

An investigation into the effects of environmental variables on the early life history stages of fish, with special emphasis on the flatfish of the West of Ireland

Ph.D. Thesis

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## **Declaration**

I hereby declare that this thesis is my own work unless otherwise stated, and that it has not been previously submitted to this or any other institution. I also give my permission to the library to lend or copy this thesis on request.

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Stephen Comerford

## Abstract

The temperate waters of the north-east Atlantic host a diverse marine ecosystem, and within that ecosystem fish are a valuable resource both in terms of ecosystem functioning and commercial exploitation. The west coast of Ireland provides nurseries for the early life stages of many species of fish whose adult forms are found both inshore within estuaries and bays and offshore in shelf waters. This study sought to examine the relationship between some of those early-stage fish and their physical environment using field data and statistical modelling techniques. An analysis of the environmental determinants of the distribution of larval and early juvenile fish of various species within the confines of Galway Bay revealed that onshore winds are a key driver, providing a mechanism for transport and retention in the bay. Growth rates during the pelagic larval stage of plaice (*Pleuronectes platessa*) from the west of Ireland from one year were compared with samples from the eastern Irish Sea and the southern North Sea using otolith microstructure. Generalised additive mixed models (GAMMs) using cumulative degree day (CDD) as the main predictor of otolith growth brought to light differences in growth patterns between the areas, that may be related to spatial variation in hydrography, distance from spawning and settlement sites, and timing of spawning events. The duration of the pelagic larval phase was found to be negatively associated with water temperatures, consistent with previous studies of plaice. Similarly, growth during the larval stages of turbot (*Psetta maxima*) from sites in Kerry in the southwest and Galway in the west of Ireland was modelled using CDD within a GAMM framework. Minor but significant differences in growth were shown between the regions and the three years of the study period. Larval durations were negatively associated with higher temperatures though the relationship was not as pronounced as that in plaice. Settlement of turbot was modelled showing that tidal height, wind and rainfall were significant predictors of settlement events. These results show that larval fish on the west coast of Ireland and elsewhere respond to fluctuations in their physical environment over a range of scales.

# **1 General introduction**

## *1.1 Recruitment theories*

The life histories of marine fish generally comprise discrete stages that are often separated in space and always in time. Harden-Jones (1968) described this as the “recruitment triangle”, a simple conceptual model in which fish of a given stock or population spawn in one area, the denatant larvae are then transported to a nursery area where they metamorphose into the juvenile form. Here the juveniles grow until reaching sufficient size and age to recruit to the adult population. The adult fish then migrate back to the original spawning grounds to complete the cycle. The dynamics of the life histories of fish are firmly anchored in biology, ecology and oceanography, but the bulk of scientific effort has been driven by man’s exploitation of fisheries. The reasons behind fluctuations in the number of fish available for capture have always been, and remain, of particular interest to fisheries scientists (Houde 2008). There have been many advances in our understanding of the complexities behind variability in recruitment of fish to the adult population. It is generally accepted that most of the variability originates in the early life history stages: the juvenile and particularly the larval phases, (Bannister et al 1973, Leggett and Deblois 1994, Nash and Geffen 2000, van der Veer et al. 2000).

The seminal early work recognising the importance of the larval phase for recruitment to the adult stock was Hjort’s “Critical Period” hypothesis (1914). This hypothesis, although since overtaken by others, still underpins much of fisheries theory. It proposes that after hatching and the consumption of the yolk-sac, fish larvae must quickly encounter sufficient food or they will die. Hjort developed the theory to include “Aberrant Drift”, by which larvae are transported away from potential nurseries; another event thought likely to end in mortality. In time further theories were developed such as Cushing’s “Match-Mismatch” (1975, 1990) which extended Hjort’s work stressing the importance of the coincidence of fish larvae with zooplankton blooms. Laskar’s “Stable Ocean” hypothesis (1978) incorporated oceanography, suggesting that features such as temporary stratification and upwellings were crucial to the survival of fish larvae. There have been other additions to the theories: wind stress and resultant micro-turbulence in the water may affect prey encounter rates: the “Optimal Environmental Window” (Cury and Roy 1989, Roy et al. 1992). It is now generally accepted that recruitment

variability in fish is driven by complex interactions of both the physical and biological environment. Age structure and size of the adult stock, timing of spawning, duration of the larval phase, mortality driven by predation in both larval and juvenile phases, density-dependent effects, growth, food availability, temperature, salinity, turbidity, oceanographic features, currents, weather and others interact to determine the fate of the pre-recruit fish (Norcross and Shaw 1984, Houde 2008).

### *1.2 Importance of hydrography*

Newly-hatched pelagic fish larvae are essentially passive particles; unable to swim sufficiently strongly to overcome the movements of the water they inhabit (Gibson 1997). As such they must become entrained in hydrodynamic features that will bring them to, or retain them in, suitable nurseries at which to metamorphose and begin the juvenile phase of life (Norcross and Shaw 1984, Werner et al. 1997). Fish populations have evolved and adapted to utilise existing pathways from spawning grounds to nurseries, the recruiting survivors of the process being those which spawned in the most advantageous areas and at the most strategic time (Gibson 1997). The features that carry the larval fish are created by forces developing and operating over a number of spatial and temporal scales. At the basin scale, ocean currents are a dominant feature, fluctuating over annual or even longer periods (Werner et al. 1997). On continental shelves tidal movements augment the currents, and vary at a daily or twice-daily scale with an underlying periodicity driven by the lunar cycle (Epifanio and Garvine 2001). Tides also have a clear effect on organisms living in and near the intertidal zones (Gibson 2003) and in estuaries (Kingsford and Suthers 1996). Wind-forcing has an effect over all scales (Norcross and Shaw 1984); in deeper water wind-driven Ekman transport dominates the upper layers of the water column in a spiral from surface to its effective depth (Bradbury and Snelgrove 2001). In shallow water the net effect of wind tends more to the direction of the wind (Werner et al. 1997). In the nearshore environment freshwater inputs from point and diffuse sources drive changes in flow, salinity, turbidity and temperature.

These hydrodynamic forces combine and interact to form features vital to the pelagic larvae. Currents, upwellings, downwellings, gyres, fronts, internal waves and slicks contain the fish and bring them towards the nurseries, or in the case of nearshore-spawning fish, retain them there (Kingsford and Choat 1986, Sabates et al. 2007, Bailey

et al. 2008). These features also contain suitable planktonic prey items as they too become entrained. In the case of nutrient-rich upwellings, plankton blooms may be stimulated, further contributing to the survival of the larval fish (Alemany et al. 2006, Prieto et al. 2009). As the larvae grow and develop the capacity to swim they may contribute their own energy to the process; where shear tidal currents exist on the horizontal plane larvae may move vertically to enter the currents on the most beneficial heading. This process, known as selective tidal stream transport, is a well-recognised strategy of particular importance to the lifecycle of some flatfish species (De Veen 1978, Rijnsdorp et al. 1985, Grioche et al. 2000, Forward and Tankersley 2001).

### *1.3 Growth*

The survival of larvae during the pelagic phase is predicated on the ability of the fish to feed and grow. Rapid growth in the larval phase confers advantages, primarily in predator avoidance and the ability to capture mobile prey items (Sogard 1997). The ability of a faster-growing larva to avoid predation may derive from increased speed due to greater size and development, or from being too big for a given predator to capture and consume (Bailey and Houde 1989). Further advantage from fast growth is evident in the ability of the larvae to sooner reach the end of the larval stage and begin metamorphosis at the nursery. The “Stage Duration” hypothesis (Houde 1987) asserts that less time spent in the larval phase results in decreased vulnerability and thus reduced mortality. If larvae have grown sufficiently and are competent to settle on reaching the nurseries they may do so immediately. Larvae that have not reached the appropriate size and age must remain in the plankton for a longer period (Searcy and Sponaugle 2000).

Growth in the pelagic phase is influenced significantly by temperature. The effect of temperature on the growth of larval fish is well understood, and has been explored in ecological studies and by aquaculturalists (Pepin 1991, Neuheimer and Taggart 2007). Within limits, higher temperatures allow higher growth rates, and larvae in warmer waters have a competitive advantage (Leggett and Deblois 1994). There is also a strongly negative relationship between the duration of the larval stage and temperature. This is well-established for plaice (*Pleuronectes platessa*) (Bolle et al. 2009), and other species have exhibited the same relationship (Seikai et al. 1986). Temperature acts not only on the metabolism of individual larvae but indirectly on the pelagic environment.

While lower temperatures depress growth rates, they also suppress predator numbers and may increase the number of survivors in a cohort. In North Sea plaice colder years give rise to strong year-classes (van der Veer and Witte 1999). Temperature is a simple parameter to control within tank experiments, but less information is available from the natural environment. Nevertheless temperature information is available for the larval phases of wild fish; temperature probes on weather buoys and similar marine apparatus can supply point information. Remotely-sensed sea surface temperature (SST) data is available from satellites at useful resolutions and while the temperatures experienced by individual fish cannot be pinpointed, valuable inference can be made as to average temperatures.

Attempts to model growth and condition of wild larval fish hinge on having good environmental information, including temperature (North et al. 2009), though information on food availability is more difficult to assess, and may not be available (Heath 2007). Huge advances have been made in computer-based models of pelagic trajectories, greatly increasing our understanding of the processes at work during the larval phase of fish (Miller 2007). Field data on changes in growth and larval duration in response to the physical environment provide useful inputs for the construction of biophysical individual-based models allowing behaviour and other parameters of modelled particles be predicted more accurately.

#### *1.4 Settlement and metamorphosis*

On reaching suitable nurseries, demersal fish settle onto a two-dimensional habitat from the three-dimensional pelagic environment. This process is particularly pronounced in flatfish (Pleuronectiformes), where the progression is usually coincident with metamorphosis (Russell 1976, van der Veer 1986, Beggs and Nash 2007) though this can be difficult to establish with accuracy (Geffen et al. 2007). The acts of settlement and metamorphosis are energetically costly and can result in increased mortality rates; though this is difficult to quantify (Chambers et al. 2001); mortality occurs coincidentally with larval immigration and juvenile emigration, making it problematic to pinpoint accurately (Nash and Geffen 2011). The cues that trigger settlement are several and not well understood. Fish must be of a size, age and condition to be able to settle and they must have arrived at a suitable site. They must receive cues to inform them to begin the process; these then produce hormonal responses in the larvae

(Yamashita et al. 2001). The directive factors may be olfactory in nature, or derive from substrate, depth, pressure, salinity, or temperature (Gibson 1997, Bergenius et al. 2005). Also the tides, currents and winds must be such as to allow settlement to proceed.

Nursery areas may be defined as habitats where juveniles have a greater opportunity to feed, grow and avoid predation than in other areas (Gibson 1994). For many species of flatfish these nurseries are sandy beaches where the juveniles inhabit the intertidal and sub-tidal zones. While the majority of year-class variability is generated in the larval phase for Wadden Sea plaice (van der Veer et al. 2000), nursery processes appear to have a moderating effect for many species (Gibson 1994, Nash and Geffen 2000). The juveniles spend one or more years on the nursery beaches before recruiting to the adult stock and returning to the spawning grounds to complete their life cycle.

### *1.5 Otoliths*

The juvenile fish that settle successfully on the nursery beaches are more readily available to the researcher than larval fish in the plankton, and can be collected using relatively inexpensive sampling methods such as beam trawling, push netting and beach seining. Inference about the period preceding capture can then be made from the otoliths, which are mechano-receptors found in the inner ears of the fish. Each fish has three pairs of otoliths, the sagittae, lapilli and asterisci, which are composed mostly of calcium carbonate and contribute to the fish's ability to hear and to orient themselves in their environment (Morales-Nin 2000). Increments visible by microscopy are laid down in the otoliths, and for most fish in normal environments these are deposited at a daily rate (Campana 2001) though exceptions exist (see Uchiyama and Strusaker 1981, Geffen 1982, Fox et al. 2003). The metamorphosis event is often visible as a disturbance in the pattern of daily increments and the formation of the accessory primordia (Toole et al. 1993). The timing of metamorphosis can be estimated from prepared otoliths by counting back the number of increments from the date of capture. Continuing to count back to the first ring laid down, usually at the hatching of the egg, yields further early life history information about the duration of the larval phase. As otolith growth is largely analogous to somatic growth the widths of each daily increment may be also used as a proxy to estimate the growth rates of the fish on a daily scale (Karakiri and von Westernhagen 1989, Campana 1990, Morales-Nin 2000). The capacity of otoliths to record and reveal age, growth and life history events has resulted



in their widespread use in fishery science. Recruitment studies routinely use information from otolith microstructure to establish mortality, assign fish to cohorts and for stock identification (Jones 1992).

### *1.6 Commercial fisheries and anthropogenic pressures*

Many fish species of the north-east Atlantic are commercially exploited, and some of the stocks are deemed to be at dangerously low levels (Marine Institute, 2010). The life cycles of many species of commercial interest including herring (*Clupea harengus*), sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), turbot (*Psetta maxima*), plaice, brill (*Scophthalmus rhombus*), dab (*Limanda limanda*) and flounder (*Platichthys flesus*), involve an inshore component. They spend the larval phase of their early life history in the plankton and rely on the bays, beaches and estuaries around the coast of Ireland for nurseries. The adult stocks are directly vulnerable to exploitation but the pre-recruit fish are also exposed to degradations caused by anthropogenic activities. The growth of human populations on our coasts increases the input of pollutants from agriculture, industry and sewage. Physical development on the coast can change the course of currents and alter the deposition and composition of sediments. This is set to a background of climate change with predicted further changes in temperatures and rainfall, rises in sea levels and an increase in extreme weather events (IPCC 2007). These alterations to the physical environment of fishes have already had quantifiable effects in the form of shifts in species compositions and the effects are predicted to increase in magnitude over time (van Hal et al. 2010, ter Hofstede et al. 2010).

### *1.7 Objectives*

This study seeks to improve our understanding of the early life history of some of these fish, and in particular to effectively model the influence of environmental drivers. While the ability to predict biological outcomes is a worthy aspiration the complexities of the marine systems often defy this realisation, certainly in a study of limited scale such as this. Nevertheless the modelling approach used here allows insight into some of the ecosystem dynamics. Aspects of the early life histories of several fish species across three spatial scales were examined. Firstly a multi-species analysis of the distribution of larval fish in the neuston and plankton in relation to environmental factors within Galway Bay in the west of Ireland was carried out over two years (Chapter 2). Secondly the growth rates and larval durations of plaice of a single year from the west of Ireland,

the Irish Sea and the southern North Sea were modelled using satellite-derived SST data (Chapter 3). Finally the relationship between SST and the larval growth rates of turbot captured over three years on the west and south-west coasts of Ireland was explored along with the environmental influences which bear on settlement events on their nursery beaches (Chapter 4). In each study statistical tools were used to reveal differences between the early life stages of fish from distinct areas and attempted to draw meaningful inference from these. In addition, an attempt was made to quantify the influence of environmental factors on a number of early life history parameters.

## **2 The role of wind-forcing in the distribution of larval fish in Galway Bay, Ireland**

### **2.1 Abstract**

Bays and estuaries are important habitats for fish and contain nursery areas vital for the growth, development and survival of larval and juvenile stages. The ichthyoplankton of Galway Bay was sampled over the spring and summer of 2007 and 2008 to determine what environmental factors influenced the distribution of larval and early juvenile fish. A total of 549 fish representing 27 species or taxa were caught. Catches decreased throughout each sampling season, and were generally poor in 2007. Catches were numerically dominated by sprat (*Sprattus sprattus*), dab (*Limanda limanda*), sand eel (*Hyperoplus immaculatus*) and whiting (*Merlangius merlangus*). Environmental factors driving distribution of fish were modelled using a binomial Generalized Linear Model (GLM). The strength and direction of wind in the five days preceding sampling was the only significant environmental factor. Sustained onshore winds increased the probability of encountering larval fish in the areas sampled. Rainfall, tidal state, tow depth and wind conditions during sampling were not significant. Among the parameters measured it appears that onshore winds sufficiently strong to overcome the residual circulation are the main physical driver for the distribution of larval fish in Galway Bay.

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## 2.2 Introduction

The distribution and abundance of larval fish in space and time are influenced by both biotic and abiotic factors in the coastal environment. Larval abundance is initially driven by the reproductive success of the adult stocks. The survival of larvae and thus their ultimate recruitment can then be modulated by their ability to get from spawning grounds to suitable nurseries, or in other cases to maintain themselves within the areas where they were spawned (Boehlert and Mundy 1988, Norcross and Shaw 1984). Various mechanisms effect the advection and dispersion of larvae such as currents (Garrido et al. 2009), mixing (Ruiz et al. 2006), fronts (Lee et al. 2005), surface slicks (Kingsford and Choat 1986), upwellings (Castro et al. 2000), and the effects of wind (Voss and Hinrichson 2003, Hernandez-Miranda et al. 2003).

The recruitment success of a year class of fish with pelagic eggs and larvae is considered to be primarily influenced by conditions experienced in their larval stage. Cushing's match-mismatch hypothesis (1990) proposes that successful cohorts of larval fish are spawned to coincide with peaks of plankton production, thus ensuring a plentiful supply of food. Van der Veer et al. (2000) found a very strong year class of North Sea plaice *Pleuronectes platessa* to be generated in the larval phase. Single strong year classes are important to the overall health and resilience of a stock. Episodic pulses of larval production are a widespread feature of marine fish, and these overlapping cohorts within a year class confer increased chances of the successful recruitment of at least part of the year's production (Secor, 2007). A review by Leggett and Deblois (1994) found that mortality during the pre-juvenile stages determined year class strength, although mortality in the later juvenile and post-juvenile stages may moderate the size of the effect. Recruitment variability is the product of complex and interacting factors at various temporal and spatial scales; during the pre-recruit stages of fish life histories both trophodynamic and physical processes influence ultimate recruitment success (Houde 2008).

The hydrodynamic systems governing the spawning and recruitment of fish along the west coast of Ireland have not been studied until now. Galway Bay is the only embayment on the west coast of Ireland to have attracted research into its nearshore ichthyoplankton community, and as such it is the sole representative of an intricate, extensive and largely unspoiled coastline on the most westerly edge of Europe. Ireland's

complex Atlantic coast provides many important habitats for fish but the transport and retention of their early stages are poorly understood. Sandy beaches within Galway Bay serve as nursery areas for several flatfish species including plaice (*P. platessa*), turbot (*Psetta maxima*), and flounder (*Platichthys flesus*) (Haynes et al. 2008, 2010, De Raedemaecker et al. 2011). The bay is also ringed with rocky shores and has an extensive littoral zone. In the past the larval and juvenile stages of up to 106 fish species have been recorded in the bay (Dunne, 1972) representing a range of larval survival strategies and adult habitat preferences. Previous work on the ichthyoplankton of Galway Bay has described the general assemblages (Dunne 1972, Fives 1970, Fives and O'Brien 1976); concentrated on the neustonic and pseudoneustonic fish (Tully and O'Ceidigh 1989 a, b); or focused on the larvae of herring (Grainger 1980).

This study was designed to describe the spring and summer ichthyoplankton assemblages of inner Galway Bay over two years, and to discover what hydrodynamic features and climatic forces contribute to their distribution. In particular, we analysed the effects of wind blows, tidal water movements and fresh water inputs on where larval fish were found. The aim was to formulate an ecological model, not to predict future outcomes but to increase our understanding of the system under investigation. Estuaries and bays are uniquely important but fragile ecosystems that are under increasing anthropogenic pressures. Inner Galway Bay is a designated Special Area of Conservation (SAC) under the EU Habitats Directive 1992 and as such is of recognised importance as a marine, littoral and terrestrial habitat. The area is also a Special Protected Area (SPA) under the EU Birds Directive 1979. The hydrodynamics of the bay are subject to potential disruption by building, development and changes in land and water use. The bay and its surrounding littoral act as nurseries for the juveniles of commercially exploited fish stocks, notably plaice, turbot, brill (*Scophthalmus rhombus*), whiting (*Merlangius merlangus*), sprat (*Sprattus sprattus*) and pollock (*Pollachius pollachius*) (Marine Institute, 2010). Perturbation of the early life history stages of fish could therefore have economic as well as ecological implications. In general, increased understanding of the mechanisms underlying the ecological functions of the system will allow greater measures of protection from potentially harmful activities.

