



1-group plaice (*Pleuronectes platessa*)



Contents

Acknowledgements:	1
Abstract:	3
Chapter 1: General introduction.....	4
Chapter 2: Fin-ray count variation in 0-group flatfish: plaice (<i>Pleuronectes platessa</i> (L.)) and flounder (<i>Platichthys flesus</i> (L.)) on the west coast of Ireland.....	15
Chapter 3: Variation in the fin ray counts of 0-group turbot (<i>Psetta maxima</i> L.) and brill (<i>Scophthalmus rhombus</i> L.) on the west coast of Ireland: 2006-2009.....	28
Chapter 4: Annual and spatial variation in the abundance length and condition of turbot (<i>Psetta maxima</i> L.) on nursery grounds on the west coast of Ireland: 2000-2007.....	41
Chapter 5: Variability in the early life stages of juvenile plaice (<i>Pleuronectes platessa</i> L.) on west of Ireland nursery grounds; 2000 – 2007.....	64
Chapter 6: The early life history of turbot (<i>Psetta maxima</i> L.) on nursery grounds along the west coast of Ireland: 2007 – 2009, as described by otolith microstructure.....	85
Chapter 7: The feeding ecology of 0-group turbot (<i>Psetta maxima</i> L.) and brill (<i>Scophthalmus rhombus</i> L.) on Irish west coast nursery grounds.....	96
Chapter 8: General discussion.....	116
References:	132

Acknowledgements

I would like to begin by sincerely thanking my two supervisors Deirdre Brophy and David McGrath, for their invaluable ideas, enthusiasm, constant support, and above all their patience over the last four years! You always believed in my work, even when as you put it David, I was unable to see the bark for the trees at times. I am extremely grateful to have had such two excellent supervisors, when most people would have been lucky to have had one.

I would like to thank everyone in the Commercial Fisheries Research Group, particularly Stephen Comerford, Bernadette O'Neill, and Fien De Raedemaecker. Without colleagues and friends such as you, much of this work would not have been possible. In particular, thank you to all who gave of their time over the years to help me with sampling. I will always remember the battles on Inch and Lahinch with Stephen, where we were up against undercurrents, fisheries officers, storms, and exhausting trecks back up the beach, after hours of beach seining, though the dinner at the end (and wine) was always worth it! I am extremely grateful to Taighde Mara Teoranta and BIM, who began the juvenile flatfish surveys. I would like to thank Paul Casburn, Vincent Browne, and all who have participated in the surveys over the years, and helped in the collection of the fish.

I am grateful to Ian O'Connor, where my research all began with the 'winkle experiment' for my third year project. From there I progressed onto a flatfish project in fourth year with David McGrath, and afterwards began a PhD. Thank you to Hans Gerritsen for the help with my transfer report, and for not 'grilling' me too much. I would like to thank Pat Dinneen for providing me with my foundation in statistics and excel throughout my degree, and for proving me wrong when I used to think "when will I ever need this again" during our Thursday afternoon three hour practical class. I am grateful to Seamus Lennon for my lecturing experience over the last few years. I would also like to thank Laura McDonagh and all in the research office their help and support, in addition to the staff in the library. Thank you also to the funding body in GMIT, which made this research possible.

Finally, I would like to thank all of my family and friends. To my parents Grace and Stephen who have always been so supportive of me as an eternal student (I will pay you back for the car

soon Dad I swear!). Thank you mum for coming to Kerry and hauling the net with me, to the admiration of many of my colleagues! I am also grateful to my brother Derek, for helping me with sampling on numerous occasions. Thank you to my grandmothers Olga and Vera, for always thinking about me, and being interested in my work. To Shauna, Ruth, and Richard, thank you for your support and understanding with my 'occasional' irritability over the duration of this thesis. Last but not least, I would like to extend a big thank you to my furry companions 'the lads' (below). Thank you for keeping my legs warm throughout all of my typing on the couch, and for forcing me away from the computer every now and then, by taking me on all of those walks and runs!



Figure 1: Hugo (left) and Davy (right) waiting patiently for a walk!

Abstract

Commercial flatfish captured in demersal fisheries along the west coast of Ireland include quota species such as plaice (*Pleuronectes platessa* L), in addition to high value non-quota species, turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.). Important non-commercial angling species of interest include flounder (*Platichthys flesus* L.). However, knowledge of the population dynamics of these flatfishes along the west coast of Ireland is lacking, and considered to be inadequate for the establishment of any population trends. In light of this, habitats along the west coast of Ireland serving as nursery grounds for the juveniles of these species were investigated (2000 – 2009). Correctly distinguishing between pairs of recently settled flatfish species, which are morphologically similar in appearance, was a prerequisite to this research. Counts of the meristic characters, fin rays, which are species specific, proved to be a reliable identification tool for juveniles. Plaice were the most abundant flatfish species present on nursery grounds, followed by turbot, and to a lesser extent brill. Assessment of nursery grounds over the eight year period, revealed both inter-annual and spatial variability in the relative abundance, growth, and condition of plaice, turbot and brill. Certain trends were revealed in these parameters, indicating the existence of both high and low quality nursery habitats. Abundances of both plaice and turbot on nursery grounds were negatively correlated with sea water temperatures during the pelagic stage. Baseline data on the timing of critical events, including hatching, larval durations, and settlement, in addition to growth experienced during early life, were established from the otolith microstructure of turbot. Post-settlement growth rate estimates of turbot also indicated certain locations as high quality nurseries. The feeding ecology of juvenile turbot and brill on nursery grounds was described, with temporal and resource partitioning revealed, implying that competition is unlikely to arise between these two morphologically similar species. A high incidence of prey was observed in the gut content of all turbot and brill, suggesting that food was not limited on Irish nursery grounds. Turbot fed on a much wider range of prey in contrast to brill, which fed almost exclusively on one prey organism. This observation may be one reason for the general sparse distribution of brill. The improved understanding of the early life history of plaice, turbot and brill may aid in the development and implementation of effective management strategies in the future; at the very least for the protection of important nursery grounds, as any loss, or decline in the quantity or quality of these areas, will undoubtedly have a negative impact on the recruitment of these species.

Chapter 1

General Introduction

1. General introduction

Flatfish are an important ecological component of continental ecosystems worldwide (Link et al., 2005), with a global distribution ranging from the Arctic to Australasia. Due to their ubiquitous nature, flatfish are exploited in many locations, and contribute significantly to global catches. In the Northeast Atlantic, total flatfish landings amounted to 346, 573 million tonnes in 2009 (Anon, 2009a). There are 21 species of flatfish known to occur in the Northeast Atlantic, (Russell, 1976), with species from the three families pleuronectidae, soleidae, and bothidae contributing significantly to flatfish catches in this area. Plaice (*Pleuronectes platessa* L.) are an important component of flatfish landings in the Northeast Atlantic, in addition to high value non-quota species such as turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.), which are captured in much lower quantities (Table 1.). In the last century, there has been a continuous decline in the abundance of both commercial and non-commercial flatfish populations inhabiting Northeast Atlantic waters, with a significant reduction in the landings of all commercial flatfish species over the previous 30 years (Anon, 2010b). Indeed, on a global scale, these highly productive waters are now one of the most heavily exploited fishing grounds (Link et al., 2002).

Table 1: Total landings in tonnes (t) of commercial flatfishes in Europe (Anon, 2009a).

Common name	Species	Landings (t)
Plaice	<i>Pleuronectes platessa</i>	78, 433
Greenland halibut	<i>Reinhardtius hippoglossoides</i>	61, 330
Sole	<i>Solea solea</i>	30, 886
Flounder	<i>Paralichthys flesus</i>	18, 724
Dab	<i>Limanda limanda</i>	10, 676
Turbot	<i>Psetta maxima</i>	5, 432
Brill	<i>Scophthalmus rhombus</i>	2, 516

1.1 Flatfish management

The Common Fisheries Policy was established to manage commercial fish stocks in the Northeast Atlantic, and is based primarily on a Total Allowable Catch (TAC) system. Data derived from stock assessments are provided annually by the International Council for the Exploration of the

Sea (ICES) and used to set quotas across different countries (Gibson, 2005). The Scientific, Technical and Economic Committee reviews the advice recommended by ICES, and subsequently provides a report to the European Union based on its findings. However, under the TAC system, the recommended quotas proposed by ICES are not always adhered to by the Council of Ministers/politicians of the various countries, and may exceed the catch levels that would allow sustainable exploitation of a particular stock (Daan, 1997). Given that stock assessments rely heavily on fisheries data, additional problems under the TAC system also include the discarding of undersized fish, or illegal or misreported landings. For example of the 14 flatfish stocks in the Northeast Atlantic for which such assessments are carried out, only four are considered to be within safe biological limits by ICES. Moreover, these assessments do not consider non-quota species such as turbot or brill.

Recent evidence suggests that declines of many commercial bottom-dwelling species including plaice, turbot, and brill, may now be even greater than previously considered (Thurstan et al., 2010). In light of the general decline in the majority of fish populations, including a predicted reduction in numbers of European turbot (Draganik et al., 2005), it is important to determine the status of stocks which have to date have not been assessed. Such information may help to determine the effects of environmental factors such as climate change that can, in combination with fishing effort, produce inter-annual variability in the size of the stock.

1.2 West of Ireland flatfish

Along the Irish west coast (ICES Divisions VIIb and VIIc) (Figure 1.), flatfish are captured in demersal fisheries. While catches may be considerably smaller in comparison to those in other areas of the Northeast Atlantic, they are an important source of income in many rural communities along the Irish west coast. Quota species such as plaice and sole (*Solea solea* Linnaeus) were worth approximately €0.5m and €0.8m respectively, in 2008 (Anon, 2009a). High value commercial species include turbot and brill, which are both non-quota flatfish, captured as by-catch in demersal fisheries. The most recent figures

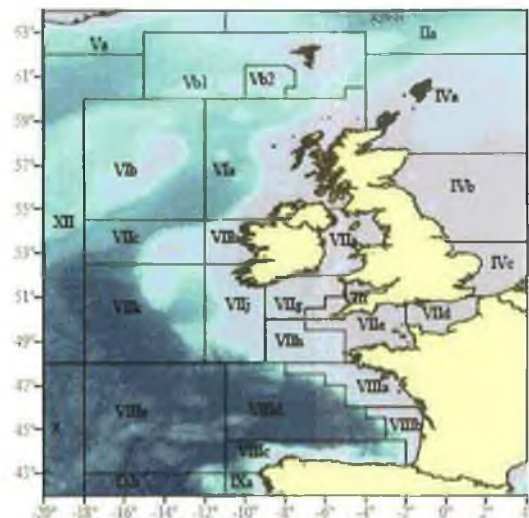


Figure 1: ICES fishing divisions around the Irish coast. (From The Marine Institute Stock Book, Ireland).

available quote turbot as being worth approximately €2.0m, with brill contributing €0.5m annually, to the Irish fishing industry (Anon, 2007). Non-commercial flatfish species include flounder (*Paralichthys flesus* L.), which is one of the most important angling fish species in

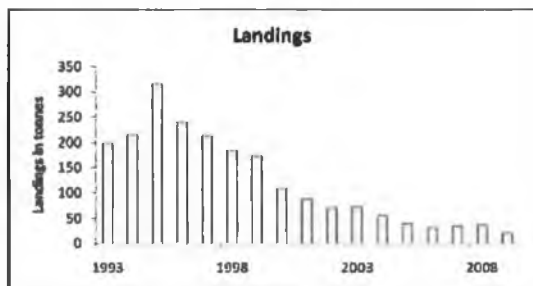


Figure 2: Official landings of plaice in Divisions VIIb & c off the west coast of Ireland. (ICES, 2010).

(Figure 2), in addition to important angling species such as flounder (Anon, 2011a). Information on the population dynamics or stock identity of flatfish species on the Irish west coast are required for their sustainable exploitation through effective management strategies (Wheatley et al., 1999).

Ireland (Anon, 2011a). Knowledge of the structure or stock biomass of flatfish populations is lacking along the west coast of Ireland. Data on plaice, one of the most abundant flatfish in this area, are considered insufficient to make any stock assessments (Anon, 2010a). There has also been an overall reduction in the landings of all commercial flatfish species in Ireland in recent years

1.3. Nursery grounds

The early life history of flatfishes has long been investigated in an attempt to establish the processes governing the recruitment of juveniles to the fishery, (Van der Veer, 1986; Sogard et al., 1997; Nash and Geffen, 2000). Nursery grounds are essentially habitats where juveniles concentrate, experience reduced predation, enhanced growth and finally where there is higher recruitment of individuals to the adult population, in comparison to other habitats (Beck et al., 2001). The nursery habitats of flatfishes range from deep offshore locations to shallow inshore areas, such as beaches and estuaries. As shallow coastal nursery grounds are easier and less costly to study in comparison to offshore locations, the majority of juvenile flatfish studies have focused on these areas. On shallow inshore habitats in the Northeast Atlantic, juvenile plaice are more often than not the most abundant flatfish species, having been

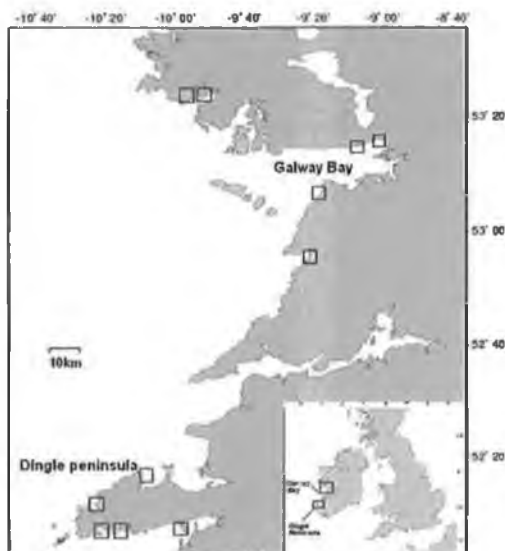


Figure 3: Juvenile flatfish nursery grounds assessed along the west coast of Ireland.

extensively studied as a result. Juvenile plaice are also the most abundant flatfish species along Irish west coast and their early life history in this location has recently been investigated (Allen et al., 2008). However, long-term trends in the population dynamics of 0-group flatfish have not been studied in this area (Figure 3).

In other areas of the Northeast Atlantic, including the Wadden Sea (Van der Veer, 1986), the North Sea, (Nielsen et al., 1998), and the Irish Sea (Nash and Geffen, 2000), the early pelagic and demersal stages of plaice have been assessed. Separate stocks of the same species may be adapted to small scale local environmental conditions, in order to increase their survival and ability to complete their life-cycle (Bailey, 1997; Nash and Geffen, 2000). There may therefore be alternative factors governing the population dynamics of west of Ireland flatfish species. In comparison to plaice, juvenile turbot (Figure 4) and brill abundances on nursery grounds are exceptionally low (Gibson, 1994). While studies have focused on the feeding ecology and growth of juvenile turbot (Jones, 1973; Aarnio et al., 1996; Sparrevohn and Støttrup, 2008), and to a lesser extent brill (Piet et al., 1998; Beyst et al., 1999), investigations of early life parameters, including hatch and settlement dates, or variability in the abundances and growth of juveniles on nursery grounds are lacking. Investigations of the early life stages should therefore be carried out for stocks in all geographical locations; this may help to elucidate the processes influencing the growth, survival, and recruitment of juveniles to the adult stock.



Figure 4: 0-group turbot captured by beach seining on an Irish nursery ground.

Not all nursery locations will provide the optimal conditions necessary for good growth and survival of juvenile flatfish (Gibson, 1994). Consequently variability in the growth of juveniles can arise both between and within nursery habitats (De Raedemaeker et al., 2010), and also between years (Beggs and Nash, 2007), with larger flatfish more likely to recruit to the adult population at the end of the nursery ground stage (Sogard et al., 1997). Hence, areas where good growth is exhibited by individuals may be used to indirectly identify high quality nursery habitats (Gibson, 1994). However, high habitat quality nursery grounds are those locations which ultimately contribute significantly more juveniles to the adult stock. Factors known to significantly influence growth include juvenile flatfish densities, temperature, food availability and type, and predation (Gibson, 1994; Van der Veer et al., 2000). In relation to recruitment, the

size of the nursery ground is considered important, as a larger area will produce a greater quantity of juveniles to replenish the adult population (Rijnsdorp et al., 1992; Van der Veer et al., 2000). As habitat loss is currently one of the main threats to coastal systems (Valiela et al., 2006), identification and protection of potentially high quality nursery habitats is essential, so as to ensure a future supply of recruits to restock the adult populations. Identification of the factors governing recruitment variability is a primary objective of fisheries scientists (Myers, 1991). For flatfish, recruitment variability is considered to be lower in comparison to other teleosts (Iles & Beverton, 2000). For the most part, flatfish recruitment is determined during the pelagic egg and larval stage, where temperature and hydrodynamics are known to significantly influence the abundance of surviving eggs and larvae (Wilderbuer et al., 2002; Van der Veer et al., 2009). In the Irish Sea, where hydrodynamic processes are of less importance due to the proximity of spawning and nursery grounds, recruitment variability can also be generated during the juvenile demersal stage (Nash and Geffen 2000), emphasising the disparity which can arise between separate stocks of the same species inhabiting different geographical locations.

Spawning areas for plaice off the Irish west coast have recently been identified by Gerritsen et al., (2010) (Figure 5). Along the west coast of Ireland, the currents run from south to north (Mohn et al., 2002). In areas where there are strong directional currents, spawning and nursery grounds of flatfish are often well separated geographically; spawning grounds are situated “upstream” of nursery grounds (Gibson, 1997). Currents may therefore play an important role in the delivery of eggs and larvae of west of Ireland flatfish species such as plaice to nursery grounds. Upon settlement to a suitable nursery habitat, recruitment is considered to be further dampened, through a combination of density independent factors such as temperature, prey quality and quantity, salinity, sediment type, and/or density dependent processes. Density dependent processes include post-settlement mortality from predation, and

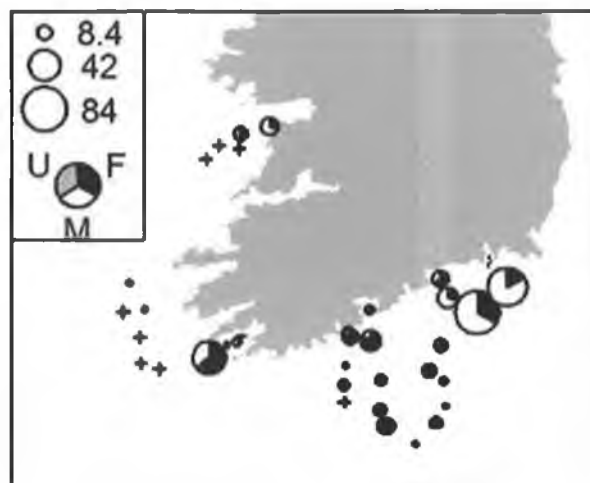


Figure 5: Distribution of three maturity classes of plaice around the Irish coast. Sex ratios are represented by pie charts: the black and white areas correspond to the proportion of females and males respectively, unsexed samples are shown as grey. (Gerritsen, 2010).

reduced growth from food limitation, as a result of the high densities of juvenile flatfish concentrating on the nursery (Iles & Beverton, 2000).

1.4. Critical events and growth during early life

Investigation of the otolith microstructure of juvenile flatfish can yield important information on the timing and duration of critical events, including estimates of hatch date, larval duration, settlement date, and growth rate (Campana, 2001). This knowledge can subsequently be used to establish mortality rates and recruitment estimates for flatfish species (Reichert et al., 2000). Otolith microstructure can also be useful for detecting underlying stock structure; for example in plaice, larval duration varied between cohorts of juveniles from different spawning grounds and analysis of this parameter revealed annual variation in the source of settling larvae (Hovenkamp, 1991).

Growth can have an important influence on the survival of fish. In general, otolith growth is related to the somatic growth of fish (Campana and Neilson, 1985). The width of otolith increments can therefore be used as an index of growth during both the larval and juvenile phases. Otolith growth rates change at a more gradual rate than morphometric condition indices (Campana and Neilson, 1985), and can provide a more accurate representation of nursery ground habitat quality. This may be beneficial when attempting to determine the habitat quality of a particular nursery ground, by identifying the factors influencing the habitat quality of a nursery, small scale temporary fluctuations in biotic or abiotic conditions might not significantly influence growth.

1.5. 0-group flatfish identification

Settlement of plaice, flounder, turbot, and brill onto west of Ireland nursery grounds occurs at different stages throughout the year (Haynes et al., 2008, 2010a). However, as some flatfish species such as turbot and brill are batch spawners, spawning on a number of occasions throughout the season, a number of different flatfish species may co-occur on the same nursery. Species such as plaice and flounder, and turbot and brill, are almost identical in appearance just after settlement, and can be difficult to differentiate as they generally lack the morphological characteristics of the adults (Russell, 1976). Hence, prior to investigations of juvenile flatfish communities, correct identification of the various species of interest is a prerequisite. To reduce the likelihood of misidentification, fin ray counts, which are species specific, are the diagnostic

characteristics recommended by Wheeler (1969) and Russell (1976) for separating similar juvenile flatfish species. Meristic characters such as fin rays can also be used to distinguish between different populations of flatfish, originating from separate spawning stocks (Nielsen et al., 1998; Burke et al., 2000).

2. Thesis objectives

This thesis investigates the early life ecology of juvenile plaice, turbot, and brill using data from juvenile flatfish surveys which were undertaken along the west coast of Ireland over a period of eight years. Given the large variability which can arise during early life, inter-annual investigations may provide a more conclusive picture of the population dynamics, including trends in abundances, growth, and overall habitat quality of flatfish nursery grounds. The identification and protection of important juvenile flatfish habitats is essential, as these areas are vital for the completion of the life-cycle, with any loss of these areas likely to negatively impact on flatfish recruitment.

The objectives of the present thesis were to:

1. Validate methods of identification for 0-group flatfish using meristic characters; fin rays.
2. Identify potentially good quality nursery grounds on the west coast of Ireland, where higher abundances of larger juvenile flatfish are found.
3. Identify spatial and temporal trends in abundance, length, and condition of 0-group flatfish.
4. Establish if surveys of sandy beach nursery areas could be used to generate a recruitment index for plaice.
5. Identify the timing of critical events, and growth rates during the early life of turbot, over temporal and spatial scales, using otolith microstructure.
6. Investigate the effects of biotic and abiotic factors on the growth and condition of 0-group turbot and brill.
7. Consider future management strategies for flatfish in light of the thesis findings.

The establishment of these baseline data for commercially important flatfish species will provide important knowledge of the processes operating on the early life stages.

3. Thesis outline

The present thesis is presented as a series of chapters which have been published, or have recently been accepted for publication, as outlined below:

Chapter 2:

Haynes, P.S., Allen, B.M., Brophy, D., McGrath D. 2008. Fin-ray count variation in 0-group flatfish: plaice (*Pleuronectes platessa* (L.)) and flounder (*Platichthys flesus* (L.)) on the west coast of Ireland. *Biology & Environment*. 108B (2). 61-67.

Species specific meristic characters, fin rays, were used to distinguish between 0-group plaice and flounder. Possible differences in the number of fin rays exhibited by both plaice and flounder, inhabiting various nursery grounds were also investigated. Finally, fin ray counts were recorded and analysed as a result of anecdotal reports suggesting the existence of juvenile plaice/flounder hybrids along the west coast of Ireland.

Chapter 3:

Haynes, P.S., Brophy, D., McGrath, D., 2010b. Variation in the fin ray counts of 0-group turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.) on the west coast of Ireland: 2006-2009. *Marine Biodiversity Records*. 3, e124 doi: 10.1017/S1755267210001144.

An identification method based on fin rays counts derived from species descriptions in the literature, was used to confirm that recently settled west of Ireland 0-group turbot and brill had been separated correctly. Both temporal and spatial variability in fin ray counts, which may indicate the existence of separate spawning stocks, was also considered.

Chapter 4:

Haynes, P.S., Brophy, D., McGrath, D., O' Callaghan, R., Comerford, S., and Casburn, P., 2010a. Annual and Spatial Variation in the Abundance Length and Condition of Turbot (*Psetta maxima* L.) on Nursery Grounds on the West Coast of Ireland: 2000 – 2007. *Journal of Sea Research*. 64 (4). 494-504.

Patterns of annual and spatial variation in the abundance, length, and condition of 0-group turbot on west of Ireland nursery grounds were assessed over an eight year period (2000 – 2007). These

data were used to identify important nursery grounds, which yield a higher number of larger juveniles in comparison to other areas. Such high quality nursery areas may subsequently produce a greater abundance of juveniles to recruit to the adult population. The potential for annual surveys of sandy beach nursery areas to serve as an index of fluctuations in the adult turbot stock was evaluated.

Chapter 5:

Haynes, P.S., Brophy, D., McGrath, D. Variability in the early life stages of juvenile plaice (*Pleuronectes platessa* L.) on west of Ireland nursery grounds; 2000 – 2007. *Journal of the Marine Biological Association of the United Kingdom*. In press (a).

Trends in abundance, length, and condition of 0-group plaice inhabiting west of Ireland nursery grounds was assessed over eight years and important nursery habitats for juvenile plaice were identified. 0-group plaice abundances were also correlated with abundances of 1-group individuals captured off the west coast in the Irish Groundfish Survey, to assess the potential of this method for generating a recruitment index.

Chapter 6:

Haynes, P.S., Brophy, D., McGrath, D., 2011. The early life history of turbot (*Psetta maxima* L.) on nursery grounds along the west coast of Ireland: 2007 – 2009 as described by otolith microstructure. *Journal of Fisheries Research*. doi:10.1016/j.physletb.2003.10.071.

A detailed examination of the early life history of 0-group turbot was conducted using otolith microstructure analysis. The timing of important events in early life, including the timing of hatching and settlement, in addition to larval and post-larval growth rates, were investigated over a three year period. Both temporal and spatial variability in these parameters was considered and the possibility that multiple spawning stocks of turbot supply west of Ireland nursery grounds was examined.

Chapter 7:

Haynes, P. S., Brophy, D., McGrath, D. The feeding ecology of 0-group turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.) on Irish west coast nursery grounds. *Journal of Fish Biology*. In press (b).

The type and quantity of prey consumed by 0-group turbot and brill was investigated between nursery grounds, over a number of months. The prey community inhabiting nursery ground sediments was also assessed, in order to determine any prey selectivity of both turbot and brill. The possibility of both temporal and resource partitioning of these morphologically similar species was also considered, in addition to any differences detected in recent growth and condition. A detailed study was also undertaken on the biotic and abiotic factors within nursery grounds; temperature, salinity, and predator abundances, which are known to influence the behavior, growth, and survival of juvenile flatfish.

To conclude the present thesis, an overall discussion considering the findings and interpretations of the six studies is presented in chapter 8. The relevance of results to the future conservation and sustainability of west of Ireland flatfish populations is considered.

Chapter 2

Fin-ray count variation in 0-group flatfish: plaice (*Pleuronectes platessa* (L.)) and flounder (*Platichthys flesus* L. on the west coast of Ireland.

Published in: *Biology & Environment*. 108B (2). 61-67.

Fin ray count variation in 0-group flatfish: plaice *Pleuronectes platessa* (L.) and flounder *Platichthys flesus* (L.) on the west coast of Ireland.

Paula S. Haynes, Brendan M. Allen, Deirdre Brophy, and David McGrath.

Abstract

0-group plaice *Pleuronectes platessa* Linnaeus and flounder *Platichthys flesus* Linnaeus were collected from beaches in Galway and Kerry on the west coast of Ireland by beach seining and push-netting respectively, in the autumn of 2005 and 2006. Characteristics used to identify adult flatfish were not discernible in these juveniles, and their fin ray counts were used to differentiate between the species, subsequent to a preliminary separation using more subtle identification techniques. Analysis of fin ray counts for both plaice and flounder showed no significant difference between the two regions studied. However, for plaice, a significant difference in dorsal fin ray numbers was observed between the Galway beaches. No evidence of plaice/flounder hybrids was observed, as identified by intermediate ray counts. There was no relationship between the number of dorsal and anal fin rays for plaice. However, a positive relationship was found between the number of dorsal and anal rays for flounder. The dorsal, anal, and caudal rays of 325 plaice and 116 flounder were counted and plotted, resulting in a clear separation between the two species. The present work demonstrates that fin ray counts may be reliably used to separate these two species on the west coast of Ireland, with the ranges observed for both species within those previously reported in the literature.

1. Introduction

Morphometric and meristic characters are commonly used to identify different species of fish. Meristic characters have been described as a number of discrete, serially repeated, countable structures that are fixed in the embryos or larvae (Turan 2004), remaining stable throughout life (Begg and Waldman, 1999). Phenotypic variation such as meristic counts continues to play an important role in stock identification among groups of fish, despite the use of genetic analysis (Swain and Foote, 1999). Such meristic counts may differ as a result of environmental differences during early development (Colman, 1976). Given the current level of global exploitation, it is essential that fish species or genetically different stocks of the same species are identified accurately, so as to obtain reliable data for the long term sustainability of that species.

Failure to discriminate between different flatfish caught in mixed catches can lead to problems in fishery management (Stankus, 2003). Fin ray counts are one type of meristic character which can be used to distinguish between different species of fish, or between different fish stocks of the same species. Fin ray numbers are influenced by a wide range of environmental factors such as salinity, light, and dissolved oxygen, with temperature being the most intensely studied parameter (Swain and Foote, 1999). As a result, different stocks of the same species living in geographically separated areas may exhibit variation in their fin ray counts. MacGregor and MacCrimmon (1977), Nielsen *et al.* (1998), and Burke *et al.* (2000) were able to differentiate between northern and southern stocks of rainbow trout, (*Salmo gairdneri* Richardson), plaice (*Pleuronectes platessa* Linnaeus), and summer flounder (*Paralichthys dentatus* Linnaeus) based on regional variation in fin ray numbers. Kinoshita *et al.* (2000) found juvenile Japanese flounder reared at higher water temperatures to have a greater mean dorsal and anal ray number. In contrast, MacGregor and MacCrimmon (1977) found the average number of dorsal and anal rays of rainbow trout (*Salmo gairdneri* Richardson), to decrease at higher incubation temperatures. Kinoshita *et al.* (2000) also found that high numbers of anal rays resulted in high numbers of dorsal rays.

Plaice and flounder (*Platichthys flesus* Linnaeus) may be readily identified and separated from each other as adults using a number of characteristics including coloration and the presence of bony tubercles on the dorsal surface (Wheeler, 1969). These identification characteristics are however not discernible in the juvenile fish of these species, and here fin ray counts can be used to differentiate between them. Significant overlap in the dorsal, anal, and caudal ray range for these species may also occur as documented by various authors (Table 1). Furthermore, the caudal fin ray range differs by only one ray between plaice and flounder, and this may permit misidentification in small individuals through miscounts.

Table 1: Fin-ray count ranges for adult plaice and flounder, as described in the literature.

Source	Dorsal ray		Anal ray		Caudal ray	
	Plaice	Flounder	Plaice	Flounder	Plaice	Flounder
Wheeler (1969)	65–79	52–67	48–59	35–46	–	–
Bagenal (1973)	65–79	52–67	48–59	35–46	–	–
Russell (1976)	–	–	43–61	34–46	19–21	16–18
Froese and Pauly (2008)	65–79	53–62	48–59	37–46	–	–

There have been anecdotal reports of flatfish with intermediate fin ray counts suggesting that a hybrid between plaice and flounder may exist off the west coast of Ireland (Gavin Keirse pers. comm.). The natural occurrence of plaice/flounder hybrids and flounder/dab hybrids have been described by Russell (1976), and Wheeler (1969) respectively. Exadactylos and Thorpe (2001) found that for 17 populations of seven species of fish, plaice and flounder were the most closely related species pair, explaining their ability to hybridize naturally. Plaice/flounder hybrids have been referred to in the literature as *Pleuronectes pseudoflesus* Linnaeus (Pape, 1935). Such fish hybrids may not always be instantly recognized, and as a result, fin ray counts have been used to identify them (Yaakub et al. 2006). The majority of known fish hybrids have been identified, based on the fact that they shared an intermediate number or range of morphometric and meristic characters compared to those of the two parent species (Garrett, 2005).

Fin rays were counted and plotted for 325 juvenile plaice, and 116 juvenile flounder. These juveniles were caught in beach seines and push-nets on a number of beaches on the west coast of Ireland in counties Galway and Kerry during 2005 and 2006. While recently flatfish such as dab may also be similar in appearance to plaice, these were not present in shallow depths on west of Ireland nursery grounds. Fin ray counts were then used to investigate the following: To determine whether geographic variation in fin ray counts existed between the plaice and flounder populations on the west and southwest coasts of Ireland. To confirm whether fin ray counts could be reliably used as a method to distinguish between the juveniles of these species on the west coast of Ireland, prior to more subtle identification techniques that distinguish shape and coloration. Finally, to look for the presence of any plaice/flounder hybrids, using the dorsal and anal fin ray counts as used by Garrett (2005).

2. Materials and Methods

0-group plaice were caught on all beaches (Table 2) sampled around Galway Bay between August 22nd and August 24th, and around the Dingle peninsula Co. Kerry (Figure 1) between September 18th and September 21st, 2005. Flounder were caught on Ballyloughaun beach in Galway Bay for 2005, and on Smerwick beach, Co. Kerry in 2006 only. Fish were caught using a beach seine, 20 m long, with a 12 mm square mesh size. A minimum of two and a maximum of six seine hauls were carried out at random locations within each beach sampled in 2005. For flounder caught on Smerwick in 2006, a Riley push net was used (Riley, 1971), with a 1.5 m x 0.3 m metal frame supported on two 70 cm x 7.5 cm skis. A 2 m long handle was attached to the frame for pushing the double-ended shrimp net. The net had a 10 mm square mesh size, and 2mm curtain mesh for the two cod ends. Flatfish caught were placed in plastic bags, and subsequently frozen.

Table 2: Beaches surveyed on the west and southwest coast of Ireland.

<i>Beach</i>	<i>Position (latitude/longitude)</i>	<i>Region</i>
Ballyloughaun	54°16.2' N / 09°01.6' W	Co. Galway
Silverstrand	53°15.2' N / 09°07.8' W	Co. Galway
Brandon	52°15.0' N / 09°01.6' W	Co. Kerry
Smerwick	52°10.7' N / 09°01.6' W	Co. Kerry

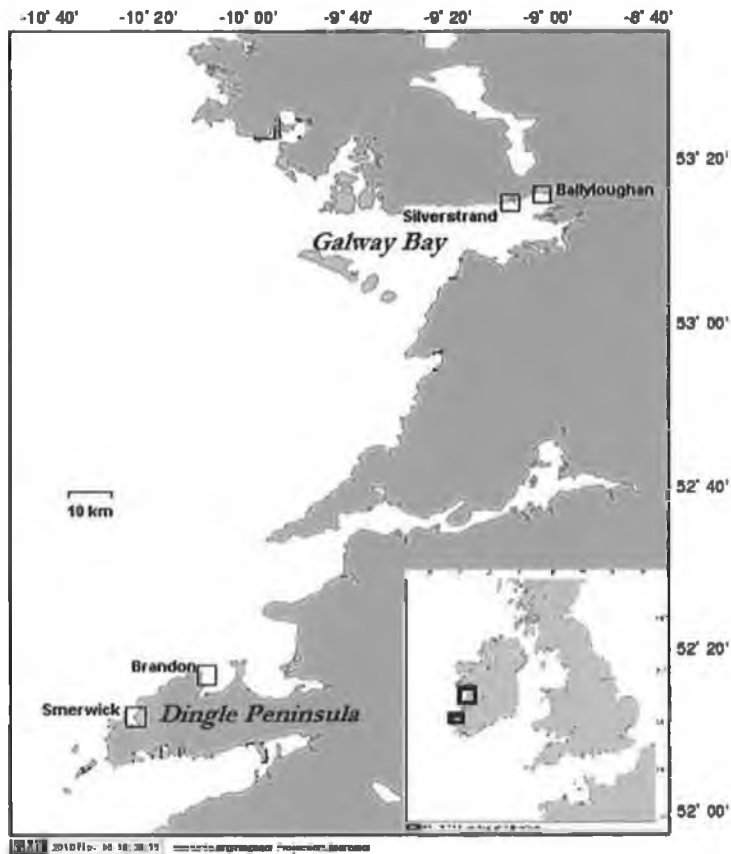


Figure 1: Two regions where 0-group flatfish were collected on the west coast of Ireland.

2.1. Laboratory analysis

Frozen 0-group flatfish were taken out of the freezer and allowed to thaw overnight. Plaice and flounder were identified according to Wheeler, (1969) and using fin ray counts. The dorsal, anal, and caudal fin rays of the juvenile plaice and flounder were counted under a stereoscopic microscope, to confirm that the two species had been separated correctly.

2.2. Statistical analysis

Statistical analysis was carried out for plaice and flounder using the statistical package MINITAB 14. Where appropriate, the data were tested for normality using the Anderson

Darling test. Homogeneity of variances was tested using Bartlett's test. A Spearman rank correlation was used to test non-parametric data. Nested ANOVAs were used to analyze the plaice data, with beach nested within each region. *Post hoc* tests were also carried out on data displaying homogeneity of variances, using Fishers multiple comparisons test. Principal Components Analysis (PCA) was carried out on the dorsal, anal, and caudal fin rays for plaice and flounder to identify any patterns in the data. PCA allows you to compress the data or a number of variables into one Principal Component (PC) without losing the information that the data is portraying (Manly, 2005). By assigning Eigen values to each PC, the variables contributing or explaining the overall picture of the data set can be identified (Manly, 2005).

