three model scenarios.

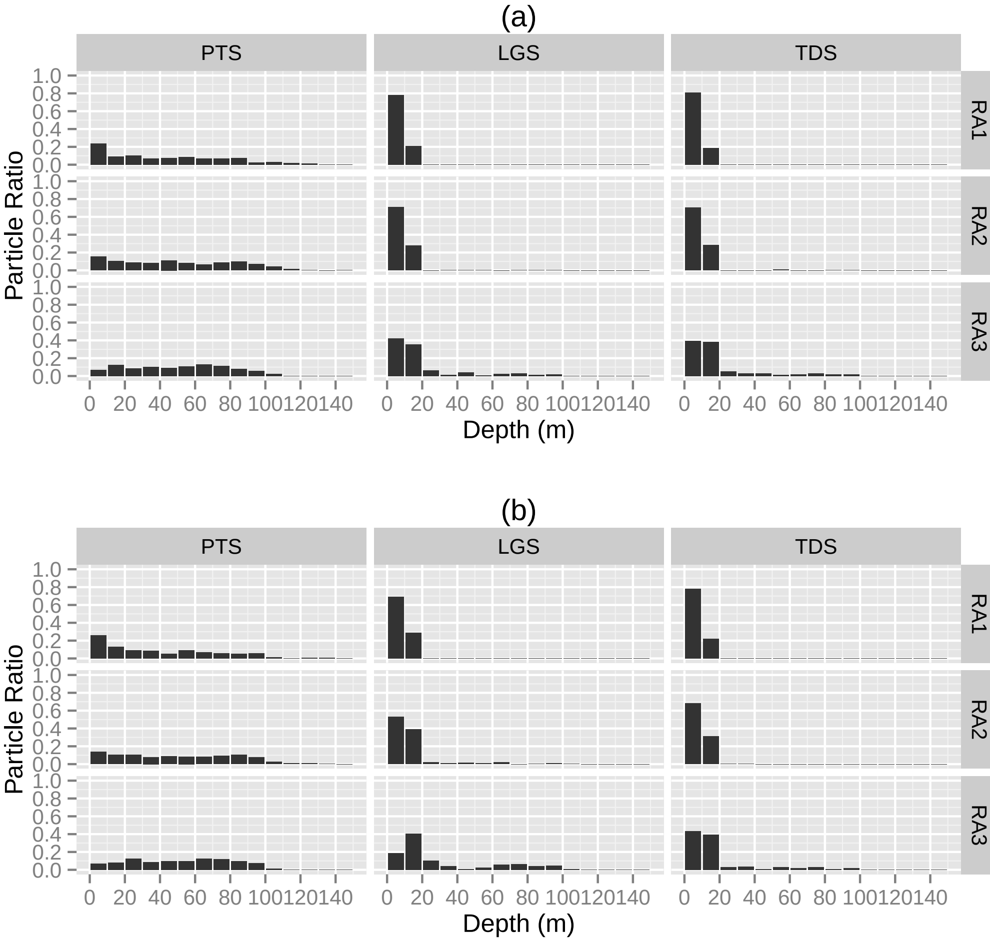
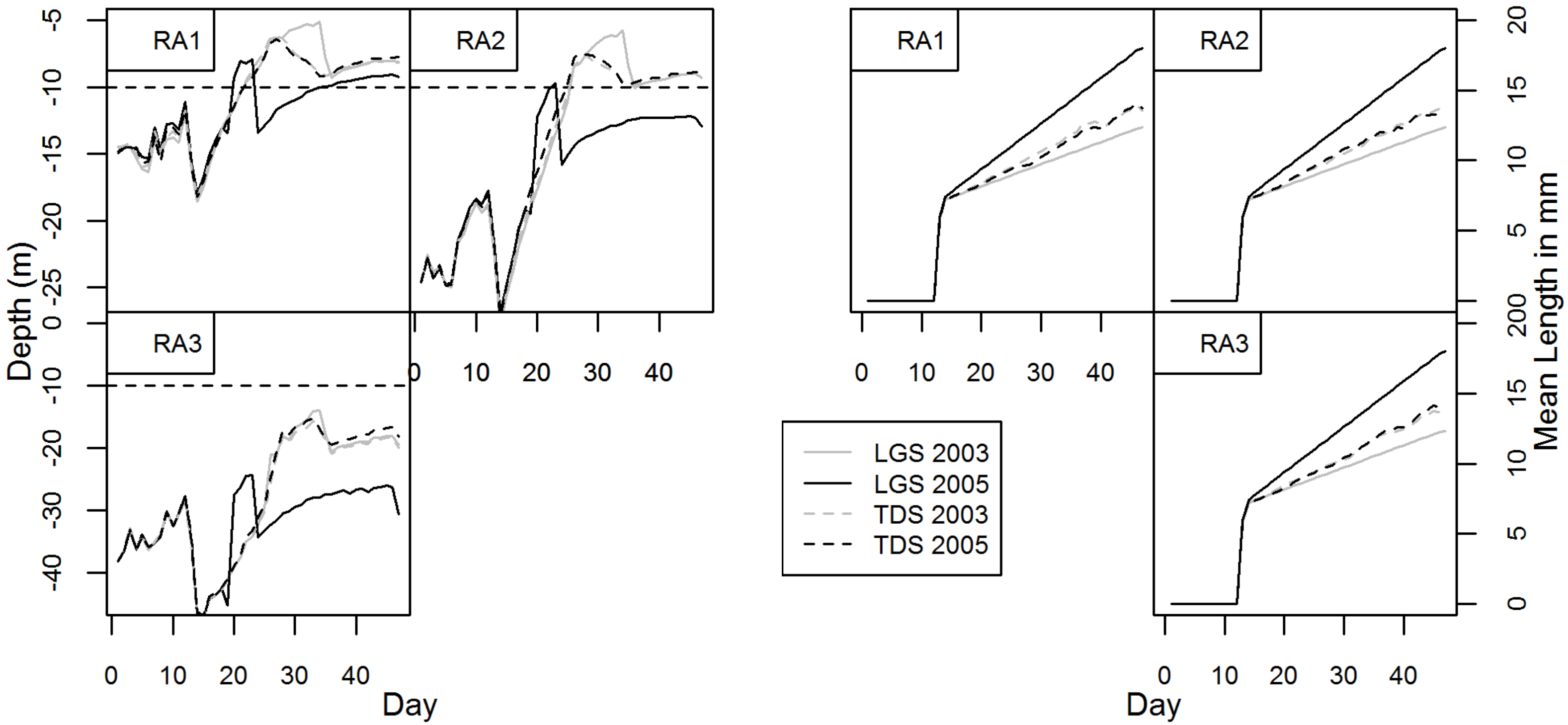


Figure 4.7: Particle ratio by depth for each model scenario and spawning/release area by year a) 2003 and b) 2005. PTS–Passive Tracer Scenario, LGS–Linear Growth Scenario, TDS–Temperature-Dependent Growth Scenario

Predicted length at the end of the model runs (i.e. size at settlement), as well as depth differed between the temperature-dependant growth scenario and the linear growth scenario. This difference was most pronounced in 2005 (Figure 4.8a and b). In the linear growth scenario, size at settlement was fixed based on field observations of a small group of survivors. In the temperature-dependant growth scenario size at settlement was influenced by the modelled



(a) (b)

Figure 4.8: a) Particle depth and b) length plotted against day since release for each spawning area and year from the temperature-dependent (TDS) and linear growth scenario (LGS). Release periods were combined for each release area (RA1, RA2 and RA3) in each scenario

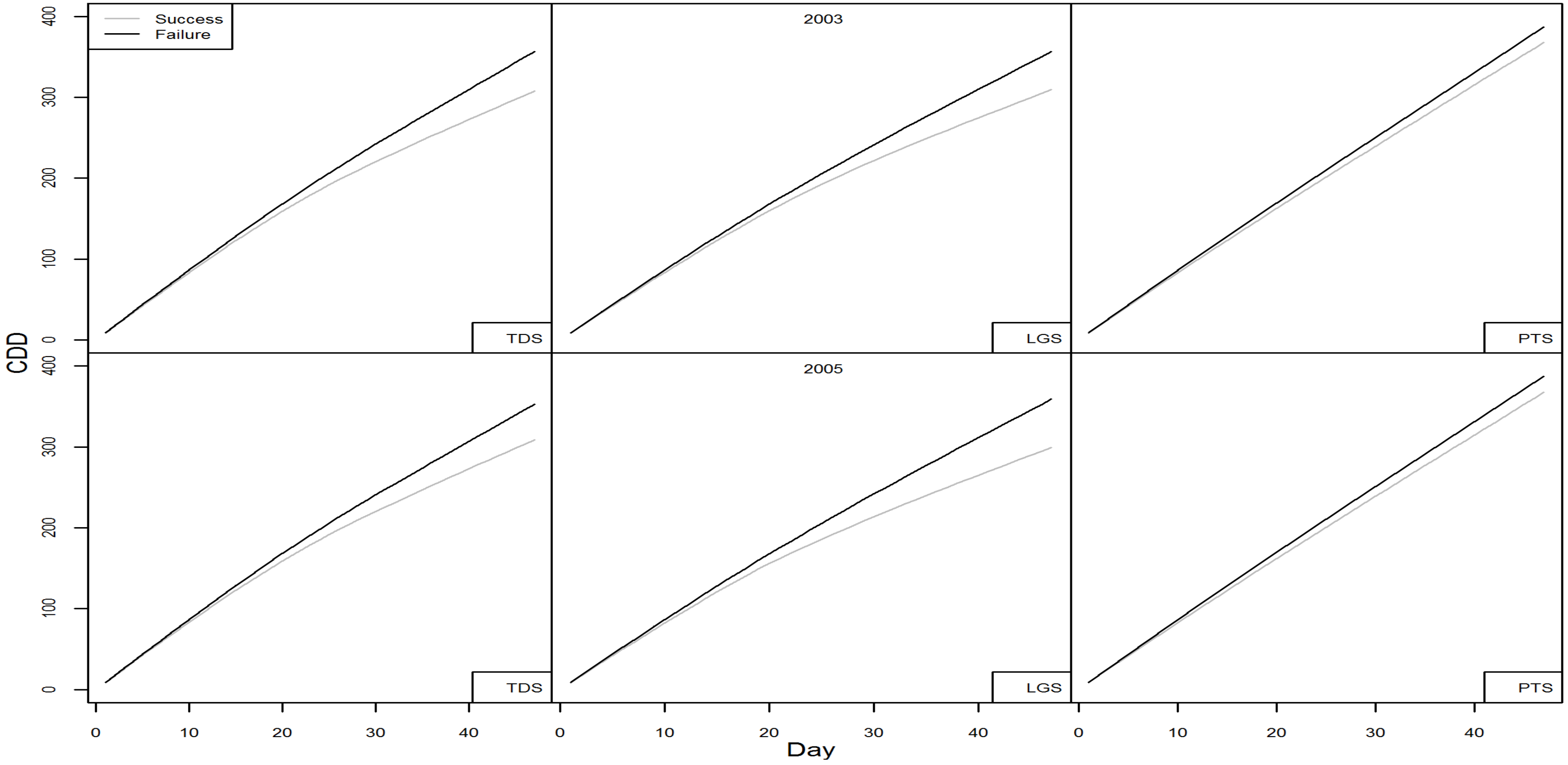


Figure 4.9: Average CDD trajectories experienced by the particles in each scenario in 2003 and in 2005 respectively. PTS–Passive Tracer Scenario, LGS–Linear Growth Scenario, TDS–Temperature-Dependent Growth Scenario. Release periods were combined for each release area (RA1, RA2 and RA3) in each scenario

temperatures experienced during the larval phase and should therefore be more reflective of the entire population (including those that do not survive the larval phase).

Table 4.5: Summary of ANOVA results indicating the days in the model runs by scenario and year by which the CDD's of the successfully settled particles and those that failed to reach settlement depth diverge significantly

Scenario	Day	CDD successes	CDD failures	p-value
PTS 2003	10	83	86	<0.001*
	15	123	128	<0.001*
	20	163	169	<0.001*
	25	201	210	<0.001*
PTS 2005	10	82	86	<0.001*
	15	122	128	<0.001*
	20	162	170	<0.001*
	25	201	210	<0.001*
LGS 2003	10	84	86	0.041
	15	123	128	0.006*
	20	160	168	0.0007*
	25	193	205	0.0002*
LGS 2005	10	82	87	0.01
	15	121	128	0.0014*
	20	156	168	<0.001*
	25	186	206	<0.001*
TDS 2003	10	83	87	0.16
	15	123	128	0.043
	20	159	168	0.012
	25	192	206	0.0006*
TDS 2005	10	83	87	0.0043*
	15	123	129	0.0005*
	20	159	168	<0.001*
	25	192	206	<0.001*

* indicates significance after Bonferroni correction (p = 0.008)

In each of the three scenarios larvae that reached < 10m had experienced lower CDD than those that did not reach this depth (Figure 4.9). This divergence was much more marked in the two scenarios that incorporated behaviour than in the passive tracer scenario. Beginning around day 20-25 (when the larvae begin vertical migration) the temperature histories of the "successful" larvae in the LGS and TDS showed a marked divergence from all of the "unsuccessful" larvae, but also from the "successful" larvae in the PTS. The difference in mean CDD ANOVA showed that across all scenarios mean CDD differed significantly between the "successful" and "unsuccessful" larvae by day 25 at the latest with the divergence occurring earlier than this in some scenarios (Table 4.5).

