Exploring connectivity of marine benthic invertebrates

by

Katherine Nisbet

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy

September 2011

Abstract

With the marine environment subjected to ever increasing anthropogenic pressures resulting in biodiversity and habitat losses, there is an urgent need to implement effective management and conservation strategies to limit these losses. One such strategy is the designation of Marine Protected Area (MPA) networks, with the central concept that individual MPAs are connected to its neighbours within the network. However, determining scales of connectivity in an environment that varies considerably both spatially and temporally is inherently difficult. Larval dispersal is a main driver of population connectivity, and planktonic larval duration (PLD) is frequently used to infer dispersal distance. Thus far studies have predominantly focused on fish and tropical species, using approaches such as larval dispersal modelling, otolith microchemistry or genetic estimates of connectivity.

This thesis aimed to assess the levels of connectivity in a range of benthic invertebrates characteristic of offshore shelf seas of the Northeast Atlantic, at a range of spatial and temporal scales. This was achieved by: (1) examining the variation in PLDs of a typical benthic assemblage, then using this information to examine the variation in realised dispersal at multiple locations using particle tracking software; (2) assessing habitat preferences for the same species, and exploring how the distribution of broad habitats would affect connectivity of species; and (3) using microsatellite markers to determine the genetic structure of the exploited scallop *Pecten maximus* at both a localised scale (Isle of Man) and a regional scale covering over half its range.

While biological variation, in the form of PLD, did affect dispersal potential of common benthic invertebrates, it was the physical factors of hydrographic regime and substrate type within a species given dispersal range that played the most important role in determining ultimate dispersal distance and location. Additionally, the scale of genetic structure of the scallop *Pecten maximus*, with Norway genetically distinct from Scotland, Ireland and Isle of Man but weaker or no structure within those regions, highlighted the interaction of biological and physical factors. Ultimately, this thesis has provided valuable insight into the drivers of connectivity in the marine benthos, but further work, particularly more collaborative studies across multiple fields, is required if MPAs are to achieve their aims in the face of a changing environment.

Acknowledgements

Firstly, I would like to thank my supervisors Leonie Robinson, Phill Watts and Chris Frid for their support and advice throughout the course of this PhD. I would also like to thank everyone in the Ecology group past and present who have been so generous with their time, especially Helen, Jon, Louise, Matt, Rob and Tony, and all those who helped me in the lab, especially Derek, Laura and Angela. Additional thanks must go to Mary Thorpe and Hannah Betts for help with ArcGIS and Bryce Beukers-Stewart and our colleagues in Norway for scallop samples.

For allowing me to participate in the CEFAS groundfish survey in 2008 and teaching me more than I thought possible to know about fish and invertebrate identification, a huge thank you to Jim Ellis and the rest of the team.

I've been incredibly lucky to meet so many brilliant people in my four years at Liverpool – too many in fact to name them all! But special mention must go to Jack Thomson, Cheryl Knowland, Lucy Abrams and Anouska Bailey. Also, Chris Cesar for providing invaluable advice and laughs in equal measure. And for being an exceptional flatmate and friend, who never once seemed fed up with my incessant questions about genetics, I thank Ian Goodhead.

To those outside of Liverpool – Anne O'Halloran, Laura Cornick, Lucy Greenhill and Jayne Irvine – thank you for helping me retain my sanity with the judicious use of many many phone calls, jaegerbombs and Muppet outfits.

Of course, thank you to Marshall for the support, chivvying along and copious Ron Abuelos. It's a truly brave man that takes on a final year PhD student, and an even braver man that takes on a Face. And for that my final year has been one of the best of my life.

And finally: Mum, Dad, Clare and Louise; for their unwavering support, encouragement and love, without which I could have not come this far.

Contents

Chapter 1

Introduction

1.1 Marine Protected Areas: management and conservation benefits

Ecosystems worldwide have come under increasing pressure from human activities, resulting in huge losses in biodiversity, habitat fragmentation and the collapse of entire systems (e.g. Skole & Tucker 1993; Pauly et al. 1998; Gardner et al. 2003; Thomas et al. 2004). For marine ecosystems, pressures from fishing, pollution and climate change have been associated with unprecedented changes in chemical, physical and biological functions (e.g. Lubchenco et al. 1995; Botsford et al. 1997; Jennings & Kaiser 1998; Watling & Norse 1998; Jackson et al. 2001; Harley et al. 2006). With the need for more effective management and conservation in the marine environment becoming increasingly apparent, numerous studies have advocated the need to apply new approaches to tackle these issues (e.g. Agardy 1994; Allison et al. 1998; Murray et al. 1999). Most notably, Marine Protected Areas (MPAs) have emerged as a popular marine management tool and have therefore attracted increasing interest from the scientific community (e.g. Allison et al. 1998; Gerber et al. 2003; Sale et al. 2005).

An MPA can be defined as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher and Kenchington, 1992). Considered by some to be the most powerful tool for conservation and management available (Agardy et al. 2011), MPAs are nevertheless limited in their usefulness, particularly when poorly planned or consulted (Ballantine 1999). These should not be confused with marine reserves which are MPAs that are considered to be fully protected from human impacts; MPAs vary considerably in the protection they afford, depending on their purpose (Lubchenco et al. 2003). Historically, they have been used as a means of protecting a specific area, habitat or species but it is argued that the design and selection of areas for the earlier MPAs was often based on little scientific justification (Allison et al. 1998). Additionally, there has historically been a bias for

establishing MPAs on coral reefs and rocky nearshore areas in temperate zones, with the sole aim being to support fisheries management (Roberts & Polunin 1991; Game et al. 2009; Agardy et al. 2010). Gradually, evidence has emerged to show that MPAs are most effective where fishing and other human activities are prohibited (i.e. marine reserves), as they are more likely to encourage (i) spillover effects where adults move outwards into unprotected areas, and (ii) increases in biomass through recruitment within the area (Man et al. 1995; Roberts et al. 2001; Gell & Roberts 2003; Halpern & Warner 2003; Hart 2006; Kellner et al. 2007). Indeed, MPAs, and marine reserves in particular, have been described as a tool but are cautioned as being viewed as the primary and only solution (Allison et al. 1998).

In the past decade, efforts have been made to indentify priority areas and optimal MPA configurations for conservation (Roberts et al. 2002; Sala et al. 2002; Balmford et al. 2004; Hall-Spencer et al. 2009). Focus has also shifted from single, isolated MPAs to the creation of networks of MPAs, whereby each MPA should provide local protection whilst being close enough to others to remain ecologically connected. A major benefit of this network approach should be to ensure that any node of the network that suffers some form of perturbation will recover more quickly as it will be seeded by other nodes, but this requires that source and seed areas are indeed connected. Field specialists came together in 2003 to assess how best networks of marine reserves could be designated and where gaps in knowledge existed (Ecological Applications, 13(1)). These studies all focused on marine reserves, though the social, economic and political issues involved (e.g. Dixon et al. 1993; Christie et al. 2003; White et al. 2010) mean that MPAs of varying protection are a reasonable and often necessary alternative to full protection. One of the major areas identified to need further work to help better design networks of MPAs, was ecological connectivity.

1.2 Connectivity in the marine environment

Simply put, connectivity is the flux of any material (e.g. gametes, genes, nutrients) between locations (Cowen & Sponaugle 2009). Population connectivity (from here on simply referred to as connectivity) implicitly describes the exchange of individuals between geographically separated subpopulations that comprise a metapopulation, though the precise definition varies between authors and

ecosystems (Calabrese & Fagan 2004). Connectivity plays a fundamental role in local and metapopulation dynamics, community structure, genetic diversity and the resilience of populations to human exploitation (Gaylord & Gaines 2000; Cowen et al. 2002; Palumbi 2003; Trakhtenbrot et al. 2005). In the marine environment, connectivity has most commonly been referred to as the extent to which populations are linked by the dispersal of larvae in sedentary species, and both larvae and adults in mobile species (Palumbi 2003). Implicit in this is the term dispersal; it is considered the driving force behind connectivity. Therefore a clear understanding of both biological (e.g. adult movement, larval strategies, habitat selection and settlement) and physical influences (e.g. hydrographic regimes, benthic habitat distribution and suitability, temperature) on dispersal is essential if connectivity is to be well understood.

One of the earliest examples linking dispersal and settlement of larvae with abundance of adults was by Petersen (1918), who studied intertidal soft-sediment communities for over 25 years. He described the anomaly of why the bivalve *Macoma balthica* was not found in areas of deeper but suitable sediments, and linked this to the dispersal of their larvae. Later, Thorson (1946, 1950), a Danish biologist, was instrumental in clearly defining the life history of many benthic invertebrates as consisting of a dispersive planktonic larval phase and a bottom-dwelling juvenile and adult phase. Since then, advances in the field of larval ecology have been significant, particularly with regards to larval development and metamorphic behaviour (Young 1990) but only within the past 30 years has larval ecology and community ecology come together to provide a view of wider community dynamics (Levin 2006). Initially much of the work focussed on post-settlement processes such as competition, predation, physical disturbance and their interaction (see Todd 1998), but studies did then begin to focus on aspects of larval settlement and recruitment, or 'supply-side' ecology (Roughgarden et al. 1985; Gaines & Roughgarden 1985; Lewin 1986; Pawlik 1993).

The role of dispersal in connectivity has developed from the field of supply-side ecology. The many driving factors that affect dispersal vary temporally, spatially and between species, with the complexity of typical benthic invertebrate life cycles in particular is such that modelling their life-cycles becomes increasingly difficult due to the variation in spatial and temporal scales between larval, juvenile and adult

phases (Eckman 1996). Indeed the heterogeneity of dispersal scales between and within species means that from a community perspective, the complexity of connectivity cannot be underestimated (Kinlan & Gaines 2003; Largier 2003). However, in parallel with advances in knowledge of larval ecology (over the past 30 years) there have also been advances in the methods for measuring and/or predicting dispersal.

1.3 Measures of dispersal and connectivity

Dispersal has been described as the 'glue' that keeps local populations together in a metapopulation (Hansson 1991) and larval dispersal in marine species has been widely accepted as the means by which populations are connected (Scheltema 1986; Shanks et al. 2003; Kinlan et al. 2005). Therefore in order to determine at what level connectivity occurs for any given species, dispersal must be measured. Understanding dispersal mechanisms and distances can then potentially aid scientists and managers to determine the optimal size, configuration and location of MPAs (Levin 2006), though examples of this principle in practice have not as yet been shown in the literature.

In oceans, the combination of species life histories and hydrodynamics allow for long-distance dispersal, potentially >1000km (Thorson 1950; Scheltema 1988; Shanks et al. 2003; Kinlan et al. 2005). However, factors such as larval behaviour, life history strategies and persistent oceanographic features can limit dispersal and sometimes lead to retention of larvae near to or within their parent population (Olson 1985; Shanks 1995; Todd 1998; Armsworth et al. 2001). While dispersal can be difficult to directly quantify, there is evidence of both extremes emerging (Bradbury & Snelgrove 2001; Mora & Sale 2002; Kinlan & Gaines 2003; Shanks et al 2003). Graham & Sebens (1996) determined three key questions relevant to determining marine invertebrate larval dispersal: (1) how long do larvae remain in the plankton? (2) How much influence, by swimming, does the larva have on where it goes? (3) What is the water flow at time of release and how will it influence the larva's ultimate destination? These questions form the basis of many approaches to measuring dispersal, including coupled physical modelling, otolith microchemistry, elemental fingerprinting, tagging experiments and genetic methods such as estimates of gene flow between populations (Levin 2006).

Many studies on connectivity have been weighted towards fish, tropical and/or rare species, but not common benthic invertebrate species within a range of habitat types. With MPA networks required to protect multiple species and habitats, more needs to be known about dispersal and connectivity of common species as well as commercial or heavily impacted species. For these species, the techniques best suited to studying connectivity have been biophysical modelling and analysis of genetic information.

Simultaneous modelling of biological traits and physical processes allows researchers to assess connectivity at varying temporal and spatial scales, and are considered critical tools for addressing the complex processes behind connectivity (Werner et al. 2007). Physical processes include wind-driven currents, tides, eddies, and fronts while the primary biological traits determining dispersal are larval development time and behaviours such as diel vertical migration. Coupled biophysical modelling approaches vary in the number of processes and traits they account for, but have progressed rapidly in terms of resolution of these processes (Kinlan et al. 2005; Werner et al. 2007). This progression has also been evident in the number of studies and variety of taxon modelled, including reef fish larvae (e.g. Cowen et al. 2000; Paris & Cowen 2004); coral larvae (James et al. 2002; Galindo et al. 2006); fish eggs and larvae (van der Molen et al. 2007); and invertebrates (Dibacco & Chadwick 2001; Pederson et al. 2003).

An indirect means of assessing larval dispersal, and therefore connectivity of populations, is through studies of genetic structure and gene flow across and between populations (Todd 1998). Gene flow is the change in gene frequency due to movement of gametes, individuals or groups of individuals between locations (Slatkin 1987), therefore estimating gene flow between populations can provide insight into the level of exchange between populations. With populations of most species showing some levels of genetic structuring (Balloux & Lugon-Moulin 2002), assessing how and at what spatial scale differentiation between populations occurs can provide estimates of species dispersal ranges. As dispersal distance is usually shorter than a species range, isolation by distance (i.e. populations in close proximity are genetically more similar than more distant populations (Balloux & Lugon-Moulin 2002)) estimates coupled with larval dispersal information can

provide a measure of where population isolation occurs (Palumbi 2003). Fisheries management in particular has become reliant on estimating population structure through genetic studies, and increasingly understanding recruitment dynamics and source-sink dynamics has been recognised to be vital for effective management (Heipel et al. 1999). Protection needs to be afforded to those populations that are self seeding but are also major sources of recruits for other populations. Wide-scale larval dispersal would be expected to suppress population differentiation (Heipel et al. 1999); indeed there are numerous examples of panmictic populations – those that are unstructured and randomly mating - in the marine environment (Palumbi 1992). Conversely, there are also examples of where population differentiation has occurred at small geographical scales, possibly due to the retention of larvae (Palumbi 1994).

1.4 Aims

It has been suggested that management decisions cannot be based on detailed species-level information on dispersal for the marine environment because of the inherent complexity (Roberts et al. 2001). Indeed, in the call for the creation of an ecologically coherent network of MPAs throughout the North-east Atlantic, the OSPAR commission stated that while it understood connectivity played a vital role in maintaining ecological coherence, lack of knowledge on connectivity should not prevent the development of the network (OSPAR 2005). Whether improved understanding of connectivity can alter designations that have already been made remains to be seen, given the difficulty in creating them in the first place.

Whilst short-term management decisions may not wait for the science to inform them, in the long-term better informed decisions are achievable. In terms of MPA networks, this requires increased understanding of how connectivity varies temporally and spatially, between species and habitats, and the biological and physical factors that affect it. By coupling available information on life history strategies of marine species, with hydrodynamic modelling and genetic analysis, it should be possible to better define connectivity in temperate benthic subtidal habitats. With the majority of the shelf seas of the north east Atlantic dominated by sedimentary habitats and their corresponding benthic species, there is an

immediate need to understand connectivity within these systems in order to provide informed protection through MPA networks.

Thus, the focus of this thesis will be to explore connectivity in a range of benthic subtidal invertebrates from the UK shelf seas, in the following way:

Chapter 2 Larval dispersal and hydrography: importance for ecological connectivity

The variation in dispersal potential of a typical subtidal benthic invertebrate assemblage was determined by first examining the differences in recorded Planktonic Larval Durations (PLD) for species with the same larval development types, then using a range of PLDs observed from these species to run dispersal scenarios in multiple locations using particle tracking software. The contributions of biological (PLD) and physical drivers (hydrographic region, specific location, depth and distance from shore) to the dispersal distances achieved were then examined using a full linear mixed model.

Chapter 3 The influence of landscape rarity, distribution and suitability on connectivity in the marine benthos

The role of habitat specificity in determining connectivity was assessed by compiling habitat preference traits for 79 species (from the same assemblage studied in Chapter 2) and examining the influence of habitat suitability, rarity and distribution on the likelihood of species being well connected in a typical regional sea (the Irish Sea). The suitability of using marine landscapes as a proxy for habitat was examined, as these are often used for classification of seascapes and designation of MPA networks may be best suited at this scale. Finally, dispersal scenarios were run using particle tracking software for several habitat specialists suited to different landscape types within the Irish Sea, to examine the likelihood of them dispersing to suitable habitat.

Chapter 4 Genetic structure of the scallop *Pecten maximus* from fishing grounds around the Isle of Man, Irish Sea

The scallop *Pecten maximus* is a relatively well studied benthic invertebrate species so that information on its life history and ecology is more accessible. We therefore have good information already available on dispersal potential and habitat

suitability so it is possible to examine the implications of this on divergence of the population over longer time scales. Using microsatellite markers, the genetic structure of a single species with a specific dispersal regime at a small geographic scale, in this case the waters surrounding the Isle of Man, was examined. By accounting for hydrographic regime and using software to make predictions of genetic divergence, implications for marine management of this highly valuable commercial species were assessed.

Chapter 5 Genetic structure of the scallop *Pecten maximus* along the North East Atlantic shelf

Continuing on from Chapter 4, this chapter examined the population structure of *Pecten maximus* at a larger geographic scale incorporating over half of its geographic range, from the northernmost limits off Norway, to the south of Ireland. Previous studies have shown varying degrees of divergence at these scales, but it may be possible to compare common genetic breaks with dispersal strategies of those species. Additionally, variations in genetic diversity of populations were examined in terms of implications for management of stocks.

Chapter 6 Discussion

The results from the preceding chapters were synthesised based on implications for MPA design, while future issues including the need for adaptive management in the face of climate change were discussed. Synthesis of results, implications for MPA network design in the UK and future directions in research.

Chapter 2

Larval dispersal and hydrography: importance for ecological connectivity

2.1 INTRODUCTION

Marine Protected Areas (MPAs) have historically been directed towards a single-purpose design, most often for fisheries or habitat protection purposes (Boersma & Paris 1999). Following recent international agreements aimed at protecting biodiversity (e.g. The *World Summit on Sustainable Development (WSSD), Johannesburg 2002)*, there is a general consensus that design must incorporate a network of connected MPAs, and there has been increased focus on how to develop and implement this (e.g. Roberts et al. 2003). As part of the creation of an MPA network in the North East Atlantic, the Oslo and Paris Convention (OSPAR) requires that any network should be 'ecologically coherent' (OSPAR 2003), a concept that is still broad in its definition (see Ardron 2008 for discussion). However, it is agreed that there are key factors which will contribute to, and be used for assessment of, ecological coherence (OSPAR 2006, 2007; Ardron 2008), including the degree of connectivity between sites and consideration of 'representativity' (where any network should cover representative areas of all major habitat types not just those that are currently at risk or degraded (DEFRA 2010)). Other contributing factors to ecological coherence are replication, viability, adequacy in size and a range of protection levels. However, a lack of knowledge on connectivity should not impede the development of an OSPAR network (Principle 10, OSPAR 2006), and management decisions in terms of size and spacing of MPAs should still allow for further advances in our understanding of the drivers of connectivity in representative habitats.

The concept of connectivity in marine populations has received considerable attention particularly in recent years (see Palumbi 2004 for review), and can simply be thought of as the exchange of individuals between populations through dispersal (Cowen and Sponagule 2008). For benthic invertebrates where the adult phase is often sessile or at least sedentary, the larval phase is critical, in which dispersion

largely occurs and greatly influences population dynamics (Crisp 1978 but see Valanko et al. 2010). A host of biological and physical factors also determine the rate and scale of dispersal of larvae, such as larval behaviour, spawning time and location, mortality, settlement cues and post-larval/juvenile dispersal (see Levin 2006 for review). Thus, accurately quantifying patterns of connectivity for a species can be difficult and even context-dependent. Accurately predicting the movement and subsequent recruitment of larvae within a metapopulation, whilst accounting for these factors, is problematic, even with the use of multiple techniques such as genetic studies, direct observations and bio-physical modelling (but see Galindo et al. 2006). Recent improvements include coupling several techniques, such as molecular data and bio-physical modelling (e.g. Gaines et al. 2003; Ketchington et al. 2006) to combine increasingly complex population and particle tracking models to predict connectivity.

To date, studies using particle tracking models have focused on single species, particularly intertidal species (e.g. limpets in Chiswell 2009; mussels in Gilg and Hilbish 2003), tropical reef species (e.g. coral in Galindo et al. 2006), or species of commercial interest (e.g. oyster in North et al. 2008; demersal fish in van der Molen et al. 2007). Where the overall dispersal potential of a species assemblage has been examined, estimates were made using information on larval development mode (e.g. Jones & Carpenter 2009), estimates of Planktonic Larval Duration (PLD), field observations, the rate of spread of introduced species (Shanks et al. 2003; Grantham et al. 2003), or genetic measures (Kinlan & Gaines 2003). These studies highlight the wide potential for dispersal, with predicted estimates of dispersal ranging from several metres to over 1,000 kilometres for representatives from all major benthic taxa.

In a study on a range of benthic species, Shanks et al. (2003) suggested dispersal distance follows a bimodal distribution. Species were characterised as having (1) PLDs <100 hours and dispersed <1 km or (2) PLDs >300 hours and dispersed >20 km. Accordingly, they proposed that a network of MPAs some 4-6km in diameter and 10-20 km apart would allow self-seeding for animals with low dispersal potential and connectivity for high dispersers respectively. Jones and Carpenter (2009) progressed beyond this dichotomy (that broadly represent non-planktotrophic and planktotrophic larvae) by categorising a selection of rare or

scarce benthic invertebrates as having low, medium or high connectivity (after Dibacco et al., 2006) and assigned potential dispersal distances and PLD ranges (Low: <1 km, <10days; Medium: 1-100 km, <1 month; High: >100 km, weeks-months, summarised from Tables 3, 4 and 5 in Jones and Carpenter (2009)). In a recent study, Roberts et al. (2010) used particle tracks to run dispersal scenarios within or around the 12-mile limit of the UK using PLDs of 1, 10, 30 and 50 days based on a range of native species. They recommended an MPA size of approximately 10-20 km across, each separated by 40-80 km in nearshore waters, and for those outside the territorial limit a size of 30-60 km across to ensure adequate protection of highly motile commercial species.

There is a clear need to provide advice on the size and spacing of MPAs so that they can form coherent networks, but we argue here that variability in realised dispersal potential of species characteristic of any particular habitat is dependent not only on generic PLD ratings but also on location (see discussion of affect of distribution of habitats, and Chapter 3). The composition of species and local hydrography will inevitably vary between habitats. Clearly an area with a current regime that facilitates retention of larvae, and is characterised by low dispersing species should be treated quite differently to an area of high advection characterised by species with high dispersal potential. In typical assemblages, such as those characterising the subtidal sediments of the UK continental shelf, there will be a range of life history characteristics displayed by the resident species. As yet, this location-specific variability has not been explored for benthic invertebrates.

In this study, using PLD of species found to characterise offshore epifaunal invertebrate assemblages around the UK shelf seas, the variation in dispersal potential between species and locations was examined. Using a simple particle tracking model coupled with a hydrodynamic model, the effect of PLD on dispersal distance was explored in locations characterised by different dispersal regimes. The overall aim of this study was to determine whether generic categorisation of species dispersal potential is appropriate when applied to typical assemblages in locations around the U.K. This was achieved by exploring the effect of (1) larval development type, (2) location and (3) hydrographic region on dispersal distance.

2.2 METHODS

2.2.1 Classification of common subtidal benthic assemblages

2.2.1.1 Selection of species

Species lists were compiled from epifaunal data collected by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) in 1998 and 1999 (see Ellis et al. 2000) and for the Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity project (MAFCONS) in 2003 and 2004 (see Callaway et al. 2003) from four regions around the southern UK continental shelf (Figure 2.1). CEFAS collected samples using a 4 m beam trawl fitted with a chain matrix and a 40 mm stretched mesh cod-end. The net was towed for 30 minutes at each station, covering an approximate area of 15,000 m^2 per tow. MAFCONS samples were collected with a 2 m beam trawl fitted with a chain matrix and a 20 mm mesh cod-end. Each tow lasted for 5 minutes, and covered an area of approximately 463 m^2. Epifauna were identified to lowest practicable taxonomic level, weighed and non-colonial species counted.

To generate a list of epifaunal invertebrate species typical of temperate subtidal benthos, species lists were reduced according to the following parameters: a species (i) occurred at ≥20 % of stations; or (ii) had a catch per unit effort (CPUE) ≥5 kg per hour at any station; or (iii) was ranked in the top five species by catch rate at any one station. This generated a list of 102 taxa that represented for 98.8 % of the biomass on average at any one station.

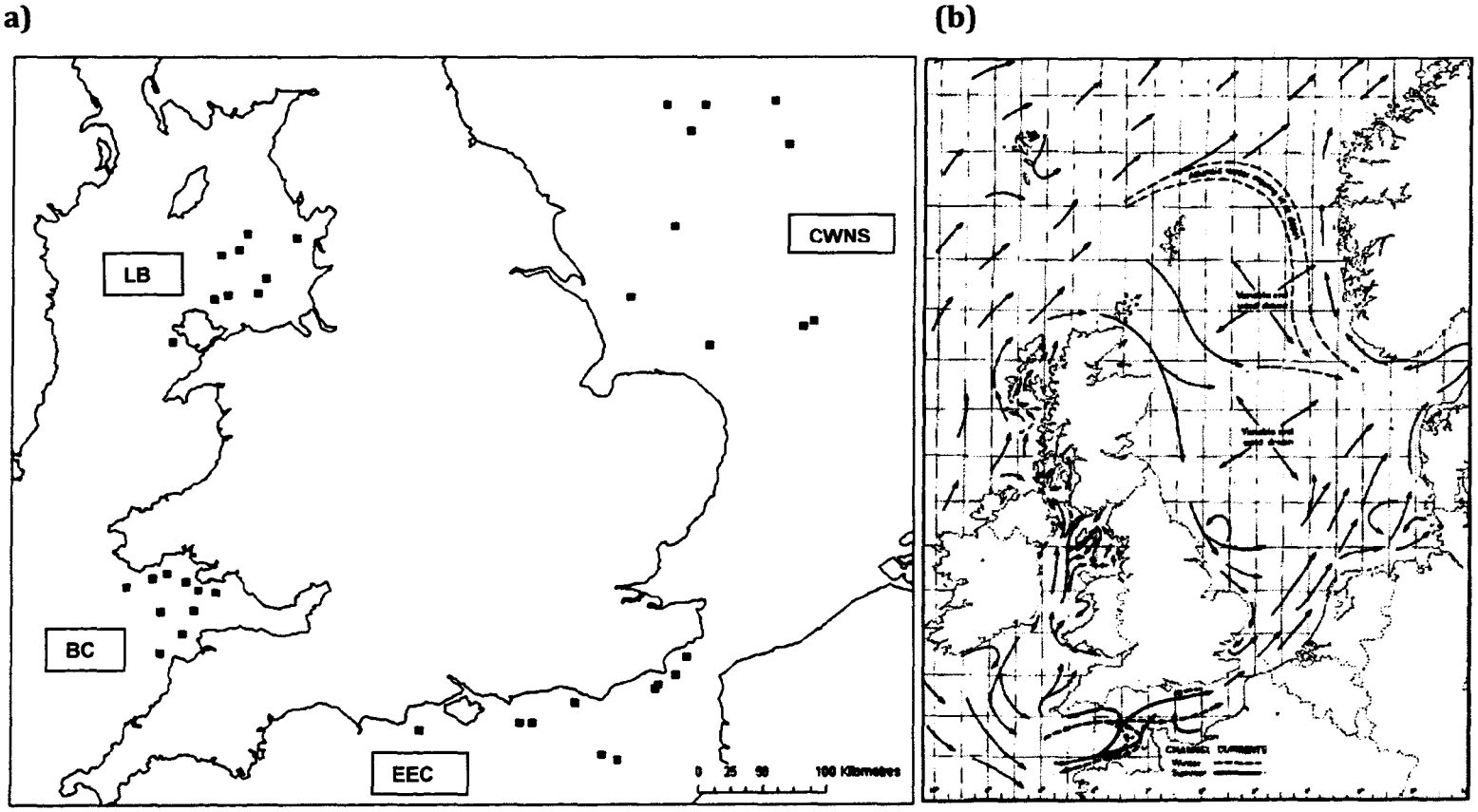


Figure 2.1 (a) Beam trawl survey area in the UK regional seas with the 39 survey station indicated. Stations were grouped into four hydrographical regions: Central West North Sea (CWNS), East English Channel (EEC), Bristol Channel (BC) and Liverpool Bay (LB). (b) Residual surface currents in UK (after Smith et al. 1996).

Literature searches were conducted for each of the 102 taxa in the reduced species list and used to identify development type and differences between taxonomic groups. Higher taxonomic classifications of species (i.e. Phylum, Class etc.) were based on Howson & Picton (1997).

PLD (equivalent to time spent in the water column) was used as a proxy to quantify larval dispersal potential of 83 of the 102 taxa. Where planktonic durations varied between sources, or a range was given from experimental data, both the maximum and minimum time was taken. As development time varies with temperature for ectotherms (Hoegh-Guldberg & Pearse 1995), estimates were further limited to the temperature range of 8-13°C, which reflects the variation in average sea surface temperatures (SST) around the UK from January to June (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month). Where estimates were only found for temperatures above this range, the longest time was used as water temperature is inversely related to length of development (O'Connor et al. 2007). If development type was known but time was not, estimates for species in the same genera and the same development type were used. Where organisms were grouped into higher taxa (e.g. Ascidians, Bryozoans), an average time was calculated based on available data describing the most common species found in the assemblage sampled.

Kruskal-Wallis tests were used to test for differences in PLD between development types and between categories in Dibacco's classification. Mann-Whitney tests were used to test for differences by species between pairs of categories. Non-parametric tests were used because PLD was non-normally distributed within categories. Bonferroni's correction was used to maintain the familywise error rate for multiple comparisons.

2.2.2 Modelling dispersal

2.2.2.1 Modelling software

Estimates of larval dispersal distance were modelled using POLPRED 2.0 (Proudman Oceanographic Laboratory), an offshore tidal computation software package with a Lagrangian particle tracking component that can be applied to different depth strata. Diffusion of particles is based on Monte-Carlo random walks (Maier-Reimer

1980), and a diffusion coefficient (m^2 s^{-1}) is specified by the user. Diffusion coefficients used for estimating larval dispersal have been described for several taxa and range from 0. 5 m^2 s^{-1} for coral larvae on tropical reefs (Oliver et al. 1993) to 10 m^2 s^{-1} for barnacle larvae on the Californian coast (Alexander & Roughgarden 1996). In this case a diffusion coefficient of 5 m^2 s^{-1} was deemed to be the most appropriate for the hydrographic and bathymetric conditions. To ascertain the effect of the number of particles and time step used on dispersal distance, and to allow for maximum efficiency, a sensitivity analysis was conducted. Dispersal scenarios were run for 500 and 1,000 particles at both 15 minute and 30 minute time steps in one location. These were run for 2, 6, 20, 42 and 90 days, and the minimum, maximum and median distances were compared. It was found that there was little difference in dispersal distance between particle number and time step combinations. As such, it was decided that 1000 particles and a time step of 30 minutes would be used. Time of release can be specified and based on species where spawning time was known (e.g. April-June (Norman & Jones 1993); December-January (Hartnoll 1975); spring (Comely and Ansell 1989)), a release date of 1st March was applied.

2.2.2.2 Location and timing of dispersal

In order to represent the sample assemblages used in this study, locations where particles were released in each dispersal scenario corresponded with station locations used by CEFAS and MAFCONS. Four areas – herein referred to as hydrographic regions - with distinct residual current patterns were identified (see Figures 2.1a & 2.1b), these being: Central West North Sea (CWNS) which has a southerly transport along the English coast then an anti-clockwise circulation through the southern North Sea; East English Channel (EEC) with a general north easterly flow through the Dover strait to the south North Sea; Bristol Channel (BC) displaying a northerly flow from the Celtic Sea meeting a westerly flow along the coast of Wales from the head of the Bristol Channel; and Liverpool Bay (LB) which has a northerly transport along the coast which meets a southerly flow from the central Irish Sea to create a clockwise circulation (Lee & Ramster 1981). A total of 10 stations in regions CWNS, EEC and BC, and nine in LC, each situated within 20-50 m depth, were chosen and their distance from shore estimated.

In order to examine dispersal distances of different development types at multiple locations, the minimum, maximum and median PLDs for BANF, lecithotrophic and

planktotrophic developers (as quantified in 2.2.1.2) were used to run dispersal scenarios at each station (see PLDs given for each development type in Table 2.3). Scenarios for BANF PLDs were run at the bottom depth level as BANF propagules are closely associated with the benthos. Lecithotrophic and planktotrophic runs were undertaken at the surface depth level.

2.2.2.3 Data Analysis

A linear mixed model was used to determine the effect of PLD, station, hydrographic region, depth and distance from shore on final dispersal distance. Dispersal distance was log-transformed because of strong right skew. Parameters were estimated by maximum likelihood to allow comparisons between models differing only in fixed effects (Faraway 2006). Both random and fixed effects were tested using likelihood ratios, which expresses the likelihood of the data fitting to one model against another (Faraway 2006). These tests are approximate but few terms of interest had borderline p-values. The lmer4 package (Bates 2005) in R version 2.9.0 (R Development Core Team 2010) was used to fit and compare models and initially included all interactions among fixed effects. Station was treated as a random effect because we have a large number of different stations, and the variability among stations is of more interest that the properties of particular stations. All other factors were treated as fixed effects. To visualise the effects of development type and region, predicted distances were obtained from the selected model for each development type and region, with depth and distance from shore fixed at their overall means.

2.3 RESULTS

2.3.1 Variation in dispersal potential of common subtidal soft sediment benthic assemblages

Dispersal, classified by either development type or using the Dibacco method, was similar with the high, medium and low classifications of the Dibacco method corresponding to planktotrophic, lecithotrophic and benthic-associated non-feeding (BANF) development respectively. Of the 102 taxa classified, 73.1% were planktotrophic/high dispersers, 15.1% lecithotrophic/medium dispersers, 4.3% were benthic-associated non-feeding (BANF) and 7.5% direct developers. When using the Dibacco et al. (2006) method, BANF and direct developers were grouped

within the 'Low' dispersal category. Mean planktonic larval duration (PLD) was 49.7 days (± 4 SE) for planktotrophic/high, 8.3 days (± 3.1 SE) for lecithotrophic/medium, 1 day for BANF larvae and 0 days for direct development, which grouped as 'low' had a mean PLD of 0.36 days (± 0.16 SE). The range of PLDs for High/Planktotrophic was large (6-90 days), with a median time of 42 days (Figure 2.2).