## 2.3 Methods and materials

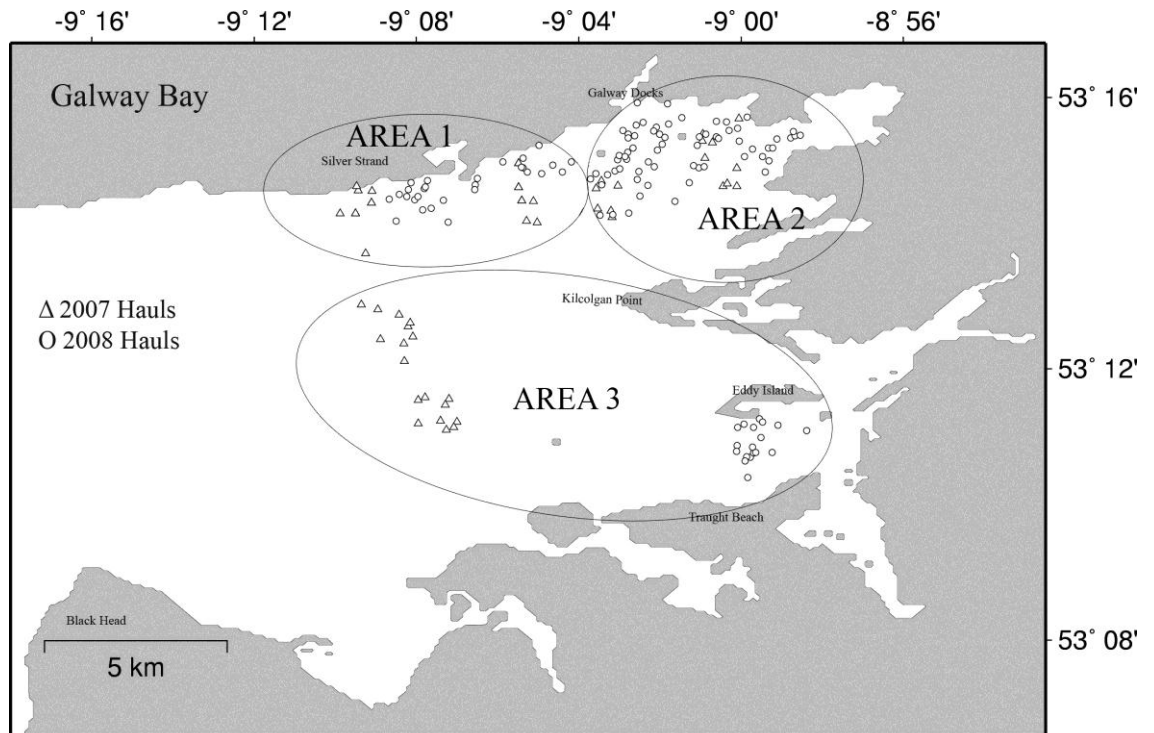
### 2.3.1 Study area

Galway Bay is a large embayment on the Atlantic coast of Ireland oriented westward. To the west the bay is open to the Atlantic, interrupted only by the Aran Islands situated approximately 35km distant from the study site. The study area was inner Galway Bay and samples were taken in an area approximately 140 km<sup>2</sup> bounded by the land to the north, east and south. Waters in this area are well mixed with no evidence of stratification during the periods sampled. The bay receives diffuse and point freshwater discharge around its perimeter, notably from the Corrib River in the north eastern corner of the bay, an estuary discharging water at an annual average of 99m<sup>3</sup>s<sup>-1</sup> through Galway City (OPW 2007). This discharge results in a thin (<1m) lens of low-salinity water along the north shore of the bay west of the Corrib River outfall (Pers. obs.) Circulation in the bay is net inward along its southern part; net outflow is westward along the north shore and the residual circulation is anti-clockwise (Booth 1975, White 1996).

Data for this study came from both dedicated sampling and surveys undertaken as part of other related projects. As a result the sampling was to some extent opportunistic and also was shaped by weather suitable for small boat work. However, there was sufficient consistency of effort and coverage of Galway Bay over the two years to justify the analysis. Inner Galway Bay was divided into three areas: off the north shore west of 009° 04' (area 1); off the north shore east of 009°04' (area 2); and south of Kilcolgan Point at 53° 13' (area 3) (Figure 2.1). In 2007, 108 tows were made in total, with 36 in each of the areas. The effort in area 3 was concentrated approximately in the middle of the bay. In 2008, 107 tows were made; 27 in area 1, 62 in area 2, and 18 in area 3. The offshore site in area 3 from 2007 was abandoned as it was very exposed and could only be sampled in particularly clement weather; in 2008 the effort in area 3 was moved further inshore in the southeast of the bay. The samples from both years in area 3 were pooled as both were from the southern part of the bay. In both years, tows were evenly split between surface (neuston) and subsurface (plankton). Sampling took place throughout the summer from May to August in 2007 and April to August in 2008. No sampling was undertaken in July of either year due to bad weather. In general sampling was abandoned or not attempted in winds > Beaufort force 5. These features of the study

had the effect of unbalancing the design to some extent but did not cause problems with the analysis.

Figure 2.1: Chart of Galway Bay, Ireland showing positions of hauls in 2007 and 2008.





### 2.3.2 Sampling

Sampling was by net with a mesh of 333  $\mu\text{m}$  towed behind a 5 metre open boat driven by a 15hp outboard engine. Tows were conducted both in the neuston and the plankton; in 2007 a frame net with rectangular opening 75cm X 35cm was employed for both types of tow with floats added for surface tows, and removed for subsurface tows. In 2008 a bongo net with twin circular frames with diameter 30cm was used instead for the subsurface tows, and the surface tows were conducted as before. This modification was not considered to influence the gear's ability to catch fish, though it decreased the estimated volume of water sampled in subsurface tows in the second year. A heavy chain depressor was used to keep the gear down for subsurface tows, and a towing depth of approximately  $5 \pm 3$  metres was controlled by boat speed and the length of warp paid out. A depth sensor attached to the net during preliminary trials indicated that the net tended to kite up and down in the water column fairly constantly. Charted depths in the areas sampled ranged from 3 to 15 metres and there is a mean spring tidal range of 4.5 metres. Surface tows were carried out at  $\sim 2.5$  knots and subsurface tows at  $\sim 2.0$  knots, both for fifteen minutes. At least three replicate samples of both the neuston and the plankton were taken during any sampling event in an area. Boat speed was monitored by a Clipper log, and the volume of water flowing through the nets was estimated using a General Oceanics flowmeter. The net was kept out of the wake of the boat by deploying the gear from the end of a short boom mounted across the beam of the boat. During surface tows the net was alongside the boat forward of the propeller wash, during subsurface tows the gear was 10 - 15 metres behind the boat. This was considered adequate to keep the gear away from the disturbance caused by the boat. Tow positions were recorded using a GPS. Temperature and salinity of the water column were measured throughout the each season using a WTW 197i TS meter, though not on every sampling date in 2008.

Larval fish were removed from the nets at sea and stored in 4% buffered formalin before transfer into methyl alcohol in the laboratory. Fish were identified to the lowest possible taxonomic level which was species except for Gobiidae (gobies) and Callionymidae (dragonets); according to Russell (1976). Larval, post larval and early juvenile planktonic or pelagic stages were caught, and for the purpose of this study it

was not necessary to differentiate between stages. As a result “larvae” may refer to any young stage of fish caught by the nets.

### 2.3.3 Data analysis

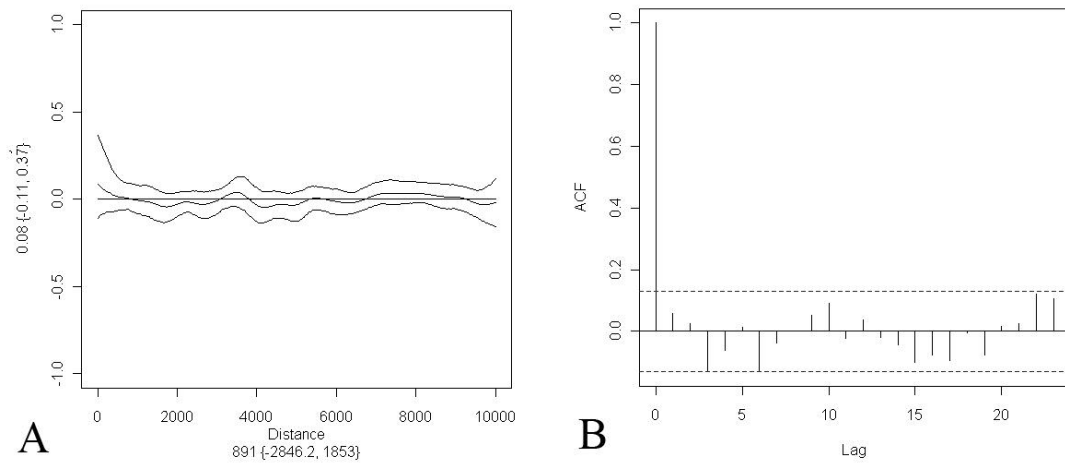
We chose a binomial model with a logistic link on the basis that it was a better descriptor of the abundance of larval fish within the system given the high numbers of catches without fish. Garrido et al. (2009) successfully modelled larval fish abundance against environmental variables using binomial models, and Stoner et al. (2001) used non-parametric binomial general additive models to examine relationships between juvenile winter flounder (*Pseudopleuronectes americanus*) and environmental variables. Logistic regression of this kind can provide simple, accurate habitat models (Norcross et al. 1999). Catch data for all the fish species captured were converted into binomial (presence/absence of fish per haul) data and modelled using generalized linear modelling (glm) with a logit link using the open source language R.

A number of candidate explanatory variables were modelled and manual backward selection was applied on the basis of AIC values (Burnham and Anderson 2002, Zuur et al. 2009), and the significance of parameters at the  $P = 0.05$  level. All possible two way interactions between explanatory variables were initially included. The candidate explanatory variables were: tidal flow (estimated volume of water flowing into or out of the bay); tidal height at Galway Port; spring or neap tide; moon phase; tow depth, i.e. neuston or plankton; wind strength and direction during sampling; rainfall preceding sampling; wind strength and direction preceding sampling; day of the year; site; and year. Wind strength was assigned a positive or negative sign to indicate an onshore (westerly) or offshore (easterly) direction, then averaged over 1,2,3,4,5,7 and 10 days preceding sampling; the number of days explaining most variation in the model was used thereafter. Rainfall preceding sampling was similarly averaged over a number of days. Tidal data was taken from the Belfield Software Tide Plotter program. Wind data came from the Met Eireann weather station at Shannon, approximately 60km from the study site, and rain data came from Met Eireann's Valentia weather station through the European Climate Assessment and Dataset website (<http://eca.knmi.nl>). As CTD measurements taken throughout the survey showed a well-mixed water column which was largely uniform around the bay, temperature and salinity were not included in the analysis.

The model was validated according to Zuur et al. (2009). Issues of temporal correlation that could potentially bias the model were investigated by plotting the correlation of

residuals from the glm model using the auto-correlation function (acf) in R (Figure 2.2). Spatial correlation between samples was tested by generating a correlogram using the spatial nonparametric covariance functions (ncf) package in R (Figure 2.2). Spatial correlation was also checked by plotting model residuals against x-y co-ordinates using the bubble function from the gstat package in R. No spatial or temporal correlation was evident which justified the use of a generalised linear model without including any correlation structure or random effect. Model residuals were plotted against fitted values and also against the predictor variables excluded during the model selection process; no patterns of any significance were observed and the model was considered robust.

Figure 2.2: Correlogram (A) showing the lack of spatial auto-correlation in the model and an Auto-Correlation Function plot (B) of model residuals, also showing the absence of any auto-correlation.



## 2.4 Results

### 2.4.1 Fish species

A total of 549 larval and juvenile fish representing 27 species or taxa were caught over the two years of sampling: In 2007, 78 were caught in 108 tows over 10 days sampling. In 2008, 471 were caught in 105 tows over 13 days sampling (Table 2.1). In 2007, 35 fish were captured from the neuston and 43 from the plankton; in 2008 274 were taken from the neuston and 197 from the plankton. Catches were dominated by larval sprat (*Sprattus sprattus*) in 2008, 124 were caught that year, although none were caught in 2007. They were evenly spread throughout the bay and were caught both in the neuston and plankton. The five-bearded rockling *Ciliata mustela* were caught in relatively high numbers (74 larvae and juveniles) across the two years, the neuston and the plankton, and all areas sampled. The greater sand eel (*Hyperoplus immaculatus*) (55 larvae) was also taken in both neuston and plankton in both years. Whiting (*Merlangius merlangus*) yielded 55 juveniles from both the neuston and the plankton; all were taken from areas 1 and 2 in the north of the bay in 2008 only. There were 74 dab (*Limanda limanda*) caught in total, again only in 2008, 71 of which came from one haul on the surface in area 3 in the south of the bay. A similar temporal pattern was seen with gobies (Gobiidae sp.); considerable numbers of each species were caught in 2008 but none were present the previous year. Throughout the survey there were no obvious patterns either spatially or between neuston and plankton. While a number of species were found exclusively in sub-surface tows, most were in small numbers ( $\leq 3$ ) with the exception of the gobies (36) and *Pomatoschistus pictus* (9). Brill (*Scophthalmus rhombus*) were the only fish found exclusively in the neuston but there were only 2 caught. Catches of all species tailed off sharply in the latter half of both years.

Table 2.1: Larval fish captured during 2007 and 2008 in Galway Bay showing larvae caught in the neuston (surface) and plankton (sub-surface).

Species	2007			2008			survey total
	neuston	plankton	total	neuston	plankton	total	
<i>Sprattus sprattus</i>	0	0	0	83	39	122	<b>122</b>
<i>Limanda limanda</i>	0	0	0	71	3	74	<b>74</b>
<i>Hyperoplus immaculatus</i>	5	5	10	35	10	45	<b>55</b>
<i>Merlangius merlangus</i>	0	0	0	19	36	55	<b>55</b>
<i>Ciliata mustela</i>	23	18	41	27	15	42	<b>83</b>
<i>Gobiidae sp.</i>	0	0	0	0	36	36	<b>36</b>
<i>Platichthys flesus</i>	0	0	0	12	12	24	<b>24</b>
<i>Blennius gattorugine</i>	1	2	3	11	8	19	<b>22</b>
<i>Pomatoschistus minutus</i>	0	10	10	0	0	0	<b>10</b>
<i>Cyclopterus lumpus</i>	2	1	3	6	0	6	<b>9</b>
<i>Pleuronectes platessa</i>	0	0	0	0	1	1	<b>1</b>
<i>Pomatoschistus pictus</i>	0	0	0	0	9	9	<b>9</b>
<i>Syngnathus rostellatus</i>	0	0	0	2	7	9	<b>9</b>
<i>Pollachius pollachius</i>	0	0	0	3	2	5	<b>5</b>
<i>Pomatoschistus minutus</i>	0	0	0	2	3	5	<b>5</b>
<i>Taurulus bubalis</i>	0	0	0	2	2	4	<b>4</b>
<i>Callionymus sp.</i>	0	0	0	0	3	3	<b>3</b>
<i>Labrus bergylta</i>	0	0	0	0	3	3	<b>3</b>
<i>Pollachius virens</i>	2	6	8	1	0	1	<b>9</b>
<i>Arnoglossus laterna</i>	0	0	0	0	2	2	<b>2</b>
<i>Centrolabrus exoletus</i>	0	0	0	0	2	2	<b>2</b>
<i>Crenilabrus melops</i>	0	0	0	0	1	1	<b>1</b>
<i>Ctenolabrus rupestris</i>	0	0	0	0	1	1	<b>1</b>
<i>Dicentrarchus labrax</i>	0	0	0	0	1	1	<b>1</b>
<i>Atherina presbyter</i>	0	1	1	0	0	0	<b>1</b>
<i>Scophthalmus rhombus</i>	2	0	2	0	0	0	<b>2</b>
<i>Hyperoplus lanceolatus</i>	0	0	0	0	1	1	<b>1</b>
<b>Totals</b>	<b>35</b>	<b>43</b>	<b>78</b>	<b>274</b>	<b>197</b>	<b>471</b>	<b>549</b>

### 2.4.2 Modelling

A number of explanatory variables were tested in the model to assess their significance in influencing the distribution of larval fish. The variables significant at the  $P = 0.05$  level were year, area, day and wind index over 5 days preceding sampling. Regressors found not to be significant at  $P = 0.05$ , and thus rejected during model selection, were tidal flow, tidal height, tidal phase, moon phase, tow depth, wind strength and direction during sampling, and rainfall over several time intervals preceding sampling. All possible two-way interactions between explanatory variables were also tested, and none were significant.

The following logistical model was fitted to the data:

$$\text{logit}(\pi_i) = \alpha + \text{Wind index}_i + \text{Area}_i + \text{Day}_i + \text{Year}_i$$

The model estimates indicated higher abundance of larval fish overall in the second year; the negative effect of time on catches throughout each season; and that area 1 on the north shore west of the Corrib Estuary was more productive than the other two areas, which were almost identical. The effect of the wind index was positive; onshore winds increased catch probability, offshore winds reduced it. Null deviance was 307.47 on 221 degrees of freedom and residual deviance was 231.33 on 216 degrees of freedom. This implies that the model explains 24.8% of the variance. All explanatory variables included were significant at  $P < 0.001$ . The model estimates were converted from logits to calculate probability ( $P$ ) by the formula:

$$P = \frac{e^x}{1 + e^x} \text{ where } x \text{ is the model estimate.}$$

To visualise the model, the probability of catches containing larval fish was plotted for both years and each of the three areas choosing the median day of April, June and August to describe the change over time and using wind as the continuous explanatory variable (Figure 2.3). Wind roses plotted the frequency, strength and direction of wind during the period of study showing the predominance of winds from the south-west (Figure 2.4)



Figure 2.3: Model output; predicted probability of catching larval fish for each area over two years. Negative values for wind indicate offshore winds averaged over five days prior to sampling, positive values indicate onshore winds. Circles top and bottom of each panel indicate positive or negative binomial data points.

