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Determining the habitat requirements of demersal fish for the design of marine protected areas

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Determining the habitat requirements of demersal fish for the design of marine protected areas

A thesis presented to the University of Bangor for the degree of
Doctor of Philosophy

By

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March 2012

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Determining the habitat requirements of demersal fish for the design of marine protected areas

Andrew F Johnson

Understanding the relationship between habitat and fish distribution is a central component in the recent shift towards ecosystem based fisheries management (EBFM). Determining the habitat requirements of commercially and ecologically important species will be essential if spatial management strategies such as marine protected areas (MPAs) are to be used successfully to conserve marine resources. A review of demersal fish habitat research highlighted numerous areas lacking in this field of habitat science. These included the propensity for studies to focus on abiotic habitat variables such as depth and sediment over large spatial scales ($\geq 100\text{s km}^2$) and the low number of studies analysing biotic habitat variables in general. I conclude that development of sound predictive science in this field is reliant on a change in research focus toward reductions in study scale, or increases in resolution for abiotic habitat variables and more integration of biotic variables into studies. The three field studies included in this thesis analyse the importance of prey resource for the distribution of demersal fishes over spatial scales ranging from hundreds of metres to tens of kilometres. The first study investigates the relationship between prey and predator abundance and prey size and predator mouth gape size for nine demersal fish species around the Balearic Islands in the Mediterranean. The results demonstrate that prey abundance and size are of significance for some demersal fish species feeding primarily on benthos and will help in defining habitat requirements of demersal fish species. Demersal fish feeding ecology is studied in more depth when I investigate the effects of a bottom trawl fishery on an invertebrate benthic community and the subsequent effects this has on two commercially important flatfishes (*P. platessa* and *L. limanda*). This chapter closes the gap between the effects of bottom fishing on benthic communities and the reduced condition of some fishes found within these areas. The results of this study suggest that alterations in prey abundances, sizes and availabilities caused by chronic bottom trawling may lead to reduced feeding efficiencies, particularly for species with narrow prey spectrums. This in turn could result in reduced conditions of affected fishes living in chronically disturbed areas. The final data chapter uses detailed habitat maps, based on differences in sediment characteristics between three sites to take a small spatial scale, high resolution approach to describing demersal fish habitat. This investigates changes in the feeding ecology of a demersal fish species, *Callionymus lyra*, with body length. Although significant differences in prey size and prey taxa selectivity were found, no significant relationships between prey resource and predator distribution were apparent for any of the year classes analysed. The potential ecological and methodological reasons for these findings are discussed in-depth. Finally, a general discussion examines the main findings and suggests areas for future development.

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CHAPTER 1

General introduction

1.1 Fisheries management and the role of habitat

Decades of over-exploitation have led to significant declines in population sizes and in some cases, the collapse of numerous commercial fish stocks (Pauly et al., 1998, Myers and Worm, 2003, Worm et al., 2009). In addition to the direct removal of fish biomass, fisheries exert further pressures on marine ecosystems through by-catch (Davies et al., 2009), food web alteration (Choi et al., 2004, Frank et al., 2011), and habitat modification and degradation (Kaiser, 1998, Kaiser et al., 2003). Growing concerns regarding the sustainability of commercial fish stocks, threatened marine species, and sensitive marine habitats have led to the development of a new ecosystem based approach to fisheries management (EBFM) (Pikitch et al., 2004). Levels of interest in this new paradigm have risen in recent years following conflicts between legislation and stake-holders, questions over the most important processes within marine systems and an increased awareness of the limitations of a single species approach to management (see Link, 2002).