PLD varied significantly between each of the three Dibacco ratings (Kruskal-Wallis H = 38.4, df = 2, $p < 0.001$) (Figure 2.2) or four development types (Kruskal-Wallis H = 38.61, df = 3, $p < 0.001$). The distribution of development types varied considerably between Phyla within the assemblage (Table 2.2). All Crustacea, 81% of the Echinodermata and 75% Mollusca were planktotrophic, but less than half of the Cnidaria were. Of the other Phyla, there were fewer than five taxa in each, which made patterns difficult to ascertain. BANF species were confined to the Bryozoa, Chordata, Cnidaria and Porifera; taxa that can also reproduce asexually (e.g. budding of Anthozoans). Mean Planktonic Larval Duration (PLD) of phyla varied considerably (Table 2.2). Crustacea had the highest mean PLD with all taxa displaying planktotrophic development while the Mollusca were lower with nearly 25% of species in the assemblages sampled being direct developers.

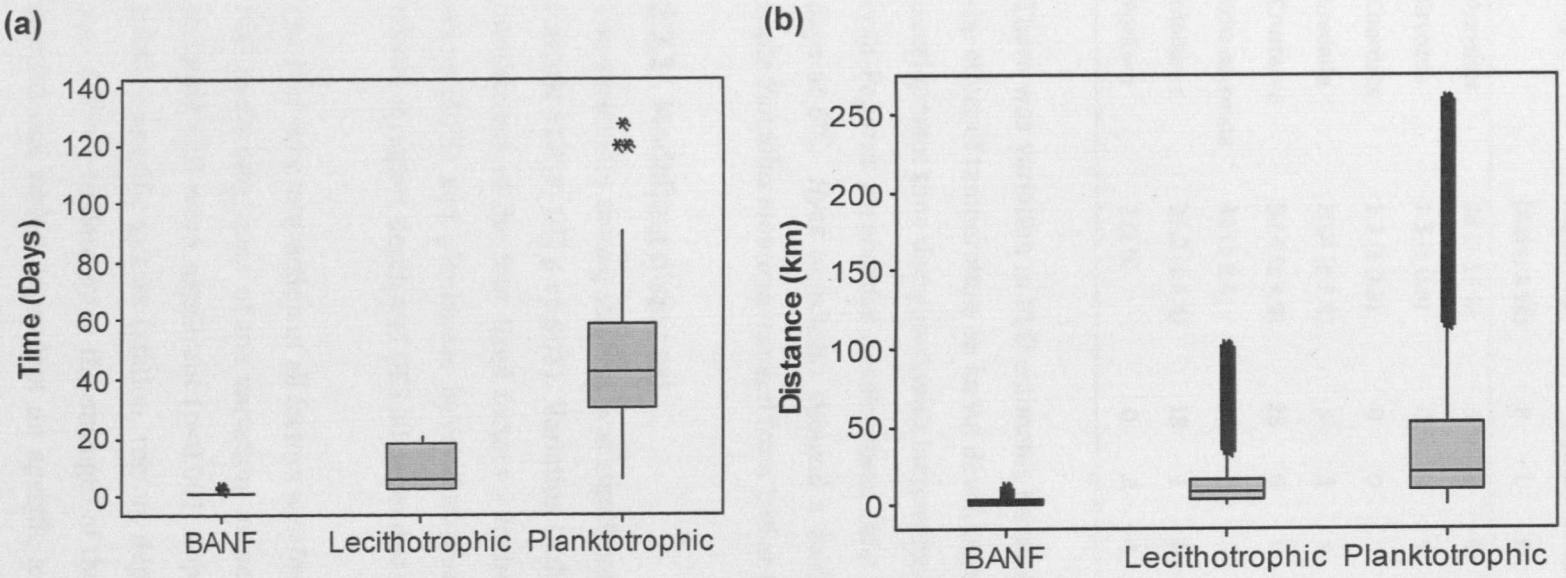


Figure 2.2 Boxplots of three larval development types (planktotrophic, lecithotrophic, Benthic Associated Non-Feeding (BANF)) from 83 taxa, showing: (A) the Planktonic Larval Duration (PLD) range; and (B) dispersal distance range where scenarios for maximum, minimum and median PLDs and for all locations have been grouped. Medians are shown by lines through the boxes, upper and lower limits of boxes represent the spread of the middle 50% of the data, and whiskers extend to the maximum and minimum data points that are not more than 1.5 times the interquartile range away from the limits of the box. Outliers are shown by an asterisk.

Table 2.2 Mean planktonic larval duration (PLD) and number of taxa of the four development types (planktotrophic (P), lecithotrophic (L), BANF (B) and direct development (D)) for eight phyla represented by 102 taxa (See Appendix 1 for full list).

Phyla	Mean PLD (days, ± SE)	Number of taxa			
		P	L	B	D
Annelida	38 (± 13.2)	3	0	0	1
Bryozoa	1.3 (± 0.3)	0	0	4	0
Chordata	1.3 (± 0.3)	0	0	3	0
Cnidaria	20.4 (± 7.8)	5	3	6	0
Crustacea	50.4 (± 4.9)	28	0	0	0
Echinodermata	42 (± 8.5)	17	2	0	2
Mollusca	25.2 (± 6.1)	18	1	0	5
Porifera	2 (± 0)	0	3	1	0

There was variation in PLD estimates for most species, most likely associated with the effect of temperature on larval development times (see Appendix 1). In general, development time decreased with increasing temperature. For example, the hermit crab *Pagurus bernhardus* development time ranged from 38 days at 18°C to 115 days at 6°C. *Hyas coarctatus* showed a similar pattern at the same temperatures while *Pandalus montagui* ranged from 10d at 12°C to 18 days at 6°C.

2.3.2 Modelling dispersal

The variability among stations was significantly greater than zero (likelihood ratio statistic 41753, 1df, p <0.001). Variation in dispersal distance was influenced by the interactions of the four fixed factors - hydrographic region, depth, distance from shore (DFS) and planktonic larval duration (PLD) (Appendix 2). However, the effects of region, depth and DFS all depended upon PLD (Appendix 2).

The four-way interaction of all factors was found to have an effect on dispersal, with PLD explaining most of the variation, as only those combinations of factors that included PLD were significant (p<0.001, Appendix 2). Given the interaction of the location-specific factors (station, region, depth, and distance from shore (DFS)) it was difficult to determine the strength of the effect of each factor individually (i.e. interactions varied dependent on specific location). For example, EEC had much

higher dispersal distances than the other regions but stations are closer to shore than, for example, CWNS where particles were more likely to be retained within a smaller area (Figures 2.3, 2.4 and 2.5). In BC and LB, stations were also closer to shore but this led to many particles either reaching land/moving outside the model limits or being locally retained so that dispersal distance was reduced. Therefore the removal of depth and DFS from future analysis may allow for clearer interpretation of the strength of location and PLD alone.

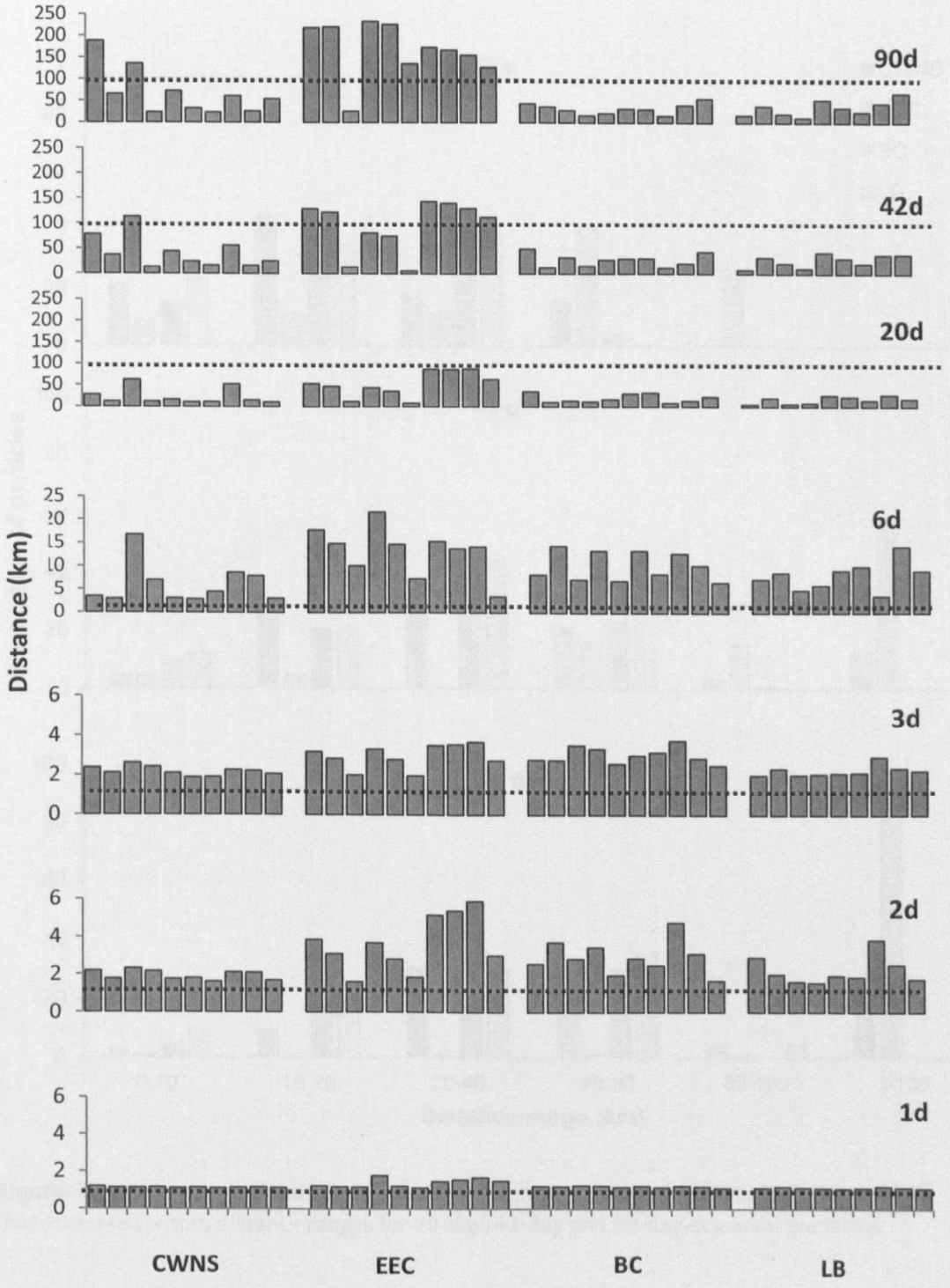


Figure 2.3 Median dispersal distance (km) of 1000 particles released at stations (1-10) in four hydrographical regions (Central West North Sea (CWNS), East English Channel (EEC), Bristol Channel (BC) and Liverpool Bay (LB)) (see Figure 1) for a range of Planktonic Larval Durations (PLD). Dotted lines indicate 1 km and 100 km limits. Note difference in scale for distance.

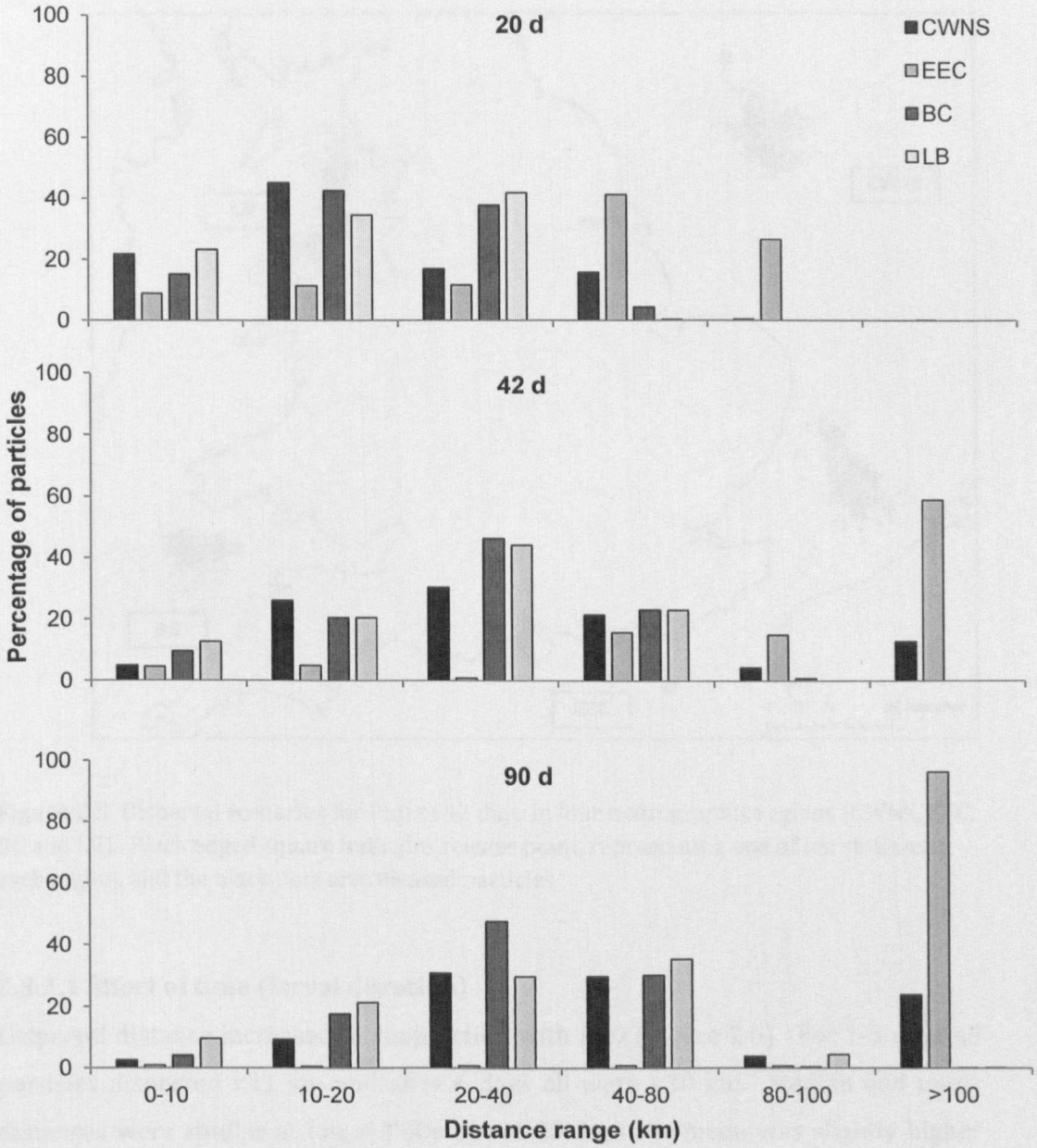


Figure 2.4 Percentage of particles in four hydrographic regions (CWNS, EEC, BC and LB) that dispersed within distance ranges for 20-day, 42-day and 90-day dispersal scenarios.

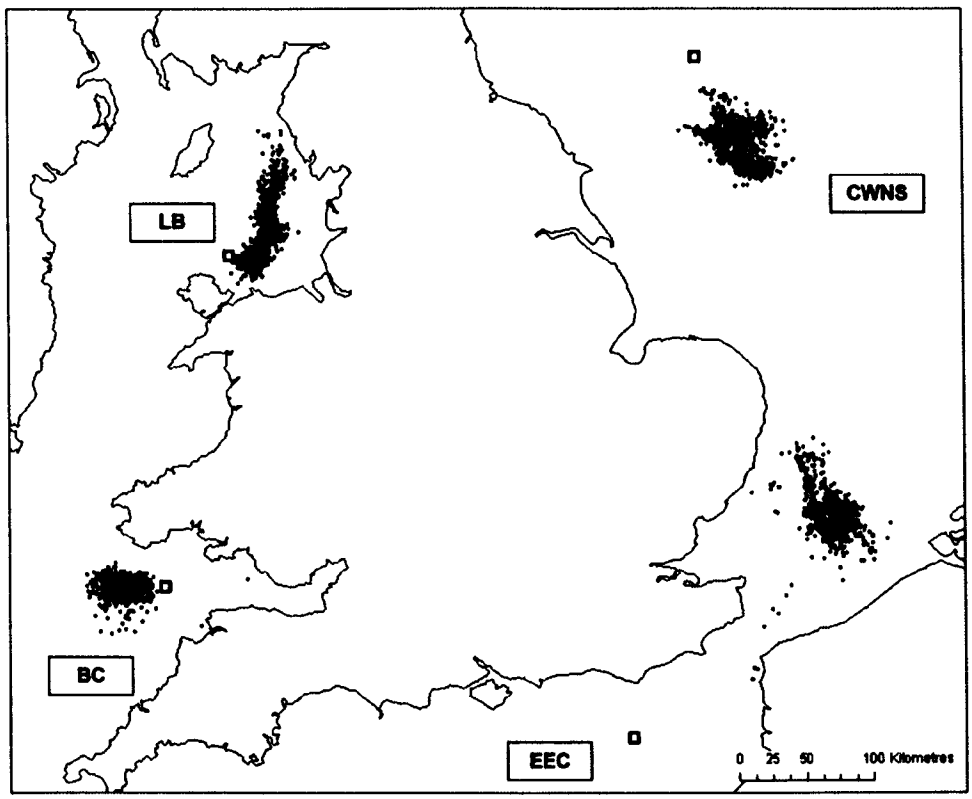


Figure 2.5 Dispersal scenarios for PLD of 42 days in four hydrographic regions (CWNS, EEC, BC and LB). Black edged square indicates release point, representing one of ten stations in each region, and the black dots are released particles

2.3.2.1 Effect of time (larval duration)

Dispersal distance increased in conjunction with PLD (Figure 2.6). For 1-3 days all particles dispersed <11 km and after 6 days all were <30 km. Median and mean distances were similar at lower PLDs but at 20 days the mean was slightly higher than median, while at 42 and 90 days it was almost double (Figure 2.6, Table 2.3). Interquartile ranges doubled from 36.7 km to 73.7 km to 146.9 km for 20, 42 and 90 days respectively, reflecting the diffusion of particles over time. Development type greatly affected dispersal distance. Greatest dispersal was predicted for planktotrophic taxa (ranging from between 1 and 260 km), whereas BANF taxa were predicted to disperse the least (between 0.1 km to 10.5 km) (Figure 2.2).

Table 2.3 Minimum, median and maximum Planktonic Larval Durations (PLD, days (d)) for three larval development types (BANF, lecithotrophic and planktotrophic) and the mean dispersal distance (km) from 39 locations.

	Minimum PLD		Median PLD		Maximum PLD		Overall Mean Distance (km) ±SE
Development Type		Mean distance (km) ±SE		Mean distance (km) ±SE		Mean distance (km) ±SE	
BANF	**1d**	**1.28** (± 0.004)	**1d**	**1.28** (± 0.004)	**3d**	**2.72** (± 0.007)	**1.99** (± 0.005)
Lecithotrophic	**2d**	**2.77** (± 0.080)	**6d**	**9.49** (± 0.027)	**20d**	**28.40** (± 0.012)	**13.47** (± 0.051)
Planktotrophic	**6d**	**9.49** (± 0.027)	**42d**	**51.30** (± 0.229)	**90d**	**83.70** (± 0.418)	**45.29** (± 0.173)

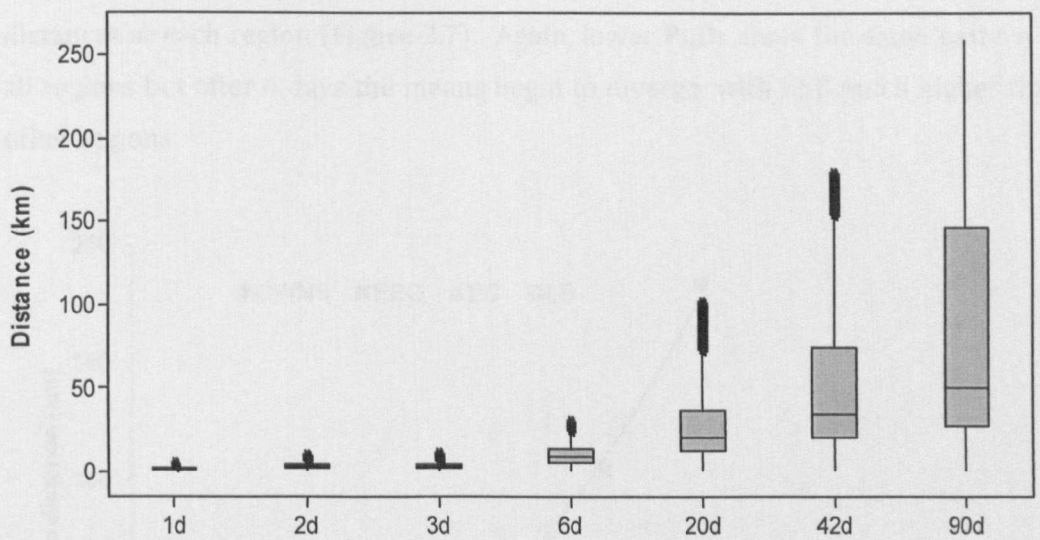


Figure 2.6 Dispersal distance for a range of Planktonic Larval Durations (PLDs) representing the maximum, minimum and median PLDs for three development types (BANF, lecithotrophic and planktotrophic). See Table 2.3 for explanation of how PLDs relate to development types

2.3.2.2 Effect of hydrographic region

Based on the median distance for 1000 particles at each station, the EEC region had consistently higher median dispersal than all other regions, with the BC and LB regions at similar levels for all PLDs (Figure 2.3). Differences in dispersal distances became more pronounced between regions as PLD increased; while regional

patterns were apparent for 42 and 90 day dispersal scenarios, they became less marked with decreased PLD. Interestingly, 2 day runs displayed greater variability than either 1 or 3 day, both of which were bottom depth runs.

At 1, 2 and 3 days, median distance for each station was within 1-6km, while at 6 days it was within 3-22km. At 90 days, median distances ranged from 11.5km in the LB region to 232km in EEC, where all stations apart from station 2 had a median dispersal distance of >100km. Only two other stations (1 & 3 in CWNS) had a median dispersal >100km. When all particles are included, 23.8% in CWNS and 96.3% in EEC dispersed over 100km (Figure 2.4). Only 0.1% and 0.04% of particles in BC and LB respectively dispersed over 100km at 90 day PLD. For the median (42 days) PLD scenario for planktotrophic dispersers, dispersal distance was <100km for all particles in BC and LB, and 87.1% of particles in CWNS. These regional differences are further highlighted when log PLD is compared to mean and median distances at each region (Figure 2.7). Again, lower PLDs show the same pattern in all regions but after 6 days the means begin to diverge, with EEC much higher than other regions.

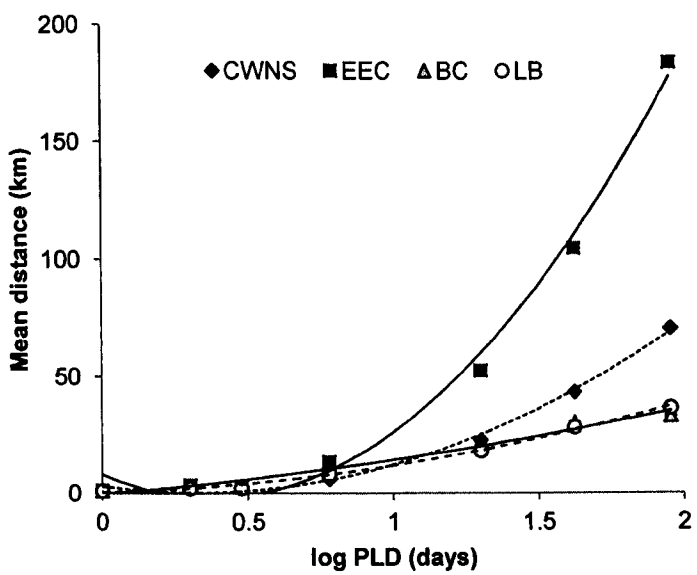


Figure 2.7 Mean dispersal distance of released particles in four hydrographical regions (CWNS, EEC, BC and LB) for minimum, maximum and median Planktonic Larval Durations (PLD) of the three development types (BANF, Lecithotrophic, Planktotrophic). PLD was log transformed. Lines of best fit were calculated using polynomial (quadratic) regression, where: CWNS $R^2 = 0.996$; EEC $R^2 = 0.9921$; BC $R^2 = 0.995$; LB $R^2 = 0.979$.

2.3.2.3 Predicted distances by region for the three main dispersive types

Predictions of dispersal distance for any given particle for the range of PLDs in each region were based on an average depth and DFS, in this case 32m and 20km respectively. Predicted distances were of a similar range to the mean distances for EEC, BC and LB (Figure 2.5) at each PLD (Table 2.4). Predictions for CWNS were higher at PLDs of 20, 42 and 90d compared to the mean and median, however the average DFS in this region was higher (109km) than used in the prediction scenario, which may account for the difference.

Table 2.4 Predicted dispersal distance of a random particle in the four hydrographic regions (CWNS, EEC, BC and LB) for minimum, maximum and median planktonic larval durations (PLD) of the three development types (BANF, Lecithotrophic, Planktotrophic).

	Region			
PLD	CWNS	EEC	BC	LB
1	1.03	1.33	0.98	1.02
2	2.25	3.78	3.20	2.34
3	2.40	3.01	3.81	2.18
6	14.73	18.65	8.19	4.72
20	57.82	53.77	35.84	12.11
42	103.99	92.04	34.59	18.32
90	149.09	189.51	37.54	21.54

2.4 DISCUSSION

Despite over 30 years of research, there remains an immediate need to understand the drivers of connectivity in order to better inform MPA design and management (Gaines et al. 2010). Larval dispersal continues to be a primary focus for research in this area. While it seems intuitive that a combination of biological and physical factors will affect the dispersal potential of larvae, the strength and variation of these effects are unknown for most species. Using a representative sample of benthic invertebrates from northern European continental shelf seas, our results demonstrate an inherent complexity and highlight the importance of biological variability, in terms of the range of dispersal potential (PLD) shown by species with the same development strategies and, crucially, the impact of location on potential dispersal due to the effect of specific physical factors of a region.

Classification of dispersal

Generic descriptors of connectivity (Dibacco et al. 2006) and dispersal potential (Jones & Carpenter 2009) based on specific traits are a useful method of broadly estimating a species dispersal ability. In particular, classification by larval development type would be most useful for identifying those species with the shortest larval dispersal period, behaviours that keep them closely associated with the benthos, and potentially those who are most likely to settle in the shortest time period (i.e. BANF species). By also using information on their minimum viable population sizes and densities, the minimum size of individual MPA could be identified (Shanks et al. 2003; Jones and Carpenter 2007). In this assemblage, 7.5% of species were classified as direct developers, with no dispersive larval phase, and 4.3% were classified as BANF and were found to disperse <10km regardless of location. By distinguishing BANF species from others, dispersal scenarios were able to be run at bottom depths where current flows can differ significantly from surface flow (Crimaldi et al. 2002). The bottom depth scenarios run for BANF species (1 & 3 days) showed less overall variation between and within regions compared to similar surface runs for lecithotrophic species under a 2-day dispersal scenario, due to less advection and diffusion overall. This suggests that location-specific differences are of less importance for the dispersal of BANF larvae. With many BANF species displaying behaviours that would encourage early settlement (Jackson 1986), it is likely that these dispersal distances would represent maximum achievable distances.

Existing estimates of larval dispersal are seen to be weighted towards low dispersing, low latitude species, which if applied to all taxa and regions may undermine conservation efforts for broadly dispersing species that dominate temperate environments. Bradbury et al. (2008) suggests that it is possible that this has led to the assumption that marine populations are more closed than previously thought, even though this may be based on a skewed subset of species. Given that 73% of species in this assemblage were planktotrophic, with PLDs between 6-90 days and dispersal distances of 1-260 km, it is essential for researchers and managers alike to account for this variation and its potential effect on connectivity. However, we acknowledge that these results are based on a passive model that does not include behaviour which might encourage retention, even at higher PLDs (e.g. Morgan & Fisher 2010).

Local and regional variations

Differences between hydrographic regions became more pronounced as PLD increased so that at PLDs >20 days regional differences were apparent. In both the BC and LB regions, almost no particles dispersed >100 km at 90 days, while over 95% of particles did in EEC. However, while the effect of PLD was significant, station location also influenced dispersal distance, with mean distances doubling or even tripling between stations within a region. While variation between some hydrographical regions might be expected, this potential for large differences within a region highlights the effect of localised current regime on dispersal. Several particle tracking studies have shown this at a large scale or for single species (e.g. Galindo et al. 2007; Paris et al. 2007); only recently have the effects of both varying PLD and hydrography begun to be explored (see White et al. 2010).

Recommendations by Shanks et al. (2003) of a network design of 4-6 km in diameter and 10-20 km apart appear realistic for locations that show evidence of retention (i.e. BC, LB and to a lesser extent CWNS). As PLD increases in these regions, there is less of a marked increase in distance. In the highly dispersive locations (EEC and some stations in CWNS), the majority of particles dispersed more than 100km and spacing of 10-20 km would seem unnecessarily precautionary. Roberts et al.'s (2010) recommendations of 10-20 km across and 40-80km apart provide more flexibility, given the variation we have found in this study. Multiple locations were found to have a unidirectional flow, indicating networks must allow for not only current flow strength but also prevalent current direction; MPAs cannot feed into one another if propagules go in the opposite direction. Therefore, in some areas (dependent on the faunal composition of habitats) sizing could be adequate at less than 10kms, and spacing may need only to be at the high end of Roberts et al.'s (2010) guidance, as long as directional flow information is incorporated. Where retention is high, closer spacing would be required. For the 39 stations in this study, assemblage composition did not vary greatly. Where assemblage composition does vary between locations, size and spacing advice would need to concentrate on the poorest dispersers. However, this may be and overly precautionary approach for the majority of benthic species given their wide distribution.

Future directions

Examining the variation in dispersal caused by physical processes on the most dispersive phase of benthic invertebrates is a first step towards understanding connectivity in UK shelf seas. Obviously dispersal does not equate directly to recruitment; larvae must survive, settle and recruit. Given that the behaviour of larvae for many benthic species is simply not known, the type of biophysical modelling completed for some fish (e.g. Paris et al. 2007) and invertebrate species (e.g. Ketchington et al. 2006) is not possible on a broad assemblage basis. Of the 102 taxa covered in this study, PLD was found for 83. Indeed the lack of information for some on life history characteristics (e.g. settlement cues, spawning times) precludes the use of more complex modelling methods. With this in mind, however, there are a number of areas where further work could improve predictions.

With ongoing concerns over projected sea temperature rises (1.5 - 4°C in UK shelf seas by the end of the century (UKCIP 2009)), our results suggest that for those species with longer PLDs, increases of only a few degrees could see significant shortening of the larval dispersal phase (see Appendix 1), and if outside their tolerance threshold, increased larval mortality (Hoegh-Gulberg 1995). Additionally, temperature may disrupt spawning time, which would be problematic for some species that, for example, spawn to coincide with the spring plankton bloom (Koeller et al. 2007). In the long term this may alter species ranges, community structure and biodiversity (O'Connor et al, 2007; ter Hofstede et al. 2010). These issues should be considered in terms of the potential need for adaptive management of MPA network design.

Incorporating environmental cues such as habitat suitability would further refine predictions. This would be possible where habitat information is available and selectivity of adults is known in terms of habitat preference. Temporal variability in, for example, current strength or flow direction will also be important and this could also be considered with the spatial aspects to consider how much actual viable dispersal areas would vary.

Here we have provided some indicative ranges that can be used to underpin guidance on size and spacing of MPA networks for representative habitats. With some further work on habitat specificity of common species and likely temporal

variability given smaller scale changes in current patterns and flow direction, it will soon be possible to set realistic criteria for particular habitat types and to vary the parameters based on local conditions using some straight-forward predictive modelling.

Chapter 3

The influence of landscape rarity, distribution and suitability on connectivity in the marine benthos

3.1 INTRODUCTION

The field of landscape ecology is well established in the terrestrial environment (e.g. Naveh & Lieberman 1984; Turner 1989; Pittman et al. 2011); it was originally conceived as an integration of ecology and geography whereby the complex relationships between communities and their environment are studied and expressed in a definite distribution pattern (Troll 1971). As such, landscapes consist of multiple habitat patches, which vary in size and distribution. A habitat can be defined as a "place where a microorganism, plant or animal lives" (Begon et al. 1996), with the suitability of a habitat for any given species dependent on multiple biotic and abiotic factors. In terrestrial systems, habitat patches are often defined by vegetation type and/or the presence of different types of anthropogenic structure (Parry et al. 2003), for example patches of forest amongst areas of urban development in Nottinghamshire, UK (Nikolakaki 2004). Landscape ecology studies in the marine environment initially lagged behind their terrestrial counterparts; however the past ten years have seen an increase in marine landscape ecology, often referred to as 'seascape' ecology in acknowledgement of the multi-dimensional nature of aquatic environments (Pittman et al. 2011). Most often these studies have focussed on either single species or single habitat types; particularly seagrass beds, coral reefs or other biogenic reefs (see Bostrom et al. 2011). As such, studies on seascapes that did not consist of easily defined or discrete units were lacking, but with the increased need to determine connectivity within multiple systems, new approaches were sought.

With landscape ecology contributing significantly to advancements in terrestrial conservation strategies (Lui & Taylor 2002), adaptations of these principles to marine conservation have inevitably followed, particularly with respect to MPA network design (Leslie 2005; Leathwick et al. 2008). One of the original proponents

to link landscape ecology theory with conservation strategies in the marine environment was Roff & Taylor (2000), who developed a method of classifying seascapes based on physical characteristics such as water temperature, hydrodynamic regime and substrate type. Their classification method was further developed by agencies in the UK (JNCC) with the resulting marine landscape maps covering all of the UKs seas to the Exclusive Economic Zone (Connor et al. 2006). For marine benthic invertebrates, the factors that determine the suitability of a habitat can include the presence of conspecifics, depth, temperature, current regime and substrate type. Thus many of the parameters used to define marine landscapes by Roff & Taylor (2000) are key to defining habitat suitability for marine invertebrates, meaning that there is potentially a close fit between habitats and marine landscapes in terms of their suitability to benthic species.

Habitat preference of subtidal benthic species and the implications this would have for connectivity in MPA networks has not been explicitly tested, particularly when using marine landscapes as a proxy for habitat. Given that landscapes are a convenient way of dividing up seascapes for management it is important to test the assumption that these landscapes can act as a proxy for habitats when considering the conservation implications of species. Thus the first aim of this study is to explore the level of habitat specificity in a range of marine benthic species to see if conservation based around broad landscape classes is relevant to the ecology of the associated assemblages.

In a previous study (Chapter 2) it was found that benthic species in offshore soft sediment communities around the UK are dominated by species with planktotrophic dispersal strategies, with potential dispersal distances ranging from <1 km to 260 km (assuming passive dispersal) where distance varied by dispersal type, specific location and local hydrographical conditions. Having explored the level of habitat specificity of the same benthic species, it will then be possible to explore the fit in terms of dispersal potential, patch area and distance between individual patches of marine landscapes grouped by their suitability to those species. In other words, if species x can disperse a maximum of 50 km, are the distances between areas of suitable landscape always less than 50 km, and/or the areas of individual patches always greater than 50km? If any species were found to show a high degree of habitat specificity this may constrain their connectivity potential and make them

more vulnerable to extirpation from disturbances in individual landscape patches. However, this is based on the assumption that the individual landscape patches suitable to these species are rare and poorly connected. If in fact suitable habitats are widespread and well connected in terms of distances between patches, specificity would not necessarily have any implications for the conservation of a species.