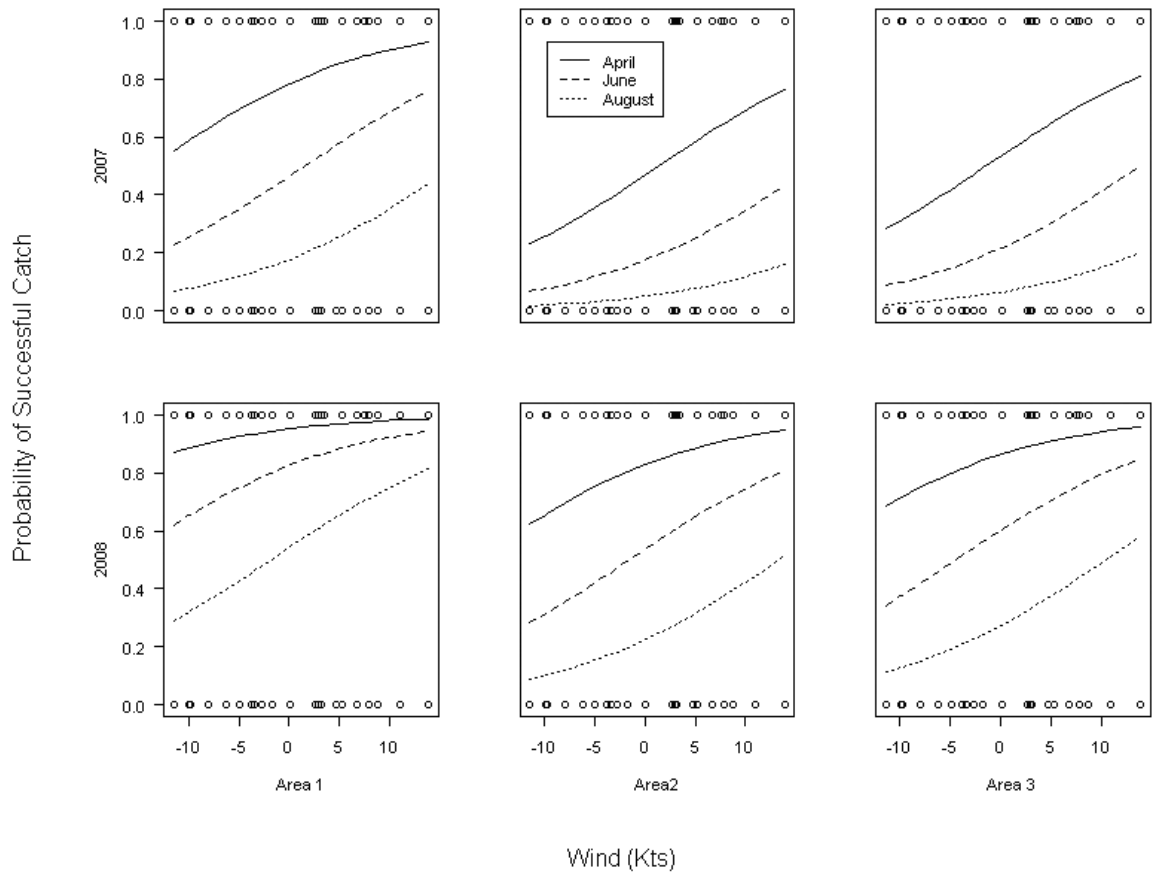
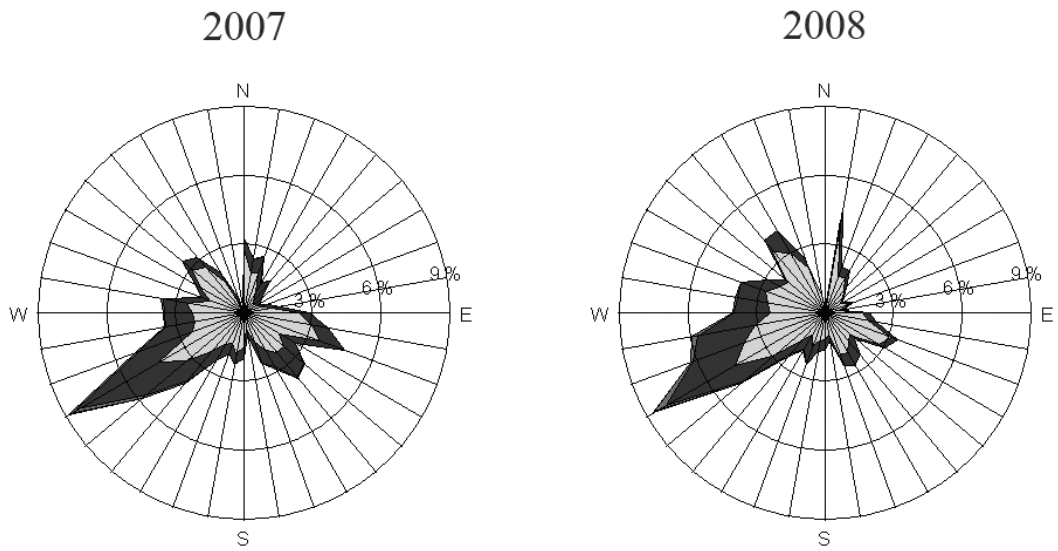


Figure 2.4: Windroses showing percentage frequency, direction and strength of winds recorded at Shannon, April to September 2007 and 2008. White 0-10kts, dark grey 11-20 kts, light grey 21-30 kts.



## 2.5 Discussion

The ichthyoplankton community of Galway Bay has been well described in the past, (Fives 1970, Dunne 1972, Fives and O'Brien 1976, Tully and O'Ceidigh 1989a, 1989b), but no attempt had been made to formally relate this community to the physical environment. Studies have established the importance of wind-forcing in the transport of fish larvae across continental shelves (Doyle et al. 2009, Epifanio and Garvine 2001), along open coastlines (Prieto et al. 2009, Nakata et al. 2000), and in estuaries (Simionato et al. 2008). Catalan et al. (2006) established that short term changes in hydrodynamic conditions caused by wind-forcing resulted in profound changes in the distribution of some species of larval fish in the Gulf of Cadiz. In the present study wind speed and direction was a significant driver of larval distribution and the model indicated that the averaged effect of wind over five days prior to sampling had the strongest impact on catch success when compared with winds averaged over shorter or longer periods. This suggests that larval fish become concentrated in inner Galway Bay following sustained blows with a westerly component and that five days is the timescale that best represents the pattern of the wind, revealing the net effect on larval fish transport. Hydrodynamic modelling work has indicated that in conditions unforced by wind or tide the residual circulation is anti-clockwise in the bay, with a prevailing current flowing west along the north shore (White 1996, C. Mohn, unpublished data). However the wind plots show that the study site was subject to frequent and occasionally strong wind blows, predominantly from the south-west, throughout the spring and summer; and these conditions appear to have driven the distribution of larvae and juveniles of the fish species sampled in this study. On a bay scale passively transported larvae have nowhere else to go but into the inner bay as the prevailing winds overcome the residual circulation. Within the bay, wind driven currents and thus the passive transport of larvae are in the direction of the wind, Ekman spirals being unable to form in shallow inshore waters (Nielsen et al. 1998, Werner et al. 1997). The implication is that should winds be exceptionally light or from an unusual direction during the spring and early summer then larval transport and retention would be adversely affected. Residual currents would tend to carry larval fish out of the bay along the north shoreline.

The present study yielded 26 species from inner Galway Bay, only one of which, *Dicentrarchus labrax* (sea bass) had not been previously recorded anywhere in the region. While the number of species recorded is the lowest of all the studies it is only generally comparable to Fives (1970) who recorded 35 species sampling in the inner bay from 1961 to 1965. The extreme scarcity of larval fish both in number of species (8) and total abundance (78) was striking in 2007. There was no obvious reason for this, the wind frequency, strength and direction were remarkably similar between the two years. The nearest available sea surface temperature for that period was at Buoy M3 off the south west coast of Ireland (Marine Institute); average temperatures for the period January 1<sup>st</sup> to April 30<sup>th</sup> for 2007 and 2008 were identical indicating that there was no temperature-related failure to spawn by offshore-spawning species. From this it is probably safe to infer that there were no major temperature anomalies affecting inshore spawning species either. Biological factors relating to spawning success remain a possibility to explain the annual differences, but it seems improbable that failure could occur across so many species representing a range of survival strategies. There was a change of gear used for subsurface tows in 2008, but this had no appreciable effect on efficiency, and actually reduced filtered volumes in the more productive year. The results from 2007 appear to show that the gear was capable of catching fish when they were present, which possibly rules out the change in equipment as a confounding factor. Nevertheless the differences in results between years are striking, and unexplained.

A physical variable indicating the wind strength and direction at the time of sampling (always < 20 knots) was not significant, which implies that short-term turbulent mixing of the water column due to wind did not affect the number of larvae available for capture, and also did not detract from the ability of the gear to catch fish. Contrasting with the importance of wind averaged over 5 days, the wind blows measured at shorter timescales may be too variable for their influence to be reflected in the distribution of the fish. In a study carried out in wind speeds of 0-22 knots approximately 70 km offshore in 80 metres of water, wave height was found to lag wind speed by about 4 hours, both in growth and decay phases (Prasada Rao and Baba 1996). In contrast to open ocean or continental shelf conditions, wind-generated wave growth rates in waters of finite depth are limited (Young 1997).

The model output plots show the decreasing probability of catching larval fish of any kind over the course of each season, while simultaneously onshore winds of greater magnitude contribute to greater catch success. The number of larval and juvenile fish captured in the plankton had fallen off markedly by August. This reflects the evolution of the larval communities over time, with the larvae of some species growing larger and becoming harder to catch, or, in other cases, leaving the neuston or plankton. Doyle et al. (2009) found that during development, stage-specific responses to physical variables during sub-intervals of life are important, and that the relationship between abundance and those variables was unique and complex among species.

Larval distribution differed significantly according to which area of the bay was sampled, and area 1 on the north shore west of the Corrib Estuary yielded more catches ( $P < 0.001$ ). Catch successes in areas 2 and 3 were almost identical to one another. This area is the only one sampled that showed any salinity anomalies, with a thin lens of lower-salinity water from the Corrib system sitting on the surface. The higher abundance is not easily explained by entrainment or passive transport; if wind-forcing alone was the driver then it could be expected that area 2 covering the mouth of the Corrib Estuary and points east of there would show the highest abundances under the influence of the prevailing wind as the larvae fetched up against the land-sea boundary. This was also the area of greatest sampling effort. During the less frequent periods of slack or offshore winds the driver for passive transport along this shore is the westward cyclonic flow (Booth 1975, C. Mohn *pers. comm*).

Different species use different strategies to locate themselves advantageously during the larval phase, employing behaviours to benefit from hydrodynamic features in their environment (reviewed in Boehlert and Mundy 1988). Selective tidal stream transport (STST) is a well-studied mechanism whereby larvae position themselves vertically according to the horizontal flow regime. It is particularly employed by larval fish entering estuaries where they maintain themselves on the bottom during ebb tides, keeping out of the main flow; then move up into the water column during flow tides to enjoy an energetically inexpensive ride upstream (De Veen 1978, Fortier and Leggett 1983, Norcross and Shaw 1984). Larval behaviour is in response to environmental cues, and tidal flux can result in accumulations of fish. However, tidal flux is a complex of potentially collinear variables including, at differing time scales, lunar phase, current

speed, freshwater input, salinity, turbidity, temperature and olfactory cues (Boehlert and Mundy 1988). We tested lunar phase, tidal phase, tidal height, estimated tidal flow, and rainfall but none were significant in the model either as main effects or in interaction with any other variables. An interaction between hydrodynamic variables and area would have been expected if there was a strong estuarial effect in the bay, but none was evident. The binomial approach used to model the presence or absence of larval fish is quite a blunt instrument with which to detect signals of temporal and spatial variability in the mouth of a small estuary such as the Corrib, and on a wider scale throughout Galway Bay. No species was caught in sufficient numbers to allow a more in-depth analysis. Future projects of this kind would need to succeed in capturing greater numbers of fish with finer temporal resolution in the early part of the season to allow a more specific inference than the general one offered here.

## **2.6 Conclusion**

The ichthyoplankton of inner Galway Bay surveyed in this study was species poor relative to previous studies in the region, and catches were meagre in the first year of the study. Nevertheless sufficient data were gathered to formulate a simple ecological model which revealed that wind forcing from the west had the greatest effect on the distribution and abundance of fish larvae compared with other physical variables. The prevailing winds appear to be a necessary component for the transport and accumulation of larval fish within Galway Bay. The community showed predictable changes over time within each year and the area of the bay west of the Corrib Estuary had the highest abundances, although the reason behind this was not clear. This study serves as the first attempt to quantify the hydrodynamic forces driving the patterns of abundance of larval fish in the nearshore environment on the west coast of Ireland. The Galway Bay area is subject to largely the same prevailing winds, moderate tidal effects and proximity to the Gulf Stream as the rest of the Atlantic coast of Ireland, and so the findings are important on a greater than bay scale. Inter-annual variation in wind regimes may contribute to recruitment variability, and longer time series could be used to test this.

### **3 Temperature effect on growth and larval duration of plaice (*Pleuronectes platessa*) in three regions of the North East Atlantic**

#### **3.1 Abstract**

Transport models for planktonic fish eggs and larvae often use temperature to drive growth because temperature data are readily available. This pragmatic approach can be criticised as too simplistic as it ignores additional factors such as food availability and growth-rate dependent mortality. We examined the extent to which temperature could explain larval duration and growth variability in post-settlement plaice from the southern North Sea, Irish Sea and west of Ireland. Larval duration and individual growth were estimated from otolith microstructure of juvenile plaice collected from nursery grounds in each region and average sea surface temperatures were reconstructed for each region from satellite data. Hatch dates, larval duration and settlement dates all differed between regions reflecting the timing of spawning and the physical characteristics of each region. Models incorporating presumed temperature history and region were able to explain 73% of variability in individual larval growth (as estimated from otolith microincrement widths). The results suggest larval duration can be estimated using a pan-regional model based on average temperature experience during the larval phase and that sea temperature can be used to drive growth models of plaice larvae although allowance must then be made for inter-regional differences.

This chapter has been accepted as Comerford, S., D. Brophy, C.J. Fox, N. Taylor, H.W. van der Veer, R.D.M. Nash and A.J. Geffen, 2012. Temperature effect on growth and larval duration of plaice (*Pleuronectes platessa*) in three regions of the North East Atlantic. Marine Ecology Progress Series *In Press*.



### 3.2 Introduction

The early life history of many flatfish species is characterised by discrete stages separated in space and time. Adult plaice (*Pleuronectes platessa*) are widely distributed in shelf waters around Ireland, the UK and mainland Northern Europe (Simpson 1959, Nielsen 1986). Spawning occurs on the continental shelf from where the pelagic eggs and larvae are transported inshore. As they arrive in shallow water, the larval fish undergo metamorphosis, settling onto the inter-tidal of sandy nursery grounds (Gibson 1997). The juveniles maintain their association with the nurseries for several years gradually moving offshore. It is during the first two phases, the pelagic larval stage and the early demersal, shallow water juvenile stage that the strength of the year class is established (van der Veer 1986, van der Veer et al. 2000, Nash and Geffen 2000). Both biotic and abiotic processes acting during the larval stage determine the size of any cohort and its success in reaching the shore (Bannister et al. 1973, van der Veer et al. 2009). Further processes in the nursery areas serve to dampen the fluctuations in abundance, moderating the effects of variation in egg supply or larval survival (van der Veer 1986, Beverton and Iles 1992). Though the size of this moderating nursery effect seems to vary throughout the range of the plaice, the importance of the larval phase to the ultimate survival of the fish on the individual, cohort and year class levels is well established (Bannister et al. 1973, Nash and Geffen 2000, van der Veer et al 2000).

The experience of any individual larval plaice results from a complex interaction of many highly variable influences. The timing of spawning and hatching and their coincidence with water temperature, large scale weather events affecting the hydrodynamic regime, food availability and predation pressures combine to determine whether, when and in what condition the fish reaches the nursery (Gibson 1997). Larval fish are susceptible to the influence of temperature. In isolation from other factors higher temperatures are correlated with higher growth rates (Blaxter 1992). Higher growth rates in fish larvae have been linked with a greater ability to escape predation (Leggett and Deblois 1994) and thus greater survivability (Bailey and Houde 1989). Conversely year class strength in plaice in the southern North Sea and other nearby areas appears to be negatively correlated with sea temperature during the larval period (van der Veer and Witte 1999, Fox et al. 2000, van der Veer et al. 2009). It has been suggested that this counter-intuitive result could be caused by several mechanisms either acting alone or in concert. Firstly wind patterns, and thus water circulation may

be atypical in colder years enhancing settlement (Nielsen et al. 1998, van der Veer et al. 1998). However, recent modelling studies from the southern North Sea have not provided strong support for this mechanism (van der Veer et al. 2009). It is difficult to reach an unequivocal conclusion however since in different years the combination of conditions may mean that most larvae reaching the nursery grounds come from different spawning areas. Secondly predator numbers and feeding rates, both in the plankton and following settlement, may be reduced in very cold years allowing greater survival (Nash and Geffen 2000, van der Veer et al. 2000, 2009).

In recent years a number of coupled, biophysical individual-based models of fish egg and larval transport have been developed (North et al. 2009). Many of these models use sea temperature to drive growth and/or survival (Heath and Gallego 1998, Fox et al. 2006, 2009, Brochier et al. 2008, Bolle et al. 2009), although food availability may also be incorporated (Hinrichsen et al. 2002). As well as being much simpler than trying to measure or model prey availability and larval feeding success, models using temperature as the main biological driver are motivated by concern about the accuracy of representation of sub-grid scale processes in hydrodynamic models (North et al. 2009).

This study was designed to examine differences between the growth rates of larval plaice from different geographic locations and to assess the extent to which growth variability could be modelled using temperature alone. To this end an analysis was conducted using archived plaice otoliths of the same year class collected during one year from three geographically distinct regions: Galway Bay in the West of Ireland, the Eastern Irish Sea, and Balgzand in the Dutch Wadden Sea (southern North Sea). The otoliths, which are calcareous structures in the ears of fish that are important for hearing, balance and orientation, grow through the formation of visible layers. In normal circumstances, and for most fish, one increment is deposited each day; and the growth rate of the otolith can be used as a proxy for somatic growth (Campana 2001). The deposition of daily increments has been confirmed for plaice larvae at temperatures greater than 5°C (Karakiri and von Westernhagen 1989).

A modelling approach is used to describe the influence of ontogeny and temperature on growth during the pelagic phase in plaice. It is hypothesised that this relationship will capture most of the regional variation in growth. In addition the relationship between

the length of the larval phase (pelagic stage duration), temperature and region is examined. The timing of hatching and settlement on the nurseries, which are the points in time that bracket the larval phase, may be significant factors for the survival of young fish, and these parameters are also examined.

### **3.3 Methods and materials**

#### *3.3.1 Sampling*

Archived otoliths came from 122 juvenile plaice captured in Ireland (n = 30), the UK (n = 44) and the Netherlands (n = 48) in 2002, as part of three independent projects. The fish were taken by a variety of methods (Table 3.1), but in all cases from the intertidal zone at or around low water. The various sampling methods were chosen to suit the individual projects. No attempt has been made in this study to compare parameters from the three regions relating to settlement and it is assumed that there has been no confounding influence of sampling gear on results relating to the pre-settlement phase.

Table 3.1: Sampling information for juvenile plaice captured from intertidal nursery areas in three regions in 2002; Ireland, the UK and the Netherlands. Fish were taken from known nursery areas.

<b>Region (Reference)</b>	<b>Nursery area</b>	<b>Sampling date</b>	<b>Gear</b>	<b>Mesh size (codend)</b>	<b>Method</b>	<b>Tow length and speed</b>
Dutch Wadden Sea  (van der Veer et al., 2009)	Balgzand	4 <sup>th</sup> April	1.9m beam trawl with one tickler chain	5x5mm	Trawl towed by boat and outboard	100m 2.1 km h <sup>-1</sup>
Irish Sea (Fox et al., 2007)	Fleet Bay Beckfoot Heysham Penmaenmawr	17 <sup>th</sup> May 20 <sup>th</sup> May 24 <sup>th</sup> May 28 <sup>th</sup> May	2m beam trawl with four ticklers chains	10mm stretched	Trawl deployed by hand, recovered by All Terrain Vehicle (ATV)	100m 5 km h <sup>-1</sup>
West of Ireland	Galway Bay Fanore Lahinch	26 <sup>th</sup> September 24 <sup>th</sup> September 24 <sup>th</sup> September	20x2m beach seine with one tickler chain	12mm diamond	Seine deployed by boat and outboard, recovered by hand	150m Speed not known

### 3.3.2 *Otolith analysis*

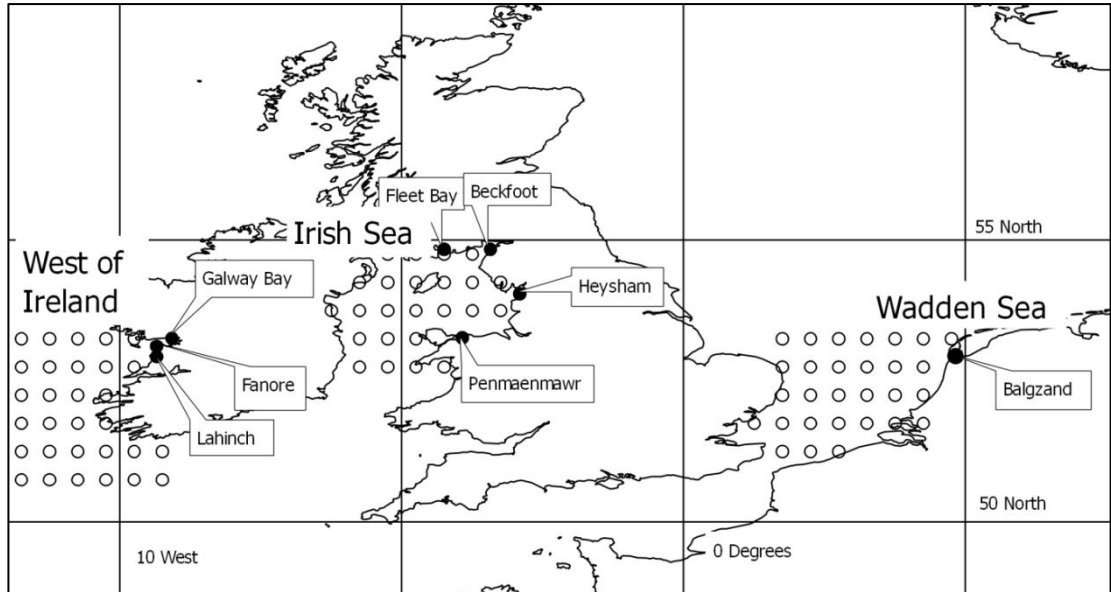
Sagittal otoliths were extracted and mounted on clear glass coverslips using thermoplastic resin (Crystalbond, Agar Scientific). Otoliths from the West of Ireland were polished on both sides to reveal the otolith core using an aluminium oxide slurry on a granite surface plate, progressing from 15  $\mu\text{m}$  grit down to 3  $\mu\text{m}$  grit. After grinding, the otoliths were polished using white jeweller's rouge. Archived otoliths from the Wadden Sea (van der Veer et al. 2009) and the Irish Sea (Fox et al. 2007) had been prepared previously using similar methods.