4.4 Discussion/Conclusions

This study found that successful larval dispersal and subsequent presumed settlement, is probably not achievable via passive transport alone as the primary mechanism for delivery to nursery grounds, since under those conditions a majority of the larvae would not reach suitable nursery areas in Galway Bay but would remain offshore (up to 93%). When tidally synchronised behaviours are included, on the other hand, larvae are retained within the Bay and much higher percentages reach suitable settlement depths (up to 78%). When temperature dependent growth is incorporated in addition to tidally synchronised behaviours, even higher percentages of larvae reach suitable settlement depth (up to 81%). The effect and importance of including behaviour in dispersal models, has been previously highlighted by other authors. Fox et al. (2006) found that if transport was limited to passive drift, larvae diffused away from spawning areas in the Irish Sea, but failed to reach nursery areas (with up to 90% remaining offshore), while when vertical swimming was included, only up to 30% remained offshore, which is in accordance with the findings of the present study. Behaviour has been found to play an important role in dispersal and retention in other species (Van der Molen et al., 2007; Watson et al., 2010), including sole (Savina et al., 2010) and King George Whiting (Jenkins et al., 1999). Therefore it has now been recognised as an essential component of dispersal models (Leis, 2007; North et al., 2009; Bradbury and Snelgrove, 2001; Vikebø et al., 2007), even if some types of behaviour, such as selective tidal stream transport, may only play a role at specific stages of dispersal (Jager, 1999; de Graaf et al., 2004). Other factors, such as pelagic larval duration (PLD), have also previously been found to have significant effects on dispersal patterns and larval delivery (Sponaugle et al., 2005; Cowen and Sponaugle, 2009; Van der Veer et al., 2009). The ICPBM incarnation presented here uses average values for PLD, rather than a range of values to account for between and within year variability as seen in the region (Allen et al., 2008) and elsewhere (Van der Veer et al., 2009), reflecting the need to find a balance between available resources and realism. The ICPBM could be modified to include variable PLD to increase realism and investigate the effect of PLD on larval delivery to west Irish nursery grounds.

In the present study and others, dispersal patterns and successful settlement to nursery areas was significantly influenced by temperature and larval growth (O'Connor et al., 2007). The temperature dependent growth scenario delivered more larvae into suitable settlement depth than the linear growth scenario, depending on spawning area and year. This is because temperature not only has an influence on the length of the pelagic phase, but also on growth and swimming capabilities (Green and Fisher, 2004). It is well established that temperature is positively correlated with growth (Green and Fisher, 2004; McCormick and Molony, 1995) and negatively correlated with PLD (a three degree change in temperature can produce a 5 day decrease in larval duration under field conditions Van der Veer et al. 2009). A recent study by Comerford et al. (2013) found that larval duration and growth could be estimated using a pan regional model of temperature experienced during the larval phase, accounting for 73% of model variability. Slower growing fish will spend longer in the pelagic phase and will develop swimming capabilities later (Green and Fisher, 2004), hence tending to disperse wider than fast growing fish (stage duration hypothesis, Houde 1989). In the linear growth model the larvae grew more quickly and so many reached settlement size prior to reaching suitable depths, settling offshore in deep water. In nature, larvae have been found to take cues from their environment for settlement, such as sediment type, vegetation, food availability and predator presence/absence (Gibson, 1997; Wennhage and Pihl, 1994). Although plaice larvae have not been found capable of delay metamorphosis, delayed settlement has been observed in plaice that have reached a suitable size for metamorphosis, in response to food supply and predator presence (Wennhage and Gibson, 1998) and slower growing fish may be able to delay settlement longer than faster growing fish (Victor, 1986). Such behaviour is currently not implemented in the model, as it lacks an explicit settlement condition.

The role of tidally synchronised behaviour in delivering larvae to nursery grounds is further emphasised by the comparison of temperature histories between particles that were delivered to depths <10m and those that remained in deeper water at the end of the model runs. After the onset of vertical swimming, some particles appear to be entrained into a cooler coastal current system which ensures their retention in shallow coastal areas, while others remain in warmer oceanic water. Although some of the particles in the passive model are dispersed to cooler shallow waters within the bay, the influence of the cool coastal current is not evident in their temperature histories. It appears therefore that in order to avail of this transport/retention mechanism, larvae need to be capable of controlling their position in the water column and also need to be within the right hydrographic conditions when they commence vertical swimming (right place, right time). This is particularly the case in the study area, given the characteristics of the local hydrography; in the entrance to Galway Bay the vertical structure of the flow can change dramatically and quickly within one tidal cycle (White, 1996). This illustrates the complexity of the interaction between biological factors (e.g. the timing and location of spawning, rates of larval development and growth) and physical features such as hydrography.

Differential growth rates may therefore be an adaptation to regional differences in hydrodynamic conditions, such as temperature and distance between spawning and nursery areas, as successful survival of the larval phase and recruitment to the juvenile phase depends on larvae taking advantage of prevalent transport and retention mechanisms (Jenkins and May, 1994) to ensure their delivery to habitats that are suitable for juvenile development. Succesful delivery rates varied according to the timing of particle release. The optimal week for release differed between years, release areas and model scenarios. The interannual variability in larval delivery observed in this study, is unlikely to be solely an artefact of the model. Although larvae that reach settlement depth before the end of the model runs may be advected out into deeper water by the currents because there is no settlement condition implemented in the model, hydrodynamic conditions, namely tidal forcing and the timing and phase of the tidal current, are different in 2003 and 2005. Wind forcing was spatially and temporally coarse, so this interannual variability is small. These slight differences in hydrodynamic and wind conditions, are therefore likely to be the main factors leading to interannual variability in delivery rates to nurseries. The link between hydrodynamic conditions and delivery of larvae to nursery grounds has been previously reported, such as by Riley et al. (1981) or Comerford and Brophy (2013), who both link the strength of onshore winds to nursery delivery, for turbot and other species respectively. The interannual variability found in the present study is relatively small (1-4%) compared to Van der Veer et al. (1998), where interannual variation was much greater (65-100%). However, the present study only covered two years, between which the temperature differential was also small, compared with seven years and greater temperature fluctuations in Van der Veer et al. (1998). Variability in larval delivery may be greater if a longer time scale is covered, in accordance with studies, such as in the North Sea or the English Channel (Bolle et al., 2009; Ellien et al., 2000), illustrating the stochastic nature of larval dispersal (Siegel et al., 2008) and temporal variability therein.

The results of this study also suggest that more rapid larval growth rates and a shorter larval duration could impair dispersal and delivery to a suitable nursery area and negatively influence survival. The effect of temperature on larval delivery is of particular relevance in view of the effects of climate change on ocean temperatures and circulation (Harley et al., 2006). Higher temperatures were found to have a negative effect on the early life stages (eggs and larvae), increasing mortality but a positive one on later stages (Hovenkamp and Witte, 1991). While species level effects are difficult to predict and regional and seasonal projections are uncertain, the ICPBM presented here could be used to simulate the effect of differing hydrodynamic conditions (wind, tidal conditions and temperature) and PLD's on larval dispersal and delivery to nursery areas from the predicted spawning grounds. Shorter larval durations, for example will likely mean that individuals may no longer be able to ensure wide enough dispersal to find suitable nursery habitat (O'Connor et al., 2007). This is because changing temperature regimes and changes in ocean circulation may lead to mis–matches in the timing of the egg and larval phase to take advantage of suitable transport conditions, resulting in larvae not being delivered and retained in suitable nursery habitats. Changes in hydrodynamic conditions due to climate change may also lead to breakdowns in connectivity between spawning and nursery areas, decreasing larval deliveries (Hufnagl et al., 2012). Changes in dispersal and larval delivery will directly impact population connectivity and effective population size, which are thought to be inversely related to ocean temperatures (O'Connor et al., 2007). With less exchange occurring between populations and replenishment through self–recruitment and influx from other populations declining, this will endanger population regulation and persistence and therefore recruitment into dependent fisheries (Cowen and Sponaugle, 2009).

Delivery into suitable settlement depth also varied significantly between spawning areas. RA1 just south east of the Aran Islands, delivering significantly more larvae under temperature dependent growth, compared to RA2 or RA3. Successful survival of the larval phase and recruitment to the juvenile phase depends on larvae taking advantage of prevalent transport and retention mechnisms (Cushing, 1990) to ensure their delivery to habitats that are suitable for juvenile development. The adaptation to regional differences in oceanographic conditions are thought to be reflected in the location of spawning areas. Suitable locations will ensure that larvae are carried with the currents to inshore nursery areas, while availing of a suitable food supply (Gibson, 1999). In areas, such as the Irish Sea, where currents are weak, spawning and nursery grounds have been found to be in close proximity to each other (Fox et al., 2006, 2009), while in areas where current are strong, spawning grounds may be further away from nursery grounds and eggs are released at an optimum direction and distance from settlement areas (Gibson, 1999). While spawning female plaice were found at the three release areas (Hans Gerritsen unpublished data; Gerritsen, 2010), the high rates of larval delivery to shallow waters in both years from RA1, are comparable to other studies (Hufnagl et al., 2012; Fox et al., 2006) and suggest that this is a probable spawning area taking into account prevalent hydrodynamic conditions and interannual variability (Bolle et al., 2009; Lacroix et al., 2012). Larval delivery decreases for those spawning areas located further offshore (RA2 and RA3) under 2003/05 conditions and therefore spawning is less likely to take place there. However, delivery rates from these areas may be higher in other years not examined in this study and the possibility that plaice spawning occurs in a number of areas as a bet-hedging strategy (Lambert and Ware, 1984) cannot be ruled out. Future field studies to validate the existence of plaice spawning grounds in the candidate areas are recommended. Although the model did not include formulations to account for mortality or horizontal swimming, these results are consistent with previous studies in other regions, both as far as the influence of behavioural characteristics is concerned, as well as the influence of differential growth and temperature regimes on dispersal (Fox et al., 2006; Bolle et al., 2009; Van der Veer et al., 2009; Hufnagl et al., 2012).

The potential nursery ground distribution (Figure 4.4 and Figure 4.5) indicated by the end positions of the larvae in the temperature dependent scenario, is consistent with the location of some of the nursery grounds previously sampled in the west of Ireland (Haynes et al., 2012), including Gurteen and Dogs Bay. The dispersal pathways also suggests some potential nursery areas further north of the Galway Bay, that merit future investigation for validation, seeing that the measurement of successful settlement employed here did not take into account factors such as habitat suitability and quality (De Raedemaecker et al., 2012). In the region indicated by the model, from

Galway Bay to Clew Bay, the shoreline is characterised by an irregular series of rocky bays with small sandy beaches (OSPAR Commission, 2000), which may be suitable for plaice settlement, with the major seabed sediment types in the region predominated by sandy cover formed into a variety of bedforms (OSPAR Commission 2000, Figure 2.2). The most probable spawning ground just south east of the Aran Islands, identified using the most realistic dispersal model and providing up to 81% of larvae to suitable settlement depth, will also require qualitative validation.

Using ICPBM to locate probable spawning and nursery grounds, as in the present study, is a valid method, as it has been shown to agree well with other measures of dispersal (Siegel et al., 2003) and can provide insight into the existence of sub–populations (Fox et al., 2009). As not all nursery grounds are of the same quality to promote growth, survival and subsequent recruitment into the population (De Raedemaecker et al., 2012; Wennhage et al., 2007), once nursery grounds in the region are known, they can be characterised and their contribution to the population quantified (Swearer et al., 1999), allowing those with the most suitable habitat characteristics and contribution to be protected via spatial habitat management. The same is true for spawning grounds (Ashford et al., 2010). The identification of spawning and nursery areas and their contribution is of paramount importance for fisheries management and conservation (Bergman et al., 1988). This especially true when taking into account the recent shift towards using Marine Protected Areas (MPA's) for fisheries conservation and management. This type of management paradigm is spatial in nature and so its effectiveness to change population sustainability, fishery yields and ecosystem properties depend on larval dispersal, juvenile and adult fish movements, habitat quality and movement of fishermen (Botsford et al., 2009; Wennhage et al., 2007; De Raedemaecker et al., 2012).

This study has identified a likely spawning ground for plaice on the west coast of Ireland. The study reconfirmed the importance of including behaviours and temperature-dependent growth formulations in ICPBM's and illustrates the effect of changing hydrodynamic conditions on larval delivery. Variability in ocean temperatures and circulation, due in part to climate change is likely to have considerable effects on dispersal patterns and larval delivery rates. The ICPBM presented here could potentially be used to explore possible effects of environmental change on dispersal, larval delivery and connectivity. Future work in the region should focus on quantitatively validating the physical model, as well as expanding its capabilities. The location of the probable spawning and nursery grounds indicated here should be verified and their relative contribution to the population/s in the region should be quantified. Future management plans will benefit from the identification of the likely spawning ground for plaice in the region and its connectivity to nursery areas.

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Chapter 5

Indirect effects of bottom trawling on fish condition and diet: influence of fish size and mobility

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Data in this chapter has contributed to Shephard, S., Minto, C., Zölck, M., Jennings, S., Brophy, D., and Reid, D. Scavenging on trawled seabeds can modify trophic size structure of bottom-dwelling fish. *ICES Journal of Marine Science*, doi.10.1093/icesjms/fst134

Abstract

Bottom trawling can cause changes in species composition and evenness in marine benthos, with implications for feeding of benthivorous fishes. This study investigates the indirect effects of bottom trawling (derived from Vessel Monitoring System data) on diet and body condition (relative weight Wr) of three flatfish (*Microstomus kitt*, *Pleuronectes platessa*, *Lepidorhombus whiffiagonis*) and one gadoid species (*Merlangius merlangus*), collected in March 2011 from the Celtic Sea (50–52°N, 5–10°W). These species represent a range of feeding and migratory strategies, from a sedentary obligate benthivore (*M. kitt*) to a mobile piscivore (*M. merlangus*). The relationship between trawling effort and condition was significantly ($p<0.05$) positive for small plaice $\leq$ 25cm and negative for small megrim $\leq$ 30cm. Condition of other species/ size groups was not related to effort. The effort effect appeared to be linked to species mobility, with condition of more sedentary species being more strongly related to effort within a 20km radius, while condition of more mobile species was related to effort in a 40km radius. For megrim, the diversity of prey items in the gut varied significantly with effort at 20km only ($p = 0.03$). These small and variable effects may reflect scavenging, compensating for changes in prey community composition.