Using the species list already compiled from Chapter 2, this chapter will examine to what degree these species display habitat preferences and how this relates to the marine landscape classifications. Furthermore, by examining the distribution of these marine landscapes and exploring the area of individual patches, as well as the distance between patches, the implications for connectivity of the different species can be explored based on their dispersal potential. The Irish Sea will be focused upon as it is semi-enclosed and therefore able to be treated as a discrete area. For a number of species with high habitat specificity larval dispersal runs will also be undertaken to examine the likelihood of them dispersing into suitable habitat given their dispersal potential, the hydrography of the area where such habitats are found and the distribution of patches of that habitat.

3.2 METHODS

3.2.1 Habitat specificity of species

Using the list of taxa created in Chapter 2 (offshore marine benthic epifauna of the UK continental shelf as sampled by a 2 metre beam trawl), additional traits related to habitat specificity were gathered for the 79 species where Planktonic Larval Duration (PLD) had been identified. For each species, details for both adults and larvae were gathered on: adult habitat preference, settlement habitat preferences and behaviours, depth and current strength preferences. In addition, any details on grain size preference, the importance of organic matter content of sediments to habitat preference and the ability to delay settlement were noted if available. Each trait was assessed by literature review, from published work and databases including the biological traits information catalogue (BioTIC) developed by the Marine Life Information Network (MarLIN). Using the species-specific information on PLD and development type gathered in Chapter 2, it was then possible to assign each species to a PLD range and distance using the distribution of distances given in

Table 2.3 of Chapter 2 where distances were averaged over location and hydrographic region (Table 3.1).

Table 3.1 Dispersal categories (High, Medium, Low) and corresponding Planktonic Larval Duration (PLD) ranges and distances for three dispersive development types: planktotrophic, lecithotrophic and BANF (Benthic Associated Non-Feeding). Distances are the mean dispersal distances for the minimum, maximum and median PLDs in each development type, as shown in Table 2.3

Development Type	Dispersal Category	PLD range	Distance (km)
BANF	L	0-1 day	1.28
BANF	H	2-3 days	2.72
Lecithotrophic	L	2-4 days	2.77
Lecithotrophic	M	5-13 days	9.49
Lecithotrophic	H	14-max	28.4
Planktotrophic	L	6-24 days	9.49
Planktotrophic	M	25-66 days	51.3
Planktotrophic	H	67-max	83.7

3.2.2 Marine Landscape distribution in the Irish Sea

Marine landscapes for the UK seas have been defined by the UKSeaMap Project (Connor et al. 2006), and were based on the findings of the Irish Sea Pilot Project, the first attempt to develop marine landscape maps in the UK (Vincent et al. 2004). The landscapes are classified in terms of simplified British Geological Society (BGS) substrate types (Figure 6 in Connor et al. 2006) along with depth, light attenuation, maximum wave base, bottom temperature and maximum near-seabed stress, which are induced by tidal currents. The whole of the UK continental shelf has been classified by marine landscape and using ArcMap v9.3 it was possible to calculate the area of each patch of each landscape type in addition to the shortest and longest distances between each patch with its closest neighbouring patch of the same landscape type (see Figure 3.1). Only landscapes with a depth greater than 10m were included as the species concerned are representative of offshore habitats, not nearshore or intertidal.

Habitat information for each species (as described in 3.2.1) was then compared to marine landscape definitions, with sediment preference matched with sediment type (based on the British Geological Society categories). After comparison, species were grouped together based on their habitat preferences and marine landscapes

matched to these to give habitat-landscape matched categories (Appendix 3). For example, the echinoderm *Anseropoda placenta* has a habitat preference for sand, muddy sand and muddy gravel, which corresponds to six marine landscapes (Shallow mixed sediment plain (strong, moderate and weak tide stress), shallow sand plain, Shelf mixed sediment plain (moderate), and shelf sand plain. This then led to a habitat-landscape grouping of Mixed/Sand. Finally, minimum patch size and maximum distance between any two patches for each of the habitat-landscape groupings was measured.

3.2.3 Habitat specificity and dispersal implications

Based on the findings from the previous sections, two species with known habitat specificity were selected to explore the likelihood of such species dispersing into areas of suitable habitat. Thus, particle dispersal scenarios were run from three points in a mud region for *Nephrops norvegicus* and three points in a rocky region for *Homarus gammarus* using POLPRED v2.0 (Proudman Oceanographic Laboratory). In total, five runs were undertaken for each site with 1000 particles released, a time step of 30 minutes and a diffusion co-efficient of 5 $m^2 s^{-1}$ was used (see justification for this in Chapter 2). *N. norvegicus* is known to release its larvae in the Irish Sea in May and June (Nichols et al. 1982) so a release date of 1st May 2008 was used for the dispersal simulations with a PLD of 47 days. Details on *H. gammarus* larval biology is limited with the only information on PLD recorded by Jorstad et al. (2005), where the planktonic stages developed over 2-3 weeks at 18-20°C. The PLD was therefore taken as 21 days as sea temperatures in the Irish Sea are lower resulting in a longer development period (see Chapter 2 for discussion). Spawning can occur from April to August (Ennis 1973) therefore a release date of 1st June 2008 was used.

3.3 RESULTS

3.3.1 Habitat preference and landscape distribution

Of the 79 species examined, information on adult habitat preference was found for 75 (Appendix 3). The majority of information on habitat preference was found using BioTIC (MarLIN) as the same substrate classification was used as that of marine landscapes (BGS). Where possible primary references were also examined. For a number of species, habitat preference was only defined as 'hard substrates' which is

not a BGS category; in these cases it was assumed that the species preferred rock. Of the additional traits related to habitat preference that were examined (e.g. larval settlement preferences, current strength preferences, organic content) there was a lack of information found for most species, therefore it was removed from further analysis.

In total, there were 28 different marine landscapes represented in the Irish Sea (Figure 3.1). Several of these are characteristic of inshore environments such as lagoons and estuaries so were discounted from further analysis. The size and distribution of marine landscapes was highly variable with, for example, two large continuous areas of mud plains contrasting with small and unevenly distributed mixed sediment plains. Average landscape patch area was 327.8 km^2 ranging from 2.9 km^2 to 4762.1 km^2. Between patches of the same landscape, the average shortest distance was 19.5 km ranging from 1.7 - 96.6 km whilst the average furthest distance was 58.6 km ranging from 12.6 – 258.9 km.

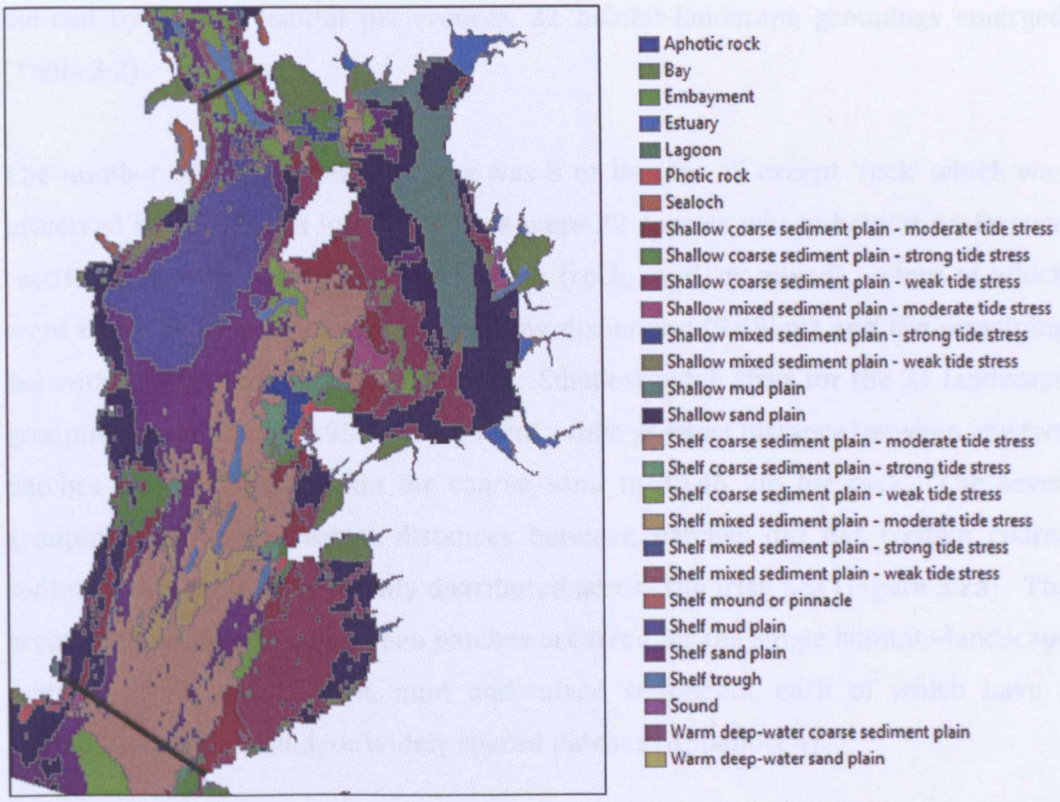


Figure 3.1 Marine landscapes of the Irish Sea (data from MESH). Black lines indicate boundary of the study area.

Upon comparison of the information available on species habitat preferences (Appendix 3), it was not possible to use the information on tide stress - a parameter used to further define marine landscapes (see Figure 3.1 landscape categories where some substrate categories are broken into weak, moderate and strong tide stress types) – because there was no information available on how tide stress affects species habitat preference. There was information for some species on flow preference but this cannot be converted to bed stress, as stress is a measure of pressure (newtons m^{-2}) while flow is a measure of velocity (bed stress varies with depth as well as current velocity). In addition as the depth ranges recorded for the species being studied (Appendix 3) tended to cover both shelf (wave base to 200m) and shallow (0m to wave base) depths (as defined by the marine landscape approach) based on the wave base distribution of the Irish Sea (Figure 10 in Connor et al. 2006, ref), it was also not necessary to disaggregate categories into shallow and shelf landscapes. Thus, the species studied were found to associate with one or more of five broad landscape classes: rock, mud, sand, coarse (gravel and sand mixtures) and mixed (mud and gravel). Using these broad landscape types, as defined by species habitat preferences, 21 habitat-landscape groupings emerged (Table 3.2).

The number of species per grouping was 8 or less for all except 'rock' which was preferred by 15 species in total. There were 22 species whose habitat preference restricted them to a single sediment type (rock, mud, or mixed), , eight of which were BANF or direct developers, four low dispersing (9.49km) and the remaining ten with a dispersal potential >28.4 km. Smallest patch sizes for the 21 landscape groupings ranged from 0.958 to 3.025 km^2, while greatest distance between any two patches ranged from 2.7 km for coarse/sand to 45.45 km for rock. The seven groupings with the greatest distances between patches did not contain coarse sediments, as these were evenly distributed across the Irish Sea (Figure 3.2a). The greatest three distances between patches occurred for the single habitat –landscape matched groupings of rock, mud and mixed sediments, each of which have a distribution of small and/or widely spaced patches (Appendix 4).

Mean dispersal distances for species varied from 0 and 1.28km for eight species each, to 83.7 km for nine species, with 37 species with a potential dispersal of 51.3 km (Appendix 3). Of the 24 species that were at higher risk of being isolated due to

the combination of their habitat preference, the distribution of the habitat-landscape matched areas and their own dispersal potential (Table 3.2), seven were low dispersing planktotrophic developers (dispersal potential of 9.49 km or less) with the remaining being BANF or direct developers. Just over half (11 of 21) of the habitat-landscape matched groupings had the potential for one or more of the associated species to become isolated due to the distance between patches being greater than their dispersal potential.

Table 3.2 Marine habitat-landscape matched groupings based on species habitat preferences. Defined for each grouping was: smallest patch size within the Irish Sea for the group; greatest distance between any two patches; percentage of species potentially isolated by greatest distances; minimum dispersal distance of species within groupings. - refers to cases where patches were continuous and therefore smallest area and greatest distance could not be calculated. See Appendix 4 for maps of each habitat-landscape matched grouping.

Landscape Groupings	Smallest patch size (km^2)	Greatest distance (km)	Percentage of species isolated	Minimum dispersal distance of all species	Total number of species
All	-	-	-	-	6
All but coarse	1.541	13.21	66	0	3
All but mud	2.894	8.05	0	28.4	3
All but rock	-	-	-	-	5
All but sand	2.945	18.05	100	1.28	2
Aphotic Rock/Sand	2.934	23.35	100	1.28	2
Coarse/Mixed/Mud	2.945	20.25	50	9.49	2
Coarse/Mixed/Sand	2.934	7.59	0	>9.49	3
Coarse/Mud/Sand	2.894	2.74	0	51.3	1
Coarse/Sand	3.005	2.70	0	>51.3	4
Mixed	2.934	26.81	33	0	3
Mixed/Mud	3.025	16.24	0	51.3	2
Mixed/Mud/Sand	3.015	20.25	100	0	1
Mixed/Sand	0.958	10.17	50	0	2
Mud	2.885	36.37	25	9.49	4
Mud/Sand	2.934	23.35	25	0	8
Rock	2.940	49.45	73	1.28	15
Rock/Coarse	2.904	16.56	0	51.3	2
Rock/Coarse/Mixed	2.963	16.25	50	9.49	2
Rock/Coarse/Sand	2.904	9.44	0	51.3	4
Rock/Sand/Mud	2.934	22.09	0	51.3	1
No information					4

3.3.2 Dispersal

Dispersal scenarios run for two species that displayed habitat specificity varied greatly in the distances travelled. Average dispersal distance of particles released from mud landscapes for *Nephrops norvegicus* over 47 days was 20.9 km (Figure 3.2a), while for the rock landscape it was double at 40.8 km for half the PLD of 21 days for *Homarus gammarus* (Figure 3.2b). Within the rock landscape, average dispersal distance from the three release points also varied, with the southernmost rock release point averaging 51.1 km compared to the 35 km for the other two release points. For all rock stations, the majority of particles travelled northwards towards the Isle of Man, and at the end of the 21 days they were dispersed over sand, coarse and mixed substrates but not rock (Figure 3.2). The southernmost mud stations saw over 90% of particles remain within the mud landscape but for the northernmost station, 95.5% of particles continued in a general northwards direction over mixed landscape types.

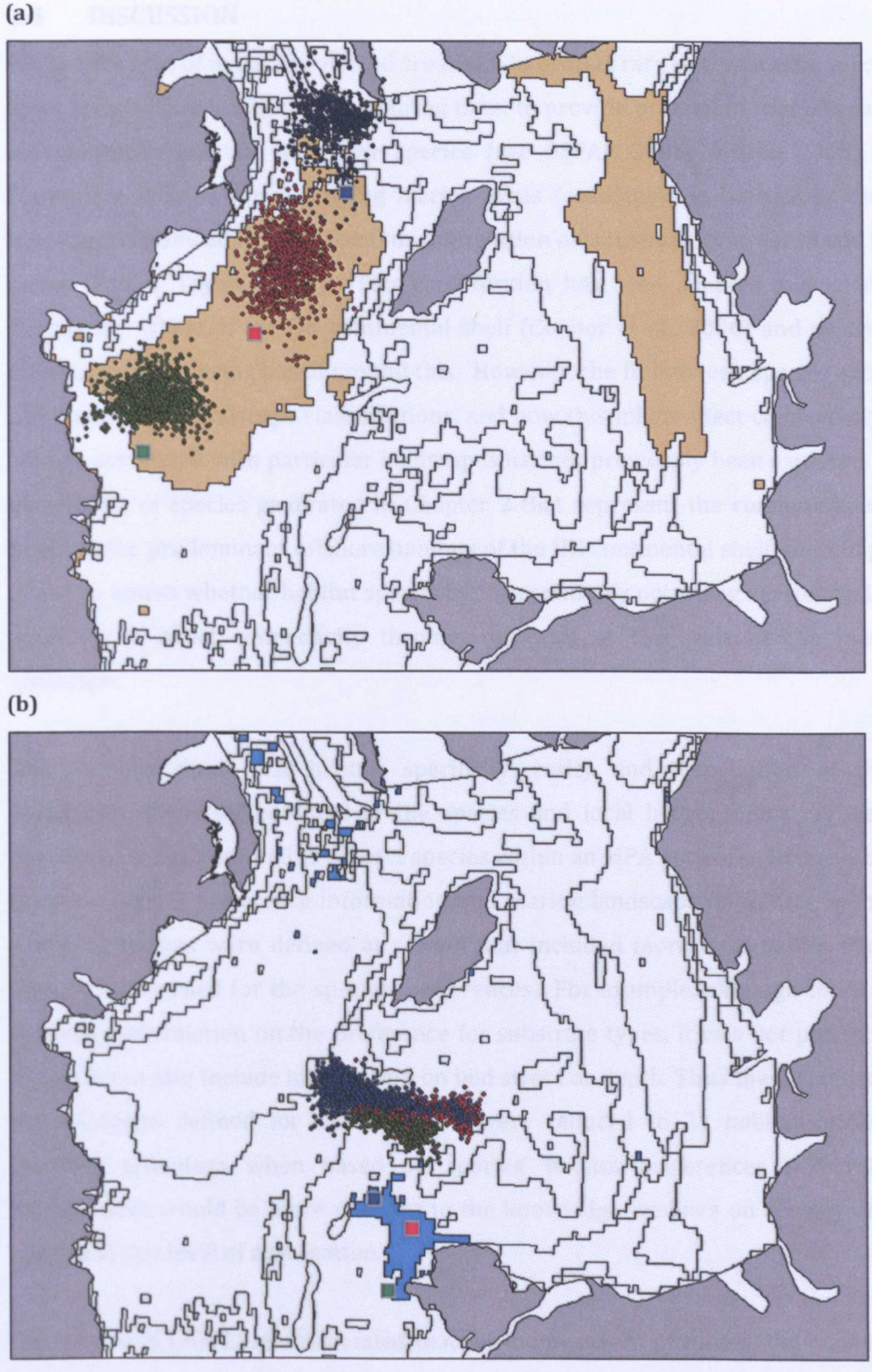


Figure 3.2 Dispersal scenarios in the Irish Sea for: (a) *Nephrops norvegicus* from a mud landscape (brown shading), and (b) *Homarus gammarus* from a rock landscape (blue shading). Particles were released from 3 locations in each landscape (squares) with the colours of particles (circles) corresponding to release points.

3.4 DISCUSSION

While networks of marine protected areas aim to protect rare or threatened species, there are also policy objectives requiring them to provide protection to the broader representative habitats and their species (see OSPAR 2006; Ardron 2008). A convenient method for classifying marine areas (seascapes) is the use of broad landscape classifications that combine information on substrate type, depth and bed stress (Rolf & Taylor, 2000). This classification has been adapted and used to classify the whole of the UK continental shelf (Connor et al., 2006) and design of MPA networks is being based around this. However, the fit between species habitat preferences and landscape classifications, and how this might affect connectivity of species associated with particular landscapes has not previously been explored. By using a list of species generated in Chapter 2 that represent the common species found in the predominant offshore habitats of the UK continental shelf, this chapter aimed to assess whether habitat specificity for commonly occurring species had the potential to affect connectivity through dispersal at the scale of the marine landscape.

The findings show that habitat specificity, rarity and distribution of those landscapes, dispersal potential of the species and local hydrographic regime all contribute to the potential to protect species within an MPA network. In terms of fit between habitat preference information and marine landscape definition, in many cases landscapes were defined at a level that included more information than is known or recorded for the species' preferences. For example, although there was generally information on the preference for substrate types, it was not possible or necessary to also include information on bed stress or depth. Thus the 28 landscape classifications defined for the Irish Sea were reduced to 21 habitat-landscape matched groupings when based on species' habitat preferences. Therefore, management would be more relevant to the knowledge we have on ecology of the species at this level of aggregation.

Bostrom et al (2011) recommended that for management purposes, the portion of habitat generalists versus specialists needs to be assessed, particularly in order to evaluate perturbation scenarios. However, it was found here that it cannot be assumed that species that are more specialist in their habitat preference (preferring

one particular landscape category, e.g. mixed sediments) are necessarily disadvantaged in terms of connectivity when compared to species that are more generalist in habitat preference (suited to any one of several broad landscape types). The distribution and rarity of the landscapes themselves is key; for the region that was explored here, the Irish Sea, any species with a habitat preference containing coarse sediments is unlikely to be isolated at any spatial scale (see Appendix 4) due to their widespread distribution. In comparison, species that are specific to rock or mixed sediments could be isolated, but so could species that appeared to be more generalist in their habitat preference if their dispersal potential is low (see Table 3.2). This study suggests that the distribution and rarity of landscapes is of equal or greater importance than the level of specialism of species that inhabit them, and this is likely to be true in any open marine system.

Distances between patches of marine landscapes were highly variable, while the patches themselves were also variable in area. The likelihood of species being isolated in different habitat-landscape matched groupings was based on straight line distances between the pair of patches that were furthest apart, and did not take into account the effects of hydrographic regime on actual dispersal. As shown by dispersal scenarios based on *Homarus gammarus* on rock, and *Nephrops norvegicus* on mud, the difference in achieved dispersal distances was driven by the hydrographic regimes of the locations, not the dispersal potential of the species. While these factors may seem obvious, the implications on connectivity are important; a landscape of mud is inherently low in current flow while a rock substrate is more likely to experience high stress. The analysis undertaken here suggests that given their distinct nature, mud plains could be entirely self seeding due to their large size and low dispersal potential while rocky patches may be more sensitive to perturbations due to their small size and high dispersal potential. In addition offshore rock areas are rare in the Irish Sea and poorly connected, which suggest that they may even require higher levels of protection than other landscape types where there is the potential for seeding from other patches.

Settlement and recruitment may be as important as dispersal in influencing connectivity for species, therefore determining the dynamics of settlement and recruitment is essential for a broader understanding (Pineda et al. 2009). However, it was only possible to find information on settlement preferences or behaviours for

7 of the 79 species investigated here. Whilst settlement behaviours may play an important role in determining the final distribution of new recruits, particularly where larvae are able to delay settlement in the face of unsuitable habitat and disperse further (e.g. *Marthasterias glacialis* Barker & Nichols 1983; *Mytulis edulis* Bayne 1965), there has been suggestion that larvae should be considered passive at large spatial scales (>m), and active choice is more important over smaller spatial scales (<m) (Butman & Grassle 1992; Grassle et al. 1992; Nellis & Bourget 1996). If this is true, behaviours would have little effect on the survival of settling individuals if they land in patches of unsuitable habitat where the patches are greater than several metres squared in area. Minimum patch size for this study was always around a square kilometre or greater, but this was limited by the resolution of the modelling used to classify landscape around the UK continental shelf. Further ground-truthing of landscape classification and patch size would help to clarify the actual potential for settlement behaviour to affect recruitment in offshore benthic species.

With marine protection strategies aiming, amongst other things, to protect representative species and habitats, knowledge of the dynamics of a range of habitats is required. In the work described here, it has been demonstrated that most subtidal benthic invertebrates of common sediments could be considered habitat generalists. For specifists and rare species, attention must be paid to habitat patch size and local hydrography if they are to be suitably protected.

Chapter 4

Genetic structure of the scallop *Pecten maximus* from fishing grounds around the Isle of Man, Irish Sea

4.1 INTRODUCTION

For sedentary or sessile benthic marine invertebrates with planktotrophic larvae, dispersal during the larval phase is thought to be the predominant means of dispersal (Jablonski & Lutz 1983; Scheltema 1986). Thus the traditional view for populations of species with dispersive larvae is that they are genetically, and often demographically, open (Scheltema 1971; Johnson 2005; Warner & Cowen 2005). However, recent studies have highlighted that larvae are not always dispersed so widely, due to biological and/or hydrodynamic factors (Cowen et al. 2007). For example, numerous studies have shown that active larval behaviour can aid retention to natal habitat, leading to reduced connectivity and possible isolation of populations (Leis 1991; Cowen & Castro 1994). Hence, it is clear that connectivity in the marine environment is not a simple corollary of life history. These issues are important for applied conservation, particularly stock management and marine protected area (MPA) design. Specifically, understanding the scale and magnitude of dispersal of sedentary benthic marine invertebrates that are exploited is essential as they face further impacts on connectivity due to the potential reduction in breeding stock through targeting of specific year size classes and habitat damage (Thorpe et al. 2000). If exploited stocks are to be successfully managed and gain from the benefits of MPAs such as spillover effects (Gell and Roberts, 2003), it is essential to understand connectivity and the mechanisms that drive it.

The scallop *Pecten maximus* (L.) is an important fishery for several fleets along the European Atlantic coast, with an annual landing of over 58,000 tonnes in 2009 (http://www.fao.org/fishery/species/3516/en). A broadcast spawning bivalve with associated high fecundity, at settlement spat prefer silt-free sand near other conspecifics (Gruffyd & Beaumont 1972), leading to large aggregations of adults which are easily exploited by dredging fisheries. The planktotrophic larvae spend between 15 to 34 days feeding in the plankton with total pelagic duration (defined

as the time between the release of gametes to settlement of spat) 18 to 42 days depending on the sea temperature (Le Pennec et al. 2003). In the Irish Sea and around the Isle of Man in particular, the commercial fishery for *P. maximus* has been ongoing since the 1930s, with 14 main grounds fished by boats from across the region (Figure 4.1(a)). With the aim of maintaining stock size and high yields, several regulations, such as a minimum landing size of 110 mm shell length, an annual closed season from June to October, and restrictions on gear type and size, were instigated from the beginning of the fishery (Brand et al. 1991). Nonetheless, the combined effects of increased demand for scallops and improved fishing methods, led to a decline in Manx scallop stocks such that by 1993 scallop landings on the Isle of Man had decreased to 650 tonnes from a peak of 2100 tonnes in 1985 (Brand et al. 1991; Heipel et al. 1999). Heavy levels of exploitation were also accompanied by a shift in age structure, with younger scallops (<5 years) dominating the catch in the 1990s (Brand 2000). The reduction in the numbers of older (and thus larger) scallops led to a decline in overall reproductive output and greater possibility of poor recruitment or even stock collapse. Crucially, for implementation of management and protection of specific stocks, the level of isolation (i.e. self-recruitment) and pattern of dispersal among Manx stocks was not known; ultimately a key question for management is whether each stock is isolated or forms part of a wider meta-population. Given the dispersal strategy of *P. maximus*, with its potential for a long planktonic period (18 - 42 d), it was assumed that grounds were highly connected to each other through the exchange of larvae; thus stocks managed by the Isle of Man have been considered open and treated as one population.

However, seascape features such as tidal and wind-driven currents, stratification of temperature or salinity, or fine-scale hydrodynamics can influence population structure. Hydrodynamic patterns within the Irish Sea have been the focus of research for a number of decades. In their 1969 paper, Ramster and Hill described the residual currents characteristic of the region. A strong northwards flow was shown to diverge once it reached the southern end of the Isle of Man, resulting in northwards flows along both the east and west coasts, which if strong enough could potentially result in isolation of populations either side of the island. The east coast current joins an anti-clockwise circulation throughout Liverpool Bay which is variable in amplitude (Lee & Ramster 1981) while the western Irish Sea continues in

a northern flow. While these residual currents may indicate no flow between east and west, fine scale currents and intra-annual variations may allow for some level of exchange. Using high resolution hydrodynamic and particle track modelling, Neill & Kaiser (2008) modelled the release of particles representing *P. maximus* larvae from different grounds around the Isle of Man. In their scenarios, there appeared to be considerable connectivity amongst the grounds but the eastern grounds of East Douglas and particularly Laxey appeared to receive fewer particles. They determined that these two sites fed into the others to the north and south but that they in turn were supplied by grounds further offshore and to the east where a high degree of commercial exploitation occurs, leading to fewer recruits to these grounds.

The idea of connectivity among stocks of *P. maximus* is generally supported by genetic studies. Thus, early work using allozymes found little genetic structure amongst individuals sampled over wide distances (Isle of Man, Scotland and France) (Beaumont et al. 1993; Wilding et al. 1998). However, in their study using Restriction Fragment Length Polymorphism (RFLP) analysis of fragments of mtDNA from the 12S and 16S genes, Heipel et al. (1999) found slight but significant differences between scallops from five grounds around the Isle of Man, with East Douglas on the east coast most different from the others. The implication is that more polymorphic genetic markers may have greater power to detect stock structure, particularly over smaller geographic ranges (see Selkoe et al. 2008 for review). Using polymorphic microsatellite loci developed for *P. maximus*, I determine the level and pattern of population differentiation between Manx scallop stocks, and examine the impact of current patterns upon the pattern of genetic structure and diversity found, with particular regard to areas that act as potential source and sinks. These data are interpreted in light of implications for connectivity and stock management. It is predicted that due to current patterns, stocks on the east coast will be more genetically similar to each other than to those on the west, with Laxey in particular isolated from the west.

4.2 METHODS

4.2.1 Sample Collection

Samples of *Pecten maximus* were collected between 2003 and 2005 at 10 locations around the Isle of Man that represent the main commercially-exploited grounds (Figure 4.1). Samples were collected by dredging at all sites except the closed areas (OCA and NCA), where divers were used. Samples were taken from the adductor muscle and stored in 100% ethanol at -20°C until DNA extraction.

4.2.2 DNA extraction and microsatellite amplification

DNA was extracted from 48 samples per location using a standard high-salt extraction method (Sambrook & Russell, 2001; Walsh et al. 1991). Samples were genotyped at eight microsatellite loci (Watts et al. 2005; Table 4.1). Between 10-50 ng of DNA was used in a 10 µl PCR containing 75 mM Tris-HCl pH 8.9, 20 mM $(NH_4)_2SO_4$, 0.01% v/v Tween-20, 0.2 mM each dNTP, 1.5-3.0 mM $MgCl_2$, 2 pmol each primer and 0.25 U *Taq* polymerase (ABgene). Forward primers were 5'-labelled with either 6-FAM, NED, PET or VIC flourophores (Applied Biosystems). Thermal cycling conditions were: 95°C for 3 min, followed by 5 cycles of (95°C for 30 s, T_a°C 45 s, 72°C 45s), 35 cycles of (95°C for 30 s, T_a°C for 45 s, 72°C for 55 s) and a final extension of 72°C for 10 mins, where T_a is the locus-specific annealing temperature for each primer (see Table 4.1).

PCR products were pooled into one of two genotyping panels along with a GENESCAN-500 LIZ size standard (Applied Biosystems) and separated by capillary electrophoresis through a denaturing polymer on an ABI3100 automated sequencer (Applied Biosystems). Allele sizes were determined using the cubic model of analysis in GENEMAPPER software (Applied Biosystems).

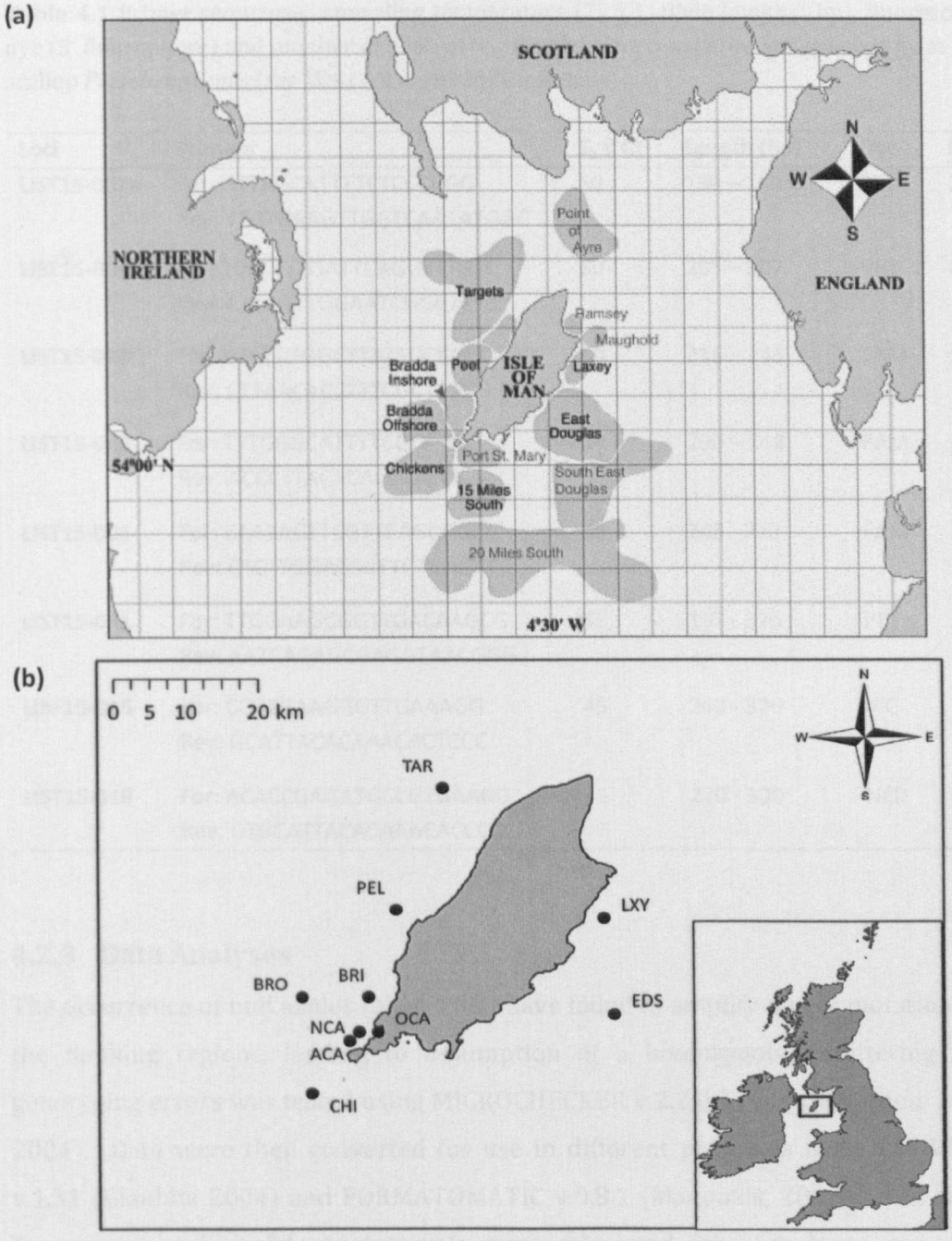


Figure 4.1 (a) Map of the Irish Sea showing the main fishing grounds of the scallop *Pecten maximus* around the Isle of Man (taken from Beukers-Stewart et al. (2003)). (b) Ten sample locations of *P. maximus* used in this study - Targets (TAR), Peel (PEL), Bradda Inshore (BRI), Bradda Offshore (BRO), Around Closed Area (ACA), New Closed Area (NCA), Old Closed Area (OCA), Chickens (CHI), East Douglas (EDS) and Laxey (LXY) - taken from seven fishing grounds around the Isle of Man between 2003 and 2005.