Broadly, EBFM aims to conserve the structure, diversity and functioning of marine ecosystems whilst satisfying societal and human needs for food and economic benefit (see FAO, 2003). Its objectives are; i) to keep fishing mortality rates low enough to prevent ecosystem-wide overfishing, ii) reduce and preferably eliminate by-catch and iii) avoid habitat-destructive activities. Hilborn (2011) also extends these main objectives adding *“There is a second phase of EBFM I call “extended EBFM” that consists of considering trophic interactions and area-based management”*. Current legislative drivers that call for an ecosystem based approach to fisheries management include the World Summit on Sustainable Development (Johannesburg, 2002), the Common Fisheries Policy green paper (2009), the FAO code on responsible fisheries (1995) as well as the European Union’s

Marine Strategy Framework Directive (MSFD) (2008). The EU's MSFD aims to achieve Good Environmental Status in Europe's seas by 2020. The directive sets out eleven high-level descriptors of good environmental status which cover all key aspects of the marine ecosystem. These include levels of biodiversity, all elements of marine food webs and sustainable catch limits for commercially exploited species as well as all the human pressures that act on marine systems. Although commonly referenced in fisheries research and policy alike, numerous experts warn that science may currently be unprepared to integrate EBFM effectively into current practices due to a lack of appreciation of the goals and objectives of its numerous approaches (Kaiser, 2005, Hilborn, 2011).

Central to EBFM is the role of habitat science (Rice, 2005). In order that fisheries research takes a primary advisory role in management, it is important that the habitat requirements and fundamental ecology of commercially and ecologically important species is understood. Legislation such as the sustainable fisheries act (SFA) (1996) in the United States highlights the drive towards an ecosystem approach and the role habitat will play in its development. In addition to reductions in overfishing and bycatch, the SFA requires management to identify essential fish habitat (EFH) of target species, defined as "those waters and substrates necessary for spawning, breeding, feeding or growth to maturity".

Considering the dynamic state of many marine systems and the proposed use of marine protected areas (MPAs) in EBFM, it will be necessary to understand how the requirements of fishes change temporally and spatially (e.g. Cheung et al., 2009, Piet and Rijnsdorp, 1998). Such information will not only aid in the development of future fishery management schemes but it will also act as a useful addition to existing strategies, with goals to restore already depleted populations (Link, 2002). Examples of local, extant fishery closures under EU law

are the herring boxes (*Clupea harengus* – numerous locations), the plaice box (*Pleuronectes platessa* – North Sea), the mackerel box (*Scomber scombrus* – SW England) and under UK law, seabass nursery grounds (*Dicentrarchus labrax* - numerous). Clearly understanding the habitat requirements of fish species will also be beneficial for scientists aiming to forecast future impacts of current fisheries as well as management bodies intending to protect stocks and habitats through the formation of MPAs.

The benefits of EBFM and habitat-based research are now better understood. However the determination of fish habitat is still lacking and many questions remain unanswered regarding species important to ecosystems and / or fisheries. Before presenting new research into the determination of demersal fish habitat in chapters 2 - 5 of this thesis, it is important to briefly discuss the terms *habitat* and *requirement* and the subjects of habitat selection and distribution in order to highlight their importance within this field.

1.2 Terminology and definitions

Without clear definitions of fundamental concepts, vagueness and ambiguity within scientific literature can lead to a lack of effective communication, comparison and progression between researchers. In order to overcome such problems it is essential that researchers clearly define terminologies used in their work, especially those that form an integral part of their aims, objectives and hypotheses. Here, and throughout past literature, the objective is generally not to call for standardised terminologies (see Hall et al., 1997) but rather reiterate the importance of clearly explaining ideas and concepts employed. It is therefore necessary to discuss the terms *habitat* and *requirement* as they both form the main structure of demersal fish habitat determination and the title of this thesis.