Keywords: Benthic impacts; Bottom trawling; Celtic Sea; Diet; Fish condition; Mobility

5.1 Introduction

Bottom trawling gear has various direct impacts on marine benthic communities (Kaiser et al., 2006). Gear impacts on the benthos differ with body type and size; fragile hard bodied organisms are particularly vulnerable (Kenchington et al., 2006) and trawling favours the removal of larger individuals and species from the system. Selective removal of organisms generally leads to a marked reduction in biomass and productivity of the benthic system (Kaiser et al., 2000; Jennings et al., 2001; Tillin et al., 2006). These negative trawling impacts on the benthos may indirectly drive declines in condition and growth of the benthivorous fish species that prey on this community

(Lloret et al., 2007; Shephard et al., 2010; Hiddink et al., 2011). In contrast, a very low level of trawling impact may facilitate a compensatory effect in the benthos: increased relative abundance (or even proliferation) of smaller opportunistic organisms (e.g. polychaetes), that are better able to withstand trawling impact (Jennings et al., 2002). This compensation seems to enhance feeding success among certain benthivorous fish species (Hiddink et al., 2008; Shephard et al., 2010; van Denderen et al., 2013), especially juvenile plaice (Rijnsdorp and Van Beek, 1991; Rijnsdorp and Van Leeuwen, 1996; Hiddink et al., 2008).

This study presents new empirical data at the scale of the Celtic Sea (1000's of km^2) to further explore indirect trawling effects on fish condition, and to investigate changes in diet as a possible driver (trawling causes changes in prey composition and biomass). Variation in condition and diet is examined across a commercial fishing effort radiant. Three flatfish species, plaice (*Pleuronectes platessa*), lemon sole (*Microstomus kitt*) and megrim (*Lepidorhombus whiffiagonis*) as well as one gadoid species, whiting (*Merlangius merlangus*) are considered. These four species represent a gradient of hypothesized dietary vulnerability to trawling impacts. Juvenile plaice, megrim and whiting in the Celtic Sea show a ontogenetic shift from a primarily benthic diet, towards a more piscivorous diet with increasing size, while lemon sole remain benthivorous throughout their life history (Pedersen, 1999; Pinnegar et al., 2003). The four species also differ in their mobility. Plaice have been shown to move over large distances, with evidence of large scale migrations, using tidal streams (Dunn and Pawson, 2002; Hunter et al., 2003, 2004), while both megrim and lemon sole are more sedentary and less mobile, showing no evidence of regular or extensive movements (Jennings et al., 1993; Gerritsen, 2010). Whiting, a pelagic species, is capable of displacements of between 53 to 123 km over the course of a year (Tobin et al., 2010). It is hypothesised that those species that are less mobile and more reliant on benthic prey, will be most likely to show an indirect effect of trawling on body condition and that this effect will be size dependent, driven by changes in benthic prey biomass and composition.

5.2 Materials and Methods

5.2.1 Sampling

Fish were collected aboard the R.V. Celtic Voyager from the 24th to the 27th of March 2011. 20 stations in the Celtic Sea were sampled (Figure 5.1). Trawl locations were selected from sampling stations used during the annual Irish Ground Fish Survey (IGFS), carried out by the Irish Marine Institute (Table 5.1).

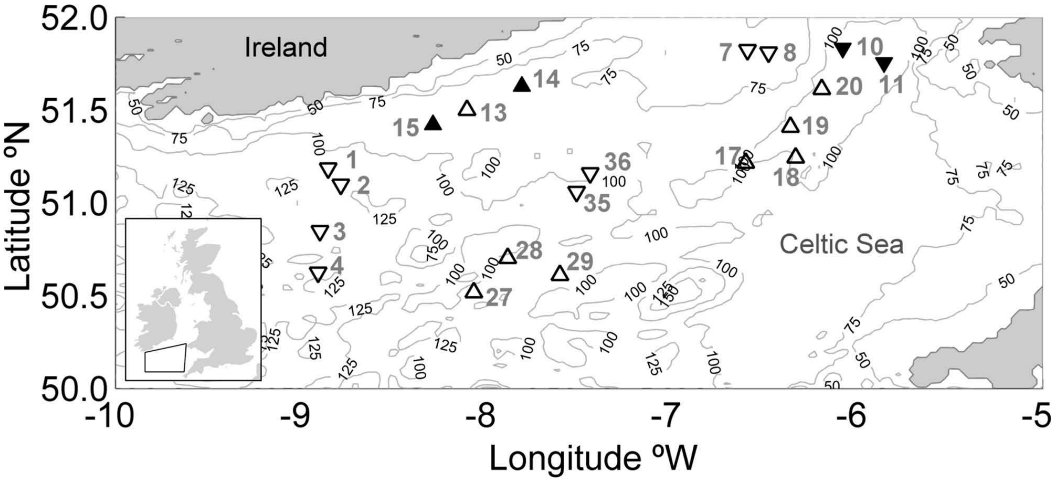


Figure 5.1: Map of sampling stations (numbered) sampled during R.V. Celtic Voyager survey 24-27 March 2011. △: High effort station on sand, ▽: Low effort station on sand, ▲: High effort station on gravel, ▼: Low effort station on gravel

To maximize the chance of detecting a trawling effect on fish condition and diet, ten sampling stations were selected from each of the upper and lower extremes of the observed fishing effort range (1 January 2009–31 December 2010), as derived from Vessel Monitoring System (VMS) records. VMS transmits the position and speed of vessels at least every two hours and data are available for all European fishing vessels over 15 metres. All mobile fishing gears (otter and beam trawls and scallop dredges) were included and speed criteria were applied to distinguish fishing activity from steaming and other non-fishing activity (Gerritsen and Lordan, 2011). Effort was quantified at two spatial scales and was calculated as follows: a) total hours fished in 2009/10 within a 20km radius of the haul midpoint (henceforth referred to as Effort 20km) and b) total hours fished in 2009/10 within a 40km radius of the haul midpoint (henceforth referred to as Effort 40km) of the sampling station. These effort levels, are cumulative (Effort 40km = Effort 20km + summed effort from 20km to 40km radius), are not consistently linearly related for a given sampling station, due to the patchiness of fishing effort. This means that for any given sampling station, fishing effort at 20km may be relatively more intense than at 40km from a station.

Summed effort data from 2009 and 2010 was combined because although the use of annual effort values for each station may allow short-term (<1 year) effects of effort on fish condition to be captured, trawling impacts on the benthos are cumulative (Hinz et al., 2009) and so changes in benthic prey availability (and hence fish condition) may persist across years. If trawling effects on prey do persist, using effort values for a single year could confound analysed effects on fish condition, if the effort regime at given stations varied markedly among years. Effort circles of 40km and 20km were selected because effort at these ranges has been closely correlated to fish community descriptors in the study area (Shephard et al., 2011, 2012). A radius of 20 and 40km likely encompasses the feeding range of individual lemon sole (Jennings et al., 1993) and possibly that of plaice, which can show fidelity to spawning sites despite being highly mobile (Hunter et al., 2003).

Dominant substrate type by survey site (Haul) was derived from MESH (Mapping European Seabed Habitats; `http://www.searchmesh.net/`). Survey sites for which biological data on study species were available were characterized as having gravel, sand or mud substrates. However, since few data for the mud substrate were available, these were combined with the sand substrate. Five stations were sampled per day. Trawls were carried out using a survey GOV trawl with a 20mm codend liner.

Fish were identified to species, measured to the nearest centimetre and weighed to the nearest gram. A sub–sample from each haul and species was taken for diet analysis. For sub–sampled individuals, the digestive tract (henceforth “guts”) was dissected out and preserved immediately in 95% ethanol.

5.2.2 Data Analysis

5.2.2.1 Diet Analysis

In the laboratory, the gut contents of each specimen were identified to Phylum, Order or Class (depending on their state of decomposition) and their numbers recorded. After excluding those fish with empty guts (out of 207 fish used for diet analysis, 106 were empty), as it was not possible to determine

Table 5.1: Summary of sampling stations, IGFS ID, shot and haul longitude and latitude, effort (summed hours fished 2009 and 2010 and High/Low) and substrate (Sand—Sd, Gravel—Gl) classification

Station	ID	Shot Lon	Shot Lat	Haul Lon	Haul Lat	Effort	Substrate	Effort 20km (h y^{-1})	Effort 40km (h y^{-1})
1	FG180	-8.854	51.186	-8.904	51.176	Low	Sd	11348	37671
2	FG141	-8.785	51.099	-8.837	51.099	Low	Sd	10352	37368
3	FG11	-8.898	50.848	-8.891	50.88	Low	Sd	3049	32213
4	CC306	-8.908	50.624	-8.872	50.598	Low	Sd	5741	38087
7	FG167	-6.592	51.823	-6.611	51.853	Low	Sd	6613	33760
8	69	-6.479	51.81	-6.51	51.838	Low	Sd	5072	38226
10	FG26	-6.079	51.833	-6.072	51.799	Low	Gl	9341	30869
11	40	-5.856	51.755	-5.901	51.734	Low	Gl	10569	33637
13	FG17A	-8.105	51.501	-8.149	51.481	High	Sd	16557	50889
14	FG18	-7.809	51.629	-7.857	51.617	High	Gl	19125	55410
15	FG134	-8.289	51.422	-8.338	51.436	High	Gl	12911	47796
17	FG39	-6.602	51.216	-6.635	51.189	High	Sd	18069	62626
18	112	-6.332	51.244	-6.338	51.211	High	Sd	24876	68974
19	111	-6.361	51.41	-6.379	51.379	High	Sd	29620	74342
20	FG139	-6.192	51.613	-6.212	51.58	High	Sd	18501	62986
27	FG133	-8.068	50.518	-8.022	50.535	High	Sd	17814	64258
28	FG53	-7.885	50.703	-7.842	50.723	High	Sd	20364	63385
29	MB30	-7.604	50.612	-7.615	50.645	High	Sd	21942	60792
35	FG36	-7.514	51.059	-7.556	51.039	Low	Sd	5543	34261
36	FG23	-7.441	51.16	-7.404	51.184	Low	Sd	8140	36926

whether these individuals had not consumed any prey or had simply ejected gut contents during capture, PRIMER (Plymouth Routines in Multivariate Ecological Research; Clarke and Gorley 2001; Clarke and Warwick 1994) was used to compute the Shannon diversity index, perform Similarity Percentages Analysis (SIMPER) and Analysis of Similarities (ANOSIM). SIMPER was conducted on the prey composition of the diet for each species and at the two effort levels. The purpose of the analysis was to determine which components of the diet of each species were most common at each effort level and which caused the most dissimilarity between them. Only samples from sandy substrates were used in this analysis, as there was not enough diet data available for gravel. ANOSIM was performed to assess the statistical significance of these similarities/dissimilarities (Clarke, 1993). All remaining statistical analyses were carried out using the R statistical package (R Development Core Team, 2011).

Generalized Additive Models (GAM) were constructed to assess the effect of bottom trawling and substrate (sand and gravel) on Shannon gut diversity index for each species. Separate models were constructed to examine the effect of effort over two spatial scales (Effort 20km and Effort 40km). The effect of substrate and effort level on diversity was computed, with the continuous effort term in the GAM taking the form of a smoother (Wood, 2006):

$$S_{ik} = f(E_{ik}) + \alpha_k + \varepsilon_{ik} \tag{5.1}$$

where S_{ik} is the Shannon index, for the ith fish on k substrate, $f(E_{ik})$ is the smoother function of effort (either 20 or 40km), α is the intercept and ε_{ik} is the variance ($\varepsilon_{ik} \sim N(0, {\sigma^2}_{\varepsilon})$). Samples were categorized according to whether they came from high or low effort areas.

5.2.2.2 Condition Analysis

Condition as indicated by Relative weight (Wr) was calculated for all fish caught during the survey according to the formulae (Blackwell et al., 2000):

$$Wr = 100 \times \frac{W}{Ws} \tag{5.2}$$

where W is the weight of the fish in grams and Ws is the predicted weight of the fish in grams, as determined from a linear regression of log weight against log length.

Relative weight rather than Fulton's condition factor (K) is used as an indicator of fish well-being because K assumes isometic growth, which is rarely the case (McGurk, 1985) and also requires comparisons to be restricted to fish of the same length. Relative weight has several advantages over other condition measures: it is simple to calculate, it does not change when using different measurement units, it compensates for changes in fish shape, changes in it are primarily due to ecological factors and it is comparable between fish of different sizes and species (Wege and Anderson, 1978).

The mean length, weight and condition of fish sampled and numbers of fish used for condition and diet analysis (by substrate and/or effort) is given in Table 5.2.

According to the presented hypothesis the trawling effects on condition would differ with fish size, due to ontogenetic shifts in diet. Hence, fish were divided into two size classes, 'small' and 'large': plaice and whiting ($\leq$ 25cm and >25cm), megrim ($\leq$ 30cm and >30cm), based on diet composition at size in the Celtic Sea (Pinnegar et al., 2003). The lemon sole sample was not split into different size classes as the size range was narrow (20–30 cm) and because this species remains an obligate benthivore throughout its life history.

Linear mixed effects models (LME) were constructed to assess the effect of bottom trawling effort and substrate on fish condition. The effects of effort on condition were examined at two spatial scales (Effort 20km and Effort 40km) using separate models. Effort level and substrate were assigned as fixed effects, while sampling station was assigned as a random effect. The mixed models were weighted with different variance structures, which could take one of three forms for the ith fish, jth sampling station, k substrate and E effort level (20 or 40km); a power variance function (varPower) of effort level ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon} \mid E_{ijk} \mid^{2\delta})$), a constant variance function (varIdent) of substrate ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon k})$ or a combination of the power and constant variance (varComb) functions($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon k} \mid E_{ijk} \mid^{2\delta})$), where δ is the variance coefficient (Zuur et al., 2009).

The mixed models were then compared to each other using the Likelihood ratio test, to find the best variance structure for each effort level and the models with the lowest Aikake Information Criterion (AIC) value were deemed to be the most suitable (Zuur et al., 2007).

The resulting models (one for each effort level), were then compared to simple Generalized Least Squares (GLS) models, weighted with the best variance structure determined previously. The most suitable models were again determined using AIC values.