Table 4.1 Primer sequences, annealing temperature (T_a,°C), allele lengths (bp), fluorescent dye (5' flourophore) and number of alleles (N_A) for eight microsatellite loci isolated from the scallop *Pecten maximus* (see Watts et al (2005) for details)

Loci	Primers	T_a (°C)	Length (bp)	Dye	N_A
LIST15-002a	For: GTTAGCATTTTCTCCCCGG Rev: TTGTGAAGTTGGTCAACATGGC	50	130 – 180	PET	21
LIST15-004	For: TCCCTTTGATTCAGGTTTGTC Rev: ATGATTTGGAATCGGCTTTG	50	295 – 307	VIC	6
LIST15-014	For: ATACCTGGCTTATTGCCGCC Rev: CTTAACACCTTTCGCTATCG	50	215 – 249	FAM	18
LIST15-020	For: TTTGGGCATTTTCGCACG Rev: ACCCTTACACACCTACCC	50	290 – 348	FAM	23
LIST15-005	For: CAATAGTTCGTTCAGCGGCG Rev: CTCTTGGATGCTTGTGAGGG	50	243 - 273	FAM	28
LIST15-011	For: TTGGAAGCGGTTGACAAGCG Rev: AATCAGAGCGAGGTAACGGG	55	197 - 376	PET	84
LIST15-016	For: CCGTGAAGGGTTGAAAGG Rev: GCATTACACAAACACTCCC	45	240 - 320	VIC	70
LIST15-019	For: ACACCGAGATGCCGTGAAGG Rev: GTGCATTACACAAACACCCC	45	220 - 300	NED	77

4.2.3 Data Analyses

The occurrence of null alleles (alleles that have failed to amplify due to mutations in the flanking regions, leading to assumption of a homozygote), stuttering and genotyping errors was tested using MICROCHECKER v.2.2.0.3 (Van Oosterhout et al. 2004). Data were then converted for use in different programs using CONVERT v.1.31 (Glaubitz 2004) and FORMATOMATIC v.0.8.1 (Manoukis, 2007). Null allele frequencies and confidence intervals were calculated for each locus and each population using GENEPOP v.4.0.11 (Rousset 2008).

The significance of any departures from expected Hardy-Weinberg equilibrium conditions (HWE) was assessed by permuting alleles among individuals within samples (1,000 permutations) using FSTAT V.2.9.3 (Goudet 2001). Basic measures of genetic diversity, including allelic richness (A_R), number of alleles (N_A), and expected (H_e) and observed (H_o) heterozygosity, and Wright's (1951) inbreeding coefficient (F_{IS}), were calculated for each population and locus using FSTAT v.2.9.3 (Goudet

2001). Population subdivision was characterised for each locus and as an average over all loci by calculating F_{ST} (Weir & Cockerham 1984), using GENEPOP v.4.0.11 (Rousset 2008).

Next, estimates of F_{ST} (averaged over all loci) between all pairs of samples were calculated using ARLEQUIN v.3.1 (Excoffier et al. 2005), and their significance tested over 10,000 permutations. The frequency of occurrence of private alleles (alleles that are only found in one population, Barton & Slatkin, 1986) and the number of shared alleles between locations was calculated using the MICROSATELLITE TOOLKIT (Park, 2001). For the latter, a score for each pairwise comparison of individuals is equal to the number of matching alleles between samples divided by the number of alleles typed, then averaged over all loci. Differences in proportion of shared alleles between all locations and between east and west locations were assessed using Kruskal-Wallis tests as the data were non-normally distributed.

Analysis of population structure was carried out using STRUCTURE v.2.3.1 (Pritchard et al. 2000). For each analysis, 10 independent runs of STRUCTURE were made, to assess output consistency and to calculate ΔK, which is the rate of change of the probability between successive runs (Evanno et al. 2005). The number of clusters (K) was varied from 1 up to 10 using the admixture model and correlated allele frequencies. All model runs were based on 10,000 Markov chain Monte Carlo replications with an initial burn-in period of 10,000 iterations. The most pronounced partition (level of population subdivision) of the data set was identified using the method of Evanno et al. (2005), with ΔK calculated using STRUCTURE HARVESTER v.0.6.7 (Earl 2011). Analysis was run with and without sample locations set as priors.

4.3 RESULTS

4.3.1 Genetic diversity and HWE

A total of 480 samples from ten locations around the Isle of Man were sampled and genotyped. Of the eight microsatellite loci used in this study, all but one were highly polymorphic with number of alleles, over all samples, ranging from 18 to 84 (Table 4.2); LIST15-004 had six alleles, and correspondingly the lowest allelic richness of 2.43, with values for A_R at the other loci ranging from 4.61 to 16.2. Mean expected

heterozygosity (H_E) was high (>0.47) for all loci except LIST15-004 which was 0.19. Five loci – LIST15-002a, LIST15-020, LIST15-011, LIST15-016 and LIST15-019 - showed departure from Hardy-Weinberg Equilibrium (HWE). Null allele frequencies (and 95% confidence intervals) for these five loci were high for most locations (Table 4.3), ranging from 0.077 (±0.035) to 0.345 (±0.263), with most loci having estimated null allele frequencies greater than 0.1. Given that these loci also show significant departure from HWE over all samples ($p<0.05$) as a result of heterozygote deficiency (Table 4.2) it is likely that the high occurrence of null alleles is responsible.

Table 4.2 Basic measures of genetic diversity (number of alleles (N_A), allele richness (A_R), expected heterozygosity (H_E) and observed heterozygosity (H_O), Inbreeding coefficient (F_{IS}) and number of private alleles(P_A) per population over all loci) for *Pecten maximus* from 10 locations around the Isle of Man, UK (see Figure 4.1 for locations). Values displayed for each locus and population, and averaged over all loci and populations. F_{IS} calculated after Weir and Cockerham, probability of deviation from Hardy Weinberg Equilibrium (HWE) *P<0.05 **P<0.01, significant for 48 out of 80 population -locus combinations.

Locus	TAR	PEL	BRI	NCA	ACA	OCA	BRO	CHI	EDS	LXY	Mean (total)
LIST15-002a											
N_A	4	9	6	7	7	7	4	7	9	7	6.7 (21)
A_R	3.21	5.71	3.05	4.56	2.92	5.35	3.22	4.23	5.89	4.73	4.61
H_E	0.37	0.58	0.23	0.52	0.20	0.63	0.42	0.44	0.67	0.60	0.47
H_O	0.02	0.04	0.23	0.27	0.13	0.29	0.38	0.29	0.29	0.44	0.24
F_{IS}	0.912**	0.888**	-0.074	0.380**	0.368**	0.459**	0.089*	0.310**	0.460**	0.202**	0.392**
LIST15-004											
N_A	4	3	5	3	4	5	3	4	3	5	3.9 (6)
A_R	2.66	1.82	2.74	2.43	2.52	2.61	2.31	2.20	2.03	2.95	2.43
H_E	0.25	0.10	0.25	0.21	0.18	0.21	0.18	0.14	0.12	0.24	0.19
H_O	0.19	0.10	0.21	0.19	0.19	0.23	0.17	0.15	0.13	0.25	0.18
F_{IS}	0.236	-0.035	0.084	0.113	-0.059	-0.081	0.054	-0.044	-0.040	-0.083	0.028
LIST 15-014											
N_A	8	12	8	9	13	10	10	9	11	12	10.2 (18)
A_R	4.95	5.62	4.38	5.34	6.39	5.03	5.14	4.46	5.18	6.05	5.29
H_E	0.49	0.62	0.49	0.58	0.62	0.51	0.52	0.42	0.48	0.66	0.54
H_O	0.42	0.58	0.38	0.46	0.67	0.52	0.44	0.42	0.42	0.63	0.49
F_{IS}	0.147*	0.056	0.153	0.205	-0.078	-0.019	0.151	-0.005	0.126	0.011	0.071
LIST15-020											
N_A	10	11	10	11	10	11	13	12	13	11	11.2 (23)
A_R	6.50	6.87	7.15	7.27	6.73	6.69	7.02	7.12	8.20	6.72	7.19
H_E	0.80	0.81	0.81	0.83	0.83	0.82	0.80	0.81	0.83	0.79	0.81
H_O	0.58	0.60	0.38	0.42	0.48	0.50	0.40	0.48	0.52	0.40	0.48
F_{IS}	0.203**	0.2342	0.473**	0.500**	0.394**	0.376**	0.496**	0.408**	0.334**	0.478**	0.390**

Table 4.2 contd...

Locus	TAR	PEL	BRI	NCA	ACA	OCA	BRO	CHI	EDS	LXY	Mean (total)
LIST15-005											
N_A	16	18	16	15	20	19	14	20	16	17	17.1 (28)
A_R	9.96	9.88	9.64	8.91	9.82	10.2	8.79	10.0	8.87	10.2	10.1
H_E	0.90	0.90	0.89	0.89	0.88	0.90	0.87	0.90	0.88	0.91	0.89
H_O	0.83	0.90	0.83	0.83	0.90	0.90	0.92	0.83	0.90	0.88	0.87
F_{IS}	0.036	0.008	0.005	0.023*	-0.046	-0.013*	-0.051	0.070	-0.024	0.040	0.005
LIST15-011											
N_A	39	41	10	41	11	42	42	39	42	36	34.3 (84)
A_R	16.5	16.1	10.0	15.6	10.1	15.2	16.1	15.5	15.5	14.9	16.2
H_E	0.98	0.98	0.90	0.98	0.93	0.97	0.98	0.97	0.97	0.97	0.96
H_O	0.58	0.77	0.06	0.65	0.06	0.69	0.73	0.81	0.69	0.71	0.58
F_{IS}	0.322**	0.212**	0.667**	0.293**	0.732**	0.275**	0.255**	0.165**	0.262**	0.236**	0.272**
LIST15-016											
N_A	34	36	28	40	35	33	32	35	30	36	33.9 (70)
A_R	15.3	15.6	15.1	15.9	16.1	15.2	14.7	15.8	14.5	15.2	15.9
H_E	0.97	0.97	0.98	0.98	0.98	0.97	0.97	0.98	0.97	0.97	0.97
H_O	0.63	0.65	0.35	0.73	0.40	0.54	0.65	0.73	0.48	0.63	0.58
F_{IS}	0.248**	0.243**	0.472**	0.166**	0.413**	0.349**	0.237**	0.203**	0.390**	0.247**	0.288**
LIST 15-019											
N_A	34	34	26	33	37	32	28	34	30	39	32.7 (77)
A_R	15.8	15.9	14.3	15.5	16.0	15.6	14.5	16.0	15.4	16.0	16.2
H_E	0.98	0.98	0.97	0.97	0.98	0.98	0.97	0.98	0.98	0.98	0.97
H_O	0.65	0.67	0.38	0.58	0.48	0.54	0.52	0.71	0.40	0.48	0.54
F_{IS}	0.065	0.063**	0.454**	0.100	0.382**	0.192**	0.191**	0.004	0.428**	0.413**	0.235**
Mean											
N_A	18.63	20.50	13.63	19.88	17.13	19.88	18.25	20	19.25	20.38	
A_R	9.36	9.67	8.29	9.44	8.82	9.48	8.98	9.41	9.44	9.59	
H_E	0.72	0.74	0.69	0.74	0.70	0.75	0.71	0.70	0.74	0.77	
H_O	0.49	0.54	0.35	0.52	0.41	0.53	0.52	0.55	0.48	0.55	
P_A	1	10	4	6	10	10	1	8	12	15	

Table 4.3 Null allele frequencies and confidence intervals (in brackets) for 10 locations around the Isle of Man across 8 microsatellite loci of the scallop *Pecten maximus*. (-) represents confidence intervals that could not be computed. See Figure 4.1 for ground codes and location.

	LIST15-002a	**LIST15-004**	**LIST15-014**	**LIST15-020**	**LIST15-005**	**LIST15-011**	**LIST15-016**	**LIST 15-019**
TAR	0.270 (*0.178*)	0.082 (*0*)	0.071 (*0.012*)	0.101 (*0.039*)	0.015 (*0*)	0.150 (*0.097*)	0.114 (*0.061*)	0.019 (*0*)
PEL	0.345 (*0.263*)	0 (-)	0.020 (*0*)	0.099 (*0.035*)	0 (-)	0.099 (*0.054*)	0.111 (*0.059*)	0.027 (*0.007*)
BRI	0 (-)	0.057 (-)	0.053 (*0*)	0.209 (*0.131*)	0 (-)	0.288 (-)	0.226 (*0.149*)	0.214 (*0.139*)
NCA	0.157 (*0.073*)	0.037 (-)	0.070 (*0.003*)	0.222 (*0.149*)	0 (*0*)	0.138 (*0.082*)	0.077 (*0.035*)	0.048 (*0.015*)
ACA	0.108 (*0.024*)	0 (-)	0 (-)	0.170 (*0.098*)	0 (-)	0.329 (*0.212*)	0.198 (*0.125*)	0.183 (*0.117*)
OCA	0.203 (*0.123*)	0 (-)	0 (-)	0.163 (*0.091*)	0 (-)	0.126 (*0.073*)	0.166 (*0.103*)	0.090 (*0.041*)
BRO	0.064 (*0.003*)	0 (-)	0.059 (*0*)	0.221 (*0.146*)	0 (-)	0.122 (*0.072*)	0.107 (*0.055*)	0.085 (*0.035*)
CHR	0.132 (*0.054*)	0 (-)	0 (-)	0.187 (*0.114*)	0.003 (*0*)	0.076 (*0.036*)	0.108 (*0.059*)	0 (-)
EDS	0.197 (*0.112*)	0 (-)	0.065 (*0.006*)	0.149 (*0.081*)	0 (-)	0.122 (*0.070*)	0.185 (*0.119*)	0.206 (*0.134*)
LXY	0.125 (*0.059*)	0 (-)	0.025 (-)	0.211 (*0.137*)	0.017 (*0*)	0.122 (*0.070*)	0.112 (*0.059*)	0.210 (*0.142*)

4.3.2 Population differentiation

There was little evidence of population subdivision, with a global F_{ST} (averaged over all loci) of 0.007; single locus estimates of F_{ST} varied from the highest values for LIST15-002a (F_{ST}=0.032) and LIST15-005 (F_{ST}=0.016), followed by LIST15-011 (F_{ST}=0.005), LIST15-014 (F_{ST}=0.004), LIST15-016 (F_{ST}=0.002) and LIST15-019 (F_{ST}=0.003) with LIST15-004 and LIST15-020 the lowest (F_{ST}=0.000 and F_{ST}=-0.001, respectively).

Between each location, the mean proportion of shared alleles ranged from 0.19 to 0.40 (Table 4.4), and overall were found to be significantly different from each other (Kruskal-Wallis H = 1129.7, df = 43, $p < 0.001$). However, when grouped by east and west locations there was no difference observed (Kruskal-Wallis H = 0.74, df = 1, $p > 0.05$). Noticeably, all BRI and ACA combinations were < 0.22 with any other station, except for their combination which showed the highest proportion of shared alleles at 0.40. When these were compared with both the other combinations it was found that they were responsible for the differences observed (Kruskal-Wallis H = 1054.5, df = 2, $p < 0.001$). Similarly, when pairwise F_{ST} comparisons were made, BRI and ACA appeared to be different from other stocks (Table 4.4) but eastern grounds were not significantly different from west. Values of F_{ST} were significant ($p<0.05$) for 15 of the 45 tests performed between grounds, with BRI and ACA significantly different from the other grounds but not each other, or BRI with OCA. Overall F_{ST} ranged from -0.003 between OCA and BRO to 0.031 between ACA and both CHI and EDS. Within the sample locations, the number of private alleles over all loci ranged from 1 to 10 for the west side locations, and 12 and 15 for the two east side locations of East Douglas and Laxey respectively (Table 4.2). Given that the total number of alleles across all populations was 327, this gives a frequency <0.05 for all locations with a mean value of <0.02, indicating few private alleles.

Table 4.4 Mean proportion of shared alleles between individuals of pairwise locations (above the diagonal) and pairwise F_{ST} values between pairwise locations (below diagonal) from ten *Pecten maximus* fishing grounds around the Isle of Man. See Figure 4.1 for ground location and codes. Values in bold are significantly different from zero ($p<0.05$), after 1000 permutations.

	TAR	PEL	BRI	NCA	ACA	OCA	BRO	CHI	EDS	LXY
TAR	0	0.32	0.20	0.32	0.21	0.33	0.34	0.34	0.33	0.29
PEL	0.003	0	0.22	0.31	0.24	0.31	0.32	0.32	0.31	0.29
BRI	**0.010**	**0.009**	0	0.20	0.40	0.20	0.20	0.20	0.19	0.19
NCA	0.004	0.003	**0.018**	0	0.21	0.31	0.33	0.33	0.31	0.29
ACA	**0.020**	**0.015**	0.000	**0.024**	0	0.22	0.22	0.21	0.21	0.20
OCA	-0.002	-0.001	0.009	0.000	**0.014**	0	0.33	0.33	0.32	0.29
BRO	-0.002	0.001	**0.012**	0.002	**0.017**	-0.003	0	0.35	0.33	0.31
CHI	0.000	0.003	**0.022**	**0.002**	**0.031**	0.000	0.000	0	0.33	0.31
EDS	0.002	0.005	**0.023**	0.006	**0.031**	0.002	0.003	-0.001	0	0.30
LXY	0.005	0.000	**0.013**	0.003	**0.015**	0.005	0.007	0.013	0.008	0

STRUCTURE failed to detect a distinct number of populations that corresponded to different geographic locations (Figure 4.2). Modal values of ΔK were identified at K=3 and 6 (Figure 4.2b); however, neither scenario allowed subsequent clustering of individuals from genetically distinct areas, but rather individuals from all stocks were estimated to have membership from each of the 3 or 6 model clusters. Such pattern is typical of weak or no population structure. In contrast to the shared allele and pairwise F_{ST} analyses, neither ACA nor BRI formed distinct clusters. When simulations were run with locations given as a prior there was no improvement in structure. Overall the results indicate that Manx scallops are not genetically distinct.

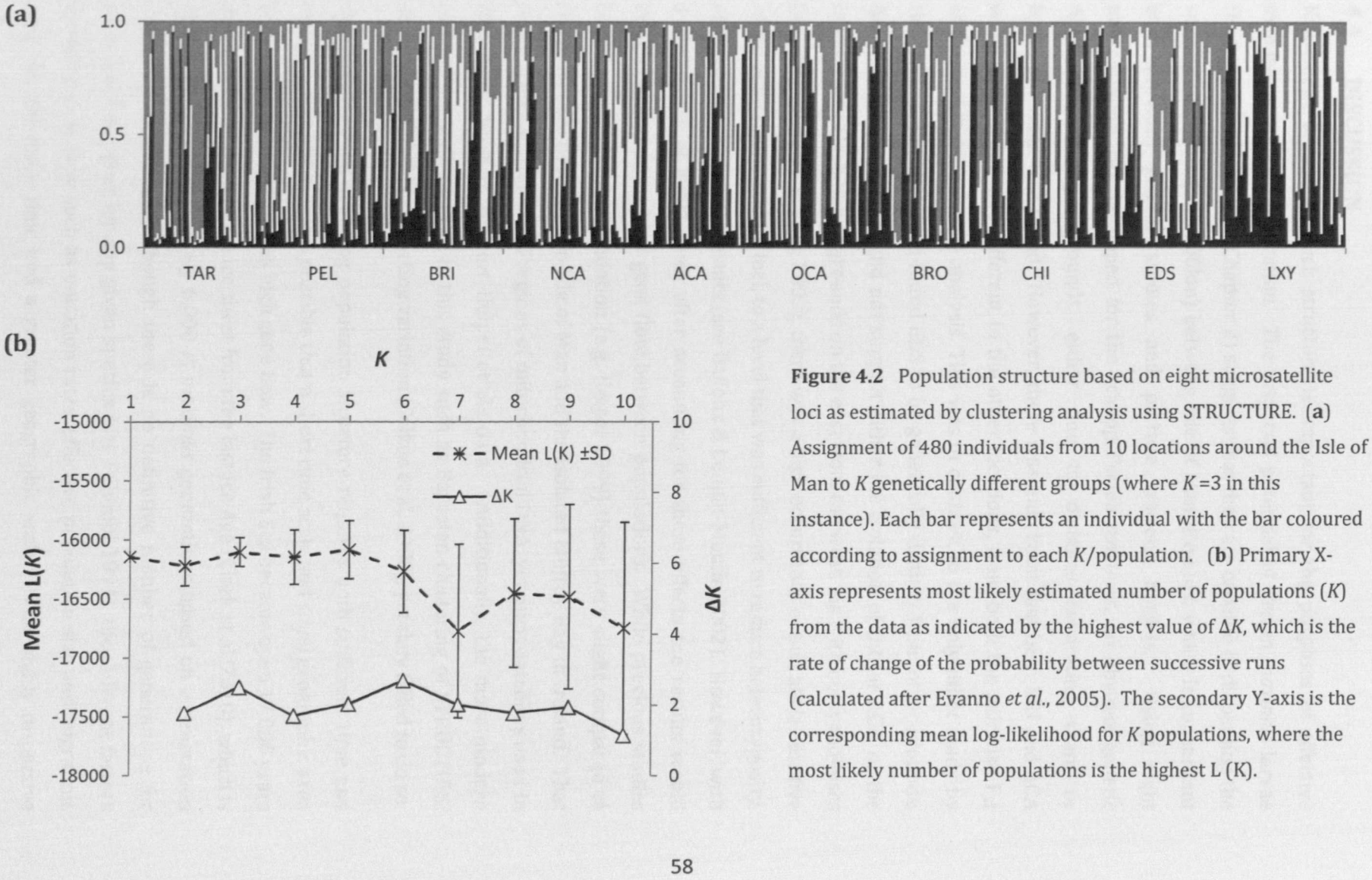


Figure 4.2 Population structure based on eight microsatellite loci as estimated by clustering analysis using STRUCTURE. (**a**) Assignment of 480 individuals from 10 locations around the Isle of Man to *K* genetically different groups (where *K* =3 in this instance). Each bar represents an individual with the bar coloured according to assignment to each *K*/population. (**b**) Primary X-axis represents most likely estimated number of populations (*K*) from the data as indicated by the highest value of Δ*K*, which is the rate of change of the probability between successive runs (calculated after Evanno *et al.*, 2005). The secondary Y-axis is the corresponding mean log-likelihood for *K* populations, where the most likely number of populations is the highest L (K).

4.4 DISCUSSION

Knowledge of scallop stock structure is important for the purposes of effective management and conservation. The dispersal potential of *Pecten maximus* larvae (based on the findings of Chapter 2) suggests that they are capable of dispersing the varying distances (all <100km) between Isle of Man grounds, which is concordant with previous genetic studies and particle tracking models. Using eight microsatellite loci developed for the scallop *Pecten maximus*, no obvious genetic differences amongst grounds, either due to distance separating them or hydrodynamics, was found. However, there was indication that both BRI and ACA were more genetically different to the other locations, from both the pairwise F_{ST} analysis and shared allele analysis. This was in contrast to the only other study by Heipel et al. (1999) which found EDS to be genetically distinct from other grounds. Analysis by STRUCTURE did not support either the isolation of BRI or ACA, or the hypothesis of isolation of grounds on the east from the west. As with many molluscs (as determined by Li et al. 2003), there was a high occurrence of null alleles for five of the eight microsatellite loci, to a level that was sufficient to reduce heterozygosity, potentially skewing the results (see Balloux & Lougin-Moulin 2002). However, with a global FST of 0.007, even after accounting for these effects the results would suggest that there is high gene flow between populations. While previous studies have found some differentiation (e.g. Heipel 1999) these were slight compared to the difference between the Isle of Man and the isolated Mulroy Bay in Ireland. That study used two conserved regions of mitochondrial DNA, yet microsatellites used in this study failed to support Heipel et als data. Additionally, the more modern methods of analysis used in this study such as Bayesian clustering of STRUCTURE are more powerful in detecting variation (Selkoe et al. 2008), yet they failed to do so.

The development of strong population structure requires both sufficient time and space; in this instance it is possible that a short time scale and small geographic area have resulted in continuous high gene flow. The Irish Sea became open 17,000 years ago with the retreat of the ice sheet from the last Ice Age (Clark et al. 2010), which is equivalent to approximately 6,000 *P. maximus* generations based on a generation time of 2 to 3 years. Though there is no definitive number of generations for divergence to occur for any given species (see Palumbi 1994), the different factors dictating gene flow such as mutation rates, effective population size and migration, may require more time and a greater geographic scale. With highly dispersive

larvae, high fecundity, large population size and the recruitment of larvae from elsewhere in the Irish Sea, *P. maximus* may require more time for divergence to occur. The whelk *Buccinum undatum*, which has a non-dispersive larval phase and adults that remain within a small area (<8km^2), has been shown to be undergoing a population bottleneck and adaptation to specific environmental factors in the northern Irish Sea (Wheetman et al. 2006). That a species which is far less dispersive than *P. maximus* is only now showing signs of population isolation now could suggest that *P. maximus* populations are in non-equilibrium conditions and are still diverging.

Scallop grounds around the Isle of Man are not part of a closed system; the possibility of other sources in the Irish Sea contributing to those grounds is likely given the hydrographic patterns and modelled dispersal scenarios of propagules described by Neill & Kaiser (2008) and Van der Molen et al. (2007). Even the occasional recruit from another population can be sufficient to maintain genetic homogeneity (Waples et al. 2008). Understanding the source-sink dynamics of *P. maximus* in the Irish Sea is key to identifying connectivity potential of grounds and to making informed management decisions. Neill & Kaiser (2008) found that the pattern of particle dispersal around the Isle of Man suggested a network of MPAs would aid stock recovery due to the retention at some grounds and the higher dispersal potential of particles from others. This may indeed be achievable, but long-term monitoring of dispersal patterns which account for temporal variation through, for example, prolonged storm activity, would need to be in place if stock recovery were to be effective.

As demonstrated in Chapter 2, median Planktonic Larval Durations (PLD) for planktotrophic species (42 days) result in dispersal distances of passive particles between <1km to 100km, depending on the strength and direction of currents. The Irish Sea is an enclosed system with specific hydrographic patterns that overall are likely to retain particles within it, unlike open coastlines such as the Atlantic or Pacific coasts of North America where particles are more likely to have the opportunity to disperse further, particularly if a uni-directional current predominates (e.g. Galindo et al. 2006; Pineda et al. 2007; van Dijk et al. 2009). In their study Van der Molen et al. (2007) modelled the dispersal of fish propagules in the Irish Sea and showed that some species, given certain larval behaviours and

characteristics of eggs in the plankton, were capable of dispersing well over 100km, which given the scale of separation between grounds, the highest being 90km between TAR and LXY, would indicate the potential for larval exchange between all grounds under the correct hydrographic conditions.

It is unclear whether *P. maximus* larvae show specific behaviours that would greatly affect dispersal potential, but given the lack of genetic structure at this geographic scale it seems unlikely. However, settling pediveligers are shown to remain close to the seafloor searching for suitable substrate and are capable of grouping together using a mucous net, possibly to allow further dispersal if the habitat is unsuitable (Le Pennec et al. 2003). Additionally, the veliger stage is capable of locomotion, with a mean swimming speed of 1.4 mm s^{-1}, but it is thought this is for vertical swimming then passive sinking, which would conserve energy (Cragg 1980; Le Pennec et al. 2003). If this behaviour is timed with the tides it is possible it may encourage retention near the parent population. Increasingly studies are showing that larval retention and self recruitment are more common that previously recognised and can be of high evolutionary value (Jones et al. 2005; Sinclair 1988; Strathmann et al. 2002). However, given the density of scallop aggregations around the Isle of Man it is possible that the entire region could be considered a retention zone, with larvae capable of finding a suitable settlement site even at their maximal dispersal range.

Here we have found no evidence of genetically distinct populations around the Isle of Man, indicating a high level of gene flow between grounds. This could be due to a number of reasons, the most likely being high dispersal potential and therefore connectivity, coupled with insufficiently strong hydrographic barriers during larval release. However, there are other effects on connectivity, which, in the short term, could result in a reduction in effective population sizes; commercially exploited species are even more susceptible to impacts on population connectivity (reduction of certain size classes, reduced reproductive output, etc), which could lead to population bottlenecks (Weetman et al. 2007). In the same way that a network of MPAs should be designed to ensure connectivity, it is not only those grounds that feed into others but those that are potentially isolated that require adequate protection. In order to determine source-sink dynamics, genetic studies need to be undertaken in combination with other methods. For example, continuous and regular sampling of scallop larvae both in the water column and recently settled,

coupled with genetic analysis of multiple year classes has been shown to be more effective in determining source-sink dynamics of localised populations (Selkoe et al. 2008). Further understanding of the population connectivity of *P. maximus* will not only provide essential information for the management of stocks but may also help gain insight into the regional connectivity of a wider range of benthic invertebrates. In conclusion, this genetic analysis suggests that scallop grounds around the Isle of Man can be treated as a single stock, but identifying source and sink grounds are essential if overall stock viability is to be maintained.

Chapter 5

Genetic structure of the scallop *Pecten maximus* along the North East Atlantic shelf

5.1 INTRODUCTION

Population differentiation can occur at varying geographical scales, but it has long been considered that the ability for high dispersal, large population sizes and lack of strong geographical barriers means that marine species show less differentiation than terrestrial species at the same geographical scales (Palumbi 1996; Caley et al. 1996). However, some marine species show higher levels of genetic differentiation than anticipated simply due to barriers to dispersal, such as hydrographic (e.g. Star et al. 2003; Sotka et al. 2004; Goldstein et al. 2009) or isolation of preferential habitat (e.g. Johnson & Black 1995; Riginos & Nachman 2001). Ultimately, the spatial scale of connectivity for populations of marine species is not dependent on any one factor but an interaction of oceanographic features, behaviour and habitat (Cowen et al. 2007). Determining where barriers lie and how these interactions affect them is essential for effective management and conservation of marine species.

The occurrence and potential causes of genetic structure has been determined for many species across the north east Atlantic shelf region. For example, the oyster *Ostrea edulis* displayed evidence of population isolation and reduced genetic diversity between Norway and the rest of the Atlantic, believed to be due to isolation by distance (IBD) alone (Launey et al. 2002), while the whelk *Buccinum undatum* was found to have distinct populations in Iceland, Canada, the Swedish Skaggerak and the rest of Europe, with what appeared to be the beginning of a population bottleneck in the Solent, UK (Weetman et al. 2006). Reduced gene flow was observed between populations of plaice (*Pleuronectes platessa*) from Norway, Iceland and the Baltic, and was determined to result from hydrographic and bathymetric barriers, particularly depth restrictions to adult movement (Hoarau et al. 2002; Was et al. 2010). The highly dispersive crustacean *Crangon crangon* was shown to have differentiation between populations in western Britain, eastern

English Channel and the Baltic Sea as a result of both IBD and hydrographic features restricting gene flow (Weetman et al. 2007). In addition to the physical factors that can affect genetic structure of populations, biological factors can be equally important. For species with high fecundities there is an inherent high variance in reproductive success and therefore a reduction in effective population size which can lead to genetic drift (Hedgecock 1994). Marine bivalves are susceptible to these effects due to their typical sedentary adult phase and high fecundity, and highly dispersive gametic and larval phases. As described in Chapter 4, *Pecten maximus* is characterised by a highly dispersive planktotrophic larval phase and an adult phase that rarely moves more than several metres (Hartnoll 1967). *P. maximus'* geographic range extends along the eastern Atlantic from northern Norway to southern Spain and includes the Azores, Madeira and the Canaries. Previous studies have found no genetic divergence over relatively large geographic distances, for example between samples from Scotland and France (Beaumont et al. 1993; Wilding 1997). Nonetheless, among areas there was evidence of major differences in their reproductive ecology which were unchanged when environmental factors were altered, suggesting a heritable component to local adaptation (Mackie & Ansell, 1993). Similarly, populations on the Norwegian coastline are not genetically different (Ridgway & Dahle 2000), even though stocks show phenotypic differentiation (Magnesen & Christophersen 2008).

Marine bivalves have consistently shown reduced heterozygosity estimates and deviation from HWE where their life history characteristics (large populations and the ability for high dispersal as larvae) would predict the opposite (David et al. 1997). As described in Chapter 4, null alleles could explain this deviation however heterozygote deficits have also been reported in bivalves when using allozymes (Zouros & Foltz 1984). Mooted hypotheses for this consistent deficit include the suggestion of some kind of selective advantage of homozygotes at the larval stage or an influence of temporal sampling effects (Gaffney et al. 1996). The influence of gene flow and genetic drift should affect all loci similarly while selection may affect the observed occurrence of polymorphisms between locations (Launey et al. 2004) leading to high levels of heterogeneity among loci. This has been shown to be particularly problematic for studies using allozymes, which have been shown to be under selection (e.g. Hilbish & Koehn, 1985; Moraga & Tanguy, 2000). Using

microsatellite markers, which are putative neutral and less polymorphic, resolution can be increased.

This chapter expands the fine-scale analysis of population structure of *P. maximus* from the Isle of Man in Chapter 4 to examine the genetic divergence that occurs from northernmost edge of *P. maximus* range in Norway, through Scotland, Ireland and the Irish Sea. Using samples from 15 locations, microsatellite analysis will be employed to determine major boundaries to gene flow, and also whether there is any indication of reduced gene flow among populations within each of the 3 regions of Norway, Scotland and Ireland, and what if any physical or ecological barriers may have influenced any observed structure.

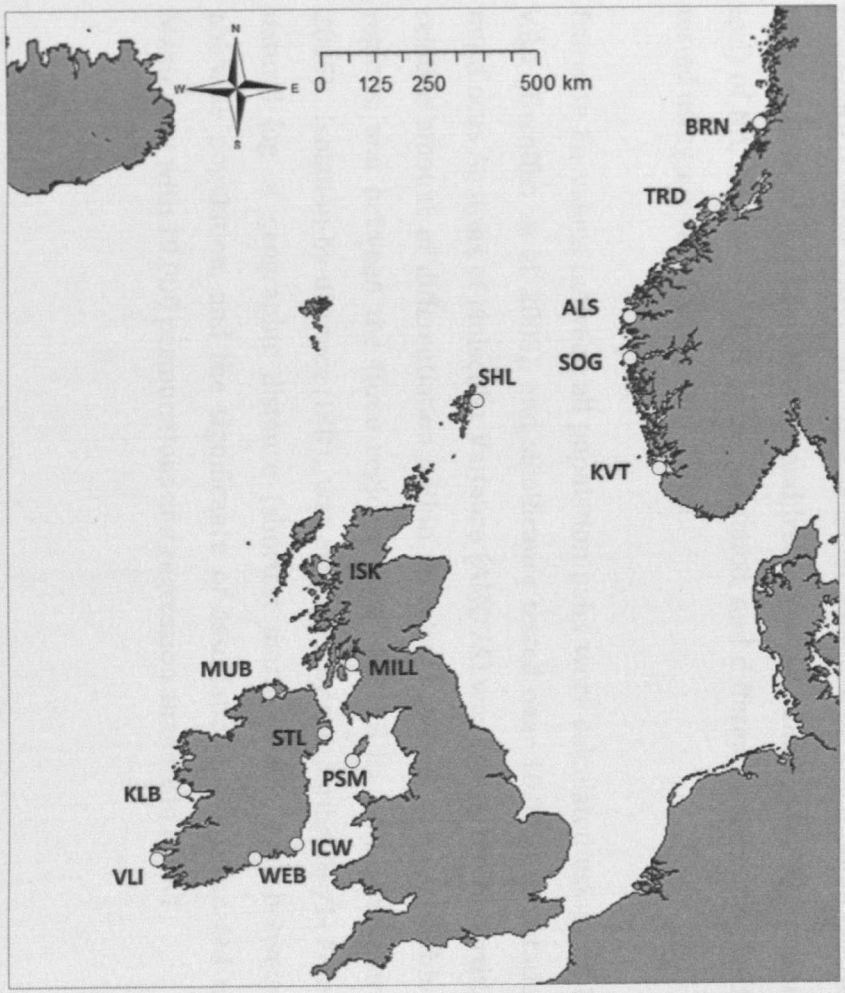
5.2 METHODS

5.2.1 Sample collection

Samples of *Pecten maximus* were collected by either divers, commercial dredges or beam trawls from locations around Ireland, Norway and the United Kingdom between 2003 and 2008 (Figure 5.1). At each location, between 9 and 30 samples were collected (Table 5.1). Tissue samples were taken from the adductor muscle and stored in 80-100% ethanol at -20°C until DNA extraction.