When comparing the fin ray counts between regions, a different number of beaches were sampled in Galway and Kerry. Furthermore, two hauls were carried out on the Galway beaches, and six hauls on the Kerry beaches. This resulted in the plaice data for the beach seining survey being unbalanced. When analyzing a balanced data set, the result obtained is more reliable compared to an unbalanced data set. As a result, two beaches were randomly selected from each region and two hauls were also randomly selected from the Kerry beaches to balance the data. Fin ray counts of 24 plaice randomly selected from each of the four beaches were made. As flounder were caught on only one beach during the beach seining, flounder collected by push-netting in Smerwick Harbour were also used. The flounder data were analyzed using a Mann-Whitney test. All fin ray data for plaice from all beaches were used when comparing the anal and dorsal fin rays.

3. Results

The total number of plaice and flounder caught per beach are shown in Table 3. As the number of plaice caught was substantially greater than that of flounder, 325 plaice were randomly selected using random number tables, and their fin rays were counted.



Table 3: Numbers of plaice and flounder caught per beach.

<i>Beach</i>	<i>Plaice</i>	<i>Flounder</i>
Ballyloughaun	67	74
Silverstrand	129	–
Brandon	274	–
Smerwick	252	42

3.1. Fin ray counts of juvenile plaice and flounder

Fin ray counts for plaice and flounder were as described in Table 4. The caudal fin ray counts for both plaice and flounder varied little, while the overall majority of flounder had 17 caudal fin rays. The overall majority of plaice had 20 caudal fin rays.

Table 4: Fin-ray count ranges for plaice and flounder on the west coast of Ireland.

<i>Fin ray</i>	<i>Plaice</i>	<i>Flounder</i>
Anal	51–59	39–46
Caudal	19–20	17–18
Dorsal	68–79	56–65

3.2. Data analysis of plaice fin ray counts

Using a nested ANOVA, with a p-value significant above 0.05 (Underwood, 1997), there was no significant difference revealed in the number of anal fin rays for plaice ($n = 96$) between regions ($p = 0.376$), or between beaches nested within regions ($p = 0.080$).

Using a nested ANOVA it was found that there was no significant difference in the dorsal fin ray numbers for plaice ($n = 96$) between regions ($df = 1$; $F = 0.27$; $p = 0.658$). However a

significant difference ($df = 2$; $F = 7.21$; $p = 0.001$) was found in the number of dorsal fin rays between beaches nested within regions. A *post hoc* analysis on the beach data showed that there was a significant difference in the dorsal fin ray numbers of plaice for Ballyloughaun ($df = 3$; $F = 5.4$; $P = 0.002$) when compared with Silverstrand, Smerwick, and Brandon.

The mean dorsal fin ray counts for plaice were calculated for each beach (\pm standard deviation, SD) (Table 5).

Table 5: Mean dorsal fin-ray counts for plaice on the west coast of Ireland.

<i>Beach</i>	<i>Mean dorsal fin-ray counts (\pm SD)</i>
Ballyloughaun	76 \pm 2
Silverstrand	73 \pm 1
Brandon	74 \pm 2
Smerwick	74 \pm 2

3.3. Data analysis of flounder fin ray counts

The anal ($n = 116$) and dorsal ($n = 116$) fin ray data were not normally distributed ($p < 0.005$). Using a Mann-Whitney test it was found that there was no difference between the anal ($p = 0.6202$) or the dorsal ($p = 0.715$) numbers of fin rays between regions.

3.4. A comparison of plaice and flounder fin ray counts

A Spearman Rank correlation was carried out for the anal and dorsal fin rays of both plaice ($n = 325$) and flounder ($n = 116$), in order to determine whether a high/low number of dorsal fin rays was associated with a high number of anal fin rays. No correlation was found between dorsal and anal fin ray counts of plaice ($p = 0.188$). However, a correlation was found between the dorsal and anal fin rays of flounder ($p = 0.000$).

3.5. PCA of the dorsal and anal fin rays of plaice and flounder

Using PCA there was a clear separation in the, dorsal, anal, and caudal fin rays for plaice and flounder (Figure 2).

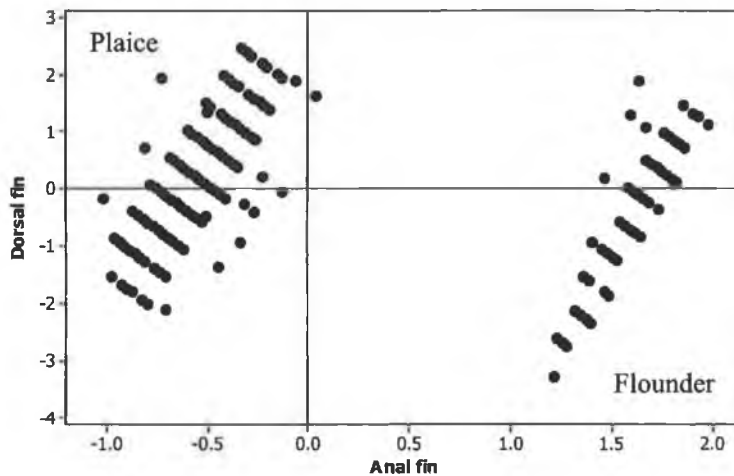


Figure 2: Plot of Principal Component Analysis for the dorsal and anal fin rays of plaice (N = 325) and flounder (N = 116) caught in Galway and Kerry in 2005 and 2006.

4. Discussion

Counting the dorsal, anal, and caudal fin ray numbers as described by Wheeler (1969) and Russell (1976) to distinguish between juvenile plaice and flounder produced a clear separation between the two species (Figure 2). This indicates that fin ray counts are a reliable method to identify juvenile flatfish on the west coast of Ireland, though genetic analyses would be necessary to confirm the separation. The fin ray counts observed for the west coast of Ireland are within the ranges previously described for plaice and flounder in Table 1 with less variation. This may be as a result of west of Ireland plaice eggs and larvae having experienced similar environmental conditions such as temperature, as those plaice documented in the literature, when the number of fin rays exhibited by individuals was being established. In the present work, the dorsal and anal fin ray ranges for both plaice and flounder did not overlap, in contrast to the fin ray ranges described in Table 1. However, this method of identification may

not be applicable to plaice and flounder outside of Irish waters, as overlap may occur in the fin ray counts in other areas. Eldon and Smith (1986) found fin ray counts not to be a suitable method for distinguishing between 0-group sand flounder (*Rhombosolea plebeia* (Richardson)) and yellow bellied flounder (*Rhombosolea leporina* Gunther). This was due to the regional variation in fin ray counts (Colman 1976), overlap in counts between the species, and the counting of fin rays being a time consuming method. For plaice and flounder, no significant difference was found in the dorsal or anal fin ray counts between the west and south west coast of Ireland, suggesting that plaice from the two regions may have experienced similar environmental conditions during their development. This is perhaps not surprising given the distances involved and the fact that currents transporting the larvae are from south to north, along the west coast of Ireland (Mohn et al, 2002).

A significant difference was found for the dorsal fin ray counts between beaches in Galway Bay for plaice only. The difference was found for Ballyloughaun beach, which had a higher mean dorsal fin ray count compared to Silverstrand in Galway, or Brandon and Smerwick in Kerry. A significant difference in dorsal fin ray counts may be more likely for Ballyloughaun, in relation to a difference in the larval supply, when compared to the Kerry beaches of Brandon and Smerwick, due to the larger geographical separation. As Ballyloughaun and Silverstrand are in close proximity to each other on the west coast, it appears improbable that larvae settling on Silverstrand are from a different spawning stock to that of Ballyloughaun. Allen (2004) found that plaice larvae had a significantly shorter larval duration on Ballyloughaun compared to that of Silverstrand. If this difference in the length of time spent by larvae in the water column were to also occur in additional years, such as that in which the present work was undertaken, then larvae on Silverstrand may have encountered additional factors influencing the fin ray count number exhibited by individuals on this beach, compared to that Silverstrand. Though only speculative, a difference in an environmental parameter experienced by larvae might be more plausible explanation rather than a difference in the larval supply between the two Galway beaches in close proximity.

The anal and dorsal fin rays of plaice were found not to be correlated in the present study. However, a significant positive correlation was found between the dorsal and anal fin rays of flounder. A correlation between the dorsal and anal fin rays for other species of flounder have been found in earlier studies. Kinoshita et al. (2000), found the dorsal and anal fin ray counts of juvenile Japanese flounder to be highly correlated. Colman (1976) found that sand flounder

sampled from the same area grouped together, based on a plot of their mean number of dorsal and anal fin ray counts. Although not tested, the plot also suggests a correlation between the dorsal and anal fin rays of sand flounder. The lack of a correlation for plaice in the present study may reflect the smaller geographical scale when compared to that of Colman (1976), who collected 2360 sand flounder from 18 different areas around the coasts of New Zealand, and Kinoshita et al. (2000) who collected Japanese flounder from 26 sites along 1700 km of coastline. However, a smaller spatial scale does not appear to have obscured the positive relationship for the lesser number of flounder sampled, as the anal and dorsal rays were positively correlated.

Although plaice and flounder hybrids have been reported by Russell (1976), no hybrids were discerned with intermediate fin ray counts of either plaice or flounder, as has been previously found for identified hybrids. It may, therefore be the case that some hybrids share the same fin ray counts as either plaice or flounder, and not an intermediate number. Wyatt *et al.* (2006) found that for roach (*Scardinius erythrophthalmus*), bream (*Abramis brama*), and rudd (*Rutilus rutilus*) some meristic characteristics such as the anal fin rays were intermediate to the two parent species, whereas overlap occurred for other characters. Garrett (2005) could not determine why hybrids were not more common, especially in areas such as Puget Sound where there is a spatial and temporal overlap of spawning between many pleuronectiform species. Plaice/flounder hybrids on the west coast of Ireland may also be extremely rare, even rarer than the hybrids found by Garrett (2005). However, for other species of fish, hybridization a mechanism utilized in instances when there is an insufficient abundance of the same species present. Alternatively, it is not known when or where plaice or flounder spawn, and there may be temporal and spatial differences in the spawning of both these species, decreasing the likelihood of hybridization. Future sampling might also need to include other beaches where flounder are also found, as the overall number of flounder caught ($n = 116$) was considerably less than that of plaice ($n = 722$). Garrett (2005) used 10 meristic characteristics, whereas only two characters were used in the present study, and additional morphological/meristic characters or indeed genetic analysis may be needed to detect such hybrids on the west coast of Ireland.

There is to date, very little published data available on variation in fin ray counts. As demonstrated by previous authors and the current study, fin rays can be used to investigate many aspects of fish or flatfish, particularly as the number of rays present appears to be influenced by environmental factors. Further studies are needed in order to try and determine

why such variation occurs. However, the primary objective of the present work, which was to determine whether fin rays could be used as a reliable method to correctly distinguish between morphologically similar 0-group flatfish species plaice and flounder subsequent to the initial separation of fish on the beach, was confirmed.

Chapter 3

Variation in the fin ray counts of 0-group turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.) on the west coast of Ireland: 2006-2009.

**Published in: *Marine Biodiversity Records*. 3, e124
doi:10.1017/S1755267210001144.**

Variation in the fin ray counts of 0-group turbot (*Psetta maxima*) and brill (*Scophthalmus rhombus*) on the west coast of Ireland: 2006-2009

Paula S. Haynes, David McGrath, Deirdre Brophy.

Abstract

Recently settled turbot *Psetta maxima* Linnaeus and brill *Scophthalmus rhombus* Linnaeus are difficult to distinguish, as they are almost identical in appearance and lack the diagnostic adult characteristics. Fin ray counts, which can be used as an aid in the identification of flatfish juveniles, are reported to show some overlap between turbot and brill. 0-group flatfish were collected from sandy beaches along the west coast of Ireland by beach seining in 2009. When counted and plotted, the dorsal and anal fin rays clearly separated the specimens into two groups; 88 turbot and 42 brill, with no overlap observed in the fin ray counts between the two species. This confirmed that fin rays could be reliably used as a diagnostic tool in west of Ireland waters, subsequent to a preliminary separation using more subtle coloration and morphological identification techniques. Additionally, temporal and spatial variability in fin ray counts was investigated, as this can be indicative of the existence of separate spawning stocks, and provide information on the environmental conditions experienced by fish during the pelagic stage. Temporal variability was observed in the fin ray counts of 490 turbot collected over a four year period (2006-2009). Counts were significantly lower in 2006 and significantly higher in 2009. The limited data suggest that these differences were related to variation in sea temperature during the larval phase. Spatial variability occurred for the fin ray counts of the brill in 2009. Individuals sampled from the nursery ground beach at Brandon exhibited a significantly higher fin ray count in comparison to that of Silverstrand. The scales of variation observed indicate that fin ray counts must be used with caution when separating species which share similar fin ray numbers.

1. Introduction

Turbot *Psetta maxima* Linnaeus and brill *Scophthalmus rhombus* Linnaeus are valuable commercial non-quota flatfish, and are caught as by-catch in demersal fisheries off the coast of Ireland (Anon, 2010b). It is not known when turbot or brill spawn, or whether separate stocks exist. The juveniles settle from the plankton onto sandy beach nursery grounds along the west coast of Ireland. Relatively little is known of the population dynamics of these two very similar species especially in the early life history stages. 0-group turbot and brill are almost identical in appearance, and distinguishing between these two species, which lack adult characteristics such as shape, coloration, and the presence of bony tubercles in the juvenile phase, can be problematic (Russell, 1976). Hence, for the correct identification of 0-group turbot and brill, fin rays are the diagnostic characteristics to be used (Russell, 1976), subsequent to more subtle identification techniques, which can be difficult to describe quantitatively. The number of fin rays exhibited by a fish is determined in the embryonic or larval life stage, and remain constant throughout the life of a fish (Lindsey, 1988). Variability in fin ray counts reported for juvenile turbot and brill in the literature, in addition to the existence of overlap in the fin ray count range, has previously not been addressed. The fin ray counts reported by Russell (1976) for turbot and brill overlap for the dorsal fin ray, and are extremely close to overlapping for the anal fin rays. In contrast, the fin ray counts reported for turbot and brill by Wheeler (1969) for the dorsal and anal fin ray counts do not overlap, showing that significant variation in counts among authors occurs. Consequently, depending on the literature source utilized, misidentification of 0-group turbot and brill could arise.

The number of fin rays are influenced by a wide range of environmental factors such as temperature, salinity, and dissolved oxygen (Nielsen et al., 1998; Swain & Foote, 1999; Kinoshita et al. 2000). In general, a longer developmental time will result in a high number of meristic characters, including fin rays, being produced, with higher numbers at more northerly latitudes (Barlow, 1961). Significant temporal and spatial variation can therefore occur between individuals of the same species originating from geographically separated stocks, and/or which have experienced different environmental conditions during the egg and larval stages. Juvenile plaice supplied to nursery grounds along the Danish coast were found to originate from separate spawning stocks based on their fin ray counts, as a result of the different environmental conditions experienced by eggs and larvae subsequent to spawning. Geographically separated stocks of rainbow trout, (*Salmo gairdneri* Richardson) and summer flounder (*Paralichthys dentatus*

Linnaeus) have also been distinguished between based on differences in their fin ray numbers (MacGregor & MacCrimmon, 1977; Burke et al. 2000).

The present study of 0-group turbot and brill is part of a larger investigation of the early life history of flatfish species on Irish west coast nursery grounds (Allen et al., 2008; Haynes et al., 2008; Haynes et al., 2010a, b; De Raedemaecker et al., 2010a, in press. Validation of identification techniques for juvenile flatfish, particularly turbot and brill, was an essential prerequisite to this research. 0-group flatfish were collected from sandy beach nursery grounds along the west coast of Ireland by beach seine. A preliminary separation of 0-group turbot and brill was carried out on the beach, based on subtle identification techniques that distinguish shape and coloration, which are not described in the literature. However, as the incorrect identification of individuals using these techniques may have occurred, fin rays were counted and plotted for the 130 0-group flatfish in 2009, in order to test the hypothesis that fin ray counts could be used as a reliable confirmatory method to distinguish between the two species, in the absence of genetic analyses. In addition, the fin ray counts of 490 juvenile turbot collected over a four year period (2006-2009) and juvenile brill collected over a one year period were also used to determine temporal or spatial scales of variation in these parameters. Significant spatial variation in fin ray counts has been shown for Irish west coast plaice by Haynes et al., (2008). No published information was available for the range of fin ray counts of turbot or brill along the west coast of Ireland, or whether fin ray counts previously determined for turbot and brill from the British Isles (Wheeler, 1969; Russell, 1976) were similar to west of Ireland counts. The objectives of the present study were therefore to:

- 1) Determine if 0-group turbot and brill could be reliably distinguished between using fin ray counts.
- 2) Determine scales of temporal and/or spatial variation in the number of fin rays of turbot and brill.

2. Methods and Materials

2.1. Fish collection

0-group turbot were collected along the west coast of Ireland in July and November between 2006 and 2009. Brill were collected in 2009 only, between May and October (Figure 1; Table

1). Sampling was carried out using a Danish style beach seine. Lengths of 0-group turbot and brill collected on Silverstrand ranged from 2.4 to 6.1 cm, and from 2.5 to 8.1 cm respectively, with the majority of individuals captured < 4 cm.. Sampling on a beach was carried out in a single day, between two hours prior to or two hours after the time of low tide during daylight hours. A preliminary separation of 0-group turbot and brill was carried out on the beach, using subtle identification techniques such as coloration and shape, prior to verification using fin ray counts. Fish were captured using a beach seine as described in Haynes et al., (2010a), and placed in plastic bags with the sample date and location and frozen in the laboratory within a number of hours of being captured for further analyses.

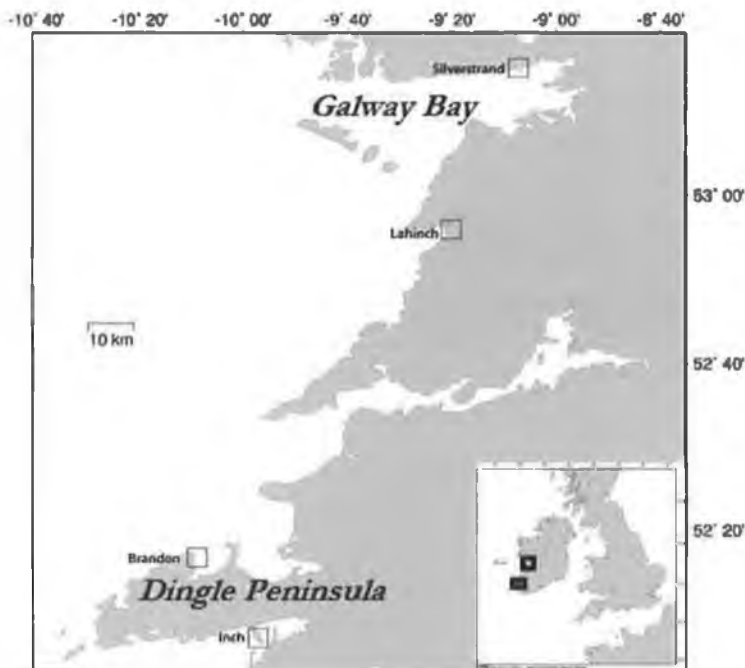


Figure 1: Beaches assessed for 0-group turbot and brill along the west coast of Ireland (2006 – 2009).

Table 1: Total abundances (n) of 0-group turbot (per year) and brill (per month in 2009) collected from Irish west coast nursery grounds. – denotes not sampled.

Month	May		June		July		August		September		October	
	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br
Inch	-	-	-	-	-	-	9	0	12	-	-	-
Brandon	-	-	-	-	0	10	3	0	-	-	-	-
Silverstrand	0	10	0	0	0	22	59	0	25	0	21	0
Lahinch	-	-	-	-	-	-	-	-	14	0	-	-

2.2. Fin ray analysis

Frozen fish were removed from the freezer and allowed to thaw overnight. In order to confirm that 0-group turbot and brill had been separated correctly in the initial identification stages, the number of dorsal, anal, and caudal fin rays, which are species specific for flatfish were counted under a stereoscopic microscope, and compared with the fin ray count given by Wheeler (1969) and Russell (1976) (Figure 2).

2.3. Temperature data

Temperature has been found to significantly influence the number of fin rays exhibited by flatfish (Kinoshita et al., 2000). Although limited, the mean spring sea surface temperature data (March April May) corresponding to the pelagic stage in turbot, were obtained and considered in the discussion, with the possibility that temporal variability in fin ray counts may have an environmental basis. Temperature data were available for three years only (2006 – 2008) and were provided by the Marine Institute from the weather buoys M1 (53.1266°N, 11.2000°W) off the west coast and M3 (51.2166°N, 10.5500°W) off the southwest coast of Ireland. These buoys are situated miles off the west coast of Ireland, and would be positioned in the pathway of currents transporting larvae from south to north along the Irish west coast (Mohn et al., 2002).

2.4. Statistical Analyses

Statistical analysis was carried out on both the dorsal and anal fin ray counts of turbot and brill using the statistical package MINITAB 15. Homogeneity of variances were tested using Levene's test, and were log transformed where appropriate (Underwood, 1997). Where the data failed to display homogeneity of variances, the non-parametric Kruskal-Wallis Test was used. Data were analysed using unbalanced ANOVA's, to test the null hypotheses that there was no significant difference in the number of dorsal and or fin ray counts of turbot between beach and year. Both beach and year were included as fixed factors. Significant differences were explored using Tukey's post hoc procedures. A One-Way ANOVA was used to test the null hypotheses that there was no significant difference in the number of dorsal or anal fin ray counts of brill between beach and month. Principal Components Analysis (PCA) was carried out on the dorsal and anal fin ray counts of 0-group flatfish, to determine if these could be used as reliable characteristics to distinguish between turbot and brill. Principal component reduces the number of characters by forming new characters that are combinations of the old ones, while retaining most but not all of the variation present in the dataset (Jolliffe, 2002). The method is used to reduce the number of characters from many to two or three, so that clusters or groupings of the characters under investigation can be more clearly distinguished or easily seen.

3. Results

The range of caudal fin rays for both turbot and brill was identical, and therefore omitted from the analyses. Fin ray counts of turbot and brill in the present study were different to those described in the literature by Wheeler (1969) and Russell (1976) (Figure 2).

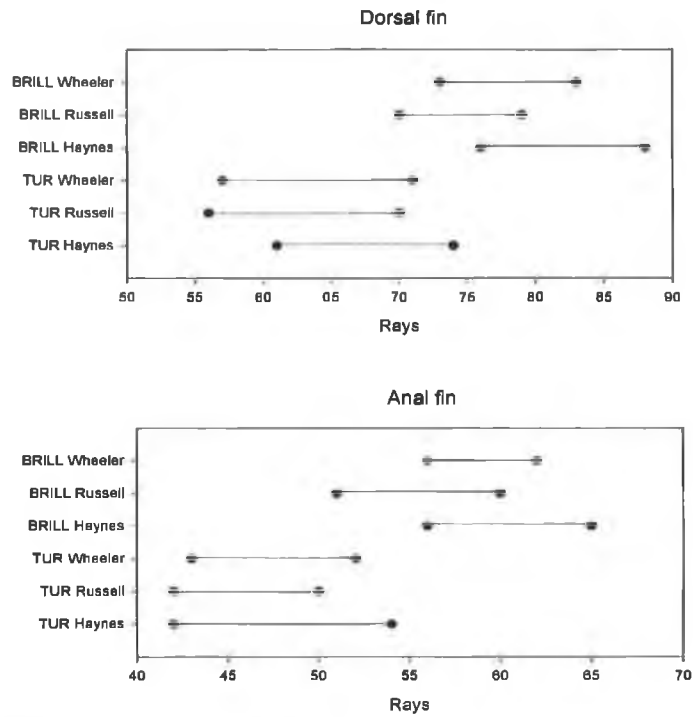


Figure 2: Fin ray count ranges for turbot and brill as described in the literature and in the present study.

3.1. Comparison of juvenile turbot and brill fin ray counts

Using PCA, the dorsal and anal fin ray counts of 0-group flatfish collected along the west coast of Ireland were found to separate into two distinct groups; turbot and brill, with no overlap detected for 2009 (Figure 3). PC1 revealed 98 % of the variation with PC2 accounting for only 2 % of the variation observed.

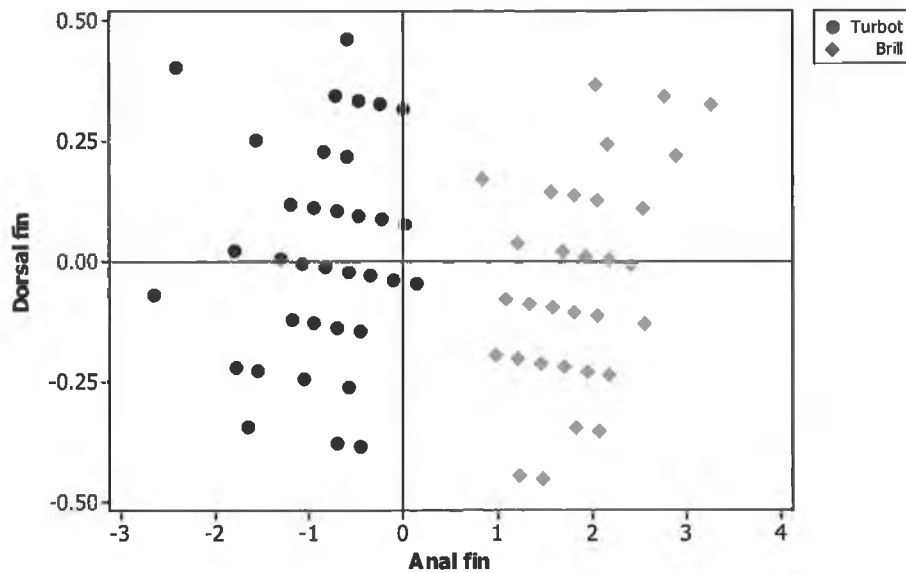


Figure 3: PCA plot of the dorsal and anal fin ray counts between 0-group turbot (n=88) and brill (n=42) collected on Silverstrand on the west coast of Ireland in 2009.

3.2. Spatial variation in the fin ray counts of brill (2009)

A One-Way ANOVA detected a significant difference in the dorsal (df = 1; F = 4.66; p = 0.037) and anal (df = 1; F = 5.43; p = 0.025) fin ray counts of brill (n = 42) between Silverstrand and Brandon. The dorsal fin ray counts on Silverstrand were significantly higher ($\bar{x} = 81 \pm 3$) in comparison to the dorsal fin ray counts on Brandon ($\bar{x} = 79 \pm 3$), with the number of anal fin ray counts on Silverstrand ($\bar{x} = 61 \pm 2$) also significantly higher in comparison to Brandon ($\bar{x} = 60 \pm 2$) (Figure 4). A One-Way ANOVA detected no significant difference in the number of dorsal (df = 1; F = 0.12; p = 0.736) or anal (df = 1; F = 0.13; p = 0.749) fin ray counts of brill between the months of May and July on Silverstrand.

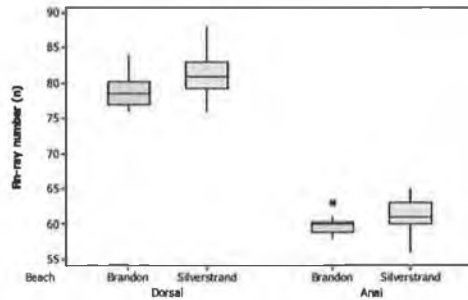


Figure 4: Spatial variation in the number of dorsal and anal fin ray counts of 0-group brill collected on beaches along the west coast of Ireland (2009).

3.3. Temporal and spatial variation in turbot fin-ray counts (2006-2009)

A Two-Way ANOVA revealed no significant differences in the number of dorsal fin ray counts of turbot ($n = 490$) between beaches ($df = 2$; $F = 1.63$; $p = 0.197$). However a significant difference occurred in the number of dorsal fin-ray counts between years ($df = 3$; $F = 60.02$; $p < 0.001$). There was no significant interaction between beach and year ($df = 6$; $F = 1.60$; $p = 0.144$). Tukey's multiple comparisons tests revealed that turbot in 2006 had significantly lower dorsal fin ray counts ($\bar{x} = 66 \pm 2$) compared to 2007 ($\bar{x} = 67 \pm 2$) 2008 ($\bar{x} = 68 \pm 2$), and 2009 ($\bar{x} = 69 \pm 2$). Furthermore, turbot in 2009 had significantly higher dorsal fin ray counts in comparison to all other years (Figure 5). A non-parametric Kruskal-Wallis found no significant differences in the anal fin rays between beaches ($H = 3.80$; $df = 2$; $p = 0.15$). However a significant difference in the number of anal fin rays occurred between years ($H = 206.12$; $df = 2$; $p < 0.001$). Tukey's multiple comparisons tests on ranked data revealed that turbot in 2006 had a significantly lower number of anal fin ray counts ($\bar{x} = 46 \pm 1$) compared to 2007 ($\bar{x} = 48 \pm 2$), 2008 ($\bar{x} = 48 \pm 2$), and 2009 ($\bar{x} = 50 \pm 2$). The mean dorsal and anal fin ray counts of 0-group turbot, collated in a given year, are presented in Table 2.

Table 2. Mean dorsal and anal fin ray counts of 0-group turbot collected on nursery grounds along the west coast of Ireland (2006 - 2009).

Year	Mean dorsal fin-ray number	Mean anal fin-ray number
2006	66 ± 2	46 ± 1
2007	67 ± 2	48 ± 2
2008	68 ± 2	48 ± 2
2009	69 ± 2	50 ± 2

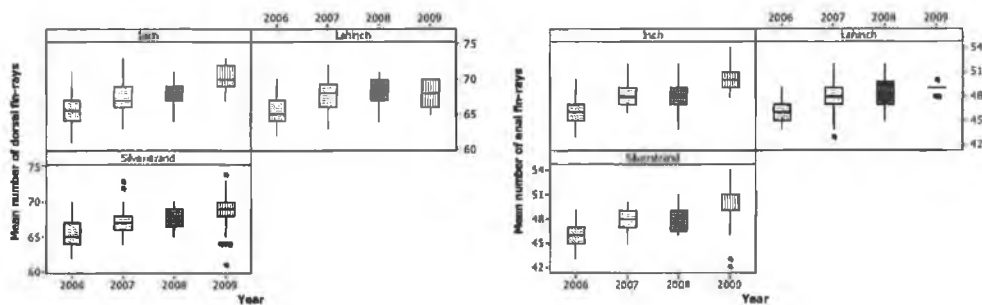


Figure 5: Temporal variation in the number of dorsal (left) and anal (right) fin ray counts of 0-group turbot collected on beaches along the west coast of Ireland (2006 - 2009).

3.4. The influence of temperature on fin ray counts

Although not statistically analysed, there was a suggestion that mean sea temperatures representing the pelagic stage of turbot along the west coast of Ireland, may have influenced the temporal variability in fin ray counts observed in the present study. The significantly lower fin ray counts exhibited by turbot in the year 2006 also corresponded with lower sea temperatures ($\bar{x} = 10.6\text{ }^{\circ}\text{C}$) in comparison to 2007 ($\bar{x} = 11.6\text{ }^{\circ}\text{C}$) and 2008 ($\bar{x} = 11.6\text{ }^{\circ}\text{C}$).

4. Discussion

Fin ray count ranges for 0-group turbot and brill along the west coast of Ireland were slightly different to those previously reported in the literature. Nonetheless, they proved to be a reliable confirmatory method for distinguishing between turbot and brill collected along the west coast of Ireland in a given year (2009), subsequent to a preliminary separation. However, given the differences between the ranges observed in the present work and those in the literature, the use of additional confirmatory identification analyses such as genetics may be required. Recently, Haynes et al., (2008) have shown that fin ray counts may be used to distinguish juvenile flounder from plaice on Irish nursery grounds, with this method previously used by Nichols, (1971), to separate plaice from other species. In contrast, fin ray counts were deemed unreliable for differentiating between 0-group sand flounder (*Rhombosolea plebeia* (Richardson)) and yellow bellied flounder (*Rhombosolea leporina* Gunther) (Eldon & Smith, 1986) due to the existence of overlap in the fin ray count ranges. Although there was no evidence of fin ray overlap between turbot and brill in 2009, the possibility that overlap in the number of fin rays may arise in other years cannot be excluded given the scales of spatial and temporal variation observed in the present investigation.

Juvenile turbot collected from nursery grounds along the west coast exhibited significantly different fin ray counts between years but not between beaches. This finding suggests that turbot present on nursery grounds along the west coast most likely experienced similar environmental conditions in the pelagic stage in a given year. In contrast, fin ray counts of juvenile brill were found to differ significantly between beaches. Fish collected from Brandon exhibited significantly lower counts compared to those collected from Silverstrand, suggesting a difference in the origin of juveniles to these areas. O'Neill et al (in review) have shown significant variation in flounder fin ray counts between Irish and Welsh populations. The scales of variation reported in the latter study and herein show that fin ray count ranges reported from temporally or spatially limited data must be treated with caution when used as the sole identification tool for juvenile flatfish.

Although the data are limited, there is the suggestion that the mean number of dorsal and anal fin ray counts of turbot is positively influenced by mean sea temperatures during the pelagic stage. Temperature has previously been reported to influence the number of fin rays exhibited by juvenile flatfish, with significant positive correlations observed for both Japanese flounder (*Paralichthys olivaceus*) (Kinoshita et al., 2000) and summer flounder (Burke et al., 2000).

Differences in environmental factors have also been reported to result in variability of pectoral fin ray counts between herring (*Clupea harengus harengus* Linnaeus) stocks (Safford & Booke, 1992). Temporal variability in fin ray counts in the present study may therefore reflect inter-annual differences in the temperature experienced by turbot eggs and larvae in the pelagic stage.

The present study demonstrates that the use of fin ray counts as a method to distinguish between 0-group turbot and brill should be applied with caution given the variability observed, with additional confirmatory identification techniques such as genetics possibly required. A longer time series is needed to further elucidate the results revealed in the present study. The suggestion that there may be different or separate cohorts of brill spawned throughout the year needs further investigation using, perhaps, otolith morphology or genetics.

Chapter 4

Annual and Spatial Variation in the Abundance Length and Condition of Turbot (*Psetta maxima* L.) on Nursery Grounds on the West Coast of Ireland: 2000 – 2007.

Published in: *Journal of Sea Research*. 64 (4). 494-504.

Annual and Spatial Variation in the Abundance Length and Condition of Juvenile Turbot (*Psetta maxima* L.) on Nursery Grounds on the West Coast of Ireland: 2000 – 2007.

Paula S. Haynes, Roisin O' Callaghan, Deirdre Brophy, David McGrath, Stephen Comerford, and Paul Casburn.

Abstract

Turbot (*Psetta maxima* Linnaeus) is a high value commercially exploited marine flatfish which occurs in European waters, from the Northeast Atlantic to the Arctic Circle, the Baltic and Mediterranean Sea. In Ireland, turbot are the most valuable commercial non-quota species. Very little is known about their population dynamics in the wild, in particular during the sandy beach nursery phase of the life history. In 2000, a survey was established to assess flatfish species on nursery grounds on the west coast of Ireland. Eleven sandy beaches were assessed for 0-group turbot by beach seining, over an eight year period (2000 – 2007) during the months of August and September. The objective of the study was to estimate juvenile turbot abundance and size structure to determine if any spatial and annual trends existed. Large scale variability in the recruitment of fish to nursery grounds may be indicative of fluctuations in the adult stock. Turbot were found to recruit to five out of the eight investigated beaches consistently over the eight year period. Temporal and spatial variability in the relative abundance and length of turbot was discerned, with no apparent overall trend. However, certain nursery grounds were shown in most of the years examined to support higher abundances of turbot in comparison to other areas over the eight year period. Turbot abundances on nursery grounds were significantly correlated with mean spring sea temperatures during the pelagic stage. The condition of turbot did not significantly differ on an annual or spatial scale. Mean densities of 0+ turbot along the Irish coast were found to be similar and at times higher than other areas in Europe, ranging from 0.1 (\pm 0.3) individuals 1000 m⁻² to 18.5 (\pm 6.9) individuals 1000 m⁻². 0-group turbot total length ranged from 2.3 cm to 9.3 cm during the months sampled. Mean lengths on beaches ranged from 3.3 cm (\pm 0.6) to 6.0 cm (\pm 1). The observed spatial and temporal variability highlights the need for long-term studies when assessing juvenile flatfish populations. Results from

the present study have provided much needed baseline data on wild juvenile turbot populations which is severely lacking for this species both on an Irish and on a European scale.

1. Introduction

Turbot (*Psetta maxima* Linnaeus) is a commercially exploited marine flatfish which occurs in European waters, from the Northeast Atlantic to the Arctic Circle, the Baltic and Mediterranean Sea. Turbot catches in Europe yield on average, 7000 tonnes annually, and in Ireland, they are the most valuable commercial non-quota species, worth €10,599 per tonne in 2002. Landings in Ireland have increased from 184 tonnes in 2002, to 321 tonnes in 2004 (Anon, 2007). There is no specific turbot fishery in Ireland, and they are caught mainly as a by-catch in demersal fisheries in other areas such as the eastern Irish Sea, and also in the Celtic Sea off the southwest coast of Ireland (Anon, 2010b). They are also an important bycatch species in other areas in Europe such as the Kattegat fisheries where turbot populations have not been assessed, and no quotas have been set (Stankus, 2003). Despite their high commercial importance, very little is known about their population dynamics in the wild (Danancher and Garcia-Vazquez, 2006; Nissling et al., 2006). Draganik et al., (2005) predict the eventual collapse of the Baltic turbot stock, as a result of an intensive fishery with increasing demands for turbot in Europe. Decreases in wild catches, and genetic evidence suggest population reductions for European turbot (Danancher and Garcia-Vazquez, 2006), and there have also been considerable reductions of turbot catches in Lithuania (Stankus, 2003).