1.2.1 Habitat

The concept of habitat is not new and its definition and meaning have been hotly debated within the ecological literature (see Hall et al., 1997, Whittaker et al., 1973, Naiman and Latterell, 2005). Two key concepts require incorporation and explanation with the use of *habitat*; scale and habitat suitability. *Habitat* can range from an organism's association with large, landscape-scale processes (e.g. climate or oceanographical cycles) through to small spatial scale associations of an individual's immediate physical environment (Hall et al., 1997). Actual descriptions of habitat are dictated by the resolution of methods employed by researchers (Diaz et al., 2004). It therefore seems prudent to ensure its definition either 1) encompasses the range of spatial scales over which processes realistically affect an individual or 2) includes an accurate description and justification (considering the methods employed) of the spatial scale at which it is used. Similarly, the range of *habitat suitabilities* over which the term *habitat* is used requires careful consideration. By definition, an organism's habitat is suitable (i.e. if an individual persists in a certain locality, the said locality must confer some advantage to that individual). Therefore broadly, *habitat* must encompass the full range of conditions within which an individual is viable and can persist unless otherwise specified.

1.2.2 Requirement

The habitat requirements of a species are thoroughly intertwined with their habitat. For many, these requirements are related to both the structure of the habitat and the landscape surrounding it (the landscape matrix) (Store and Jokimaki, 2003). The extent to which *requirement* is defined (a consideration which is often missed altogether) is determined by the objectives of the investigation and the identified habitat(s) of interest. For example, if one is concerned with determining the habitat requirements of a species during its spawning

season, it would be inappropriate to attempt to determine the full range of known conditions within which the species can exist, especially if the spawning grounds are in notably different localities from those inhabited outside of spawning periods. A clear and precise definition of both *habitat* (e.g. spatial and temporal description of the area that produces successful and viable spawning) and *requirements* (e.g. the specific abiotic and biotic conditions within the aforementioned habitat needed to produce the successful and viable spawning) are therefore needed to focus research effort. Without this, research may set out to answer specific questions regarding the habitat requirements of a species but return with a large suite of parameters which, without further refinement, do not accurately fulfil the specific primary objectives of the investigation. Clear descriptions of *habitat* and *requirement*, and justifications for their chosen use will also be necessary to prevent misinterpretations both within and between studies.

1.3 Relating distribution to habitat

The majority of work determining the habitat requirements of demersal fish species primarily sets out to map the population distribution in a known area through direct catch and then quantify the selected habitat parameters within the area of each catch. Differences in distributions of fishes are then compared to variations in the parameters analysed, using a correlative approach (Rice, 2005). It is often assumed that areas of high population density are areas of high habitat suitability. However, it is important to note that abundance can be a misleading indicator of habitat quality especially for already impacted systems and occupancy *versus* non-occupancy may not accurately inform us about the suitability of a habitat (Store and Jokimaki, 2003). With this in mind, consideration of the actual distribution of populations only partially elucidates a habitat's suitability. It is therefore greatly

advantageous to measure suitability in terms of survival, fitness (condition) and / or reproductive output of a species (MacCall, 1990, Shepherd and Litvak, 2004, Stoner, 2003). It is also important to consider that a “suitable” habitat may contain a mixture of different patches. Ideally, investigators will therefore have apriori knowledge of habitat types in the vicinity of the study area as well as the suite of parameters important to the study species in order to clearly interpret settling decisions (Orians and Wittenberger, 1991, Shepherd and Litvak, 2004). The scale of the neighbouring area analysed is likely to depend on the visual / sensory range of the species in question, their “normal” patterns of movement and the resolution / spatial scale of the whole investigation

1.4 Habitat selection

Few studies of habitat requirements determine the distribution of individuals relative to others (i.e. intra and interspecific competition and predation) (Hixon and Jones, 2005, Lindholm et al., 2001, Auster et al., 2003). Analysing distributions at such high resolutions is often impracticable, not in line with overall study scales and is a likely reason it is often dismissed. Although adding another level of complexity, which is often overshadowed by other habitat variables acting over larger scales, the consideration of such factors allows increased understanding of the distribution of fish populations and adds another important dimension to the requirements of a fish species (Bjornstad et al., 1999, Hiddink et al., 2005). For example, what densities of both congeners and interspecific competitors are required that allows persistence in a species habitat?