5.2.2 DNA extraction, microsatellite amplification and sequencing

DNA was extracted from samples using a standard high-salt extraction method (Sambrook & Russell 2001; Walsh et al. 1991). Samples were genotyped at eight microsatellite loci (Watts et al. 2005; Table 4.1). Between 10-50 ng of DNA was used in a 10 µl PCR containing 75 mM Tris-HCl pH 8.9, 20 mM $(NH_4)_2SO_4$, 0.01% v/v Tween-20, 0.2 mM each dNTP, 1.5-3.0 mM $MgCl_2$, 2 pmol each primer and 0.25 U *Taq* polymerase (ABgene). Forward primers were 5'-labelled with either 6-FAM, NED, PET or VIC flourophores (Applied Biosystems). Thermal cycling conditions were: 95°C for 3 min, followed by 5 cycles of (95°C for 30 s, T_a°C 45 s, 72°C 45s), 35 cycles of (95°C for 30 s, T_a°C for 45 s, 72°C for 55 s) and a final extension of 72°C for 10 mins, where T_a is the locus-specific annealing temperature for each primer (see Table 4.1). PCR products were pooled into one of two genotyping panels along with a GENESCAN-500 LIZ size standard (Applied Biosystems) and separated by capillary electrophoresis through a denaturing polymer on an ABI3100 automated sequencer



Code	Location	Sample size
	Norway	
BRN	Bronnoy	15
TRD	Trondelag	30
ALS	Alesund	30
SOG	Sogn	15
KVT	Kvitsoy	49
	Scotland	
SHL	Shetland	30
ISK	Isle of Skye	15
MILL	Millport	13
	Northern Ireland, Ireland & Irish Sea	
PSM	Port St Mary	9
STL	Strangford Lough	10
MUB	Mulroy Bay	25
KLB	Kilkieran Bay	15
VLI	Valentia Island	10
WEB	Western Bay	10
ICW	Irish Coast Wexford	10

Figure 5.1 Sample locations of *Pecten maximus* from 15 grounds along the North East Atlantic coast; **Table 5.1** Number, location name, location code and sample size

(Applied Biosystems). Allele sizes were determined using the cubic model of analysis in GENEMAPPER software (Applied Biosystems).

5.2.3 Data analysis

Data conversions for use in different programs were made using CONVERT v.1.31 (Glaubitz 2004). The occurrence of null alleles, stuttering and genotyping errors was tested using MICROCHECKER v.2.2.0.3 (Van Oosterhout et al. 2004). Additionally, null allele frequencies and confidence intervals for all populations at each locus were then assessed using GENEPOP v.4.0.11 (Rousset 2008).

Measures of genetic diversity including allelic richness (A_R), number of alleles (N_A), expected heterozygosity (H_e) and observed heterozygosity (H_o) were calculated for each population and locus using FSTAT v.2.9.3 (Goudet 2001) and ARLEQUIN v.3.1 (Excoffier et al. 2005). FSTAT was also used to assess both deviations from Hardy-Weinberg equilibrium (HWE) across all loci and populations using the inbreeding coefficient F_{IS} (Weir & Cockerham 1984), and the overall levels of population differentiation as determined by values of F_{ST} (Weir & Cockerham 1984). Significance between population groups was tested by a random permutation procedure (Goudet 2001). To assess whether genetic diversity differed between the three regions of Norway, Scotland and Ireland, mean values (over all locations and loci) of NA, AR, HE and FST were calculated, and differences among regions were tested using a permutation test in FSTAT.

Pairwise F_{ST} values between all population pairs were calculated using ARLEQUIN v.3.1 (Excoffier et al. 2005), and significance tested over 10,000 permutations. A multilocus Analysis of Molecular Variance (AMOVA) was conducted to partition the relative amount of differentiation within samples, between samples within the 3 regions, and between the three regions, using ARLEQUIN v.3.1 (Excoffier et al. 2005). Isolation-by-distance (IBD), was examined by comparing F_{ST} /1- F_{ST} and the natural log of geographic distance (shortest marine route, km) between each pairwise population, and the significance of associations was estimated using a Mantel test with 10,000 permutations and regression analysis in FSTAT.

Analysis of population structure was carried out using STRUCTURE v2.3.1 (Pritchard et al. 2000). For each analysis, 10 independent runs of STRUCTURE were made, to assess output consistency and to calculate ΔK (Evanno et al. 2005). The number of clusters (K) was varied from 1 up to 10 using the admixture model and correlated allele frequencies. All model runs were based on 500,000 Markov chain Monte Carlo replications with an initial burn-in period of 50,000 iterations. The most pronounced partition (level of population subdivision) of the data set was identified using the method of Evanno et al. (2005) where the second order rate of change of the likelihood function with respect to K (ΔK) was calculated using STRUCTURE HARVESTER v.0.6.7 (Earl 2011). When data sets have few markers, few individuals or weak structure, using sampling locations as prior information assists the program in clustering by using LOCPRIOR models (Hubisz et al. 2009), which can provide accurate inference of population structure where the standard models are unable to. In this instance, locations were grouped based on hypothesised populations of Norway, Scotland and Ireland.

5.3 RESULTS

Of the eight microsatellite loci LIST15-011, LIST15-016 and LIST15-019 failed to amplify sufficiently in enough samples for analysis. For the other loci, null allele frequencies were relatively low at all locations for LIST15-002a, LIST15-004, LIST15-014 (Table 5.1). At loci LIST15-005 frequencies ranged from 0 to 0.1403 while for LIST15-020 frequencies were highest at up to 0.353. At MILL, STL and PSM, null allele frequencies could not be generated for two of the five loci (Table 5.1). These correlated with the loci where only one allele was scored, which meant that other measures of diversity for these loci at these locations could not be calculated (Appendix 1). For each location, at each locus, the number of alleles (N_A) ranged from 1 to 13 with the total number of alleles for each locus over all locations from 7 at LIST15-002a to 21 at LIST15-005 (Appendix 5). Mean expected heterozygosity (H_E) was high (>0.53) for all loci except LIST15-004 (0.20) (Table 5.2). Global Fst was 0.06 (CI 0.029-0.082) while global FIS was 0.08 (CI -0.142-0.223) (Table 5.2)

Table 5.1 Null allele frequencies for 5 microsatellite loci at 14 locations along the North East Atlantic coast. – indicates not enough information to compute frequencies while only confidence intervals that could be calculated are shown in italics. See Figure 5.1 for location codes.

	02a	4	14	20	5
BRN	0	0	0.063	0.098 *±0.022*	0.126 *±0.027*
TRD	0	0	0	0.138 *±0.052*	0.0281 *±0*
ALS	0	0	0.025 *±0*	0.092 *±0.022*	0.031
SOG	0.013	0	0	0	0
KVT	0	0.093 *±0.01*	0.005 *±0*	0.056 *±0.003*	0.0722 *±0.019*
SHL	0.042	0.101	0.014	0.138 *±0.043*	0.059 *±0.013*
ISK	0	0	0	0.251 *±0.118*	0
MILL	-	-	0	0	0
MUB	0	0.085	0.088 *±0.003*	0.176 *±0.067*	0
KLB	0	0	0	0.291 *±0.145*	0.1403 *±0.033*
VLI	0	0	0.130	0.110	0
STL	0	-	-	0	0
PSM	0	-	0	0.310	-
WEB	0	0	0.197	0.102	0
ICW	0	0	0	0.353	0

Table 5.2 Summary statistics for five microsatellite loci of the scallop *Pecten maximus* pooled from 15 locations across the north east Atlantic shelf. N_A: number of alleles; H_O: observed heterozygosity; H_E: expected heterozygosity. Significant values (P<0.05) of F_{ST} and F_{IS} (calculated after Weir and Cockerham (1984)) are denoted in bold.

Locus	N_A	H_O	H_E	F_{ST}	F_{IS}
LIST15-002a	7	0.71	0.53	0.07	-0.31
LIST15-004	9	0.20	0.20	0.00	**0.13**
LIST15-014	17	0.59	0.66	0.08	**0.09**
LIST15-020	16	0.49	0.76	0.09	**0.30**
LIST15-005	21	0.81	0.88	0.02	**0.11**
Overall	14	0.56	0.61	0.06	0.08

Diversity measures at latitude indicated no correlation between both allele richness and expected heterozygosity and latitude (Figure 5.2). The mean number of alleles showed a positive relationship with latitude ($R^2 = 0.3496$) however.

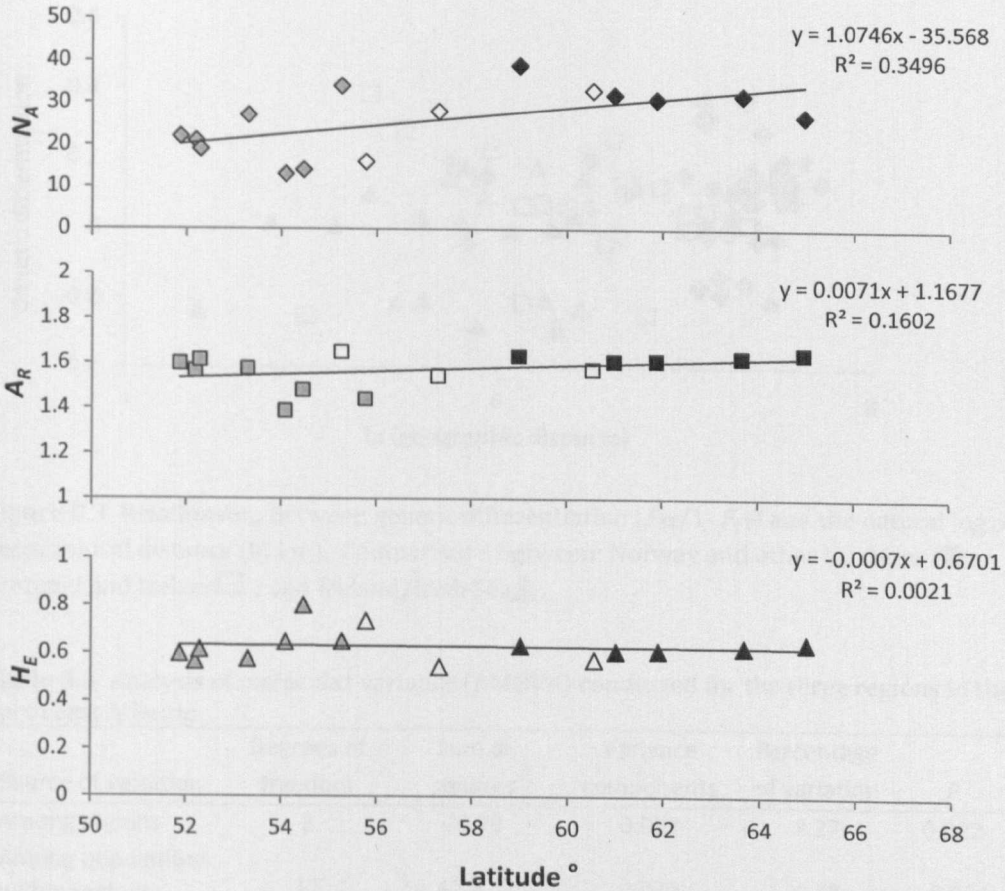


Figure 5.2 Measures of genetic diversity (Number of Alleles (N_A), Allele richness (A_R) and Expected Heterozygosity (H_E)) for *Pecten maximus* at different latitudes from 15 locations along the north east Atlantic shelf. Locations are shaded by region: Norway (black), Scotland (white) and Ireland (grey).

Between Norway and Scottish locations, pairwise F_{ST} values were significantly different (Table 5.4). Norway was also significantly different to most Ireland/Irish Sea populations except PSM and STL, which were two locations with only one allele at two loci. Additionally, MUB, an enclosed bay on the north-west coast of Ireland also showed significant differences with other Irish locations but not with three of the five Norway locations. There appeared to be no significant ($p>0.05$) correlation between genetic differentiation and geographic distance ($R^2 = 0.052$) though the rank correlation test was significant ($p = 0.019$) (Figure 5.3). An AMOVA (Table 5.3) indentified all sources of variation to be significant, with among regions component accounting for 2.27% of the total variance, among populations within regions 4.28% and within populations 7.77%.

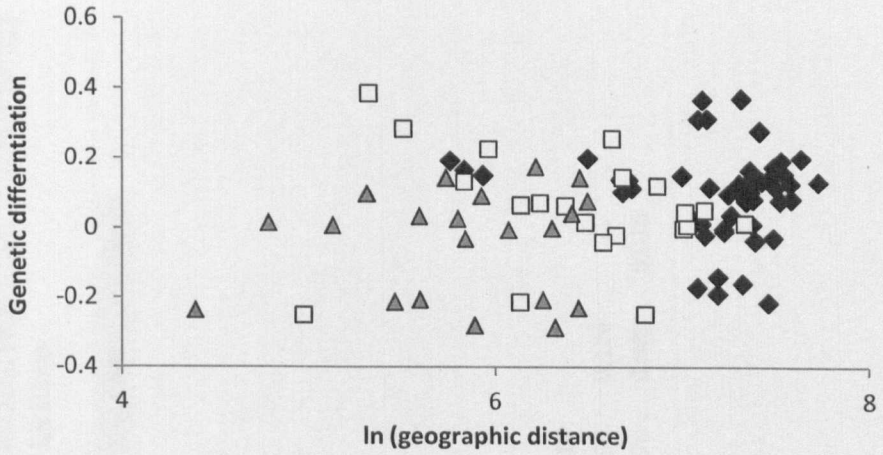


Figure 5.3 Relationship between genetic differentiation (F_{ST}/1- F_{ST}) and the natural log of geographical distance (ln km). Comparisons between: Norway and other locations ◆ ; Scotland and Ireland□ ; and Ireland/Irish Sea▲.

Table 5.3 Analysis of molecular variance (AMOVA) conducted for the three regions in the north east Atlantic

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation	*P*
Among regions	2	20.79	0.037	2.27	0.022
Among populations within regions	12	42.815	0.070	4.28	<0.001
Within populations	1077	348.009	0.126	7.77	<0.001
Total	1091	730.614	1.624		

Fixation indices: F_{SC} – 0.0438, F_{ST} = 0. , F_{CR} = 0.

Clustering analysis using STRUCTURE indicated a distinct grouping of Norway locations with no variation amongst them (Figure 5.4) based on the highest log likelihood value where K = 2 and the highest ΔK value where K = 5 (Figure 5.5). In addition, as K increased from 2 to 5, it became evident that the three locations in Scotland formed another cluster which was different to Norwegian and Irish populations. The remaining populations in Ireland and the Irish Sea showed little distinct structure, though at K's of 2, 3 and 4 they shared most similarity with Scottish locations. Overall the major barrier appeared to be Norway and the other locations, with a Scotland/Ireland split which is not very strong in terms of membership to separate mode clusters.

Table 5.4 Pairwise F_{ST} values between locations along the north east Atlantic shelf, grouped as Norway (dark grey), Scotland (White) and Ireland/Irish Sea (light grey). Values in bold are significantly different from zero ($p<0.05$) after 10,000 permutations. See Figure 5.1 for locations.

	BRN	TRD	ALS	SOG	KVT	SHL	ISK	MILL	MUB	KLB	VLI	STL	PSM	WEB
TRD	-0.014													
ALS	-0.016	0.005												
SOG	-0.007	0.012	-0.016											
KVT	-0.008	0.005	-0.011	-0.009										
SHL	**0.122**	**0.166**	**0.142**	**0.161**	**0.131**									
ISK	**0.105**	**0.131**	**0.102**	**0.121**	**0.093**	**0.027**								
MILL	**0.218**	**0.271**	**0.239**	**0.269**	**0.238**	0.058	**0.181**							
MUB	0.011	**0.036**	0.013	0.029	**0.016**	**0.127**	**0.117**	**0.221**						
KLB	**0.073**	**0.119**	**0.087**	**0.113**	**0.089**	-0.001	0.016	**0.059**	**0.075**					
VLI	**0.077**	**0.104**	**0.076**	**0.094**	**0.072**	**0.049**	-0.021	**0.204**	**0.084**	0.008				
STL	-0.272	-0.190	-0.232	-0.164	-0.205	-0.329	-0.271	-0.334	-0.260	-0.401	-0.299			
PSM	-0.029	-0.037	-0.009	-0.002	-0.020	**0.108**	**0.061**	**0.278**	0.026	**0.071**	0.040	-0.310		
WEB	**0.117**	**0.167**	**0.135**	**0.162**	**0.135**	0.014	**0.044**	0.066	**0.126**	-0.006	0.033	-0.390	**0.126**	
ICW	**0.113**	**0.149**	**0.119**	**0.142**	**0.113**	0.009	-0.042	**0.184**	**0.149**	-0.001	-0.032	-0.270	**0.089**	0.015

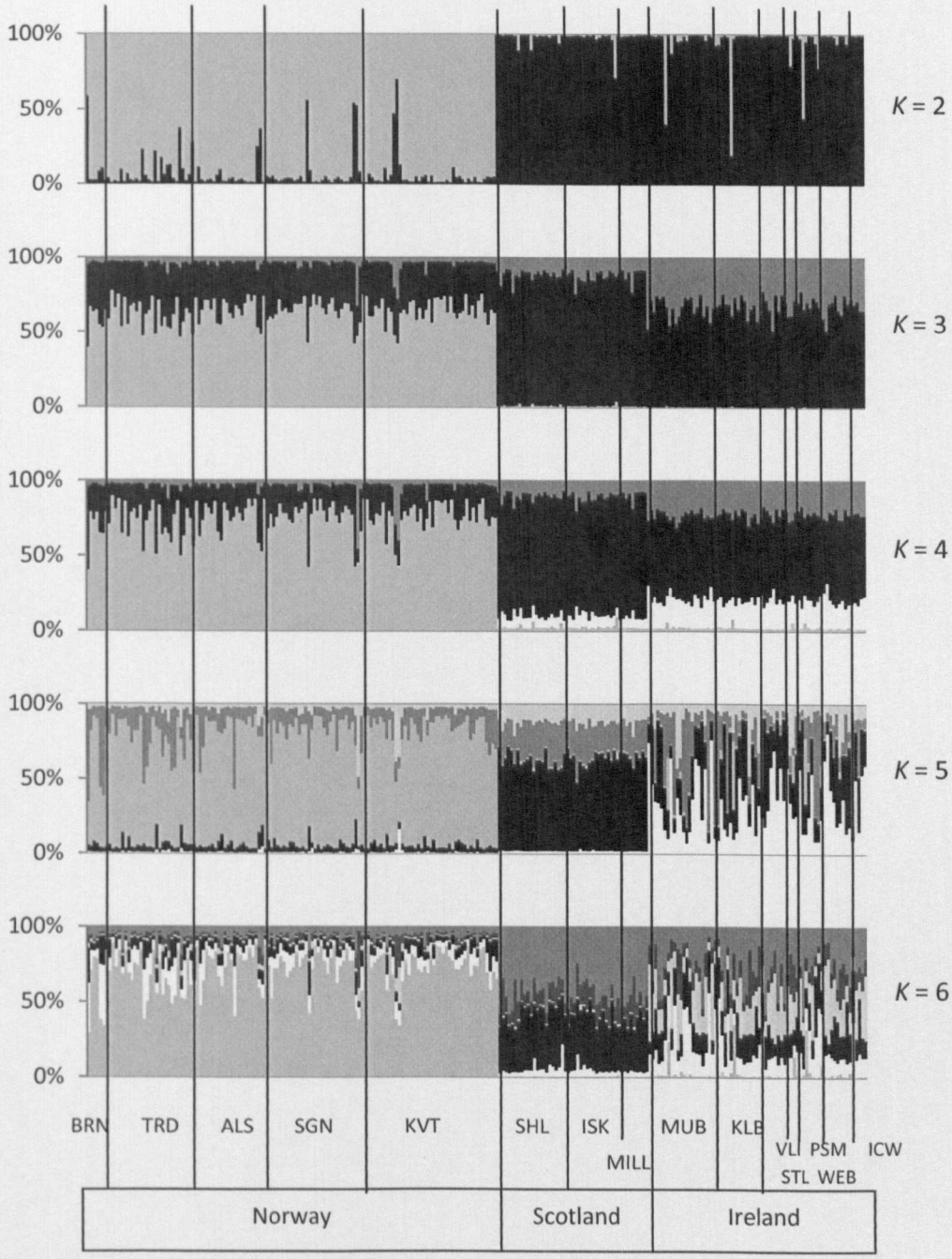


Figure 5.4 Population structure based on five microsatellite loci as estimated by clustering analysis using STRUCTURE, with the assignment of 480 individuals from 10 locations around the Isle of Man to *K* genetically different groups (where *K* =2 to 6 in this instance). Each bar represents an individual with the bar coloured according to assignment to each *K*/population.

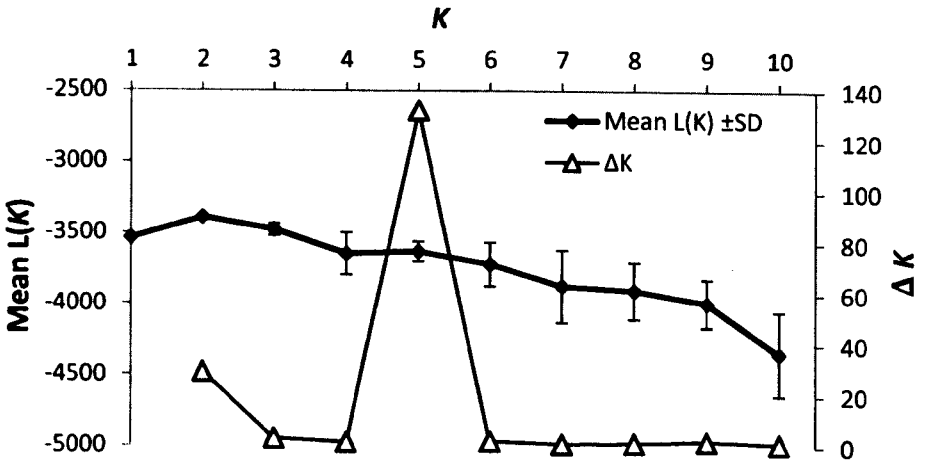


Figure 5.5 Population structure based on five microsatellite loci as estimated by clustering analysis using STRUCTURE. Primary X-axis represents most likely estimated number of populations (*K*) from the data as indicated by the highest value of Δ*K*, which is the rate of change of the probability between successive runs (calculated after Evanno *et al.*, 2005). The secondary Y-axis is the corresponding mean log-likelihood for *K* populations, where the most likely number of populations is the highest L (*K*).

5.4 DISCUSSION

By determining the genetic diversity and structure of a species throughout its geographic range, the scale at which populations are connected can be assessed. Using microsatellite and sequencing analysis on samples of *Pecten maximus* from 15 locations from the northernmost edge to the middle of its range, this study has shown that there is a distinct barrier to gene flow separating populations in Norway from those in Scotland and Ireland, with another, weaker barrier between Scotland and Ireland. Given the results of Chapter 4 where no genetic structure was observed between grounds around the Isle of Man, genetic structuring was more likely to be observed at larger geographical scales. However, the reasons behind the observed patterns of structure found here need to be addressed.

As discussed in Chapter 4, the retreat of the ice sheet at the last glaciation period began approximately 17,000 years ago from the southern Irish Sea (Clark et al. 2010), coinciding with the southernmost sampling sites in this study. Recolonisation of the region would have happened gradually, with the assumption that the northernmost locations would have been the last to be colonised. At the edge of species range limits, populations are hypothesized to show reduced

diversity and variability along with a smaller effective population size (e.g. Lind et al. 2007; Maggs et al. 2008; Was et al. 2010). While gene diversities were middling to high (mean H_E = 0.61) for all populations, there was no reduction in genetic diversity in the northern populations in comparison to the rest (Figure 5.2). It is possible that these differences may be observed when compared to samples from the full extent of *P. maximus* range or it may simply be the case that fishing pressures have reduced population sizes and therefore genetic diversity across all populations, masking any patterns. Additionally, there is evidence that during the last glaciation period some species survived in small periglacial refugia, which would dampen the effects of genetic diversity reduction in northern regions (Maggs et al. 2008).

The sharp genetic break isolating Norway from the other locations, coupled with no reduction of genetic diversity at the northernmost locations, is indication that there has been sufficient time since the glacial retreat for populations to diverge. However, the mechanisms by which Norway has become isolated need to be examined. Initially, isolation-by-distance (IBD) could be assumed to be responsible for this pattern, but there was no evidence of IBD through either the mantel test or from comparison of genetic differentiation and distance (Figure 5.3). Indeed, individuals from Shetland are more genetically related to those in the south of Ireland >1500 km away than those in Norway <350 km away. Given that *P. maximus* have a PLD of between 18 and 42 days, it is unlikely larvae could cross the >300km between Shetland and Norway, even if currents were strong enough to ensure exchange. Indeed current patterns of the northern North Sea show a flow southwards from Shetland, which joins a general flow into the Baltic, coupled with variable and wind-driven patterns in central areas (Lee & Ramster 1981; Smith et al. 1996). Furthermore, there is a strong contrasting northwards flow along the Norway coast. With dispersal scenarios in Chapter 2 attaining a maximal distance of 250 km for a particle at 42 days (though this was in the Eastern English Channel where flow speeds are much higher than elsewhere), dispersal potential between Shetland and Norway is likely to be low or nonexistent. The distance between Shetland and Norway would not necessarily result in reduced connectivity if there were grounds acting as stepping stones between. However, any such stepping stone grounds are likely to have been severely depleted and their habitat compromised by the intense fishing activities characteristic of the North Sea (e.g. Turner et al. 1999; Frid et al. 2000).

While these factors impact directly upon the dispersal of larvae, there is also the possibility of environmental variations creating a phenotypic barrier between the two. With large range of sea temperatures found across the sampling range, larvae may not be able to successfully recruit into populations if they are not adapted to local conditions. Additionally, variations in reproductive timings indicating phenotypic differences have been shown between locations in Norway (Magnesen & Christophersen 2005) and between scallops from France and Scotland (Mackie & Ansell 1993), even while no genetic variation was found. This may be indication of adaptive divergence between populations, which may correlate with reduced connectivity.

Over similar geographic distances in shelf seas, genetic differentiation has been found for many species such as the scallop *Placopecten magellanicus* in the northwest Atlantic (Ketchington et al. 2005), the shrimp *Crangon crangon* between Britain and the Baltic (Weetman et al. 2007) and the limpet *Cellana strigilis* across New Zealand and the sub-Antarctic (Goldstein et al. 2009). As with this study, divergence did not occur at much smaller geographic scales, therefore it may be that processes of genetic differentiation are similar in all shelf regions. There has been inference of the isolation of Mulroy Bay (MUB), an enclosed bay on the northwest coast of Ireland, resulting in genetic isolation (e.g. Heipel et al. 1999) but this was not consistent with the results of this study. The weak genetic break between Scotland and Ireland demonstrated in STRUCTURE is interesting. Hydrographic fronts in the northern channel of the Irish Sea and could feasibly isolate the west coast of Scotland from STL, PSM, ICW and WEB. However, the populations on the west coast of Ireland (KLB and VLI) are not subject to a strong hydrographic barrier; indeed there is a strong northerly residual current along the west coast of Ireland towards the Isle of Skye (ISK). This may explain why as *K* increased, the distinction of the two regions became less pronounced (Figure 5.4).

The lack of genetic structure within broad regions has implications for management of *P. maximus* populations and sedentary marine invertebrates in general, both locally and across the entire study range. While genetic diversity was uniform across all populations, fishing pressures can reduce effective population size leading to a reduction in genetic diversity (Hauser et al. 2002). As many scallop fisheries are within the territorial limit, they are subject to a high degree of local management

and in cases such as the Isle of Man, have been effective in recovering stocks after crashes (e.g. Beukers-Stewart et al. 2003, 2005). But these crashes may have already affected genetic structure of populations, particularly in terms of diversity. Additionally, phenotypic diversity may be as important to maintain if adaptations are temperature dependent; with projected average sea temperature rise as high as 4°C by the end of the century (UKCIP 2009), the geographic range to which species are adapted, whether for larval development or reproductive timing, will be altered. Therefore, understanding patterns of connectivity at a genetic level will help in pre-emptive management strategies.

Chapter 6

Discussion

With widespread disturbance, alteration and even species or habitat loss due to anthropogenic pressures on the marine environment (e.g. Pauly et al. 1998; Frid et al. 2000; Jackson et al. 2001), effective management and conservation strategies are essential if biodiversity loss is to be stabilised and sustainable use of the environment to be achieved. Networks of marine protected areas (MPAs) are a popular method for protecting biodiversity (e.g. Roberts et al. 2002; Gaines et al. 2010), but the benefits of a network can only be achieved if the design takes full account of the factors that influence ecological coherence, which include the adequacy and viability of the individual MPA sites selected and the ecological connectivity between these.

Despite over 30 years of research, there still remains an immediate need to improve our understanding of the drivers of ecological connectivity, particularly with respect to the design and management of MPA networks (Gaines et al. 2010). While early studies were predominantly focussed on determining connectivity of fish and/or coral reefs, few studies explored this for temperate benthic invertebrates, particularly those common to offshore habitats. Policy drivers now require the protection of representative areas of the full range of biodiversity that is native to a given area (e.g. OSPAR 2006) and this therefore requires advice on network design that is relevant to the full range of species and habitats.

This thesis aimed to explore connectivity of marine benthic invertebrates of temperate continental shelf seas. This was done first by assessing the variation in dispersal potential of a typical benthic invertebrate assemblage, due to the effects of larval development type and Planktonic Larval Duration (PLD), and due to specific location, hydrography, depth and distance from shore (Chapter 2). Using the same species, the level of habitat specificity and the implications of this and the distribution and rarity of habitat types on dispersal potential was then examined in Chapter 3. In the following two chapters, the genetic structure of an exploited sessile benthic invertebrate, the scallop *Pecten maximus*, was determined at both

localised and regional geographic levels. The findings of this thesis have demonstrated both the importance of biological variation within typical benthic assemblages of the UK shelf seas, and the need to account for local hydrography and habitat suitability and distribution when determining dispersal potential. Furthermore, while no genetic structuring of *Pecten maximus* was evident at a localised scale (the Isle of Man), the variation and pattern of both genetic diversity and genetic structure across the north east Atlantic highlights the complexities of connectivity amongst populations.

6.1 Scaling policy with connectivity

Policy drivers act at different temporal and spatial scales, and given that networks of MPAs are one of the potential management measures that can be sought to achieve the objectives of these policies, it is important to understand at what spatial and temporal scales connectivity works. Within Europe, the Marine Strategy Framework Directive (MSFD) operates over broad regional sea areas (Northeast Atlantic, Baltic Sea, Black Sea and the Mediterranean). It strongly encourages the co-operation of the countries bordering these seas when implementing their management measures (EC 2008). The regional sea conventions (e.g. OSPAR, HELCOM) also act at the regional sea scales, though their definitions of regional seas do not always match those of the MSFD. For example, OSPAR has management areas within the northeast Atlantic such as the greater North Sea. Additionally, there are national objectives for MPA network designation, and in reality while many of the major directives and conventions operate at the regional scale, it is the individual countries that will instigate management measures. It is therefore crucial to understand the scales at which connectivity operates in order to assess the level of transboundary cooperation needed to design networks of MPAs that work to their full potential.

Strong hydrographical features (such as major fronts) can operate as barriers to dispersal, which may act to reduce connectivity of a species within its geographic range (Gaylord & Gaines 2000; Werner et al. 2007). Using genetic marker techniques, a barrier between individuals of the scallop *Pecten maximus* in Norway and individuals of the same species around Scotland and Ireland was clearly evident (Chapter 5), with a weak barrier also suggested between Scottish and Irish coasts. The genetic divergence noted between Norwegian and UK/Ireland populations has

also been described for plaice (Hoarau et al. 2006; Was et al. 2010), while similar barriers have been noted between Iceland, Faroe and the Barents Sea for a range of species (e.g. Hutchison et al. 2001; Luttikhuizen et al. 2003; Weetman et al 2006; Danancher & Garcia-Vazquez 2011). Clearly, even for invertebrate species with highly dispersive larvae, genetic connectivity operates in most cases within regional sea scales (100 km or less). Thus management should also be designated at this level (although see section on adaptation to climate change in 6.3).

Findings from Chapters 2-4 highlighted the factors that affect connectivity within regional seas and these are discussed further in Section 6.2 below. However, it is important to note that designations at the national scale, where the influence of outlying but fully connected areas is not taken into account, may also lack ecological sense. In particular, the lack of genetic structure in scallop populations found around the Isle of Man (Chapter 4) highlights that knowledge of surrounding source and sink areas must also be considered in designing national networks, and supports the need for cooperation of countries surrounding regional seas. Our results demonstrate that with the variation in hydrographic regime (Chapter 2) and distribution of preferred habitats (Chapter 3), designation of spatial management tools for any policy objective, whether it operates for national, regional or international interests, should be done at the scale of regional seas and should involve transboundary cooperation of countries in designing networks of MPAs.

6.2 Factors affecting connectivity within regional seas

Explicit advice on size and spacing of MPA networks, based on a range of species, varies from nodes of 4-6 km in diameter and 10-20 km apart (Shanks et al. 2003), to 10-20km across and 40-80km apart (Roberts et al. 2010). The latter study was conducted within the UK, and seemed more appropriate given the findings of Chapter 2, although it is clear from the findings of both Chapters 2 and 3 that using simple rules on size and spacing will not necessarily result in the most efficient design of a network, particularly when local hydrographic conditions and habitat distributions are not taken into account. Dispersal scenarios run in both chapters also support the need to take into account direction of dispersal in designating connected MPA nodes within a network.