As adults, turbot inhabit sandy or rocky bottoms, from the sublittoral down to 70 – 80 m (Nielsen et al., 1986). Turbot are a highly fecund fish, with females producing between 8 and 10 million (Draganik et al., 2005), and even up to 13 million eggs (Kalinina, 1960). In the North Sea, adults migrate towards shallow coastal areas to spawn between April and August (Molander, 1964; Jones, 1974; Nielsen, 1986). It has been reported that turbot spawn over a broad area in the Kattegat, at depths of between 10 and 40 m (Støttrup et al., 2002). In the Baltic Sea, spawning takes place from late May to July also in coastal waters, at depths of between 3 and 40 m (Nissling et al., 2006). In Ireland, it is not known when turbot spawn, or where the turbot spawning grounds are located. Turbot settle from the plankton onto shallow sandy beach habitats and are reported to have very specific and more restricted nursery grounds, such as highly exposed areas, where they settle in more shallow

waters (Riley et al., 1981; Gibson, 1994), in comparison to other flatfish species. This may be one reason for their low occurrence on nursery grounds (Gibson, 1994; Nissling et al., 2006), despite their high fecundity and lack of predators (Draganik et al., 2005). Once metamorphosis has occurred at around 2.5 cm (Jones, 1973) juvenile turbot can remain in a nursery area for up to three years before migrating to deeper waters (Jones, 1973; Rae, 1957).

Although low in comparison to other teleost species, flatfish can exhibit interannual variation in recruitment, with variability in many species attributed to the different processes acting on the early life stages (Leggett and Frank, 1997; Burke et al., 1998). Nursery grounds are more often than not shallow coastal habitats (Sogard et al., 2001) such as sandy beaches, where growth is optimised (Gibson, 1994). Recruitment for some flatfish populations has been found to be related to the availability of a suitable nursery area (Gibson, 1994), with the abundance of flatfish larvae reaching these nursery areas determining year class strength (Nissling et al., 2006). However, interannual variation in larval abundance is thought to be dampened by density-dependent processes operating during the juvenile phase (Nash and Geffen, 2000). In addition, hydrodynamic processes transporting the larvae between the spawning and nursery grounds will affect the growth and survival of juveniles on nurseries (Dou et al., 2003). In particular, the transport of larvae to nursery grounds and subsequent year class strength has been related to wind conditions for plaice (Nielsen et al., 1998) and turbot (Riley et al., 1981). Assessing nursery areas is extremely important as they will ultimately supply the recruits to the adult stocks (Støttrup et al., 2002). Many nursery ground studies aim to define good quality habitat for juvenile flatfish (Gilliers et al., 2004; Amara et al., 2007; Glass et al., 2008), with densities of juvenile plaice indirectly related to the quality of a nursery area (Wennhage et al., 2007). Determining the growth and condition of flatfish in a particular nursery, and the effects of environmental or anthropogenic factors on individuals can also help to indirectly determine habitat quality (Gilliers et al., 2004). Condition in turn can also affect recruitment, with nutritional condition of larvae and juvenile's one of the key factors in determining their survival (Tanaka et al., 1989). However, it is ultimately the actual number of juveniles recruiting from a particular nursery ground to the adult stock, which will define the quality of a particular location (Beck et al., 2001). The same authors also put forward that as this is difficult to determine, potentially high quality nursery grounds should be protected, due to their vulnerability to anthropogenic impacts, until such a time that their habitat quality can be confirmed.

Although the assessment of sandy beach nursery areas on a continuous basis can provide crucial information in determining the state of flatfish stocks, long-term studies on early life history stages of flatfish species are rare (Van der Veer et al., 1994; Sogard et al., 2001), with few studies (Rijnsdorp and Van Leeuwen, 1996; Sogard et al., 2001) assessing temporal trends over a long time period. Long-term data are needed on the local processes operating within a nursery area when assessing recruitment variability in flatfish populations. A juvenile flatfish survey was established by Taighde Mara Teoranta in nursery areas around the Dingle peninsula on the south-west coast of Ireland in 2000 to assess and monitor the juvenile stages of commercially important flatfish populations on an annual basis. The survey was then extended to the west coast in 2002. The aims of the present study were to analyse an eight year historical data set collected on turbot, to identify key turbot nursery areas, and determine any spatial and temporal variability in abundance, growth, and condition on nursery grounds over several spatial scales. Such information provides baseline data which are severely lacking in Ireland and Europe for this species.

2. Materials and Methods

2.1. Study areas

A combination of exposed and sheltered sandy beaches (Table 1) were assessed from two regions; the west and south-west coasts of Ireland, from 2000 – 2007 (Figure 1). Five beaches were sampled in the southwest of the country in Co. Kerry. In the west, the survey sampled four beaches in Galway Bay and two beaches on the Clare coast. The flatfish survey commenced in the southwest in 2000 and was extended to the west in 2002. At the beginning of the survey, beaches in the west and southwest were assessed in both May and September. However due to the very low numbers of juvenile flatfish present on the beach, sampling in May was discontinued. Beaches yielding very low numbers of juvenile flatfish were also omitted from the survey after the first few years (Table 2).

Table 1: Name, location, and description of the beaches assessed for turbot on the southwest and west coast of Ireland during the juvenile flatfish survey (2000 – 2007).

<i>Beach</i>	<i>latitude/longitude</i>	<i>Description</i>	<i>Length (km)</i>
Inch	52° 08.3' N 09° 58.8' W	Exposed shore	7
Smerwick	52° 10.9' N 10° 24.8' W	Sheltered bay	3
Ventry	52° 07.0' N 10° 22.3' W	Sheltered bay	5
Brandon	52° 14.1' N 10° 06.8' W	Exposed shore	11
Dingle Harbour	52° 08.4' N 10° 16.8' W	Sheltered bay	0.5
Lahinch	52° 08.3' N 10° 16.8' W	Exposed shore	3.5
Fanore	53° 07.2' N 09° 07.6' W	Exposed shore	1.5
Silverstrand	53° 14.9' N 09° 07.6' W	Sheltered shore	5
Ballyloughaun	53° 16.2' N 09° 01.1' W	Sheltered shore with freshwater influence	0.5
Gurteen	53° 22.6' N 09° 57.6' W	Semi closed shore	5
Dogsbay	53° 22.7' N 09° 57.8' W	Semi closed shore	2



Figure 1. Beaches assessed for 0+ turbot on the west and southwest coast of Ireland (2000 – 2007).

2.2 Fish collection

Juvenile flatfish were collected from nursery areas on the west and southwest coasts between 2000 and 2007 (see Table 2 and 3). In addition to turbot, information based on other juvenile flatfish species collected during the survey such as plaice, flounder, brill, and dab have been published (Allen 2008; Haynes et al., 2008), or are currently under investigation. When attempting to determine patterns of fish abundance and distribution, timing of sampling in terms of tidal, lunar, and day/night effects can have a significant influence (Nash et al., 1994b; Gibson et al., 1996). In order to reduce variability, and to avoid the confounding effects of differences in the timing of sampling, fish were collected on all beaches over the eight year period on a spring tide during daylight hours. Sampling on a beach was carried out in a single day, between two hours prior to or two hours after the time of low tide. There was a maximum of four days between the first and last beach assessed in a given

region (see Table 2 and 3). On the west coast a period of a month elapsed between sampling in 2005, 2003 and 2007 (Table 2 and 3).

Fish were captured using a beach seine, 20 m long, and 2 m deep, with a 13 x 13 mm mesh size. The swept area of the beach seine was calculated at approximately 1380 m², allowing for the calculation of fish densities. There were two 150 m ropes attached to the net for hauling purposes. A weighted footrope and a floated head rope were also attached to the seine net. Although a beach seine is size and species specific as regards its catch efficiency (Gibson et al., 1996), it has been used to adequately assess spatial and temporal variability in flatfish abundance and composition (Gibson et al., 1993). In addition, a beach seine was chosen because of its suitability for use in shallow waters (Brown and McLachlan, 1990), and because juvenile turbot have been previously captured in depths of less than 4 m by Jones (1973) and in less than 2 m by Riley *et al.* (1981). A diver swimming alongside the beach seine in certain years, did not observe the net to life up, or detect any fish escaping.

An inflatable boat was used to shoot one of the seines ropes perpendicular to the shore. The net was then deployed from the boat into the water, parallel to the shore. The boat then travelled back towards the shore with the second 150 m rope. The net was hauled onto the beach with even pressure on both ropes. In the south-west, the net was hauled by quad bikes in all years, except in 2000. This allowed the attachment of an extra tickler chain to the net to increase the catch efficiency of juvenile flatfish (Sogard et al, 2001). In the west, the hauling of the net was carried out by hand due to the small size of the beaches, without the addition of the extra tickler chain. This resulted in different sampling procedures between the south-west and west coasts. In addition, there was a time difference of a number of weeks between sampling in the west and southwest (Table 2 and 3). Therefore the two regions were treated separately in subsequent analyses.

Depending on the size of the beach, a minimum of two and a maximum of ten hauls per beach were carried out in each year over the eight year period. From 2000 to 2002, sampling areas on the beach were chosen to ensure the absence of weed or rock. From 2003 onwards, random number tables were used to choose the area, which was paced out on the beach. All species caught in the beach seine were identified on the shore, and frozen in the laboratory within a number of hours of being captured for further analyses.

Table 2: Information and results of 0+ turbot caught during the juvenile flatfish survey at beaches on the south-west coast of Ireland (2000 – 2007).

<i>Beach</i>	<i>Date of survey per year</i>	<i>Number of hauls per beach</i>	<i>Total number of turbot caught per beach</i>	<i>Mean density ± SD per 1000m²</i>	<i>Mean lengths (cm) ± SD</i>	<i>Mean condition K</i>
Inch	05-09-00	2	13	5.1± 3.1	4.4± 1.1	-
	04-09-01	4	54	13.0± 5.7	4.8± 1.2	-
	09-09-02	4	75	18.5± 6.9	4.1± 0.8	-
	09-09-03	6	21	2.0± 1.9	4.0± 1.0	-
	15-09-04	6	44	5.8± 4.9	4.3± 0.9	-
	20-09-05	6	70	8.4± 6.3	4.1± 0.7	- 0.02
	11-09-06	6	62	7.5± 2.5	4.6± 1.5	0.02
	11-09-07	10	20	1.8± 1.7	5.8± 1.4	0.03
Smerwick	08-09-00	3	15	4.8± 2.7	5.5± 0.9	-
	06-09-01	4	15	2.6± 2.7	5.1± 0.8	-
	11-09-02	5	21	4.2± 2.3	4.0± 0.8	-
	11-09-03	5	1	0.1± 0.3	3.3± 0.6	-
	14-09-04	3	7	1.7± 1.8	4.2± 1.1	-
	19-09-05	6	19	2.3± 1.1	4.7± 1.1	- 0.01
	13-09-06	6	13	1.6± 0.8	4.4± 0.8	0.01
	12-09-07	5	14	2.5± 1.7	5.8± 1.4	- 0.02
Ventry	09-09-00	4	0	-	-	-
	09-09-01	4	1	0.2± 0.4	7.1± 0	-
	08-09-02	3	1	0.2± 0.4	4.0± 0	-
	13-09-03	4	6	1.1± 0.4	6.2± 4.3	-
	22-09-04	4	6	1.1± 0.4	4.7± 2.0	-
	14-09-05	4	0	-	-	-
	14-09-06	4	0	-	-	-
	10-09-07	4	0	-	-	-
Brandon	07-09-00	4	17	3.1± 2.3	5.1± 1.2	-
	05-09-01	4	11	2.4± 2.0	5.8± 0.8	-
	10-09-02	6	43	6.5± 4.4	4.4± 1.2	-
	10-09-03	6	2	0.3± 0.4	6.0± 1.0	-
	16-09-04	3	5	0.9± 1.1	4.6± 0.7	-
	21-09-05	6	4	0.5± 0.9	5.6± 0.7	-
	12-09-06	7	19	0.5± 0.9	4.3± 1.5	-
	13-09-07	4	8	2.1± 1.1 0.7± 0.6	5.8± 1.4	-
Dingle	08-09-00	1	0	-	-	-
Harbour	04-09-01	1	0	-	-	-

Table 3: Information and results of 0+ turbot caught during the juvenile flatfish survey at beaches on the west coast of Ireland (2003 – 2007).

<i>Beach</i>	<i>Date of survey per year</i>	<i>Number of hauls per beach</i>	<i>Total number of turbot caught per beach</i>	<i>Mean density ± SD per 1000m²</i>	<i>Mean lengths (cm) ± SD</i>	<i>Mean condition K</i>
Lahinch	24-09-02	3	2	0.7 ± 0.6	5.0 ± 0	-
	23-09-03	4	12	2.2 ± 2.9	8.8 ± 1.0	-0.01
	22-08-05	3	37	8.9 ± 9.8	3.9 ± 0.7	0.01
	07-09-06	5	44	6.4 ± 7.5	5.4 ± 0.9	-0.01
	27-09-07	4	34	3.6 ± 0.6	5.2 ± 1.3	0.02
Fanore	24-09-02	2	12	4.3 ± 1.0	6.8 ± 3.4	-
Silverstrand	26-09-02	2	0	-	-	-
	26-09-03	2	12	4.3 ± 1.0	4.5 ± 1.1	0.00
	24-08-05	2	35	12.7 ± 14.9	3.8 ± 1.0	-0.01
	05-09-06	2	27	10.1 ± 2.0	4.5 ± 0.8	-0.01
	28-09-07	2	22	10.0 ± 7.7	5.2 ± 1.5	0.01
Dogsbay	25-09-02	2	4	1.4 ± 0	6.6 ± 4.3	-
	24-09-03	2	0	-	-	-
	23-08-05	2	4	2.5 ± 0.5	4.5 ± 0.7	-
	06-09-06	3	7	-	-	-
	26-09-07	2	0	-	-	-
Gurteen	25-09-02	2	0	0.7 ± 0	5.6 ± 0.1	-
	24-09-03	2	0	0.4 ± 0.5	8.1 ± 3.8	-
	23-08-05	2	1	-	-	-
	06-09-06	3	1	-	-	-
Ballyloughan	26-09-07	2	5	-	-	-
	26-09-02	2	0	-	-	-
	26-09-03	2	3	1.1 ± 1.5	4.0 ± 0.3	-
	24-08-05	2	16	5.8 ± 2.9	4.0 ± 1.1	-
	05-09-06	2	10	3.6 ± 0	5.2 ± 1.3	-
	28-09-07	2	0	-	-	-

2.3. Laboratory Analysis

Frozen fish were removed from the freezer and allowed to thaw overnight. 0+ turbot lack the distinctive bony tubercles that are characteristic of the species, and are almost identical to juvenile brill (*Scophthalmus rhombus* Linnaeus). The number of fin rays for various flatfish are species specific, and described by Wheeler (1969). The dorsal, anal, and caudal fin rays were counted under a stereoscopic microscope and used in the identification of juvenile flatfish. The standard length (SL) from the tip of the mouth to the where the caudal fins begin, was measured to the nearest 0.1 cm. The weight of the turbot was measured to the nearest 0.1 g.

2.4. Temperature data

Temperature is known to exert a significant influence on the growth and development of fish (Yamashita et al., 2001). In the present study, the mean sea surface temperature data of April May June, corresponding to the pelagic stage, and the mean sea surface temperature data of July August September, were used to investigate if interannual variation in the relative abundance and size of juvenile turbot had an environmental basis. Temperature data were provided by the Marine Institute from the weather buoys M1 (53.1266°N, 11.2000°W) off the west coast and M3 (51.2166°N, 10.5500°W) off the south-west coast of Ireland. These buoys are situated miles off the west coast of Ireland, and would be positioned in the pathway of currents transporting larvae from south to north along the Irish west coast (Mohn et al., 2002).

2.5. Fish condition and density dependence

Length-weight residuals were used to examine fish condition among years and sites. Residuals were calculated using regression log of length against log of weight. Where appropriate length-weight residual data were squared and log transformed to achieve equal variances (Underwood, 1997). Length-weight residuals are also useful when determining the condition of fish from different size classes (Blackwell et al., 2000). Residuals of the length-weight relationship have previously been utilized to calculate condition, and hence indirectly provide information on the habitat quality of 0-group flatfish (Gilliers et al., 2006). A similar condition index using length and weight was used by Imsland et al., (1995) for reared turbot juveniles. A large negative mean residual value signifies that

fish are in poor condition, a large positive mean residual value is indicative of good condition and a mean residual value close to zero signifies fish in average condition (Blackwell et al., 2000).

Due to intra-specific competition, high densities of juvenile fish on nursery grounds can lead to slower growth (Van der Veer and Witte, 1993) which in turn may affect the overall condition of a fish. Pearson's correlation analysis on the mean density and the mean condition of turbot was carried out.

2.6. Statistical Analysis

The number of turbot collected per beach was divided by the number of hauls carried out, and was used as an index of relative abundance. Although each haul was carried out in a similar manner, the possibility that the area covered by the beach seine for each haul was variable cannot be excluded. It was also assumed that the catchability of the beach seine was similar for each beach sampled. Mean turbot densities on each beach were calculated as numbers per 1000m⁻² for each year, for comparisons with turbot densities in other studies. Length weight data over the eight year period were not always available as a result of inconsistent recording (Table 2 and 3).

Statistical analysis was carried out on turbot abundance, length, and condition data from beaches on the west and south-west of the country using the statistical package MINITAB 15. Inconsistencies in the number of hauls taken and the number of fish caught on each beach in each year introduced imbalance into the data. The analysis of unbalanced data using ANOVA can be problematic as the tests for main effects and interactions are not independent of each other. Computational methods designed for unbalanced data overcome these issues by using a range of methods to calculate the sum of squares for each effect (Type I – III according to SAS terminology) (Shaw and Mitchell-Olds, 1995). This approach is preferable to imposing balance on the data by removing replicates which can greatly reduce the power of the analysis. The most widely used method is Type III sum of squares; the sum of squares for each effect is adjusted to account for the contribution from the other effects in the model. With severely imbalanced data, multicollinearity can reduce the power of a Type III analysis and real effects may not be detected due to Type II error. For this reason, some authors recommend the use of Type II sum of squares in favour of Type III (Langsrud, 2003). The Type II method is based on the assumption that interactions are negligible and has greater statistical power

than Type III. In this study all data were analysed using unbalanced Type III ANOVA's in Minitab, to test the null hypotheses that there was no difference in the relative abundance, length, and condition of turbot between beaches and years. Both year and beach were included as fixed factors. When main effects and interactions were deemed non-significant, a Type II sum of squares analysis was conducted using the car package in R (Fox, 2008, R development core team, 2008) to verify this conclusion. All significant differences were explored using Tukey's post hoc procedures with correction for multiple comparisons as described by Underwood (1997). Prior to the analysis the data were tested for normality using the Anderson-Darling test. Homogeneity of variances was tested using Levene's test, and the data were log transformed where appropriate (Underwood, 1997).

3. Results

3.1. Spatial and temporal variability in turbot relative abundance

A total of 931 juvenile turbot were caught on the west and south-west coast of Ireland between 2000 and 2007, (Table 2 and 3). Mean densities (\pm SD) of juvenile turbot ranged from 0.1 (\pm 0.3) individuals 1000m⁻² to 18.5 (\pm 6.9) individuals 1000 m⁻².

For beaches on the south-west coast, eight years of turbot abundance data (2000 - 2007) were available for the beaches Inch, Brandon, Smerwick and Ventry. Only two years of abundance data were available for Dingle, so this beach was excluded from further analysis. Log transformed turbot relative abundances (n = 579) differed significantly between beaches (df = 3; F = 51.7; p < 0.001) and between years (df = 7; F = 6.11; p < 0.001). A significant interaction between beach and year factors occurred (df = 21; F = 2.39; p = 0.004) (Type III sum of squares). Due to the interaction, interannual variation was investigated for each beach separately and spatial variation was investigated within each year using Tukeys's multiple comparison tests. Spatial variability in turbot relative abundance was inconsistent between years, however some general trends could be discerned; Turbot relative abundance on Inch was significantly equal to or greater than all other beaches in each year, while relative abundance on Ventry was significantly lower than or equal to all other beaches in all years (Table 2; Figure 2). Temporal variability was also inconsistent between beaches, with relative abundances for all beaches equal in the majority of years (Figure 2).

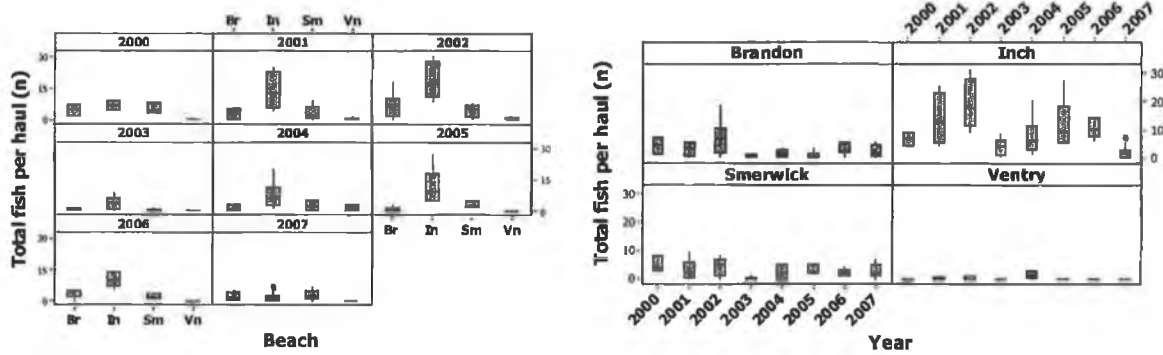


Figure 2: Plots showing patterns of spatial (left) and temporal (right) variation in mean juvenile turbot abundance at nursery areas on the south-west of Ireland during the period 2000-2007. Bn = Brandon, In = Inch, Sm = Smerwick, Vn = Ventry.

On the west coast four years of abundance data (2003, 2005-2007) were available for the beaches Lahinch, Silverstrand, Ballyloughan, Gurteen and Dogsbay. Only one year of data was available from Fanore, which was therefore excluded from further analysis. Turbot relative abundance was significantly different between beaches ($df = 4$; $F = 4.51$; $p = 0.006$), but not between years ($df = 3$; $F = 1.52$, $p = 0.23$). There was no significant interaction between beach and year factors and this was removed from the model ($df = 12$, $F = 0.27$, $p = 0.99$). Tukey's post-hoc tests revealed that turbot relative abundance was higher on Silverstrand and Lahinch in comparison to Ballyloughan, Gurteen, and Dogs Bay ($p < 0.01$) (Figure 3).

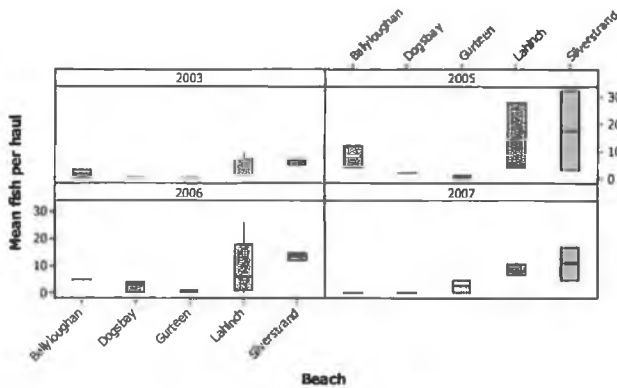


Figure 3: Plots showing patterns of temporal variation in mean juvenile turbot abundance at nursery areas on the west coast of Ireland (2003, 2005, and 2006).

3.2. Spatial and temporal variability in turbot length

Mean lengths (\pm SD) of turbot ranged from 3.3 (\pm 0.6) cm on Smerwick in 2003, to 6.0 (\pm 1) cm on Brandon in 2003 (Table 3 and Figure 4).

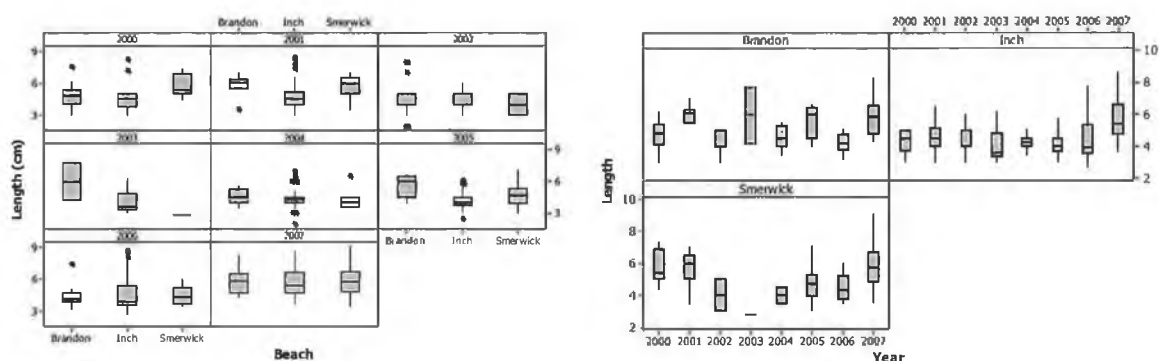


Figure 4: Plots showing patterns of spatial (left) and temporal (right) variation in mean juvenile turbot length (TL, cm) at nursery areas on the south-west of Ireland during the period 2000-2007.

The smallest juvenile turbot caught in the beach seining survey was 2.3 cm on Silverstrand in 2005. The largest juvenile turbot was 9.3 cm from Silverstrand in 2007.

On the south-west coast, spatial and temporal variation in turbot length was investigated using data from the beaches where turbot consistently occurred: Inch, Brandon, and Smerwick for all years (2000 – 2007). Turbot lengths ($n = 571$) differed significantly between beaches ($df = 2$; $F = 8.37$; $p < 0.001$) and between years ($df = 7$; $F = 12.20$; $p < 0.001$). There was a significant interaction between beach and year factors ($df = 14$; $F = 2.04$; $p = 0.014$). In terms of spatial variability, turbot were significantly smaller on Inch in certain years, in comparison to the other two beaches (Figure 4). On a temporal scale turbot lengths in 2007 were greater than or equal to all other years on the three nursery areas in the southwest (Figure 4).

On the west coast sufficient numbers of turbot occurred on Lahinch, Silverstrand, and Ballyloughan for three years (2003, 2005, and 2006) only. Mean turbot length did not differ significantly between beaches ($df = 2$; $F = 2.71$; $p = 0.07$). Lengths were found to differ significantly between years ($df = 2$; $f = 24.3$; $p < 0.001$). There was no significant interaction between beach and year factors, so this term

was removed from the model ($df = 4$; $f = 1.75$; $p = 0.14$). Further analysis, using multiple comparisons tests (Tukeys's) indicated that turbot collected in 2006 were larger than turbot collected in 2005 and 2003. Turbot in 2005 were also smaller than turbot collected in 2003 and 2006 (Figure 5).

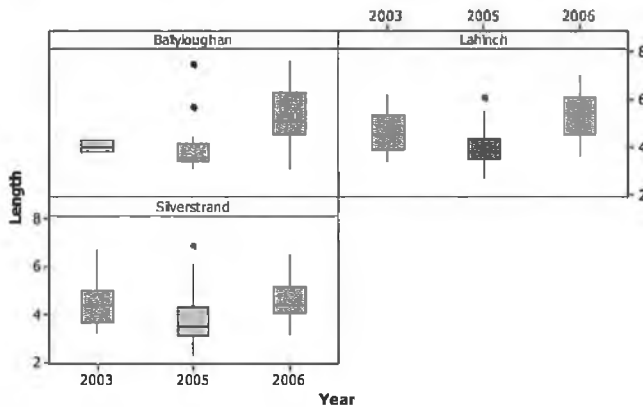


Figure 5. Plots showing patterns of temporal variation in juvenile turbot lengths at nursery areas on the west of Ireland during the period 2003, 2005, and 2006.

3.3. Spatial and temporal variability in turbot condition

The mean residual condition index of turbot on nursery grounds ranged from -0.02 to 0.03 on the south-west coast, and from -0.01 to 0.02 on the west coast.

On the south-west coast turbot condition data were available on the southwest coast Inch and Smerwick for three years (2005 – 2007). The condition of turbot in the southwest ($n = 200$) was not significantly different between beaches ($df = 1$; $F = 0.00$; $p = 0.97$), or years ($df = 2$; $F = 0.87$; $p = 0.42$). There was no significant interaction between beach and year factors ($df = 2$; $F = 1.39$; $p = 0.25$).

On the west coast turbot condition data were available on Lahinch and Silverstrand for four years (2003, 2005, 2006, 2007). The condition of turbot in the west ($n = 195$) was not significantly different between beaches ($df = 1$; $F = 0.02$; $p = 0.89$), or years ($df = 3$; $F = 0.31$; $p = 0.82$). There was no significant interaction between beach and year factors ($df = 3$; $F = 2.28$; $p = 0.08$).

3.4. Density dependence of turbot

There was no significant correlation between the mean condition and the mean density of turbot over three years (2005, 2006, and 2007) on the south-west coast (Inch, and Smerwick) ($R^2 = 0.336$, $p = 0.606$), and over four years (2003, 2005 – 2007) on the west (Lahinch and Silverstrand) ($R^2 = 0.065$, $p = 0.746$) coast of Ireland.

3.5. Temperature effects on turbot abundance and length

Turbot abundances on the south-west coast (2001 – 2007) were found to be negatively correlated with the spring mean sea temperature (April, May, June) (AMJ), corresponding to the larval phase ($R^2 = 0.608$, $p = 0.039$) (Figure 6). However no such correlation was observed between turbot abundance and the mean summer temperatures (July, August, September) corresponding to the juvenile benthic stage ($R^2 = 0.6154$, $p = 0.085$). Turbot mean length (2001 – 2007) was not significantly correlated with mean sea temperature (July, August, September) on southwest ($R^2 = 0.011$, $p = 0.678$), or west ($R^2 = 0.268$, $p = 0.483$) nursery grounds.

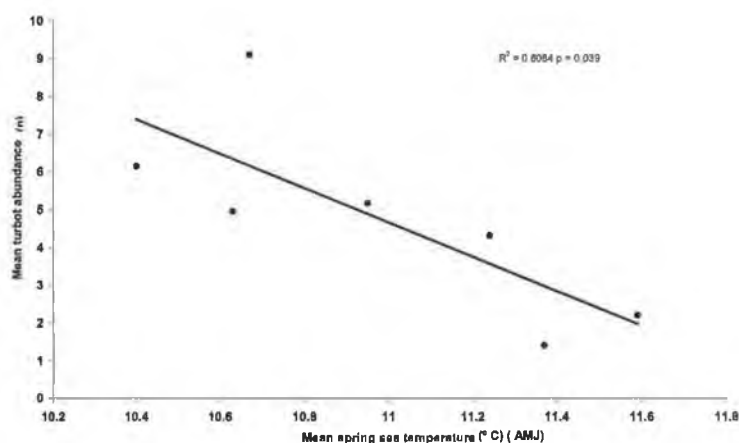


Figure 6: Correlation between mean turbot abundance per year on south-west nursery grounds, and mean spring sea temperature (2002 – 2007).

4. Discussion

4.1. Turbot abundance and size over spatial and temporal scales

Turbot larvae recruited to sandy beach nursery areas in the present study in each of the eight years of the investigation. Turbot consistently recruited to three beaches in the south-west in every year over a nine year period, and to two beaches in the west in every year over a four year period. Although turbot have been reported in the literature to favour exposed areas (Jones, 1973; Stankus, 2003, Nissling et al., 2007; Paulsen and Støttrup, 2004), the present study found high abundances of turbot in a sheltered area (Silverstrand), with an average density of 9.7 individuals 1000 m⁻² over a four year period. Juvenile turbot have also been found in sheltered areas along the Danish coast (Sparrevohn and Støttrup, 2008a). Densities of turbot on Irish nursery areas ranged from 0.1 ± (0.3) on Smerwick in 2003 to 18.5 ± (6.9) on Inch in 2002, and are similar to densities in other areas around Europe. Using a beam trawl, turbot densities ranging from 0 to 23 per 1000 m⁻² were recorded off the coast of Lithuania over a three year period (Stankus, 2003), with 4.9 individuals per 1000 m⁻² recorded off the coast of Wales (Jones, 1973). However, the above studies may not be directly comparable, given the differences in the timing of these studies, in addition to variability in the selectivity of the different types utilised.

On southwest nursery grounds, turbot relative abundances were found to vary both spatially and temporally over the eight year period (2000 – 2007), whereas on the west coast, turbot abundance varied only on a spatial scale in 2003 and 2005 – 2007. Furthermore, high abundances of turbot have also been found in certain years on an estuarine nursery ground (Ballyloughan) with average densities of 3.5 individuals 1000m⁻² over a three year period. Salinities here are highly variable, ranging from 10 to 26 (Allard, Pers. Comm). Reared turbot have been reported to be euryhaline, with good growth, which was dependent on temperature, was observed at 15 ‰ and 25 ‰ (Imsland et al., 2001). Although there are no reports in the literature on the salinity preference of turbot when settling in the wild, their occurrence on this estuarine nursery ground demonstrates that optimum salinities for growth may be similar to that of reared turbot.

In the present study, the geographical position of nursery areas might be an important feature in determining the abundance of turbot that occupy them. Although there were no apparent physical

differences between nursery areas in the southwest, or between nursery areas in the west, near-shore currents may be responsible for the delivery of metamorphosing larvae to beaches, as has been found for turbot along the Kattegat coast (Sparrevohn and Støttrup, 2008b). Changes in transportation patterns of currents are also thought to play a crucial role in the number of settling turbot larvae in the Baltic Sea (Nissling et al., 2006). Hence, hydrodynamic processes along the west coast of Ireland may also play an important role in the abundances of turbot larvae delivered to nursery grounds. Small scale variation in flatfish abundances on nursery grounds has also been attributed to a combination of environmental factors, which also influences the distribution of most fish species (Gibson, 1994). In the present study mean spring sea temperature was found to be significantly negatively correlated with turbot abundance on nursery grounds in the south-west coast over the eight year study. Temperature has a profound effect on the spawning, recruitment, and distribution of fish (Marshall and Elliott, 1998), with colder temperatures during the egg and larval stage resulting in a reduction in the number of larval predators (Van der Veer et al., 2000), or a decrease in the effects of pathogenic bacteria on eggs (Fonds 1995). This observation suggests that the abundance of juveniles recruiting to nursery areas on the west coast of Ireland is generated during the egg and larval stage, with temporal variability in currents and temperature resulting in variability in fish abundance.

While spatial variation was not entirely consistent across years, some beaches showed a general tendency for low (Gurteen, Dogsbay and Ventry) or high (Inch) juvenile turbot abundance. In contrast, no areas along the Kattegat were found to consistently support higher abundances of juvenile turbot over various periods during 1950 – 2000 (Sparrevohn and Støttrup, 2008b). Turbot distribution in the present study may also reflect underlying differences in the habitat quality of these nursery areas. It may be that in years when sufficiently high numbers of larvae are delivered to nursery areas, those with high quality habitat can support higher densities than those with poorer quality habitat. There is a tendency, although not consistent, for smaller fish on Inch in certain years. If fish on Inch were younger due to later hatching and settlement, then this may explain the tendency for higher abundances on this beach, as fish would not have been exposed to mortality for as long as the fish on other beaches. However, higher abundances were also observed on Inch in years when no variation in length occurred and mean density was not correlated with mean condition. The inter-annual variability in this spatial signal highlights that studies on nursery ground dynamics of fish populations should take place over a long period of time, so as to discern more conclusive trends. As no information on the biotic and abiotic characteristics of the eleven beaches of this study is currently

available, the underlying cause of the observed spatial trends in abundance can only be speculated. However, studies are currently being carried out to investigate the effects of predation, prey availability, and interspecific competition on turbot for nursery areas along the west coast.

Predation, which has found to be the main cause of mortality in juvenile turbot on the west coast of Spain (Iglesias et al., 2003), will also significantly influence the distribution and abundance of flatfish on nursery areas (Amara and Paul, 2003). Lockwood (1980) suggested that predation may be greater on more open coasts compared to shallow bays, as there are a greater range of size and species of predators. However turbot which are larger at settlement compared to other flatfish species, may attain a size refuge from predators such as *Crangon* in a shorter time period compared to flounder, which has a size refuge of 2.4 cm (Taylor, 2005), and plaice which has a size refuge of 3 cm, (Van der Veer and Bergman, 1987; Burrows et al., 2001). Interspecific competition and prey availability on nursery grounds will also affect species distribution. Turbot are fast swimming selective predators compared to other flatfish such as plaice which prey on a wider range of organisms (De Groot, 1971). Dominant prey items found in the stomach of juvenile turbot consisted of mysids, *Crangon*, and fish, whereas the main prey items found in the stomach of juvenile plaice consisted of polychaetes, postlarval *Crangon*, and bivalves (Beyst et al., 1999). The same author also observed clear niche segregation between plaice and turbot occupying a nursery area. On nursery grounds in the Baltic Sea, the diet of turbot and flounder has also been found to differ (Florin and Lavados, 2009). Temporal partitioning of turbot and plaice has been observed on the west coast of Ireland. Turbot settle later in the year than plaice, and have also been found to be the only flatfish present on nursery grounds in the months of October and November (Pers. obs). This observation, coupled with difference in prey suggests that interspecific competition may not occur between plaice, which is the dominant flatfish on the west coast of Ireland and turbot.