Table 5.2: Summary table showing fish mean length, weight and condition (Wr) as well as number of fish used for condition and diet analysis (divided by substrate and effort). Numbers in brackets are total number of fish collected and number used in diet analysis. PLA - Plaice, MEG - Megrim, WHG - Whiting, LEM - Lemon Sole

	Fish collected			**Condition Analysis**		**Diet Analysis**			
						High Effort		**Low Effort**	
Species	**Length (cm)**	**Weight (g)**	**Condition (Wr)**	**Sand**	**Gravel**	**Sand**	**Gravel**	**Sand**	**Gravel**
PLA (158, 53)	24.58	160.68	99.99	125	33	12	5	12	0
MEG (139, 56)	29.55	235.68	100.02	122	17	11	3	7	1
WHG (311, 64)	27.06	190.09	100.01	206	105	10	3	15	9
LEM (99, 34)	24.75	197.36	99.99	77	22	1	3	9	0

Table 5.3: Best model for each species by size class ((a) small fish (b) large fish) and effort level for condition analysis (Response variable relative weight). Variance Structures are defined as: varIdent ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon k})$; varPower ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon} \mid E_{ijk} \mid^{2\delta})$); varComb ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon k} \mid E_{ijk} \mid^{2\delta})$); Normal ($\varepsilon_{ijk} \sim N(0, {\sigma^2}_{\varepsilon})$. PLA - Plaice, MEG - Megrim, WHG - Whiting, LEM - Lemon Sole

		Effort 20 km				Effort 40 km			
		PLA	MEG	WHG	LEM	PLA	MEG	WHG	LEM
	Model Parameter								
	Effort	*	*	*	*	*	*	*	*
	Substrate	*	*	*	*	*	*	*	*
	Interaction	*	*	*	*	*	*	*	*
	Random Effects			Station					
(a)	**Variance Structure**								
	varIdent							*	
	varPower	*	*			*	*		
	VarComb			*					
	Normal				*				*
	Model Parameter								
	Effort	*	*	*	-	*	*	*	-
	Substrate	*	*	*	-	*	*	*	-
	Interaction	*	*	*	-	*	*	*	-
	Random Effects			Station	-			Station	-
(b)	**Variance Structure**								
	varIdent				-			*	-
	varPower				-				-
	VarComb		*	*	-		*		-
	Normal	*			-	*			-

5.3 Results

5.3.1 Effects of effort and substrate on condition

The best models for each species and size class by effort level for condition analysis are summarized in Table 5.3.

The results of the analysis for each species are summarized in Table 5.4. Condition of small plaice was significantly positively related to fishing effort at the 40km effort scale, while at the 20km scale the effort effect was just below the 0.05 significance level, with a greater effect on gravel than sand (Figure 5.2), which was also significant at the 40km scale. When Bonferroni correction was applied to the p-values to account for the examination of the effort effect at two spatial scales (p crit. = 0.025), the trawling effect for small plaice at 40km was just above the critical value (p = 0.027). Bearing in mind however, that the correction is very conservative, this effect should not be dismissed. There was no significant effect of either trawling effort or

Table 5.4: Effects of continuous fishing effort and substrate on condition (relative weight) for (a) small fish (plaice (PLA), whiting (WHG) $\leq$ 25cm and megrim (MEG) $\leq$ 30cm) and (b) large fish >25cm (plaice and whiting) and $>$ 30cm (megrim), showing significance level for each model parameter

		Effort 20 km				Effort 40 km			
		PLA	MEG	WHG	LEM	PLA	MEG	WHG	LEM
(a)	Effort	0.06.	0.003**	0.88	0.48	0.027*	0.05*	0.8	0.64
	Substrate	0.23	0.004**	0.81	0.61	0.12	0.08.	0.56	0.78
	Interaction	0.09.	0.004**	0.92	0.54	0.04*	0.08.	0.64	0.75
	d.f.	93	77	118	99	93	77	118	99
(b)	Effort	0.91	0.45	0.45	-	0.91	0.13	0.39	-
	Substrate	0.43	0.72	0.37	-	0.55	0.44	0.23	-
	Interaction	0.81	0.61	0.27	-	0.96	0.32	0.18	-
	d.f.	65	62	161	-	65	62	161	-

Signif. levels: ***0.001 **0.01 *0.05 ·0.1 Bonferroni correction p = 0.025

substrate on condition of large plaice.

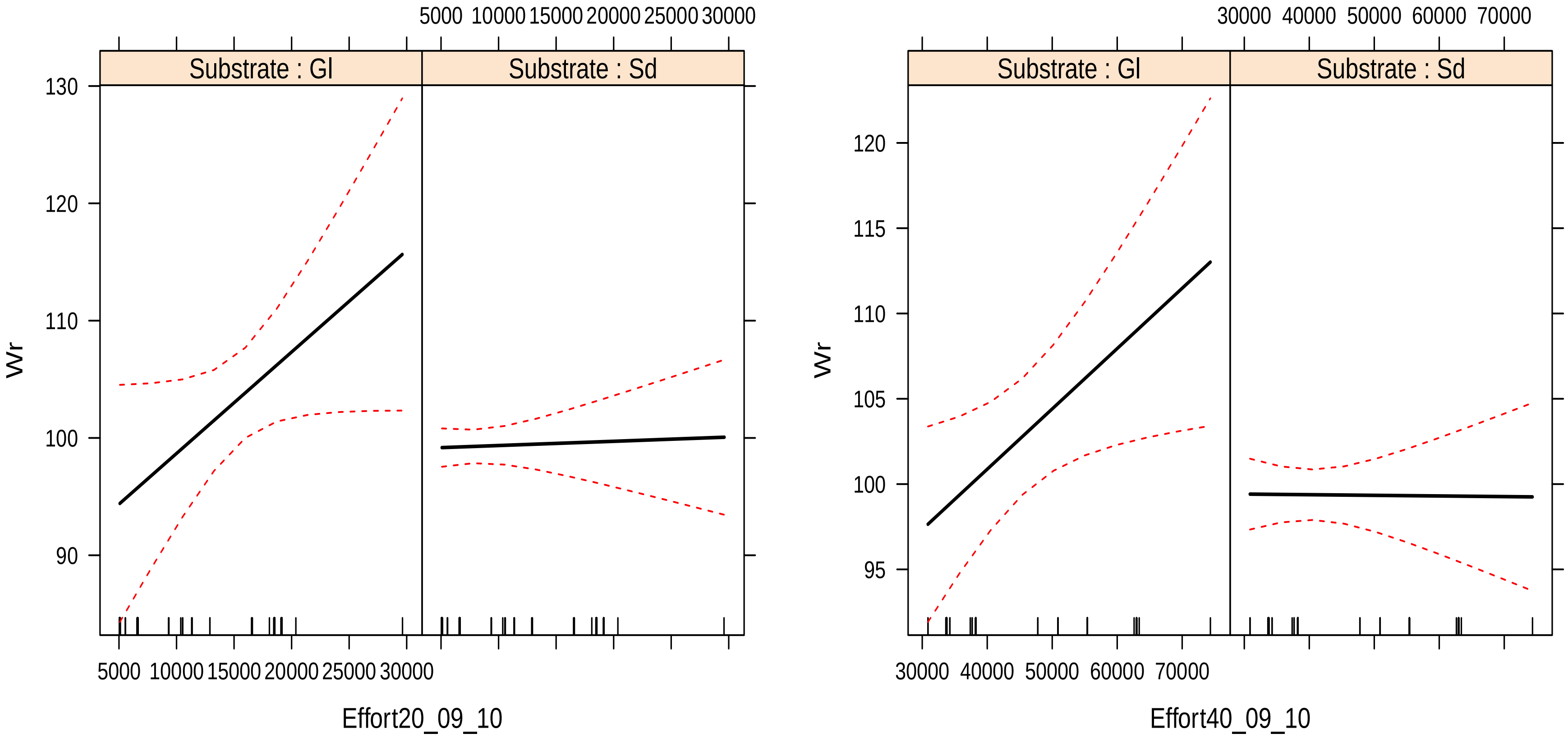
Condition of small megrim ($\leq$ 30cm) was significantly negatively affected by effort at 20km only, while at 40km this effect was just at the significance threshold of 0.05. There was a significant substrate effect and a significant interaction between effort and substrate at the 20km effort scale. After applying Bonferroni correction, only the effects at 20km effort remained significant. As with small plaice, condition was more affected by trawling on gravel than on sand substrate (Figure 5.3), although here the relationship was negative. There was no significant effect of either trawling effort or substrate on condition of large megrim.

Condition of whiting and lemon sole was not significantly affected by bottom trawling effort or substrate.

5.3.2 Effect of effort and substrate on prey diversity

In megrim the diversity of prey items in the gut varied significantly with effort at 20km only ($p = 0.03$), while at 40km there was no significant effect of effort on diversity. After applying Bonferroni correction, however, this effect was no longer significant. No effect on prey diversity was detected in either plaice or whiting (Table 5.5). Sample size was too small to split the species into small and large ontogenetic groups.

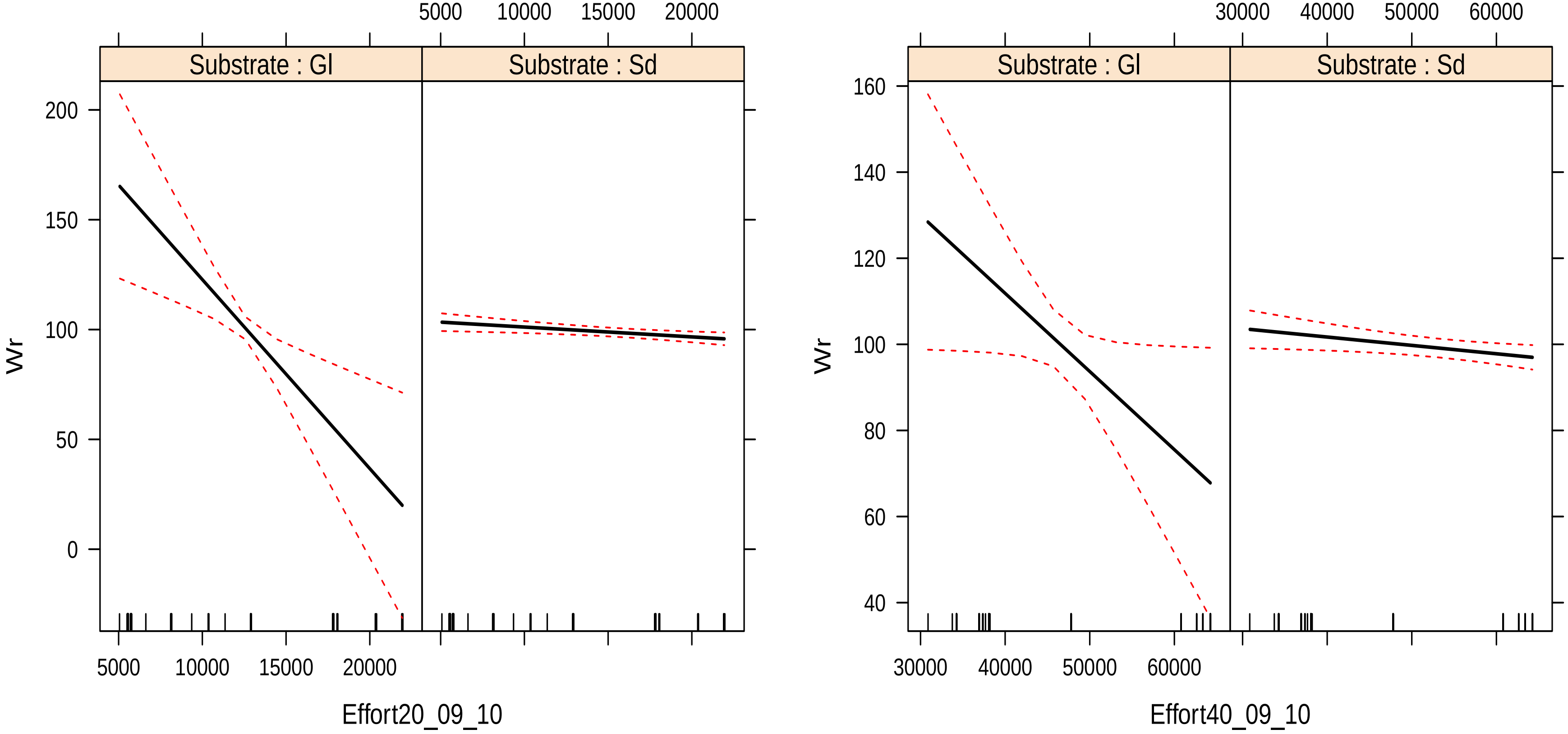
As described above, the analysis indicated some correlations between effort and the diet composition for megrim that were in accordance with the original



(a)

(b)

Figure 5.2: Effect of effort and substrate (Sand – Sd, Gravel – Gl) on condition (Wr) of plaice ($\leq$ 25cm) at (a)20km and (b)40km Effort



(a)

(b)

Figure 5.3: Effect of effort and substrate (Sand – Sd, Gravel – Gl) on condition (Wr) of megrim ($\leq$ 30cm) at (a)20km Effort and (b)40km Effort

Table 5.5: Effects of fishing effort and substrate on Shannon Diversity Index for each species (PLA–Plaice, MEG–Megrim, WHG–Whiting), showing significance level for each model parameter as well as degrees of freedom (d.f.) and percentage deviance explained. Statistical power (β) for sample size (N – number of Hauls), as well as N to achieve $\beta_{0.80}$ is also given

	Effort 20 km			Effort 40 km		
	PLA	MEG	WHG	PLA	MEG	WHG
Effort	0.23	0.03*	0.41	0.31	0.49	0.59
Substrate	0.18	0.32	0.95	0.32	0.19	0.78
d.f.	4.12	4.6	3	3.93	3	3
Dev	63.4%	73.1%	6.9%	58.1%	23.3%	3.4%
N	12	13	14	12	13	14
β	0.21	0.55	0.17	0.17	0.14	0.12
$\beta_{0.80}$	60	26	168	60	221	378

Signif. levels: ***0.001 **0.01 *0.05 ·0.1 Bonferroni correction p = 0.025

hypothesis, however, sample size was also low. Therefore, post–hoc power analyses were conducted to determine the likelihood of detecting a significant effect when one exists, given the observed sample sizes, variance and effect size (Bolker, 2008).

In all cases, the statistical power (β) of the analysis for the given sample size (number of hauls) was below the conventionally acceptable power of 0.80, ranging between 0.12 and 0.55. The results of the power analysis indicated that if sample size were increased (by a factor of 2-27 depending on the species and effort level), a statistically significant relationship between fishing effort and diet in megrim may be detected (Table 5.5).