In terms of variation in development types and PLDs, the fact that these species ranges are within UK and Ireland shelf seas, and in most cases have a minimum geographic range from Norway to Spain, means the species information gathered can be applied throughout the North East Atlantic. Obviously, temperatures across the region vary so this would have to be taken into account in terms of dispersal potential as temperature does correlate with PLD (see Chapter 2, Appendix 1). Ultimately, each region must take into account the physical parameters of temperature, hydrographic regime and habitat suitability and distribution when considering MPA network design but within regions, the scales of realised dispersal described in this thesis can be considered as indicative of the sorts of species found in temperate offshore habitats.

As stated previously, even a small number of recruits would ensure genetic homogeneity amongst grounds; it is possible that the large area of scallop grounds around the Isle of Man, and therefore the large area of release points of gametes, ensures larvae disperse widely enough for this to occur. Furthermore, not only are scallop grounds themselves large around the Isle of Man (see Figure 4.1a), but the habitat preference of *Pecten maximus* is broad enough that they can find suitable habitat (based on sediment type) throughout the Irish Sea (Figure 6.1). While they are found in large aggregations, which form the basis of the fishery not only around the Isle of Man but across the Irish Sea, this does not mean they are not found more sparsely dispersed throughout their entire range.

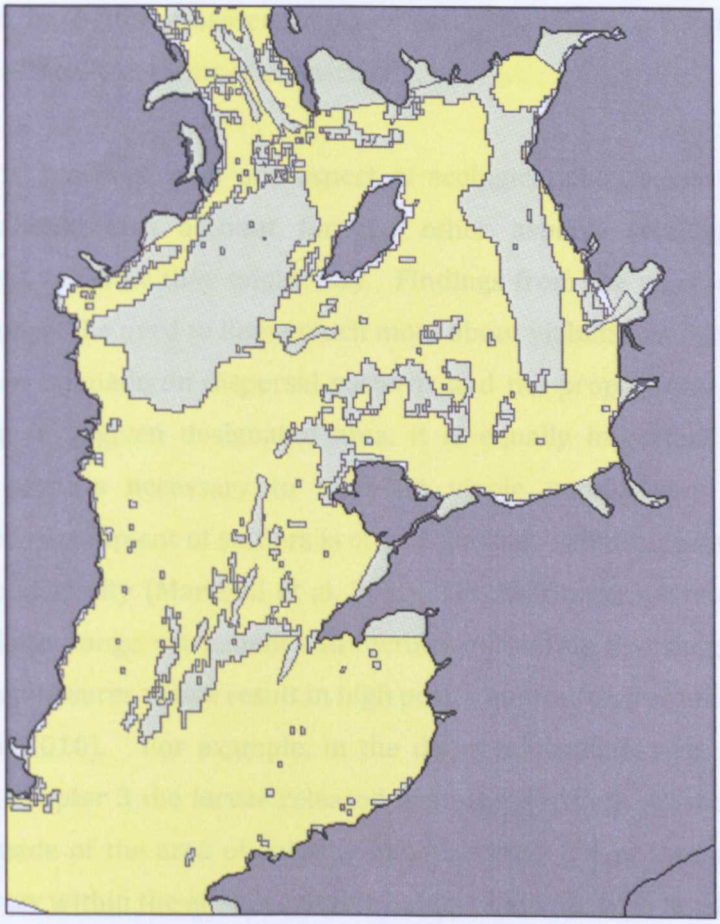


Figure 6.1 Distribution of 'coarse/sand' habitat-landscape grouping (yellow shading) in the Irish Sea, which is suitable for the scallop *Pecten maximus*.

Connectivity is a key component of ensuring overall ecological coherence, relating directly to our ability to assess whether an MPA network "interacts and supports the wider environment". Initial definitions of ecological coherence were vague, (Ardron 2008); however, in 2007 OSPAR published a working definition, where an ecologically coherent network of MPAs: (i) interacts and supports the wider environment and (ii) maintains the processes, functions, and structures of the intended protected features across their natural range. The OSPAR definition is itself still vague in practice, but the findings of this thesis suggest it would be possible to expand on these concepts to give more specific guidance on what should be assessed in determining the ecological coherence of an area (thus a stricter definition of ecological coherence itself). By combining information on species composition and dispersal potential, habitat distributions and hydrographic regime,

networks can be better assessed as to whether they are achieving ecological coherence, specifically in terms of connectivity.

Connectivity is, however, only one aspect of ecological coherence; MPA network designation should also account for the other aspects (viability, adequacy, representation) and how they might vary. Findings from the work undertaken in this thesis support the need to know much more about viability, as even where good predictions can be made on dispersal patterns and the proportions of larvae that might end up in a given designated area, it is equally important to know the numbers of recruits necessary to maintain viable populations, as successful settlement and recruitment of settlers is one of the main requirements to sustaining population connectivity (Marshall et al. 2010). Furthermore, while dispersal may occur over a large range, settlement and recruitment within that range is subject to high selection pressures which result in high post-colonisation mortality (Chia 1989; Marshall et al 2010). For example, in the dispersal scenarios run for *Nephrops norvegicus* in Chapter 3 the larvae released from the northern-most station mainly dispersed outside of the area of suitable habitat. With 5% of the larvae released predicted to stay within the area of suitable habitat and with high levels of fecundity, it could be that this would be enough to self-seed the area even allowing for mortality. However, without a clearer idea of population dynamics and recruitment levels required it is impossible to advise on this.

The survival of both larvae and adults are dependent on many factors, not least of which is the suitability of the habitat. In their review of these factors Marshall et al. (2010) demonstrated that the scale of selection pressures vary, but are often smaller than the scale of dispersal potential. They argued that this would bias survival against exogenous colonisers, and was therefore a phenotype-environment mismatch, a term used to describe a reduction in fitness when an organism specialised to one environment finds itself in another environment (defined by DeWitt et al. 1998). With indications of phenotypic differences in *Pecten maximus* within Norway grounds (Ridgeway & Dahle (2000), and between France and Scotland (Beaumont et al. 1993), the scale of connectivity at a phenotypic level is smaller than microsatellite analysis would indicate. This highlights the importance of considering connectivity at shorter temporal scales than genetic time scales. If entire regions are treated as genetically identical based solely on microsatellite

markers, important local adaptations to the physical environment could be reduced if populations are impacted. This is particularly important if populations are to be resilient to a changing environment.

6.3 Further work

While this thesis has examined a number of approaches to determining connectivity in the marine benthos, it has not been possible to validate predictions against actual data on the characteristics of individual species over time. It is apparent that the complexity of both determining and measuring connectivity, even in more discrete systems such as coral reefs, should not be underestimated. As such, there has been increasing awareness for the need to use a combined approach to address these issues and the viability of MPA networks. For example, Sale & Kritzer (2003) described the need for large-scale, multidisciplinary, and collaborative research programs, which were undertaken in association with natural resource managers. Additionally, Pineda et al. (2009) examined approaches to recruitment and population dynamics of benthic systems, and described the use of reductionist approaches, where complex systems are studied one parameter at a time, and simplified approaches, where the numbers of processes within a system are reduced to make the problem more manageable. They found that simplified approaches can 'muddle' understanding of complex processes, leading to mistaken inferences of results. They concluded that understanding each component is essential if systems are to be understood as a whole.

It will be a continued challenge to integrate multiple and novel methods to address the complexity of connectivity in the marine benthos, but collaborations between benthic ecologists, oceanographers, statistical modellers and molecular ecologists will be a much more productive than a lone-method approach. Already successful examples of these approaches can be found. For example, by examining the genetic structure of three species within a region and combining this with environmental data that would affect genetic patterns such as habitat patch size, temperature and hydrodynamics, Selkoe et al. (2010) showed that while slight differences in diversity and pairwise differentiation across sampling sites could be viewed as genetic patchiness or noise, they might in fact actually indicate ecologically meaningful

differences. Clearly these collaborative approaches will be key in unravelling the complexities of connectivity in the future.

One of the most essential factors in MPA network design will be the ability for adaptive management; networks must be able to be altered, not only in the face of a changing environment through, for example, climate change, but also with improvement of scientific knowledge. While decisions on the design of MPA networks are being made (or in the case of the UK have been made (MCZ designations in 2011)), the number of scientific studies on dispersal and connectivity have increased exponentially (Figure 6.2). Fewer than 10 studies a year were undertaken through the 1990s and early 2000s, but by 2005 studies began to increase exponentially, with over 80 in 2010. Clearly, the findings of each of these could potentially have implications for how MPA networks are designed, and if the findings are not disseminated to managers, designs may be ill-informed and potentially useless in terms of their aims.

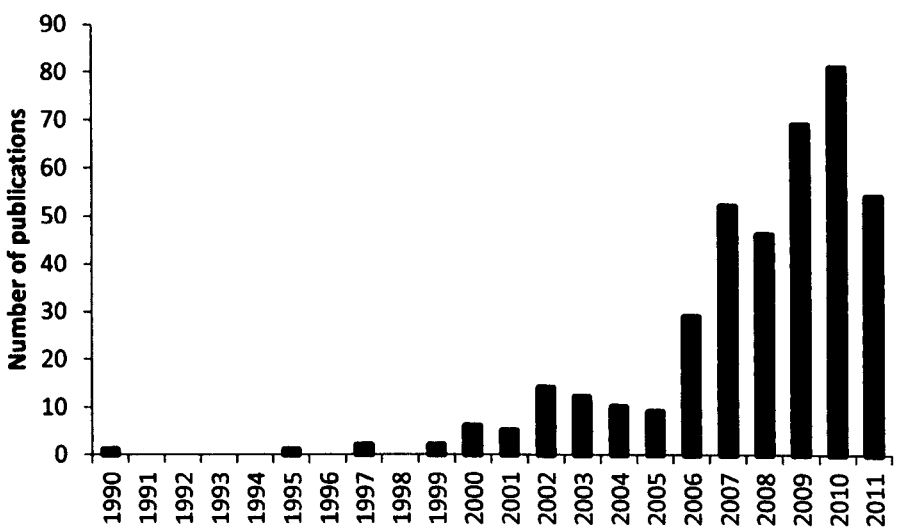


Figure 6.2 Number of publications since 1990 on larval dispersal and connectivity. Data from a Web of Science search on topic.

MPA network design in the UK has been undertaken by governmental bodies at local and national levels, with Scotland and Northern Ireland working independently from England and Wales. Each region is using sites already afforded some level of

protection (e.g. Ramsar sites and Special Areas of Conservation (SACs)) as the first part of the network. Designation of additional locations in England and Wales has been established through the Marine Conservation Zone (MCZ) Projects. Overall the network is to adhere to the design principles of representativity, replication, adequacy and connectivity (JNCC/Natural England 2010). For connectivity, the lack of detailed information available led the guidelines to state that it should be considered of secondary importance to the other principles. What has been recommended, is that if species-specific dispersal estimates are available they should be used to determine spacing, but where this information is not known, spacing between MPAs of similar habitat should not be more than 40 - 80 km (as recommended by Roberts et al. (2010)). Indeed, it is the findings of Roberts et al. (2010) which form the basis of guidelines on connectivity for the UK's designations. It is made clear that connectivity will vary depending on location, but there are no clear recommendations for how hydrographic regime or habitat distribution could be incorporated into network design, only that they will play a role in connectivity.

The findings of this thesis, particularly those covered in Chapters 2 and 3 describe the variation in connectivity between locations, both due to hydrography and habitat distributions. It would be a relatively simple process for managers to use the same methods to assess connectivity of the proposed MCZs, thereby allowing for location-specific variations in connectivity to be incorporated. Furthermore, at the national and international scale, the genetic breaks shown in Chapter 5, coupled with the findings of other genetic studies, highlight the need for cross-regional collaboration to ensure that the larger MPA network is indeed connected.

Although the potential effects of a number of key drivers on connectivity were explored in this thesis, it was not possible to cover the likely effects of changes in temperature. It has long been recognised that the development time of a larva is highly variable (Scheltema 1986), but as already discussed in Chapter 2, sea temperature is negatively related to development time. Dispersal potential is therefore reduced at higher temperatures, though for any given species the effects of this relationship are highly variable (O'Connor et al. 2007). While many studies are conducted in optimal conditions, there is often a high mortality rate at extremes of temperature ranges. For example, an ovigerous female of *Corystes cassivelaunus* was maintained in an aquarium at 15°C and the resulting eggs maintained in batches of

10°C, 15°C and 20-25°C (Ingle & Rice 1972). Survival to the megalopa stage only occurred at 15°C, with the fastest mortality shown for the 20-25°C group. It may be that larvae remain competent at temperatures that adults are acclimatised to, though mortality may be high. In this case, 15°C was higher than what adults and larvae would normally experience in British waters during spring or summer (Ingle & Rice 1972). With projected sea temperature rises of 3°C on average (IPCC), but potentially much higher localised increases, a reduction of larval dispersal potential and competency may be seen.

However, the temperature limits of adults were not so clear. While geographic and therefore temperature ranges were large for the majority of species studied here, it is possible local populations cannot adapt quickly enough to increased temperatures. Additionally, if species live at the edge of their limits already then increases may have severe impacts on them (e.g. Hammond & Hofmann 2010). For example, even with its range extending across the world, *Carcinus maenas* has been shown to not be able to mate at >18°C. In another study, juveniles of *Panadlus borealis* have been shown to be more sensitive to temperature changes than adults (Koeller et al. 2009; Daoud et al. 2010), which could have major implications for the structure and dynamics of populations throughout their range. Additionally, reduced pH from increasing CO_2 will have an effect on larval development, leading to high mortality and reduced PLD which will therefore reduce dispersal (Ericson et al 2010). From a fisheries perspective, one potentially positive aspects of rising sea surface temperature has been shown in Isle of Man scallop populations, where rising spring temperatures have seen increased gonad development, leading to greater gamete production which may be the cause of increased recruitment success amongst stocks (Shephard et al. 2010). Ultimately, the potential impacts of climate change on mortality and dispersal of species throughout their life history must continue to be examined. If MPA networks are to have any hope of achieving their aims, they must be able to adapt to accommodate these changes.

6.4 Conclusions

Though the establishment of MPAs are often restricted by economic and socio-political factors, they still play an important and viable role in conservation. While there are examples of successful MPAs, Mora & Sale (2011) found that not enough

are being established at a fast enough rate to match the accelerating loss of species and habitats, and that the shortcomings of most MPAs mean they should not be viewed as the only solution to manage and reduce habitat and biodiversity loss. There are some human pressures, such as overfishing, which must be tackled through different management measures, such as reduction of effort, but there are still many issues where MPA networks can help. Mora & Sale (2011) go on to describe the lack of connectivity between MPAs, and the single focus of sites (e.g. fish stock protection) that reduce their effectiveness in protecting against a broad range of threats, as being a major barrier to their usefulness. Thus, there is a need to find both additional means of protecting habitats and species and to continue to improve designation of MPA sites within a network.

In the face of a changing environment, connectivity of species and systems will naturally change. Thus there is a clear need for adaptive capability in network designations. Given this, designations at any given time need to account for a number of key factors that include: the dispersal potential of the species involved; the habitat requirements of those species and the distribution and rarity of those habitats; and the hydrography of the area and site-specific conditions. Designations should occur within regional sea areas where major hydrographical barriers define the boundaries of those areas, and it is critical that individual countries communicate with neighbouring countries to account for connectivity that goes beyond their jurisdictional areas. Continued efforts to understand ecological coherence should also focus on viability and the level of recruitment required to maintain viable populations of a range of species representative of native biodiversity. In terms of ecological connectivity, there is still room for increases in understanding but the rate of knowledge growth in this area has increased considerably since this thesis began. Any further work on connectivity will benefit the field most with increased collaborations across scientific fields and better dissemination to policy makers and marine managers.

REFERENCES

Agardy MT (1994) Advances in marine conservation: the role of marine protected areas. TREE 9:267-270

Agardy T, di Sciara GN, Christie P (2011) Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar Pol 35:226-232

Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. Ecol Monogr 66:259-275

Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecol Apps 8:79-92

Ardron J (2008) The challenge of assessing whether the OSPAR network of marine protected areas is ecologically coherent. Hydrobiologia 606:45-53

Armsworth PR, James MK, Bode L (2001) When to press on or turn back: dispersal strategies for reef fish larvae. Amer Nat 157:434-450

Ballantine B (1999) Marine reserves in New Zealand: the development of the concept and the principles. Proceedings of the International Workshop on Marine Conservation for the New Millennium, Korean Ocean Research and Development Institute, Cheju Is. pp3-38

Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. Mol Ecol 11: 155-165

Balmford A, Gravestock P, Hockley N, McClean CJ, Roberts CM (2004) The worldwide costs of marine protected areas. Proc Nat Acad Sci USA 101:9694-9697

Barker MF, Nichols D (1983) Reproduction, recruitment and juvenile ecology of the starfish *Asterias rubens* and *Marthasterias glacialis*. J Mar Biol Ass UK 63:745-765

Barton NH, Slatkin M (1986) A Quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. Heredity 56:409-415

Bates, D 2005. Fitting linear mixed models in R. R News 5: 27.30

Bayne BL (1965) Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1-47

Beaumont AR, Morvan C, Huelvan S, Lucas A, Ansell AD (1993) Genetics of indigenous and transplanted populations of *Pecten maximus*: no evidence for the existence of separate stocks. J Exp Mar Biol Ecol 169: 77-88

Begon M, Harper JL, Townsend CR (1996) Ecology (3rd Ed.) Blackwell Science, Oxford, UK

Beukers-Stewart B, Mosley MWJ, Brand AR (2003) Population dynamics and predictions in the Isle of Man fishery for the great scallop (*Pecten maximus*, L.). ICES J Mar Sci 60:224-242

Beukers-Stewart B, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of closed area protection for a population of scallops. Mar Ecol Prog Ser 298:189-204

Boersma PD, Parrish JK (1999) Limiting abuse: marine protected areas, a limited solution. Ecol Econ 31: 287-304

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps and challenges. Mar Ecol Prog Ser 427:191-217

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277:509-515

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144-150

Bradbury IR, Snelgrove PVR (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. Can J Fish Aquat Sci 58:811-823

Bradbury IR, Laurel B, Snelgrove PVR, Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. Proc R Soc Lond B 275:1803-1809

Brand AR, Allison EH, Murphy E J (1991) North Irish Sea scallop fisheries: a review of the changes. In An International Compendium of Scallop Biology and Culture, pp. 204–218. Ed. by Shumway SE and Sandifer PA. World Aquaculture Society, Baton Rouge.

Brand AR (2000) North Irish Sea scallop (*Pecten maximus* and *Aequipecten opercularis*) fisheries: effects of 60 years of dredging on scallop populations and the environment. Alaska Department of Fish and Game, Division of Commercial Fisheries, Special Publication 14. pp. 37–43

Bullard SG, Whitlatch RB, Osman RW (2004) Checking the landing zone: Do invertebrate larvae avoid settling near superior spatial competitors? Mar Ecol Prog Ser 280: 239-247

Butman CA, Grassle JP, Webb CM (1988) Substrate choices made by marine larvae settling in still water and in a flume flow. Nature 333:771-773

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Envir 2:529-536

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Ann Rev Ecol Syst 27:477-500

Callaway R, Robinson L, Greenstreet SPR (2003) Methods Manual. MAFCONS Project report no: 2003:001: EC project number Q5RS-2002-00856. 83pp.

Chia FS (1989) Differential larval settlement of benthic marine invertebrates. In: Reproduction, genetics and distributions of marine organisms, 23rd European Marine Biology Symposium. Eds. Ryland JS & Tyler PA. pp. 3-12

Chiswell SM (2009) Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. II. Oceanographic connections. Mar Ecol Prog Ser 388: 121-135

Christie P, McCay BJ, Miller ML, Lowe C, White AT, Stoffle R, Fluharty DL, McManus LT, Chuenpagdee R, Pomeroy C, Suman DO, Blount BG, Huppert D, Eisma RLV et al (2003) Toward developing a complete understanding: A social science research agenda for marine protected areas. Fisheries 28(12):22-25

Clark CD, Hughes ALC, Greenwood SL, Jordan C, Sejrup HP (2010) Pattern and timing of retreat of the last British-Irish Ice Sheet. Quat Sci Rev XX:1-35

Comely CA, Ansell AD (1989) The reproductive cycle of *Echinus esculentus* L. on the Scottish west coast. Est Coast Shelf Sci 29:385-407

Connor DW, Gilliland PM, Golding N, Robinson P, Todd D, Verling E (2006) UKSeaMap: the mapping of seabed and water column features of UK seas. Joint Nature Conservation Committee, Peterborough

Cowen RK, Castro LR (1994) Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. Bull Mar Sci 54:228-244

Cowen RK, Lwiza KM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of Marine Populations: Open or Closed? Science 287:857-859

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold S, Werner F (2002) Population connectivity in marine systems. Report of a workshop to develop science recommendation for the National Science Foundation.

Cowen RK GG, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: an overview. Oceanography 20:14-21

Cowen RK, Sponaugle S (2008) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1: 443-466

Cragg SM (1980) Swimming behaviour of the larvae of *Pecten maximus* (L.) (Bivalvia). J Mar Biol Ass UK 60:551-564

Crimaldi JP, Thompson JK, Rosman JH, Lowe RJ, Koseff JR (2002) Hydrodynamics of larval settlement: the influence of turbulent stress events at potential recruitment sites. Limnol Oceanogr 47:1137-1151

Crisp DJ (1978) Genetic consequences of different reproductive strategies in marine invertebrates. In: Battaglia B, Beardmore JA (eds) Marine organisms: genetics, ecology and evolution. Plenum, New York, pp 257-27

Danancher D, Garcia-Vazquez E (2011) Genetic population structure in flatfishes and potential impact of aquaculture and stock enhancement on wild populations in Europe. Rev Fish Biol Fisheries 21:441-462

David P, Perdieu MA, Pernot AF, Jarne P (1997) Fine-grained spatial and temporal population genetic structure in the bivalve *Spisula ovalis*. Evolution 51:1318-1322

DEFRA (2010) Guidance on selection and designation of Marine Conservation Zones (Note 1). Department of Environment, Food and Rural Affairs, UK

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. TREE 13:77-81

DiBacco C, Chadwick DB (2001) Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California and nearshore coastal habitats using elemental fingerprinting. J Mar Res 59:53-78.

Dibacco C, Levin LA, Sala E. (2006) Connectivity in marine ecosystems: the importance of larval and spore dispersal. In: Crooks KR, Sanjayan M, editors. Connectivity conservation. Cambridge: Cambridge University Press; 2006. p. 184-212

Dixon JA, Scura LF, van't Hof T (1993) Meeting ecological and economic goals: Marine parks in the Caribbean. Ambio 22:117-125

Earl DA (2011) Structure harvester v0.6.1. Available at: http://taylor0.biology.ucla.edu/struct_harvest/index.php (last accessed 10/08/11)

Eckman JE (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. J Exp Mar Biol Ecol 200:207-237

Ellis J, Rogers S, Freeman S (2000) Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel. Est Coast Mar Sci 51: 299-315

Ennis GP (1973) Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. J Mar Biol Ass UK 53:531-538

EC (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive)

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the sofware Structure: a simulation study. Mol Ecol 14:2611-2620

Excoffier L, Laval G, Schneider (2005) Arlequin v. 3.0: An Integrated software package for population genetics data analysis. Evol Bioinf Online 1:47-50

Faraway JJ (2006) Extending the linear model with R: Generalised linear, mixed effects and non-parametric regression methods. Chapman and Hall/CRC Boca Raton (pp 158-159)

FAO http://www.fao.org/fishery/species/3516/en (last accessed 23/08/11)

Frid CLJ, Harwood KG, Hall SJ, Hall JA (2000) Long-term changes in the benthic communities in North Sea fishing grounds. ICES J Mar Sci 57:1303-1309

Gaffney PM, Scott TM, Koehn RK, Diehl WJ (1990) Interrelationships of Heterozygosity, Growth Rate and Heterozygote Deficiencies in the Coot Clam, *Mulinia lateralis*. Genetics 124:687-699

Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Acad Nat Sci USA 82:3707–3711

Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. Ecol Apps 13: 32-46

Gaines SD, White C, Carr MH, & Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. PNAS 43:18286-18293

Galindo HM, Olson DB, Palumbi SR (2006) Seascape genetics: A coupled oceanographic-genetic model predicts population structure of caribbean corals. Curr Biol 16:1622-1626

Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, et al. (2009) Pelagic protected areas: the missing dimension in ocean conservation. TREE 24:360–9

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-Term Region-Wide Declines in Caribbean Corals. Science 301:958-960

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Amer Nat 155:769

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. TREE 18:448-455

Gerber LR, Botsford LW, Hastings A, Possingham HP, Gaines SD, Palumbi SR, Andelman S (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecol Apps 13:S47-S64

Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: Coupling genetics with fine-scale physical oceanography. Ecology 84: 2989-2998

Giovanni online data system developed and maintained by the NASA GES DISC. http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month

Glaubitz JC (2004) CONVERT: A user-friendly program to reformat diploid genotypic data for commonly used population genetic software packages. Mol Ecol Notes 4:309-310

Goldstein SJ, Gemmell NJ, Schiel DR (2009) Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. I. Genetic Connections. Mar Ecol Prog Ser 388:111-119

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www.unil.ch/izea/softwares/fstat.html

Graham KR, Sebens KP (1996) The distribution of marine invertebrate larvae near vertical surfaces in the rocky subtidal zone. Ecology 77:933-949

Grantham BA, Eckert GL, Shanks AL (2003) Dispersal potential of marine invertebrates in diverse habitats. Ecol Apps 13:108-116

Grassle JP, Butman CA, Mills SW (1992) Active habitat selection by *Capitella* sp. I larvae. 11. Multiple-choice experiments in still water and flume flows. J Mar Res 50:717-743

Gruffydd LD, Beaumont AR (1972) A method for rearing *Pecten maximus* larvae in the laboratory. Mar Biol 15:350-355

Hall-Spencer JM, Tasker M, Soffker M, Christiansen S, Rogers S, Campbell M, Hoydal K (2009) Design of Marine Protected Areas on high seas and territorial waters of Rockall Bank. Mar Ecol Prog Ser 397:305-308

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc B 270:1871-1878

Hansson L (1991) Dispersal and connectivity in metapopulations. Biol J Linn Soc 42:89-103

Harley CDG, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Hart DR (2006) When do marine reserves increase fishery yield? Can J Fish Aquat Sci 63:1445–1449

Hartnoll RG (1967) An investigation of the movement of the scallop *Pecten maximus*. Helg Mar Res 15:523-533

Hartnoll RG (1975) The annual cycle of *Alcyonium digitatum*. Est Coast Mar Sci 3:71-72

Hauser L, Adcock GJ, Smith PJ, Bernal Ramirez JH, Carvalho GR (2002) Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). PNAS 99:11742-11747

Hedgecock D (1994) Does variance in reproductive success limit effective population size of marine organisms? Pp. 122–134 in *Genetics and Evolution of Aquatic Organisms*. A. Beaumont, ed., Chapman & Hall, London.

Heipel DA, Bishop JDD, Brand AR (1999) Mitochondrial DNA variation among open-sea and enclosed populations of the scallop Pecten maximus in western Britain. J Mar Biol Assoc UK 79:687-695

Hendrick VJ, Foster-Smith RL (2006) Sabellaria spinulosa reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. J Mar Biol Assoc UK 86:665-677

Hilbish TJ, Koehn RK (1985) Dominance in physiological phenotypes and fitness at an enzyme locus. Science 229:52-54

Hoegh-Guldberg O, Pearse J (1995) Temperature, food availability, and the development of marine invertebrate larvae. Amer Zool 35:415-425

Hoarau G, Rijnsdorp AD, van der Veer HW (2002) Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large-scale spatial and temporal homogeneity. Mol Ecol 11:1165–1176

Howson CM, Picton BE (1997) The species directory of the marine fauna and flora of the British Isles and surrounding seas. Ulster Museum, Belfast and The Marine Conservation Society, Ross-on-Wye

Hubisz M, Falush D, Stephens M, Pritchard J (2009) Inferring weak population structure with the assistance of sample group information. Mol Ecol Res 9:1322-1332

Hutchison WF, Carvalho GR, Rogers SI (2001) Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Mar Ecol Prog Ser 223: 251-260

Jablonski D & Lutz RA (1983) Larval ecology of marine benthic invertebrates: paleoecological implications. Biol Rev 58:21-89

Jackson JBC (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species distributions and genetic structure of local populations. Bull Mar Sci 39: 588-606

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001)

Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293:629-637

James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: modeling larval dispersal and retention patterns. Proc Biol Sci 269:2079-86

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201-352

Johnson MP (2005) Is there confusion over what is meant by 'open population'? Hydrobiol 544:333-338

Johnson MS, Black R (1995) Neighbourhood size and the importance of barriers to gene flow in an intertidal snail. Heredity 75:142-154

Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. Current biology 15:1314-1318

Jones PJS, Carpenter A (2009) Crossing the divide: The challenges of designing an ecologically coherent and representative network of MPAs for the UK. Marine Policy 33:737-743

Jørstad KE, Prodöhl PA, Kristiansen TS, Hughes M, Farestveit E, Taggart JB, Agnalt A-L, Ferguson A (2005) Communal larval rearing of European lobster (*Homarus gammarus*): Family identification by microsatellite DNA profiling and offspring fitness comparisons. Aquaculture 247:275-285

Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. Ecol Apps 17:1039–1054

Kenchington EL, Patwary MU, Zouros E, Bird CJ (2006) Genetic differentiation in relation to marine landscape in a broadcast-spawning bivalve mollusc (*Placopecten magellanicus*). Mol Ecol 15: 1781-1796

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007-2020

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Diversity Distrib 11:139-148

Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S, Richards A, Ouellet P, Orr D, Skúladóttir U, Wieland K, Savard L, Aschan M (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the north Atlantic Ocean. Science 324:791-793.

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecol Apps 13: s71-s89

Launey S, Ledu C, Boudry P, Bonhomme F, Naciri-Graven Y (2002) Geographic structure in the European Flat Oyster (*Ostrea edulis* L.) as revealed by microsatellite polymorphism. J Heredity 93:331-351

Leathwick JR, Moilanen A, Francis M, Elith J, Taylor P, Julian K, Hastie T (2008) Novel methods for the design and evaluation of marine protected areas in offshore waters. Conserv Lett 1:91–102

Lee AJ, Ramster JW (1981) Atlas of the Seas around the British Isles. Ministry of Agriculture, Fisheries and Food, Ordnance Survey, Southampton.

Leis JM (1991) Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. Mar Biol 109:157-166

Le Pennec M, Paugam A, Le Pennec G (2003) The pelagic life of the pectinid *Pecten maximus* - a review. ICES J Mar Sci 60:211–223

Leslie HM (2005) A synthesis of marine conservation planning approaches. Conserv Biol 19:1701–1713

Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. Integr Comp Biol 46:282-297

Lewin R (1986) Supply-Side Ecology. Science 234:25-27

Li G, Hubert S, Bucklin K, Ribes V, Hedgecock D (2003) Characterization of 79 microsatellite DNA markers in the Pacific oyster *Crassostrea gigas*. Mol Ecol Notes 3:228–232

Lind CE, Evans BS, Taylor JJU, Jerry DR (2007) Population genetics of a marine bivalve, *Pinctada maxima*, throughout the Indo-Australian Archipelago shows differentiation and decreased diversity at range limits. Mol Ecol 16:5193–5203

Lubchenco J, Allison GW, Nararrete SA, Mange BA, Castilla JC, Defeo O, Folke C, Kussakin O, Norton T, Wood AM (1995) Biodiversity and ecosystem functioning: Coastal Systems *in* United Nations Environment Programme, Global Diversity Assessment. Cambridge University Press, Cambridge, UK

Lubchenco JP, Palumbi SR, Gaines SD, Andelman S (2003) (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecol Apps. 13:s3-s7

Lui J, Taylor WW (2002) Integrating landscape ecology into natural resource management. Cambridge University Press

Luttikhuizen PC, Drent J, Baker AJ (2003) Disjunct distribution of highly diverged mitochondrial lineage clade and population subdivision in a marine bivalve with pelagic larval dispersal. Mol Ecol 12:2215-2229

Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, Olsen J, Perez KE, Stam W, Väinölä R, Viard F, Wares J (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology 89:S108-S122

Maier-Reimer E (1980) On the formation of salt wedges in estuaries In: Sundermann J and Holz KP (Eds) Mathematical modelling of estuarine physics. Springer-Verlag

Mackie LA, Ansell AD (1993) Differences in reproductive ecology in natural and transplanted populations of *Pecten maximus*: evidence for the existence of separate stocks. J Mar Biol Ecol UK 169:57-75

Magnesen T, Christophersen G (2008) Reproductive cycle and conditioning of translocated scallops (*Pecten maximus*) from five broodstock populations in Norway. Aquaculture 285:109-116

Man A, Law R, Polunin NVC (1995) Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biol Conserv 71:197-204

Manoukis NC (2007) FORMATOMATIC: A program for converting diploid allelic data between common formats for population genetic analysis. Mol Ecol Notes 7:592 - 593

MarLIN (Marine Life Information Network) (2009) *Marine Life Information Network.* Plymouth: Marine Biological Association of the United Kingdom. Available from: www.marlin.ac.uk

Marshall DJ, Monro K, Bode M, Keough MJ, Swearer S (2010) Phenotype-environment mismatches reduce connectivity in the sea. Ecol Lett 13:128-140

Mora C, Sale PF (2010) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. Mar Ecol Prog Ser 434:251-266

Moraga D, Tanguy A (2000) Genetic indicators of herbicide stress in the Pacific oyster *Crassostrea gigas* under experimental conditions. Environ Toxicol Chem 19:706-711

Morgan SG, Fisher JL (2010) Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. Mar Ecol Prog Ser 404:109-126

Murray SN, Ambrose RF, Bohnsack JA, Botsford LW, Carr MH, Davis GE, Dayton PK, Gotshall D, Gunderson DR, Hixon MA, Lubchenco J, Mangel M, MacCall A, McArdle DA, Ogden JC, Roughgarden J, Starr RM, Tegner MJ, Yoklavich MM (1999) No-take Reserve Networks: Sustaining Fishery Populations and Marine Ecosystems. Fisheries 24:11-25

Naveh Z, Lieberman AS (1984) Landscape ecology: theory and application. Springer, New York.

Neill SP, Kaiser MJ (2008) Sources and sinks of scallops (*Pecten maximus*) in the waters of the Isle of Man as predicted from particle tracking models. Fisheries & Conservation report No. 3, Bangor University

Nellis P, Bourget E (1996) Influence of physical and chemical factors on settlement and recruitment of the hydroid *Tubularia larynx*. Mar Ecol Prog Ser 140:123-139

Nichols JH, Bennett DB, Symonds DJ, Grainger R (1982) Estimation of the stock size of adult Nephrops norvegicus (L.) from larvae surveys in the western Irish Sea in 1982. J Nat Hist 21:1433-1450

Nikolakaki P (2004) A GIS site-selection process for habitat creation: estimating connectivity of habitat patches. Landsc Urb Plan 68:77-94

Norman CP, Jones MB (1993) Reproductive ecology of the velvet swimming crab, *Necora puber* (Brachyura: Portunidae), at Plymouth. J Mar Biol Ass UK 73:379-389

North E, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS (2008) Vertical swimming behaviour influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar Ecol Prog Ser 359: 99-115

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci USA 104:1266–1271

Oliver JK, King BA, Willis BL, Babcock RC, Wolanski E (1992) Dispersal of coral larvae from a lagoonal reef II. Comparisons between model predictions and observed concentrations. Con Shelf Res 12: 873-889

Olson RR (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. Ecology 66:30-39

OSPAR (2003) OSPAR Convention for the Protection of the Marine Environment of the Northeast Atlantic. Recommendation 2003/3 on a Network of Marine Protected Areas. OSPAR 03/17/1-E; Annex 9

OSPAR (2006) OSPAR Convention for the Protection of the Marine Environment of the Northeast Atlantic. Guidance on developing an ecologically coherent network of OSPAR Marine Protected Areas. BDC 06/3/7

OSPAR (2007) OSPAR Convention for the Protection of the Marine Environment of the Northeast Atlantic. Background Document to Support the Assessment of Whether the OSPAR Network of Marine Protected Areas is Ecologically Coherent. ICGMPA 07/03/01-rev.