Habitat selection is an almost universal activity among animals (Orians and Wittenberger, 1991). Following the ideal free distribution (IFD) (Fretwell and Lucas, 1969, MacCall, 1990, Simpson and Walsh, 2004), habitat preferences will generally decline with increased population density. The amount of competition and predation within a population is likely to dictate the amount of habitat selection occurring (Gilliam and Fraser, 1987, Rosenzweig, 1991). Therefore, neglecting to consider the smaller scale density dependent effects of habitat selection may cause conclusions of overall habitat requirements to be inaccurate in terms of their suitability, an effect likely to be magnified if results are extrapolated to larger spatial scales. For example, if site A shows a higher abundance of species X than site B, it is naturally assumed that site A is of a higher quality. This conclusion however overlooks density dependent effects which if accounted for (and acting as the IFD predicts) would tell us that the fitness / condition within sites A and B are likely to be similar due to the action of density dependent habitat selection (DDHS) (see Fretwell and Lucas, 1969). If accounting for density dependent habitat processes and following the IFD within this scenario, the correct conclusion would be that both sites A and B are of similar habitat quality / suitability. Sheperd and Litvak (2004) explain that for DDHS to exist fish species must make informed decisions on habitat suitability along a gradient. They go on to hypothesise that preference gradients are unlikely to exist for flatfish species due to the high heterogeneity of the seafloor. The existence of habitat suitability gradients is however likely to be highly dependent on the systems under study and the species home range involved. Consequently it is useful for small spatial scale habitat requirement studies as well as some larger scale investigations to consider DDHS effects where such processes may play an influential role in species distributions.

1.5 Thesis outline

The overall aim of the thesis is to improve our knowledge of the link between demersal fishes and their habitat.

Chapter 2 provides the base upon which the other chapters were designed and written. Within this chapter I use a literature review to introduce the field of demersal fish habitat determination. The main hypothesis of this work is that researchers in the field of demersal fish habitat determination are not always looking at suitable spatial and temporal scales for the habitat parameters analysed and the majority of management strategies aiming to use MPAs. I then summarise work carried out, demonstrating patterns seen in this field and evaluate whether or not these are wholly justified. This highlights areas lacking and common themes that require evaluation if research in this field is to progress effectively and be used in the management of demersal fish stocks.

Chapter 3 takes an in-depth look at prey abundance, a habitat variable traditionally analysed over very small (cm^2) or large ($\geq 100\text{s km}^2$) spatial scales. I hypothesise that prey abundance and size are important factors determining the distribution of demersal fishes over medium spatial scales (10s – 100s km^2). In addition I analyse the importance of prey size arguing that although a prey item is present in an area it may not be available depending on its size and the mouth gape limitation of the predators present. This is a story that I believe is fundamental in understanding the influence of benthic prey communities on the distribution of demersal fishes.

Chapter 4 adds an anthropogenic element to the story of demersal fish habitat determination. Here, over relatively small spatial scales (10s km^2) I look at the effects of benthic disturbance

caused by a bottom trawl fishery on the diet and feeding ecology of two demersal fish species. This chapter joins the loose ends between the impacts of a trawl fishery on the benthic community (Hinz et al., 2009) and the reduced condition of fishes found within the same area (Hiddink et al., 2011). I test the hypothesis that the reduced condition of plaice found by Hiddink et al. (2011) is caused by a reduction in feeding efficiency in highly trawled areas as well as the low quality of prey available to plaice compared to dab. The spatial scale of the study, the gradient of impacts within the area and the morphometric similarities of the fish species analysed provides a unique opportunity to use foraging theory to describe how the consequences of a bottom fishery can affect demersal fishes through alterations in their prey community.