Otoliths from the Irish Sea (Fox et al. 2007) and the North Sea (van der Veer et al. 2009) samples had previously been read in separate studies, but all otoliths were re-read to remove any inter-reader effects. Images of the otoliths were captured by a single reader at 200x and 1000x magnification using an Olympus BX51 light microscope and QImaging Retiga 2000k camera. Images were processed using the image analysis software ImagePro Analyser version 6.2. Distances from the centre of the core to the hatch ring and the first accessory growth centres (AG) were recorded. Individual increments widths were measured from the first hatch ring to the AG providing growth-proxy data for the pelagic larval phase. In order to estimate the temperature experience of the larvae during the planktonic drift, estimates of post-larval duration were also required. Post-larval duration was estimated by counting increments from the first complete increment outside of the AG to the edge of the otolith. Post-larval increments were generally clear for otoliths from the Wadden Sea and Irish Sea but West of Ireland otoliths were harder to interpret as the fish were older at capture (Table 3.1). In these cases at least two counts of post-larval duration were made on each otolith. If the co-efficient of variation (CV) between them was <5% then an average value was taken. If not then a third count was made and an average taken of the two closest values, again only if the CV was <5%. If the third count failed to achieve a sufficiently low CV the otolith was excluded from the analysis. Hatch dates were estimated by subtracting the total post-hatch age (larval duration + post-settlement duration) of the fish from the sampling date.

### *3.3.3 Satellite temperature data*

Global sea surface temperature (SST) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on the Terra EOS AM satellite were downloaded from the NASA OceanColor website and processed using the SeaWiFS data analysis system SeaDAS version 6.1. Relevant data were extracted from the global SST datasets using Quantum GIS version 1.5.0. SST data were 8-day averages and level 3 binned daytime observations were used. Data were collected from a grid 0.5° latitude x 0.5° longitude, approximately equal to 55.5 x 55.5km. Data points were chosen to broadly represent the presumed larval drift pathways between spawning grounds and the nursery grounds sampled. Likely paths have been modelled for the southern North Sea (Harding et al. 1978, Talbot 1978, van der Veer et al. 2009) and the Irish Sea (Fox et al. 2006, 2009, van der Molen et al. 2007). Far less information is available for drift of larval plaice on the west coast of Ireland. Based on the general oceanographic circulation it was assumed that drift would be largely south to north (Figure 3.1).

Figure 3.1: Map showing locations (open circles) for SST data. Black circles show nursery areas where samples were taken.





### 3.3.4 Data analysis

Regional differences in larval duration, settlement date, hatch date and final degree day at settlement were tested by Kruskal-Wallis as data were non-normal and heteroscedastic. Post-hoc differences were tested using Mann-Whitney-Wilcoxon with a Bonferroni correction for multiple comparisons.

The continuous predictor, degree day was calculated as the time integral of the average daily temperature across the regions shown in Figure 3.1 which were assumed to represent the drift range during the period corresponding to the larval phase of the individual fish.

$$DD = \sum_n t_1 + t_2 + \dots + t_n$$

Otolith increment width data were log transformed and modelled using generalized additive mixed models (GAMMs). Data exploration indicated that the data followed a gamma distribution after transformation therefore the Gamma family with a log link function was used.

Generalized additive models (GAMS) were used to examine the relationship between larval duration and temperature. Data were modelled on the average SST over the larval period of each fish using the Poisson distribution with a log link. The factor “region” was tested for its significance within the model using the ANOVA routine. These data were also modelled using traditional linear regression methods to compare results with previous studies Bolle et al. (2009).

The GAM methods use penalized regression splines to smooth the relationship between response and predictor variables (Wood 2006). Model outputs include the term “effective degrees of freedom” (edf); ranging from zero to infinity, higher values of edf imply greater non-linearity in the relationship (Zuur et al. 2009).

Data were analysed using R version 2.11.1 and packages mgcv and nlme.

### 3.3.5 Model selection

Model selection was carried out using Akaike Information Criteria (AIC), lower AIC values indicating a better model (Burnham and Anderson 2002), however, only variables significant at the  $P < 0.05$  level were included. The suite of models applied to otolith increment width data were generalized additive mixed models (GAMMs), modelling log transformed otolith larval growth increment widths on sea surface temperature (SST), degree day (DD), larval duration (LD) of the individual fish, and region. Region was treated as a factor with three levels: Irish Sea, Wadden Sea and West of Ireland, and was allowed to interact with the continuous predictor variables. Non-parametric smoothers were applied to SST, DD and LD. DD described the otolith growth better than LD or SST. A mixed effects model was necessary to account for the temporal correlation characteristic of data of this kind. A corAR1 temporal correlation structure was applied to the model allowing for correlation at a daily (otolith increment) level nested in each individual fish. Auto-correlation in modelling violates assumptions of independence and can lead to incorrectly inflated significance (Zuur et al. 2009). Traditional linear regressive methods to model data collected in a time series immediately violate the assumption of an independent  $x$  variable. Critically, failing to account for auto-correlation increases the risk of Type I errors, which give falsely positive results, and parameter estimation may also be adversely effected (Zuur et al. 2009). Otolith increment growth data are an excellent example of temporally correlated data, each daily increment width being necessarily highly correlated with the one before and the one after (Chambers and Miller 1995, Butler and Folkvord 2000).

Final models were checked for validity by plotting histograms of residuals, residuals against linear predictor, response against fitted values and deviance residuals against theoretical quantiles using the `gam.check` routine in `mgcv`. Auto-correlation function (ACF) plots were generated to check for remaining auto-correlation of the modelled residuals. There was no evidence of any patterns in the plots to indicate problems with model specification, poor fit, unequal variances, missing predictors or auto-correlation so the final models were considered robust.

### 3.4 Results

#### 3.4.1 Hatch dates and larval duration

Hatch dates and assumed settlement dates showed significant differences between regions (Kruskal-Wallis,  $P < 0.001$ , both parameters). Post-hoc testing indicated that each region was significantly different from the others (Mann-Whitney-Wilcoxon,  $P < 0.001$ , both parameters). The median hatch date for plaice from the Wadden Sea was 22<sup>nd</sup> January, from the Irish Sea it was over one month later (6<sup>th</sup> March) and from the West of Ireland it was even later, 11<sup>th</sup> April. The order of median settlement dates was similar; Wadden Sea (25<sup>th</sup> March); Irish Sea (20<sup>th</sup> April); West of Ireland (15<sup>th</sup> May) (Figs. 2, 3 and 4).

Larval duration (Figure 3.4) was significantly different between regions (Kruskal-Wallis,  $P < 0.001$ ), with all regions differing from each other (Mann-Whitney-Wilcoxon,  $P < 0.001$  in all cases). Mean larval duration in the Irish Sea was 46.0 days  $\pm$  6.53; in the West of Ireland it was 34.1 days  $\pm$  3.99; and in the Wadden Sea it was 62.1 days  $\pm$  6.04.

It is important to note that fish were sampled relatively soon after settlement in the Wadden Sea (mean post-larval duration 10.2 days  $\pm$  4.26), somewhat later in the Irish Sea (mean post-larval duration 30.2 days  $\pm$  9.97) but much later in the West of Ireland (mean post-larval duration of 135 days  $\pm$  19.52). At the time of sampling settlement may not have concluded in the Wadden Sea and Irish Sea (Fox et al. 2007).

Figure 3.2: Histograms of hatch dates for larval plaice in the three regions.

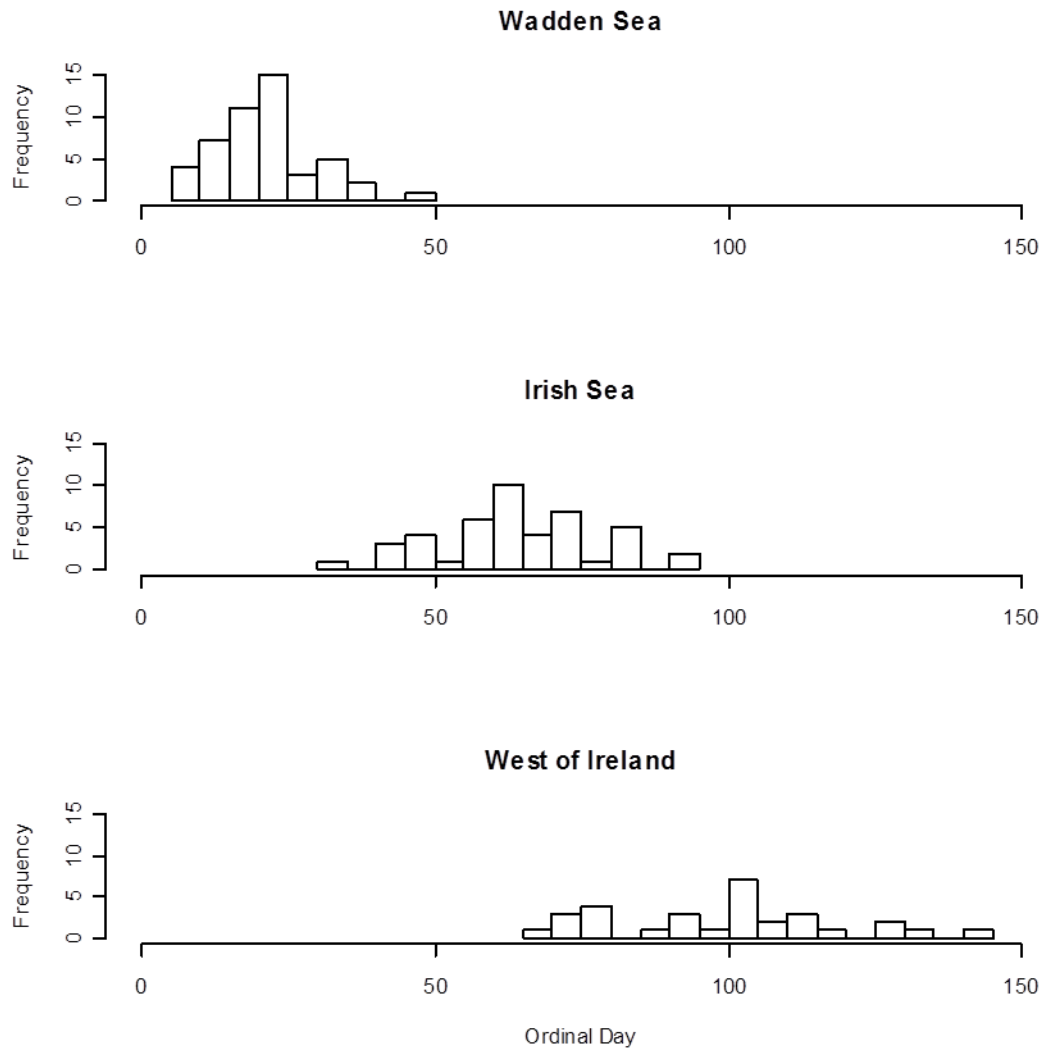
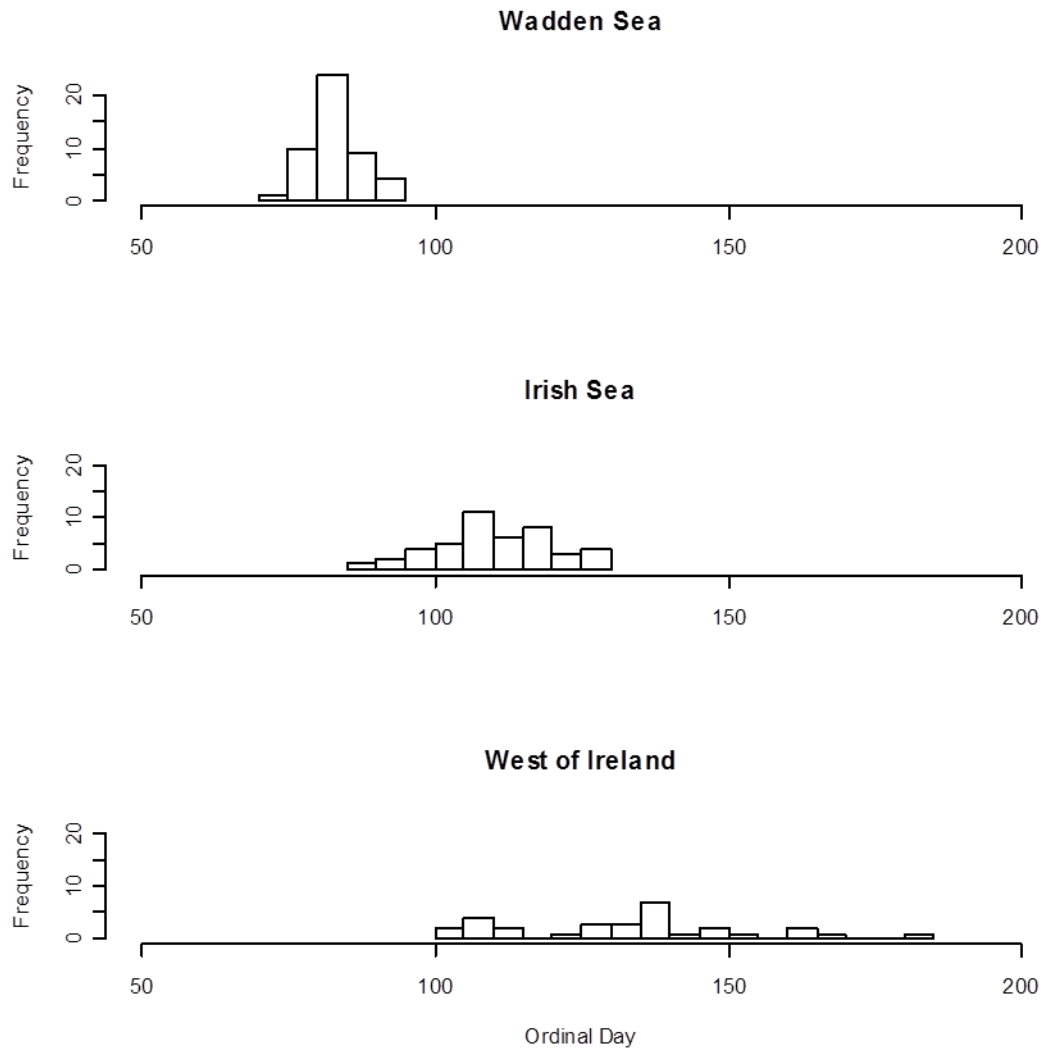


Figure 3.3: Histograms of settlement dates for larval plaice in the three regions.



### 3.4.2 Sea surface temperatures and larval duration

Figure 3.5 shows the eight day averages of SST for the three regions over the estimated larval period. The trend was generally upward through the period, though all regions showed some short-term decreases in temperature which were strongest in the Wadden Sea and Irish Sea. Wadden Sea and Irish Sea temperatures tracked each other quite closely during the period of temporal overlap, with the Irish Sea warmer on average; but the West of Ireland temperatures were considerably warmer overall.

There was a significant negative relationship between larval duration and mean temperature during the drift period (GAM,  $P < 0.001$ , edf = 2.72, R-sq (adj) = 0.85) which was linear at the lower temperatures but began to level off at around 9 °C. At temperatures above 10.5 °C there was no apparent effect of temperature on larval duration (Figure 3.6). Region was a non-significant parameter in this model implying that the relationship between larval duration and temperature is consistent across regions. The same data were also modelled using traditional linear regression (Figure 3.7). Although the GAM described the relationship between larval duration and temperature better than the linear model, the linear parameters were calculated for comparison with Bolle et al (2009).

$$\text{This study:} \quad \ln(\text{LD}) = 5.15 - 0.15 (\text{SST})$$

$$\text{Bolle et al.:} \quad \ln(\text{LD}) = 5.00 - 0.15 (\text{SST})$$

where LD is larval stage duration and SST is average sea surface temperature.

These results are strikingly similar, and also agree broadly with van der Veer et al. (2009), who found that larval duration of plaice in the Balgzand was negatively correlated with temperature over eight years, though the effect was not as marked as in this study.

Although the effect of temperature on larval duration was regionally consistent, the combined effects of larval duration and temperature revealed significant variation between areas (Kruskal-Wallis,  $P < 0.001$ ). Analysis of the degree day at settlement showed similar values for the Irish Sea and West of Ireland, but higher values for Wadden Sea fish (Figure 3.9).

Figure 3.4: Boxplots of plaice larval duration, hatch dates and settlement dates by region: WS (Wadden Sea), IS (Irish Sea), WOI (West of Ireland). Dates are in ordinal days. Kruskal-Wallis tests indicated that all parameters were significantly different by region ( $P < 0.001$ ). Post-hoc tests confirmed that each region was significantly different from the others (Mann-Whitney-Wilcoxon,  $P < 0.001$ , all parameters).

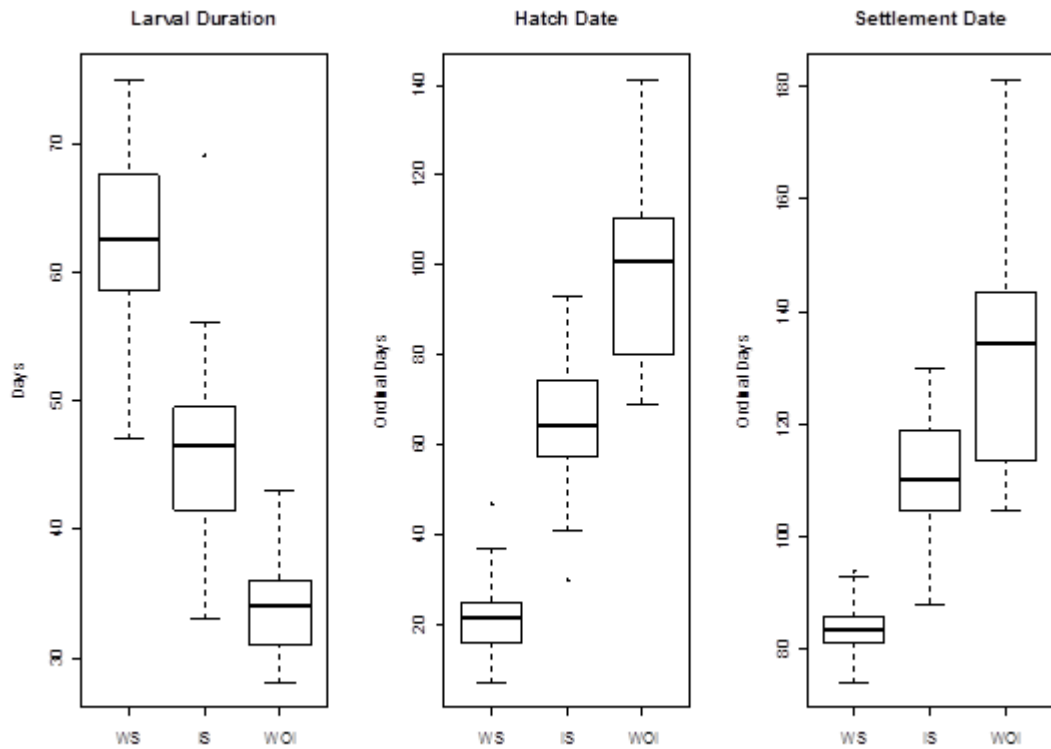


Figure 3.5: SST (8 day averages) during the estimated larval drift of plaice in each region. Mean overall temperatures for the regions during the periods of interest were Wadden Sea  $7.0 \pm 0.24$  °C sd; Irish Sea  $8.2 \pm 0.36$  °C sd; West of Ireland  $10.7 \pm 0.58$  °C sd.