Palumbi SR (1992) Marine speciation on a small planet. TREE 7:114-118

Palumbi SR (1994) Genetic Divergence, Reproductive Isolation, and Marine Speciation. Annu Rev Ecol System 25:547-572

Palumbi SR (1996) What can molecular genetics contribute to marine biogeography? An urchin's tale. J Exp Mar Biol Ecol 203:75-92

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Apps 13:146-158

Palumbi SR (2004) Marine reserves and ocean neighbourhoods: the spatial scale of marine populations and their management. Annu Rev Environ Resour 29: 31-68

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limonol Oceanog 49:1964-1979

Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity Mar Ecol Prog Ser 347: 285-300

Park SDE (2001) Trypanotolerance in West African cattle and the population genetic effects of selection. Ph.D. thesis, University of Dublin

Parry DM, Kendall MA, Pilgrim DA, Jones MB (2003) Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. J Exp Mar Biol Ecol 285:497-511

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing Down Marine Food Webs. Science 279:860-863

Pawlik J (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

Pedersen OP, Aschan M, Rasmussen T, Tande KS, Slagstad D (2003) Larval dispersal and mother populations of *Pandalus borealis* investigated by a Lagrangian particle-tracking model. Fish Res 65:173–90

Petersen CGJ (1918) The sea bottom and its production of fish food. A survey of the work done in connection with valuation of the Danish waters from 1883–1917. Rep Danish Biol Stat 25:1–61

Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean: consequences for population connectivity. Oceanography 20:22-39

Pineda J, Reyns N, Starczak V (2009) Complexity and simplification in understanding recruitment in benthic populations. Pop Ecol 51:17-32

Pittman SJ, Kneib RT, Simenstad CA (2011) Practicing coastal seascape ecology. Mar Ecol Prog Ser 427:187-190

POLPRED (v 2.0) Proudman Oceanographic Laboratory, Liverpool

Pritchard JK SM, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945-959

R Development Core Team 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramster JW, Hill HW (1969) Current system in the northern Irish Sea. Nature 224: 59 -61

Ridgeway GMI, Dahle G (2000) Population genetics of Pecten maximus of the Northest Atlantic coast. Sarsia 85:167-172

Riginos C, Nachman MW (2001) Population subdivision in marine environments: the contributions of isolation by distance, discontinuous habitat, and biogeography to genetic differentiation in a blennioid fish, *Axoclinus nigricaudus*. Mol Ecol 10: 1439-1453

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fish 1:65-91

Roberts CM, Halpern B, Palumbi SR, Warner RR (2001) Designing marine reserve networks: why small, isolated protected areas are not enough. Conserv Pract 2:10-17

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280-1284

Roberts CM, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie H, Lubchenco J, McArdle D, Ruckelshaus M, Warner RR (2003) Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecol Apps 13:215-228

Roberts CM, Hawkins JP, Fletcher J, Hands S, Raab K, Ward S (2010) Guidance on the size and spacing of Marine Protected Areas in England. Natural England Commissioned Report NECR037

Roff JC, Taylor ME (2000) National frameworks for marine conservation – a hierarchical geophysical approach. Aquat Conserv Mar Freshwat Ecosyst 10:209-223

Roughgarden J, Isawa Y, Baxter C (1985) Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54–67

Rousset F (2008) Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Mol Eco Res 8:103-106

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. Science 298:1991–1993

Sale PF, Kritzer JP (2003) Determining the extent and spatial scale of population connectivity: decapods and coral reef fishes compared. Fish Res 65:153-172

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trend Ecol Evol 20:74-80

Sambrook J, Russel DW (2001) Molecular Cloning: a Laboratory Manual. Cold Spring Harbor Laboratory Press, New York.

Scheltema RS (1971) Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol Bull 140:284-322

Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull Mar Sci 39:290-322

Scheltema RS (1988) Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the East Pacific Barrier. Biol Bull 174:145-152

Selkoe KA, Henzler CM, Gaines SD (2008) Seascape genetics and the spatial ecology of marine populations. Fish & Fisheries 9:363-377

Selkoe KA, Watson JR, White C, Horin TB, Iacchei M, Mitarai S, Siegel DA, Gaines SD, Toonen RJ (2010) Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. Mol Ecol 19:3708-3726

Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. (Ed. LR McEdward) in. Ecology of marine invertebrate larvae. CRC. Boca Raton, Florida, USA. pp 324–367

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Apps 13:159-169

Sinclair M (1988) Marine Populations: An Essay on Population Regulation and Speciation. Washington Sea Grant Program, Seattle

Skole D, Tucker C (1993) Tropical Deforestation and Habitat Fragmentation in the Amazon: Satellite Data from 1978 to 1988. Science 260:1905-1910

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236:787-792

Smith JA, Damm PE, Skogen MD, Flather RA, Pätsch J (1996) An investigation into the variability of circulation and transport on the north-west European shelf using three hydrodynamic models. Ocean Dynamics 48:325-348

Sotka EE, Wares JP, Barth JA, Grosberg RK, Palumbi SR (2004) Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. Mol Ecol 13:2143-2156

Star B, Apte S, Gardner JPA (2003) Genetic structuring among populations of the greenshell mussel *Perna canaliculus* revealed by analysis of randomly amplified polymorphic DNA *ktA. Mar Ecol Prog Ser 249:171-182

Strathmann RR, Hughes TP, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002) Evolution of local recruitment and its consequences for marine populations. Bull Mar Sci 70:377–396.

ter Hofstede R, Hiddink JG, Rijnsdorp AD (2010) Regional warming changes fish species richness in the eastern North Atlantic Ocean. Mar Ecol Prog Ser 414:1-9

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145-148

Thorpe JP, Sole-Cava AM, Watts PC (2000) Exploited marine invertebrates: genetics and fisheries. Hydrobiologia 420: 165-184

Thorson G (1946) Reproduction and larval development of Danish marine bottom invertebrates. Med Komm Hovunder Serie Plankton 4:1–523

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Todd CD (1998) Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375/376:1-21

Trakhtenbrot A, Nathan R, Perry G et al (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181

Troll C (1971) Landscape ecology (geoecology) and biogeocenology– a terminology study. Geoforum 2:43–46

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171-197

Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell GA (1999) Fishing impacts and the degradation or loss of habitat structure. Fish Manag Ecol 6:401-420

UKCIP (2009) http://ukclimateprojections.defra.gov.uk/ Last accessed 26/11/10

Valanko S, Norkko A, Norkko J (2010) Strategies of post-larval dispersal in non-tidal soft-sediment communities. J Exp Mar Biol Ecol 384: 51-60

van der Molen J, Rogers SI, Ellis JR, Fox CJ, McCloghrie P (2007) Dispersal patterns of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. J Sea Res 58: 313-330

van Djik JK, van Tussenbroek BI, Jimenez-Duran K, Marquez-Guzman GJ, Ouborg J (2009) High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. Mar Ecol Prog Ser 390: 67-77

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4: 535–538

Vincent MA, Atkins SM, Lumb CM, Golding N, Lieberknecht LM, Webster M (2004) Marine nature conservation and sustainable development - the Irish Sea Pilot. (Report to DEFRA). Peterborough: Joint Nature Conservation Committee.

Walsh PS, Metzger DA, Higuchi R (1991) Chelex-100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Biotechniques 10:506-513.

Waples RS, Punt AE, Cope JM (2008) Integrating genetic data into management of marine resources: how can we do it better? Fish and Fisheries 9:423-449

Warner RR & Cowen RK (2005) Local retention of production in marine populations: evidence, mechanisms and consequences. Bull Mar Sci 70:245-249

Was A, Gosling E, Hoarau G (2010) Microsatellite analysis of plaice (*Pleuronectes platessa* L.) in the NE Atlantic: weak genetic structuring in a milieu of high gene flow. Mar Biol 157:447-462

Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conserv Biol 12:1180-1197

Watts PC, Mallanaphy WJ, McCarthy C, Beukers-Stewart BD, Mosley MWJ, Brand AR, Saccheri IJ (2005) Polymorphic microsatellite loci isolated from the great scallop, *Pecten maximus* (Bivalvia : Pectinidae). Mol Ecol Notes 5:902-904

Weetman D, Hauser L, Bayes MK, Ellis JR, Shaw PW (2006) Genetic population structure across a range of geographic scales in the commercially exploited marine gastropod *Buccinum undatum*. Mar Ecol Prog Ser 317:157-169

Weetman D, Ruggiero A, Mariani S, Shaw PW, Lawler AR, Hauser L (2007) Hierarchical population genetic structure in the commercially exploited shrimp *Crangon crangon* identified by AFLP analysis. Mar Biol 151: 565-575

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358-1370.

Werner FE, Cowen RK, Paris CB (2007) Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. Oceanography 20:54-69

Wilding CM, Latchford JW, Beaumont AR (1998) An investigation of possible stock structure in *Pecten maximus* (L.) using multivariate morphometrics, allozyme electrophoresis and mitochondrial DNA polymerase chain reaction-restriction fragment length polymorphism. J Shell Res 17:131-139

White JW, Botsford LW, Hastings A, Largier JL (2009) Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. Mar Ecol Prog Ser 398:49-67

Wright S (1951) The genetic structure of populations. Ann Eugen 15: 323-354

Young CM (1990) Larval ecology of marine invertebrates: a sesquicentennial history. Ophelia 32:1-48

Zouros E, Foltz DW (1984) Possible explanations of heterozygote deficiency in bivalve molluscs. Malacologia 25:583-591

APPENDIX 1

Development type and time of 102 taxa typical of a UK shelf benthic invertebrate assemblage. Development type was classified as: Benthic-Associated Non-Feeding (BANF); Direct Development (DD); Lecithotrophic (L); or Planktotrophic (P). Development time (used as a proxy for PLD) was compiled for a range of temperatures (6°C to ≥16°C) if available, or a range based on available data. A final time for each species was calculated (1) if a time was available at 8-13°C, otherwise (2) times outside this temperature limit. At temperatures ≥13°C the longest time was used as development is inversely related to temperature. Where temperature was not specified, a time in the middle of a range was used.

		Development time (days) at a range of temperatures (°C)													
Taxon	**Development Type**	**Not specified**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**≥16**	**Final Time**	**References**
Aphrodita aculeata	DD													**0**	Thorson, 1946
Lanice conchilega	P	60												**60**	McHugh, 1993
Lygdamis muratus	P											42	30-42	**42**	Wilson, 1977
Sabellaria spinulosa	P	40-60												**50**	Wilson, 1970
Alcyonidium diaphanum	BANF	≤ 1												**1**	Potter, 2001
Bryozoa	BANF													**2**	Hayward & Ryland, 1995
Flustra foliacea	BANF	≤ 1												**1**	Hayward & Ryland, 1996
Pentopora foliacea	BANF	≤ 1												**1**	Hayward & Ryland, 1995; Keough & Chernoff, 1987
Ascidians	BANF	≤ 1												**1**	McHenry, 2005
Ascidiella scabra	BANF	≤ 1												**1**	McHenry, 2005
Ciona intestinalis	BANF										1-5			**2**	Havenhand & Svane, 1991
Abietinaria filicula	BANF	≤ 1												**1**	Boero, 1984
Actinauge richardi	P														Hayward & Ryland, 1995

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Alcyonium digitatum	L	2-10												**10**	Hartnoll, 1975
Calliactis parasitica	P													**30**	Chia, 1976
Caryophyllia smithii	P											56-70		**70**	Tranter et al., 1982
Epizoanthus incrustatus	BANF	≤ 1												**1**	Ryland et al., 2000
Hydrallmania falcata	BANF	≤ 1												**1**	Hayward & Ryland, 1995; Henry & Kenchington, 2004
Hydroids	BANF	≤ 1												**1**	Boero, 1984
Lafoea dumosa	BANF														Hayward & Ryland, 1995
Metridium senile	P													**60**	Hoffman, 1987
Pennatula phosphorea	L														Edwards & Moore, 2008
Stomphia coccinea	P								8-16					**16**	Sadro, 2005; Siebert, 1973
Tubularia larynx	BANF	2-4												**3**	Nellis & Bourget, 1996
Urticina eques	L								11-27					**27**	Chia & Spaulding, 1972
Anapagurus laevis	P	≤ 39												**39**	see *Pagurus prideauxi*
Atelecyclus rotundatus	P						82-136					48-89		**82**	Hong & Ingle, 1987
Balanus	P														Pyefinch, 1948
Balanus crenatus	P														Pyefinch, 1949
Cancer pagurus	P	60-180					----------30-60----------							**120**	Nichols et al, 1982, Ungfors, 2007

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Carcinus maenas	P											39-41		**41**	Mohamedeen & Hartnoll, 1989
Corystes cassivelaunus	P	60												**60**	Ingle & Rice, 1971
Crangon allmanni	P					68.7			36.2					**52**	Criales & Anger, 1986
Crangon crangon	P								35-42					**42**	Temming & Damm, 2002
Eualus gaimardii	P														Hayward & Ryland, 1995
Galathea squamifera	P											50		**50**	Christiansen & Anger, 1990
Geryon trispinosus	P											38		**38**	Ingle, 1979
Homarus gammarus	P												14-21	**21**	Jørstad et al 2005
Hyas coarctatus	P		108			68			46			36.5	30	**80**	Anger, 1984
Inachus dorsettensis	P	30-46												**38**	Lebour, 1927
Liocarcinus depurator	P								48-64					**56**	Choy, 1991
Liocarcinus holsatus	P								48-64					**56**	Choy, 1991
Lithodes maja	L					45-51								**48**	Anger, 1996
Macropodia spp.	P	>30												**30**	Lebour, 1927
Maja squinado	P	>30												**30**	Lebour, 1927
Munida sarsi	P														Hartnoll et al., 1991

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Necora puber	P								55-73					**64**	Choy, 1991
Nephrops norvegicus	P													**47**	Dickey-Collas et al., 2000
Pagurus bernhardus	P		107-112						49-54				33-35	**80**	Dawirs, 1979
Pagurus prideauxi	P												18-39	**39**	Goldstein & Bookhout, 1972
Pandalus montagui	P		10-16			7-10			6-8					**10**	Schultze & Anger, 1997
Processa canaliculata	P													**30**	Gurney, 1923
Spirontocaris lilljeborgi	P														Lebour, 1937
Amphiura chiajei	P												8	**8**	Fenaux, 1970
Anseropoda placenta	DD													**0**	Guilllou & Diop, 1988
Asterias rubens	P	87-100												**87**	Barker & Nichols, 1983
Astropecten irregularis	P													**25**	Benitez-Villalobos, 2005; Newth, 1925
Brissopsis lyrifera	P													**39**	see *Echinocardium chordatum*
Crossaster papposus	L	19-20												**20**	Gemmill, 1920
Echinocardium cordatum	P	39											15-24	**39**	Kashenko, 1994; Nunes & Jangoux, 2007

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Echinus esculentus	P	45-60											21-23	**52**	Jimmy et al., 2003; MacBride 1903
Leptasterias muelleri	DD													**0**	Britt & Petersen, 1982
Luidia ciliaris	P	≤ 120												**120**	Mortensen, 1913
Marthasterias glacialis	P	127-141												**127**	Barker & Nichols, 1983
Ophiothrix fragilis	P													**21**	Morgan & Jangoux, 2005
Ophiura albida	P	28-56												**42**	Tyler, 1976; Tyler pers. comm.
Ophiura ophiura	P	28-56												**42**	Tyler, 1976; Tyler pers. comm.
Porania pulvillus	P	56												**56**	Gemmill, 1915
Psammechinus miliaris	P												28	**28**	Kelly et al., 2000
Solaster endeca	L														Britt & Petersen 1982; Gemmill, 1912
Spatangus purpureus	P	21												**21**	Mortensen, 1913
Spatangus raschi	P														Rees, 1953
Stichastrella rosea	P														Benitez-Villalobos, 2005
Strongylocentrotus droebachiensis	P					24-39								**32**	Hart & Scheibling, 1988
Acanthocardia spp	P	≤ 21												**21**	Creek, 1960
Aequipecten opercularis	P	21-35												**28**	Brand et al., 1980; MacLeod et al., 1985
Antalis entalis	P	6												**6**	Jones & Baxter, 1987

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Aporrhais pespelecani	P														Lebour, 1933
Aporrhais serresianus	P														Lebour, 1934
Archidoris pseudoargus	P													**90**	Thompson, 1966
Arctica islandica	P				----------55-60----------					32				**57**	Landers, 1976; Lutz et al., 1982
Astarte sulcata	P														Saleuddin, 1964
Buccinum undatum	DD													**0**	Martel et al., 1986
Colus gracilis	DD													**0**	inferred from *C. jeffrysianus* and *Buccinum undatum*
Colus jeffreysianus	L														Colman et al., 1986
Corbula gibba	P														Jensen, 1988
Crepidula fornicata	P											26-31		**31**	Pechenick & Lima, 1984
Dosinia exoleta	P														Hayward & Ryland, 1995
Eledone cirrhosa	DD													**0**	Collins et al., 2002
Mactra stultorum	P												16	**16**	Nakajima et al., 1997
Modiolus modiolus	P			----------11-30---------									19	**20**	Brown, 1984; de Schweinitz & Lutz, 1976
Mytilus edulis	P						30-60							**45**	Bayne, 1965
Neptunea antiqua	DD													**0**	Power & Keegan, 2001
Ostrea edulis	P										49		26	**49**	Davis & Calabrese, 1969

Appendix 1 continued...

Taxon	Development Type	Development time (days) at a range of temperatures (°C)												Final Time	References
		Not specified	6	7	8	9	10	11	12	13	14	15	≥16		
Pecten maximus	P						----------25--------						16-38	**25**	Gruffydd & Beaumont, 1972; Lui et al., 2007; Paulet et al., 1988
Philine aperta	P								40	35				**40**	Hansen & Ockelmann, 1991
Sepiola atlantica	DD													**0**	Yau & Boyle, 1996
Spisula subtruncata	P														Gaspar & Monteiro, 1999
Axinella	L														Hayward & Ryland, 1995
Halichondria bowerbanki	BANF													**2**	Amano, 1986; Woollacott, 1990
Halichondria panicea	BANF													**2**	Amano, 1986; Woollacott, 1990
Porifera	BANF													**2**	Amano, 1986; Hayward & Ryland, 1995; Woollacott, 1990

REFERENCES

Amano S (1986) Larval release in response to a light signal by the intertidal sponge *Halichondria panicea*. Biol Bull 171:371-378

Anger K (1984) Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda, Majidae) reared in the laboratory. Mar Ecol Prog Ser 19:115-123

Anger K (1996) Physiological and biochemical changes during lecithotrophic larval development and early juvenile growth in the northern stone crab, *Lithodes maja* (Decapoda: Anomura). Mar Biol 126:283-296

Barker MF, Nichols D (1983) Reproduction, recruitment and juvenile ecology of the starfish, *Asterias rubens* and *Marthasterias glacialis*. J Mar Biol Assoc UK 63:745-765

Bayne BL (1965) Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1-47

Benitez-Villalobos F (2005) Reproduction and larval biology of North Atlantic asteroids related to the invasion of the deep sea. PhD dissertation, University of Southampton, UK

Blanc A, Pinczon du Sel G, Daguzan J (1998) Habitat and diet of early stages of *Sepia officinalis* L. (Cephalopoda) in Morbihan Bay, France. J Moll Stud 64:263-274

Boero F (1984) The ecology of marine hydroids and effects of environmental factors: a review. Mar Ecol 5:93-118

Brand AR, Paul JD, Hoogesteger JN (1980) Spat settlement of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. J Mar Biol Ass UK 60:379-390

Britt I, Petersen F (1982) Breeding season and egg morphology of echinoderms in Balsfjorden, northern Norway. Sarsia 67:215-221

Chia FS, Spaulding JG (1972) Development and juvenile growth of the sea anemone, *Tealia crassicornis*. Biol Bull 142:206-218

Chia FS (1976) Sea anemone reproduction: patterns and adaptive radiations. In: Mackie GO (ed) Coelenterata ecology and behaviour, pp.261-270. Plenum Press, New York

Choy SC (1991) Embryonic and larval biology of *Liocarcinus holsatus* and *Necora puber* (Crustacea: brachyura: portunidae). J Exp Mar Biol Ecol 148:77-92

Christiansen ME, Anger K (1990) Complete larval development of *Galathea intermedia* Lilljeborg reared in laboratory culture (Anomura: Galatheidae). J Crustac Biol 10:87-111

Colman JG, Tyler PA, Gage JD (1986) The reproductive biology of *Colus jeffreysianus* (Gastropoda: Prosobranchia) from 2200m in the N.E. Atlantic. J Molluscan Stud 52:45-54

Creek GA (1960) The development of the lamellibranch *Cardium edule* L. Proc Zool Soc Lond 135:243-260

Criales MM, Anger K (1986) Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. allmanni*. Helgol Mar Res 40:241-265

Davis HC, Calabrese A (1969) Survival and growth of larvae of the European oyster (Ostrea edulis L.) at different temperatures. Biol Bull 136: 193-199

Dawirs RR (1979) Effect of temperature and salinity on larval development of *Pagurus bernhardus* (Decapoda, Paguridae). Mar Ecol Prog Ser 1:323-329

de Schweinitz EH, Lutz RA (1976) Larval development of the northern horse mussel, *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. Biol Bull 150:348-360

Edwards DCB, Moore CG (2008) Reproduction in the sea pen *Pennatula phosphorea* (Anthozoa: Pennatulacea) from the west coast of Scotland. Mar Biol 155:303-314

Fenaux L (1970) Maturation of the gonads and seasonal cycle of the planktonic larvae of the Ophiuroid *Amphiura chiajei* Forbes. Biol Bull 138:262-271

Gaspar MB, Monteiro CC (1999) Gametogenesis and spawning in the subtidal white clam *Spisula solida*, in relation to temperature. J Mar Biol Assoc UK 79:753-755

Gemmill JF (1912) The development of the starfish *Solaster endeca* Forbes. Trans Zool Soc Lond 20:1-71

Gemmill JF (1915) The larva of the starfish *Porania pulvillus* (O.F.M.) Q J Microsc Sci 61:27-50

Gemmill JF (1920) Memoirs: The development of the starfish *Crossaster papposus*, Müller and Troschel. Q J Microsc Sci s2-64:155-187

Giangrande A (1997) Polychaete reproductive patterns, life cycles and life histories: an overview. Oceanogr Mar Biol Annu Rev 35:323–386

Goldstein B, Bookhout CG (1972) The larval development of *Pagurus prideauxi* Leach, 1814, under laboratory conditions (Decapoda, Paguridea). Crustaceana 23:263-281

Gruffydd LD, Beaumont AR (1972) A method for rearing *Pecten maximus* larvae in the laboratory. Mar Biol 15:350-355

Guillou M, Diop M (1988) Ecology and demography of a population of *Anseropoda placenta* (Echinodermata: Asteroidea) in the Bay of Brest, Brittany. J Mar Biol Ass UK 68:41-54

Gurney R (1923) The larval stages of *Processa canaliculata* Leach. J Mar Biol Ass UK 13:245-265

Hansen B, Ockelmann KW (1991) Feeding behaviour in larva of the opisthobranch *Philine aperta* I. Growth and functional response at different developmental stages. Mar Biol 111:255-261

Hart MW, Scheibling RE (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. Mar Biol 99:167-176

Hartnoll RG (1975) The annual cycle of *Alcyonium digitatum*. Est Coast Mar Sci 3:71-72

Hartnoll RG, Rice AL, Attrill MJ (1991) Aspects of the biology of the galatheid genus *Munida* (Crustacea, Decapoda) from the Porcupine Seabight, northeast Atlantic. Sarsia 76:231-246

Havenhand JN, Svane Ib (1991) Roles of hydrodynamics and larval behaviour in determining spatial aggregation in the tunicate *Ciona intestinalis*. Mar Ecol Prog Ser 68:271-276

Hayward PJ, Ryland JS (eds) (1995) Handbook of the marine fauna of northwest Europe. Oxford University Press

Henry LA, Kenchington ELR (2004) Ecological and genetic evidence for impaired sexual reproduction and induced clonality in the hydroid *Sertularia cupressina* (Cnidaria: Hydrozoa) on commercial scallop grounds in Atlantic Canada. Mar Biol 145:1107-1118

Hoffman RJ (1987) Short-term stability of genetic structure in populations of the sea anemone *Metridium senile*. Mar Biol 93:499-507

Hong SY, Ingle RW (1987) Larval development of the circular crab, *Atelecyclus rotundatus* (Olivi) (Crustacea: Brachyura: Atelecyclidae) reared in the laboratory. J Nat Hist 21:1539-1560

Ingle RW, Rice AL (1971) The larval development of the masked crab, *Corystes cassivelaunus* (Pennant) (Brachyura, Corystidae) reared in the laboratory. Crustaceana 20:271-284

Ingle RW (1979) The larval and post-larval development of the brachyuran crab *Geryon tridens* Krøyer (Family Geryonidae) reared in the laboratory. Bull Br Mus (Nat Hist) Zool **36**:217–232

Jensen, JN (1988) Recruitment, growth and mortality of juvenile *Corbula gibba* and *Abra alba* in the Limfjord, Denmark. Kieler Meeresforsch Sonderh 6:357-365

Jimmy RA, Kelly MS, Beaumont AR (2003) The effect of diet type and quantity on the development of common sea urchin larvae *Echinus esculentus*. Aquaculture 220:261-275

Jørstad KE, Prodöhl PA, Kristiansen TS, Hughes M, Farestveit E, Taggart JB, Agnalt AL, Ferguson A (2005) Communal larval rearing of European lobster (*Homarus gammarus*): Family identification by microsatellite DNA profiling and offspring fitness comparisons. Aquaculture 247:275-285

Jones AM, Baxter JM (1987) Molluscs: Caudofoveata, Solenogastres, Polyplacophora and Scaphopoda: keys and notes for the identification of the species. Brill, for the Linnean Society of London and the Estuarine and Brackish-Water Sciences Association, London

Kashenko SD (1994) Larval development of the heart urchin *Echinocardium cordatum* feeding on different macroalgae. Biol Morya 20:385-389.

Kelly MS, Hunter AJ, Scholfield CL, McKenzie JD (2000) Morphology and survivorship of larval *Psammechinus miliaris* (Gmelin) (Echinodermata: Echinoidea) in response to varying food quantity and quality. Aquaculture 183:223-240

Keough MJ, Chernoff H (1987) Dispersal and population variation in the Bryozoan *Bugula neritina*. Ecology 68:199-210

Landers WS (1976) Reproduction and early development of the ocean quahog, *Arctica islandica*, in the laboratory. Nautilus 90:88-92

Lebour MV (1927) Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity, with a description of the larval stages of *Inachus Dorsettensis*, *Macropodia longirostris* and *Maia squinado*. J Mar Biol Ass UK 14:795-821

Lebour MV (1933) The eggs and larvae of *Turritella communis* Lamarck and *Aporrhais pes-pelicani* (L.). J Mar Biol Ass UK 18:499-506

Lebour MV (1937) The newly hatched larva of *Spirontocaris spinus* (Sowerby) Var. *Lilljeborgi* Danielssen. J Mar Biol Ass UK 22:101-104

Liu H, Kelly MS, Campbell DA, Dong SL, Zhu JX, Wang SF (2007) Exposure to domoic acid affects larval development of king scallop *Pecten maximus* (Linnaeus, 1758). Aquat Toxicol 81:152-158

Lutz RA, Mann R, Goodsell JG, Castagna M (1982) Larval and early post-larval development of
Arctica islandica. J Mar Biol Ass UK 62:745-769

MacBride EW (1903) The development of *Echinus esculentus* together with some point on the development of *E. miliaris* and *E. acutus*. Philos Trans R Soc Lond B 195:285-330

Macleod JAA, Thorpe JP, Duggan NA (1985) A biochemical genetic study of population structure in queen scallop (*Chlamys opercularis*) stocks in the Northern Irish Sea. Mar Biol 87:77-82

Mangold K, Boletzky S, Frösch D (1971) Reproductive biology and embryonic development of Eledone cirrosa (Cephalopoda: Octopoda). Mar Biol 8:109-117

McHenry MJ (2005) The morphology, behaviour and biomechanics of swimming in ascidian larvae. Can J Zool 83:62-74

Martel A, Larivee DH, Klein KR, Himmelman JH (1986) Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. Mar Biol 92:211-221

McHugh D (1993) A comparative study of reproduction and development in the polychaete family Terebellidae. Biol Bull 185:153-167

Mohamedeen H, Hartnoll RG (1989) Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* (L.) J Exp Mar Biol Ecol 134:1-24

Morgan R, Jangoux M (2005) Larval morphometrics and influence of adults in settlement in the gregarious Ophiuroid *Ophiothrix fragilis* (Echinodermata). Biol Bull 208:92-99

Mortensen T (1913) On the development of some british echinoderms. J Mar Biol Ass UK 10:1-18

Nakajima K, Okumura H, Takabatake S (1997) Effect on growth and survival of reared larvae of Sunray surf clam, *Mactra chinensis* Philippi of single and mixed feeds of *Pavlova lutheri* and *Chaetoceros gracilis*. Sci Rep Hokkaido Fish Exp Stn 50:27-33

Nellis P, Bourget E (1996) Influence of physical and chemical factors on settlement and recruitment of the hydroid *Tubularia larynx*. Mar Ecol Prog Ser 140:123-139

Newth HG (1925) The early development of *Astropecten irregularis*, with remarks on duplicity in echinoderm larvae. Q J Microscop Sci 69:519–554

Nunes CDAP, Jangoux M (2007) Larval growth and perimetamorphosis in the echinoid *Echinocardium cordatum* (Echinodermata): the spatangoid way to become a sea urchin. Zoomorphology 126:103-119

Paulet YM, Lucas A, Gerard A (1988) Reproduction and larval development in two *Pecten maximus* (L.) populations from Brittany. J Exp Mar Biol Ecol 119:145-156

Pechenik JA, Lima GM (1984) Relationship between growth, differentiation, and length of larval life for individually reared larvae of the marine gastropod, *Crepidula fornicata*. Biol Bull 166:537-549

Porter JS, Hayward PJ, Spencer Jones ME (2001) The identity of *Alcyonidium diaphanum* (Bryozoa: Ctenostomatida). J Mar Biol Ass UK 81:1001-1008

Power AJ, Keegan BF (2001) Seasonal patterns in the reproductive activity of the red whelk, *Neptunea antiqua* (Mollusca: Prosobranchia) in the Irish Sea. J Mar Biol Ass UK 81:243-250

Pyefinch KA (1948) Methods of identification of the larvae of *Balanus balanoides* (L.), *B. Crenatus* Brug. and *Verruca stroemia* O. F. Müller. J Mar Biol Ass UK 27:451-463

Rees CB (1953) The Larvae of the Spatangidae. J Mar Biol Ass UK 32:477-490

Ryland JS, de Putron S, Scheltema RS, Chimonides PJ, Zhadan DG (2000) Semper's (zoanthid) larvae: pelagic life, parentage and other problems. Hydrobiologia 440:191-198

Sadro S (2001) Cnidaria (Coelenterata). In: Shanks A (ed) Identification guide to larval marine invertebrates of the Pacific Northwest, Oregon State University Press

Saleuddin ASM (1964) The gonads and reproductive cycle of *Astarte sulcata* (Da Costa) and sexuality of *A. elliptica* (Brown). *Proc Malacol Soc Lond* 36:141-148

Schultze K, Anger K (1997) Larval growth patterns in the Aesop Shrimp *Pandalus montagui*. J Crust Biol 17:472-479

Siebert AE (1973) A description of the sea anemone *Stomphia didemon* sp. nov. and its development. Pac Sci 27:363-376

Temming A, Damm U (2002) Life cycle of *Crangon crangon* in the North Sea: a simulation of the timing of recruitment as a function of the seasonal temperature signal. Fish Oceanogr 11:45-58

Thorson G (1946) Reproduction and larval development of Danish marine bottom invertebrates. Medd Kom Dan Fisk Havunders Plankton 4:1-523

Thompson TE (1966) Studies on the reproduction of *Archidoris pseudoargus* (Rapp) (Gastropoda Opisthobranchia) Philos Trans R Soc Lond B 250:343-374

Tranter PRG, Nicholson DN, Kinchington D (1982) A desctiption of spawning and post-gastrula development of the cool temperate coral, *Caryophyllia smithi*. J Mar Biol Assoc UK 62:845-854

Tyler PA (1976) The ecology and reproductive biology of the genus Ophiura with special reference to the Bristol Channel. PhD dissertation, University of Wales, UK

Wilson DP (1970) The larvae of *Sabellaria spinulosa* and their settlement behaviour. J Mar Biol Ass UK 50:33-52

Wilson DP (1977) The distribution, development and settlement of the Sabellarian polychaete *Lygdamis muratus* (Allen) near Plymouth. J Mar Biol Ass UK 57:761-792

Woollacott RM (1990) Structure and swimming behaviour of the larva of *Hallichondria melanodocia* (Porifera: Demospongiae) J Morphol 205:135-145

Yau C, Boyle PR (1996) Ecology of *Sepiola atlantica* (Mollusca: Cephalopoda) in the shallow sublittoral zone. J Mar Biol Ass UK 76:733-748

APPENDIX 2

Comparison of full linear mixed model containing the fixed effects of region, depth, distance from shore (DFS) and planktonic larval duration (PLD) and all their interactions, with simpler models. Station was included as a random factor nested within region. Loglik refers to the log likelihood and significant interactions are highlighted in bold.