Chapter 5 primarily addresses the importance of including ontogenetic considerations in the determination of demersal fish habitat. Here I use a small spatial scale (100s m²), high resolution approach to describe the feeding ecology and distribution of one fish species over a pre-defined area for a range of year classes. I analyse the relationship between predator and prey distribution and discuss the effects of season, bottom type and prey community composition on the ontogenetic distribution of this fish species. I hypothesise that there are significant differences in the diets of juvenile and adult fishes and that these differences will have a significant effect on their distribution. The approach taken also permits a brief discussion of the use of benthic maps (in this case multi-beam habitat maps) based on sediment / topographic information to define habitats of demersal fish species.

Chapter 6 summarises the findings of the thesis and discusses areas for future development emerging from them.

The following chapters have been published and appear in this thesis as they do in the published article.

Chapter 2: Johnson et al. (in press). Linking temperate demersal fish species to habitat: scales, patterns and future directions. 2012. . *Fish and Fisheries*.

Chapter 3: Johnson et al. (2012). Effect of prey abundance and size on the distribution of demersal fishes. *Canadian Journal of Fisheries and Aquatic Sciences*. **69**. 191-200. doi:10.1139/F2011-138.

These articles were written by the author of this thesis and contributions of co-authors were restricted to supervision of the thesis and comments on manuscripts prior to submission.

CHAPTER 2

Linking temperate demersal fish species to habitat: scales, patterns and future directions

2.1 Abstract

Adoption of the ecosystem approach to fisheries management relies on recognition of the link between fish and other components of the ecosystem, namely their physical and biological habitat. However identifying the habitat requirements of marine fishes and hence determining their distribution in space and time is scientifically complex. We analysed the methodologies and findings of research on temperate, demersal fish habitat requirements to highlight the main developments in this field and to identify potential shortfalls. Many studies were undertaken over large spatial scales ($\geq 100\text{s km}^2$) and these generally correlated abundances of fish to abiotic variables. Biological variables were accounted for less often. Small spatial scale ($\leq \text{m}^2$), experimental studies were comparatively sparse and commonly focused on biotic variables. While the number of studies focusing on abiotic variables increased with increasing spatial scale, the proportion of studies finding significant relationships between habitat and fish distribution remained constant. This mismatch indicates there is no justification for the tendency to analyse abiotic habitat variables at large spatial scales. Innovative modelling techniques and habitat mapping technologies are developing rapidly, providing new insights at the larger spatial scales. However there is a clear need for a reduction in study scale, or increase in resolution additional to the integration of biotic variables. We argue that development of sound predictive science in the field of demersal fish habitat determination is reliant on a change in focus along these lines. This is especially important if spatial management strategies, such as Marine Protected Areas (MPAs) or No Take Zones (NTZs) are to be used in future ecosystem based approaches to fisheries management.

Keywords: abiotic and biotic habitat descriptors, conservation, demersal fish, ecosystem approach, Essential Fish Habitat, habitat association,

2.2 Introduction

Resource exploitation, habitat modification, pollution and climatic shifts are having widespread and detrimental consequences for marine ecosystems globally (Vitousek, 1997, Jackson et al., 2001, Kaiser et al., 2002). With more than 20% of the world's human population living in biodiversity hotspots (Cincotta et al., 2000) and over 60% living within 60km of the coast (Alongi, 1998), marine ecosystems are now under huge pressure from anthropogenic activities and increasingly demonstrate a reduced capacity to withstand these pressures (Folke et al., 2004). Of particular concern to managers and conservationists are the impacts of bottom trawl fisheries on benthic ecosystems. The modification and degradation of habitats associated with bottom fishing can have long-term consequences for benthic biota, reducing productivity, biomass and species richness (Hiddink et al., 2006a, Queiros et al., 2006, Hinz et al., 2009). Following growing concerns regarding the long-term sustainability of marine fish exploitation (Pauly et al., 2005), fisheries collapses from food web restructuring (Frank et al., 2005), and reduced abilities of chronically impacted benthic communities to sustain previous stock levels (Shephard et al., 2010, Hiddink et al., 2011), traditional and often single-species management practices are being evaluated. The result has been the development of a new ecosystem-based fisheries management (EBFM) paradigm (Pikitch et al., 2004, Frid et al., 2005) which aims to maintain a sustainable ecosystem state by integrating knowledge of biotic, abiotic and human components of ecosystems and applying them to fisheries within ecologically meaningful boundaries (Link, 2002).