The smallest turbot caught in the present study was on Silverstrand in Co. Galway in 2005 at 2.3 cm, while the largest turbot, 9.3 cm, was also caught on Silverstrand in 2007. Jones (1973) found the smallest turbot caught off the coast of Wales to be 2.7 cm in length. In North-West Spain Iglesias et al, (2003), found turbot to settle at between 2.5 and 3.5 cm in the shallowest area of an exposed beach. On the Irish west coast, significant differences were observed in the length of turbot on an annual and spatial scale on the southwest coast, but no consistent trend was apparent. On the west coast there were no significant differences in the length of turbot between beaches, only between

years. Interannual length differences were more consistent in the west compared to the southwest, and in certain years (e.g. 2006) larger fish were found across all beaches, whereas in other years (2005), fish were smaller. As no age data are available for these fish, it is not possible to determine if these size differences reflect variation in juvenile growth rates, timing of hatching or settlement, or timing of sampling (four week difference between 2005 and 2003). Length variability may also be attributed to the selectivity of the beach seine. However, the sampling conditions in the present work remained consistent throughout the eight year time series, with the detection of consistent signals, such as both larger and smaller turbot occurring on certain beaches in the majority of years investigated.

Temperature, dissolved oxygen, salinity, and food quality and quantity have been found to be the main factors affecting the growth of juvenile flatfish (Gibson, 1994; Yamashita et al., 2001), and both hatching and growth would be influenced by interannual variability in environmental conditions, albeit at different stages in the early life history. Temperature was shown to affect the growth of plaice in the North Sea (Zijlstra et al., 1982), while variability in the growth rates of reared turbot have been reported where food is scarce (Carter et al., 1996). However, no correlation was observed in the present study between the mean sea summer temperatures and the mean length of turbot on south-west or west nursery grounds. Additional biotic and abiotic factors may be influencing turbot growth, and fine-scale local beach data combined with age estimates are currently being analysed in separate studies, which may help to elucidate spatial and temporal trends in the size of juvenile turbot. The contrasting results for the west and the southwest show that the factors influencing variation in length at turbot nursery grounds can operate over both large (as in the south-west) and small (as in the west) scales.

Juvenile turbot condition on nursery grounds was not significantly different in the south-west or west. This suggests that the two regions might provide similar nursery ground conditions in terms of habitat quality for turbot, such as temperature, salinity, food availability, and predation. This result is important for the protection of important nursery areas, particularly for rare turbot beaches which might be all of equal habitat quality, and should therefore all be conserved. However, the use of several condition indices is recommended, as no one measure provides an accurate depiction of habitat quality (Gilliers et al., 2004). Therefore the biochemical index RNA: DNA or growth index of otolith increment analysis may also be needed to detect any temporal or spatial differences in

condition in the present study. In general, fish condition is used to estimate habitat quality on a spatial scale only (Wang et al., 2001; Gilliers et al., 2004; Gilliers et al., 2006; Amara et al., 2007; Vinagre et al., 2008), and temporal variability of frequently changing habitats (Gibson, et al., 1996) is not considered. Even though no significant differences in turbot condition were detected, turbot condition ranged from slightly below average condition (0), to just above average condition. The present study has also examined variability on both a temporal and spatial scale, and may therefore provide a more conclusive description of nursery ground habitat quality.

Numerous studies have reported density dependence in flatfish (Van der Veer, 1986; Nash et al., 1994a; Modin and Pihl, 1994; Lorenzen and Enberg, 2002). However in the present study no evidence of density dependence was discerned, as turbot density was not correlated with fish condition. For plaice, density dependence is less likely to have a significant impact on the population unless there are very high densities of fish present (Modin and Pihl, 1994). As turbot densities in the present study are much lower in comparison to other flatfish species, it may be that densities are simply never high enough to produce density-dependent growth or mortality. Density dependence was not observed for plaice on the west coast of Ireland (Allen et al., 2008), which occur in much higher numbers in comparison to turbot. It may be that predation or competition for food does not appear to affect the growth of flatfish on the west coast of Ireland. However, given the large variety of additional fish species/juvenile flatfish competitors also captured during the surveys, the possibility of competition for the available resources on west of Ireland nursery grounds cannot be excluded. While the overall carrying capacity of the different nursery grounds is expected to vary, particularly given the size differences, studies investigating the productivity of west of Ireland nursery grounds have in general revealed a high abundance of available food resources (De Raedemaeker et al., 2010; 2011; Haynes et al., 2011). Nonetheless, in the absence of intra-specific competition, differences detected in the growth and condition of west of Ireland juvenile flatfish species in these studies may be attributed to inter-specific competition with non-flatfish species on the nursery.

Although no apparent large scale spatial trends have been identified along the coast of Ireland, important turbot nursery areas along the coast of Ireland have been identified, with high turbot abundances occurring on both sheltered and exposed shores. Variation in abundance and length has been found to occur at the beach level, and to change on an annual basis suggesting that local small

scale processes may be influencing the recruitment of turbot on the southwest and west coasts. It is evident that more often than not, certain nursery areas along the Irish coast such as Inch beach produce higher abundances of turbot compared to other areas, suggesting that this might be a more important nursery ground. Local adaptations of species have evolved according to local hydrographic conditions (Nissling et al., 2006), and temperature in the pelagic phase appears to affect the number of turbot arriving on beaches on the south-west coast. As additional biotic factors come into effect at the beach level, their influence on juveniles may be more difficult to extrapolate at the nursery ground phase. However, current ongoing studies on the early life stages of flatfish on the Irish coast are currently investigating the effects of local factors and oceanographic processes operating in nursery areas. Identifying the factors that influence early life history stages is one of the keys to understanding recruitment and population dynamics of any species (Walsh, 1996), and as there is very little information available on wild turbot populations, assessing turbot nursery grounds may provide important information on the processes governing recruitment. Results from the present study have provided much needed baseline data on wild juvenile turbot populations which is severely lacking for this species both on an Irish and on a European scale. Such data may be utilised in future assessments attempting to understand the population dynamics of west of Ireland turbot populations.

Chapter 5

**Variability in the early life stages of juvenile plaice
(*Pleuronectes platessa*) on west of Ireland nursery
grounds; 2000 - 2007.**

Journal of the Marine Biological Association of the United Kingdom. In press

Variability in the early life stages of juvenile plaice (*Pleuronectes platessa*) on west of Ireland nursery grounds; 2000 - 2007.

Paula S. Haynes, Deirdre Brophy, David McGrath.

Abstract

Plaice (*Pleuronectes platessa* L.) are the most abundant juvenile flatfish present on west of Ireland nursery grounds. 0-group plaice were collected from eleven sandy beach nursery areas along the west coast of Ireland by beach seining (2000-2007). In the majority of years examined, certain beaches were found to support a higher abundance of juvenile plaice, or individuals that were larger in size and exhibited good condition, suggesting that differences in habitat quality exist between beaches. Monthly mean densities of plaice in ranged from 2.4 (\pm 2.4) to 100 (\pm 1.3) individuals 1000 m⁻². Mean lengths of plaice ranged between 6.0 (\pm 1.0) and 10.1 (\pm 0.5) cm. No evidence of density dependent growth was detected over the eight years of the study. The length and condition of juvenile plaice also differed between hauls, indicating the existence of microhabitat effects and emphasising the importance of selecting an appropriate spatial resolution to adequately assess an area. Similar to other locations in Europe, juvenile plaice abundances on nursery grounds were inversely related to mean spring sea water temperatures during the pelagic stage. Abundances of 0-group plaice were not related to the number of either 1 or 2-group individuals collected during bottom-trawl surveys off the Irish west coast, demonstrating the difficulties associated with developing a recruitment index for plaice.

1. Introduction

The European plaice, (*Pleuronectes platessa* Linnaeus), is a commercially important and widely distributed flatfish species. Plaice early life history has been extensively studied in many areas of the Northeast Atlantic. Adult plaice spawn offshore, with pelagic eggs hatching after approximately 1 to 2 weeks. Upon reaching a suitable sandy beach nursery habitat, larval plaice undergo metamorphosis and remain on nursery grounds for a number of years, before joining the adult population (Fox et al., 2009). The abundance and distribution of juvenile flatfish inhabiting nursery grounds is dependent on the initial number of larvae delivered to the area (Gibson, 1997). It is therefore during the pelagic life stage that recruitment, or the year class strength of plaice is determined, with factors such temperature and hydrodynamics known to have a profound effect on the survival of eggs and larvae (Fox et al., 2000; Van der Veer et al., 2009). However, the year class strength of plaice has also been shown to be established through density-dependent processes operating during the nursery ground stage, demonstrating that the factors influencing recruitment may not be the same for different stocks of the same species (Nash and Geffen, 2000).

Though nursery grounds are in general considered to be areas where good growth is promoted and survival is enhanced (Gibson, 1994), the quality of these habitats can vary substantially. Faster growing or larger individuals are more efficient at feeding and predator evasion; therefore, high quality habitats will contribute significantly more juveniles to the adult stock in comparison to sub-optimal nursery grounds (Power et al., 2006). The quantity or size of a nursery ground can also influence recruitment and larger habitats are known to give rise to a greater number of juvenile plaice for the adult population (Van der Veer et al., 2000). Exposure and habitat structure of the nursery influences larval supply and levels of predation after settlement, thus affecting juvenile plaice densities, while sediment structure is important in terms of prey availability (Pihl and Van der Veer, 1992). Given the increase in habitat degradation of coastal areas in recent times, identification and protection of high quality nursery grounds is essential, as a reduction in these areas will negatively affect flatfish recruitment (Zijlstra, 1972). Adequate assessment of a location should also be considered when attempting to identify important flatfish nursery habitats, given the small scale variation in growth and condition which can arise within a nursery (De Raedemaeker et al., 2010).

While a considerable number of studies have been carried out on the early life history of plaice in the North Sea, the Dutch Wadden Sea, and the Irish Sea, information for the west coast of Ireland

is lacking. Plaice are the most abundant juvenile flatfish species present on west of Ireland nursery grounds where they are known to settle between March and April (Allen et al., 2008). Recent evidence from an Irish national biological sampling survey series indicates that plaice spawn to the southwest of the country (Gerritsen, 2010) (Figure 1). There has been a reduction in the landings of plaice off the west coast of Ireland over the last three decades, with landings reaching an all time low in 2006 (Anon, 2010b). Moreover, ICES (International Council for the Exploration of the Sea) consider the information available for plaice stocks in areas VIIb and VIIc off the Irish west coast as insufficient for the evaluation of any stock trends (Anon, 2010b). Hence, for the sustainable management of the Irish west coast plaice population, it is essential that stocks from this area are assessed.

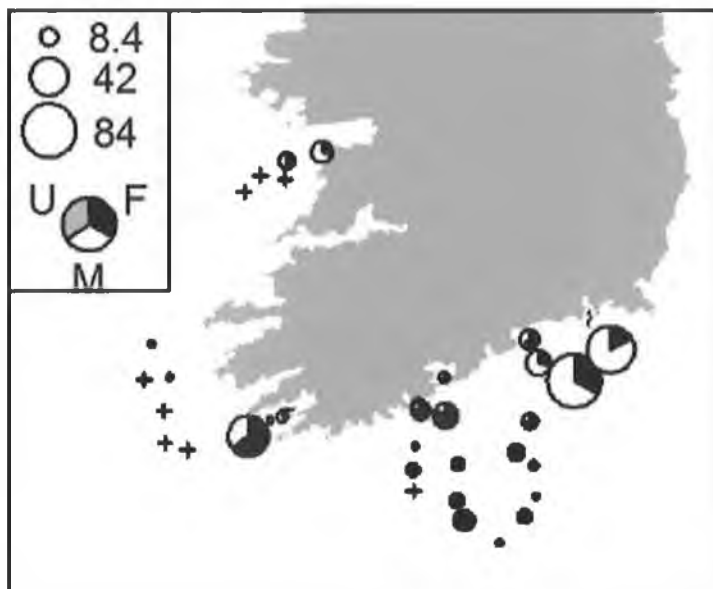


Figure 1: Distribution of three maturity classes of plaice around the Irish coast. Sex ratios are represented by pie charts for species of which the catch was sexed: the black area represents the proportion of females, white for males, unsexed samples are shown as grey. (Gerritsen, 2010).

Estimating the quantity of juveniles inhabiting a nursery ground can provide an indication as to the overall health of the adult population. A juvenile flatfish survey was established around the Dingle peninsula on the southwest coast of Ireland in 2000 to assess and monitor juvenile flatfish populations occupying sandy beaches on an annual basis and to identify any long-term temporal or

spatial trends in abundance, length, and condition. The survey was then extended to the west coast in 2002. The data collected from these surveys were used to: (1) investigate spatial and temporal trends in juvenile plaice abundance, length, and condition; (2) identify nursery grounds of high habitat quality, as indicated by high abundance and/or enhanced growth and condition); (3) determine if temperatures corresponding with the pelagic and juvenile life stage of plaice were related to plaice abundance or length; (4) determine if density-dependent growth operated on west of Ireland nursery grounds by comparing juvenile plaice densities and lengths; (5) establish if the abundance of 0-group of plaice can be used to reliably predict the abundance of 1 and 2-group plaice in bottom trawl surveys along the Irish west coast in subsequent years.

2. Materials and Methods

Study areas

A combination of both sheltered and exposed sandy beach nursery grounds, with varying levels of wave exposure and sediment types were assessed on the west coast of Ireland over an eight year period (Table 1).

Table 1: Name, location, and description of beaches assessed for juvenile plaice on the southwest and west coast of Ireland during the juvenile flatfish survey (2000 – 2007).

<i>Beach</i>	<i>Latitude/longitude</i>	<i>Description</i>	<i>Length (km)</i>
Inch	52° 08.3' N 09° 58.8' W	Exposed shore	7
Smerwick	52° 10.9' N 10° 24.8' W	Sheltered bay	3
Ventry	52° 07.0' N 10° 22.3' W	Sheltered bay	5
Brandon	52° 14.1' N 10° 06.8' W	Exposed shore	11
Dingle Harbour	52° 08.4' N 10° 16.8' W	Sheltered bay	0.5
Lahinch	52° 08.3' N 10° 16.8' W	Exposed shore	3.5
Fanore	53° 07.2' N 09° 07.6' W	Exposed shore	1.5
Silverstrand	53° 14.9' N 09° 07.6' W	Sheltered shore with freshwater influence	5
Ballyloughaun	53° 16.2' N 09° 01.1' W	Sheltered shore with freshwater influence	0.5
Gurteen	53° 22.6' N 09° 57.6' W	Semi closed shore	5
Dogsbay	53° 22.7' N 09° 57.8' W	Semi closed shore	2

The sample dates for each beach over the eight year period are provided in Table 2.

Table 2. Sample dates for beaches assessed along the west and southwest coast of Ireland (2000 – 2007).

<i>Southwest beaches</i>	<i>Date of survey per year</i>	<i>West beaches</i>	<i>Date of survey per year</i>
Inch	05-09-00	Lahinch	24-09-02
	04-09-01		23-09-03
	09-09-02		22-08-05
	09-09-03		07-09-06
	15-09-04		27-09-07
	20-09-05		
	11-09-06		26-09-02
	11-09-07	Silverstrand	26-09-03
Smerwick	08-09-00		24-08-05
	06-09-01		05-09-06
	11-09-02		28-09-07
	11-09-03	Dogs Bay	25-09-02
	14-09-04		24-09-03
	19-09-05		23-08-05
	13-09-06		06-09-06
	12-09-07		26-09-07
Ventry	09-09-00	Gurteen	25-09-02
	09-09-01		24-09-03
	08-09-02		23-08-05
	13-09-03		06-09-06
	22-09-04		26-09-07
	14-09-05		
	14-09-06	Ballyloughan	26-09-02
	10-09-07		26-09-03
Brandon	07-09-00		24-08-05
	05-09-01		05-09-06
	10-09-02		28-09-07
	10-09-03		
	16-09-04		
	21-09-05		
	12-09-06		
	13-09-07		

Salinity can be highly variable on certain nursery locations (10 ‰ – 26 ‰) as a result of freshwater runoff, which can also result in excess growth of filamentous algae on the nursery. The study area was divided into two regions: west and southwest. Five beaches were assessed in the southwest; these were located on the Dingle peninsula in Co. Kerry. On the west coast the survey targeted four beaches within Galway Bay, and one beach on the Co. Clare coast (Figure 2). At the beginning of the survey, beaches in the west and southwest were assessed in both May and September. However due to very low abundances of juvenile flatfish captured, the survey in May was discontinued. Two beaches yielding very low or no numbers of juvenile flatfish were also omitted from the survey after 2004. Data presented in the current work was for 0-group plaice

captured in September only. Due to differences in the sampling procedures used and the timing of the survey between the southwest and west coasts, data collected from the two regions were analysed separately (Haynes et al., 2010a). Data were not available for the west coast region in 2004.

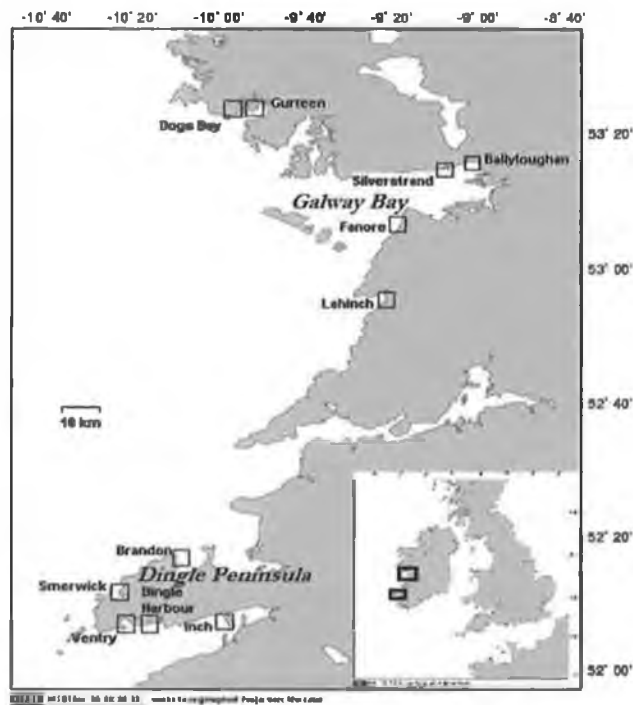


Figure 2: 0-group plaice nursery grounds assessed along the west coast of Ireland.

1.1. Fish collection

Sampling on a beach was carried out in a single day, within two hours either side of low tide. There was a maximum of four days between the first and last beach assessed in any one year, in a given region. On the west coast, fish were caught approximately one month earlier in 2005 in comparison to 2003 and 2007. When attempting to determine patterns of fish abundance and distribution, timing of sampling in terms of tidal, lunar, and day/night effects can have a significant influence (Gibson et al., 1996). In order to reduce this source of variability, and to avoid the confounding effects of differences in the timing of sampling, fish were collected on all beaches over the eight year period on a spring tide during daylight hours.

Fish were captured from nursery grounds along the west and southwest coast of Ireland, using a Danish style beach seine, which was 20 m long and 2 m deep, with a 13×13 mm mesh size. The swept area of the beach seine was approximately 1380 m², and described in greater detail in Haynes et al., (2010a). Mean plaice densities of plaice ± the standard deviation (SD) were calculated on each beach as the numbers per 1000 m², for comparisons with plaice densities in other studies. All species captured in the beach seine were identified on the shore. Juvenile plaice were placed in plastic bags with the sample date and location, and frozen in the laboratory within a number of hours of being captured for further analyses.

1.2. Laboratory Analyses

Frozen fish were removed from the freezer and allowed to thaw overnight. Juvenile plaice and flounder are similar in appearance, and may be difficult to distinguish. Therefore, the number of dorsal, anal, and caudal fin rays, which are species specific for flatfish (Wheeler, 1969), were counted under a stereoscopic microscope. This method has previously been used for the successful identification of plaice and flounder along the west coast of Ireland (Haynes et al., 2008). The standard length of plaice (SL) from the tip of the mouth to the where the caudal fins begin, was measured to the nearest 0.1cm, and weight was measured to the nearest 0.1g.

1.4. Separation of 0- and 1-group plaice

To distinguish between 0- and 1-group plaice captured throughout the eight year survey, the length frequency distribution of all plaice captured in the eight year survey (n = 5305) was plotted. However, no clear modes were observed. Age data were available for juvenile plaice collected on the southwest and west coast nursery grounds for three and two years respectively, from an unpublished MSc. thesis (Allen, 2004). 11 cm was the largest 0-group plaice captured, so this length used as a cut off point to exclude 1+ fish in the current study.

1.5. Temperature data

Temperature has been found to be the main environmental factor controlling the growth and development of fish (Gibson, 1994; Yamashita et al., 2001). Mean spring sea surface temperatures (January February March, JFM: the period corresponding to the pelagic stage) (Allen et al., 2008), and mean summer sea surface temperatures (July, August and September, JAS) were therefore

used to determine if interannual variation in the relative abundance and size of juvenile plaice on southwest nursery areas had an environmental basis. For the southwest region, seven years of temperature and plaice data were available (2001-2007); for the southwest coast, five years of data (2002-2007, excluding 2004) were available. Temperature data were provided by the Marine Institute from the weather buoys M1 (53.1266°N, 11.2000°W) off the southwest coast, and M3 (51.2166°N, 10.5500°W) off the west coast of Ireland.

1.6. Density dependent growth

The density of juvenile plaice was calculated as the number of individuals per 1000m². Due to intra-specific competition, high densities of juvenile fish on nursery grounds can lead to reduced growth, which in turn may affect the overall condition of a fish. As density dependence has been previously observed for plaice on nursery grounds (Van der Veer, 1986; Nash and Geffen, 2000), Pearson's correlation analysis was carried out on the mean density and the mean length of plaice captured on all nursery grounds in all years to determine if higher densities on nursery grounds were associated with a reduced mean length of plaice along the west coast of Ireland.

1.7. Condition analyses

Length and weight data were not available for every year of the survey due to inconsistent recording; hence plaice condition was calculated for the years 2003, 2005, and 2006 only. Morphometric indices based on such easily obtainable data have been reported to be good indicators of fish condition and habitat quality, as they incorporate all aspects of the life history of juvenile fish in a nursery area (Gilliers et al., 2006). Residuals from the linear regression of log₁₀ length and log₁₀ weight were used to calculate the condition for each plaice. This method is useful when determining the condition of fish from different size classes (Blackwell et al., 2000). Such condition indices assume that a fish of a heavier weight at a particular length are in better condition and can subsequently provide an indication as to the habitat quality of a nursery ground (Gilliers et al., 2004). A positive residual value indicates higher than average condition, whereas a negative residual value indicates lower than average condition.

1.8. Recruitment

Several authors have previously attempted (Nielsen et al., 1998; Van Beek et al., 1989) and some have been successful (Nash and Geffen, 2000) in relating abundances of 0-group flatfish to 1 or 2-group abundances. To investigate the correlation between two indices of relative abundance for juvenile plaice on the west coast of Ireland, the mean abundance of 0-group plaice collected in August and September for seven years of the survey (2003 - 2007) was plotted against the mean abundance of 1 and 2-group plaice of the corresponding year classes captured between October and December along the southwest coast of Ireland (ICES division VIIj) during the Marine Institute's Irish Groundfish Survey (IGFS) onboard the *RV Celtic Explorer*. The relationship between the mean abundance of 1 and 2-group plaice was also investigated, as it may not be until a later age that future population abundances are established.

1.9. Statistical Analyses

Data were tested for normality using the Anderson-Darling test. Homogeneity of variances was tested using Levene's test, and data were log transformed where necessary (Underwood, 1997). Once the assumptions of parametric analysis of variance were confirmed unbalanced type III nested ANOVAs were used to investigate temporal and spatial variability in the measured parameters. The null hypotheses that there was no difference in the numbers of plaice caught per haul (relative abundance) between beaches or years were tested. Length and condition of plaice was also compared between beaches years, and hauls. Beach was treated as a fixed factor, while year and haul were treated as random factors. Where the data failed to display homogeneity of variances even upon transformations, the non-parametric Kruskal-Wallis Test was performed. All significant differences were explored using Tukey's post hoc procedures with correction for multiple comparisons as described by Underwood (1997). Tukey's post hoc procedures were performed on ranked data where homogeneity of variances failed to occur (Zar, 1996). All non-parametric data were ranked in order to carry out Tukey's post hoc analyses. All statistical analyses were carried out using MINITAB 15.

2. Results

2.1. Relative abundance of plaice

A total of 5112 plaice were captured on the southwest and west coasts of Ireland over the eight year period 2000 – 2007 inclusive. Mean densities (\pm SD) of plaice ranged from 2.4 (\pm 2.4) on Ventry in 2004 (Table 3), to 100 (\pm 11.3) individuals per 1000 m⁻² on Ballyloughan in 2006 (Table 4).

Table 3: Mean densities per 1000 m⁻² (\pm SD) and mean lengths (cm \pm SD) of juvenile plaice from nursery grounds on the southwest coast of Ireland (2000 - 2007).

Year	Brandon		Smerwick		Inch		Ventry	
	Mean density (\pm SD) per 1000m ⁻²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ⁻²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ⁻²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ⁻²	Mean length (cm \pm SD)
2000	32.6 \pm 22.3	6.5 \pm 0.1	21.0 \pm 13.8	7.0 \pm 0.1	3.6 \pm 1.0	8.5 \pm 0.5	27.0 \pm 29.7	6.5 \pm 0.1
2001	15.6 \pm 0	7.2 \pm 0.2	42.0 \pm 26.2	6.6 \pm 0.1	65.0 \pm 25.2	8.5 \pm 0.1	25.0 \pm 20.1	6.7 \pm 0.1
2002	38.9 \pm 18.4	8.8 \pm 0.2	42.2 \pm 30.6	7.1 \pm 0.1	35.2 \pm 8.3	8.5 \pm 0.1	14.3 \pm 9.4	6.0 \pm 0.2
2003	6.3 \pm 0	8.7 \pm 1.1	9.2 \pm 12.5	8.2 \pm 0.2	4.8 \pm 1.6	7.3 \pm 0.2	8.0 \pm 4.9	6.7 \pm 0.2
2004	8.7 \pm 0	9.7 \pm 0.1	5.8 \pm 3.2	8.1 \pm 1.4	8.1 \pm 3.3	8.8 \pm 0.2	2.4 \pm 2.4	6.2 \pm 0.3
2005	32.4 \pm 14.4	8.6 \pm 0.1	31.0 \pm 9.1	7.9 \pm 0.1	3.6 \pm 1.0	6.7 \pm 0.2	3.4 \pm 2.9	7.4 \pm 0.4
2006	18.4 \pm 6.1	8.2 \pm 0.1	38.4 \pm 30.0	7.4 \pm 1.1	11.7 \pm 5.5	8.5 \pm 0.1	6.0 \pm 6.9	6.2 \pm 0.3
2007	3.2 \pm 4.0	10.1 \pm 0.2	24.6 \pm 10.8	7.3 \pm 0.1	8.7 \pm 9.7	8.5 \pm 0.1	17.8 \pm 10.0	6.9 \pm 0.1

Table 4: Mean densities per 1000 m² (\pm SD) and mean lengths (cm \pm SD) of juvenile plaice from nursery grounds on the west coast of Ireland (2002 - 2007). N/A denotes where no fish were captured.

Year	Silverstrand		Ballyloughan		Gurteen		Dogs bay		Lahinch	
	Mean density (\pm SD) per 1000m ²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ²	Mean length (cm \pm SD)	Mean density (\pm SD) per 1000m ²	Mean length (cm \pm SD)
2002	7.6 \pm 5.6	8.1 \pm 0.2	10.1 \pm 1.0	8.9 \pm 0.2	20.3 \pm 3.6	8.4 \pm 0.1	21.4 \pm 26.1	8.2 \pm 0.1	3.6 \pm 0	7.3 \pm 0.6
2003	25.4 \pm 15.4	8.0 \pm 0.1	8.3 \pm 3.6	7.7 \pm 0.3	27.9 \pm 12.8	7.4 \pm 0.1	15.8 \pm 3.6	7.4 \pm 0.2	2.5 \pm 1.5	7.6 \pm 0.4
2005	46.4 \pm 31.8	6.3 \pm 0.1	24.3 \pm 13.8	7.4 \pm 0.1	14.1 \pm 9.7	6.0 \pm 0.2	24.3 \pm 16.9	5.7 \pm 0.2	4.1 \pm 2.9	5.8 \pm 0.2
2006	36.2 \pm 11.3	6.1 \pm 0.1	100 \pm 11.3	6.2 \pm 0.1	24.9 \pm 17.0	5.7 \pm 0.1	28.0 \pm 19.0	6.5 \pm 0.1	11.3 \pm 13.8	7.2 \pm 0.3
2007	18.5 \pm 4.6	7.2 \pm 0.2	N/A	N/A	N/A	N/A	18.8 \pm 6.1	N/A	15.9 \pm 8.0	7.7 \pm 0.1

Eight years of juvenile plaice abundance data (2000 - 2007) were available for nursery grounds on the southwest coast. Non-parametric Kruskal-Wallis Tests revealed that the abundance of plaice (n = 3723) differed significantly between beaches (df = 3; H = 16.47; p < 0.001) and also between years (df = 7; H = 36.4; p < 0.001). Tukeys's multiple comparison tests showed that in the abundances of 0-group plaice were higher on Smerwick in 2002, 2003, 2006 and 2007, in comparison with the other southwest beaches (Figure 3). Ventry consistently yielded low abundances of plaice over the eight year study. Inter-annual variation in 0-group plaice abundances was observed on all beaches (Tukey's post hoc test, p<0.05) but no consistent pattern emerged.

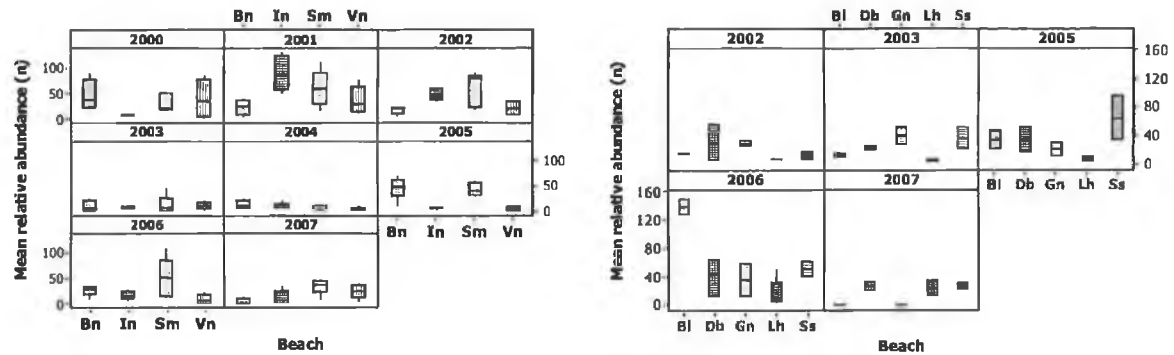


Figure 3: Plot showing patterns of spatial variation in mean juvenile plaice abundances (n) at nursery areas on the southwest (left) and west (right) coast of Ireland (2000-2007). Bn = Brandon, In = Inch, Sm = Smerwick, Vn = Ventry. Bl = Ballyloughan, Db = Dogs Bay, Gn = Gurteen, Lh = Lahinch, Ss = Silverstrand.

On the west coast, juvenile plaice abundance data were available for the years 2002, 2003, 2005, 2006, and 2007. ANOVA showed that a significant interaction between beach and year occurred ($df = 16$; $F = 3.23$; $p = 0.003$). However, the main effects were not significant with no significant variation in the relative abundance of plaice ($n = 1389$) between beaches ($df = 4$; $F = 0.99$; $p = 0.442$) or years ($df = 4$; $F = 2.42$, $p = 0.09$).

2.2. Plaice lengths

Mean lengths (\pm SD) of 0-group plaice ranged from 5.7 ± 1.0 cm on Gurteen in 2005, to 10.1 ± 0.2 cm on Brandon in 2007 (Table 3). For nursery grounds on the southwest coast, non-parametric Kruskal-Wallis Tests revealed that the lengths of plaice differed significantly between beaches ($df = 3$; $H = 590.01$; $p < 0.001$) years ($df = 7$; $H = 299.25$; $p < 0.001$) and hauls ($df = 6$; $H = 50.26$; $p < 0.001$). Tukeys's multiple comparison tests found that the mean length of plaice was highest on Brandon, followed by Inch and Smerwick (2002 – 2005, and 2007). Plaice were, in general, consistently smaller on Ventry (Figure 4). High inter-annual variability in the mean length of plaice occurred on each beach, with no overall pattern discerned.

On the west coast, data for the lengths of plaice ($n = 1403$) were available for the years 2002, 2003, 2005, 2006, and 2007. Using non-parametric Kruskal-Wallis Tests, the lengths of plaice were found to differ significantly between beaches ($df = 2$; $H = 21.91$; $p < 0.001$) years ($df = 4$; $H = 444.40$; $p < 0.001$) and hauls ($df = 3$; $H = 9.92$; $p = 0.019$). Tukeys's tests indicated that there was no consistent trend in the mean length of plaice between beaches and years (Figure 4).

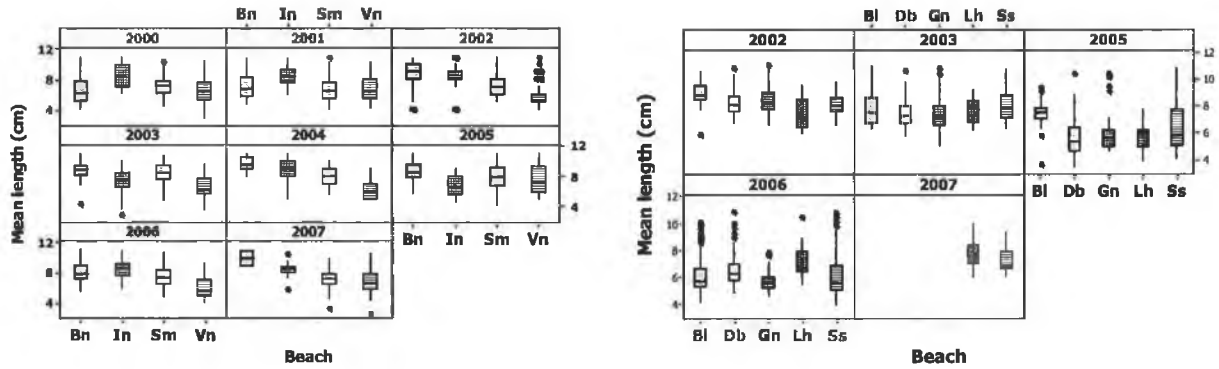


Figure 4: Plots showing patterns of spatial variation in mean juvenile plaice lengths (cm) at nursery areas on the southwest (left) and west (right) coast of Ireland (2000-2007). Bn = Brandon, In = Inch, Sm = Smerwick, Vn = Ventry. Bl = Ballyloughan, Db = Dogs Bay, Gn = Gurteen, Lh = Lahinch, Ss = Silverstrand.

2.3. Plaice condition

Using residuals of the length-weight relationship as a condition index, the mean condition of 0-group plaice in a given year ranged between 0.04 on Brandon in the year 2006 and -0.10 on Dogs Bay in the year 2005. Data for the condition of plaice on the southwest coast were available for the years 2003, 2005, and 2006. Using non-parametric Kruskal-Wallis Test, the condition of plaice differed significantly between beaches ($df = 3$; $H = 99.35$; $p < 0.001$) years ($df = 2$; $H = 289.02$; $p < 0.001$) and hauls ($df = 6$; $H = 90.24$; $p < 0.001$). Multiple comparisons tests revealed that plaice on Inch (0.01) exhibited the highest overall mean condition, followed by Brandon (0.00) and Smerwick (0.00). Plaice on Ventry had a significantly lower mean condition (-0.04) in contrast to other southwest nurseries (Figure 5).

On the west coast, data for the condition of plaice were available for the years 2003, 2005, and 2006. Using non-parametric Kruskal-Wallis, the condition of plaice differed significantly between beaches ($df = 4$; $F = 201.8$; $p < 0.001$) years ($df = 2$; $F = 127.70$; $p < 0.001$), and hauls ($df = 4$; $F = 18.14$; $p < 0.001$), with no overall pattern discerned (Figure 5).