5.3.3 Diet composition and effort

Due to the lack of sufficient samples on gravel substrate, the relationship between trawling effort and diet composition could only be analysed for sand substrates. Percentage diet composition by prey type for the study species at high and low effort is shown in Table 5.6.

Diet composition for plaice showed high within group variability in both high and low effort groups (average similarity 23.56% and 32.43%, respectively). Polychaetes, bivalves and nematodes were the main diet components.

Diet composition between high and low effort groups differed by an average of 71.02%; polychaetes and bivalves were more abundant at low effort, while nematodes were more abundant at high effort.

Table 5.6: Percentage prey composition of study species stomach contents at high and low fishing effort. Sample size for each species and fishing effort is given

Prey	% Low Effort	% High Effort	Change Low:High
Plaice			
	n = 12	n = 12	
Polycheates	65.1	51.0	Decrease
Bivalves	19.9	10.3	Decrease
Nematodes	5.5	10.3	Increase
Cniderians	2.7	10.3	Increase
Mysids	2.1	0.0	Decrease
Echinoderms	2.1	5.5	Increase
Annelids	0.7	3.4	Increase
Gastropods	0.7	3.4	Increase
Malacostracans	0.7	0.0	Decrease
Nemertea	0.7	4.1	Increase
Spincula	0.0	1.4	Increase
Megrim			
	n = 7	n = 11	
Mysids	42.9	81.8	Increase
Nematodes	21.4	7.8	Decrease
Malacostracans	14.3	6.5	Decrease
Fish	7.1	0.0	Decrease
Euphausids	7.1	0.0	Decrease
Nemertea	7.1	0.0	Decrease
Hemichordates	0.0	1.3	Increase
Bivalves	0.0	1.3	Increase
Decapods	0.0	1.3	Increase
Whiting			
	n = 15	n = 10	
Nematodes	42.3	72.0	Increase
Mysids	38.2	8.0	Decrease
Fish	10.6	8.0	Decrease
Nemertea	4.1	0.0	Decrease
Malacostracans	3.3	0.0	Decrease
Annelids	0.8	6.0	Increase
Polycheates	0.8	2.0	Increase
Bivalves	0.0	2.0	Increase
Amphipods	0.0	2.0	Increase
Lemon Sole			
	n = 9	n = 1	
Hemichordates	0.9	0.0	Decrease
Nematodes	53.8	0.0	Decrease
Polycheates	13.7	11.1	Decrease
Annelids	10.3	0.0	Decrease
Nemertea	8.5	0.0	Decrease
Cniderians	6.8	0.0	Decrease
Spincula	3.4	0.0	Decrease
Decapods	0.9	44.4	Increase
Gastropods	0.9	0.0	Decrease
Malacostracans	0.9	0.0	Decrease
Mysids	0.0	44.4	Increase

Megrim diet composition showed much more within group variability (average similarity 12.36% and 7.94% at high and low effort respectively). Their diet was composed mainly of nematodes and malacostracans (including mysids). Megrim diet differed by 86% between high and low effort groups; mysids, malacostracans and nematodes were more abundant at high than low effort.

Whiting diet composition showed an intermediate within group variability (average similarity 15.30% and 14.49% at high and low effort, respectively). At high effort whiting diet was mostly composed of mysids and small fish. At low effort nematodes dominated the diet, followed by mysids. Whiting diet differed by 88.39% between high and low effort groups; nematodes and small fish were more abundant at high effort that low effort, while mysids were more abundant at low effort.

Due to the low number of lemon sole samples available, their diet composition was not analysed. The differences in diet composition with effort for all three species described above were not found to be significant when an Analysis of Similarities (ANOSIM) was performed, in all likelihood due to the low sample size and high within group variability.

5.4 Discussion/Conclusions

Bottom trawling affects biomass and species composition in the marine benthos (Kaiser et al., 2000). This can result in changes in prey availability and type for benthivorous fishes and has been related to shifts in diet and body condition (Choi et al., 2004). This study found that bottom trawling effects on condition and diet composition were dependent on fish species and size, as well as substrate. The effects of trawling effort on condition were most apparent in small plaice and megrim. For plaice, condition increased with trawling effort and the relationship was more strongly significant at the larger spatial scale examined (effort within a 40km radius). In contrast, the condition of megrim decreased with fishing effort at a more local spatial scale (within a 20km radius). In both cases fishing impacts appeared more pronounced on gravel substrate than on sand substrates, and in the case of megrim substrate and interaction effects were significant. The study results thus support small and variable indirect effects of bottom trawling on feeding success of benthivorous fishes (Shephard et al., 2013).

Observed inter-specific differences in the relationships between condition and fishing effort likely occur due to variation in dietary preference, foraging behaviour and mobility. Obligate benthivores will be more vulnerable than species with a wider prey spectrum. The spatial range over which fish move to forage for food may influence how their condition responds to fishing effort. More mobile species can forage over greater distances and so may have greater access to areas less impacted by fishing, where prey availability may be higher. More sedentary species will be less able avoid negative impacts of fishing on food availability.

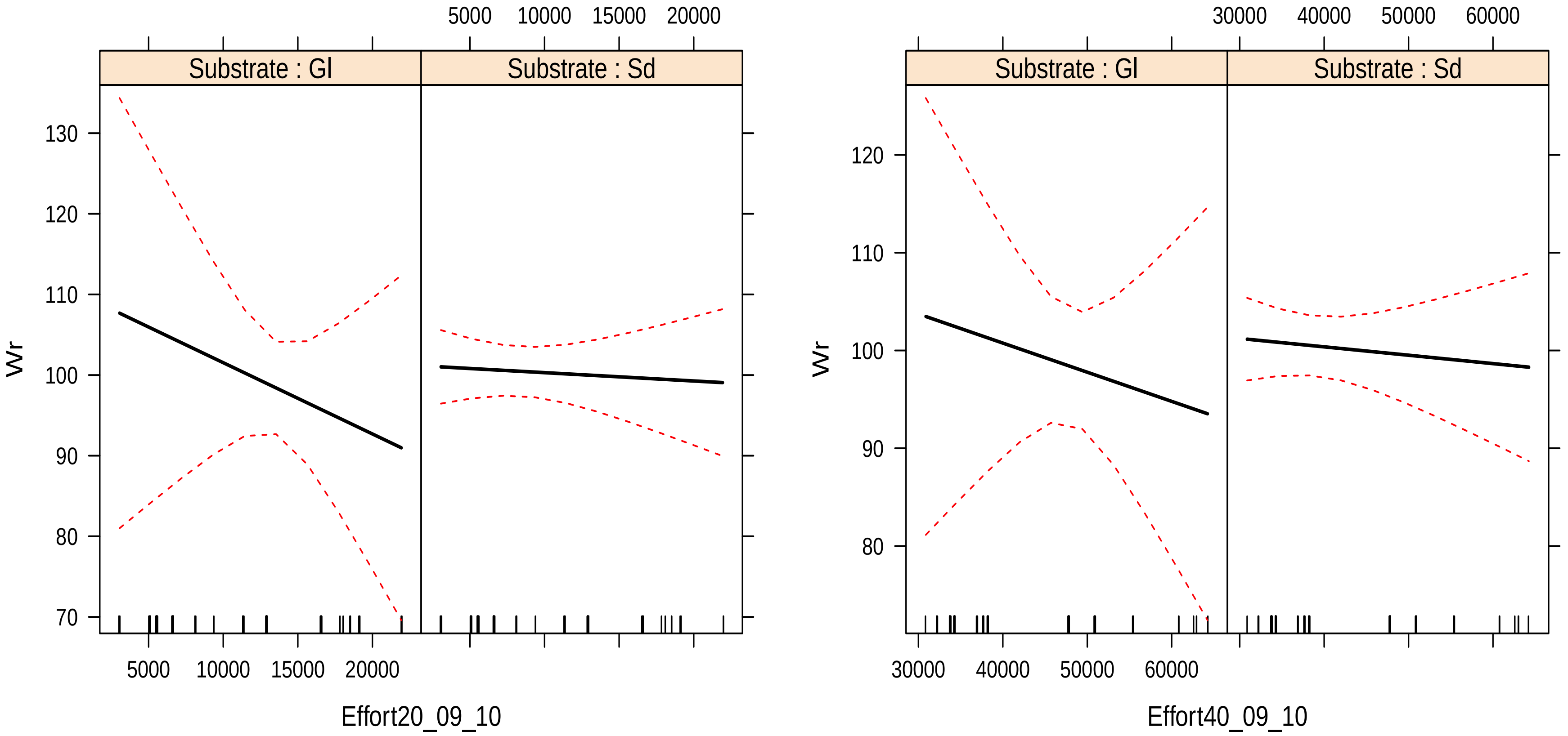
Plaice have a relatively wide range of preferred prey, feeding mostly on polychaetes and molluscs, echinoderms, crustaceans and small bivalves (Piet et al., 1998). Smaller plaice concentrate on ploychaete prey, some of which may actually proliferate at low levels of bottom trawling (Hinz et al., 2009; Shucksmith et al., 2006). While polychaete and bivalve prevalence decreased slightly in plaice stomach contents from high to low effort, other prey items, such as echinoderms, annelids and gastropods increased. This putative increase in their prey likely explains the observed positive relationship between body condition of small plaice and bottom trawling intensity and conforms to the modelling results of van Denderen et al. (2013). Large plaice are also highly mobile, capable of large scale movements (Amezcua et al., 2003; Hinz et al., 2006; Hunter et al., 2003; Jennings et al., 1993), making them more able to exit areas with unfavourable conditions and unsuitable food. Hence, as implied by the results of the present study, large plaice are less likely to show a response to local trawling impacts on the benthos.

In contrast to plaice, megrim have a much more restricted preferred prey range, that consists mostly of mysids and small benthic fish (Šantić et al., 2009). Smaller individuals feed on small bivalves and echinoderms as well as other benthic infauna such as nematodes, malacostracans and euphausids, some of which may be adversely affected by bottom trawling, reducing their biomass and production (Hiddink et al., 2008). As megrim are less mobile than plaice (Gerritsen et al., 2010; Pinnegar et al., 2003), they may be less able to exit an area with poor food availability or may not move, lacking the necessary cues, to search for preferred prey species (Hiddink et al., 2005). In the absence of their preferred prey, they have been shown to switch their prey (Garrison and Link, 2000). The observed decline in condition with fishing effort of small megrim at a more local scale (20km), is consistent with this hypothesis, as is the observed change in stomach contents, with less nematodes, malacostracans and fish but increases in bivalves and decapods. Larger megrim are more mobile and show strong shifts towards piscivory, becoming less reliant on benthic prey and less likely to reflect local trawling impacts on the benthos.

Nematodes are an important component of whiting diet, although there is also a shift towards piscivory with increasing size. Although overall species numbers, diversity and species richness of the nematode community can decrease with chronic high trawling intensity, overall abundance appears not to be affected at low or medium effort levels (Schratzberger and Jennings, 2002), indicating that this type of meiofauna may be more resilient to trawling impacts (Schratzberger et al., 2002). The increase of bivalves, polychaetes and annelids in the diet of whiting at high effort observed in the present study, may occur because whiting scavenge on more prevalent organisms or prey items that are damaged by trawling. Whiting have been observed to target bivalves when scavenging on damaged prey (Kaiser and Spencer, 1994; Groenewold and Fonds, 2000; Shephard et al., 2013). This together with the pelagic nature of whiting (higher mobility), may explain the lack of a trawling effect (Trenkel et al., 2005).

Failure to detect a relationship between condition and fishing effort in lemon sole was surprising. This species may substitute nematodes, their dominant prey at low effort, for mysids and decapods in more heavily trawled areas (Table 5.6). Such prey switching may reduce the impact of trawling on lemon sole condition. However, only one fish was available from the high effort station, so dietary differences must be interpreted with caution. Although the relationships were not statistically significant, condition appeared to decrease slightly with effort on gravel but not on sand (Figure 5.4). This may be indicative of their narrow prey range, consisting mainly of nematodes and polychaetes, which are found primarily on sandy substrates and may be less affected by trawling (Hiddink et al., 2008). A larger sample size would better support investigation of the trawling effects on this species.

The results of this study support those reported by Shephard et al. (2010), in that there was also an increase in condition of plaice associated with effort. However, the study did not find a decline in condition with effort on gravel. This may be due to the larger spatial scale (ICES rectangle) at which habitat was classified in Shephard et al. (2010). In the present study, substrates were defined according to precisely where the sampling station was located on MESH substrate maps, which may be more appropriate for capturing habitat effects on the relationship between fishing and condition. No effects of fishing effort on condition of whiting were detected in this study; this is



(a)

(b)

Figure 5.4: Effect of effort and substrate (Sand – Sd, Gravel – Gl) on condition (Wr) of Lemon Sole at (a)20km Effort and (b)40km Effort

in accordance with the results of Hiddink et al. (2011). However, that study reported a negative effect of trawling frequency on condition of plaice, in contrast to the positive relationship reported in the present study. Hiddink et al. (2011) investigated the impacts of fishing on condition on a much smaller spatial scale, in an area of low natural disturbance, in relative proximity to the coast. Their study area may have been more susceptible to trawling impacts and subject to higher cumulative fishing effects than the Celtic Sea. The apparent differences between gravel and sand substrates, are likely driven by their differential responses to trawling impacts and the differences in the infaunal and epifaunal communities that inhabit them.

Assuming that fishing effects on condition are driven by trawling impacts on food availability, one would expect to see differences in diet between areas of high and low fishing effort. Correspondingly, this study found evidence ($p = 0.03$) for change in prey diversity between high and low effort areas, and these effects corresponded to the fish species and size class for which negative trawling effects on condition were observed (megrim). The statistical power of the analysis was relatively low, but could be improved to acceptable levels by moderate increases in sample size (Table 5.5). However, even with some evidence of a possible link with diet, as reported previously in other areas (Smith et al., 2013), other mechanisms may also contribute to the observed relationships between trawling intensity and condition. As sampling took place during the latter part of the spawning season, the effect of reproductive status on feeding should be taken into account. Plaice have been shown to cease feeding during this period (Rijnsdorp, 1989) and this may have influenced our results. Additionally, fish may adapt to fishing pressure by switching to scavenging on, and switching to, abundant and locally available benthic prey (Smith et al., 2013), so that while trawling may affect them, they can compensate so that effects become very difficult to detect. The observed differences in the stomach contents between fish from heavily trawled and fish from less impacted areas lends support to this hypothesis, although sample size was low. This was one possible explanation put forward by Shephard et al. (2013), for small but variable effects of bottom trawling on trophic level structure of the same fish species. Further investigation would be required to confirm diet as the mechanism underlying the relationship between fishing, substrate and prey diversity/diet composition.