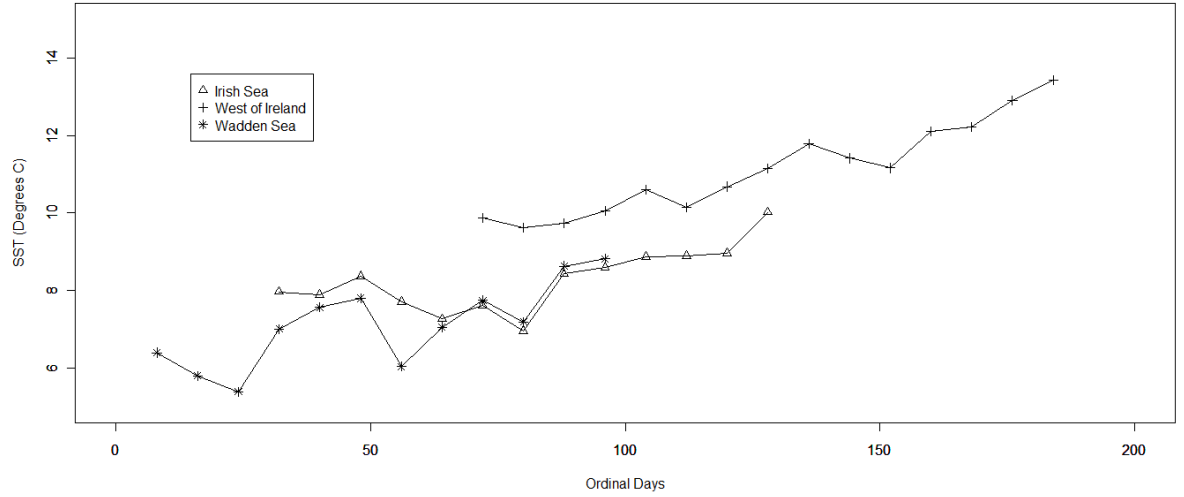




Figure 3.6: GAM plot showing smoothed relationship between average estimated SST during the larval phase and larval duration ( $P < 0.001$ , edf = 2.72, R-sq (adj) = 0.85,  $N = 122$ ). There were no differences in the relationship between regions (ANOVA,  $P = 0.578$ ) and this factor was not included in the model. Tick marks on the x-axis represent temperature data points.

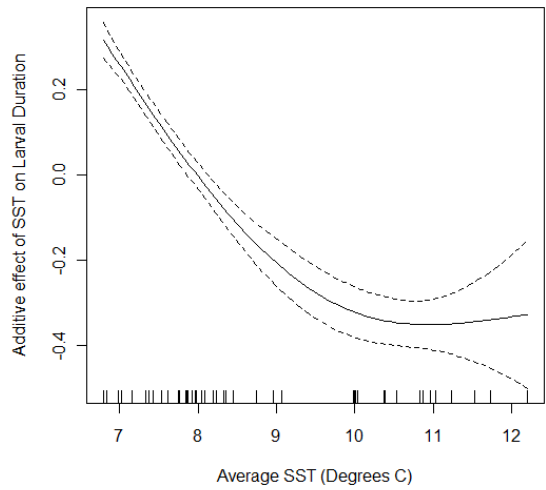
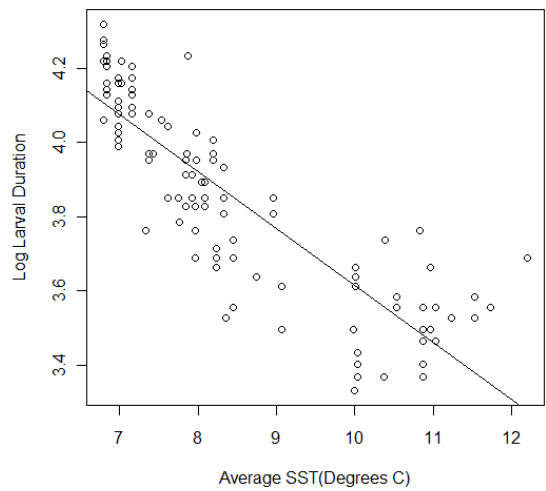


Figure 3.7: Linear regression of Log transformed larval stage duration (LD) modelled on average SST. Model estimate was  $\ln(LD) = 5.15 - 0.15 (SST)$ , R-sq(Adj) = 0.752, intercept and estimate both significant at  $P < 0.001$ .



### 3.4.3 Growth

Individual growth, as indicated by otolith increment width, was strongly correlated with the variables larval duration (LD), degree day (DD), and mean sea surface temperature (SST). The model selection process summarised in Table 3.2 illustrates the improvement in the model fit as indicated by reducing AIC values when DD is included as a predictor variable instead of LD. AIC was even lower when SST was substituted into the model but in this case the model was not valid; predictors were non-significant, residual plots were poor, and the R-sq value was very low. AIC of the model that included degree days without the correlation structure was high, but the ACF plot of the model residuals showed strong auto-correlation, rendering it invalid.

The model chosen to describe the larval growth data was:

$$\ln(\text{Otolith increment width}) \sim \text{Region} + s(\text{Degree Day}) : \text{Region}$$

Where  $s$  denotes a non-parametric smoother applied to the continuous predictor variable, and the smoother was allowed to interact with the factor Region. Degree day was significant at  $P < 0.001$  for each smoother and the factor region was also significant at  $P < 0.001$ . The GAM curves were non-monotonic for all regions, and the growth rate trend was largely positive (Figure 3.8). In plaice from the Irish Sea and Wadden Sea, growth rates slowed after hatching over the first period of about 80 DD, and then increased consistently until inflecting at about 350-400 degree days. West of Ireland plaice otolith increment widths increased consistently from hatch until decreasing at around the same degree day value as the other two regions.

Table 3.2: Results of GAMMs of plaice larval growth (otolith increment width) modelled on the smoothed predictors degree day (DD), larval duration (LD), and sea surface temperature (SST) interacting with region, a factor with three levels. Model validity was assessed on examination of residual plots, ACF plots and the significance of variables. Lower AIC values indicate better model fit, i.e. a model with AIC of -10 has more support than a model with AIC of -5

<b>Response</b>	<b>Predictor 1</b>	<b>Predictor 2</b>	<b>Correlation structure</b>	<b>AIC</b>	<b>R-sq(adj)</b>	<b>Model valid</b>
<i>Ln</i> Otolith increment width	DD	Region	corAR1	-4872.36	0.728	Yes
<i>Ln</i> Otolith increment width	LD	Region	corAR1	-4835.53	0.712	Yes
<i>Ln</i> Otolith increment width	SST	Region	corAR1	-5005.62	0.131	No
<i>Ln</i> Otolith increment width	DD	Region	None	-539.01	0.729	No

Figure 3.8: GAM plots showing additive effect of degree day on Log transformed otolith increment width during the larval phase interacting with the three regions, Irish Sea ( $P < 0.001$ , edf = 6.524), West of Ireland ( $P < 0.001$ , edf = 5.031), and Wadden Sea ( $P < 0.001$ , edf = 7.263). Solid lines are modelled estimates; dashed lines represent Bayesian credible intervals. Increasing credible intervals towards the end of the curves reflect the variation in the age of larvae at settlement; this means there were fewer data points on the right of the x-axis. Raw otolith increment width data are shown in the lower plots. Regions are significantly different (ANOVA,  $P < 0.001$ ).

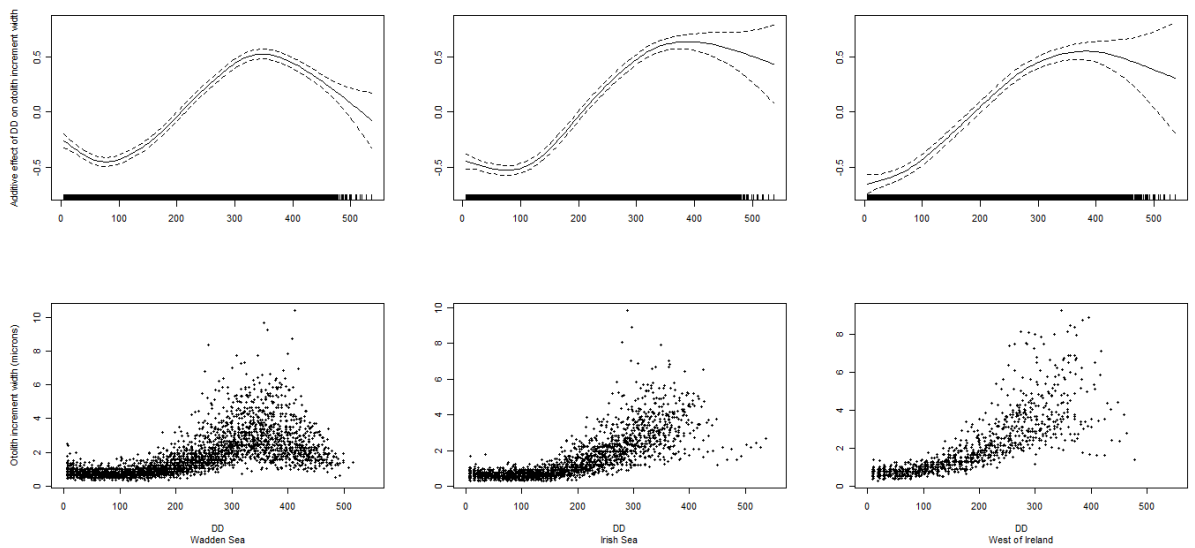
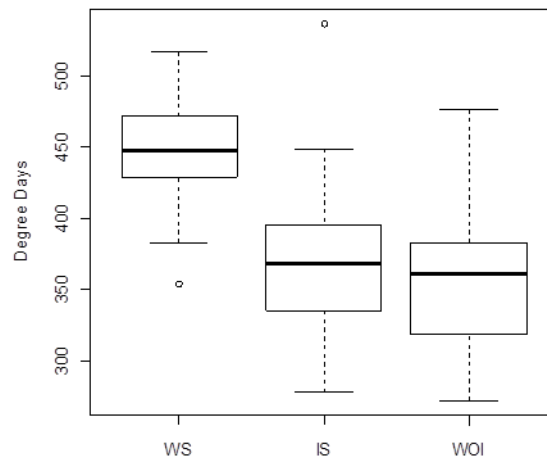


Figure 3.9: Boxplot of the degree day value at settlement by region, which were significantly different overall (Kruskal-Wallis,  $P < 0.001$ ). Post-hoc tests indicated that the Irish Sea (IS) and West of Ireland (WOI) results were not significantly different from each other (Mann-Whitney-Wilcoxon,  $P = 0.798$ ); the Wadden sea (WS) results were significantly different from the other two ( $P < 0.001$ ).



### 3.5 Discussion

The direct effect of temperature on the growth of fish larvae is well established (Blaxter 1992, Kielbassa et al. 2010). Karakiri and von Westernhagen (1989) also found a positive relationship between temperature and development, larval duration in plaice was over 100 days at 5°C but 40-50 days at 10°C. In the same paper they also reported an effect on growth of reduced salinity but this is probably not so significant in the field as most of the pelagic larval phase occurs offshore (Fox et al. 2006, Bolle et al. 2009). Higher temperatures have also been shown to induce earlier metamorphosis in flounder (*Platichthys flesus*) (Hutchinson and Hawkins 2004). In general, the durations of early life history stages of fish are shorter at higher temperatures (Pepin 1991).

Degree days are expected to reflect the temperature experience of a fish more accurately than using average temperatures over the planktonic phase (Neuheimer and Taggart, 2007). The development of larval fish has been successfully predicted by degree days in tank experiments (Malzahn et al. 2003, Weltzien et al. 1999) whilst Neuheimer and Taggart (2007) extended the concept (defined as growing degree days, GDD) to field data. In the present study, the analysis illuminated the daily integration of varying ambient temperatures on otolith growth. Instantaneous larval growth was analysed by modelling individual increment widths, and the results show that degree day best described this growth, and was a clear improvement over age as a predictor.

There were differences in the pattern of early instantaneous growth (as estimated by the proxy, otolith increment width) between the regions. In the West of Ireland region the growth rate rose constantly from hatching whilst in the Irish and North Seas there was an initial decrease. Similar shifts in plaice larval growth have been previously noted in the southern North Sea (Hovenkamp and Witte 1991). In the Irish Sea and southern North Sea a substantial portion of plaice larvae hatch into cooling waters as temperatures typically decrease early in the year reaching a minimum in late Feb – mid March (Fig. 2 this study, Fox et al. 2007, van der Veer et al. 2009). In contrast, larvae in the west of Ireland region were estimated to have hatched from day 60 onwards, and into warming waters (Fig. 4). Towards the end of the larval period, mean modelled increment widths decreased in all regions, but this was particularly prominent for Wadden Sea fish. Wennhage and Gibson (1998) showed that settlement behaviour of recently metamorphosed larvae was influenced by the presence of suitable prey in the

sediment and the presence or absence of predators and growth might slow if suitable conditions are not encountered. However, reduced growth rates might also result from changes in salinity as late larval fish enter inshore waters (Karakiri and Westernhagen 1989) or from the metabolic demands of metamorphosis (Christensen and Korsgaard 1999, Geffen et al. 2007). Metamorphosis in flatfish seems to be more related to size than age (Borski et al. 2010); for plaice Hovenkamp and Witte (1991) reported that slow-growing and fast-growing larvae metamorphosed at similar sizes. Although plaice may be able to delay settlement for some days after they have reached a suitable size for metamorphosis, (Wennhage and Gibson 1998), it is generally considered that this ability is limited and that fish which do not reach suitable nursery grounds relatively quickly will be lost to the population (Fox et al. 2006).

Although the degree day values at settlement showed little difference between the West of Ireland and the Irish Sea, they were considerably higher for Wadden Sea fish. The extended larval durations of the Wadden Sea fish and the longer period between peak growth and settlement, compared with the other regions, may explain this. In the Irish Sea, spawning and nursery grounds are in close proximity. The initial transport of the eggs and larvae is largely wind-forced but tidally-synchronised vertical migration of older larvae seems to be required to concentrate settling fish into known inshore nursery grounds (Fox et al. 2006, 2009). In contrast, spawning and nursery grounds in the southern North Sea are further apart but are connected by strong tidal streams (Harding et al. 1978, van der Veer et al. 1998, Bolle et al. 2009). The presence of vertical migration behaviour does not seem to have such a dramatic effect on larval transport although it is still important for immigration of late larval stages into tidal nursery grounds such as the Wadden Sea (Bolle et al., 2009). Earlier spawning in the southern North Sea into colder waters may result in transport over longer distances because of the increased larval duration. Unfortunately there is no information in the published literature about the location of plaice spawning grounds off the west coast of Ireland. Further field surveys and transport modelling are required to establish connectivity pathways between spawning and nursery grounds in this region.

The fish sampled had relatively short hatch and settlement periods in the Wadden Sea, and these took place earlier in the year than in the other two regions. The hatch and settlement periods were most protracted in the West of Ireland. This is likely to be an artefact of the time elapsed between settlement and sampling, the Wadden Sea fish

having been sampled very shortly after settlement (and before the completion of settlement), and the West of Ireland fish not sampled until September. The Irish Sea fish were intermediate between the two. More fish will have settled over a longer time period in the Wadden Sea and the Irish Sea after sampling took place, although these are not represented in in this study. Allen et al. (2008) sampled juvenile plaice on six occasions from mid-March to the beginning of April in Galway Bay, West of Ireland in 2003. Using the same methods to back-calculate dates from otolith increment counts, mean larval durations were found to be almost identical to the fish sampled in 2002 in this study. However he found plaice that on the 10<sup>th</sup> March that year, more than a month earlier than the first settled fish from this study (14<sup>th</sup> April 2002). This implies either different settlement patterns in 2002 on the west coast, or that earlier settled fish in 2002 may have suffered mortality on the nursery between settlement and sampling. The recognised moderating effect of nursery ground processes on the year class strength of plaice (Nash and Geffen 2000, van der Veer et al. 2000) may have influenced the West of Ireland fish, possibly removing earlier or later settling fish, slower or faster growers, or fish with longer or shorter larval durations.

By necessity the fish sampled in this study represent a small component of the surviving larvae spawned that year. The existence of sub-cohorts in settling plaice is well known (Hovenkamp 1992, Allen et al. 2008, Geffen et al. 2011) and may be a confounding factor in our understanding of larval growth and mortality (Geffen et al. 2011). Timing of peak spawning in plaice has been shown to vary year on year (Nash and Geffen 1999, Fox et al. 2007, van der Veer et al. 2009), and the fish sampled in the different regions in this study had spent varying lengths of time on the nurseries prior to capture. However the results indicate that the general relationship between growth and temperature is represented by the models even in the absence of a fully balanced sampling design.

We have assumed that otolith increment widths reflect somatic growth in individual plaice larvae and that increments are deposited daily. Karakiri and von Westernhagen (1989) reared larvae at 5 and 10°C and demonstrated that both assumptions held at these temperatures. They also suggested that 5°C was the lower limit at which plaice larvae would grow. Hovenkamp and Witte (1991) noted this problem in relation to age determination of larvae from the southern North Sea collected in particularly cold years. However, errors arising from narrow initial increment are unlikely to be a major factor



in this study since the initial narrow increment widths ranged from 0.3 to 0.8  $\mu\text{m}$  in slow-growing larvae at the lowest average temperatures experienced (estimated to be 6°C in the southern North Sea).

For the North and Irish Seas, estimated hatch and settlement dates in the present study largely agreed with previous estimates from Fox et al. (2009) and van der Veer et al. (2009). However, a difference of about eight days exists between larval duration estimates for 2002 Wadden Sea fish from van der Veer et al. (2009) and the present study. The Wadden Sea fish in the present study are a sub-sample of those analysed in the earlier paper and the differences may be attributable to those fish chosen, or to differences in interpretation of otolith microstructure. In van der Veer et al. (2009) the number of unclear early growth increments immediately post-hatch was estimated by dividing the distance from the hatch ring to the first clear increment by an average increment width of 0.6  $\mu\text{m}$ . This was not done in the present study as increments were visible right in to the hatch-ring. Considerable uncertainty and potential bias in otolith reading can occur between readers and laboratories (Campana 2001), but in the present study all otoliths were read by a single reader at least guaranteeing internal consistency. Even if the absolute estimates of larval age were biased in either study, comparative patterns between regions should be realistic.

Our models assume that degree days can be estimated from satellite data as the average over a large sea area assumed to encompass the region of larval drift. Fox et al. (2007), however, showed that there can be as much as a 4°C difference in water temperatures between inshore and offshore waters of the eastern Irish Sea at the time plaice larvae would be in the plankton. Although otolith microchemistry can be used to re-construct temperatures (Høie et al. 2004, Shephard et al. 2007), this cannot usually be achieved for the larval stage, so we are limited to indirect estimates of ambient thermal history. Even with the application of particle tracking models it is usually impossible to know the exact transport history of settling fish and this remains a key limitation for modelling (North et al. 2009). Even so this study serves to strengthen our understanding of the fundamental role played by temperature in the larval stage of plaice. The differences in growth patterns illustrate the variation in early life histories across regions while the consistency of the relationship between larval duration and temperature is a key feature of the strategy to get larvae to the nurseries coincident with their

competence to settle there. The findings indicate that future modelling work may incorporate temperature as the main driver for larval development in plaice.