Major drivers of this new approach have been the formation of numerous conventions and legislations that have highlighted the importance of defining habitat requirements of key species. Examples include the Conservation of Antarctic Marine Living Resources (1982),

and the Sustainable Fisheries Act (SFA) (1996), in the United States. The SFA added Essential Fish Habitat (EFH) provisions to the existing Magnuson Stevens Fishery Act (1976) requiring the National Oceanographic and Atmospheric Administration (NOAA) to facilitate the long-term protection of “those waters and substrates necessary for spawning, breeding, feeding or growth to maturity”. The SFA highlights the importance of defining physical, chemical and biological properties that are used by fish, and those that are necessary to support a sustainable fish biomass for each of the fish species listed. Similar initiatives aiming to define the habitat requirements of marine fish species are now being echoed globally (Europe – Directive on the Conservation of Natural Habitats and Wild Fauna and Flora (1992/43/EEC), Australia – Environment Protection and Biodiversity Conservation Act 1999, Canada – Fisheries Act (reforms - sect.35, 1985) and Species At Risk Act (Bill C-5, 2002)).

Despite the drive towards ecosystem conservation, and long histories of commercial fishing in Europe, Canada and America (Pauly et al., 2005), still relatively little is known about the habitat requirements and basic ecology of many temperate demersal fish species (Benaka, 1999). With declining marine fish stock levels (Pauly et al., 2005) and an increased awareness of the impacts of bottom fisheries (Kaiser, 1998), understanding the specific habitat requirements of demersal fishes is more important than ever. Management strategies aiming to attain sustainable exploitation levels of fish stocks can vary widely, from fishing quota implementation (Karagiannakos, 1996) or the establishment of no take zones (NTZ) and marine protected areas (MPA) (Gaines et al., 2010), to stock restoration projects involving artificial habitat construction (Seaman, 2008) and re-stocking (Heenan et al., 2009). The latter initiatives are often only feasible over certain habitat types and scales. For example, artificial habitat construction is a relatively straightforward process for tropical reef

fish species, that often have small home ranges and require complex 3-dimensional habitats (Roberts and Ormond, 1987) and has been implemented successfully in numerous locations over generally small spatial scales (Seaman, 2008). Temperate systems on the other hand often consist of relatively homogeneous, soft sediment habitat types that may span thousands of square kilometres over which habitat manipulation is not practicable.

Spatial management measures, such as NTZs and MPAs, can range from access restrictions for certain users at specified times to full protection from all anthropogenic activity within the designated area. These may vary from closing areas greater than 1000 square kilometres for the protection of multi-species communities with relatively low habitat specificity and wide distributions as illustrated by ground fish stocks in the Western Gulf of Maine, New England, USA (see Murawski et al., 2000) to the closures of smaller areas less than 100 square kilometres to deal with single species in areas of high habitat suitability such as the Red mullet (*Mullus barbatus*, Mullidae) in the Gulf of Castellamare, northwestern Sicily, Italy (see Fiorentino et al., 2008)). Such approaches are now common-place; however their aims with regard to fisheries may vary, from the protection of certain life stages of specific species, to the overall enhancement of multiple fisheries (Koss et al., 2005, Frost and Andersen, 2006, Ardron, 2008, Gelcich et al., 2009). Studies that accurately describe the habitat requirements of target species and the scales over which they operate can facilitate decisions on the type of management strategies that are most viable for the species of concern.