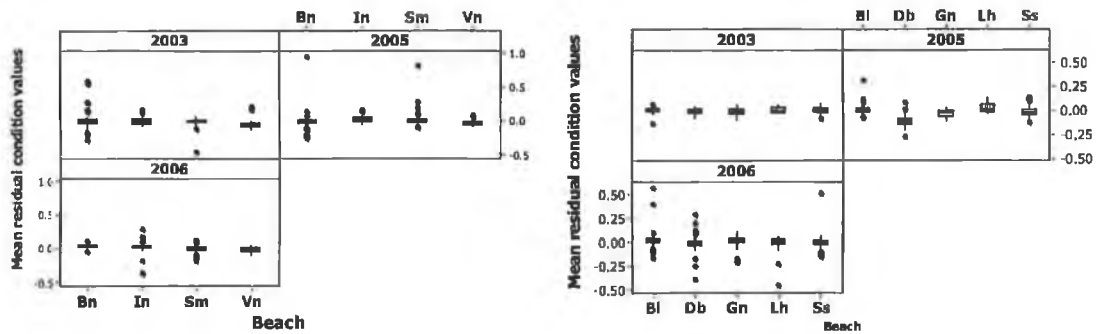


Figure 5: Plots showing patterns of spatial variation in mean juvenile plaice condition at nursery areas the southwest (left) and west (right) coast of Ireland (2003 2005 2006). Bn = Brandon, In = Inch, Sm = Smerwick, Vn = Ventry. Bl = Ballyloughan, Db = Dogs Bay, Gn = Gurteen, Lh = Lahinch, Ss = Silverstrand.

2.4. Density dependent growth

There was no evidence of density dependent growth on nursery grounds in the present study. No significant correlation between the mean density and the mean length of plaice on all nursery grounds was detected ($p = 0.085$).

2.5. Temperature and plaice abundance

0-group plaice abundances on the southwest coast (2001 – 2007) were significantly inversely correlated with the mean spring sea temperature (January, February, March), corresponding to the larval stage ($r^2 = 0.885$, $p = 0.005$) (Figure 6). However, no such correlation was observed between juvenile plaice abundances and mean summer temperatures (July August September) corresponding to the juvenile benthic stage ($r^2 = 0.287$, $p = 0.640$). 0-group plaice abundances on the west coast (2002 – 2007, excluding 2004) were not significantly correlated with the mean spring sea temperature or summer temperatures ($p > 0.05$).

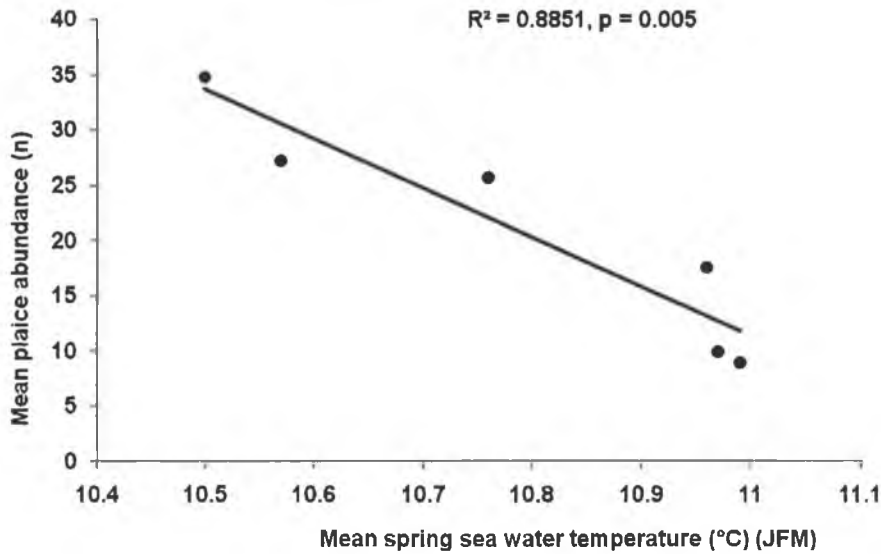


Figure 6: Correlation between mean plaice abundance per year on southwest nursery grounds, and mean spring sea temperature (JFM, 2002 – 2007).

2.6. Recruitment

There was no relationship discerned between the mean abundance of 0-group plaice collected from southwest nursery grounds, and the mean abundance of 1 or 2 year plaice collected in the following year during the Irish Groundfish Survey, off the southwest coast (ICES area VIIj), over a 7 year period ($p = 0.597$).

3. Discussion

3.1. Plaice abundances

Plaice successfully recruited to nine nursery grounds in each year of the study, with the exception of 2007 when plaice were absent from two beaches. Mean densities of juvenile plaice on nursery grounds ranged between $2.4 (\pm 2.4)$ and $100 (\pm 11.3)$ individuals 1000 m^{-2} over the eight year period. This is similar to reports from other areas in the Northeast Atlantic; densities of plaice collected in August/September in the Kattegat ranged from 31 to 28 individuals 1000 m^{-2} (Nielsen et al., 1998), in the Dutch Wadden Sea there were 1.7 individuals 1000 m^{-2} (Zijlstra et al., 1982),

and between 4.4 and 6.5 individuals 1000 m^{-2} were observed in the Irish Sea in autumn (Nash et al., 1994a). Density dependent growth, most likely due to food limitation, has been found to occur at plaice densities > 5 individuals m^{-2} (Wennhage et al., 2006). The current study found no evidence of density dependent growth in 0-group plaice in August/September. However, density dependent processes may have impacted on growth earlier in the year in the period just after settlement. In the Irish Sea, density related processes on nursery grounds were described as the most likely factors affecting 0-group plaice abundances over a seven year period (Nash and Geffen, 2000). Other studies have also noted that an increase in the density of juvenile plaice impacted negatively on growth (Nash et al., 1994a; Modin and Pihl, 1996).

On the west coast of Ireland plaice abundances fluctuated temporally and spatially without any consistent trend emerging, which is common in juvenile plaice studies (Van der Veer, 1990, Nash and Geffen 2000, Riou et al., 2000). However, the nursery Smerwick supported a higher number of plaice in the majority of years. In general, juvenile plaice abundances are determined by differences in larval supply, resulting in interannual variability in recruitment (Bolle et al., 2009; Van der Veer et al., 2009), which is subsequently modified by processes operating on the nursery such as variation in habitat type (Wennhage and Pihl, 2001). Given the recent observations of plaice spawning to the southwest of the country (Gerritsen et al., 2010), the nursery Smerwick in the current study may be situated in a favourable geographical location in relation to the supply of settling larvae. Smerwick is also a moderately exposed habitat in comparison to other nursery locations; higher densities of plaice have been reported on semi-exposed shores in comparison to more exposed and sheltered areas (Pihl and Van Der Veer, 1992). The finer sediment structure of Smerwick in comparison to more exposed locations might enhance the burial ability of 0-group plaice for predator evasion. In contrast to other southwest nursery areas, Ventry produced a consistently lower quantity of juvenile plaice over the eight years, indicative of a suboptimal nursery, possibly due to different benthic fauna types on this beach (De Raedemaecker et al., 2010). This nursery can, on occasion, also be characterised by a large volume of filamentous green algae (Pers. obs.), which is known to reduce plaice densities (Pihl and Van Der Veer, 1992).

Plaice abundances on southwest nursery grounds were inversely related to mean spring sea temperatures during the pelagic stage. This negative relationship has also been observed in the Irish and North Seas (Fox et al., 2000; Van der Veer et al., 2009). The consistency in the relationship between temperature and juvenile plaice abundance across the distribution of the species indicates that temperature is a major driver of recruitment success which overrides other

more local processes. Colder sea temperatures during the pelagic and early demersal stages of flatfish are believed to significantly reduce the abundance of predators, which are more sensitive to the drop in sea temperature (Rijnsdorp and Van der Veer, 2008). It has also been put forward that colder sea temperatures during the pelagic stage will reduce the activity of pathogenic bacteria on plaice eggs (Fonds, 1995).

No relationship was detected between plaice abundances and temperature on west coast nurseries, perhaps due to the lower number of years available for analysis. No significant relationship was identified between plaice abundances on Irish west coast nurseries and mean summer sea temperatures (during the early juvenile benthic stage). This indicates that survival after settlement may be under the influence of local nursery ground processes rather than broad scale environmental factors such as temperature. Predation has been shown to significantly reduce the densities of newly-settled plaice (Van der Veer et al., 1990; Pihl and Van der Veer, 1992; Gibson et al., 1995). The size and quality of the nursery are also important determinants of abundance. Along the Swedish coast, it was revealed that the largest nursery grounds, in terms of surface area, did not produce to the highest abundances of juvenile plaice at the end of the nursery ground stage (Wennhage et al., 2006). This is also indicated in the present work; the larger beaches in terms of suitable habitat available for 0-group flatfish (Inch and Brandon) did not always support high densities of 0-group plaice.

3.2. Plaice length and condition

Mean lengths of west of Ireland 0-group plaice collected in September ranged between 5.7 (\pm 1.0) and 10.2 (\pm 0.2) cm. This is similar to reports from other areas such as the Irish Sea (\bar{x} of 7.5 cm in September; et al., 1994a) and the Wadden Sea (7.5 cm, end of August; Berghahn et al., 1995) (8.5 cm in September; Zijlstra et al., 1982). Smaller 0-group plaice were observed along the Swedish coast (3.5 – 5.5 cm) in August; (Modin and Pihl, 1996); this may reflect differences in the age of the fish at capture.

On the southwest coast in the present study, both temporal and spatial variability in the mean lengths and condition of plaice were observed, with both good growth and condition of plaice exhibited on certain beaches. Faster growth experienced by juvenile flatfish on the nursery will reduce the time during which an individual is vulnerable to predation (Taylor, 2003). Hence,

survival will be greatest on nursery grounds where juvenile flatfish experience rapid growth (Gibson, 1994; Sogard et al., 2001). However, given that differences in the lengths of plaice between nursery grounds in the present study may have arisen from differences in the timing of hatching or settlement, the use of additional indices such as the condition of plaice is also important, as this index provides information on the wellbeing of the fish, irrespective of age differences. In general, over the eight year period plaice on Brandon and Inch were larger and also in better condition while plaice on Ventry had lower mean lengths and condition compared with other nursery areas. These results are in agreement with those of an earlier study, where significantly lower otolith growth rates and morphometric condition in 0-group plaice inhabiting Ventry were detected, in comparison to Inch and Smerwick (De Raedemaecker et al., 2010). Differences in the growth of plaice between nursery areas imply variation in habitat quality which may be related to environmental conditions on the beaches. De Raedemaecker et al., (2010) proposed that variation in otolith growth and condition of plaice at these west of Ireland nursery grounds could be linked to the variety of prey in the diet. Shifting between different types of prey throughout the nursery ground stage, was also considered to influence the growth rates of juvenile plaice in the Wadden Sea (Van der Veer et al., 2010), with limited food availability put forward as the causative factor for the reduced growth rates of juvenile plaice in the Irish Sea (Ciotti et al., 2010), and also in the North Sea (Teal et al., 2008). However, there is no evidence to suggest that food is limiting on west of Ireland nursery grounds (De Raedemaecker et al., in press; Haynes et al., in press (b)). The growth of 0-group flatfish is reported to be determined primarily by temperature, with higher growth observed at higher temperatures (Van der Veer & Witte, 1993). Although there is little information available on the environmental conditions on Irish southwest nursery grounds, a freshwater input on the nursery Ventry may have resulted in lower temperatures on this beach.

As well as the broad scale differences observed between beaches in the southwest region, small scale variability in length and condition were also observed between hauls on all beaches, which is consistent with the findings of De Raedemaecker et al., (2010) for plaice on southwest nursery grounds. This may reflect the patchy distribution of prey and emphasises the importance of appropriate spatial coverage when assessing habitat quality of inshore locations. Similar to length variability in the present investigation, fluctuations in the condition of plaice between hauls imply differences in the quality or the quantity of prey within nursery grounds, and emphasise the importance of adequate assessment of inshore locations.

The establishment of recruitment indices are valuable tools for predicting the future size of fish stocks. Some studies have been successful in the formation of a recruitment index. In the North Sea, Van Beek et al., (1989) found a significant relationship between estimates of 0- and 1-group plaice abundances and year class strength estimates from virtual population analysis (VPA). However, in the present study no consistent pattern in recruitment was discerned, with 0-group plaice abundances not related to mean abundances of either 1 or 2-group individuals captured off the west coast of Ireland over a six year period. Moreover, mean abundances of 1 and 2-group plaice were not significantly correlated. When attempting to establish a recruitment index, the accurate estimation of the species of interest, collected at the appropriate time when the year class strength is set, is required. Previous juvenile flatfish investigations have shown that the abundance of 0-group plaice was only correlated with numbers of 1-group fish at a specific point in the nursery period (Nash and Geffen, 2000). 0-group plaice in the present study were collected over a one week period during the summer months in each year of the flatfish survey. At this time, abundance estimates may have been confounded by emigration into deeper waters. On the other hand, sampling conditions along the west coast of Ireland remained consistent throughout the eight year time series and abundance estimates were not influenced by variation in catch efficiencies of the selected gear (Nash et al., 1994a). Results should therefore provide reliable estimates of the relative abundance of juvenile flatfish and a good indication of fluctuations in the juvenile populations. This is supported by the detection of consistent signals, such as the relationship between abundance and spring temperatures in the southwest region and the consistently high relative abundances on some beaches. In relation to the collection of 1- and 2-group plaice along the west coast of Ireland, the Irish groundfish survey does not assess shallow inshore areas. Therefore, its spatial coverage may not be appropriate for estimating the abundance of 1- and 2- group plaice, which have been found to remain within their original coastal nursery area before moving offshore to deeper waters and recruiting to the adult stock (Lockwood, 1974).

In summary, important plaice nursery grounds on the west coast of Ireland have been identified and densities of 0-group plaice over an eight year period have been estimated. Certain nursery areas were found to support relatively high abundances of 0-group plaice; in addition, growth and condition appear to be enhanced in these areas. Further evidence of the influence of temperature during the pelagic larval phase on year class strength of plaice was presented. The present study has provided an improved understanding of the early life history of plaice on the Irish west coast. Long-term studies such as this are valuable for investigating habitat quality and the processes governing recruitment in flatfish.

Chapter 6

The early life history of turbot (*Psetta maxima* L.) on nursery grounds along the west coast of Ireland: 2007 – 2009, as described by otolith microstructure.

Journal of Fisheries Research.
doi:10.1016/j.physletb.2003.10.071.

The early life history of turbot (*Psetta maxima* L.) on nursery grounds along the west coast of Ireland: 2007 – 2009, as described by otolith microstructure

Paula S. Haynes, Deirdre Brophy, David McGrath.

Abstract

The early life history of turbot (*Psetta maxima* Linnaeus) was investigated over a three year period (2007-2009). 0-group turbot were collected in September of each year, from three nursery areas along the Irish west coast. The timing of hatching and settlement and the duration of the larval stage were estimated using otolith microstructure analysis. Otolith increment widths were used to derive an index of relative growth rates before and after settlement. Turbot were estimated to have hatched between May and June and settled onto nursery grounds between June and July over the three years of the study. No inter-annual differences in the timing of hatching or settlement were observed. Spatial variability was detected, with turbot collected from one location hatching and settling significantly earlier compared to other locations. Turbot from the same location also displayed higher post-settlement otolith growth rates suggesting that this may be a nursery of high habitat quality. Turbot captured in 2009 exhibited significantly shorter larval durations and higher larval otolith growth rates compared to turbot collected in other years. Post-settlement growth rates displayed the opposite trend, with turbot showing lower post-settlement growth in 2009. The results provide valuable baseline data on critical events in the early life history of a data-poor species.

1. Introduction

Turbot (*Psetta maxima* Linnaeus) is a highly valued flatfish species, occurring in both marine and estuarine waters around Europe. Despite its high commercial value, there are currently no analytical assessments carried out for turbot, and little is known of the stock structure of wild populations (Anon, 2010b). However, stocks are considered to be overexploited around Europe, including the Baltic (Draganik et al., 2005) and North Seas (Anon, 2010a).

Adult turbot spawn in shallow waters just offshore, between April and August in the North Sea (Jones, 1974) and between late May and July in the Baltic Sea (Nissling et al., 2006). Turbot produce pelagic eggs and larvae, with the exception of the Baltic Sea, where eggs are demersal. Similar to many flatfish species, juvenile turbot inhabit shallow inshore nursery areas (Riley et al., 1981), settling at a length of between 2 and 3 cm onto predominantly exposed shores (Jones, 1973b; Nissling et al., 2006).

In Ireland, turbot is one of the most valuable commercial non-quota species with landings increasing in recent years as a result of a more concentrated fishing effort (Anon, 2007). There is no specific turbot fishery in Ireland, and they are caught mainly as by-catch in demersal fisheries in the eastern Irish and Celtic Seas. The timing or location of spawning along the Irish coast is not known. However, a recent study identifies a number of turbot nursery grounds on the Irish west coast (Haynes et al., 2010b).

Otolith microstructure analysis can provide important information on the timing of critical events in flatfish early life history. Daily increment deposition has been confirmed for many flatfish species (Nash and Geffen, 2005). A laboratory study has shown that for turbot, the rate of ring deposition is daily under rearing conditions that promote higher growth rates but that less than one ring is deposited each day when growth rates fall below 2mm day⁻¹ (Geffen, 1982). In general, where unfavorable conditions are not experienced otolith increments are assumed to be deposited at a daily rate and can be used to estimate age and as a proxy for growth (Campana and Neilson, 1985). When a flatfish undergoes metamorphosis from the pelagic to the flattened benthic form, the shape of the otolith changes dramatically producing distinctive checks known as accessory primordia (AP's) in the otolith microstructure (Nash and Geffen, 2005). Metamorphosis is coincident with settlement onto nursery grounds in the majority of flatfish species (Geffen et al. 2007) including turbot (Üstündağ, 2003); therefore the presence of AP's in the otolith

microstructure allows the timing of settlement to be estimated. Given the lack of information available on wild turbot, the aim of the present work was to establish baseline data for hatch dates, larval durations, timing of settlement, and relative growth rates, in addition to identifying any temporal or spatial variability in the investigated parameters.

2. Materials and Methods

2.1. Sampling of fish

0-group turbot were collected from one sheltered and two exposed sandy beaches along the west coast of Ireland (Figure 1) in September 2007 - 2009. Sampling occurred within 2 hours either side of the low tide during daylight hours. In 2009 one location was sampled early in the settlement period (late August) in order to assess the extent to which the measured parameters in the population could change due to post-settlement mortality. Sampling details are summarized in Table 1.

Sampling was conducted using two Danish style beach seines. The seine used in 2008 and 2009 was 5.5 m long and 2 m deep, with a 5×5 mm mesh size. In 2009 a 20 m long and 2 m deep seine, with a 13×13 mm mesh size was used. Both nets captured a similar size range of juvenile turbot. Between two and 10 hauls were carried out, depending on the size of the beach. Sampling locations on each beach were randomly selected. Juvenile turbot were frozen on the day of capture before further analysis.

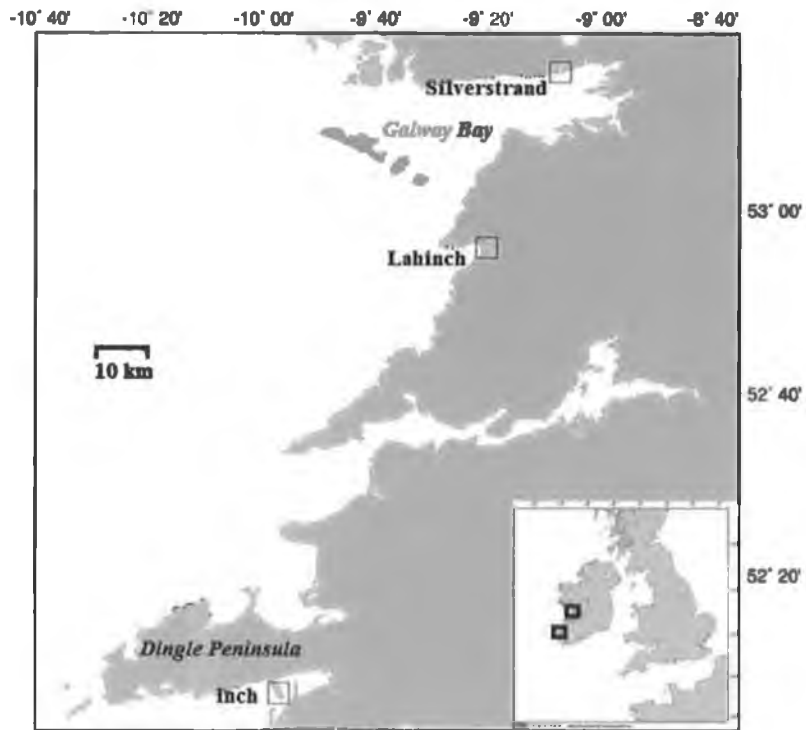


Figure 1: Beaches assessed for 0-group turbot along the west coast of Ireland (2006 – 2009).

Table 1: Date of capture, number of otoliths analyzed, hatch and settlement dates, and growth of 0-group turbot (2007-2009).

<i>Beach</i>	<i>Date of capture</i>	<i>Number of otoliths analyzed</i>	<i>First hatch date</i>	<i>Mean larval duration ± SD (days)</i>	<i>First Settlement date</i>	<i>Mean larval otolith growth rates ($\mu\text{m day}^{-1} \pm \text{SD}$)</i>	<i>Mean post-settlement otolith growth rates ($\mu\text{m day}^{-1} \pm \text{SD}$)</i>
Inch	07/09/2007	12	May-02	36 (± 8)	Jun-16	2.1 (± 0.7)	9 (± 1.2)
	04/09/2008	11	May-01	38 (± 4)	Jun-16	2.6 (± 0.7)	9.2 (± 1.0)
	10/09/2009	9	Jun-09	32 (± 5)	Jul-13	3.1 (± 0.5)	6.7 (± 0.9)
Silverstrand	27/09/2007	12	Jun-19	33 (± 4)	Jul-24	2.8 (± 0.6)	6.5 (± 1.2)
	15/09/2008	13	May-27	37 (± 6)	Jul-06	2.6 (± 0.4)	7.1 (± 0.8)
	18/09/2009	13	May-06	33 (± 3)	Jul-11	3 (± 0.6)	6.4 (± 0.1)
	26/08/2009	10	June-20	29 (± 5)	Jul-23	-	-
Lahinch	28/09/2007	11	Jun-16	39 (± 8)	Jul-27	2.3 (± 0.7)	6.4 (± 1.0)
	16/09/2008	15	Jun-01	39 (± 6)	Jul-11	2.7 (± 0.8)	6.6 (± 0.9)
	17/09/2009	11	Jun-07	34 (± 3)	Jun-10	3.3 (± 0.5)	5.5 (± 0.4)

2.2. Otolith preparation and analysis

Sagittal otoliths were removed from 117 0-group turbot and cleaned. One of the pair was randomly selected for analysis. Otoliths were polished using the technique described by Brophy and Danilowicz (2002), until rings from the core to the outer edge of the otolith could be seen. Cracked or unreadable otoliths were rejected. Polished sections were examined using an Olympus BX51 compound microscope under 400X and 1000X magnifications, interfaced with a PC and the Image Pro Plus Analyzer version 6.2 software. The three life history stages examined were the larval (the region bounded by the first increment after the hatch check and the last full increment before the first accessory primordium or AP); metamorphic (the increments between the first and last AP), and post-settlement stages (the first complete increment after the last AP to the edge of the otolith) (Figure 2). The first six increments after the final AP were used as an index of juvenile

growth rate. Increments were measured to the nearest 0.1 μm , and counted along the longest axis. Hatch dates were estimated from total increment counts. To assess the reader's ageing precision, 25 otoliths were randomly selected and daily increments were counted for a second time, with no prior knowledge of the first count. The overall mean % coefficient of variation between the initial and second reading was calculated at 6.8%. All measured parameters were compared between right and left otoliths from a subsample of 10 fish and no significant differences were found (paired t-test, $p < 0.05$), justifying the use of randomly choosing the right or left otolith for the analysis.

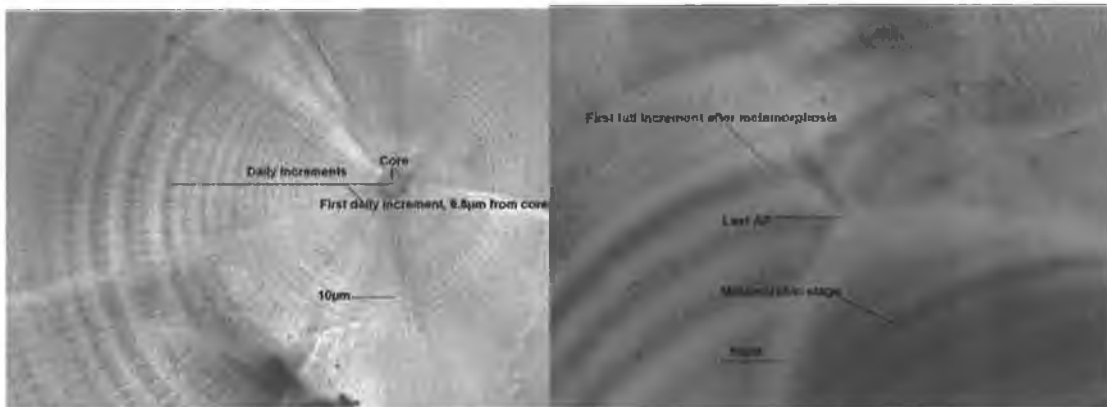


Figure 2: Sagittal otoliths of 0-group turbot viewed at 1000X. Daily increments during the larval (left) and settlement (metamorphic and post-settlement) stage (right) are presented. The first increments deposited after hatching can be seen on the left, with the final AP representing the end of metamorphosis visible on the right.

2.3. Data Analyses

After confirming that the assumptions of normality and equal variance were met, ANOVAs were used to examine variation in the measured parameters between locations and years. Beach was included as a fixed factor and year as a random factor. All significant differences were explored using Tukey's post hoc procedures with correction for multiple comparisons as described by Underwood (1997). Correlation analysis was used to investigate if post-settlement otolith growth rates were related to larval duration or larval otolith growth rates.

3. Results

Results of the otolith microstructure analysis are summarized in Table 1 and Fig. 2. Hatch dates were not significantly different between years ($F = 0.93$; $p = 0.39$), but differed between beaches ($F = 0.83$; $p < 0.001$), with no interaction between beach and year ($F = 2.32$; $p = 0.06$). Turbot collected on Inch hatched significantly earlier by 5 and 6 days in comparison to Lahinch and Silverstrand respectively, over the three years (Tukey's post-hoc test; $p < 0.001$). Larval durations were not significantly different between beaches ($F = 1.97$; $p = 0.14$), but differed between years ($F = 7.56$; $p < 0.001$). There was no interaction between beach and year ($F = 1.32$; $p = 0.29$). Turbot collected in 2009 had significantly shorter larval durations (\pm SD) ($\bar{x} = 33 \pm 4$ days) compared to turbot collected in 2008 ($\bar{x} = 38 \pm 5$ days) ($p < 0.05$). Mean increment widths were calculated for the first 23 days of life (the shortest larval duration observed); mean increment widths were not significantly different between beaches ($F = 0.76$; $p = 0.47$), but differed between years ($F = 12.30$; $p < 0.001$). There was no interaction between beach and year ($F = 2.17$; $p = 0.08$). Turbot collected in 2009 showed significantly higher mean larval otolith growth rates (\pm SD) ($\bar{x} = 3.1 \pm 0.6 \mu\text{m day}^{-1}$) for the first 23 increments compared to turbot collected in 2008 ($\bar{x} = 2.6 \pm 0.6 \mu\text{m day}^{-1}$), and 2007 ($\bar{x} = 2.4 \pm 0.7 \mu\text{m day}^{-1}$), ($p < 0.001$).

Settlement dates were not significantly different between beaches ($F = 3.61$; $p = 0.13$), or years ($F = 0.06$; $p = 0.94$). An interaction occurred between beach and year ($F = 2.88$; $p = 0.03$). Turbot settled earlier on Inch in 2007 ($F = 13.61$; $p < 0.001$) and in 2008 ($F = 4.34$; $p = 0.02$) by approximately one month and two weeks respectively, compared to Lahinch and Silverstrand. Mean post-settlement otolith growth rates were significantly different between beaches ($F = 22.25$; $p < 0.001$) and years ($F = 8.90$; $p < 0.001$), with no interaction between beach and year ($F = 0.64$; $p = 0.64$). Turbot on Inch showed significantly higher post-settlement otolith growth rates (\pm SD) ($\bar{x} = 8.3 \pm 1.3 \mu\text{m day}^{-1}$) compared to Lahinch ($\bar{x} = 6.0 \pm 1.1 \mu\text{m day}^{-1}$), and Silverstrand ($\bar{x} = 6.5 \pm 1.1 \mu\text{m day}^{-1}$) over the three years ($p < 0.001$). Turbot collected in 2009 had lower post-settlement growth ($\bar{x} = 5.7 \pm 1.0 \mu\text{m day}^{-1}$) compared to 2007 ($\bar{x} = 7.5 \pm 1.4 \mu\text{m day}^{-1}$), and 2008 ($\bar{x} = 7.2 \pm 2.0 \mu\text{m day}^{-1}$), ($p < 0.003$). Mean-post settlement otolith growth rates were negatively correlated with mean larval otolith growth rates ($r = -0.47$; $p < 0.001$). There was no correlation between post-settlement otolith growth rates and larval duration ($p > 0.05$).

Turbot collected from Silverstrand in August 2009 were compared to turbot collected from the same site in September 2009. No significant differences in larval duration, hatching or settlement

dates were detected ($p = 0.211, 0.129, \text{ and } 0.113$ respectively) suggesting that the estimates were not influenced by post-settlement mortality and/or migration of fish from the inter-tidal in the weeks after settlement.

4. Discussion

The current study provides estimates of the timing of critical life history events for juveniles that successfully recruit on west coast of Ireland nursery grounds. This represents a valuable contribution to current knowledge of a data-poor species. However, the limitations of the otolith age estimation technique must be considered. Although daily increment formation during normal growth periods is well established for many flatfish species, increments within accessory growth centers may be non-daily (Nash and Geffen, 2005) and otolith asymmetry around metamorphosis can introduce errors into age estimation (Sogard, 1991). Pre-settlement otolith increment widths recorded in this study were relatively wide ($2.1 - 3.3 \mu\text{m}$ on average) and there was no evidence of the narrowing increments that are indicative of poor growth conditions (Sogard et al., 2001). Hatching and settlement times estimated turbot with few or no AP's collected in August were similar to estimates derived from turbot collected from the same area in September, suggesting that the metamorphic region could be read with the same degree of reliability as the larval region. Previous surveys conducted by the authors on the same beaches throughout the year show that turbot first appear in the samples between the end of July and the middle of August (unpublished data); this is consistent with the settlement dates reported in this study and supports the accuracy of the age estimates. Nonetheless, further validation of daily increment formation during flatfish metamorphosis is needed to support the interpretation of otolith increment counts from wild caught juveniles. It should also be borne in mind that the frequency distribution of hatching and settlement dates is subject to any size selectivity of the sampling gear; it is possible that larger (either older or faster growing) 0-group turbot may have escaped, or avoided the seine net (Nash et al., 1994b).

Turbot captured in September on the Irish west coast were estimated to have hatched between May and June and settled onto nursery grounds between June and July in 2007-2009. In the North Sea, turbot arrive on beaches in June and July (Jones, 1973), and in Gotland they settle between the end of July and the end of August (Nissling, et al., 2006). Turbot on the nursery Inch hatched and settled significantly earlier compared to other locations. This could be an artefact of the timing of sampling; turbot were collected from Inch seven to 20 days earlier than from the other two

sites. Size selective post-settlement mortality or migration into deeper water may have removed older turbot from the other two beaches in the interval between sampling events. However, the comparison of early life history parameters estimated from August and September caught fish from Silverstrand in 2009 shows that in that area, post-settlement mortality or migration did not produce detectable differences in hatch date within a 21 day period. Alternatively, recruits to Inch may have originated from an earlier hatched cohort, or from a separate stock. More intensive sampling, coincident on the three nursery areas would be needed to confirm this.

Shorter larval durations and higher larval growth rates were observed in 2009 compared to the other two years. Larval growth rates and the duration of the pelagic phase are linked to temperature and food availability during larval life (Van der Veer et al. 2009). Rapid larval growth and completion of the planktonic phase can enhance survival and recruitment success (Houde, 1994). In flatfish, the duration of the larval phase is also critical in terms of timely delivery to a suitable nursery area (Van der Veer, et al. 2000). Therefore inter-annual variability in larval duration and growth rates is likely to be an important determinant of recruitment success (Van der Veer and Leggett, 2005). A more detailed examination of annual variation in larval growth and duration of turbot on the west coast of Ireland might provide insights into the factors governing recruitment variability.

Post-settlement otolith growth varied temporally and spatially. The higher post-settlement growth observed on Inch suggest that this area might be a high quality nursery. This is consistent with previous observations that Inch can support higher densities of turbot relative to other nursery areas (Haynes et al. 2010b) and reports of enhanced growth and condition of juvenile plaice from the same location (De Raedemaecker et al. 2010). However, the redistribution of faster growing fish into deeper waters during the interval between sampling events cannot be ruled out. The observed inter-annual variation in post-settlement growth may be indicative of large scale environmental fluctuations, whereas spatial variation in growth in a given year is most likely due to small scale local variability. While temperature has been described as the dominant factor controlling the growth of individuals on nursery grounds, a combination of interacting biotic and abiotic additional factors (Gibson, 1994), can also affect juvenile flatfish growth.

The negative correlation between pre- and post-settlement otolith growth rates, which was unrelated to age at settlement, may occur due to compensatory growth mechanisms, whereby fish which have experienced a period of reduced growth due to food deprivation or lowered

temperatures show accelerated growth rates once conditions improve (e.g. Niecieza and Metcalfe, 1997). The costs associated with compensatory growth include a reduction in the energy available for tissue repair and metabolic maintenance and greater vulnerability to predators due to increased foraging time and reduced swimming speeds (Sogard and Olla, 2002). Therefore, slow growth during the larval phase may continue to reduce the chance of survival even after settlement. This highlights the importance of inter-annual variation in larval duration and growth for recruitment variability.

The information presented here on turbot early life history and its spatial and temporal variability can contribute to understanding of the processes governing recruitment to the adult stock and when combined with oceanographic information could help to identify the origin of larvae supplying the nursery areas. The identification of nursery areas which potentially support high growth rates is important given the current widespread degradation of the coastal zone and the need to protect high quality nursery areas (Beck et al., 2001).

Chapter 7

**The feeding ecology of 0-group turbot (*Psetta maxima* L.)
and brill (*Scophthalmus rhombus* L.) on Irish west coast
nursery grounds.**

Journal of Fish Biology. In press.

The feeding ecology of 0-group turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.) on Irish west coast nursery grounds.

Paula S. Haynes , Deirdre Brophy, Fien De Raedemaeker, David McGrath.

Abstract

The feeding ecology of 0-group turbot *Psetta maxima* Linnaeus and brill *Scophthalmus rhombus* Linnaeus was investigated in 2009 on sandy beach nursery areas along the Irish west coast. The main prey groups present in the gut of both species were identified. Turbot consumed six types of crustaceans, in addition to polychaetes. In contrast, brill fed almost exclusively on mysids, even though nine taxonomic prey groups were identified in the sediment. Both turbot and brill avoided non-motile organisms such as gastropods and bivalves, which were present in high abundances in the sediment. The growth and condition of either turbot or brill, was not significantly related to the quantity or type of prey consumed, temperature, or salinity. A high incidence of feeding was detected for both turbot and brill over the duration of the study, suggesting that food was not limiting on west of Ireland nursery grounds. Temporal partitioning of settlement was detected between turbot and brill, suggesting that inter-specific competition for food on west of Ireland nursery grounds does not occur between these two flatfish species.

1. Introduction

Shallow inshore coastal areas serve as nursery grounds for many flatfish species during early life. These areas are described as highly productive habitats, with the availability of prey, considered to be one of the key factors determining the quality of flatfish nursery grounds in terms of growth and survival (Gibson, 1994). While several authors investigating the feeding ecology of juvenile flatfish have concluded that food availability on nursery grounds is never limited (Karakiri et al., 1991; Amara et al., 2001), others have reported that variability in the type and quantity of prey available both within and between nursery areas can arise (Van der Veer and Witte, 1993; De Raedemaeker et al., 2010). Seasonal fluctuations in benthic productivity within the nursery ground, can also affect the growth and survival of juveniles (De Raedemaeker et al., in press). Such differences may determine the abundance of juveniles eventually recruiting to the adult population, with larger individuals more likely to survive the nursery ground stage (Sogard et al., 2001).

Within a nursery ground, both intra and inter-specific competition, for available food resources can occur (Martinsson and Nissling, 2011). However, certain strategies have evolved to reduce competition both between and within flatfish species, thereby increasing the foraging efficiency and subsequent growth of individuals. Tactics exhibited by many flatfish species include temporal and spatial partitioning, whereby different species settle onto nursery grounds at different times throughout the year, and/or at different depths within the nursery. Resource partitioning, or different feeding habits have also evolved, with ontogenetic shifts in diet reducing intra-specific competition (Florin and Lavados, 2009). While competition is an important determinant of density-dependent mortality on nursery grounds, it may ultimately only arise if exceptionally high densities of juvenile flatfish occur (Nash et al., 2007).

In Ireland, turbot and brill are valuable non-quota commercial flatfish species, with the juveniles known to inhabit nursery grounds along the west coast of Ireland (Haynes et al., 2010a). In general, temporal partitioning between the two species occurs along the Irish west coast, with 0-group brill settling onto beaches in March and April (Haynes et al., in review) in July, whereas 0-group turbot do not arrive on the nursery grounds until later on in the year, in June and July (Haynes et al., 2011), and are present on beaches up until October/November (Pers. obs). However, on occasion, both 0-group turbot and brill of a similar size may co-occur, as a result of several cohorts spawned

throughout the year. This suggests that competition between these two morphologically similar species might arise (Piet et al., 1999).