### **3.6 Conclusion**

This study serves to strengthen our understanding of the fundamental role played by temperature in the larval stage of plaice. The differences in growth patterns illustrate the variation in early life histories across regions while the consistency of the relationship between larval duration and temperature is a key feature of the strategy to get larvae to the nurseries coincident with their competence to settle there. The findings indicate that future modelling work may incorporate temperature as the main driver for larval development in plaice.

## **4 The influence of environment on the growth and settlement of larval turbot (*Psetta maxima* L.) on the Atlantic coast of Ireland**

### **4.1 Abstract**

Turbot are a rare, valuable and commercially-exploited flatfish found in Irish continental shelf waters which use sandy beaches on Irish coasts for nurseries. Analysis of juvenile turbot otoliths can reveal information from their pelagic larval phase. In this study Juvenile (0+) turbot were sampled from two nurseries on the west and southwest coasts of Ireland over three years. Sagittal otoliths were taken from the fish and processed to ascertain larval growth rate, larval duration and settlement dates. Cumulative degree days (CDD) were derived from satellite-sensed sea surface temperature (SST) data assumed to represent larval drift in conjunction with the ages of the larvae at a daily scale and were used to model larval growth using generalized additive mixed modelling (GAMM). This revealed differences in growth patterns between regions and years, which may indicate that separate stocks supply larvae to the nurseries. Larval duration was negatively associated with mean temperature during the larval period using a negative binomial generalized linear model (glm), but there was no regional or annual effect. This result is in agreement with similar analyses of plaice (*Pleuronectes platessa*). Analysis of variance showed that turbot from the western nursery ground had experienced warmer mean temperatures during the larval period, and larval durations differed over years. Turbot settlement on the nurseries was modelled on a daily scale using a logistic glm. Three environmental drivers were found to significantly influence the timing of settlement (as indicated by the deposition of the first accessory primordium in the otolith): tidal amplitude on the day of settlement was negatively associated, mean rainfall over three days prior to settlement was positively associated and mean wind speed over three days was negatively associated. Wind direction was not significant in the model, although year-class strength in turbot has been correlated with onshore winds in the past. This study is the first attempt to quantify the importance of environmental variables to the early life stages of turbot from the north eastern Atlantic.

This chapter is in review as Comerford, S., P.S. Haynes and D. Brophy, 2012. The influence of environment on the growth and settlement of larval turbot (*Psetta maxima* L.) on the Atlantic coast of Ireland. Journal of Sea Research.

## 4.2 Introduction

The life cycles of flatfish comprise discrete stages, in most cases requiring the passage of pelagic eggs and larvae from spawning grounds to nurseries, where a demersal habit is adopted following metamorphosis from a symmetrical body plan to the familiar flatfish shape (Gibson, 2005). The turbot (*Psetta maxima* L.) of the North East Atlantic spawn in continental shelf waters and the developing larvae are conveyed by current and wind over a period of weeks to shallow sandy coastal nurseries. Here the juveniles settle in the late summer and early autumn to spend one or two years feeding and growing before migrating offshore where they join the adult stock to spawn (Jones 1973, Haynes 2010a).

Little has been established about the larval period of turbot; their rarity means that they are infrequently recorded in plankton surveys, and then in small numbers (see e.g. Tully and O'Ceidigh 1989a). However it is in the larval period and in the early juvenile stage that the year class strength of the much-studied plaice (*Pleuronectes platessa* L.) is established (van der Veer 1986, Nash and Geffen, 2000). The timing and location of spawning determine the length of time spent in the plankton and the conditions encountered during the journey from the spawning site for any flatfish species. These conditions then control mortality due to predation or starvation, and the growth and thus fitness of the survivors to metamorphose and settle at the nurseries.

The growth of larval fish is greatly influenced by temperature (Blaxter 1992). Higher temperatures drive faster growth and faster growing fish reach the refuge of size sooner, as bigger larvae have an advantage in escaping predators (Bailey and Houde 1989, Leggett and Deblois 1994). Conversely predator abundance may be depressed in colder years resulting in greater survival of larval fish (Nash and Geffen 2000, van der Veer et al. 2000, 2009). Juvenile turbot abundance on Irish nurseries was negatively correlated with average spring-time water temperatures over an eight year period (Haynes 2010a). Environmental conditions affect larvae in other ways too; turbot year class sizes have been shown to be positively correlated with onshore winds on UK coasts (Riley et al. 1981). Surface turbulence associated with high winds may also affect the ability of turbot larvae to find prey items, as their late larval stage is found in the hypo-neustal layer (Last 1979).

Nursery area effects serve to further regulate numbers in many flatfish species, although it may be inferred that turbot do not suffer density-dependent effects given their scarcity on the nurseries (Sparrevohn et al. 2008, Haynes 2010a, 2011). Studies on sole (*Solea solea* L.), and plaice indicate a positive relationship between surface area of nursery grounds available and the numbers of juvenile fish recruiting into the adult stock (Van der Veer et al. 2000). This nursery size hypothesis may partially explain the relative rarity of turbot since their nursery areas are restricted to a narrow band on the coasts. Surveys of 0+ flatfish around the UK coasts usually found juvenile turbot in salinities higher than 32 PSU and never in depths greater than 2m (Riley et al. 1981). Fish that are very specific in their habitat requirements are likely to be less abundant than species that can inhabit a broader range of habitat; juvenile turbot inhabit restricted distributions in shallow waters, and are rare (Gibson 1997).

This study is based on data from the otoliths of juvenile turbot captured over three consecutive years from nurseries on the west and southwest coasts of Ireland. Otoliths are calcareous structures associated with orientation found in the ears of teleost fish, and conveniently their growth is strongly correlated with somatic growth. In most cases increments are laid down daily on the otoliths (Campana 2001), and in the otoliths of juvenile fish these increments are visible using microscopy following processing. The fish can therefore be aged at the daily scale, and their somatic growth rates inferred from the relative widths of the daily increments. Tank experiments have shown that increment deposition in turbot otoliths occurs at a daily rate, though this may be disrupted under stressful conditions (Geffen 1982). In this paper we sought to establish the importance of sea surface temperatures during the larval stage to both the growth of the larvae and the duration of the larval period of turbot. It was hypothesised that regional differences in growth and larval duration, possibly relating to different contributing adult stocks, would be revealed.

Metamorphosis of the larval fish, which is concurrent with settlement onto the benthic habitat in many flatfish species (Geffen et al. 2007), causes visible disruption to the otolith thereby marking the event in time (Campana 2001). In this paper turbot metamorphic events were modelled at daily level to reveal the contribution environmental factors make to the transition between the planktonic and demersal life stages. As the success of any year class is determined in the early life history stages, and the rarity of turbot appears to be regulated by their restrictive habitat choice at nurseries;

then an understanding of the act of settlement and the importance of the physical drivers leading to successful settlement would provide further insight into their ecology.

Turbot are commercially exploited, although they do not have a fishing quota assigned to them in Irish waters (CSO, 2007). Historically they have been considered “prime” fish, and still maintain a high value, though they do not support a directed fishery in the area studied. They are taken as bycatch, usually by trawlers. Turbot are thus vulnerable as a species on three fronts: they are the subject of an unregulated fishery, and are valuable; they exclusively use sandy beaches as nurseries, and are subject to the vagaries of coastal anthropogenic pressures; and they are subject to the temperature increases and associated environmental changes predicted due to global warming (IPCC 2007, Vinagre et al. 2009, ter Hofstede et al. 2010). The fish analysed here have already been the subject of enquiry into aspects of their early life history (Haynes et al. 2011). Parameters relating to hatch dates, larval duration, and settlement dates have been established and a comparison made between pre- and post-settlement growth rates. This paper seeks to reveal further characteristics of larval turbot, specifically those relating to the environment; and to contribute to our understanding of the ecology of this scarce and insufficiently understood flatfish.

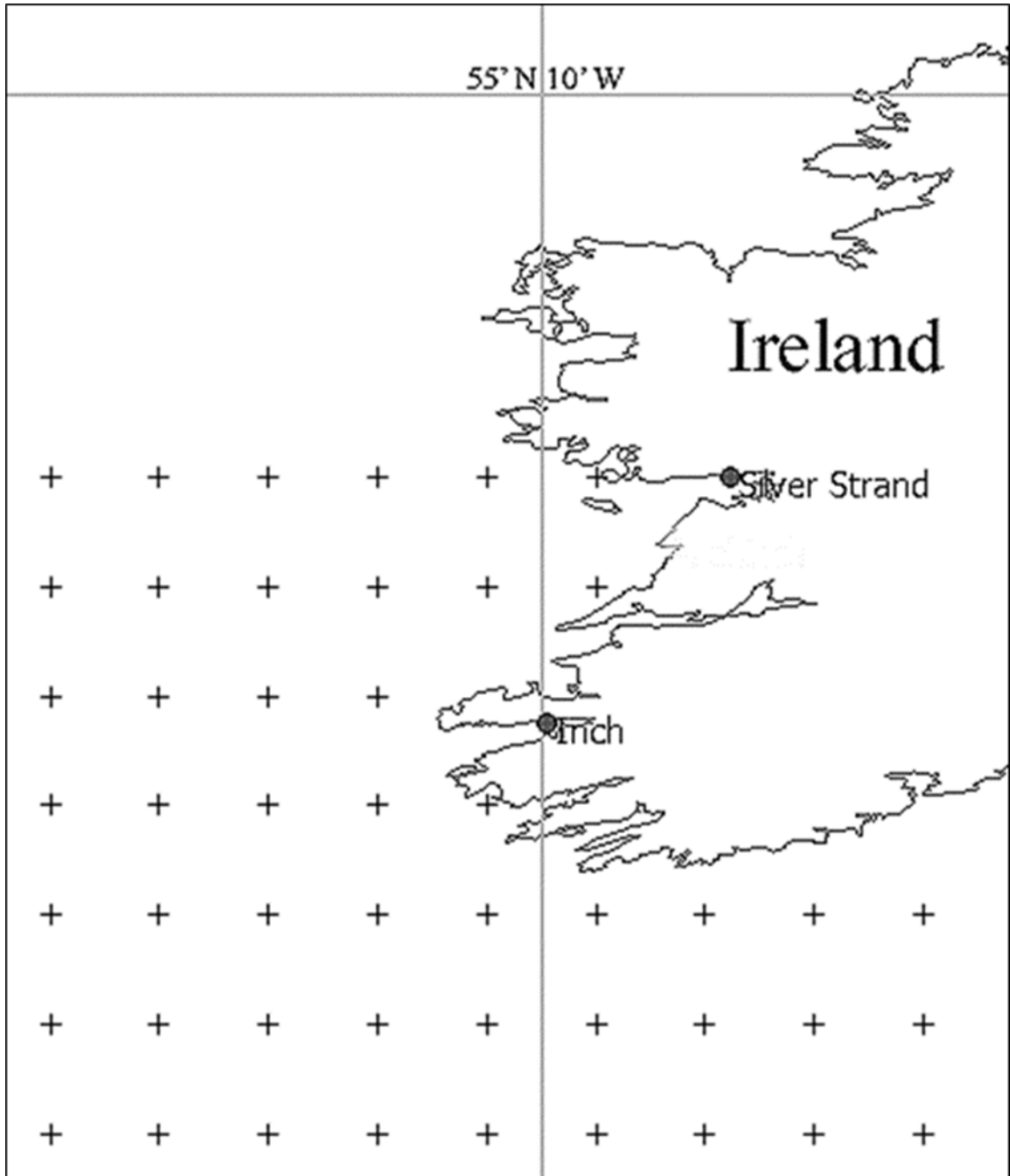
### **4.3 Methods and materials**

#### *4.3.1 Sampling*

A total of 59 juvenile (0+) turbot were analysed from 2007, 2008 and 2009. Of these 31 were from Inch beach in Co. Kerry and 28 from Silver Strand beach in Co. Galway, representing all years. The beaches are relatively exposed, though Silver Strand enjoys some shelter within Galway Bay. Inch is west-facing and more exposed to the Atlantic swells. Sampling took place each year during the month of September as near as possible to the spring tide within two hours either side of low tide. Each beach was sampled on a single day. Sampling was by Danish beach seine; in 2007 a 20 x 2m net with 13 x 13mm mesh was deployed by dinghy. In 2008 and 2009 a 5.5 x 2m net with 5 x 5mm mesh was deployed by wading from the shore. Nets were recovered manually, except in 2007 at Inch when they were recovered with the aid of two quad bikes. Both nets successfully captured newly settled turbot, and their substitution was not considered a confounding factor. †



Figure 4.1: Map showing nurseries in Galway (Silver Strand) and Kerry (Inch) where turbot were captured. Crosses indicate points at which sea surface temperatures (SST) were remotely sensed by satellite.



#### 4.3.2 Otolith analysis

The juvenile turbot were placed in plastic bags and frozen on the day of capture. They were thawed in the lab and identified by means of fin ray counts to distinguish them from brill (*Scophthalmus rhombus* L.) according to Russell (1976). Sagittal otoliths were removed from the thawed fish under a dissecting microscope then cleaned and mounted on glass slides with Crystalbond™. Left and right-side otoliths were chosen randomly and polishing was carried out according to Brophy and Danilowicz (2002) to reveal the increments deposited during the larval and post-larval growth periods. The larval part of each otolith was measured along its longest axis from the hatch ring to the last full increment prior to the accessory primordium (AP), and each increment was counted and its width recorded. A count was then made of all increments from the AP to the edge, representing the post-settlement period. The timing of the larval period of each individual fish was estimated by subtracting both the larval and post-larval daily otolith increment counts from the capture date. For the purposes of this study metamorphosis as indicated by the AP was assumed to be synchronous with settlement (Üstündağ 2003).

Otoliths from a subsample of 25 fish were chosen randomly and re-analysed without knowledge of prior results. This test gave a coefficient of variation of 6.8% between readings which was considered satisfactory. The left and right otoliths of a further subsample of 10 fish were measured, and there was no significant difference between the results (paired t-test,  $P < 0.05$ ). This justified the random selection of left and right otoliths.

### 4.3.3 Data analysis

Data were analysed using the open-source software R version 2.11.1. To determine regional differences in average temperatures experienced by the larval fish, and their larval stage duration, analysis of variance testing was used. These data were non-normal and heteroscedastic so the non-parametric Kruskal-Wallis test was chosen.

The predictor cumulative degree day (CDD) was calculated as the time integral of the average daily temperature ( $t$ ) across the regions shown in Figure 4.1 which were assumed to represent the drift range during the period corresponding to the larval phase of the individual fish.

$$\text{CDD} = \sum_n t_1 + t_2 + \dots + t_n$$

Generalized additive mixed models (GAMMs) were applied to otolith larval growth data, which were log transformed to account for heteroscedasticity. Data exploration indicated that the data followed a gamma distribution after transformation therefore the Gamma family with a log link function was used. CDD, larval age and SST were tried as continuous variables in a model selection process; the factors year (three levels) and region (two levels) were also tried, and interactions were considered. Model selection was carried out manually on the basis of significance of predictors at the  $P < 0.05$  level and lower AIC values resulting from inclusion or omission from the model (Burnham and Anderson 2002, Zuur et al. 2009). The R packages `mgcv` and `nlme` were employed for GAMMs which use penalized regression splines to smooth the relationship between response and predictor variables (Wood 2006). A `corAR1` temporal correlation structure was applied to the model allowing for correlation at a daily (otolith increment) level nested in each individual fish. This use of a mixed model was to counteract the effects of auto-correlation in the data which violates assumptions of independence and can lead to incorrectly inflated significance (Zuur et al. 2009). Model outputs include the term effective degrees of freedom (edf); ranging from zero to infinity, higher values of edf imply greater non-linearity in the relationship.

Settlement of turbot on the nurseries was modelled using a binomial generalized linear model (glm) with a logistic link. Dates on which fish settled were coded 1, dates when there was no settlement were coded 0. All dates bounded by the first and last settlement event of each year were included. This approach allowed the probability (P) of fish

settlement to be calculated for the explanatory variables in the final model by the formula:

$$P = \frac{e^x}{1 + e^x} \quad \text{where } x \text{ is the model estimate.}$$

A number of explanatory variables were tried in the model and the best model was selected on the basis of lowest AIC values with variables only included at the  $P < 0.05$  level. Factors considered were region, and year and month of settlement. Continuous variables considered were moon phase; maximum tidal height; wind speed averaged over 1,2,3,5 and 7 days; rainfall averaged over the same periods; an index of wind speed with a directional component for onshore/offshore winds, also averaged over the same period; and wind direction. Interactions were also tested. Nagelkerke's generalised  $R^2$  generated by the Design package in R was used to give a measure of variance explained by the model.

The relationship between larval duration and average sea surface temperatures experienced by each fish during its larval period was modelled using a negative binomial glm with an identity link from the package MASS. This was used to account for overdispersion found when using a glm. Models were all validated by examination of residual plots and by using the Auto-correlation (ACF) function.

Wind and rainfall data were supplied by Met Eireann, the Irish meteorological office. Wind data came from Shannon in Co. Clare, situated between the two regions of interest. Rain data came from rain gauges in Galway City and Valentia in Co. Kerry. Average values of the two stations were used in the settlement model as the two weather stations bracket the study area. Tidal height data were taken from the tide gauge at Galway Harbour maintained by the Irish Marine Institute and were downloaded from the Marine Institute website. Global sea surface temperature (SST) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on the Aqua EOS PM satellite were downloaded from the NASA OceanColor website and processed using the SeaWiFS data analysis system SeaDAS version 6.1. Data were collected from a grid 0.5° latitude x 0.5° longitude, approximately equal to 55.5 x 55.5km (Figure 4.1).

## 4.4 Results

### 4.4.1 Growth

Larval growth as represented by logged otolith increment widths was modelled using GAMM. The best predictor of growth as indicated by lowest AIC (-4970.9) was the smoother for thermal integral cumulative degree day (CDD) with no other predictors included, which explained 84% of the variability in the model. For ease of interpretation another model was fitted to the data which allowed the smoother for CDD to change over each year and region. While this model disimproved the AIC (-4882.3) the smoother was still significant at  $P < 0.0001$  and the factors were significant at  $P = 0.0018$ . This model explained 86% of the variation in the data. Larval age in days and SST as an independent variable were also tried during selection but did not improve the model. The single smoother fitted to the data in Figure 4.2 shows linear growth up until approximately 300 CDD after which growth slows, but continues to increase until settlement at the end of the curve. Similarly the fitted smoothers in Figures 4.3 and 4.4 show that growth in both regions and over the three years was linear and with similar slopes until approximately 300 CDD, thereafter the growth curves differed more markedly. Otolith growth prior to settlement in Galway in 2007 evidently slowed and the rate declined, while in Kerry that year the curve was more typical of the combined growth curves. Growth appears similar across the two regions in 2008. In 2009 the curve for Galway was short, reflecting the shortest larval durations for the study period; the curve for Kerry in 2009 was also short, but with a characteristic dip where growth rates slowed markedly before increasing again prior to settlement.

Figure 4.2: Otolith growth data for turbot modelled on cumulative degree day (CDD) over three years and two regions. One smoother is fitted which is significant ( $P < 0.0001$ ). Dotted lines indicate Bayesian credible intervals. The amount of variability explained by the model is 84% ( $R\text{-sq adj} = 0.843$ ). This was the best model determined by AIC.

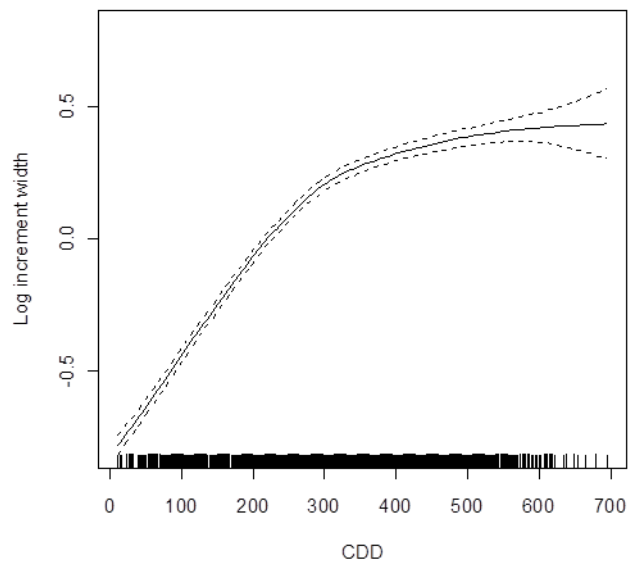


Figure 4.3: Output of GAMM model for Galway when year and regions were included as factors. The factors were significant at  $P = 0.0018$ . The additive effect of CDD on logged otolith increment width is shown in the left hand column; the raw data is shown in the right hand column. This model explained 86% of the variability in the data ( $R\text{-sq adj} = 0.861$ ).