The complexity of observed relationships between bottom trawling, fish condition and diet highlight the imperative for fine scale ecological knowledge in fisheries management. Measures applied without taking into account habitat-specific effects and their interactions with fishing, may have unexpected results (Lloret and Planes, 2003). A well known example is the 'Plaice box' in the North Sea. This technical measure was expected to improve recruitment, spawning stock biomass and abundance (Pastoors et al., 2000). Instead it has led to a shift in distribution and decrease in abundance of juvenile plaice inside the box (Van Keeken et al., 2007). It is hypothesized that the exclusion of trawling inside the box may have resulted in a decline in food production for small plaice. This in turn has caused the plaice to forage for food outside the box, where productivity is higher due to the displacement of fishing effort (Hiddink et al., 2008). This is consistent with our results of enhanced condition of small plaice in more heavily fished areas, which may lead to changes in the benthos that favour their preferred prey (Rijnsdorp and Vingerhoed, 2001). However, the impact of eutrophication and pollution in the area, can also not be discounted as an explanation for the observed changes in the benthos and therefore the indirect effect on plaice condition (Heip, 1995).

The European Union has adopted an ecosystem approach to manage fisheries and the marine environment in the Marine Strategy Framework Directive (MSFD, 2008/56/ EC), which has the main objective of maintaining the good status of marine waters, habitats and resources (Borja et al., 2010). Identifying drivers of change in feeding success and thus condition of target fish species may have implications for fisheries management, as this will guide decisions as to how fishing effort should be distributed in space (habitat) and time (intensity and season).

The current study, while suggesting an indirect link between bottom trawling and condition of benthivorous fishes and identifying a possible mechanism by which this occurs (diet), illustrates the need for habitat specific ecosystem based management. It also highlights the complexity in interactions between trawling effort, fish condition and habitat. The mechanisms behind these processes will require further investigation.

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Chapter 6

General Discussion

6.1 Overview

"I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea fisheries, are inexhaustible; that is to say, that nothing we do seriously affects the number of the fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless."

Thomas Henry Huxley PC FRS, Inaugural Address 1883 Fisheries Exhibition, London

Humans have been exploring the oceans and making use of the resources it provides for thousands of years. When Huxley gave his famous inaugural address in 1883, while problems of overexploitation with inland fisheries were acknowledged, the oceans fishery resources seemed plentiful and boundless. It was almost inconceivable at the time, although there were dissenting opinions and cautions (Lankester, 1884), that this could change. The vast industrialisation and mechanisation that characterises modern fishing fleets today was, after all, unimaginable in an era when the tall ships still ruled the high seas.

As sailing vessels were replaced by steam and later diesel powered boats, and refrigeration capabilities and gear efficiency improved, the exploitation of fisheries resources also grew in scale and range. As industrialisation and mechanisation progressed, allowing for more and more fish to be caught, it was soon found that the great sea fisheries were anything but inexhaustible. Today, many commercially exploited fish species and ecosystems are experiencing increasing pressure from fishing, resulting in marked declines in abundance (Callaway et al., 2007; Hutchings et al., 2010), the restructuring of exploited communities and sometimes regime shifts to an alternate ecosystem state (Choi et al., 2004; Collie et al., 2000). The Canadian cod fishery is perhaps one of the best known and well studied cautionary tales in fisheries science in this regard. The cod has been called "the fish that changed the world" (Kurlansky, 1998) because it had such an historic impact on the fishing industry and associated communities, but perhaps it deserves the distinction even more for its impact on fisheries science and management.

Fisheries scientists, managers, marine ecologists and biologists all face a problem that many of their terrestrial colleagues do not have. The study species, habitats and oceanographic processes they are interested in are normally not readily available to them. The early life stages of many commercially important fish species are highly mobile, small and very difficult, if not impossible, to observe or follow directly in a non-laboratory setting. The habitats they inhabit are diverse, may change depending on life cycle stage and are often difficult for scientists to access. The species of interest interact with other species and their environment within complex ecosystems, which are in a constant state of change as a result of climate change, pollution, coastal development and overfishing.

While the body of work on fisheries biology and ecology grows and new questions arise, it is perhaps not surprising that there are divergent schools of thought about the current state and future of our fisheries resources (Hilborn, 2010). There are those that advocate for drastic reductions in fishing pressure to avoid further depletions in biodiversity, which ultimately lead to fishing down the food web (Pauly et al., 1998; Pauly, 2009). Worm et al. (2006) maintained that if current exploitation trends continue all fish stocks would collapse by 2048. Others, advocate for a more balanced approach, while agreeing that there are problems that need to be addressed in order to achieve the common goal of higher abundances and lower fishing pressure (Murawski et al., 2007). It was subsequently shown, that not all fish stocks would collapse by 2048 (Branch, 2008). While a considerable number of stocks are still below sustainability target levels and 30% of fish stocks for which data is available are overfished, fishing pressure had been reduced to a point where all but 17% could recover above overfished levels at current fishing rates (Worm et al., 2009; Hilborn, 2010). The concept of fisheries systematically fishing down marine food webs (Pauly et al., 1998) has recently been challenged; changes in the trophic level of catches may reflect the targeting of different species (that may have a lower trophic level) to maximise economic benefits (Essington et al., 2006), rather than a real change in community structure (Sethi et al., 2010). Furthermore, the trophic level of landings may not accurately reflect the trophic level of the ecosystem (Branch et al., 2010) and top predators are less affected by fishing pressure than would be expected (Hutchings et al., 2010), while lower level species show higher rates of collapse (Pinsky et al., 2011).

Even if the above schools of thought may never be reconciled, there is wide agreement that current fishery management systems need to be overhauled to take on a more precautionary ecosystem based approach. This type of management approach works best in areas were abundant information is available, such as the North Sea (ICES, 2012), while for data poor areas and stocks, only basic measures such as precautionary catch reductions can be taken. Efforts to provide basic information on the ecological and oceanographic processes that affect a species, are the first step in a bottom up approach of information gathering, upon which future management plans for these data poor stocks and ecosystems can be based. Providing up to date information on these processes is vital in view of fisheries induced evolution, that can shift the reference points used in fisheries management (Heino et al., 2013), and the ability of populations to adapt to the predicted impacts of climate change (IPCC, 2007).

Information obtained from otoliths has been used to provide insight into a range of issues that are pertinent to fisheries management, including larval dispersal, population connectivity, larval and juvenile growth and survival and recruitment variability (reviewed in Sponaugle, 2010). This thesis is part of such efforts to provide information on aspects of the early life history, growth and condition of plaice populations in Irish and Scottish waters for which currently only limited data are available. While it may not be of immediate use to fisheries managers, it does increase our understanding of the biology, ecology and early life history characteristics of the plaice populations in these regions, while providing information on the influence of environmental conditions on these traits. In so doing it provides a small piece in the puzzle that scientists are trying to piece together to understand the drivers of variability in fish stocks occurring at all stages of the life cycle. This information can then inform the development of predictive models, taking account of environmental variability. The assessments based on these predictive models, will allow fisheries managers to make scientifically sound, informed decisions to manage fisheries sustainably in a changing environment, while protecting the ecosystems they are a part of.

6.2 Early life history and Growth

Age and growth information obtained from otoliths and other calcified structures such as scales, have formed the basis of single species models used in fisheries management for decades. The importance of the early life stages and their fate to fish population dynamics was highlighted by Hjort in 1914 (Houde, 2008). The discovery of daily increments in otoliths by Pannella (1971) has allowed scientists to qualitatively and quantitatively investigate many aspects of larval and juvenile ecology. Identifying the ecological and oceanographic processes that affect these stages is important, because of their impact on population replenishment and recruitment, which have consequences for population persistence and resilience (Cowen and Sponaugle, 2009). Currently, for management purposes, fish populations are divided up into management units, which do not always reflect the actual population structure or take account of connectivity and exchange. This can increase the risk of overexploitation or depletion (Ying et al., 2011).

Growth information stored in otoliths can provide insight into population structure. Groups of fish that are exposed to different environmental conditions during their lives, are likely to possess distinct otolith growth trajectories. In addition, population based differences in the growth marks associated with life history transitions (hatching, settlement and migration) can occur (Geffen, 1992; Campana, 2005; Folkvord et al., 1997, 2004). Otolith growth marks have been used to elucidate population structure in many species and environments (Brophy and Danilowicz, 2002; Clausen et al., 2007; Begg et al., 2001; Dawson, 1991; Buratti and Santos, 2010). Spatial variation in early life history characteristics and growth patterns, can also be indicators of larval and juvenile origin, connectivity and habitat quality (Brophy and King, 2007; Gibson, 1994; Van der Veer et al., 2010; De Raedemaecker et al., 2012).

It has been hypothesised that larval traits, such as fast growth rates, can carry over into juvenile life and beyond. Much of the support for the hypothesis comes from extensive investigations in coral and temperate reef fish has been hypothesised and investigated extensively in coral reef fish (Smith and Shima, 2011; Sponaugle et al., 2006; Sponaugle and Grorud-Colvert, 2006; Grorud-Colvert and Sponaugle, 2006). When pre–recruitment growth affects subsequent growth and age at first spawning, this can have implications for lifetime fecundity (Brophy and Danilowicz, 2003). In this study, larval growth rates were significantly correlated with juvenile growth 30 days after settlement (Chapter 2), which may reflect such a “carry over” effect. However, the correlation may also be indicative of variable habitat quality. Differences in juvenile habitat quality may also explain the regional differences observed in otolith growth trajectories. The growth of many juvenile flatfish in coastal nursery areas, including plaice, has been shown to be influenced by spatial variation in habitat quality, via factors such as food availability (Van der Veer et al., 2010; Wennhage and Gibson, 1998), sediment type (Amezcua and Nash, 2001; Hinz et al., 2006), temperature (Gibson et al., 2002) and salinity (Augley et al., 2008).

This study provides basic early life history and growth information on the relatively data poor plaice populations in Irish and west Scottish waters. This is an initial step towards informing the management of these stocks. Population specific growth differences can have direct applications to stock assessment and management. For example in herring, otolith growth patterns have been used to separate spawning components within mixed fisheries and assess temporal variability therein (Bierman et al., 2010; Clausen et al., 2007; Brophy and Danilowicz, 2003; Brophy et al., 2006; Burke et al., 2009), to quantify stock mixing (Geffen, 2009), and to assess larval and juvenile origin and connectivity between spawning and nursery areas (Brophy and King, 2007; Brophy and Danilowicz, 2003). Management needs to take account of such information, because single stock management may not be appropriate in situations where exploitation is not uniform across spawning or population components, leading to loss of diversity (Bierman et al., 2010), loss of subpopulations and productivity (Holland and Herrera, 2012). Information on larval and juvenile origin can inform spatial habitat management and is also important in terms of quality and quantity of recruits, as fish from different nursery grounds may show variable growth, maturation and recruitment (Brophy and Danilowicz, 2003). Currently the plaice stocks in the west of Ireland and west of Scotland are not of high commercial interest. However, this may change as stocks in other regions or catches of current target species decline. Thus, the information provided by this study, in combination with data from for example microchemical or dispersal studies (Ashford et al., 2010), will increase understanding of population structure and will be valuable for future assessments. It may also allow us to detect possible detrimental effects of current fishing levels.

Temperature has been well established as an important influence on plaice larval growth and the duration of the pelagic phase (Chapter 2; Van der Veer et al., 2009; Green and Fisher, 2004; McCormick and Molony, 1995; Comerford et al., 2013). Temperature effects on growth and larval duration, as well as changes in oceanographic conditions may also lead to changes in dispersal pathways of larvae (Chapter 4), changing population connectivity and thus affecting population replenishment and persistence (O'Connor et al., 2007). Increasing temperatures, associated with climate change could therefore impact growth, survival and dispersal of plaice (Teal et al., 2008; Van Keeken et al., 2007; Van der Veer et al., 1998). Ecosystem shifts potentially triggered by climate change could thus impact exploited fish populations, such as plaice, throughout their life cycle. Global ocean temperatures are predicted to rise, with extreme weather events thought to increase as a result of global warming (IPCC, 2007). Changing seasonal temperatures are likely to affect the timing of fish spawning and could influence egg development and growth rates (Fox et al., 2003), size at hatching and survival, particularly among larval fish, which are more sensitive to environmental fluctuations (Pankhurst and Munday, 2011). Global warming is also likely to shift the distributions and geographic ranges of fish species (Stenevik and Sundby, 2007), while climate-driven changes in the suitability of nursery grounds will directly affect their productivity (Hufnagl et al., 2012). The movement of other species into new habitats, affects marine food webs, impacting on commercial species such as plaice in the North Sea via juvenile predation and competition for food sources (Van Hal et al., 2010). In the Baltic Sea, size in the summer plankton community has been shown to decrease in response to climate change, lowering energy availability for zooplankton and planktivorous fish (Suikkanen et al., 2013). Increasing temperatures may also affect habitat quality of nursery areas. It is proposed that this may have positive impacts on some flatfish species e.g. sole and negative impacts on others e.g. North Sea plaice (Teal et al., 2008). In view of this wide range of possible impacts, it may be necessary for more uncertainty to be incorporated into predictive models to account for the greater fluctuations in recruitment likely to result from climate change.