Both 0-group turbot and brill are described as visual day light hunters, feeding primarily on moving organisms such as mysids and amphipods, as opposed to sedentary prey items (De Groot, 1971). While fish are reported to be the main choice of prey for the juveniles of both species > 10 cm (Holmes and Gibson, 1983; Sparrevojn and Støttrup, 2008a), studies have also found smaller turbot (3 - 5 cm, Aarnio et al., 1996; 2.5 – 6cm, Beyst et al., 1999), and brill (> 6 cm, Braber and De Groot, 1973; > 5 cm, Beyst et al., 1999), to include fish in their diet. In contrast to other juvenile flatfish such as plaice or flounder, turbot and brill are reported to feed on a narrow range of prey items (Beyst et al., 1999), with 0-group brill known to be highly selective in the type of prey that they consume (Cabral, et al., 2002). This restrictive diet may negatively affect the number of brill surviving to the end of the nursery ground stage, particularly if the preferred prey item within the inhabited nursery ground is scarce.

On the west coast of Ireland, recent studies have provided valuable baseline knowledge on the early life history of turbot (Haynes et al., 2010a, b, 2011). However, basic data on the biology and ecology of juvenile brill from this geographical location is lacking. The sparse distribution of brill, in addition to their inconsistent recruitment to nursery grounds in any location of the Northeast Atlantic, has resulted in very little published information being available in the literature. In an attempt to expand on, or improve the data previously established for juvenile flatfish on the west coast of Ireland, the feeding ecology and behavior of 0-group turbot and brill was investigated.

The objectives of the present study were to:

- 1) Describe the type of prey consumed by juvenile turbot and brill inhabiting nursery grounds, and investigate any differences in the availability of prey across months.
- 2) Examine any temporal, spatial, or resource partitioning between 0-group turbot and brill.
- 3) Identify the type of prey available in the sediment on nursery grounds, to determine if turbot or brill were actively selecting specific prey items.
- 4) Determine whether either the growth or condition of turbot and brill was related to the abundance or type of prey consumed, or temperature and salinity values within nursery locations.

2. Materials and Methods

2.1. Nursery grounds assessed

Four shallow sloping sandy beaches were assessed for 0-group turbot and brill along the west coast of Ireland (Figure 1). Inch and Brandon are located on the southwest of the country in Co. Kerry and Lahinch is on the west coast in Co. Clare; all three are exposed shores composed of coarse sediment. Silverstrand is composed of finer/soft sediment and is situated on the west coast, to the north side of Galway Bay.

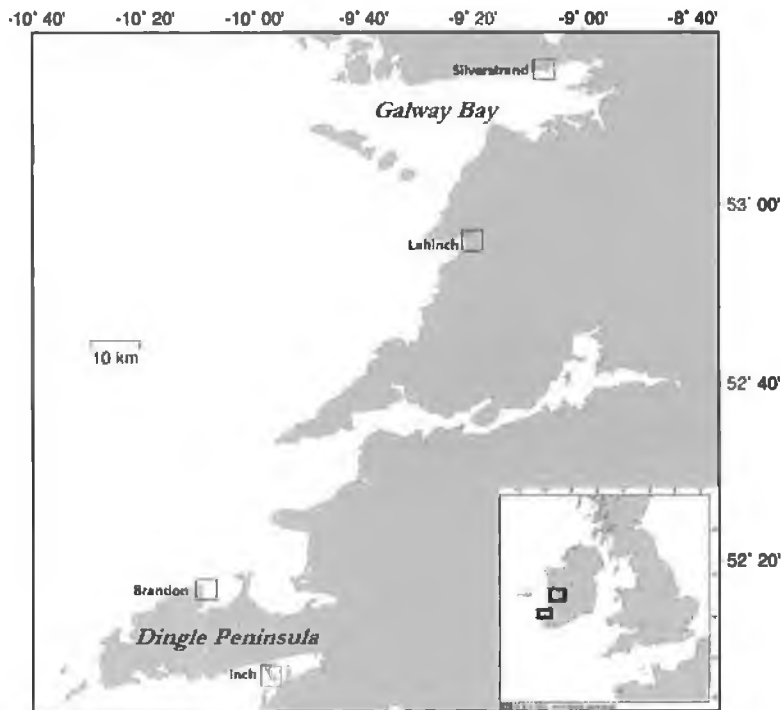


Figure 1: 0-group turbot and brill nursery grounds assessed along the west coast of Ireland.

2.2. Sampling procedure

The collection of fish was weather dependent and the number of sampling replicates taken from each beach was inconsistent (Table 1). Sampling on the nursery Silverstrand was undertaken between March and November and the remaining nursery grounds were assessed intermittently,

between May and September (Table). Fish were captured using a small beach seine, 5.5 m long and 2 m deep, with a 5×5 mm mesh size. Sampling was carried out at depths of between 0 and 1 m. 0-group turbot and brill are known to reside predominantly in shallow depths on nursery grounds (Aarnio et al., 1996; Sparrevohn and Støttrup, 2008; Draganik et al., 2005) and 0-group turbot in the Baltic Sea are reported to favor depths of between 0.2 and 0.6 m (Martinsson and Nissling, 2011). Sampling on a beach was carried out in a single day on a spring tide during daylight hours for the purpose of consistency. The number of hauls ranged between four and 13 depending on the beach. Preliminary identification of all 0-group flatfish captured in the beach seine was carried out on the shore using morphological characters. Juvenile flatfish were then placed immediately into liquid nitrogen, prior to being transferred to a - 80 °C freezer in the laboratory. Sampling was carried out at approximately one hour before the time of low tide. Sampling on Silverstrand was also undertaken in June. However, no 0-group flatfish were captured given the high level of weed present on this beach during two sampling trips.

Table 1: Numbers of 0-group turbot and brill collected in each month from Irish west coast nursery grounds. - denotes not sampled.

Month	March 30 th		April 25 th		May 22 nd , 23 rd , & 26 th		June 7 th & 22 nd		July 7 th , 16 th , 20 th , 21 st , 24 th , & 29 th		August 16 th -19 th , 21 st & 26 th		September 03 rd & 17 th		October 08 th & 22 nd		November 6 th	
Beach	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br
Inch	-	-	-	-	-	-	-	-	-	-	9	0	12	-	-	-	-	-
Brandon	-	-	-	-	-	-	-	-	0	10	3	0	-	-	-	-	-	-
Silverstrand	0	0	0	0	0	10	0	0	0	22	59	0	25	0	21	0	0	0
Lahinch	-	-	-	-	-	-	-	-	-	-	-	-	14	0	-	-	-	-

Bottom sea temperatures of the intertidal zone were recorded from randomly chosen locations (< 1 m depth) within each nursery ground on each sampling occasion, in addition to salinity. To investigate the availability of prey within nursery grounds, four Van Veen grab samples (0.025m²) were taken from randomly chosen areas where 0-group turbot and brill were captured (0 - 1 m),

within each beach on each sample date. Mean temperature and salinity values for each month are provided in Table 2.

Table 2: Mean temperature and salinity values recorded for each month on each nursery ground assessed. - denotes not recorded

Month	May		June		July		August		September		October	
Beach	Temp °C	Sal ‰	Temp °C	Sal ‰	Temp °C	Sal ‰	Temp °C	Sal ‰	Temp °C	Sal ‰	Temp °C	Sal ‰
Inch	-	-	-	-	-	-	17.2 (±0.2)	31.3 (±1.3)	16.7 (±0.2)	30.0 (±1.0)	-	-
Brandon	-	-	-	-	17.2 (±0.3)	27.6 (±1.6)	17.2 (±0.3)	27.6 (±1.6)	-	-	-	-
Silverstrand	11.9 (±0.1)	26.4 (±0.8)	43.7 (±0.4)	29.2 (±0.7)	17.9 (±0.2)	31.7 (±0.9)	17.9 (±0.2)	31.4 (±0.7)	16.0 (±0.8)	30.0 (±1.6)	15.1 (±0.1)	29.0 (±0.9)
Lahinch	-	-	-	-	-	-	-	-	16.8 (±0.2)	31.7 (±0.8)	-	-

2.3. Laboratory analyses

Frozen fish were removed from the freezer and allowed to thaw overnight. As newly settled 0-group turbot and brill are almost identical, fin ray counts, which are species specific (Wheeler, 1969) were made for all fish captured in order to verify that individuals had been correctly separated on the shore (Haynes et al., 2010b).

Sediment samples were sieved through a 0.5 mm mesh size, so as to remove larger particles and retain any benthic organisms for identification at a later stage (ostracods were the smallest benthic organism detected at < 1.5 mm). All remaining prey and sediment particles were preserved in 10 % formalin. Sediment samples were completely sorted under a stereoscopic microscope, with prey counted and identified to their main taxonomic group using the key by Hayward and Ryland (2003).

2.4. Morphological analyses

The standard length from the tip of the mouth to where the caudal fin begins was measured to the nearest 0.1 cm, and weight was measured to the nearest 0.1 g. The total abundance of prey present in the gut, stomach fullness, and the total length and weight of the digestive tract were recorded in order to assess whether any of these characters influenced the growth or condition of fish. Fish whose gut contents were emerging or absent were excluded from subsequent analyses. Stomach fullness was calculated by dividing the proportion of the gut containing prey (mm) by the total length of the gut (mm) to obtain a percentage. The preferential selection of prey from the sediment by juvenile flatfish was assessed using the Manly-Chesson selectivity index according to the following formula;

$$\alpha_i = \frac{(d_i/N_i)}{\sum_{j=1}^k (d_j/N_j)}$$

Where $i = 1, 2, \dots, k$ and k is the number of prey categories, d_i is the number or proportion of prey type in the diet, and N_i is the density or proportion of prey in the environment (sediment samples). Prey types which are consumed relative to their abundance in the environment or are not selected, will have $\alpha_i = 1/k_i$. $\alpha_i > 1/k_i$ indicates a preference for a particular prey type and $\alpha_i < 1/k_i$ indicates selection against a specific item of prey (Mittelbach, 2002).

2.5. Temporal and spatial partitioning

Temporal, spatial, and resource partitioning between 0-group turbot and brill was investigated between the months of May and October, on the nursery ground Silverstrand. Every month, the numbers of turbot and brill captured in each haul was recorded and the co-occurrence of the two species was examined. Gut content analysis was carried out for these fish in order to determine if there was any overlap in the prey consumed. Temporal partitioning was also investigated for 0-group turbot and brill collected in August and September on Silverstrand, over a six year period, as part of an annual juvenile flatfish survey carried out on west of Ireland nursery grounds (see Haynes et al., 2010a). The total number of fish captured on a particular beach was divided by the number of hauls carried out, to compare the relative abundances of turbot and brill in each month.

2.6. *Growth*

Otolith increment widths were used to derive an index of daily growth after settlement. The first six and seven post-settlement increments (corresponding to six and seven days after the deposition of the final accessory primordium (AP)), deposited by turbot and brill respectively, were measured to the nearest 0.1 μm along the longest axis. The selected number of increments for each species corresponded to the minimum number present on the otolith in the majority of individuals. Increments deposited upon completion of metamorphosis, or after the final AP, are more likely to represent the period when fish are feeding on the nursery (Geffen, 2007). Sagittal otoliths were removed and cleaned and one of the pair was randomly selected for analysis. Cracked or unreadable otoliths were rejected. The selected otolith was mounted on a slide in crystalbond, and polished until all increments in the region of interest could be clearly observed. Polished sections were examined using an Olympus BX51 compound microscope under a 1000X magnification, with analysis aided by Image Pro Plus Analyzer version 6.2 software.

2.7. *Condition*

Residuals of the length-weight relationship were used as a measure of condition in turbot and brill. This method of assessing condition is appropriate when dealing with a range of size classes (Blackwell et al., 2000). Residuals were calculated for each individual fish, using the regressions \log_{10} of length against \log_{10} of weight. Residuals of the length-weight relationship have previously been utilized to calculate the condition, and hence provide information on the habitat quality of 0-group flatfish (Gilliers et al., 2006). A similar condition index based on length and weight was used by Imsland et al., (1995) for reared turbot juveniles. A large negative mean residual value signifies that fish are in poor condition; a large positive mean residual value is indicative of good condition, and a residual value close to zero indicates that fish are in average condition (Blackwell et al., 2000). As the prey type and quantity of consumed is known to have an effect on the growth and condition of juvenile flatfish, the biodiversity Shannon-Wiener index describing the diversity of prey in the gut was calculated for each individual, and plotted against the residual condition.

2.8. Data analyses

Pearson's correlation was used to investigate if growth and condition were related to prey abundance and type, temperature and/or salinity using the statistical package MINITAB 15. Prey composition and abundance in the gut of turbot and brill were analyzed using a non-metric multidimensional scaling (MDS) ordination technique in PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 statistical package (Clarke, 1993). Where large differences in scale occurred between variables the data were square root transformed and a Bray-Curtis coefficient was calculated to produce a similarity matrix. To investigate differences in the taxonomic composition of prey in the gut between months, a one-way nested analysis of similarities (ANOSIM) was performed. Significant differences were explored using the R-statistic value, whereby a value close to one indicated a large difference between samples, with an R value close to zero indicating a low difference between samples. Similarity percentages (SIMPER) were generated to determine the main taxonomic groups accounting for up to 90 % of all prey consumed by turbot and brill on each beach. Given the low number of both turbot and brill collected on beaches differences in the prey consumed by fish inhabiting separate locations were not statistically investigated, but were described. Average values of the investigated parameters are also calculated \pm the standard deviation (SD).

3. Results

3.1. Gut content

3.1.1. Turbot

A total of nine juvenile turbot collected over the duration of the study had empty guts; these tended to be smaller individuals (< 3.5 cm) and were not included in the analyses. Across beaches in the present study, juvenile turbot (4.5 -7.5 cm) consumed a total of 7 taxonomic groups of prey, with four groups dominating the gut content of all captured individuals. The average % (n) of prey items present in the gut of individual turbot is presented in Figure 2.



Figure 2: Plot depicting the similarity in the diets of 0-group turbot collected on the nursery ground Silverstrand between August and October. Each symbol represents an individual fish.

The more detailed temporal analysis of the nursery ground Silverstrand revealed that juvenile turbot (2.5 -7.5 cm) revealed that turbot consumed a total of 8 taxonomic groups of prey between August and October, with four groups dominating the gut content of all captured individuals. The MDS plot showed that the taxonomic prey groups found in the guts of 74 turbot on Silverstrand were similar across months with a large amount of overlap observed (Figure 3). ANOSIM detected no significant difference in the prey composition over the months of August, September, and October on Silverstrand ($R = -0.03$, $p = 0.626$). The diet of turbot collected from Silverstrand between August, September, and October was characterized by cumaceans (70 %), mysids (15 %), polychaetes (6 %), and amphipods (1.3 %). Additional prey items which featured in low abundances (< 10 %) in the diet of turbot on Silverstrand included isopods, decapods, and amphipods. An average % fullness of the gut of all turbot calculated at $70 (\pm 3) \%$.

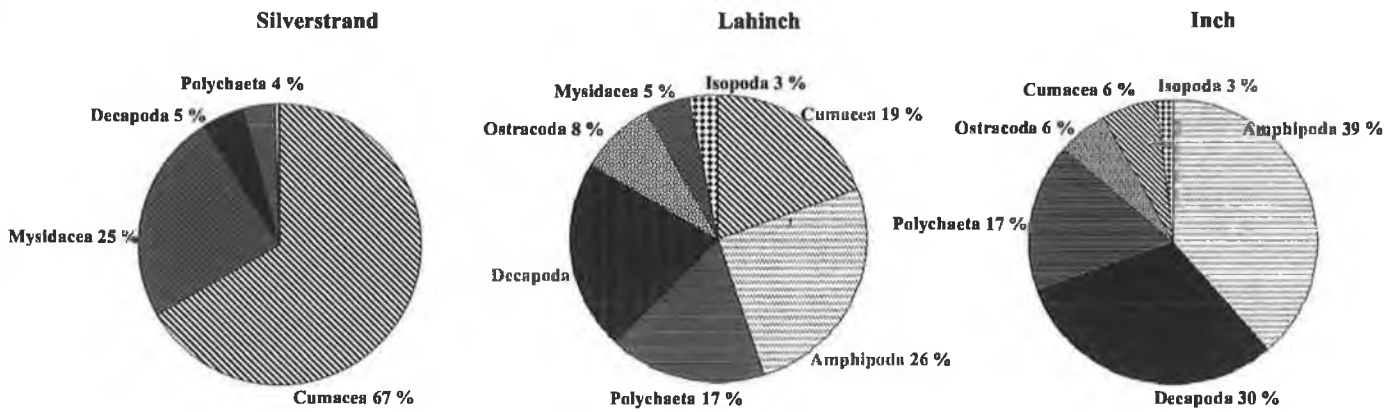


Figure 3: Average % of prey groups present in the gut of individual 0-group turbot on west of Ireland nursery grounds.

3.1.2. Brill

Juvenile brill consumed a total of three taxonomic prey groups; their gut contents were dominated by mysids and contained smaller proportions of amphipods and cumaceans. The MDS plot revealed a large amount of overlap in the type of prey consumed by 25 brill in May and in July on Silverstrand, with ANOSIM finding no significant difference in the prey items consumed ($R = 0.028$, $p = 0.247$). The average % gut fullness of brill collected on Silverstrand in May and July was 85 ± 12 (SD) %. The prey consumed by brill was also similar across beaches, consisting predominantly of mysids, regardless of the habitat occupied (Figure 4).

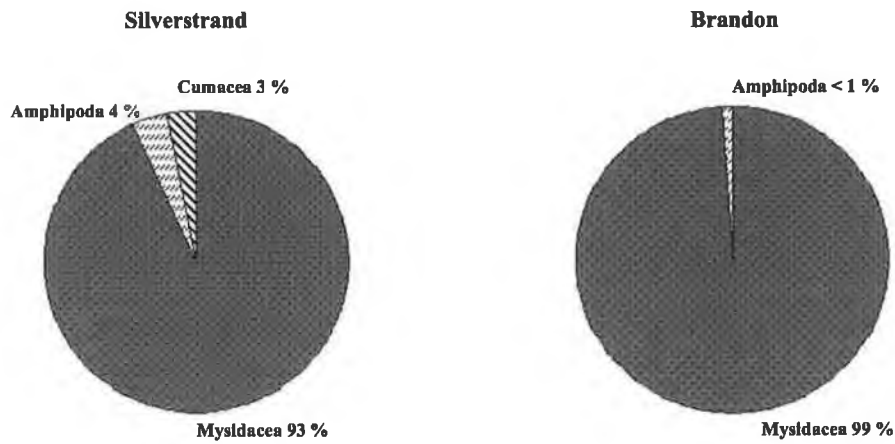


Figure 4: Average % of prey groups present in the gut of individual 0-group brill on west of Ireland nursery grounds.

3.2. Prey availability

A total of 9 groups of prey items were identified in the sediment across all four beaches, and consisted predominantly of crustaceans, polychaetes, bivalves, and gastropods (Figure 5). ANOSIM did not detect a significant difference in the number of prey items between hauls ($R = 0.012$, $p = 0.620$).

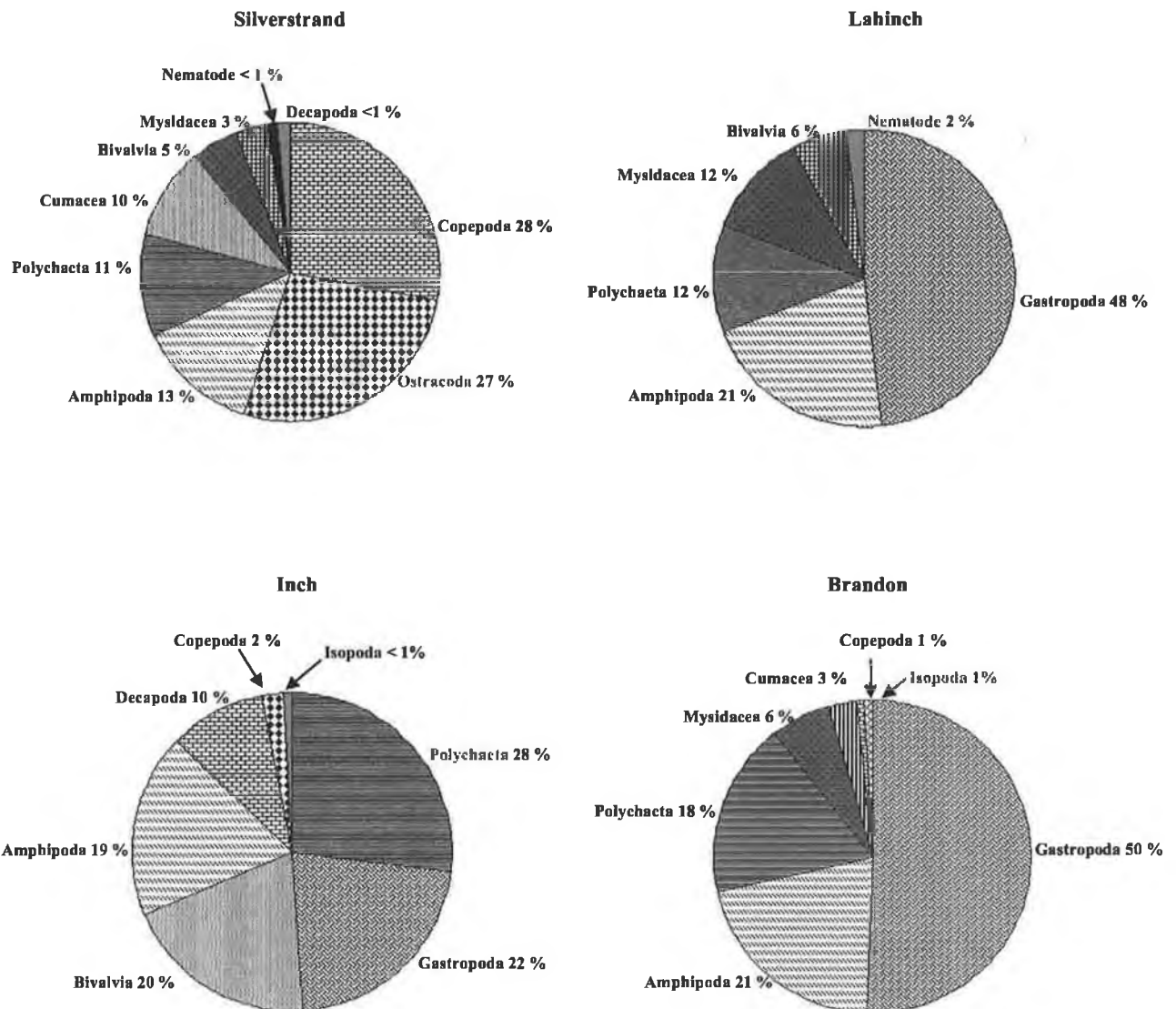


Figure 5: Average (%) of all prey groups present per grab sample (0.025m²) on west Ireland nursery grounds.

3.3. Prey selectivity

The Manly-Chesson Index of prey selectivity showed that turbot exhibit a positive preference for six groups of crustaceans, in addition to polychaetes, with the main taxonomic group selected differing between nursery grounds. Juvenile brill showed a preference for mysids and amphipods.

The highly abundant sessile organisms, gastropods, and bivalves were avoided in all areas by both turbot and brill (Table 3).

Table 3: Prey selectivity calculated using the Manly-Chesson Index for juvenile turbot and brill on west of Ireland nursery grounds. + shows a preference for a particular prey item, while - represents selection against a prey item. Where fish were not present is denoted by N/A.

<i>Beach</i>		<i>Inch</i>	<i>Brandon</i>	<i>Silverstrand</i>	<i>Lahinch</i>
<i>Species</i>	<i>Fish</i>				
C. Polychaeta	Turbot	-	n/a	-	+
	Brill	n/a	-	-	n/a
C. Bivalvia	Turbot	-	n/a	-	-
	Brill	n/a	-	-	n/a
C. Gastropoda	Turbot	-	n/a	-	-
	Brill	n/a	-	-	n/a
O. Amphipoda	Turbot	+	n/a	-	+
	Brill	n/a	-	+	n/a
O. Mysidacea	Turbot	-	n/a	+	+
	Brill	n/a	+	+	n/a
O. Cumacea	Turbot	-	n/a	+	-
	Brill	n/a	-	-	n/a
O. Ostracoda	Turbot	+	n/a	-	-
	Brill	n/a	-	-	n/a
O. Decapoda	Turbot	+	n/a	+	-
	Brill	n/a	-	-	n/a
O. Copepoda	Turbot	-	n/a	-	-
	Brill	n/a	-	-	n/a
O. Isopoda	Turbot	+	n/a	-	-
	Brill	n/a	-	-	n/a

3.4. Temporal partitioning

The patterns of distribution of 0-group turbot (2.7 - 7.5 cm) and brill (2.9 - 7.5 cm) on the nursery ground Silverstrand suggested that temporal partitioning occurred between the two species; brill occurred in catches from May until August while turbot were found in the catches from August to October with peak densities occurring in early September (Figure 6).

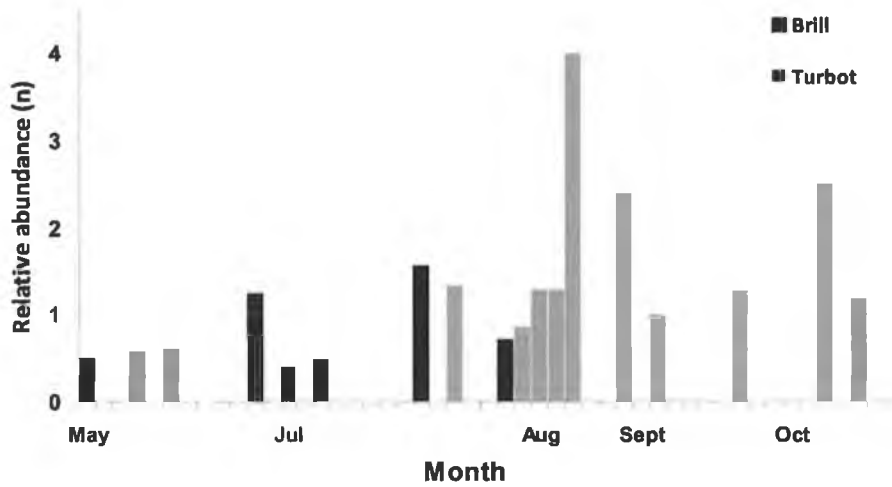


Figure 6: Total abundance of 0-group turbot and brill collected from the nursery ground Silverstrand (May-October, 2009).

There was an interval of 16 days when no sampling occurred, between the last recording of brill and the first recording of turbot; however, it is unlikely that either species occurred at high densities during this period as peak settlement of turbot on the beach occurs in August/September (Haynes et al., 2011), whereas and brill settle in March/April (Haynes et al., in review). Surveys conducted in August and September over a six year period also showed little temporal overlap in the distribution of turbot and brill (Figure 7).

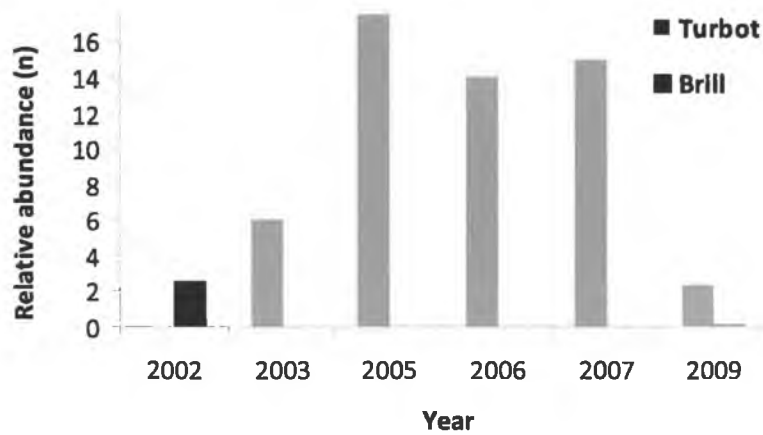


Figure 7: Total abundance of 0-group turbot and brill collected from Silverstrand on the west of Ireland on a single sampling occasion in August/September; 2002 - 2009.

3.5. Temperature and salinity

Across nursery grounds bottom sea temperatures ranged between 11.8 and 18.2 °C, with salinity values of between 25 ‰ and 34 ‰ also recorded between May and October.

3.6. Growth and condition correlations

The growth and condition of each individual fish was not related to % gut fullness or the abundance (n) of prey in the gut for turbot or brill. Mean growth and condition for each species on each sampling visit was not correlated with temperature or salinity values recorded on nursery grounds ($p > 0.05$). There was no significant correlation between the growth or condition of either turbot or brill, and the Shannon-Wiener prey index ($P > 0.05$).

4. Discussion

Juvenile turbot inhabiting nursery grounds along the west coast of Ireland consumed predominantly cumaceans, mysids, amphipods, decapods, and polychaetes during the months when they were present. The limited data available from three nursery grounds indicated a high degree of spatial overlap in the taxonomic prey items ingested by juvenile turbot although there was a lower incidence of cumaceans and a higher abundance of amphipods and decapods in the gut of fish collected from the two exposed shores (Lahinch and Inch), compared to the sheltered shore (Silverstrand). Although more replicate sites would be needed to confirm that these differences relate to the level of exposure of the beaches, the observations may reflect differences in the habitat structure between the locations (Nissling et al., 2007; Florin et al., 2009).

With the exception of cumaceans, the main benthic groups consumed by juvenile turbot along the Irish west coast were similar to those reported in studies of other nursery grounds in the Northeast Atlantic. Juvenile turbot were observed to feed predominantly on mysids and crangon in the Kattegat (Sparrevohn and Støttrup, 2008a) and on amphipods and mysids in the Baltic Sea (Florin and Lavados, 2009); polychaetes were also present in the guts of turbot in the North Sea (Jones, 1973). In contrast to other studies (Sparrevohn and Støttrup, 2008; Aarnio et al., 1996; Ustups et al., 2007; Florin and Lavados, 2009), fish were notably absent from the diet of 0-group turbot in the present study; this may reflect the size range of the turbot examined. Although gobies are reported to occur in the diet of juveniles < 6 cm (Aarnio et al., 1996; Beyst et al., 1999), in many areas fish are not included as a food item until turbot reach larger sizes: 7 - 8 cm in the Baltic Sea (Stankus, 2003), 10 cm along the Spanish coast (Iglesias et al., 2003), between 10 and 15 cm in the Southern North Sea and the Irish Sea (Braber and De Groot, 1973; Jones 1973). Alternatively, the absence of fish in the diet may be due to the low abundance of suitable fish prey on the nursery grounds (Beyst et al., 1999); no gobies were caught in beach seines on the nursery grounds in the current study (personal observation).

Brill fed on a much smaller range of prey items than turbot in the current study, their diet consisting almost exclusively of mysids on both beaches examined. Selection of mysids by brill is common in other locations (Cabral et al., 2002). Brill reportedly start to consume fish at relatively small sizes (5 cm) (Braber and De Groot, 1973; Beyst et al., 1999). However, as with turbot, no fish were identified in the gut of juvenile brill collected on the Irish west coast. Whether or not turbot and

brill here are forced to consume less favorable prey items such as crustaceans in the absence of fish is not known, though this has been previously suggested for juvenile turbot occupying other areas (Nissling et al., 2007). Consuming less favorable prey can negatively affect the growth and hence survival in juvenile flatfish (Sparrevohn and Stottrup, 2008).

In this study, both brill and turbot avoided non-motile prey items such as gastropods and bivalves, which were present in high numbers in the sediment but were not identified in the diet of either flatfish species. This is consistent with the known feeding behavior of both turbot and brill juveniles, which are more likely to consume mobile, fast moving prey in preference to sessile organisms (Holmes and Gibson, 1983). In general, juvenile flatfish are opportunistic feeders and are reported to consume the most available prey item within the nursery (Cabral et al., 2002; Darnaude et al., 2001). However, in this study we found evidence of selective feeding in 0-group turbot and brill. Turbot on Silverstrand preferentially fed on cumaceans, mysids, and decapods rather than the more abundant copepods and ostracods. A preference for mysids has previously been reported in the Kattegat where 0-group turbot actively consumed mysids and gobies, even in the presence of similar abundances of chironomids and amphipods (Florin and Lavados, 2009). Juvenile brill exhibited a high level of prey selectivity for mysids, followed by amphipods, and did not consume the most abundant type of prey available as indicated by the sediment analysis.

In contrast to the more varied feeding behavior noted for turbot, juvenile brill exhibited a high level of prey selectivity for mysids, followed by amphipods, and did not consume the most abundant type of prey available as indicated by the sediment analysis. The results suggest that turbot are more flexible than brill in terms of feeding behaviour and may more readily adapt their prey choice to in response to food availability; this may partly explain the higher abundance and more widespread distribution of turbot on west of Ireland nursery grounds. Estimates of prey abundance in the environment relied on four grab samples from each beach on each sampling date. However, there was no significant difference detected in the number of total prey items collected per haul on each beach. This suggests that although limited, the sediment data collected by the grab provided an accurate description of the feeding conditions within each beach. While the prey selectivity results must therefore be interpreted with caution, they do signal some important differences in feeding strategies between turbot and brill and also indicate that feeding behaviour can vary between nursery areas. A more comprehensive sediment analysis would help to substantiate these observations.

Very little temporal overlap was observed in the distribution of juvenile turbot and brill on west of Ireland nursery grounds. In general, the two species did not co-occur on the nursery ground Silverstrand between May and October in 2009 or in August/September over a six year period. This may not reflect direct avoidance of competition by the two species; the timing of spawning and subsequent development rate of eggs and larvae are likely to have evolved to coincide with favourable conditions during the larval phase, such as prey availability, an absence of predators, or suitable transport processes (Bailey et al., 2005). In any case the observed temporal segregation of settlement in turbot and brill will either directly or indirectly reduce inter-specific competition on the nursery grounds. When two species of 0-group juvenile flatfish co-occur, negative interaction or competition for available resources can occur; feeding in juvenile turbot in the Baltic Sea was found to be negatively correlated with juvenile flounder densities (Martinsson and Nissling, 2011). In this study, there was a high incidence of feeding for all captured individuals over the duration of the study and very few fish had empty guts. This suggests that food was not limiting and these fish did not experience competition when foraging for prey. Temporal partitioning is likely to maximize the feeding success of 0-group juvenile flatfish that inhabit the same nursery grounds.

Growth and condition of turbot and brill were not related to the prey diversity, % fullness of the gut, prey numbers in the gut, or mean temperature and salinity values recorded on nursery grounds. A significant positive relationship was previously observed between the condition of plaice on western Irish nursery grounds, and the diversity of prey items present in the gut (De Raedemaeker et al., 2010). However, that study also observed considerable spatial and temporal variation in diet which was absent in the current study. Attempting to link otolith growth with biotic or abiotic variables can also be problematic, as otolith growth responds more gradually to changes in feeding conditions and metabolic rate, and represents a running average of fish growth rather than an instantaneous measure (Campana and Neilson, 1985). A longer time series or additional indices of growth and condition may be required, in order to identify any significant relationship between the investigated parameters. Gilliers et al., 2006 recommends that with several biological indicators are used for assessing the habitat quality of 0-group flatfish.

The present study has described the feeding ecology and behavior of 0-group turbot and brill in a previously understudied location within their distribution range. Similar to other locations in the Northeast Atlantic, turbot and brill on the Irish west coast consumed a narrow range of prey groups. Turbot and brill appear to target different prey groups, settle onto the nursery areas and occur at low

densities; competition between these two morphologically similar flatfish species is therefore unlikely. The high prey selectivity exhibited by brill, both here and also in other locations, may explain their exceptionally low occurrence in all areas of the Northeast Atlantic (Gibson, 1994). Nonetheless, given the high incidence of feeding observed for both turbot and brill over the duration of the present work, food did not appear to be limited on west of Ireland nursery grounds.

Chapter 8

General discussion

Conclusions

General Discussion

1. Methods of identification for 0-group flatfish using fin rays

Juvenile flatfish surveys carried out along the west coast of Ireland revealed that pairs of recently settled flatfish species, which were morphologically similar in appearance, co-occurred on sandy beach nursery grounds. In the absence of confirmatory identification techniques such as genetics,



Figure 1: Adult turbot (Anon, Fishbase.org)

fin ray counts were deemed to be a reliable tool to correctly distinguish between the similar pairs of flatfishes; plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*), and turbot (Figure 1) (*Psetta maxima*) and brill (*Scophthalmus rhombus*) (Haynes et al., 2008, 2010b; Chapters 2 & 3). The number of fin rays recorded for west of Ireland turbot and brill were outside of the ranges previously reported in the literature. This observation emphasises the need for caution when

utilising fin rays to identify 0-group flatfish, as the counts can vary depending on the location, and also the time at which they are recorded. The number of fin rays exhibited by fish is determined during the larval stage, and is influenced by environmental parameters such as temperature (Lindsey, 1988). So the observed discrepancy between the fin ray counts observed here and those reported in the literature may reflect geographic variation in the larval rearing environment.

Although rarely considered in favour of more advanced techniques such as genetics, variability in meristic characters such as fin ray numbers, can be used in combination with other methods including morphometrics or DNA (Cadrin, 2000), to delineate fish stocks (Swain and Foote, 1999). For example, morphometric and meristic measurements have proved more useful than genetic and tagging data for distinguishing between some herring stocks (Armstrong and Cadrin, 2001). While spawning stocks may not be genetically isolated, the rate of exchange between them may be so low as to justify their separate management. In these cases, phenotypic traits such as meristics can help to define stock boundaries.