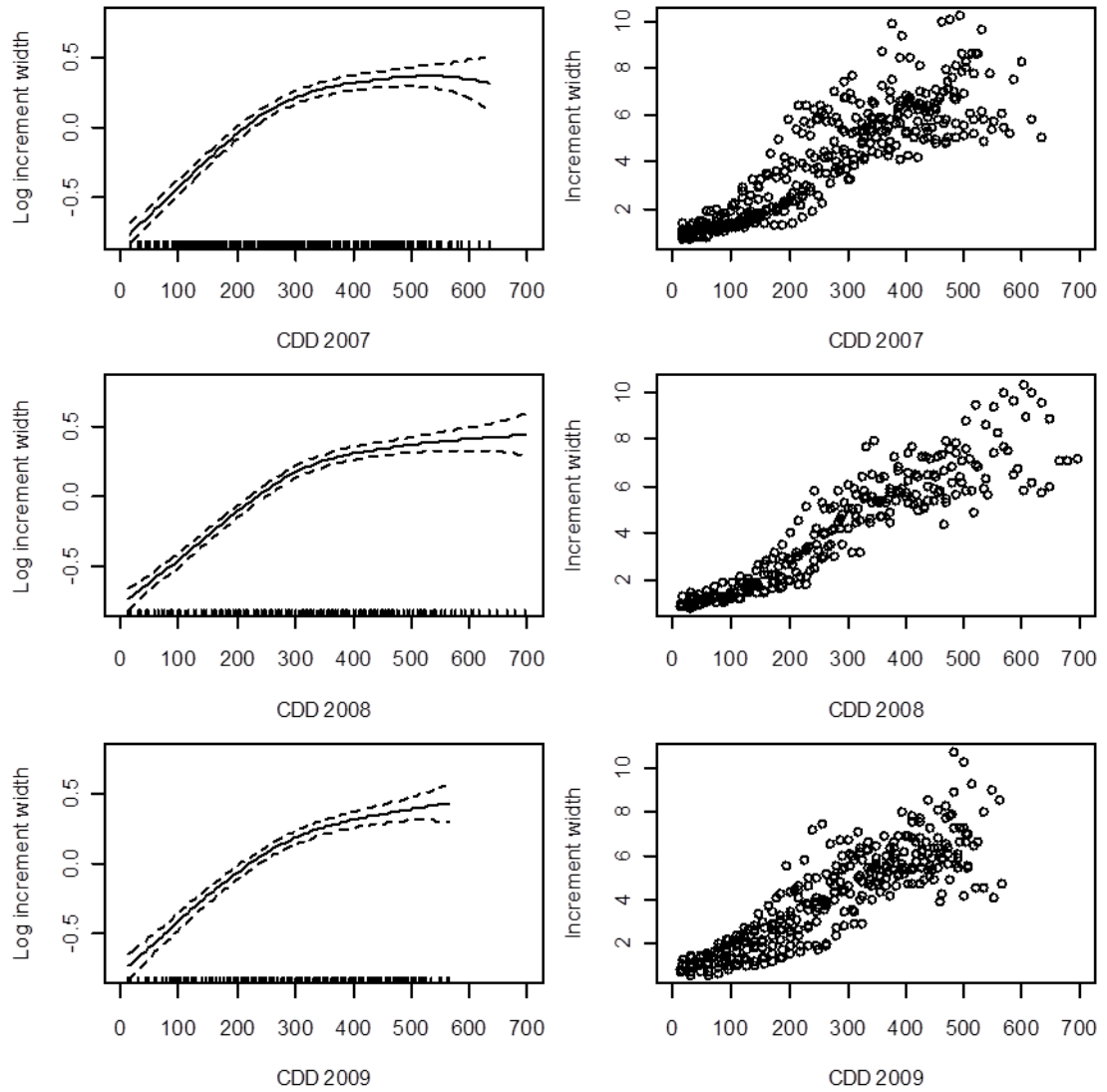
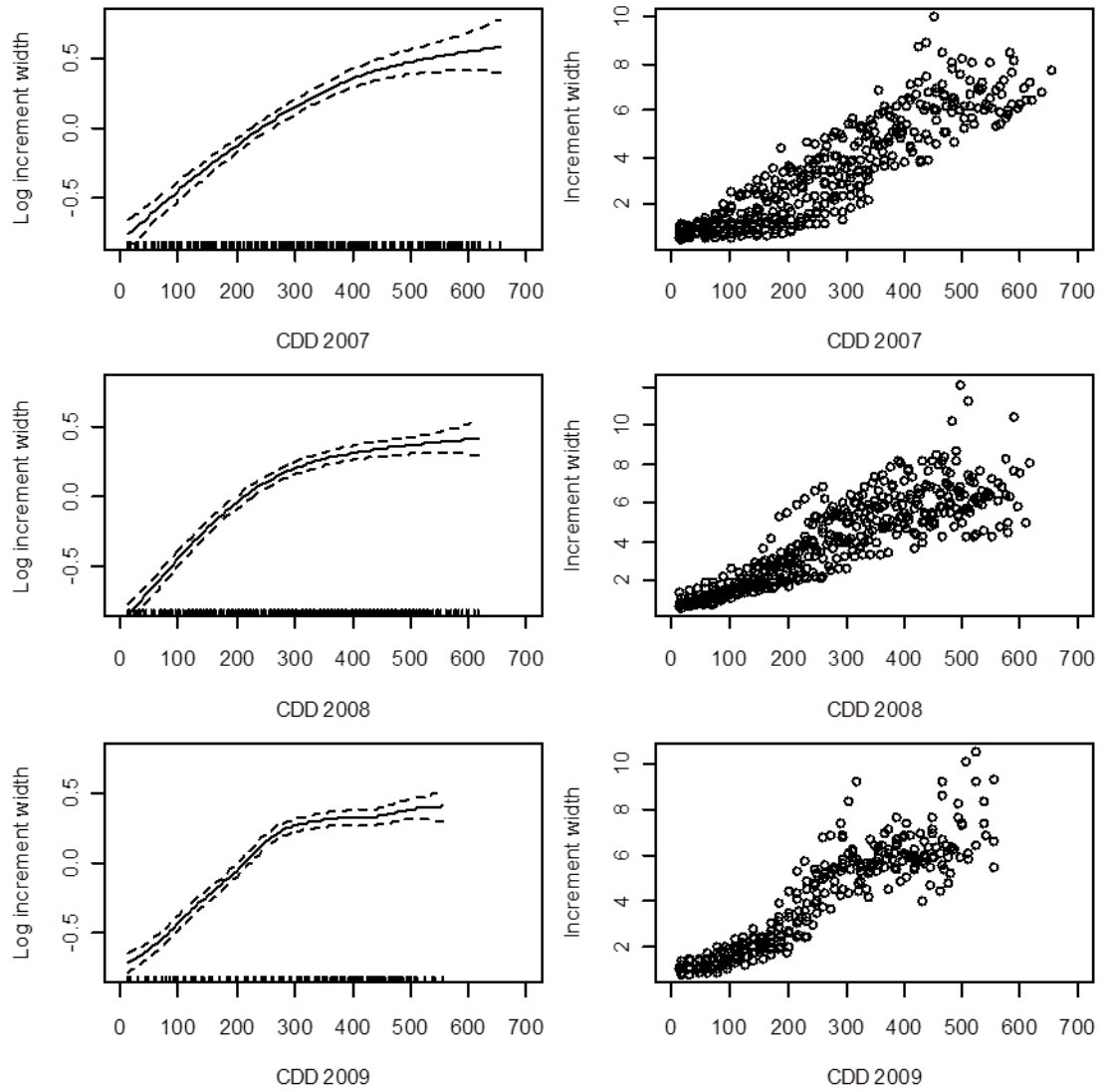


Figure 4.4: Output of GAMM model for Kerry when years and regions were included as factors. The additive effect of CDD on logged otolith increment width is shown in the left hand column; the raw data is shown in the right hand column.

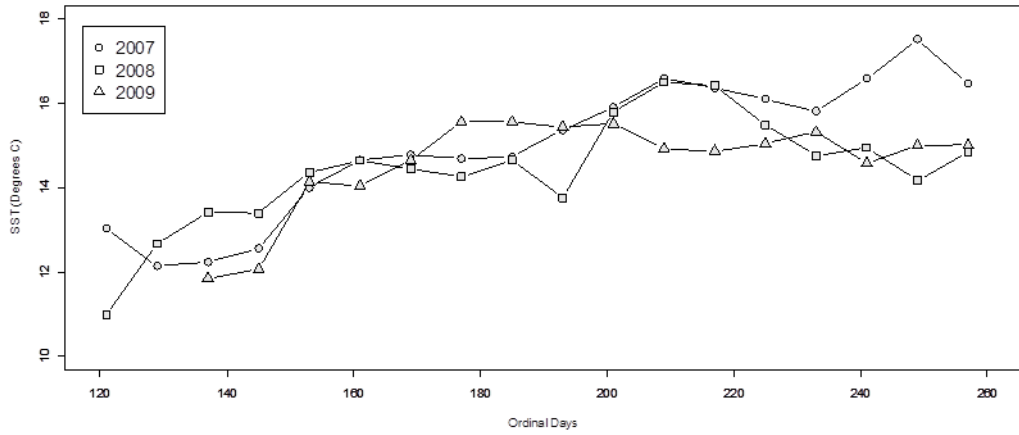




#### 4.4.2 *Sea surface temperature*

Eight-day average SST for the area approximating the drift of turbot larvae were plotted over the time the larvae were present in the plankton (Figure 4.5). Temperatures ranged from a low of 11.0°C in 2008 to a high of 17.5°C in 2007. The average temperature for the three years was 14.7°C; Kruskal-Wallis testing confirmed that there was no difference in the average temperatures experienced by the individual larval fish between years ( $P = 0.35$ ). When average SST values experienced by the larval fish were divided by region however, a significant difference was found (Kruskal-Wallis,  $P = 0.003$ ). The temperatures for the fish from the western region were warmer (Figure 4.7). Temperature trends were generally upward for the early half of each season. Some cooling can then be seen in 2008 and 2009, though the temperatures in 2007 continue to trend generally upwards.

Figure 4.5: Average sea surface temperatures over the larval periods of turbot for three years. Data points are 8-day averages for the study area.



#### 4.4.3 Larval duration

The relationship between the duration of the larval period of an individual fish and the average temperatures experienced by that fish was explored. A negative binomial glm was applied and the negative trend was found to be significant ( $P = 0.006$ ) (Figure 4.6). When the factors year and region were included in the model they were not found to influence the relationship. Potential differences in larval duration over years and regions was tested separately by analysis of variance and the years were found to be significantly different (Kruskall-Wallis,  $P = 0.0012$ ) (Figure 4.7). Mean larval duration was 34.0 days in 2007 (range 23 – 47); 37.7 in 2008 (range 29 – 46); and 32.8 in 2009 (range 21 – 37). Larval durations across regions were not found to be significantly different (Kruskall-Wallis,  $P = 0.232$ ).

Figure 4.6: Larval duration (LD) as a function of the average SST during the larval period of individual fish. Fitted line is the output from a negative binomial glm ( $P = 0.007$ ).

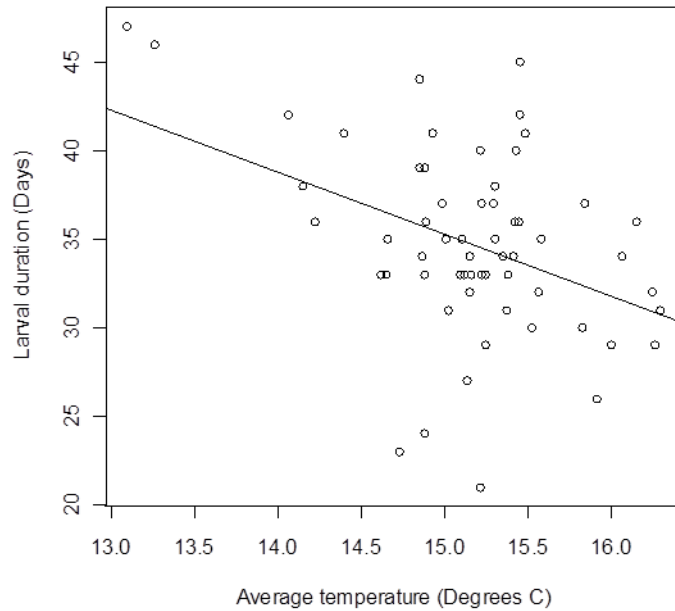
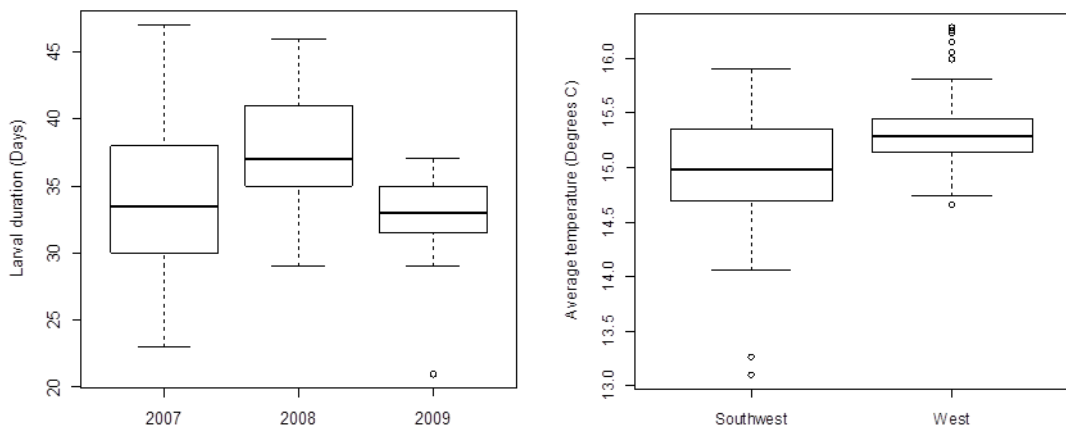


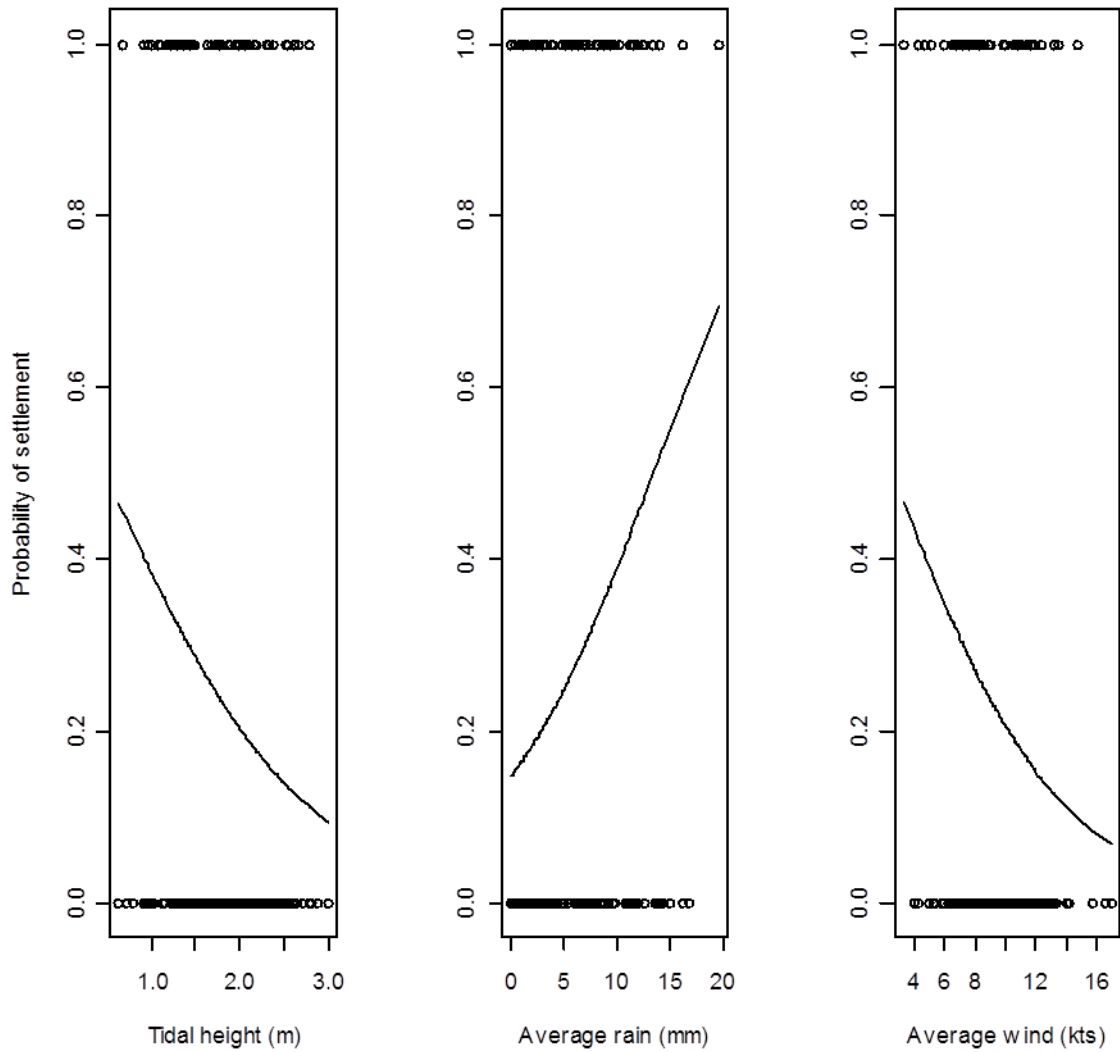
Figure 4.7: Boxplots of larval duration by year and average SST by Region, results are significantly different (Kruskal-Wallis,  $P < 0.05$ ).



#### 4.4.4 Settlement

The importance of environmental variables in driving the settlement of larval turbot was explored using a binomial glm. The factors found to be significant following model selection were maximum daily tidal height ( $P = 0.007$ ); average rain ( $P = 0.001$ ); and wind strength ( $P = 0.020$ ). Nagelkerke's generalised  $R^2$  for the model was 0.116. The relationship with tidal height was negative, with more settlement during periods of neap tides when tidal heights were lower. Rain had a positive effect; higher rainfall in the three days previous increased the probability of settlement. Wind, also averaged over three days, had a negative effect. Periods of higher winds reduced the probability of turbot settling on the beaches (Figure 4.8). Moon phase, wind direction, year, month and region were included in model selection but were not significant and thus not retained.

Figure 4.8: Probability curves for settlement of turbot driven by environmental variables. Tidal height is maximum height of tide at Galway Harbour; average rain is rainfall at Galway and Valentia averaged over three days; average wind is wind speed at Shannon averaged over three days. All variables were significant in the binomial settlement model at  $P < 0.05$ . (Nagelkerke's  $R^2$  Index = 0.116).