6.3 Larval and juvenile origin

The life cycles of many marine organisms, including flatfish, are complex, making it difficult to trace the offspring from egg to the larval, through the juvenile to the adult stage. In order for ecosystem based management systems to be effective however, it is vital to know not only the natal origins (spawning grounds) and nursery areas of the fish, but also the connectivity and exchange that exist between them. Without such knowledge, two tenets of ecosystem based management cannot be met, namely the delineation of appropriate spatial scales and stock units over which such management should occur, as well as the specification of sub-areas within the larger management unit that should be protected from exploitation (Fogarty and Botsford, 2007). The modelling approach used in (Chapter 4) allowed for the identification of likely spawning grounds and larval dispersal pathways. The observed differences in otolith growth trajectories (Chapter 2) and elemental composition (Chapter 3) could potentially be used to assess connectivity of plaice spawning and nursery grounds. The outputs of this thesis will therefore assist progress towards more ecosystem based management of plaice in Irish and Scottish waters.

Marine Protected Areas (MPA's), have been proposed as a solution to failure of conventional fisheries management (Worm et al., 2006). The purpose of MPA's is to increase fish density, biomass, mean size and diversity. This should theoretically spill over into fished areas, increasing yields. However, a study by Halpern (2003) showed mixed success of MPA's with 37% showing no increase in density, 4-10% no increase in biomass, 11-20% no size increases and 24-41% no increases in diversity. Conversely, a study using discrete time models by Rodwell and Roberts (2004) found that marine reserves could increase the probability of reaching target levels of biomass, while reducing catch variability in neighbouring fisheries, and adequate marine reserve coverage could prevent fishery collapse, with reserve size depending on prevailing levels of exploitation. Overall, while the effectiveness of MPA's may vary between taxa and fishing intensity inside and outside the area needs to taken into consideration prior to implementation, the positive effects outweigh the negative (Lester et al., 2009). However, for MPA's to be effective management tools, high resolution data on fish population structure and dynamics is required. The potential insights into population connectivity, offered by regional and nursery ground specific differences in otolith growth (Chapter 2) and composition Chapter 3, could inform the planning and implementation of MPA's for plaice.

Otolith microchemistry has been used extensively in recent years to inform fisheries management and can, in some cases, provide higher resolution data than even genetic techniques (Thresher, 1999; Campana et al., 2000). For example, in Atlantic herring, the elemental composition of otoliths has been used to assess the extent of mixing between herring populations to the west of the British Isles (Geffen et al., 2011), which could not be distinguished using genetic techniques, although they show sufficient behavioural and ecological separation to benefit from segregated management (Brophy and King, 2007).

Otolith microchemistry has been used in other species to discriminate stock identity (Swan et al., 2003), elucidate migration histories (Tzeng and Tsai, 1994; Correia et al., 2003; Feyrer et al., 2007), give insight into early life history events (Toole et al., 1993; Arai et al., 1999; Correia et al., 2004), assess the influence of environmental conditions on larval quality (Shima and Swearer, 2009), provide information on dispersal histories and mixing (Miller and Shanks, 2004; Di Franco et al., 2011) and to identify spawning and nursery origin of larvae and juvenile fish (Schaffler et al., 2009; Gillanders and Kingsford, 2000; Vasconcelos et al., 2007, 2008; Brown, 2006). The relative contribution from different nursery grounds to spawning aggregations can also be assessed (Yamashita et al., 2000; Tobin et al., 2010), as can connectivity of estuarine and coastal habitats (Gillanders, 2005). While otolith microchemistry can be used to trace large scale movements of fish with higher resolution and at different life stages (Darnaude and Hunter, 2008), than conventional tagging methods, it has also been shown to be of use to inform of small scale juvenile movements within and between nurseries (Fodrie and Herzka, 2008). Thus otolith microchemistry is capable of providing fine scale insight into habitat utilization and habitat shifts between juvenile and adult stages. All of these insights are of importance to management, as they allow for the effective application of spatial habitat management tools. Information derived from elemental composition of otoliths is therefore useful to fisheries management because it can give very fine scale insight into population structure and connectivity of many fish species, in both marine and freshwater habitats, including commercially important species, such as sole in the North Sea (Cuveliers et al., 2010).

Otolith elemental composition may be useful to eventually provide information on population structure and connectivity of both Scottish and western Irish Sea plaice populations, which although currently not directly targeted, may become so in the future. In this study (Chapter 3), sufficient variation was found in otolith elemental composition to allow successful classification of juvenile plaice at both regional and local (nursery ground) scales.

Whole adult otolith elemental fingerprints are mostly used to track fish movements or identify the components of mixed populations over short periods of time, while analyses of the larval or juvenile otolith core are more useful as direct markers of stock or nursery origin (Campana, 2005). Whole otolith chemistry has been applied to elucidate the migrations and mixing of cod stocks in Canada (Campana et al., 2000). In Iceland, the juvenile source of spawning adult cod was determined using the chemical signature of the juvenile portion of the adult otolith Thorisson et al. (2011). In the future, whole otolith chemistry may allow us to assess the extent of mixing among plaice populations in western Scotland and the western Irish Sea, and thereby the contribution of the different components to any eventual fishery.

Nearshore estuaries and marine ecosystems, such as sandy beaches, seagrass beds, marshes and mangrove forests serve as important sources of primary and secondary production and harbour a large and diverse number of fishes and invertebrates (Beck et al., 2001). These areas also serve an important ecological function as nurseries for many fish species, as there they tend to experience lower rates of predation and higher rates of growth than in other habitats (Gillanders et al., 2003). The link between juvenile (nursery) habitat and adult habitat is important to fisheries management because these habitats export substantial amounts of juvenile biomass into the adult population (Beck et al., 2001; Gillanders et al., 2003) and thus serve an important function in the recruitment process of many species, including plaice (Bergman et al., 1988). Thus, it is not only important for management to identify areas that provide high juvenile densities, enhanced growth and survival, but also to assess their relative contribution to the adult stock. This has been done for a variety of species, including northern bluefin tuna in the Pacific and some flatfish species (Vasconcelos et al., 2008; Brown, 2006). Along the Portuguese coast, the estuarine origin of five commercially important fish species, including sole, flounder and sea bass, was successfully discriminated using otolith elemental composition of juvenile otoliths (Vasconcelos et al., 2007). Analysing the juvenile core of adult fish will allow fish to be traced back to their nurseries using this elemental habitat tag, establishing connectivity between estuarine and coastal habitats. The population structure of black seabream (*Spondyliosoma cantharus*), was also successfully analysed using whole otoliths and cores, suggesting the population consist of distinct local population units, that share a spawning ground, which exports recruits to different coastal fishing areas (Correia et al., 2012a). Otolith chemistry can also be used, to assess to what extent fish move away from their nurseries to supply other nurseries and/or fisheries (Gillanders, 2002a). The dispersal pathways of the coral reef fish *Chromis viridis* (Pomacentridae), were investigated by Ben-Tzvi et al. (2008), who found that the populations originated from different sources, dispersing along various routes. Small scale fish movements within and between nursery areas as examined by Fodrie and Herzka (2008), using otolith elemental fingerprints, are also important to establish the integrity of population units, to allow for adequate spatial habitat management. This will ensure that misclassification of adults to nursery areas remains at a minimum, due to similarities in elemental fingerprints from similar environmental conditions. Fisheries management can make use of such information to assess whether or not a population is capable of self-sustaining, or dependent on input from other populations, to persist. Further it also allows management to assess the scale on which management measures should take place, at the local or regional level and whether international collaboration may be required.

For this approach to be used to link juvenile and adult habitats in the regions examined in this study, ideally all, but certainly the major nursery areas in the regions, would need to be characterised. A library of nursery specific elemental fingerprints could then be established, taking temporal stability into account, for use in stock identification and connectivity studies (Gillanders, 2002b). In the case of the west coast of Scotland, the spawning ground(s) of plaice in the region would need to be located, so that adult fish could be traced back to their origin and their contribution to the population assessed. Eventually, data from such microchemistry studies can be integrated with data from other sources (Bradbury et al., 2008; Waples et al., 2008; Smith and Campana, 2010; Correia et al., 2012b; Ashford et al., 2010) to provide more holistic and fine scale insight into stock identity, population structure and connectivity of plaice populations in Irish and west Scottish waters for future assessment and management purposes.

6.4 Dispersal

Population connectivity, whereby populations are linked via the dispersal of their larvae, juveniles and/or adults, requires individual exchange between these respective populations and successfully settlement into the recipient population (Sale et al., 2005; Lacroix et al., 2012). The spatial scales over which these exchanges occur can be as wide ranging as the purpose, such as feeding, reproduction and finding suitable habitat. These movements thus result in a myriad of connections so that a process taking place at one location has to potential to impact processes at another location (Gaines et al., 2007). Thus, it is important for management purposes to elucidate connectivity at all phases of the life cycle, but in particular during the early life stages, where due to the difficulty associated with tracking them, there are still knowledge gaps (Lacroix et al., 2012). Of particular importance is the connectivity between spawning and nursery grounds and the processes that affect larval dispersal and retention (Gaines et al., 2007; Cowen and Sponaugle, 2009). As the use of Marine Protected Areas to manage highly mobile species becomes more prevalent, the spatial scale of larval dispersal, the factors influencing it and the connectivity of spawning and nursery grounds becomes even more important. This is because the distance and direction in which larvae disperse, termed dispersal envelopes, will determine three key issues, namely a) the size of the reserve or the area needed to ensure sufficient self-recruitment to safeguard persistence, b) the placement and spacing of these areas to promote persistence of the target populations by dispersal among them and c) the potential benefit that the size, spacing and placement of these areas will provide to neighbouring fisheries by via recruitment subsidies (Sale et al., 2005).

Obtaining information on these dispersal envelopes is difficult, because the larval stages of marine species impossible to track directly (Gaines et al., 2007), and dispersal patterns are species, site and time specific, affected by a complex interplay of sensory capabilities, behavioural responses and hydrodynamic conditions (Sale and Kritzer, 2003; Sale et al., 2005). Individually-Based Coupled Physical Biological Models (ICPBM), as their name suggests, combine the physical environment with biological information to allow us to bridge this knowledge gap. The incorporation of behavioural characteristics has been recognised as an essential component of these models (Leis, 2007), as larval behaviour has been shown to significantly affect growth, mortality and dispersal patterns (Fiksen et al., 2007).

On the west coast of Ireland, the locations of plaice spawning grounds are currently unknown. The Atlantic coast of Ireland is regularly in the path of strong weather systems, with south westerly prevailing winds and northward offshore currents (Fernand et al., 2006). Galway Bay thus is ideally located to act as a catchment area for larvae spawned on the continental shelf just inside or outside the Bay. The Bay itself has an anticlockwise residual current, also aiding ingress of larvae from outside (White, 1996). These oceanographic conditions would suggest the location of the spawning ground delivering larvae to nursery areas in Galway Bay to be to the south of the entrance. In this study, a region specific ICPBM for the west coast of Ireland was developed to simulate plaice larval dispersal from proposed spawning grounds to nursery areas in Galway Bay (Chapter 4). While the main aim was to locate the probable spawning ground of the settlers that ingress into Galway Bay, the model was also used to investigate the relative importance of passive transport, behaviour and individual growth rates on successful delivery of larvae to nursery areas. A likely spawning area was located and the importance of individual behaviour for delivering larvae to shallow coastal areas was highlighted. The model outputs also show how interannual variability in temperature and larval growth rates could potentially influence plaice dispersal.

ICPBM's have been used successfully to describe larval dispersal and elucidate spawning grounds of other species in other regions, including commercially important fish species such as plaice, sole, haddock and King George whiting (Van der Molen et al., 2007; Fox et al., 2006, 2009; Van der Veer et al., 1998, 2009; Savina et al., 2010; Lacroix et al., 2012; Brickman and Frank, 2000; Jenkins et al., 2000), crabs (Peliz et al., 2007) and coral reef fishes (Porch, 1998; Danilowicz and Sale, 1999). Coupled biophysical models can potentially assist in conservation, management and recovery efforts. They are currently capable of simulating transport patterns, temperature and prey abundance; thus providing insight into early life stage dynamics variability, connectivity and the influence on environmental variability on recruitment (Hinrichsen et al., 2011).

The applications of ICPBM's are not limited to modelling dispersal patterns alone. For Anchovy (*Engraulis encrasicolus*) in the Bay of Biscay, ICPBM's were used to produce a survival index and determine the impact of fluctuations in survival on recruitment variability (Allain et al., 2007; Huret et al., 2010). Spatially explicit information, provided by ICPBM's, can be used in conservation and management efforts, to protect areas of importance because of their contribution to recruitment, but also to find areas to sample for particular life stages or even evaluate possible impacts of climate change (Hinrichsen et al., 2011). Mortality estimates derived from ICPBM's can be incorporated into population dynamic models, to provide more realism and improve their outputs, when testing the effectiveness of spatial management measures under various recovery scenarios (Lehuta et al., 2010; Hinrichsen et al., 2011).

In order to identify spawning grounds that had the potential to enhance the survival of the early life stages of cod and sprat, Daewel et al. (2008, 2011) combined a hydrodynamic model, a particle tracking model, a foraging and growth model and a lower trophic level model incorporating nutrients, zooplankton, phytoplankton and detritus (Hinrichsen et al., 2011). The study confirmed that the North Sea was an important nursery area for both species and the location of survival enhancing spawning grounds was in accordance with Fox et al. (2008). Temperature was found to affect cod survival rates but not sprat, with cod doing better in colder years. The lower trophic level model and particle tracking model, showed that this was due to higher prey abundance and favourable oceanographic conditions for cod (Daewel et al., 2008, 2011; Hinrichsen et al., 2011).

Oceanographic conditions have been shown to be of particular importance for species with specific habitat requirements, such as flatfish (Van der Veer et al., 1998). Connectivity of spawning and nursery grounds has been examined using modelling approaches (Bolle et al., 2009). Using a hydrodynamic model, including temperature dependent development and stage specific behaviour, Hufnagl et al. (2012) tested the hypothesis that the location of spawning grounds is determined by the location of nursery grounds and prevailing current between them. The 31 year simulation period also allowed Hufnagl et al. (2012) to investigate the effects of climate change on the distribution of active spawning grounds. Temporal trends in transport success were linked to changes in circulation patterns, temperature and currents. Therefore, climate change would be expected to affect the suitability of nursery areas with consequences for plaice distribution and productivity (Hufnagl et al., 2012). The behaviour of larvae has been shown to be an essential component of modelling approaches, as it can play a significant role in model outputs (North et al., 2009; Pineda et al., 2007), as was also illustrated in the present study. Therefore improving the behavioural algorithms of models to achieve increased realism should be attempted when possible.