Spatial variability in fin ray counts of brill was detected in the present thesis. This corresponded with spatial variation in otolith microstructure, suggesting that individuals inhabiting the two nursery areas were of different larval origin (Haynes et al., in review). As meristic traits are established during the larval phase and are not subsequently altered, the observed variation in fin

ray counts could be useful, in combination with other markers, for determining the larval or juvenile origin of adult brill from the west coast of Ireland. However, a more in-depth investigation, covering a wider geographical range and over a longer time period would be required in order to fully describe spatial variation in fin ray counts and to establish if they remain consistent between years. Cadrin et al., (2004) advocates the use of “multidisciplinary stock identification” using various genetic, morphometric, and meristic disciplines when discriminating between fish stocks. A combination of meristic characters, including fin rays and gill rakers, and morphometrics, were successfully used to discriminate between Mediterranean horse mackerel *Trachurus mediterraneus* stocks (Turan, 2004), thus emphasising the merits of the multi-marker approach.

2. Recruitment of flatfish to nursery grounds

Over the eight years of flatfish surveys on west of Ireland nursery grounds, juvenile plaice were the most abundant species present. Moreover, plaice successfully recruited to nine of the eleven inshore locations in each year of the eight year study. This high incidence and widespread distribution of juvenile plaice is a common finding in other locations, including the Irish Sea (Nash et al., 1994), the Scottish coast (Gibson et al., 1996), along the English Channel (Selleslagh and Amara, 2008), and also on the Belgian coast in the North Sea (Beyst et al., 1999). Juvenile turbot were the second most abundant flatfish species present on Irish nursery grounds. However, in contrast to plaice, turbot juveniles appeared only at a few specific locations and at much lower abundances. This finding is in agreement with earlier studies, which reported turbot to be more selective in their nursery habitat requirements in comparison to other flatfish species (Gibson, 1994). Earlier studies on juvenile turbot have also stated that this species is found only on exposed nurseries (Jones, 1973; Nissling et al., 2007). However, juvenile turbot along the west coast of Ireland settled consistently onto both sheltered (Figure 2) and exposed nursery habitats. This suggests that turbot may be adapted to a wider range of nursery habitats than has previously been documented.



Figure 2: Inch on the southwest coast of Ireland

In contrast to plaice and turbot, the recruitment of brill to nursery grounds along the west coast of Ireland was highly inconsistent between locations and years (Haynes et al., in press, b; chapter 7).

Furthermore, when juvenile brill were captured on Irish nursery grounds, numbers were inadequate for the detection of any population trends. This exceptionally low occurrence of juvenile brill, and the general lack of published information available for this species in other areas of the Northeast Atlantic, suggests that this flatfish is not common. Adult brill are seldom captured in Irish Groundfish surveys (Anon, 2010b), and low abundances were also reported by Amezcua and Nash (2001) in surveys conducted in the Irish Sea. Surveys conducted in both the eastern English Channel and in southern North Sea, found that the relative abundances of brill and turbot were extremely low in comparison to other flatfish species such as plaice, sole (*Solea solea*), and dab (*Limanda limanda*) (Parker-Humphreys, 2005). Catch summary statistics of turbot and brill collected during the International Bottom Trawl Survey (IBTS) in the North Sea, also provide evidence that juvenile abundances of both of these flatfish species are low (Anon, 2010c). In the present research, juvenile brill occurred primarily in sheltered habitats. Gibson (1994) concluded that similar to turbot, brill are highly selective in their nursery habitat requirements, and that this would subsequently result in lower numbers of juveniles recruiting to the adult stocks. The possibility that brill settle onto sandy beach habitats along the west coast of Ireland, which were not surveyed in this study cannot be excluded. Brill might settle in deeper waters (> 2 m), as the nursery ground habitats of juvenile flatfishes are known to vary from deep offshore waters, to shallow inshore locations (Miller et al., 1991). Though depths > 2 m were not assessed in the present work, it is unlikely that the majority of 0-group brill were residing in sub-tidal habitats. For one particular location on the west coast of Ireland (Silverstrand), very few juvenile brill were collected during a beam trawling survey, carried out over a two year period, in depths of between 2 and 5 m (De Raedemaeker, Pers. Comm.). Beach seine hauls at the same location (Chapter 7, this thesis) captured comparatively high numbers of 0-group brill. This does not reflect differences in the efficiency of the two gear types as the beam trawl is more efficient for capturing juvenile flatfish in comparison to the beach seine (Kuipers et al., 1992). Therefore, 0-group brill most likely occur at higher densities in shallow waters (< 2 m), at least at Silverstrand.

Along the west coast of Ireland, individuals of both plaice and turbot were consistently collected in each year of the study, and failure to recruit to their characteristic nursery was rarely observed for either species. However, whether this finding infers consistent or good recruitment of plaice and turbot to the adult stocks is not known. Episodic peaks in recruitment or, exceptionally strong year classes of flatfishes can occur; for example in the North Sea there were strong year classes of plaice in 1963, 1981, 1985, and 1996 (Millner et al., 2005) while the years 1947, 1958, 1963, and 1987 produced strong year classes of sole (Millner and Whiting, 1996). This high survival of eggs and larvae is reported to sustain high recruitment to the fishery for at least a decade, in addition to

producing subsequent strong year classes (Secor, 2007). Along the west coast of Ireland, no obvious peaks in the abundance of any flatfish species were noted over the duration of the study. This may accurately reflect trends in the stock during that time period. However the possibility that the location and timing of the surveys were not appropriate for detecting peaks in juvenile abundance must also be considered. The juvenile flatfish surveys were only undertaken in either August or September of each year. Strong year classes may not be detected if there is substantial migration into deeper water before August. Plaice and brill first settle onto nursery grounds along the Irish west coast in March (Allen et al., 2008) and have reached a size of up to 11 cm and 9 cm respectively by September (Haynes et al., in press (a)). While emigration of larger individuals may have commenced by the time the surveys are undertaken, Burrows et al., (2004) have shown that 0-group plaice display strong site fidelity, and are unlikely to move distances > 200 m outside of the nursery. Furthermore, throughout the eight year survey, high numbers of both 1- and 2- group plaice were captured. Both 1- and 2-group turbot and brill were also captured in these surveys, though their numbers were substantially lower in comparison to plaice. These findings suggest that it is not just 0-group individuals which utilise nursery grounds on the Irish west coast in September. It is therefore unlikely that substantial emigration has commenced, given the high number of 1-, and to a lesser extent 2-group individuals which are also present. Indeed, 1- and 2- group plaice have been found to remain within their original coastal nursery area before eventually moving offshore to deeper waters and recruiting to the adult stock (Lockwood, 1974).

It is improbable that there are any substantial areas not surveyed in this thesis and previous surveys for juvenile flatfish along the Irish west coast, which support high abundances of 0-group flatfish. Throughout the eight year survey, most of the suitable habitat; that is sandy beaches was assessed. Separate beach seining surveys were also carried out along the northwest coast, where very low, if any, numbers of 0-group plaice, turbot, or brill were captured (O'Callaghan, pers. comm.). Inland Fisheries Ireland have also conducted annual fish surveys of coastal, or transitional waters on the northwest coast of the country, using beach seining, fyke netting, and beam trawling. Very low numbers of plaice and zero abundance of turbot and brill were captured in these surveys (Anon, 2008, 2009b). This implies that the sandy beaches assessed in the annual juvenile flatfish survey represent the key flatfish nursery grounds along the Irish west coast.

Climate change is likely to have a negative impact on flatfish populations. In the Northeast Atlantic predicted future changes include an increase in sea temperature, and changes in the direction and strength of prevailing winds, productivity, and salinity, which will vary depending on the geographic location. Although knowledge of the factors influencing all life stages of fish is

necessary to predict the effects of climate change on populations, it is in the early life stages that fish will be most negatively affected (Rijnsdorp et al., 2009). Any changes in either temperature, or the direction of currents running between the spawning and nursery grounds is likely to have a negative effect on abundances of surviving eggs and larvae (Rijnsdorp and Van der Veer, 2008). This may be of particular relevance for turbot and plaice along the Irish west coast, given that higher abundances of both species were found on nursery grounds in years when sea temperatures were colder during the pelagic stage, as observed in the current thesis. Colder sea temperatures during the pelagic and early demersal stages of flatfish are believed to significantly reduce the abundance of predators, which are more sensitive to the drop in temperature (Rijnsdorp and Van der Veer, 2008). Hence, any increase in temperatures during both the pelagic and juvenile stage, is likely to increase the abundances of predators in the pelagic stage, or result in the earlier arrival of predators onto nursery grounds, thus increasing the predation rates of newly settled flatfish (Rijnsdorp and Van der Veer, 2008).

While juvenile flatfish may respond to higher temperatures on the nursery ground by moving into cooler deeper waters as in the North Sea (Van Keeken et al., 2004), this may make individuals more vulnerable to predation, which is considered to be higher at greater depths (Gibson et al., 2002). While any increases in temperature on west of Ireland nursery grounds may result in the redistribution of juveniles to more northerly nursery grounds, these areas may not offer habitats of high quality, in terms of supporting high abundances of flatfish experiencing good growth and condition. Changes in productivity are thought to have resulted in food limitation, and hence lower growth of 0-group plaice and sole towards the end of the nursery ground stage on North Sea nursery grounds, (Teal et al., 2008), likely making smaller individuals more vulnerable to mortality. Given the influence of temperature and hydrodynamics on the pelagic stages of flatfish (Riley et al., 1981; Nielsen et al., 1998; Bolle et al., 2009; Van der Veer et al., 2009), the potential impacts of climate change should be considered in future studies.

3. Spatial and temporal trends in abundance, length, and condition of 0-group flatfish.

Juvenile flatfish assessments of Irish west coast nursery grounds revealed both spatial and temporal differences in the abundance, length, and condition of plaice, turbot, and brill. This variability in juvenile flatfish investigations is common, and is reported to arise in response to fluctuations in a multitude of biotic and abiotic factors (Gibson et al., 1996). In the present thesis, some general trends were detected in the abundance, length, and condition, of juvenile flatfish species, which appeared to be related to the quality of particular nursery habitats. There were several findings

which indicated that the nursery ground Inch (Figure 2), in the southwest of the country was a habitat of good quality. Firstly, this nursery was observed to support, more often than not, a higher abundance of both plaice and turbot over the eight year flatfish survey. Given the large surface area of Inch, a higher number of juveniles may therefore join the adult stocks from this location (Rijnsdorp et al., 1992). Turbot also exhibited significantly higher growth rates during the early stages of settlement on Inch over a three year period, providing further support for the hypothesis that Inch is an optimal nursery habitat for this species (Haynes et al., 2011; chapter 6). In a separate investigation at the nursery ground Inch, juvenile plaice also displayed higher recent growth rates in comparison to other nursery locations (De Raedemaeker et al., 2010). Consistently larger fish, exhibiting good condition on Inch, would be less likely to suffer size-selective predation mortality, and would be more likely to survive and recruit to the adult stock (Sogard, 1997).

The present study also found evidence of sub-optimal nursery grounds. Over the eight year juvenile flatfish survey, both turbot and plaice collected from the nursery ground Ventry were consistently smaller in length. Furthermore, juvenile plaice inhabiting this beach also displayed slower growth rates (De Raedemaeker et al., 2010) and were in poor condition (Haynes et al., in press (a); chapter 5) compared to plaice in other areas. This could make both plaice and turbot more vulnerable to mortality, given that faster growth experienced by juvenile flatfish on the nursery will reduce the time during which a fish is likely to be predated upon (Taylor, 2003). Hence, survival is likely to be greatest on nursery grounds where juvenile flatfish experience optimal growth rates (Gibson, 1994; Sogard et al., 2001). The relatively consistent trends revealed in the abundance, size, and condition of west of Ireland juvenile flatfish species may help to define and protect essential high quality flatfish habitats.

4. Establishment of a recruitment index using abundances of 0 and 1-group flatfish.

An essential prerequisite to juvenile flatfish research is the type of gear chosen for assessments, which can influence both the density estimates and also the size of the fish captured. There are large differences in the efficiency of the gear selected for juvenile flatfish surveys (Gibson, 1993; Nash et al., 1994b), with beach seines (Figure 3) reported to have highly variable catch efficiencies for juvenile flatfish, ranging between 40



Figure 3: The smaller beach seine utilised for capturing 0-group flatfish on west of Ireland nursery grounds.

and 90 % (Pierce et al., 1990). Kuipers et al., (1992) estimate that the efficiency of a beam trawl for capturing juvenile plaice is around 30 %, and given their fixed width, beam-trawls are considered to have a higher efficiency for estimating juvenile flatfish abundances on nursery grounds, in comparison to other sampling methods such as beach seines. Other authors suggest that abundances of fish captured in trawls are underestimated (Wennhage et al., 1997), with Gibson et al., (1996) recommending cross calibrations between the various types of gear available for juvenile flatfish investigations, in addition to the use of at least two gear types, as no single fishing method is considered to be 100 % reliable. Inaccurate abundance estimates of juvenile flatfish may be obtained, if the sampling conditions affecting the efficiency of the gear type vary over the duration of a population study. Factors known to influence the efficiency of the gear include substrate type, temperature, and weather conditions (Kuipers et al., 1992). However, while flatfish abundance estimates may vary between gear types, and the juvenile densities observed along the west coast of Ireland may not be comparable with those reported in other areas using different fishing methods, the sampling conditions in the present thesis remained consistent throughout the eight year time series. Results should therefore provide reliable estimates of the relative abundance of juvenile flatfish and a good indication of fluctuations in the juvenile populations. This is supported by the detection of consistent signals, such as the relationship between 0-group turbot and plaice abundances and spring temperatures in the southwest region, and the consistently high relative abundances of both flatfish species on some beaches.

Many studies have identified significant relationships between juvenile flatfish abundances and environmental conditions experienced during the larval stage (Nielsen et al., 1998; Henderson and Seaby, 2005; Van der Veer et al., 2009). While these studies undoubtedly provide valuable insights into the processes influencing recruitment throughout the early life stages, accurate prediction of the number of juveniles eventually recruiting to the adult population has not yet been achieved. In the present thesis, abundances of 0-group plaice collected from nursery grounds over a six year period were not related to the number of 1- and 2-group individuals captured in Irish Groundfish surveys in subsequent years off the west coast of Ireland. When attempting to establish a recruitment index, accurate estimates of abundance for the species of interest, collected at the appropriate time when the year class strength is set, is required. 0-group plaice in the present thesis were collected over a one week period during the summer months in each year of the flatfish survey. As discussed above, sampling conditions remained consistent throughout the eight year time series. The results should therefore provide reliable estimates of 0-group flatfish relative abundances and a good indication of fluctuations in the juvenile populations.

Previous juvenile flatfish investigations have shown that the abundance 0-group plaice were only correlated with numbers of 1-group fish at a specific point in the nursery period, when immigration of new individuals to the population had ceased, and emigration of larger fish into deeper waters had not yet commenced (Nash and Geffen, 2000). If substantial emigration of larger 0-group plaice had commenced prior to the juvenile flatfish survey in August/September, this could confound estimates of juvenile abundance. However, as discussed in section 3, emigration of 0-group plaice is unlikely to have commenced, given the large number of 1-group plaice collected in all years of the survey in September. On an Irish Sea nursery, Nash et al., (1992) captured overwintering 1- group fish (September – April) in depths of up to 10 m. Based on these previous findings, the spatial coverage of the Irish groundfish survey may not be appropriate for estimating abundances of 1- and 2- group plaice, as it does not assess shallow inshore areas.

There is little information available regarding the movements or migration patterns of 0-group turbot or brill within nursery habitats. It is therefore difficult to evaluate whether or not shallow water surveys are appropriate for establishing recruitment indices for these species. 0-group turbot are reported to remain predominantly in shallow waters (< 2 m) on the nursery (Riley et al., 1981). However, individuals have been found at atypical depths of up to 8 m, in response to a lack of suitable prey in shallow areas (Sparrevohn and Støttrup, 2008). At shallow depths, predators are, in general, less abundant and there is a higher availability of food (Gibson, 1994; Gibson et al., 2002). Hence, the area or zone occupied by juvenile flatfish on the nursery ground will represent a 'trade-off' between acquiring suitable prey, and the risk of being predated upon (Burrows et al., 1994). In order to find the necessary food for survival, juvenile flatfish may move into deeper waters, thus increasing their vulnerability to predators. The extent to which this behaviour influences distribution is difficult to establish for scarce species such as turbot and brill. Redistribution of fish into deeper waters during periods of low prey availability would confound abundance estimates obtained from beach seining surveys. Given the difficulties associated with the collection of sufficiently high numbers of individuals for species such as turbot and brill, both in Irish waters and other areas of the Northeast Atlantic, the formation of a recruitment index for either species might not be possible. Nursery ground assessments may therefore be more appropriate for identifying potentially high quality nursery (areas of relatively high abundances) and studying the processes governing juvenile growth and survival.

5. Timing of critical events, and growth exhibited during the early life of turbot

Fast growth experienced by flatfish during early life, is considered to increase the likelihood of an individual surviving the pelagic and benthic stages, and ultimately recruiting to the adult stock. Faster growing larvae are likely to spend less time in the vulnerable planktonic stage, where substantial mortality is known to occur (Bailey et al., 2005). Therefore fast larval growth can confer a survival advantage (Anderson, 1988; Miller et al., 1991; Hovenkamp, 1990). On the nursery ground, larger juvenile flatfish are also less likely to suffer mortality from predation (Anderson, 1988; Ellis and Gibson, 1995). Therefore, variability in the growth rates of juvenile flatfish could potentially produce fluctuations in survival and recruitment to the adult stock (Sogard et al., 2001). Assessing the growth exhibited by flatfish, in both the larval and juvenile benthic stage may therefore indirectly provide information on recruitment, as there is in general, a positive relationship between high growth rates and survival (Campana, 1996). In the present thesis, both temporal and spatial variability was detected in the growth of 0-group turbot using otolith microstructure (Figure 4). Juveniles collected on all Irish nursery grounds in 2009, exhibited significantly higher growth during the larval stage. While fast larval growth is reported to be an important prerequisite for a strong year class (Anderson, 1988), the significantly higher larval growth of turbot collected in 2009, was followed by lower post-settlement growth on the nursery. This lower growth was also reflected by the smaller length of fish at capture. Fast growth and reduced mortality during the larval phase of flatfishes, might not confer an advantage in terms of the growth experienced during the juvenile phase.

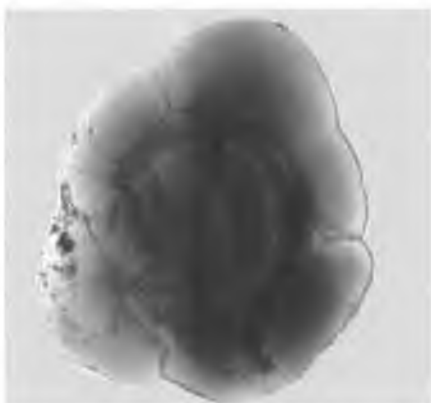


Figure 4: Sagittal otolith of 0-group turbot viewed at 20X.

An important finding from the examination of turbot otolith microstructure in the present thesis was that fish collected from the nursery Inch exhibited consistently higher growth rate estimates over the three year investigation. If juveniles occupying this nursery ground are consistently larger, as the results suggest, then they would be more likely to survive the nursery ground stage. As higher growth is only an indirect measurement of habitat quality, determining the contribution or actual number of juveniles recruiting from this area to the coastal stock, would be needed to establish its value as a nursery

ground. The lack of data available for the movement and distribution of juveniles, particularly to the adult stages (Beck et al., 2001) can be improved upon with technological advances such as stable

isotope analysis or otolith microchemistry (Gillanders, 2002). For example, Brown (2006) was able to classify juvenile English sole (*Pleuronectes vetulus*) and speckled sanddab (*Citharichthys stigmaeus*) from estuarine and coastal habitats with 80% accuracy, using otolith microchemistry. Tagging experiments have also been successfully used to investigate the movements of juvenile flatfish. Using this method, Burrows et al., (2004) were able to confirm site fidelity in juvenile plaice by tracking their movements. The incorporation of these methods into future juvenile flatfish investigations would lead to an improved understanding of the contribution of individual nursery grounds to the adult stock. However, in contrast to plaice, numbers of adult turbot and brill off the Irish west coast are likely to be too low for these techniques to be successfully applied. Indirect measurements of habitat quality, such as good growth of juveniles on a particular nursery ground (Inch in the present thesis), might therefore be the best estimate of juvenile flatfish survival. Juvenile flatfish nursery grounds are necessary to ensure completion of the life-cycle and replenishment of the adult stocks. It is therefore better to 'err on the side of caution', and to use indirect data (higher densities and growth) as evidence of potentially high quality habitats, rather than to allow the deterioration of nursery areas (Beck et al., 2001).

6. The effects of biotic and abiotic factors on 0-group turbot and brill

Juvenile flatfish experiencing good growth and condition on the nursery ground are considered to be more likely to survive the nursery ground stage (Tanaka, 2005). Suitable temperatures and a sufficient quantity of prey are two factors considered to promote fast growth, resulting in juveniles which will be less vulnerable to predation (Reichert 2003). However, large variability in the growth and condition of individuals can arise both between and also within nursery grounds. While some authors have found variability in growth and condition between nurseries to occur primarily due to fluctuations in water temperature (Van der Veer *et al.*, 1990; Karakiri *et al.*, 1991), others have put forward that it is food quantity and quality which are the factors responsible (Van der Veer and Witte, 1993; Sparrevohn and Støttrup, 2008). Examination of the local factors operating within the nursery may therefore elucidate the cause of such variability.

An investigation of the biotic and abiotic factors known to significantly influence the growth, and survival of juvenile flatfish was carried as part of the present research, over a one year only. Foremost, the feeding ecology of west of Ireland juvenile flatfish was investigated. However, analyses of the diet composition of juvenile turbot and brill did not account for any detected fluctuations in growth or condition across sites. In the present work offshore or in situ temperatures were not directly related to the growth of 0-group plaice, turbot, or brill on Irish nursery grounds

(Haynes et al., 2010a; Haynes et al., 2011; Haynes et al., in press(a); Chapters 4, 5, & 7). While local temperatures within each nursery ground would be more representative of the temperature conditions experienced by fish on the nursery, as opposed to offshore temperatures, a longer time series may be required in order to understand the link between temperature and juvenile flatfish growth and condition. The difficulties of attempting to elucidate the key parameters controlling the growth and survival of juvenile flatfish is emphasised by Gilliers et al., (2006), who put forward that it may be a combination of factors on the nursery, acting in concert. Further long-term studies, with the collection of additional biotic and abiotic data on the processes operating within the nursery ground are required in order to determine the factors influencing the growth and survival of west of Ireland juvenile flatfish.

Growth and survival of juvenile flatfish residing in inshore nursery grounds are linked with the quality and quantity of these locations (Gibson, 1994). Anthropogenic activities in coastal areas, which cause pollution and habitat destruction, can reduce the quality and availability of nursery grounds, impacting negatively on the recruitment of juveniles to the adult population (Le Pape et al., 2003). Chemical contaminants on nursery grounds have resulted in the disease and reduced growth and condition of juvenile flatfish (Johnson et al., 1998; Gilliers et al., 2004). The outflow of organic effluent onto has been shown to influence the settling behaviour of juvenile plaice on nursery grounds, which favour bare sand (Wennhage & Pihl, 1994). While there were no obvious signs of habitat degradation on the investigated nursery grounds in the present thesis, organic effluent is known to flow into certain area resulting in the growth of filamentous green algae. Potentially good quality nursery grounds such as Inch in the present thesis, should therefore be monitored and protected in coastal zone management, from any degradation in habitat quality. The identification of essential fish habitat is vital for the replenishment of the adult population (Beck et al., 2001).

The co-occurrence of several flatfish species on nursery grounds, as observed in the current work, can lead to competition for available food resources (Rooper et al., 2006). Strategies which can reduce competition such as resource and temporal partitioning (Beyst et al., 1999) were detected between plaice and brill and between turbot and brill respectively (De Raedemaecker et al., 2010; Haynes et al., in press (b); chapter 7). Bailey et al., (2005) state that in flatfish, the timing of spawning and the subsequent development rate of the eggs and larvae are likely to have evolved to coincide with favourable conditions such as prey availability, an absence of predators, and suitable transport processes. Hence, the observed temporal partitioning identified between the morphologically similar turbot and brill along the west coast of Ireland may reflect a response of

these species to such factors, rather than competition avoidance. Furthermore, regarding turbot and brill, abundances of these flatfish species on nursery grounds, might also be too low for competition to arise. However, competition between juvenile flatfish and other species may also occur on west of Ireland nursery grounds. Other fish species such as the sand goby (*Pomatoschistus rninutus*), which is present on west of Ireland nursery grounds, may compete with juvenile flatfish species such as plaice, for available resources (Evans, 1983). Above a certain size threshold, competition can also occur between plaice and invertebrate predators such as *Crangon crangon*, and *Carcinus maenas* (Gibson, et al., 1998). These species could also potentially compete with turbot and brill.

7. Additional juvenile flatfish assessment techniques

Nursery ground assessments can provide valuable information on the early life history of juvenile flatfish species and are less costly or labour intensive than offshore flatfish surveys. In order to reveal the biotic and abiotic factors influencing populations, the use of additional fish assessment techniques may be necessary. Stoner et al., (2007) advocate the use of advanced techniques (see below), improved data collection and modelling to obtain currently lacking baseline data on the biology and ecology of juvenile flatfish. One advanced technique employed in various studies is an in situ underwater camera, which can record densities and behaviour of both juvenile flatfish and that of their predators (Burrows et al., 1994; Gibson et al., 1998; Spencer et al., 2005). Spencer et al., (2005) concluded that in turbid waters, the use of a camera sled attached with a tickler chain, was a far superior method for the accurate estimation of densities of juvenile English sole, (*Pleuronectes vetulus*), in comparison to that of a beam trawl. These methods can also provide insight into behaviour such foraging and predator avoidance, which will not be detected by more common fishing methods, such as trawls or grabs (Stoner et al., 2007). Determining these behaviours is important, as they are associated with the survival of juvenile flatfish on the nursery, for example, the ability of juvenile flatfish to bury when attempting to avoid or escape from predators will influence survival. The accurate estimation of juvenile flatfish densities is important when investigating variability between different locations, and/or attempting to relate juvenile densities to various influential parameters such as temperature.

8. Flatfish management

An initial survey undertaken by the Marine Institute in 1993, to determine the state of west of Ireland fish stocks including plaice and sole, concluded that commercial catch per unit effort (CPUE) data were not representative of the fishing activity in the area (Wheatley et al., 1999). The

same authors also found that plaice and sole eggs were rarely encountered in egg and larval surveys, and the location of their respective spawning grounds was unknown. While recent work carried out by the Marine Institute has now identified plaice and sole spawning grounds along the west coast of Ireland (Gerritsen et al., 2010), there is, as yet, currently no management plan in place for these quota flatfish species (Anon, 2010b). It is therefore unlikely that any management plan will be put in place for non-quota species such as turbot and brill in the medium term. As any basic data on the adult stages of plaice, turbot, and brill populations are, to date lacking (Anon, 2010a), conservation of the juvenile flatfish nursery grounds identified in the present thesis, should be part of the overall management for west of Ireland flatfish (Wheatley et al., 1999). The protection of potentially high quality nursery grounds may also be of particular relevance for west of Ireland flatfish, where the biomass of stocks are undoubtedly smaller in comparison to other locations such as the North Sea. Adult flatfish stocks off the Irish west coast may be considered too small for the implementation of an effective management plan, given the scarcity of data collected in the initial survey carried out in 1993 for plaice and sole.

In other parts of the Northeast Atlantic, management plans have been devised for the conservation and protection of flatfish stocks. In the Baltic Sea, an action plan has been established for the ‘long-term management of flatfishes’, including plaice, turbot, and brill (Anon, 2010d). The report

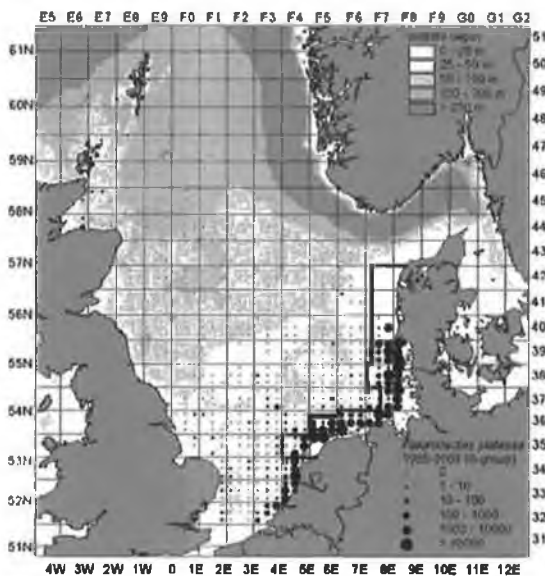


Figure 5: The plaice box (solid black line) and spatial distribution of juvenile plaice in the North Sea. (From ICES.dk/marineworld).

concluded that overall, the development of management plans for flatfish is ‘lagging behind’; with the lack of knowledge on the state of stocks considered to be the main cause. In the North Sea, a management plan for both plaice and sole was implemented in 2008, with preliminary results suggesting that the stocks have been restored to within safe biological limits. The ‘plaice box’ (PB) (Figure 5) is an area established within the North Sea to protect against bycatch and discarding of juvenile plaice. However, the spawning stock biomass (SSB) of plaice has continued to decline (Pastoors et al., 2000). It is difficult to determine the exact cause of this, as there are many interacting factors which may be affecting the SSB, including growth rates, recruitment levels, natural mortality, and fishing mortality (Beare et al., 2010). There has been an off-shore movement

of juvenile plaice out of the PB, possibly in response to a decline in food availability, as a result of a decrease in eutrophication in the area (Philippart et al., 2007). Though larger fishing vessels have been excluded from the PB, there has been an increase in the number of small beam trawls, which may also have contributed to the decline of juvenile plaice inside of the PB, with the complete exclusion of larger vessels inside the PB not always enforced (Beare et al., 2010). It has been suggested that heavily trawled areas inside the PB increased the abundance of small opportunistic benthic species such as polychaetes, thereby enhancing food availability for juvenile plaice. However, other studies state that the changes in diet and overall food supply are more likely related to a decline in eutrophication and/or climate influences, though no definite conclusion has been drawn. Overall, a report on the effectiveness of the PB has concluded that the reduction in juvenile plaice inside is due to changes in the environment or fishing activities, rather than as a result of the establishment of the PB itself (Beare et al., 2010). While the protection of juvenile flatfish habitats may not have resulted in a subsequent increase in the adult population, it is believed that the state of plaice stocks in the North Sea would be far worse if the PB had not been established (Beare et al., 2010). Protected areas such as the PB in the North Sea may not be directly comparable to the west coast of Ireland, if such a similar protected area was to be established here. However, in light of the North Sea findings, with proper enforcement, a complete ban on all fishing activities within the protected area, and in-depth analysis, where possible, of all factors influencing the abundance, growth, and distribution of juvenile flatfish, there is the potential for protected areas to function effectively.

Conclusions

In the absence of any conclusive evidence to date on the state of west of Ireland flatfish species, the value of juvenile flatfish assessments has been emphasised in the current work, with nursery grounds of both good and sub-optimal habitat quality revealed. While comparing the quality of nursery grounds by examining the abundance, growth and condition of flatfish species, does not infer the number of juveniles which will successfully recruit to the adult stock from a particular location, the continuation of these juvenile investigations is critical for non-quota species such as turbot and brill, which are not even considered in offshore assessments. The complexity of the life-cycle of flatfishes and the multitude of factors which can operate within their habitats makes the establishment of an accurate recruitment index difficult. Nonetheless, considering the baseline data established, the main focus should now be on the conservation of west of Ireland nursery grounds, as any loss in the quantity or quality of these habitats would certainly have a negative impact of flatfish recruitment. A time may arrive in the future when it will be possible to determine the

contribution of west of Ireland nursery grounds, in terms of the abundance of juveniles joining the adult stock. The improved understanding of the early life history of plaice, turbot and brill may aid in the development and implementation of effective management strategies in the future; at the very least for the protection of important nursery grounds.

References

- Aarnio, K., Bonsdorf, E., Rosenback, N. 1996. Food and feeding habits of juvenile flounder *Platichthys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Aland Archipelago, Northern Baltic Sea. *Journal of Sea Research*. 36 (3-4), 311-320.
- Allen, B.M. 2004. Distribution, seasonal occurrence, recruitment and growth of juvenile flatfish species on the west coast of Ireland. Unpublished M.Sc. thesis, Galway-Mayo Institute of Technology.
- Allen, B.M., Brophy, D., McGrath, D., King, P.A. 2008. Hatching times, larval duration, settlement and larval growth of plaice (*Pleuronectes platessa* (L.)) in Galway Bay determined using otolith microstructure. *Biology and Environment*. 108 (3), 127-134.
- Amara, R., Laffargue, P., Dewarumez, J.M., Maryniak, C., Lagardere, F., Luzac, C. 2001. Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *Journal of Fish Biology*. 58 (3), 788-803.
- Amara, R., Paul, C. 2003. Seasonal patterns in the fish and epibenthic crustaceans community of an intertidal zone with particular reference to the population dynamics of plaice and brown shrimp. *Estuarine Coastal and Shelf Science*. 56, 807-818.
- Amara, R., Meziane, T., Gilliers, C., Hermel, G., Laffargue, P. 2007. Growth and condition indices in juvenile sole *Solea solea* measured to assess the quality of essential fish habitat. *Marine Ecology Progress Series*. 351, 201-208.
- Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*. 8, 55-66.
- Anon, 2007. <http://www.cso.ie>. Government body responsible for compiling Irish official statistics. Accessed 04/03/11.
- Anon, 2008. <http://www.wfdfish.ie/index.php/category/transitional-waters-2008/>. Accessed 10/08/11.
- Anon, 2009a. <http://www.fao.org/figis/servlet/TabSelector>. Accessed 13/08/11.
- Anon, 2009b. <http://www.wfdfish.ie/wp-content/uploads/2009/12/WRFB-TW-preliminary-report-2009.pdf>. Accessed 10/08/11.
- Anon, 2010a. <http://www.ices.dk/committe/acom/comwork/report/2010/2010/tur-2232.pdf>. Accessed 14/07/11.
- Anon, 2010b. The stock book, annual review of fish stocks in 2009 with management advice for 2010. Marine Institute, Galway.

- Anon, 2010c. [http://datras.ices.dk/Documents/Manuals/Addendum_1_Manual_for_the_IBTS_Revision_VII I.pdf](http://datras.ices.dk/Documents/Manuals/Addendum_1_Manual_for_the_IBTS_Revision_VII_I.pdf). Accessed 11/08/11.
- Anon, 2010d. <http://www.ices.dk/fish/CATChSTATISTICS.asp>. Accessed 04/08/11.
- Anon, 2011a. <http://www.sea-angling-ireland.org/>. Accessed 11/08/11.
- Anon, 2011b. <http://www.fishbase.org>. Accessed 14/08/11.
- Armstrong, M.P., Cadrin, S.X. 2001. Morphometric variation among spawning groups of the Gulf of Maine-Georges Bank herring complex. Herring: Expectations for the New Millennium. Univ. Alaska Sea Grant, AK-SG-01-04, Fairbanks.
- Bagenal, T.B. 1973. Identification of British fishes. Amersham, U.K. Hulton Educational.
- Bailey K.M., 1997. Structural dynamics and ecology of flatfish populations. *Journal of Sea Research*. 37, 269-280.
- Bailey, K.M., Nakata, H., Van der Veer, H.W., 2005. The planktonic stages of flatfishes: physical and biological interactions in transport processes. Chapter 5. Pp 94-114. In R.N. Gibson (ed) Flatfishes: Biology and Exploitation. Blackwell Science Ltd, Oxford.
- Barlow, G.W. 1961. Causes and significance of morphological variation in fishes. *Systematic Zoology*. 10, 105-17.
- Beare, D., Rijnsdorp, A., Van Kooten, T., Fock, H., Schroeder, A., Kloppman, M., Witbaard, R., Meesters, E., Schulze, T., Blaesbjerg, M., Damm, U., Quirijns F. Study for the Revision of the plaice box – Final Report. 2010. Wageningen IMARES. Report number C002/10.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P. 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51, 633–641.
- Begg, G., Waldman, J. 1999. A holistic approach to fish stock identification. *Journal of Fisheries Research*. 43 (1-3), 35 - 44.
- Beggs, S.E., Nash, R.D.M. 2007. Variability in settlement and recruitment of 0-group dab *Limanda limanda* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research*. 58 (1), 90-99.
- Berghahn R., Ludemann K., Ruth M. 1995. Differences in individual growth of newly settled 0-group plaice (*Pleuronectes platessa* L.) in the intertidal of neighbouring Wadden Sea areas. *Netherlands Journal of Sea Research*. 34 (1-3), 131-138.
- Beyst, B., Cattrijsse, A., Mees, J. 1999. Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. *Journal of Fish Biology*. 55, 1171-1186.