		Bottom runs (1d, 3d)				Surface runs (2d, 6d, 20d, 42d, 90d)			
Model	**Interaction Removed:**	**loglik**	**X^2**	**Df**	**p-value**	**loglik**	**X^2**	**Df**	**p-value**
4-way		-73325				-146301			
3-way	4-way	-73370	89.898	3	**<2.2e^{-16}**	-147897	3193.6	12	**<2.2e^{-16}**
	Depth*DFS*PLD	-73372	4.2591	1	**0.03904**	-148331	867.74	4	**<2.2e^{-16}**
	Region*DFS*PLD	-73383	26.006	3	**9.51e^{-6}**	-152279	8762.3	12	**<2.2e^{-16}**
	Region*Depth*PLD	-73386	31.805	3	**5.753^{-7}**	-148599	1402.1	12	**<2.2e^{-16}**
	Region*Depth*DFS	-73373	6.9156	3	0.07464	-147899	3.6259	3	0.3048
2-way	3-way	-73454				-153842			
	Region*Depth	-73455	1.2365	3	0.7443	-153845	4.9643	3	0.1767
	Region*DFS	-73454	0.4634	3	0.9269	-153847	10.167	3	**0.0172**
	Region*PLD	-73565	221.89	3	**<2.2e^{-16}**	-166145	24606	12	**<2.2e^{-16}**
	Depth*DFS	-73454	0.4703	1	0.4929	-153844	3.7491	1	0.05284
	Depth*PLD	-73490	72.037	1	**<2.2e^{-16}**	-155754	3823	4	**<2.2e^{-16}**
	DFS*PLD	-73480	51.672	1	**6.56e^{-13}**	-154137	589.64	4	**<2.2e^{-16}**

APPENDIX 3

Habitat-landscape groupings of 79 common subtidal benthic invertebrates, determined by comparing species' habitat preference with marine landscape type (denoted by an *x*). Additionally, for each species development type (DT, defined in Appendix 1), Planktonic Larval Duration (PLD), dispersal distance (DD) category (High (H), Medium (M), Low (L)), and mean dispersal distance (km, based on dispersal scenarios in Chapter 2) is given for each species. Marine Landscapes 1-16 are defined at the end of this appendix.

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
All	*Cancer pagurus*	P	bedrock, cobbles, gravel, pebbles, sandy mud, muddy sand, fine clean sand, coarse clean sand, muddy gravel	Lower shore to 100m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	120	H	83.7
All	*Carcinus maenas*	P	All	Lower shore to 60m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	41	M	51.3
All	*Crepidula fornicata*	P	Small boulders, cobbles, pebbles, muddy gravel, gravel, fine clean sand, coarse clean sand, muddy sand, sandy mud, mud, mixed	0 to 60m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	31	M	51.3
All	*Marthasterias glacialis*	P	rock, mud, sand, gravel, mixed	0 to 180m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	127	H	83.7
All	*Modiolus modiolus*	P	bedrock, large to very large boulders, small boulders, gravel, muddy gravel, coarse clean sand, fine clean sand, sandy mud, muddy sand, mud, mixed	0 to 280m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	20	L	9.49
All	*Ostrea edulis*	P	bedrock, large to very large boulders, small boulders, gravel, cobbles, pebbles, muddy gravel, muddy sand, mud	0 to 80m	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	49	M	51.3

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
All but coarse	*Mytilus edulis*	P	bedrock, large to very large boulders, small boulders, muddy gravel, sandy mud, muddy sand, mixed	<100m	x	x				x	x	x	x	x				x	x	x	45	L	51.3
All but coarse	*Buccinum undatum*	DD	bedrock, large to very large boulders, small boulders, muddy gravel, coarse clean sand, fine clean sand, muddy sand	0 to 1200m	x	x				x	x	x		x				x		x	0	–	0
All but coarse	*Leptasterias muelleri*	DD	Bedrock, large to very large boulders, mixed	0 to 800m	x	x				x	x	x						x			0	–	0
All but mud	*Crossaster papposus*	L	pebbles,gravel, coarse clean sand, fine clean sand, mixed, gravelly sand	0 to 50m	x	x	x	x	x	x	x	x		x	x	x	x	x		x	20	H	28.4
All but mud	*Hyas coarctatus*	P	Sandy, hard, muddy sand and gravel	0 to 500m	x	x	x	x	x	x	x	x		x	x	x	x	x		x	80	H	83.7
All but mud	*Psammechinus miliaris*	P	Large to very large boulders, cobbles, muddy gravel, mixed, bedrock, small boulders, gravel, muddy sand	0 to 100m	x	x	x	x	x	x	x	x		x	x	x	x	x		x	28	M	51.3
All but rock	*Neptunea antiqua*	DD	Coarse clean sand, fine clean sand, sandy mud, muddy sand, mud, gravelly sand, gravelly mud	15 to 1200m			x	x	x	x	x	x	x	x	x	x	x	x	x	x	0	–	0
All but rock	*Ophiura ophiura*	P	Coarse clean sand, fine clean sand, sandy mud, muddy sand, mud, gravelly sand, gravelly mud				x	x	x	x	x	x	x	x	x	x	x	x	x	x	42	M	51.3

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
All but rock	*Pagurus prideauxi*	P	Muddy gravel, coarse clean sand, fine clean sand, sandy mud, muddy sand, mud, gravelly sand, sandy gravelly mud, gravelly mud	LWST to 90m			x	x	x	x	x	x	x	x	x	x	x	x	x	x	39	M	51.3
All but rock	*Pandalus montagui*	P	Muddy gravel, sandy mud, muddy sand, mud, mixed, gravelly sand, gravelly mud	4 to700m			x	x	x	x	x	x	x	x	x	x	x	x	x	x	10	L	9.49
All but rock	*Processa canaliculata*	P	Coarse clean sand, fine clean sand, muddy sand, mud, mixed, gravelly sand, muddy gravelly sand	5 to 200m			x	x	x	x	x	x	x	x	x	x	x	x	x	x	30	M	51.3
All but sand	*Alcyonidium diaphanum*	BA NF	Attached to boulders, stones, cobbles but also detached	LWST to 100m	x	x	x	x	x	x	x	x	x		x	x	x	x	x		1	L	1.28
All but sand	*Flustra foliacea*	BA NF	Bedrock, large to very large boulders, small boulders, cobbles, mixed	LWST to 200m	x	x	x	x	x	x	x	x	x		x	x	x	x	x		1	L	1.28
Aphotic Rock/Sand	*Hydrallmania falcata*	BA NF	Pebbles, coarse clean sand, fine clean sand	20 to 100m	x				x											x	1	L	1.28
Aphotic Rock/Sand	*Pentapora foliacea*	BA NF	bedrock, large to very large boulders, artificial	11-80m	x																1	L	1.28
Coarse/Mixed/Mud	*Acanthocardia spp*	P	Muddy gravel, mud, muddy sandy gravel, muddy gravelly sand				x	x	x	x	x	x	x		x	x	x	x	x		21	L	9.49
Coarse/Mixed/Mud	*Maja squinado*	P																			30	M	51.3
Coarse/Mixed/Sand	*Anapagurus laevis*	P	Gravel, muddy gravel, muddy sand, gravelly sand	20 to 200m			x	x	x	x	x	x		x	x	x	x	x		x	39	M	51.3
Coarse/Mixed/Sand	*Atelecyclus rotundatus*	P	Sand and gravel	12 to 300m			x	x	x	x	x	x		x	x	x	x	x		x	82	H	83.7

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
Coarse/ Mixed/Sand	*Spatangus purpureus*	P	Gravel, muddy gravel, coarse clean sand, muddy sand, gravelly sand	0 to 900m			x	x	x	x	x	x		x	x	x	x	x		x	21	L	9.49
Coarse/ Mud/Sand	*Corystes cassivelaunus*	P	Coarse clean sand, sandy mud, fine clean sand, muddy sand, gravelly sand	0 to 90m			x	x	x				x	x	x	x	x		x	x	60	M	51.3
Coarse/ Sand	*Aequipecten opercularis*	P	gravel, coarse clean sand, fine clean sand, muddy sand, gravelly sand	0 to 100m			x	x	x					x	x	x	x			x	28	M	51.3
Coarse/ Sand	*Astropecten irregularis*	P	Gravelly sand, muddy sand, fine clean sand, coarse clean sand	10 to1000m			x	x	x					x	x	x	x			x	25	M	51.3
Coarse/ Sand	*Luidia ciliaris*	P	coarse clean sand, fine clean sand, muddy sand, gravelly sand	4 to 400m			x	x	x					x	x	x	x			x	120	H	83.7
Coarse/ Sand	*Pecten maximus*	P	coarse clean sand, muddy sand, gravel, fine clean sand	10 to 110m			x	x	x					x	x	x	x			x	25	M	51.3
Mixed	*Eledone cirrhosa*	DD	Mixed							x	x	x						x			0	–	0
Mixed	*Lygdamis muratus*	P	Muddy sand, pebbles and stones							x	x	x						x			42	M	51.3
Mixed	*Macropodia spp.*	P	Mixed, often associated with hydroids	0 to 168m						x	x	x						x			30	M	51.3
Mixed/Mud	*Crangon allmanni*	P	Muddy gravel, sandy mud, muddy sand, mud, mixed, gravelly sand, gravelly mud	10 to 250m						x	x	x	x					x	x		52	M	51.3
Mixed/Mud	*Porania pulvillus*	P	muddy gravel, sandy mud, mud, gravelly mud	10 to 300m						x	x	x	x					x	x		56	M	51.3
Mixed/Mud /Sand	*Aphrodita aculeata*	DD	fine clean sand, coarse clean sand, mixed, mud, muddy sand, muddy gravel, sandy mud	10 to >1000m						x	x	x	x	x				x	x	x	0	–	0

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
Mixed/Sand	*Anseropoda placenta*	DD	sand, muddy sand, muddy gravel	10 to 500m						x	x	x		x				x		x	0	_	0
Mixed/Sand	*Liocarcinus depurator*	P	Muddy gravel, muddy sand, fine clean sand, coarse clean sand	0 to 450m						x	x	x		x				x		x	56	M	51.3
Mud	*Amphiura chiajei*	P	Mud, muddy sand	9 to 1000m									x						x		8	L	9.49
Mud	*Brissopsis lyrifera*	P	Mud, muddy sand	5 to 500m									x						x		39	M	51.3
Mud	*Geryon trispinosus*	P	Mud	40-2200m									x						x		38	M	51.3
Mud	*Nephrops norvegicus*	P	Mud, sandy mud	20 to 800m									x						x		47	M	51.3
Mud/Sand	*Antalis entalis*	P	soft ocean bottoms	<2000m									x	x					x	x	6	L	9.49
Mud/Sand	*Arctica islandica*	P	fine clean sand, coarse clean sand, muddy sand, sandy mud	4 to 256m									x	x					x	x	57	M	51.3
Mud/Sand	*Colus gracilis*	DD	coarse clean sand, fine clean sand, sandy mud, muddy sand	30 to 80m									x	x					x	x	0	_	0
Mud/Sand	*Crangon crangon*	P	fine clean sand, mud, muddy sand, sandy mud	Lower shore to 150m									x	x					x	x	42	M	51.3
Mud/Sand	*Echinocardium cordatum*	P	Coarse clean sand, fine clean sand, muddy sand, sandy mud	0 to 30m									x	x					x	x	39	M	51.3
Mud/Sand	*Lanice conchilega*	P	Coarse clean sand, sandy mud, fine clean sand, muddy sand	0 to 1700m									x	x					x	x	60	M	51.3
Mud/Sand	*Ophiura albida*	P	Fine clean sand, sandy mud, muddy sand	4 to 850m									x	x					x	x	42	M	51.3

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
Mud/Sand	*Philine aperta*	P	Muddy sand, sandy mud, fine clean sand	0 to 500m									x	x					x	x	40	M	51.3
Rock	*Abietinaria filicula*	BA NF	bedrock, large to very large boulders, small boulders, cobbles			x	x															1	L
Rock	*Alcyonium digitatum*	L	bedrock, large to very large boulders, small boulders, cobbles, artificial	LWST to 50m	x	x															10	M	9.49
Rock	*Archidoris pseudoargus*	P	Thought to be associated with Halichondria spp.	0 to 300m	x	x															90	H	83.7
Rock	*Ascidiella scabra*	BA NF	bedrock, large to very large boulders, artificial, small boulders, cobbles	HW to 300m	x	x															1	L	1.28
Rock	*Ciona intestinalis*	BA NF	bedrock, large to very large boulders, artificial, small boulders	Lower shore to 500m	x	x															2	L	1.28
Rock	*Echinus esculentus*	P	Bedrock, large to very large boulders, small boulders, artificial	0 to 1200m	x	x															52	M	51.3
Rock	*Epizoanthus incrustatus*	BA NF	Mollusc shells, hard substrates		x	x															1	L	1.28
Rock	*Halichondria bowerbanki*	BA NF	bedrock	0 to 90m	x	x															2	H	2.72
Rock	*Halichondria panicea*	BA NF	bedrock, cobbles, large to very large boulders, small boulders	0 to 569m	x	x															2	H	2.72
Rock	*Homarus gammarus*	P	bedrock, crevices, large to very large boulders	0 to 150m	x	x															21	L	9.49
Rock	*Metridium senile*	P	bedrock, large to very large boulders, artificial, small boulders, cobbles	Lower shore to >200m	x	x															60	M	51.3
Rock	*Sabellaria spinulosa*	P	Hard substrates, bedrock, boulders, cobbles		x	x															50	M	51.3

Appendix 3 continued...

Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
Rock	*Stomphia coccinea*	P	shells, stones		x	x															16	L	9.49
Rock	*Tubularia larynx*	BA NF	bedrock, large to very large boulders, small boulders, cobbles	Lower shore to 25m	x	x															3	H	2.72
Rock	*Urticina eques*	L	bedrock, large to very large boulders, small boulders, crevices	Lower shore to at least 100m	x	x															27	H	28.4
Rock/ Coarse	*Necora puber*	P	Bedrock, large to very large boulders, pebbles, gravel	0 to 70m	x	x	x	x	x						x	x	x				64	M	51.3
Rock/ Coarse	*Strongylocentrotus droebachiensis*	P	Rock, hard substrata, gravel	0 to 1200m	x	x	x	x	x						x	x	x				32	M	51.3
Rock/ Coarse/ Mixed	*Liocarcinus holsatus*	P	Bedrock, large to very large boulders, gravel, mixed	6 to 350m	x	x	x	x	x	x	x	x			x	x	x	x			56	M	51.3
Rock/ Coarse/ Mixed	*Ophiothrix fragilis*	P	Bedrock, large to very large boulders, small boulders, cobbles, pebbles, gravel, maerl, muddy gravel		x	x	x	x	x	x	x	x			x	x	x	x			21	L	9.49
Rock/ Coarse/ Sand	*Asterias rubens*	P	Gravel, coarse clean sand, bedrock	0 to 650m	x	x	x	x	x					x	x	x	x			x	87	H	83.7
Rock/ Coarse/ Sand	*Calliactis parasitica*	P	*Pagurus bernhardus*, shells	sublittoral to 60m	x	x	x	x	x					x	x	x	x			x	30	M	51.3
Rock/ Coarse/ Sand	*Caryophyllia smithii*	P	bedrock, large to very large boulders, cobbles, other species, sandy areas, mud between boulders	up to 100m for var. smithii	x	x	x	x	x					x	x	x	x			x	70	H	83.7

Appendix 3 continued...

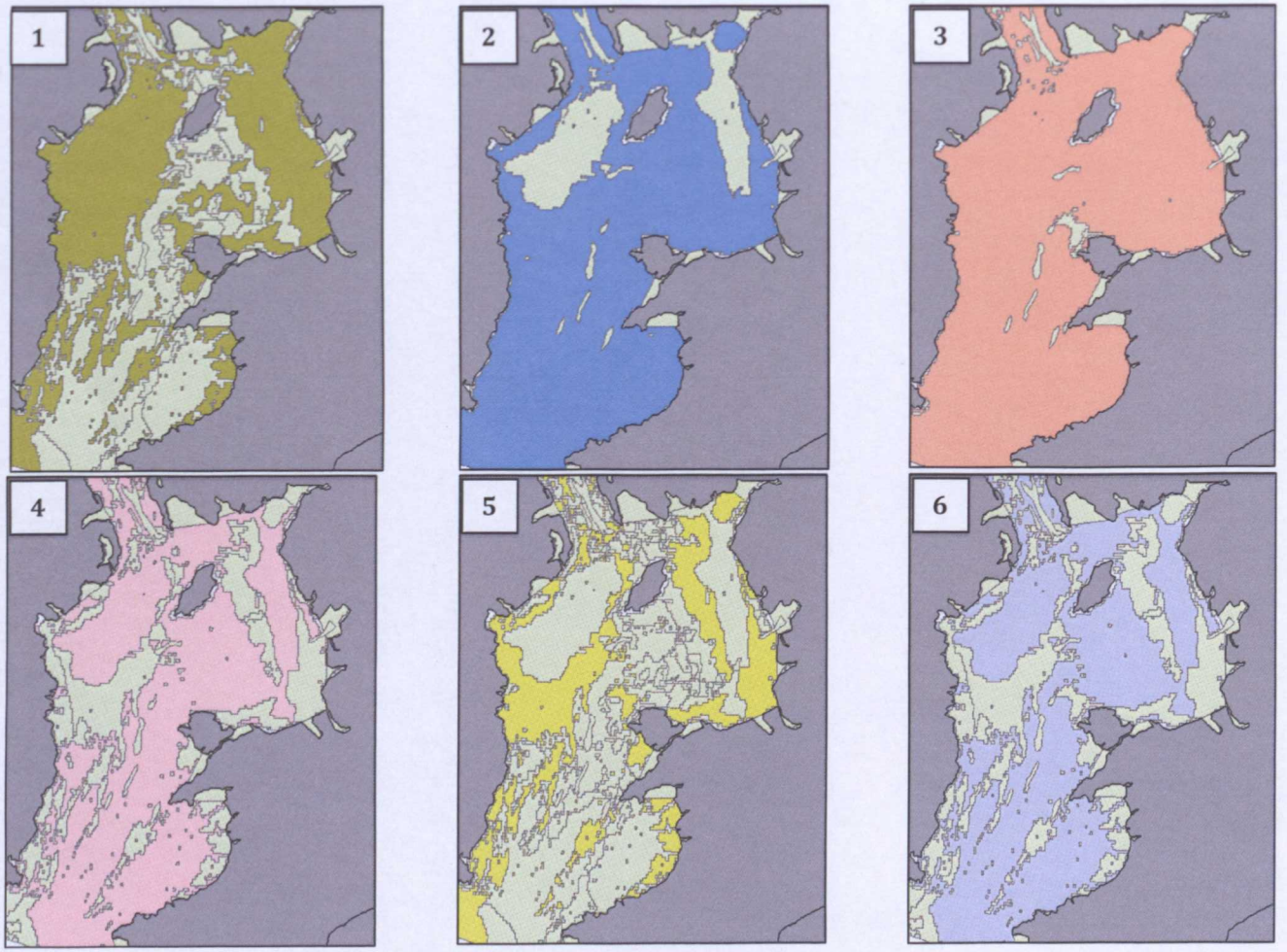
Habitat-Landscape Groupings	Species	DT	Habitat preference	Depth limits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	PLD	DD distance category	Mean distance (km)
Rock/ Coarse/ Sand	*Pagurus bernhardus*	P	Bedrock, large to very large boulders, coarse clean sand, fine clean sand, gravelly sand	MTL to 140m, rarely to 500m	x	x	x	x	x					x	x	x	x			x	80	H	83.7
Rock/Sand/ Mud	*Inachus dorsettensis*	P	Pebbles, coarse clean sand, fine clean sand, sandy mud, mud, muddy sand	0 to 300m	x	x							x	x					x	x	38	M	51.3
	Galathea squamifera	P		8-100m																	50	M	51.3
	Lithodes maja	L		10 to 600m																	48	H	28.4
	Mactra stultorum	P																			16	L	9.49
	Sepiola atlantica	DD																			0	–	0

Number	Marine Landscape
1	Aphotic Rock
2	Photic Rock
3	Shallow coarse sediment plain- strong tide stress
4	Shallow coarse sediment plain - moderate tide stress
5	Shallow coarse sediment plain - weak tide stress
6	Shallow mixed sediment plain - moderate tide stress
7	Shallow mixed sediment plain - strong tide stress
8	Shallow mixed sediment plain - weak tide stress

Number	Marine Landscape
9	Shallow mud plain
10	Shallow sand plain
11	Shelf coarse sediment plain - moderate tide stress
12	Shelf coarse sediment plain - strong tide stress
13	Shelf coarse sediment plain - weak tide stress
14	Shelf mixed sediment plain – moderate tide stress
15	Shelf mud plain
16	Shelf sand plain

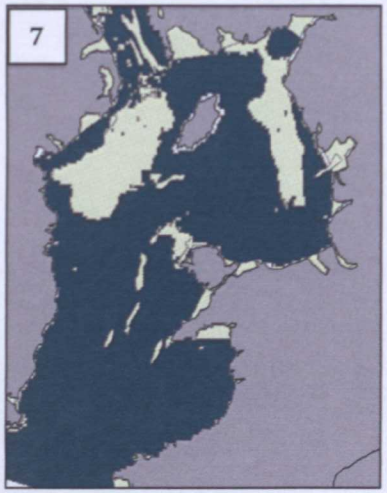
APPENDIX 4

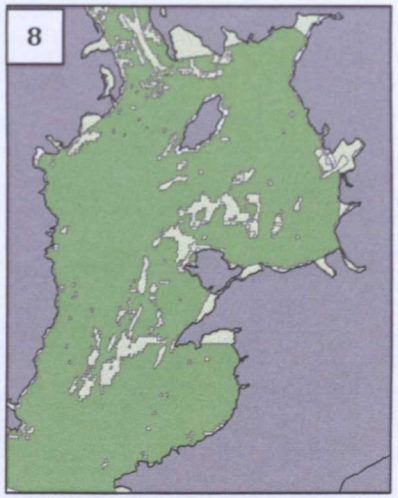
Marine landscape groupings in the Irish Sea as defined by habitat preferences of 79 common subtidal benthic invertebrate species. Solid coloured areas represent the landscapes (ungrouped areas in pale green).

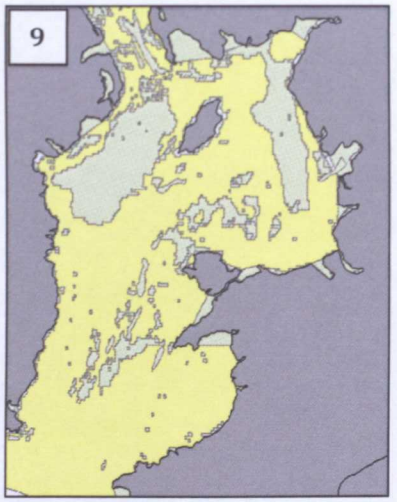


1. All but coarse
2. All but mud
3. All but rock
4. All but sand
5. Aphotic rock/Sand
6. Coarse/Mixed/Mud

APPENDIX 4 continued...



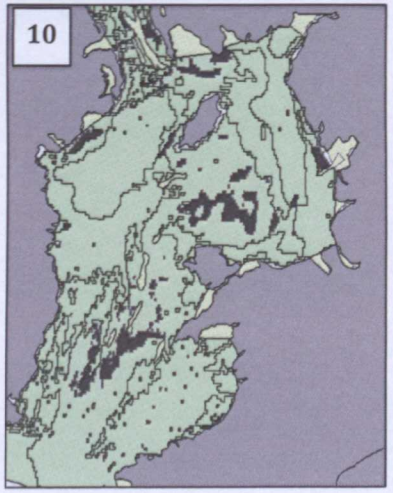


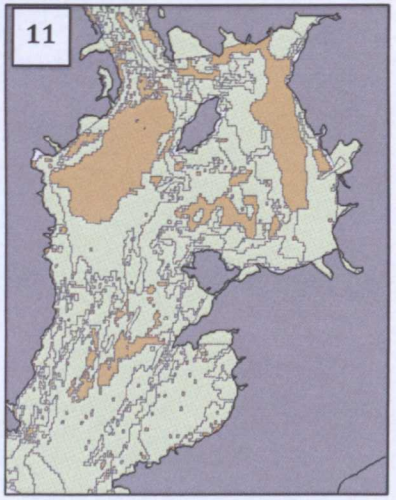


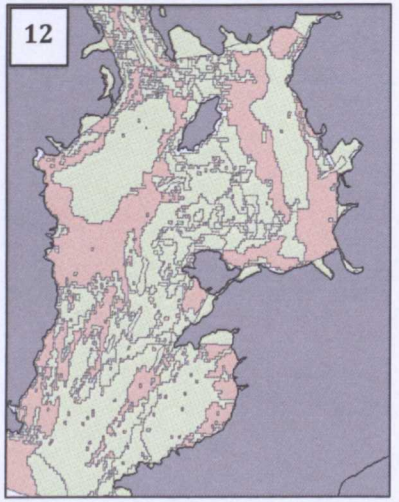
7. Coarse/Mixed/Sand

8. Coarse/Mud/Sand

9. Coarse/Sand





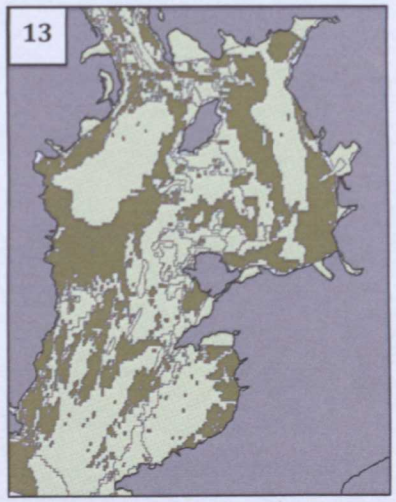


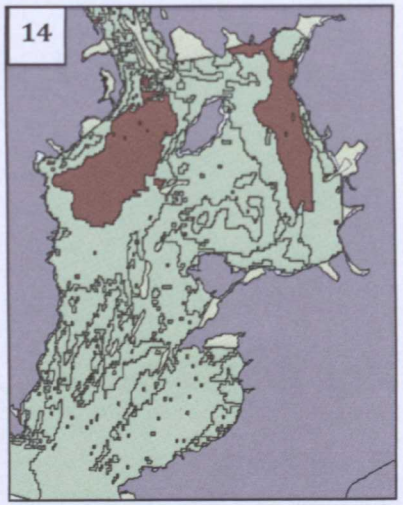
10. Mixed

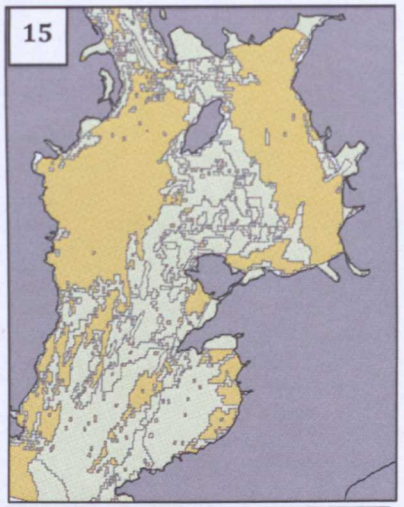
11. Mixed/Mud

12. Mixed/Mud/Sand

APPENDIX 4 continued...



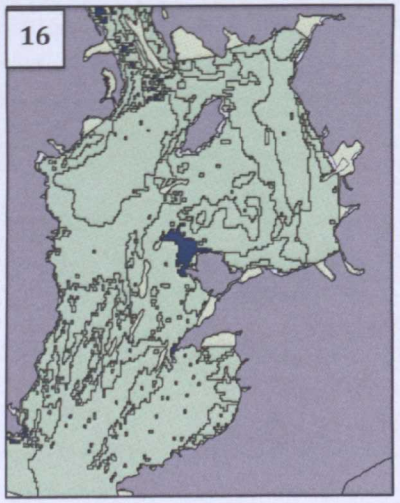


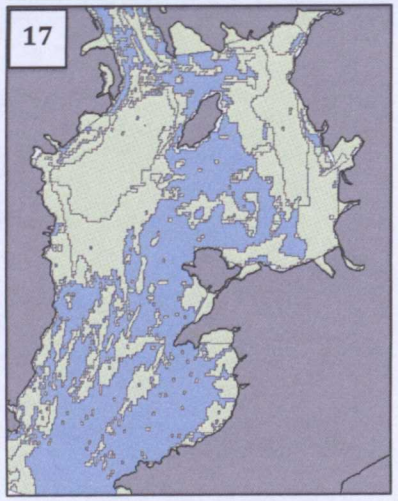


13. Mixed/Sand

14. Mud

15. Mud/Sand



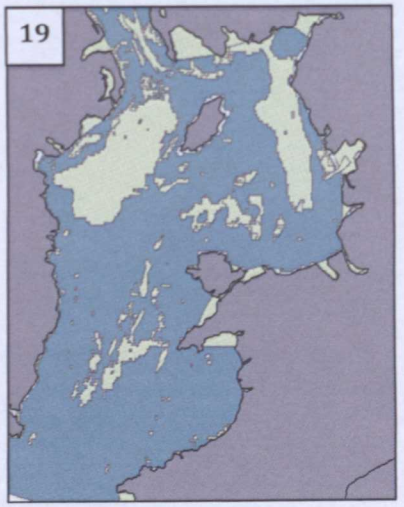


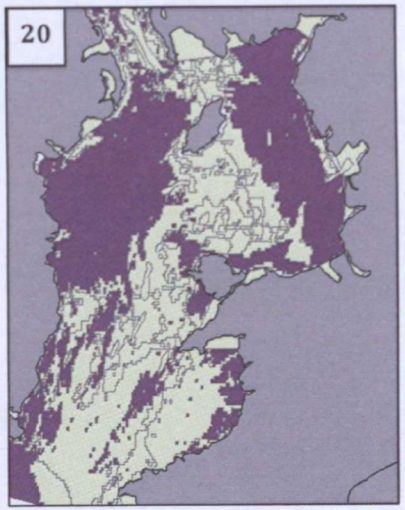
16. Rock

17. Rock/Coarse

18. Rock/Coarse/Mixed

APPENDIX 4 continued...





19. Rock/Coarse/Sand

20. Rock/Sand/Mud

APPENDIX 5

Basic measures of genetic diversity (number of alleles (N_A), allele richness (A_R), expected heterozygosity (H_E), observed heterozygosity (H_O), and the inbreeding coefficient (F_{IS})) for *Pecten maximus* from 15 locations in the north east Atlantic shelf (see Figure 5.1 for locations). N/A indicates not enough information for calculation. F_{IS} calculated after Weir and Cockerham, probability of deviation from Hardy Weinberg Equilibrium (HWE) *P<0.05 **P<0.01, significant for 21 out of 75 population -locus combinations.

		LIST15-002a	LIST15-004	LIST 15-014	LIST15-020	LIST15-005
BRN						
	N_A	3	2	5	7	10
	A_R	1.60	1.09	1.80	1.83	1.91
	H_E	0.60	0.09	0.80	0.83	0.91
	H_O	0.92	0.09	0.67	0.67	0.64
	F_{IS}	-0.571	0	0.17	0.207*	0.314**
TRD						
	N_A	3	3	6	9	11
	A_R	1.53	1.15	1.73	1.84	1.89
	H_E	0.53	0.14	0.73	0.84	0.89
	H_O	0.74	0.15	0.74	0.58	0.83
	F_{IS}	-0.398	-0.036	-0.013	0.316**	0.075
ALS						
	N_A	3	2	6	8	12
	A_R	1.57	1.17	1.80	1.77	1.76
	H_E	0.57	0.17	0.80	0.77	0.76
	H_O	0.59	0.18	0.73	0.62	0.70
	F_{IS}	-0.042	-0.077	0.093	0.201*	0.083*
SOG						
	N_A	4	3	7	9	9
	A_R	1.62	1.13	1.79	1.72	1.79
	H_E	0.62	0.13	0.79	0.72	0.79
	H_O	0.60	0.14	0.79	0.80	0.73
	F_{IS}	0.032	-0.033	-0.001	-0.114	0.084
KVT						
	N_A	3	4	8	11	13
	A_R	1.58	1.25	1.78	1.76	1.81
	H_E	0.58	0.25	0.78	0.76	0.81
	H_O	0.76	0.18	0.76	0.67	0.67
	F_{IS}	-0.305	0.278**	0.035	0.121**	0.176**
SHL						
	N_A	5	5	6	6	11
	A_R	1.50	1.18	1.53	1.76	1.91
	H_E	0.50	0.18	0.53	0.76	0.91
	H_O	0.48	0.12	0.46	0.50	0.78
	F_{IS}	0.042	0.378*	0.133	0.343**	0.145*
ISK						
	N_A	2	2	7	8	9
	A_R	1.52	1.08	1.46	1.81	1.87
	H_E	0.51	0.08	0.46	0.81	0.87
	H_O	0.93	0.08	0.40	0.38	0.87
	F_{IS}	-0.867	0.000	0.138	0.535**	0.000

		LIST15-002a	LIST15-004	LIST 15-014	LIST15-020	LIST15-005
MILL						
	N_A	1	1	6	3	5
	A_R	1.00	1.00	1.68	1.60	1.93
	H_E	N/A	N/A	0.68	0.60	0.93
	H_O	N/A	N/A	0.71	0.67	1.00
	F_{IS}	N/A	N/A	-0.053	-0.143	-0.091
PSM						
	N_A	2	1	5	4	1
	A_R	1.53	1.00	1.73	1.69	1.00
	H_E	0.53	N/A	0.73	0.69	N/A
	H_O	0.50	N/A	0.71	0.14	N/A
	F_{IS}	0.063	N/A	0.016	0.806*	N/A
STL						
	N_A	3	1	1	4	5
	A_R	1.61	1.00	1.00	1.87	1.93
	H_E	0.61	N/A	N/A	0.87	0.93
	H_O	0.75	N/A	N/A	0.67	0.67
	F_{IS}	-0.286	N/A	N/A	0.273	0.333
MUB						
	N_A	2	4	9	8	11
	A_R	1.51	1.28	1.85	1.74	1.88
	H_E	0.51	0.28	0.85	0.74	0.88
	H_O	0.81	0.22	0.71	0.41	0.81
	F_{IS}	-0.619	0.220*	0.167*	0.455**	0.079
KLB						
	N_A	2	2	8	6	9
	A_R	1.43	1.08	1.66	1.81	1.91
	H_E	0.43	0.08	0.66	0.81	0.91
	H_O	0.58	0.08	0.67	0.27	0.70
	F_{IS}	-0.375	0.000	-0.017	0.674**	0.236*
VLI						
	N_A	2	3	5	3	8
	A_R	1.53	1.31	1.56	1.53	1.92
	H_E	0.53	0.31	0.56	0.53	0.92
	H_O	1.00	0.33	0.33	0.33	1.00
	F_{IS}	-1.000	-0.091	0.415*	0.385	-0.098
WEB						
	N_A	2	3	4	5	8
	A_R	1.40	1.28	1.58	1.79	1.96
	H_E	0.40	0.27	0.58	0.79	0.96
	H_O	0.50	0.29	0.25	0.50	1.00
	F_{IS}	-0.273	-0.043	0.582*	0.388	-0.053
ICW						
	N_A	2	3	3	5	6
	A_R	1.53	1.44	1.32	1.86	1.93
	H_E	0.53	0.44	0.32	0.86	0.93
	H_O	0.83	0.50	0.33	0.17	1.00
	F_{IS}	-0.667	-0.154	-0.053	0.821**	-0.091

	LIST15-002a	LIST15-004	LIST 15-014	LIST15-020	LIST15-005
All populations					
N_A	7	9	17	16	21
A_R	1.56	1.18	1.76	1.84	1.87
H_E	0.53	0.20	0.66	0.76	0.88
H_O	0.71	0.20	0.59	0.49	0.81
F_{IS}	-0.31	**0.13****	**0.09***	**0.30****	**0.11****