ICPBM's are thus valuable tools for management. While they provide us with greater insight primarily on the physical processes affecting marine life, they can also give insight not only into connectivity, but also survival, settlement success, transport of different life stages, as well as the effects of temperature and food availability in a quantitative manner. They can thus be used to enhance management plans, as information obtained can be used to improve stock recruitment relationships, re-evaluate biological reference points, estimate the necessary scale and location of marine protected areas, as well as investigate the direct and indirect effects of climate change (Hinrichsen et al., 2011). In this regard their hindcast ability may be a valuable feature, as we may be able to better understand the biotic and abiotic processes, that have lead to the distributions and abundances of fish species today, thus allowing us to learn from the past to shape the future of our fisheries resources.

6.5 Ecosystem effects of Fishing

Fishing activities have both direct and indirect effects on marine ecosystems. As well as increasing the mortality of the target and by–catch species (Lewison et al., 2004), fishing gears can result in habitat disturbance and destruction

(Pranovi et al., 2000; Moran and Stephenson, 2000). Discarding by fisheries is also problematic because while it can provide food for scavenging species, it can also result in high numbers of immature fish being killed (Borges et al., 2005). Fisheries also remove prey of other fish, birds and mammals (Tasker et al., 2000) and reduce predator populations. This will cause imbalances in competitive interactions between species, sometimes leading to proliferations of other non-target or undesirable species, from a human point of view (Jennings and Kaiser, 1998; Shiganova and Bulgakova, 2000).

Owing to the complexity of the ecosystems in which fisheries operate, it is not surprising that trying to quantitatively describe the ecosystem effects of fishing, will lead to unexpected (Hutchings et al., 2010; Pinsky et al., 2011) and sometimes contradictory results (Shephard et al., 2010; Hiddink et al., 2011). In addition, fisheries induced evolution results in shifting reference points, making it even more difficult to estimate fishing impacts (Heino et al., 2013). With the predicted increase in world population, demand for fish is likely to exceed current supply. While this is likely to result in the overexploitation or even stock collapses of target species, the effects on non-target species and ecosystems as a whole are not clear, although changes in structure and function can be expected (Gislason et al., 2000). Maintaining sustainable fisheries, capable of satisfying demand, requires healthy and productive marine ecosystems. Therefore, it is paramount to elucidate ecosystem wide effects of fishing in order to design efficient management plans, that will maintain ecosystem health and productivity.

While fishing activities have considerable quantifiable direct effects, such as marked declines in abundance (Callaway et al., 2007; Hutchings et al., 2010), population collapse, restructuring of marine communities and ecosystem regime shifts (Choi et al., 2004; Collie et al., 2000), they are also likely to have indirect effects that may not be as readily quantifiable. Fishing induced reduction in biomass and production of the benthos, is speculated to indirectly drive declines in condition and growth rate of several fish species that prey on this community (Hiddink et al., 2011; Lloret et al., 2007; Shephard et al., 2010).

In an attempt to provide further insight into this issue and elucidate a possible explanatory mechanism, in this study, the indirect effects of bottom trawling on diet and body condition of three flatfish (*Microstomus kitt*, *Pleuronectes platessa*, *Lepidorhombus whiffiagonis*) and one gadoid species (*Merlangius merlangus*) were investigated (Chapter 5). Any such indirect effects of fishing were likely to be very difficult to quantify, and this was the case in the present study. While the relationship between trawling effort and condition was significantly positive for small plaice and negative for small megrim as expected, the condition of the other species and size groups was not affected significantly, although condition of small lemon sole declined somewhat. The observed effort effect appeared to be linked to species mobility, with condition of more sedentary species being more strongly related to effort within a smaller spatial range, while condition of more mobile species was related to effort over a larger spatial range. Although there seemed to be a size and mobility effect related to fishing effort, this was not consistent, and while stomach content analyses suggested that diet may be a possible driver, as previously reported (Smith et al., 2013), prey diversity was only significantly affected in one species. These inconsistencies may be a reflection of the ability of some of these species to substitute their usual prey by scavenging. This may lead to small but variable effects of bottom trawling, such as those reported by Shephard et al. (2013), that may not be profound enough to result in a significant effect on condition in species where this may be expected.

The impact of natural mortality and predator prey relationships need to be taken into account when assessing fisheries impacts on marine ecosystems. Fishing may directly affect species composition as the relative sensitivity of species to increased mortality may differ. This is because species with a low natural mortality are thought to be more sensitive to exploitation than species with high natural mortality, because increases in fishing mortality will increase overall mortality rates (Daan et al., 2005). Predator/prey relationships are also important, as they may impact the effectiveness of management measures. Sprat and herring prey on the eggs of many commercially important fish species, including plaice and cod. In the Irish Sea sprat were found to consume up to 73% of plaice eggs spawned (Plirú et al., 2012). Thus, the abundance and distribution of this pelagic predator may have important consequences for the recruitment dynamics of other fish species and therefore need to be taken into account in management and recovery strategies.

Fisheries have also been linked to changes in plankton community structure, through grazing changes. This affects marine ecosystems at the lowest trophic levels, via both bottom up and top down effects (Reid et al., 2000). Such top down effects have been shown to occur in other areas, such as kelp forests and coral reefs, where fishing has lead to proliferation of sea urchins (Tegner and Dayton, 2000) and reduction of herbivory (McManus et al., 2000), respectively. This resulted in the reduction of productivity of kelp forests and loss of habitat for other species, that use kelp forests as shelter. Reduced herbivory on coral reefs, through removal of grazing fish, has resulted in algal proliferation and organic pollution, even without eutrophication (McManus et al., 2000). Fish species experience the direct effects of fishing through increased mortality in the short term. Over longer time periods, fisheries will impact their size structure, and on a system wide scale, the diversity of the fish community, as has been shown for demersal fish species (Bianchi et al., 2000). Even though the trophic guild structure of some systems may remain stable under various forms of exploitation, in the long term, heavily exploited species will decline in abundance and their distributional range will decline, decreasing overlap with other species. The opposite is the case for weakly exploited species, as shown for the fish community in Georges Bank (Garrison and Link, 2000). The fishing methods themselves can also have direct impacts. Fish aggregation devices (FAD's), used in tuna fisheries, have been shown to impact migration and productivity of this species (Ménard et al., 2000). Some marine ecosystems have also been shown to be more severely impacted by fishing activities than others. Deep sea and continental slope fish are particularly vulnerable to overexploitation, due to their spatial and reproductive isolation, slow growth and low fecundity (Koslow et al., 2000). In some cases, such as enclosed seas, the effects of fisheries and anthropomorphic impacts, such as nutrient inputs, may be difficult to disentangle. In these cases while fisheries impacts are serious, they may be secondary and synergistic, but potentially catastrophic under hypoxic conditions, since eutrophic processes make demersal ecosystems particularly sensitive to disturbance of bottom habitats (Caddy, 2000).

As we move away from single species management towards ecosystem based management systems, employing multi-species models (Hollowed et al., 2000), the assessment of the past, present, and future states of marine ecosystems and the impact of anthropomorphic and climate effects are crucial to the scientific advice required for their implementation (Livingston et al., 2005). The production of environmental assessments and impact statements has been part of environmental protection legislation for many decades, such as mandated by the National Environmental Policy Act of 1969 in the United States (Livingston et al., 2005). However, until recently they have not been seen as useful tools in fisheries management, to scientifically evaluate ecosystem impacts of fisheries. Their use would provide useful advice on impact reduction, allowing informed choices to be made by fisheries managers selecting management strategies and measures (Livingston et al., 2005). The ecosystem based management framework has been applied in the United States to the Alaska groundfish fishery. This has resulted healthy fisheries, providing yields of 2 million tonnes a year (Witherell et al., 2000). The applied approach is multi-faceted, employing the precautionary principle and involves public participation, reliance on scientific research and advice, conservative catch quotas, comprehensive monitoring and enforcement, by-catch controls, gear restrictions, temporal and spatial distribution of fisheries, habitat conservation, and other biological and socio-economic considerations (Witherell et al., 2000).

Indicators of fisheries impacts, that are used to quantify the state of the system, include measuring the total catch and trophic level of catch (although caution is warranted, see Essington et al. (2006)) to assess disruption of predator/prey relationships and ingress of non-native species. The availability of forage fish is determined by assessing trends in key forage species, in this case walleye pollock and Atka mackerel. By-catch trends are monitored, including those of important non-commercial species and forage fish, as are qualitative impacts on marine mammals and birds (Livingston et al., 2005). To assess the ecosystem effects on the stock, prey availability and abundance trends, predator population trends and physical and biological changes in habitat quality, are used as indicators. Fishery specific effects are monitored using incidental catches of forage species, structural habitat biota, marine mammals, birds and sensitive non-target species (Livingston et al., 2005). Impacts on community structure as a whole can be assessed using diversity and similarity indices, ordination methods, metrics of aggregate community properties, and metrics derived from ecosystem models. Such models include Ecopath, which simulates marine food webs, structure and function, and other models that quantify changes in biomass and trophic interactions in time (Ecosim) and space (Ecospace) (Pauly et al., 2000).

As not all ecosystems are the same, and a myriad of indicators and biological reference points exist, simulation models have been used to evaluate the ability of a suite of indicators to alert us to changes in marine ecosystems under various ecological and exploitation scenarios (Fulton et al., 2005). Fulton et al. (2005) found that indicators at the community level are the most reliable, and that a variety of indicators need to be used simultaneously to detect the full range of fishing impacts (Link et al., 2002). It will also be necessary to continually revise and update these indicators and reference points to take account of fisheries induced evolution, which has been shown to affect even precautionary limits and reference points (Heino et al., 2013). Thus, while ecosystem effects of fishing will still be difficult to assess and be prone to high levels of uncertainty, implementing management systems that use biological indicators and reference points, rather than simply individual quotas of target species alone, will move us towards the ultimate goal of sustainable, ecologically sound fisheries.

6.6 Future Research

An inherent attribute of studies such as this is that, with every question answered, another question arises that, if only to satisfy scientific curiosity, should be answered. The growth attributes examined in the first part of the study suggested possible carry over effects. The state space model showed no correlation between pre-settlement growth rate and post-settlement growth acceleration, which illustrates the value of such a modelling approach to link larval and juvenile growth when trying to assess variability in juvenile growth, as this information would have been lost otherwise. Transplanting recently settled plaice between nursery grounds should answer this question, as if carry over effects exist, change in habitat should not affect growth rates. A common garden experiment would also allow us to assess the suggested differences in site quality, which were not formally assessed in the study. The state space model, used in the present study, should also be parameterized for cumulative degree day or sea surface temperature, to allow for comparison of goodness of fit when using time alone. This would make it possible to more directly assess the effects of temperature on growth. It would also be a valuable tool to use to inform dispersal models with stage specific growth rates. The planktonic envelopes suggest the location of spawning grounds for west Scottish plaice that are in accordance to (Coull et al., 1998), but only disperal models, which are currently under development for this stock (Dr Clive J. Fox, Scottish Association for Marine Science, personal communication), will confirm their likely location.

Otolith microchemistry has been shown in the second part of this study to be a promising tool to assess population structure and connectivity in the western Irish Sea and western Scotland. Future work should focus on characterisation of the most likely nursery grounds so that a full assessment of western Irish and Scottish plaice population structure and connectivity can be made. Laser ablation inductively coupled mass spectroscopy can then be used to assess life stage specific differences in composition. The effect of temperature and growth on the elemental composition of otoliths is difficult to disentangle and one possible avenue of research that has been proposed is the separation of the carbonate and protein constituents of the otolith matrix to analyse their composition. It is thought that the carbonate part of the otolith would reflect mainly temperature effects, while the organic (protein) part is likely to reflect feeding effects and temperature (Dr. Steven E. Campana, DFO, personal communication). Such an endeavour would allow us to more directly assess elemental composition in terms of growth and temperature effects.

The dispersal model presented in the third part of this study still has a lot of scope for refinement. Future work in this area should firstly attempt to quantitatively validate the model itself, as currently this has only been done qualitatively. The spawning ground location indicated by the model should also be quantitatively validated. The model itself would benefit from including algorithms for settlement behaviour, horizontal swimming as well as mortality formulations and finer scale physical forcing. Variable pelagic larval durations would also improve the realism of the model. The model could then be used to not only hindcast dispersal patterns but also to assess the effects of changes in circulation and weather patterns as well as temperature on these.

The dietary mechanism suggested for the effects of fishing on fish condition in the fourth part of this study should be investigated further using larger sample sizes in various habitat types, ideally outwidth the spawning season of the species investigated. The possibility of fish species switching to scavenging in trawled areas should also be further investigated, as this may have consequences for the integrity of marine food webs, if species that are normally not scavengers switch their prey preference.

6.7 Conclusions

This thesis provides significant new information on the early life history, growth, population connectivity, dispersal and condition of plaice on Irish and Scottish coasts. As such, it is part of the larger and wider ranging effort by scientists, to provide the scientific basis required to fully develop and implement fisheries management on an ecosystem basis. While some may argue that sustainable fisheries management is not so much hindered by lack of scientific advice but rather the lack of political will to make the necessary changes in governance, incentive structure, fisheries capitalization and subsidies, science can, in the meantime, provide the means and wherewithal with which to inform, assess, measure, model and monitor the ecosystems and management plans, that will result. The uncertainty associated with scientific advice and assessments used in such management systems, due to lack of sufficient data, should not be a hindrance to their implementation. Novel ways to deal with uncertainty exist, such as the new ecological risk assessment framework applied in Australia, termed Ecological Risk Assessment for the Effects of Fishing (ERAEF) (Hobday et al., 2011), where the amount of information required increases through the hierarchy, and allows application in data limited situations. The implementation of such frameworks will require bringing together stakeholders, scientists and managers, a feature that is perhaps lacking currently, but is essential if we are to reach our common goal of sustainable and productive fisheries in healthy ecosystems, that will meet our demands for generations to come.

6.8 References

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