- Blackwell, B.G., Brown, M.L., Willis, D.W., 2000. Relative weight (W_r) and current use in fisheries assessment and management. *Reviews in Fisheries Science*. 8 (1), 1- 44.
- Bolle, L.J., Dickey-Collas, M., van Beek, J.K.L., Erftemeijer, P.L.A., Witte, J.I.J., S.J. an der Veer, H.W., Rijnsdorp, A.D. 2009. Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. *Marine Ecology Progress Series*. 390, 195-211.
- Braber, L., de Groot, S.J. 1973. The food of five flatfish species (Pleuronectiformes) in the southern North Sea. *Netherlands Journal of Sea Research*. 6, 163-172.
- Brophy, D., Danilowicz, B.S. 2002. Tracing populations of Atlantic herring (*Clupea harengus* L.) in the Celtic and Irish Seas using otolith microstructure. *ICES Journal of Marine Science*. 59, 1305-1313.
- Brown, A.C., McLachlan, A. 1990. Ecology of sandy shores. *Elsevier*, Amsterdam, the Netherlands.
- Brown, J.A. 2006. Classification of juvenile flatfishes to estuarine and coastal habitats based on the elemental composition of otoliths. *Estuarine Coastal and Shelf Science*. 66, 594-611.
- Burrows, M.T. 1994. An optimal foraging and migration model for juvenile plaice. *Evolutionary Ecology*. 8, 125-149.
- Burrows, M.T., Gontarek, S.J., Nash, R.D.M., Gibson, R.N. 2001. Shrimp predation on 0-group plaice: contrasts between field data and predictions of an individual-based model. *Journal of Sea Research*. 45, 243-254.
- Burrows, M.T., Gibson, R. N., Robb, L., Maclean, A., 2004. Alongshore dispersal and site fidelity of juvenile plaice from tagging and transplants. *Journal of Fish Biology*. 65, 620-634.
- Burke, J.S, Ueno, M., Tanaka, Y., Walsh, H., Maeda, T., Kinoshita, I., Seikai, T. Hoss, D.E., Tanaka, M. 1998. The influence of environmental factors on early life history patterns of flounders. *Journal of Sea Research*. 40, 19 -32.
- Burke, J.S., Monaghan, J.P. and Yokoyama, S., 2000. Efforts to understand stock structure of summer flounder (*Paralichthys dentatus*) in North Carolina, USA. *Journal of Sea Research*. 44 (1-2), 111-22.
- Cabral, H.N., Lopes, M. Loeper, R. 2002. Trophic niche overlap between flatfishes in a nursery area on the Portuguese coast. *Scientia Marina (Barcelona)* 66, 293-300.
- Cadrin, S.X. 2000. Advances in morphometric identification of fishery stocks. *Reviews in Fish Biology and Fisheries*. 10, 91-112.
- Cadrin, S.X., Bolles, K.L., Overholtz, W.J., Armstrong, M.P., Friedland, K.D. 2004. Using Multidisciplinary Stock Identification to Optimize Morphometric Discrimination of Atlantic

- Herring Spawning Groups off New England. *International Council for the Exploration of the Sea*. K:09.
- Campana, S.E., Neilson, J.D. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*. 42, 1014-1032.
- Campana S.E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*. 135, 21-26.
- Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. 59, 197-242.
- Carter, C.G., Houlihan, D.F., Thomas, P. 1996. The effect of decreased ration on feeding hierarchies in groups of greenback flounder (*Rhombosolea taparina*: Teleostei). *Journal of Marine Biological Association U.K.* 76, 505–516.
- Ciotti B.J., Targett T.E., Nash R.D.M., Batty R.S., Burrows M.T., Geffen A.J. 2010. Development, validation and field application of an RNA-based growth index in juvenile plaice *Pleuronectes platessa*. *Journal of Fish Biology*. 77 (5), 2181-2209.
- Clarke, K.R., Ainsworth M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*. 92, 205-219
- Colman, J. 1976. Geographical variation in fin ray numbers in the New Zealand sand flounder *Rhombosolea plebia*. *New Zealand Journal of Marine and Freshwater Research*. 10 (3), 485-97.
- Daan, N. 1997. TAC management in North Sea flatfish fisheries. *Journal of Sea Research*. 37, 321–341.
- Danancher, D., Garcia-Vazquez E. 2006. Turbot – *Scophthalmus maximus*. In: “Genetic effects of domestication, culture and breeding of fish and shellfish, and their impacts on wild populations.” A European network. WP1 workshop “Genetics of domestication, breeding and enhancement of performance of fish and shellfish”, Viterbo, Italy, 6 pp.
- Darnaude, A.M., Harmelin-Vivien M.L, Salen-Picard C. 2001. Food partitioning among flatfish (Pisces, Pleuronectiforms) juveniles in Mediterranean coastal shallow sandy areas. *Journal of the Marine Biological Association of the United Kingdom*. 81, 119.-127.
- De Groot, S.J. 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). *Netherlands Journal of Sea Research*. 5, 121-196.
- De Raedemaeker, F., Keating J., Brophy D., O’Connor I., and McGrath D., 2010. Spatial variability in the diet, condition and growth of juvenile plaice (*Pleuronectes platessa*) at

- sandy beach nursery grounds on the south west coast of Ireland. *Journal of the Marine Biological Association of the United Kingdom*. DOI: 10.1017/S0025315410001505.
- De Raedemaeker, F., O'Connor, I., Brophy, D., Black, A. Macrobenthic prey availability in flatfish nursery grounds and the potential for food competition between 0-group plaice and dab. *Journal of Fish Biology*. In press.
- De Veen, J.F., 1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. *Netherlands Journal of Sea Research*. 12, 115–147.
- Dou, S., Masuda, R., Tanaka, M., Tsukamoto, K. 2003. Identification of factors affecting the growth and survival of the settling Japanese flounder larvae. *Paralichthys olivaceus*. *Aquaculture*. 218 (1-4), 309-327.
- Draganik, B., Maksimov, Y., Ivanov, S., Psuty-Lipska, I. 2005. The status of the turbot *Psetta maxima* (L.) stock supporting the Baltic fishery. *Bulletin of the Sea Fisheries Institute*. 1 (164), 23-53.
- Eldon, G., Smith, G. 1986. Quick laboratory identification of juvenile flounders (*Rhombosolea plebia* and *R. leporine*). *New Zealand Journal of Marine and Freshwater Research*. 20, 77-9.
- Ellis, T., Gibson, R.N. 1995. Size selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Marine Ecology Progress Series*. 127, 27-37.
- Evans, S. 1983. Production, predation and food niche segregation in a marine shallow soft-bottom community. *Marine Ecology Progress Series*. 10, 147-157.
- Exadactylos, A., Thorpe, J. 2001. Allozyme variation and genetic inter-relationships between seven flatfish species (Pleuronectiformes). *Zoological Journal of the Linnaean Society* 132, 487-99.
- Florin, A.-B., Sundblad, G., Bergström, U. 2009. Characterisation of juvenile flatfish habitats in the Baltic Sea. *Estuarine Coastal and Shelf Science*. 82, 294–300.
- Florin, A.-B., Lavados, G. 2009. Feeding habits of juvenile flatfish in relation to habitat characteristics in the Baltic Sea. *Estuarine Coastal and Shelf Science*. 86 (4), 607-612.
- Fonds, M., 1995. Effect of winter temperature on the brood success of flatfish. Annual Report 1995. *Netherlands Institute for Sea Research Texel*.
- Fonds, M., Cronie R., Vethaak, A.D., Van der Puy, P. 1992. Metabolism, food consumption, and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands Journal of Sea Research*. 29, 127-143.
- Fox, C.J., Planque, B.P., Darby C.D. 2000. Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L) around the United Kingdom and the influence of sea temperature. *Journal of Sea Research*. 44 (1-2), 159-168.

- Fox, C.J., McCloghrie P., Nash R.D.M. 2009. Potential transport of plaice eggs and larvae between two apparently self-contained populations in the Irish Sea. *Estuarine Coastal and Shelf Science*. 81 (3), 381-389.
- Fox, J., 2008. The car (companion to applied regression) package for R, version 1.2-9.
- Froese, R., Pauly, D. 2008. FishBase, available at <http://www.fishbase.org> (Accessed 09/07/08).
- Garrett, D. 2005. A new intergeneric hybrid flatfish (Pleuronectiformes: Pleuronectidae) from Puget Sound and adjacent waters. *Copeia*. 3, 672-6.
- Geffen, A.J. 1982. Otolith ring deposition in relation to growth in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. *Marine Biology*. 71, 317-326.
- Geffen, A.J., van der Veer, H.W., Nash, R.D.M. 2007. The cost of metamorphosis in flatfishes. *Journal of Sea Research*. 58, 35-45.
- Gerritsen, H. 2010. "Survey Report: Herring Recruit and Biological Sampling Survey 22 February – 2 March 2009 South-west and south of Ireland", Marine Institute, Ireland.
- Gibson, R.N., Ansell, A.D., Robb, L. 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Marine Ecology Progress Series*. 98, 89 – 105.
- Gibson, R.N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research*. 32 (2), 191-206.
- Gibson, R.N., Yin M.C., Robb L. 1995. The behavioural basis of the predator-prey size relationships between shrimp (*Crangon crangon*) and juvenile plaice (*Pleuronectes platessa*). *Journal of the Marine Biological Association of the United Kingdom*. 75, 337-349.
- Gibson, R.N., Robb L., Burrows M.T., and Ansell A.D. 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Series*. 130, 1-17.
- Gibson, R.N. 1997. Behaviour and the distribution of flatfishes. *Journal of Sea Research*. 37, 241-256.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H. Nickell, L. A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability, and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series*. 165, 145-159.
- Gibson, R.N., Robb, L., Wennhage, H., Burrows, M.T., 2002. Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Mar. Ecol. Prog. Ser.* 229, 233 – 244.
- Gibson, R.N., 2005. Flatfishes, Biology and Exploitation. (Ed.) Gibson R.N. Blackwell publishing. 213-231.

- Gillanders, B.M. 2002. Temporal and spatial variability in elemental composition of otoliths: implications for determining stock identity and connectivity of populations. *Canadian Journal of Fisheries and Aquatic Sciences*. 59, 1-11.
- Gilliers, C., Amara, R., Bergeron, J.P. 2004. Comparison of growth and condition indices of juvenile flatfish in different coastal nursery grounds. *Journal of Environmental Biology of Fishes*. 71 (2), 189-198.
- Gilliers, C., Le Pape, O., Désaunay, Y., Morin, J., Guérault, D., Amara, R. 2006. Are growth and density quantitative indicators of essential fish habitat quality? An application to the common sole *Solea solea* nursery grounds. *Estuarine Coastal Shelf Science*. 69, 96-106.
- Haynes, P.S., Allen B.M., Brophy D., McGrath D. 2008. Fin-ray count variation in 0-group flatfish: plaice (*Pleuronectes platessa* (L.)) and flounder (*Platichthys flesus* (L)). on the west coast of Ireland. *Biology and Environment*. 108B (2), 61-67.
- Haynes, P.S., Brophy D., McGrath D., O' Callaghan R., Comerford S., Casburn P. 2010a. Annual and Spatial Variation in the Abundance Length and Condition of Turbot (*Psetta maxima* L.) on Nursery Grounds on the West Coast of Ireland: 2000 – 2007. *Journal of Sea Research*. 64 (4), 494-504.
- Haynes, P.S., McGrath, D., Brophy D., 2010b. Variation in the fin ray counts of 0-group turbot (*Psetta maxima*) and brill (*Scophthalmus rhombus*) on the west coast of Ireland: 2006-2009. *Marine Biodiversity Records*. *Marine Biodiversity Records*. 3, e124 doi: 10.1017/S1755267210001144.
- Haynes, P.S., Brophy D., McGrath, D. 2011. The use of otolith microstructure to describe the early life history of turbot (*Psetta maxima* L.) on nursery grounds along the west coast of Ireland: 2007 – 2009. *Journal of Fisheries Research*. doi:10.1016/j.physletb.2003.10.071.
- Haynes, P.S., Brophy, D., McGrath, D. Variability in the early life stages of juvenile plaice (*Pleuronectes platessa* L.) on west of Ireland nursery grounds; 2000 – 2007. *Journal of the Marine Biological Association of the United Kingdom*. In press (a).
- Haynes, P.S., Brophy, D., De Raedemaeker, F., McGrath, D. The feeding ecology of 0-group turbot (*Psetta maxima* L.) and brill (*Scophthalmus maximus* L.) on Irish west coast nursery grounds. *Journal of Fish Biology*. In press (b).
- Haynes, P.S., Brophy, D., McGrath, D. Early life history of brill (*Scophthalmus rhombus* L.) along the west coast of Ireland as described by otolith microstructure. *Marine Biodiversity Records*. In review.

- Haynes, P.S., Shephard, S., Brophy, D., McGrath, D., Boele, S.J. Relative abundance of juvenile turbot *Psetta maxima* and brill *Scophthalmus rhombus* suggests negative interactions on nursery grounds. *Unpublished manuscript*. Galway-Mayo Institute of Technology.
- Hayward, P.J., Ryland, J.S. 2003. Handbook of the marine fauna of North-West Europe (eds). *Oxford Science Publications*, Oxford.
- Henderson, P.A., Seaby, R.M. 2005. The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*. 85, 197-204.
- Holmes, R.A., Gibson, R.N. 1983. A comparison of predatory behaviour in flatfish. *Animal Behaviour*. 31, 1244-1255.
- Hovenkamp, F. 1990. Growth differences in larval plaice (*Pleuronectes platessa* L.) in the Southern Bight of the North Sea as indicated by otolith increments and RNA/DNA ratios. *Marine Ecology Progress Series*. 58, 205-215.
- Hovenkamp, F. 1991. Immigration of larval plaice *Pleuronectes platessa* in the North Sea. *Journal of Sea Research*. 70, 105-116.
- Houde, E.D. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science*. 51, 91-97.
- Iglesias, J., Ojea, G., Otero, J.J., Fuentes, L., Ellis, T. 2003. Comparison of mortality of wild and released reared 0-group turbot, *Scophthalmus maximus*, on an exposed beach (Ría de Vigo, NW Spain) and a study of the population dynamics and ecology of the natural population. *Fisheries Management and Ecology*. 10 (1), 51-59.
- Iles, T.C., Beverton, R.J.H. 2000. The concentration hypothesis: the statistical evidence. *ICES Journal of Marine Science*. 57, 216-227.
- Imsland, A.K., Folkvord, A., Stefansson, S.O. 1995. Growth, oxygen consumption and activity of juvenile turbot (*Scophthalmus maximus* L.) reared under different temperatures and photoperiods. *Netherlands Journal of Sea Research*. 341, 49-159
- Imsland, A.K., Sunde, L.M., Folkvord, A., Stefansson, O. 1996. The interaction of temperature and fish size of juvenile turbot. *Journal of Fish Biology*. 49 (5), 926-940.
- Imsland, A.K., Foss, A., Gunnarsson, S., Berntssen, M., FitzGerald, R., Bonga, S.W., van Ham, E., Nævdal, G., Stefansson, S.O. 2001. The interaction of temperature and salinity on growth and food conversion in juvenile turbot (*Scophthalmus maximus*). *Aquaculture*. 198, 353- 367.
- Johnson, L.L., Misitano, D., Sol, S., Nelson, G., French, B., Ylitalo, G., Hom, T. 1998. Contaminant effects on ovarian development and spawning success in rock sole (*Lepidopsetta*

- bilineata*) from Puget Sound, WA. *Transactions of the American Fisheries Society*. 127, 375-392.
- Jolliffe, I.T. 2002. *Principal Component Analysis*, 2nd edn. New York: Springer-Verlag.
- Jones, A. 1973. The ecology of young turbot, *Scophthalmus maximus* (L.), at Borth, Cardiganshire, Wales. *Journal of Fish Biology*. 5, 367-383.
- Jones, A. 1974. Sexual maturity, fecundity and growth of the turbot *Scophthalmus maximus* L. *Journal of the Marine Biological Association of the United Kingdom*. 54 (3), 109-125.
- Karakiri, M., Berghahn, R., Van der Veer, H.W. 1991. Variations in settlement and growth of 0-group plaice (*Pleuronectes platessa* L.) in the Dutch Wadden Sea as determined by otolith microstructure analysis. *Journal of Sea Research*. 55, 15-22.
- Kalinina, E.M. 1960. The peculiarities of brill portioned spawning. *Issues of Ichthyology*. 16, 137-143. Cited in Stankus, S., 2003.
- Kinoshita, I., Seikai, T., Tanaka, M., Kuwamura, K. 2000. Geographic Variations in Dorsal and Anal Ray Counts of Juvenile Japanese Flounder, *Paralichthys olivaceus*, in the Japan Sea. *Environmental Biology of Fishes*. 57, 305-313.
- Kuipers, B.R, MacCurrin B, Miller, J.M., Van der Veer H.W., Witte, J.I. 1992. Small trawls in juvenile flatfish research: their development and efficiency. *Netherlands Journal of Sea Research*. 29, 109-117
- Langsrud, Y. 2003. ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Statistics and computing*. 13, 163-167
- Leggett, W.C., Frank, K.T. 1997. A comparative analysis of recruitment variability in North Atlantic flatfishes — testing the species range hypothesis. *Journal of Sea Research*. 37, (3-4), 281-299.
- Le Pape, O., Holley, J., Guérault, D., Désaunay, Y. 2003. Quality of coastal and estuarine essential fish habitat: estimations based on the size of juvenile common sole (*Solea solea* L.). *Estuarine Coastal and Shelf Science*. 58, 793-803
- Lindsey, C.C. 1988. Factors controlling meristic variation. *Journal of Fish Physiology*. 11 B, 197-274.
- Link, J.S., Bolles, K., Milliken, C.G. 2002. The feeding ecology of flatfishes in the Northwest Atlantic. *Northwest Atlantic Fisheries Science*. 30, 1-17.
- Link, J.S., Fogarty, M.J., Langton, R.W. 2005. Chapter 9. The trophic ecology of flatfishes. Pp. 185-196. In R.N. Gibson (ed) *Flatfishes: Biology and Exploitation*. Blackwell Science Ltd, Oxford.

- Lockwood, S.J. 1974. The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L.) in Filey Bay, Yorkshire. *Journal of Fish Biology*. 6, 465–477.
- Lockwood, S.J., 1980. Density-dependent mortality in 0-group plaice (*Pleuronectes platessa* L.) populations. *ICES Journal of Marine Science*. 39 (2), 148-153.
- Lorenzen, K., Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society of London Biological Science*. 269, 49 – 54.
- MacGregor, R., MacCrimmon, H. 1977. Evidence of genetic and environmental influences on meristic variation in the rainbow trout, *Salmo gairdneri* Richardson. *Environmental Biology of Fishes*. 2 (1), 25_33.
- Manly, B.F.J. 2005. Multivariate statistical methods: a primer, 3rd edn. London. Chapman & Hall/CRC Press.
- Marshall, S., Elliott, M. 1998. Environmental influences on the fish assemblage of the Humber estuary. *U.K. Estuarine Coastal Shelf Science*. 46, 175 -184.
- Martinsson, J., Nissling, A. 2011. Nursery area utilization by turbot (*Psetta maxima*) and flounder (*Platichthys flesus*) at Gotland, central Baltic Sea. *Boreal Environment Research*. 16 (1), 60 – 70.
- Miller, J.M., Burke, J.S., Fitzhugh, G.R. 1991. Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. *Netherlands Journal of Sea Research*. 27, 261-275.
- Millner, R.S., Whiting, C.L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES Journal of Marine Science*. 53, 1185–1195.
- Millner, R.S., Walsh, S.J., De Astarloa, J.M.D. 2005. Chapter 11. Atlantic flatfish fisheries. Pp 240 – 269. In R.N. Gibson (ed) *Flatfishes: Biology and Exploitation*. Blackwell Science Ltd, Oxford.
- Mittlebach, G.C. 2002. Fish foraging and habitat choice: a theoretical perspective. In *Handbook of Fish and Fisheries*. (Hart P.J.B. & Reynolds, J.D. eds.) (1), pp 251-266. Oxford Blackwell Science.
- Modin, J., Pihl, L. 1994. Differences in growth and mortality of juvenile plaice, *Pleuronectes platessa* L., following normal and extremely high settlement. *Netherlands Journal of Sea Research*. 32 (3-4), 331-341.
- Modin, J., Pihl L. 1996. Small-scale distribution of juvenile plaice and flounder in relation to predatory shrimp in a shallow Swedish bay. *Journal of Fish Biology*. 49 (6), 1070-1085.

- Mohn, C., Bartsch, J., Meinke, J. 2002. Observations of the mass and flow field at Porcupine Bank. *ICES Journal of Marine Science* 59, 380-392.
- Molander, A.R. 1964. Underordning plattfiskar. In *Fiskar och fiskar i Norden*. 90-113. Ed. by K. A. Andersson. *Natur och Kultur*, Stockholm pp. 90-113.
- Myers, R.A., 1991. Recruitment variability and range of three fish species. *NAFO Science Council Studies*. 16, 21-24.
- Nash, R.D.M., Geffen, A. J., Hughes, G. 1992. Winter growth of juvenile plaice on the Port Erin Bay (Isle of Man) nursery ground. *Journal of Fish Biology*. 41, 209-215.
- Nash, R.D.M., Geffen, A.J., Hughes, G. 1994a. Individual growth of juvenile plaice (*Pleuronectes platessa* L.) on a small Irish Sea nursery ground (Port Erin Bay, Isle of Man, UK). *Netherlands Journal of Sea Research*. 32 (3-4), 369-378.
- Nash, R.D.M., Santos, R.S., Geffen, A.J., Hughes, G. Ellis, T.R. 1994b. Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin Bay, Isle of Man and Porto Pim Bay, Faial, Azores). *Journal of Fish Biology*. 44, 35-45.
- Nash, R.D.M., Geffen, A.J. 2000. The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research*. 44, 101-110.
- Nash, R.D.M., Geffen, A.J. 2005. Chapter 7. Age and growth. Pp. 138-163. In R.N. Gibson (ed) *Flatfishes: Biology and Exploitation*. Blackwell Science Ltd, Oxford.
- Nash, R.D.M., Geffen, A.J., Burrows, M.T. Gibson, R.N. 2007. Dynamics of shallow-water juvenile flatfish nursery grounds: application of the self-thinning rule. *Marine Ecology Progress Series*. 344, 231-244.
- Nichols, J.H. 1971. Pleuronectidae, Fiches d'identification des oeufs et larves de poissons. 4-6 *International Council for the Exploration of the seas*, Copenhagen, pp. 18.
- Nicieza, A.G., Metcalfe, N.B. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology*. 78, 2385-2400
- Nielsen, J., Tortonese, E., Editors. 1986. Fishes of the North-Eastern Atlantic and the Mediterranean. *UNESCO, Paris*. 3, 1287-1293.
- Nielsen, E., Bagge, O., MacKenzie, B. 1998. Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research*. 39 (1-2), 11-28.
- Nissling, A., Johansson, U., Jacobsson, M. 2006. Effects of salinity and temperature conditions on the reproductive success of turbot (*Scophthalmus maximus*) in the Baltic Sea. *Journal of Fisheries Research*. 80, (2-3), 230-238.

- Nissling, A., Jacobsson, M., Hallberg, M. 2007. Feeding ecology of juvenile turbot *Scophthalmus maximus* and flounder *Pleuronectes flesus* at Gotland, Central Baltic Sea. *Journal of Fish Biology*. 70 (6), 1877-1897.
- O' Neill, B., McGrath, D., Brophy, D. Scales of variability in fin ray counts of flounder on Irish and Welsh coasts. *Biology and Environment* (In review).
- Pape, A., 1935 Contribution to the natural history of *Pleuronectes pseudoflesus*, a hybrid between plaice and flounder. *Helgoländer Wissenschaftliche Meeresunters. Kiel N. F.* 22, 53-88.
- Parker-Humphreys, M. 2005. Distribution and relative abundance of demersal fishes from beam trawl surveys in eastern English Channel (ICES division VIIId) and the southern North Sea (ICES division IVc) 1993-2001. *Science Series Technical Report*. CEFAS Lowestoft, 124: 92pp.
- Pastors, M.A., Rijnsdorp, A.D., Van Beek, F.A. 2000. Effects of a partially closed area in the North Sea ('plaice box') on stock development of plaice. *ICES Journal of Marine Science*. 57, 1014-1022.
- Paulsen, H., and Støttrup, J.G. 2004. Growth rate and nutritional status of wild and released reared juvenile turbot in southern Kattegat, Denmark. *Journal of Fish Biology*. 65, (1), 210-230.
- Philippart, C.J.M., Beukema, J.J., Cadee, G.C., Dekker, R., Goedhart, P.W., Van Iperen, J.M., Leopold, M.F., Herman, P.M.J. 2007. Impacts of nutrient reduction on coastal communities. *Ecosystems*. 10, 95D118.
- Pierce, C.L., Rasmussen, J.B., Leggett, W.C. 1990. Sampling littoral fish with a seine: Corrections for variable capture efficiency. *Canadian Journal of Fisheries and Aquatic Sciences*. 47, 1004-1010.
- Piet, G.J., Pfisterer, A.B., Rijnsdorp, A.D. 1998. On factors structuring the flatfish assemblage in the southern North Sea. *Journal of Sea Research*. 40, 143-152.
- Pihl, L. Van der Veer H.W. 1992. Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L., in coastal nursery areas. *Journal of Sea Research*. 29 (1-3), 145-152.
- Power, J.H., Burger M.J., Stokes A.M. 2006. Mass, volume, and length relationships in plaice (*Pleuronectes platessa*) juveniles. *Journal of Sea Research*. 57, 230-235.
- R development core team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Rae, B.B. 1957. A preliminary account of the turbot in Scottish waters. *Scottish Fisheries Bulletin* Number 8.

- Reichert, M.J.M. 2003. Diet, consumption and growth of juvenile fringed flounder (*Etropus crossotus*): a test of the 'maximum growth/optimum food hypothesis' in a subtropical nursery area. *Journal of Sea Research* 50, 97–116. doi: 10.1016/S1385-1101(03)00081-9.
- Rijnsdorp, A.D., Beek, F.A.V., Flatman, S., Millner R.M., Riley J.D., Giret, M., Clerck R.D. 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northwest Atlantic. *Netherlands Journal of Sea Research*. 29, 173-192.
- Rijnsdorp, A.D., and van Leeuwen, P.I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES Journal of Marine Science*. 53, 1199-1213.
- Rijnsdorp, A.D., Van der Veer, H.W. 2008. RECLAIM . RESolving CLimAtic IMPacts on fish stocks. Specific Targeted Research Project on "Modernisation and sustainability of fisheries, including aquaculture-based production systems" 1.6 Report of WP1. Chapter 22 – Plaice pp 1-9.
- Rijnsdorp A., Peck M. A., Engelhard G.H., Möllmann C., Pinnegar J.K. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*. 66, 1570-1583.
- Riley, J. D., Symonds, D. J., Woolner, L. 1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. The early life history of fish: recent studies. *Conseil International pour l'Exploration de la Mer*. 178, 223-228.
- Riley, J.D. 1971. The Riley push-net. In *Methods for the Study of Marine Benthos* (Holme, N. & McIntyre, A.D., eds), pp 286 – 290. Oxford: Blackwell.
- Riou, P., Le Pape, O., Rogers S. 2001. Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel: application of a combined method using Generalized Linear Models and a Geographic Information System. *Aquatic Living Resources*. 14, 125-135.
- Rooper, C.N., Gunderson, D.R., Armstrong, D.A. 2006. Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington. *Fishery Bulletin*. 104, 616-622.
- Russell, F.S. 1976. The eggs and planktonic stages of British marine fishes. London. Academic Press. 524 pp.
- Safford S.E., Booke H. 1992. Lack of biochemical genetic and morphometric evidence for discrete stocks of northwest Atlantic herring *Clupea harengus harengus*. *Fishery Bulletin* (US) 90, 203–210.
- Secor, D.H. 2007. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research*, 57, 91-103.

- Selleslagh, J., Amara, R. 2008. Inter-season and interannual variations in fish and macrocrustacean community structure on a eastern English Channel sandy beach: Influence of environmental factors. *Estuarine Coastal and Shelf Science*. 77 (4), 721-730.
- Shaw, R.G., Mitchellolds, T. 1995. Anova for Unbalanced Data - an Overview. *Ecology*. 74, (6) 1638-1645.
- Sogard, S.M. 1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation and somatic growth relationships. *Canadian Journal of Fisheries and Aquatic Sciences*. 48, 1862-1871.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science*. 60 (3), 1129-1157.
- Sogard, S.M., Able, K.W., Hagan, S.M. 2001. Long-term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *Journal of Sea Research*. 45 (3-4), 189-204.
- Sogard, S.M. Olla, B.L. 2002. Contrasts in the capacity and underlying mechanisms for compensatory growth in two pelagic marine fishes. *Marine Ecology Progress Series*. 243, 165-177.
- Spencer, M.L., Stoner, A.W., Ryer C.H., Munk, J.E. 2005. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: comparison with beam trawls and divers. *Estuarine Coastal and Shelf Science*. 64, 497-503
- Sparrevohn, C.R., Støttrup, J.G., 2008a. Diet, abundance, and distribution as indices of turbot (*Psetta maxima* L.) release habitat suitability. *Reviews in Fisheries Science*. 16 (1-3), 338-347.
- Sparrevohn, C.R., Hinrichsen, H.H., Rijnsdorp, A.D. 2008b. Spatial and annual variations in the abundance of age-0 turbot (*Psetta maxima*) and its implication for stock enhancement strategies. Unpublished manuscript.
- Stankus, S. 2003. The peculiarities of turbot (*Psetta Maxima* L.) Biology and their role in the ecosystem of the Baltic Sea coastal zone of Lithuania. *Acta Zoologica Lituanica*. 13, 217-238.
- Stoner, A.W., Spencer, M.L., Ryer, C.H. 2007. Flatfish-habitat association in Alaska nursery grounds: use of continuous video records for multi-scale spatial analysis. *Journal of Sea Research*. 57 (2-3), 137 - 150.
- Støttrup, J.G., Sparrevohn, C.R., Modin, J., Lehmann, K. 2002. The use of releases of reared fish to enhance natural populations. A case study on turbot *Psetta maxima* (Linne, 1758). *Fisheries Research*. 59, 161-180.

- Swain, D., Foote, C. 1999. Stocks and chameleons: the use of phenotypic variation in stock identification. *Fisheries Research*. 43, 113-28.
- Tanaka, M., Goto, T., Tomiyama, M., Sudo, H. 1989. Immigration, settlement, and mortality of flounder (*Paralichthys olivaceus*) larvae and juveniles in a nursery ground, Shijiki Bay, Japan. *Netherlands Journal of Sea Research*. 24, 57-67.
- Tanaka Y, Yamaguchi H, Gwak WS, Tominaga O, Tsusaki T, Tanaka, M. 2005. Influence of mass release of hatchery-reared Japanese flounder on the feeding and growth of wild juveniles in a nursery ground in the Japan Sea. *Journal of Experimental Marine Biology and Ecology*. 314, 137-147.
- Taylor, D.L. 2003. Size-dependent predation on post-settlement winter flounder *Pseudopleuronectes americanus* by sand shrimp *Crangon septemspinosa*. *Marine Ecology Progress Series*. 263, 197-215.
- Taylor, D.L. 2005. Predatory impact of green crab (*Carcinus maenas* Linnaeus) on post-settlement winter flounder (*Pleuronectes americanus* Walbaum) as revealed by immunological dietary analysis. *Journal of Marine Experimental Biology and Ecology*. 324, 112-126.
- Teal, L.R., De Leeuwen, J.J., Rijnsdorp, A.D. 2008. Effects of climate change on growth of 0-group sole and plaice. *Marine Ecology Progress Series*. 357. doi:10.3354/meps07367.
- Thurstan, R.H., Brockington, S., Callum, M.R. 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nature Communications*, 1, Article 15.
- Turan, C. 2004. Stock identification of Mediterranean horse mackerel (*Trachurus mediterraneus*) using morphometric and meristic characters. *ICES Journal of Marine Science*. 61, 774-81.
- Underwood, A.J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge, Cambridge University Press.
- Üstündağ, C. 2003. Seed production of turbot (*Psetta maxima*). *CFRI YUNUS Research Bulletin*. 3:4, 6-11.
- Ustups, D., Uzars, D., Muller-Karulis, B. 2007. Structure and feeding ecology of the fish community in the surf zone of the eastern Baltic Latvian coast. *Proceedings of the Latvian Academy of Sciences*. Section B. 61, 20-30.
- Valiela, I. 2006. Global coastal change. Blackwell Publishing: Carlton, VIC (Australia). ISBN 1-4051-3685-5. 368 pp.
- Van Beek, F.A., Rijnsdorp A.D., de Clerck R. 1989. Monitoring juvenile fish stocks in the Wadden Sea and the coastal areas of the southeastern North Sea. *Helgoländer Wissenschaftliche Meeresunters*. 43, 461-477.

- Van der Veer, H.W. 1986. Immigration, settlement, and density dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Marine Ecology Progress Series*. 29, 223–236.
- Van der Veer, H.W., Bergman, M.J.N. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa*, population in the Western Wadden Sea. *Marine Ecology Progress Series*. 35, 203-215.
- Van der Veer H.W., Pihl, L., Bergman M.J.N. 1990. Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*. *Maine Ecology Progress. Series*. 64, 1–12.
- Van der Veer, H.W., Witte, J.IJ. 1993. 'maximum growth/optimal food condition' hypothesis: a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. *Marine Ecology Progress Series*. 101, 81-90.
- Van der Veer, H.W., Berghahn, R. Rijnsdorp, A.D. 1994. Impact of juvenile growth on recruitment in flatfish. *Netherlands Journal of Sea Research*. 32 (2), 153-173.
- Van der Veer, H.W., Berghahn, R., Miller, J.M., Rijnsdorp, A.D. 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the flatfish symposia. *ICES Journal of Marine Science*. 57, 202–215.
- Van der Veer, H.W., Leggett, W.C. 2005. Recruitment In Flatfishes: Biology and Exploitation (Gibson, R. N., ed.), pp. 120–137. London: Blackwell Science.
- Van der Veer, H.W., Bolle L.J., Geffen A.J., Witte J.IJ. 2009. Variability in the transport of fish eggs and larvae. IV. Interannual variability in larval stage duration of immigrating plaice in the Dutch Wadden Sea. *Marine Ecology Progress Series*. 390, 213-223.
- Van der Veer H.W., Freitas V., Koot J., Witte J.IJ., Zuur, A.F. 2010. Food limitation in epibenthic species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*. 416, 215-227.
- Van Keeken, O., Van Hoppe, M., Grift, R.E. Rijnsdorp, A.D. 2004. The effect of changes in the spatial distribution of juvenile plaice in the North Sea (*Pleuronectes platessa*) on the management of its stocks. - ICES paper CM 2004/K: 25.
- Vinagre, C., Fonseca, V., Maia, A., Amara, R., Cabral, H. 2008. Habitat specific growth rates and condition indices for the sympatric soles *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup 1858, in the Tagus estuary, Portugal, based on otolith daily increments and RNA-DNA ratio. *Journal of Applied Ichthyology*. 24(2), 163-169.
- Walsh, S.J. 1996. Life history and ecology of long rough dab *Hippoglossoides platessoides* (F) in the Barents Sea. *Journal of Sea Research*. 36 (3-4), 285-310.

- Wang, L., Lyons, J., Kanehl, P. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management*. 28 (2), 255–266.
- Wennhage, H., Pihl, L. 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous microalgae. *Netherlands Journal of Sea Research*. 32, 343–351.
- Wennhage, H., Gibson, R.N., Robb L. 1997. The use of drop traps to estimate the efficiency of 2 beam trawls commonly used for sampling juvenile flatfishes. *Journal of Fish Biology*. 51,441-445.
- Wennhage, H., Pihl L. 2001. Settlement patterns of newly settled plaice (*Pleuronectes platessa*) in a non-tidal Swedish fjord in relation to larval supply and benthic predators. *Marine Biology*. 139, 877–889.
- Wheatley, S.B., Connolly, P.L., Woods, F., Keating, M., Doherty, M. The state of stocks of cod whiting sole and plaice on the west and southwest coasts of Ireland. Irish Fisheries Investigations (New Series) No. 3 – 1999. Marine Institute, Galway.
- Wheeler, A., 1969. The Fishes of the British Isles and North-West Europe. London: Macmillan.
- Wilderbuer, T.K., Hollowed, A.B., Ingraham, W.J., Spencer, Jr., P.D., Connors, M.E., Bond, N.A., Walters, G.E. 2002. Flatfish recruitment response to decadal climate variability and ocean conditions in the eastern Bering Sea. *Progress in Oceanography*. 55, 235-247.
- Wyatt, P., Pitts, C., Butlin, R. 2006. A molecular approach to detect hybridization between bream *Abramis brama*, roach *Rutilus rutilus*, and rudd *Scardinius erythrophthalmus*. *Journal of Fish Biology*. 69, 52-71.
- Yaakub, S.M., Bellwood, D.R., van Herwerden, L., Walsh, F.M. 2006. Hybridization in coral reef fishes: introgression and bi-directional gene exchange in *Thalassoma* (family Labridae). *Molecular Phylogenetics and Evolution*. 40, 84–100
- Yamashita, Y., Tanaka, M., Miller, J.M. 2001. Ecophysiology of juvenile flatfish in nursery grounds. *Journal of Sea Research*. 45, 205-218.
- Zar, J.H. 1996. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, NJ.
- Zijlstra, J. 1972. On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. *Symposium Zoological Society of London*. 29, 233-258
- Zijlstra, J., Dapper, R., Witte, J. 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. *Netherlands Journal of Sea Research*. 15 (2), 250-272.