## 4.5 Discussion

The relationship between temperature and growth is well understood for turbot (Weltzien et al., 1999) and other fish species (Pepin 1991, Kielbassa et al. 2010). Cumulative degree day is an excellent descriptor of growth, allowing the effects of ontogeny and temperature to be combined in a biologically meaningful way (Neuheimer and Taggart 2007). CDD, along with the GAMM method, make modelling of the larval growth period intuitive and statistically robust. The method also allows for minor differences to be revealed, i.e. the differences in otolith growth patterns of the larval period between years and regions. No consistent spatial or temporal patterns emerged from the analysis of growth, and the variations in growth rates serve to illustrate the complexity of the hydrodynamic regime and the sensitivity of larval turbot to fluctuations in their environment. Growth can also be expected to respond to variations in food supply, but the food availability for larval fish is difficult, if not impossible, to infer. Variations in temperature at a scale too fine to model with the available data may have contributed to the differences, in general the accuracy of temperature-based models is subject to the resolution of the temperature data available (North et al. 2009). Haynes et al. (2011) did not find annual differences in hatch times for these turbot, however fish from Kerry did settle a few days earlier than those from Galway during the study period. In this paper there was no difference found in larval duration between the regions, but there were differences between years, and temperatures were lower during the larval periods of the Kerry fish. All of these results indicate the intrinsic variability in the early life history parameters of turbot larvae that succeeded in settling on the nurseries.

Higher temperatures during the larval period led to shorter larval durations. This has also been established for plaice (Bolle et al. 2009, van der Veer et al. 2009). When modelled in this study, there was no evidence of any regional or annual effect in this relationship, indicating a fundamental relationship between the parameters. Species richness in the eastern North Atlantic has already been demonstrated to have changed due to temperature increases over time (ter Hofstede et al. 2010); the demonstrated importance of temperature on all aspects of the larval life of turbot shows that they are vulnerable to changes in the temperature regime. Further increases in temperature projected due to global warming can be expected to affect turbot populations, though the mechanisms and results are not clear. Increased growth rates may confer

competitive advantages in feeding and survival, but reduced larval durations may interfere with the timing of settlement on the nurseries. Year class strength of plaice is known to be negatively related to sea temperatures, it is proposed that in colder years predator numbers are depressed, allowing greater numbers of larvae through to the settlement stage (Nash and Geffen 2000, van der Veer et al. 2000, 2009).

The settlement model showed that among the parameters for which data were available, tidal height, rainfall and wind influenced the settlement of turbot. Tidal height at a daily scale is an index of the volumes of water moving in the sea, and thus the strength of currents at any given time. The relationship was negative, with settlement more likely at lower tidal heights. Tidal height is collinear with both moon phase and the spring/neap cycle of tides, though it gave a clearer signal of effect in the model. Strong currents causing hydrodynamic features such as fronts and eddies entrain larval fish; and currents are often alongshore within bays (Kingsford and Suthers 1996). Turbot larvae may therefore find it easier to break free from these features and to settle on the beach during periods of reduced current flow. Alternatively the effect may be more indirect, rhythmicity of spawning events may be centred around the lunar cycle, and the tidal signal in the model could be a lagged effect of spawning times. Geffen et al. (2011) did not find any relationship between settling plaice larvae and tidal amplitude at Port Erin Bay on the Isle of Man. Plaice settle earlier in the year and in greater numbers than turbot; that study found multiple settlement events with sub-cohort size decreasing over time. In this study there was no evidence of cohorts, though sample sizes were small and sampling was carried out on a single day on each beach and sampling later each season may have revealed cohorts.

The processes of settlement and metamorphosis represent critical times for flatfish (Chambers et al. 2001, Yamashita et al. 2001). Metamorphosis is energetically expensive and may involve a period during which feeding ability is reduced (Tanaka et al. 1996, Geffen et al. 2007). The timing of arrival at the nurseries is important, as is the size, age and condition of the candidate fish. They must have reached an ontogenetic stage at which they are competent to settle, and then respond to signals orienting them to the nursery and providing cues for settlement (Boehlert and Mundy 1988, Miller 1988). These may include any hydrodynamic parameter such as salinity, temperature, substrate, turbulence, pressure, depth, turbidity or olfactory cues (Kingsford et al. 2002), but which of these are important is unknown for turbot.



Results show that turbot settlement events increased following rainfall. Reduced salinity close to shore following periods of wet weather may provide a cue assisting the larval fish in orientation, indicating that the nursery is near. Although turbot can live in salinities as low as those found in the Baltic Sea (Nissling et al. 2006), in Atlantic waters the juveniles show a preference for higher salinities (Riley et al. 1981), and are not normally found in estuaries. The preference settling turbot larvae have for low salinities in this study must then relate to the mechanisms of settlement and does not signify a habitat preference in the post-larval stage.

Wind strength also had a significant effect on the larval turbot, periods of higher winds appearing to reduce or prevent settlement. Turbot occupy the upper, neustal layers of the plankton in their later larval stages (Last 1979, Tully and O'Ceidigh 1989a) meaning that they are susceptible to the action of wind on the water surface. Wind direction did not have any discernible effect in the model, which is counter-intuitive; it would be expected that sustained onshore winds would force the larvae against the land-sea boundary. Year-class strength of turbot has been correlated with onshore winds (Riley 1981), implying a relationship with wind over a larger spatial scale than that relating to the act of settlement on the nurseries. Prevailing winds are south-westerly in Ireland, which is an onshore condition for all of the nurseries sampled. Strong winds cause turbulence at the surface, and may compel the larvae to go deeper in the water column, and thus may force settlement to be postponed. Larvae may also be driven ashore by strong onshore winds, and may die. If this is the case it further explains the rarity of turbot on the Irish western seaboard, given the propensity for strong onshore winds throughout the year. Settling larvae may simply be unable to maintain contact with the substrate during periods of high winds; this may cause mortality or possibly induce delayed metamorphosis, though this appears to be rare in fish larvae (Bradbury and Snelgrove 2001, Searcy and Sponaugle 2000) and has not been documented for turbot.

The shortcomings of the settlement model must be considered here. Sample size was small, and although the predictors were significant only about 12% of variation was explained by the model. Due to the structure of the data, settlement dates rather than individual fish were modelled. This prevented the application of a mixed model which could have accounted for the effect of hatch date on settlement events. Although larval duration is variable it would still be expected that hatch dates would influence

settlement but it was not possible to disentangle the information. Studies of turbot on the Atlantic coast of Ireland have been consistently hindered by the small sample sizes arising from the scarcity of the fish on the nursery grounds (Haynes et al. 2010a, 2010b, 2011). Their very rarity however adds urgency to attempts to increase our knowledge of their life history and ecology. Regardless of sample size this paper offers insight into the influences of environmental factors on the vulnerable early life stages of turbot, and provides a baseline of information with which to assess future changes to the climate, the environment and the population of turbot on Irish coasts. A modelling framework has also been established to investigate drivers of settlement which can be applied to other fish species.

## **4.6 Conclusion**

The relationship between the early life history stages of turbot on Ireland's western seaboard and the physical environment have been explored here for the first time. Sea temperature data from satellites enabled accurate models of larval growth to be developed, which revealed differences in growth patterns which were not consistent across regions and years. Larval durations were also influenced by temperature, with higher temperatures driving shorter larval durations, consistent with other flatfish species. The influences of wind, rain and tide on the settlement of turbot onto the nurseries were tentatively established. These findings demonstrate the importance of weather patterns to the larval and metamorphosing turbot and show their vulnerability to a changing climate.

## **5 General discussion**

### *5.1 Overview*

Man has had a long association with the seas and the fish contained in them, our prehistoric ancestors having fished as soon as they had the means to do so. The questions that have concerned humans have mostly been to do with the mechanics and profitability of exploitation, and fisheries science has developed alongside the ever-increasing prosecution of the world's fish stocks. Scientists are of course interested in the biology and ecology of fishes for many reasons, but the main driver for research has tended to be exploitation, therefore much of the work concentrated on fish of commercial interest. Marine ecology is limited by many intrinsic aspects of the study subject, fish are mobile, the ecosystems are complex, and they are often inaccessible and invisible to us. Most of all though workers are trying to hit a moving target; as our understanding of marine ecosystems increases and the body of work grows, the subjects of our studies are changing drastically through coastal development, pollution, overfishing and climate change.

It has long been understood that processes at work in the larval stages of fish are important, Hjort (1914) proposed the "Critical Period hypothesis" to explain recruitment variability and fisheries scientists have since devoted great attention to better understanding of the unpredictability of year class strength in fish, the "recruitment problem" (see Houde 2008). As our perception of the incredible complexity of marine ecosystems develops we now accept that there are many interacting predictors of recruitment variability. This bottom-up approach to questions regarding fisheries is valid and has provided huge ecological insight over time, and this thesis is another part of the overall attempt to understand the early life histories of fish. It is not however an attempt to solve the "recruitment problem". The influence of natural variability in recruitment to the overall health of fish stocks pales in comparison to the increasingly degrading effects of overfishing, pollution, habitat degradation and climate change. Small scale studies such as this may not be of immediate value as tools for fishery managers, but they do serve to increase our overall understanding of the vulnerability of larval, juvenile and adult fish to changes in their environment. This in turn informs environmental management decisions and improves our ability to protect whole ecosystems.

## *5.2 Physical environment*

The life histories of pre-recruit fish are determined by a complex interaction of biotic and abiotic factors; during the larval part of their life cycle their growth, condition, location and very survival are regulated by extrinsic forces (Gibson 1997). Regardless of the timing of their spawning or of the traits bestowed by the genetics of the previous generations; once the eggs are fertilised, the hydrodynamics of the water in which they find themselves largely determine their fate (Norcross and Shaw 1984, Bailey et al. 2008). The ontogenetic journey from fertilisation through hatching and larval life to metamorphosis into the juvenile form relies entirely on a confluence of physical events and conditions for the physical journey from spawning site to nursery to be successful.

## *5.3 Wind*

At the bay scale the most important environmental driver for the distribution of larval fish within Galway Bay was wind (Chapter 2). Tidal currents, rainfall and lunar phase failed to give any signal in the model, indicating the singular importance of the prevailing wind. The action of wind over water influences the movement of that water across ocean basins and in shallow coastal waters, though not uniformly. Ekman spirals form in deeper waters resulting in currents acting at angles to the wind according to depth and in which hemisphere they occur (Price et al. 1987). In shallow waters the currents caused by the winds tend to be along the wind's trajectory (Young 1997). At all scales wind effects the distribution of larval fish (Nielsen et al. 1998, Voss and Hinrichsen 2003, Doyle et al. 2009) and can cause secondary effects such as upwellings (Allemany et al. 2006). In this study onshore winds seemed to push larval fish into the bay, concentrating them in such a way as to increase catches during sampling. In doing so the wind seemed to exert a greater influence than the residual circulation. Larval fish must be adapted to local conditions to allow them find suitable nurseries in sufficient numbers to recruit to the adult populations (Gibson 1997). The west of Ireland is subject to strong and frequent onshore wind events from Atlantic weather systems and it is reasonable to suppose that the larval fish populations of all species have spawning and early life history strategies to take account of local wind conditions. The west-facing aspect of Galway Bay presents an end-point to any larval fish spawned either within the bay or out on the continental shelf. The offshore currents tend northward (Fernand et al. 2006) and the prevailing winds are south-westerly, implying that shelf spawners such as

the flatfishes must spawn south of the entrance to the bay. Residual currents within the bay are anti-clockwise (Booth 1975, White 1996), also favouring larval transport off the shelf into the bay from the south. Any consideration of the wind regime in the Bay must of course take account of predicted increases in extreme wind events (IPCC 2007) which have the potential to disrupt patterns of larval transport.

#### *5.4 Temperature*

Temperature has been shown to influence early growth rates in flatfish (Ryland and Nichols 1975, Seikai et al. 1986, Hutchinson and Hawkins 2004) and this was the case for both plaice and turbot in this study (Chapters 3 and 4), with cumulative degree day predicting most of the variation in growth. In both cases regional differences in growth were highlighted by the models, the differences may have been driven by differing larval durations, differing temperature regimes during the larval phase, variations in available food, or genotypic or phenotypic differences in populations sampled. Temperature variation at a scale finer than the resolution of the data used for modelling may also have contributed to the observed differences. Temperature acts at all levels of organisation in fish, it acts on the metabolism of fish at the cellular and individual levels, higher temperatures increasing metabolic rates within limits and driving higher growth rates (Pepin 1991). Higher growth rates increase chances of survival according to the “bigger is better” hypothesis, larger larvae being more capable of avoiding predation (Bailey and Houde 1989). Higher temperatures therefore may confer cohorts of larvae competitive advantage over conspecifics.

Higher temperatures also reduce larval durations (van der Veer and Witte 1999, van der Veer et al. 2009) and this held true for both plaice and turbot in this study. Shorter larval durations may confer advantage in reducing the time the fish is in the more vulnerable larval phase (Houde 2008). This must be considered in view of the physical journey larvae must make from spawning site to nursery; reduced larval durations may disadvantage fish if they are competent to metamorphose, and in the case of flatfish to settle, but have not yet reached a suitable site for settlement. Delayed metamorphosis could counteract this to some extent but plaice do not appear to have that ability (Gibson and Batty 1990) and there is no reference to it in the published literature for turbot. Ability to metamorphose is associated more with size than age (Chambers and Leggett 1992), larvae that have reached competence to metamorphose but not their

physical destination may be lost (Nash and Geffen 2011). Temperature influences the early life history of fish in indirect ways too. For example colder years are correlated with bigger year classes in plaice, the mechanism appearing to be a temperature induced reduction in predator numbers allowing more larvae through to the nurseries (Bannister et al. 1973, van der Veer and Witte 1999, Fox et al. 2000).

Changes in the distribution and abundance of several species of adult fish have been observed due to shifts in temperature (Hollowed et al. 2012, Hermant et al. 2010, van Hal et al. 2010). Large-scale climatic factors have been shown to influence early life history events in winter flounder *Pseudopleuronectes americanus* (Sogard et al. 2001). Temperature of course ultimately drives weather; extreme and unusual weather events may disrupt the larvae's journey and cause mass mortality. Extreme weather is predicted (IPCC 2007) but its effects on complex systems remain unknown.

### *5.5 Settlement*

The ability of larval fish to metamorphose and settle is primarily driven by size, age and arrival at a suitable nursery (Gibson 1997, Yamashita et al. 2001); we explored which changes in the physical environment might drive peaks in turbot settlement (Chapter 4). While the sample size was small and the data noisy, nevertheless a significant signal was detected indicating that rainfall, tide and wind influenced settlement. Periods following higher rainfall saw increased settlement implying an olfactory cue. Encountering lower-salinity water may inform candidate settlers that they are approaching a suitable nursery. Immature fish are sensitive to changes in salinity (Gibson 1994, Yamashita et al. 2001) and they may utilise this ability at the end of the larval journey. Other potential cues to settlement are depth, substrate, turbidity and temperature (Gibson 1997, Kingsford et al. 2002). Settlement activity peaked around neap tide periods, possibly indicating that it is less energetically expensive to break out of entrainment in currents then. During periods of greater tidal movements around the spring tide period larvae may be carried alongshore by the currents and be unable to swim perpendicular to those currents to the shores. Alternatively settlement may coincide with neap tides simply as a result of synchronisation of spawning events with lunar cues. Wind strength was negatively associated with settlement; turbot settled in greater numbers following periods of light wind, and wind direction had no detectable influence. While it could be expected that onshore winds would encourage settlement,

particularly as turbot larvae are found in the upper layers of the water in their late larval stages (Last 1979, Tully and O’Ceidigh 1989a), this was not the case. High winds appeared to prevent settlement, larvae may have the ability to remove themselves from the neuston during high wind events to prevent being washed up on the beaches, or being carried back offshore.

### *5.6 Modelling*

The use of GLMs and GAMs is particularly suited to fishery research (Venables and Ripley 2002) and the suitability of non-linear methods for modelling environmental drivers is well demonstrated here. In this study binomial logistic regressions have been used to establish the importance of physical factors in forcing responses in larval fish within noisy datasets with a great deal of natural variability. While inference in logistic regression is largely limited to stating the significance and direction of a relationship nevertheless the information is valuable and ecologically meaningful. Bigger datasets may have allowed more detailed inference be made as to the magnitude of responses; in any case biological data in studies such as this often contain many zero results, making modelling difficult (Zuur et al. 2009). There are difficulties associated with gathering enough information about potential drivers; principally, missing covariates weaken models and may lead to incorrect conclusions (Zuur et al. 2009). Rigorous model validation was pursued in this study, and false deductions were avoided. Generalised additive modelling (GAM), which applies a smoothing function to continuous predictors (Wood 2006), proved very effective in revealing the relationship between growth and temperature for both plaice and turbot, and allowed a fine-scale interpretation of growth patterns and the geographic differences between those patterns. The addition of a correlation structure to mixed models enabled the problems caused by the inherent auto-correlation of otolith data be circumvented, and ensured that the significance of factors was not falsely inflated (Zuur et al. 2009). SST estimates were incorporated into the daily age of each fish through the use of CDD as a predictor of otolith increment width, an approach that explained a great deal of the variation in growth. While satellite-derived SST data is limited in its precision, and cannot track the temperature history of individual fish at a fine spatial or temporal scale it still modelled the growth of the species in this study satisfactorily. This modelling approach has potential for modelling larval growth of other species and will be useful when incorporating predicted growth of fish into individual-based models (IBMs). The



proliferation of biophysical IBMs in recent years has allowed considerable insight into the processes influencing the pelagic stages of larval fish development, and increasing the accuracy of the information input into the models improves inference (Peck and Hufnagl 2012, North et al. 2009).

GAMs were also applied to plaice larval duration data and demonstrated their non-linear relationship with average temperatures during the larval phase. This approach was compared with linear regressions applied to previous plaice analyses from the literature and the GAM substantially improved the model, though when linear regression was applied to the dataset from this study the estimates were almost identical. Firstly this demonstrates that the relationship between temperature and larval duration pertained with a high degree of similarity across a broad geographical area. Secondly it shows the value of GAM as a method to show this non-linear relationship in more detail. Interestingly turbot also showed a significant negative relationship between larval duration and temperature but in this case the application of a smoother did nothing to improve the model which was linear throughout its extent.

### *5.7 Study limitations*

The first part of this study carried out within Galway Bay was limited in its inference due in part to poor catches of larval fish. Limitations in gear size due to the employment of a small boat reduced the physical volume of water that could be sampled. These limitations were further confounded by bad weather restricting sampling opportunities. The presence of larvae in the water column decreased markedly over time; to counteract this sampling should have been concentrated earlier in the season, however bad weather in the early spring impeded our ability to sample when larvae were most abundant. Unfortunately these problems are inherent in projects undertaken on the inhospitable west coast of Ireland. The plaice study was well-balanced geographically with samples of juvenile fish coming from the west of Ireland, the Irish Sea and the Dutch Wadden Sea. However issues were encountered with the dates on which the samples were taken. The fish from the west of Ireland were captured as late as September which caused problems in the first instance with reading the otoliths which were larger due to the ages of the fish, and in the second instance with the un-knowable selection processes undergone on the beaches since settlement. These confounding factors could have been avoided with a better-balanced experimental design allowing for sampling at the same

point in time following first settlement. While the ability of otoliths to integrate data from the larval period is fundamental to studies of this kind, it would be advantageous to compare cohorts that have undergone the same processes. The turbot study was well spatially balanced, covering two separate areas on the west coast of Ireland; and temporally, with samples from three years taken during the same period each year. The only disadvantage was a small sample size and this is an enduring problem with Irish turbot (Haynes et al. 2010). The rarity of the fish on the nurseries necessitates an intense sampling effort, but the demands of the survey must be balanced against awareness that the population may be effected by removing too many fish.

### *5.8 Conclusion*

The adult fish of the west of Ireland are not subject to the same scientific scrutiny as those of the North Sea or the Irish or Celtic Seas (Marine Institute 2010). Several flatfish species have been the subject of recent research into their juvenile stages within Galway Bay and further afield along the western seaboard of Ireland (Allen et al. 2008, Haynes et al. 2010a, 2010b, 2011, De Raedemaeker et al. 2011, O'Neill et al. 2011). While the larval fish populations of Galway Bay (Fives 1970, Tully and O'Ceidigh 1989a, 1989b), and further offshore (O'Brien and Fives 1995) have been described in the past this thesis is the first effort to complete the "recruitment triangle" and to understand some of the dynamics influencing the larval fish, and particularly flatfish, of the west of Ireland. The physical environment has proved to significantly influence each of the early life history parameters measured in this study and at all of the spatial scales considered.

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