In order to aid in the sustainable exploitation of demersal fish stocks, researchers must uncover the most important habitat variables determining the distributions of species as well as the range of temporal and spatial scales over which they operate (Hinz et al., 2003). Many

studies in this field however use widely spaced sampling stations (10s to 100s km) and combine data collected across temporal scales. Consequently, habitat variables influencing demersal fish habitat distributions that operate over smaller scales may well be overlooked. For example, combinations of monthly to annual data are likely to mask differences in habitat use between seasons. Similarly, collection of data over a scale of hundreds of square kilometres may not allow for inference about differences in distributions at smaller spatial scales. Mismatches between spatial scales examined and the actual scale at which processes occur, may at best mean that patterns are missed, and at worst result in drawing erroneous conclusions. Management interventions supported by such outputs may therefore produce questionable management strategies and a lack of sustainable and efficient protection.

The determination of EFH commonly involves relating the abundance of the species under investigation to measured habitat variables thought to be important to the species distribution (Rice, 2005). Habitats accommodating the study species are assumed to be of some importance. Stoner (2003) however points out that seemingly appropriate habitats, may never be occupied, with specific locations being more important than particular habitat forms. Ideally the determination of EFH should be based on more than abundance alone and should also address the growth and survival of individuals, thus considering how their current distribution may affect future generations. This is especially important if predictions derived from research are to be used in management. Such approaches combining measures of growth and fitness are however often restricted to small scale manipulative experiments, as such data collection over large areas is often constrained by methodologies and cost.

Although work in the field of demersal fish habitat determination is becoming an important part of the ecosystem based approach to fisheries management, we are currently lacking a

critical synthesis that assesses the importance of biotic and abiotic habitat variables at different spatial scales. This means that we are currently unaware if there are particular spatial scales over which different habitat variables affect the distribution of demersal fishes. In this paper we analyse the number of different habitat variables that have been studied and the spatial scales over which they determine the distribution of temperate, demersal fishes from square metres to more than a hundred thousand square kilometres. We restrict our analysis to temperate, demersal species as the habitat variables determining the distribution of tropical and pelagic species are likely to differ considerably (see Shepherd and Litvak, 2004). Over the period 1980 to 2011 we aim to quantify the following parameters in this field of research: 1) the number of studies in the field of demersal fish habitat identification and the geographic locations in which they were undertaken, 2) the life stages and fish species analysed, 3) the types and numbers of habitat variables commonly investigated and the spatial scale of work undertaken, 4) the proportion of studies reporting significance for each habitat variable over the spatial range studied and 5) the temporal scales considered in the literature. In order to examine whether trends in research were justified we compared the relationships between the total number of studies and the proportion of studies reporting significance for each separate habitat variable, as well as for all abiotic and all biotic variables, across the range of spatial scales analysed. Our analyses permits a critical evaluation of current trends and patterns in the field of demersal fish habitat determination. We hypothesise that: i) many studies focus at large spatial scales due to the origin of the data used within them, ii) few studies analyse the effects of biotic habitat variables on the distributions of demersal fishes and iii) few studies take a temporal approach to the analysis of demersal fish habitat requirements. With rising expectations of managers to meet sustainability targets and the growing pressures on marine ecosystems, continued research in the field of demersal fish habitat determination is required if we are to sustainably exploit our bottom fisheries

resources. This analysis is therefore both timely and necessary to assess what research has been undertaken in this field to date, in order that we drive future research efforts in the appropriate direction.

2.3 Methods

2.3.1 Search criteria

We conducted a literature search for peer-reviewed publications, published in English over the period 1980 to 2011, describing the habitat requirements of temperate, marine, demersal fish species. Within any particular publication, one or a number of different investigations may be described. We therefore define ‘article’ as a published journal paper and ‘study’ refers to the separate investigations of different habitat variables undertaken within an article. The period was chosen due to the accessibility of online articles and because it corresponded approximately with the time over which fisheries science wholly embraced research into the anthropogenic impacts on demersal resources and demersal fish habitat determination (following the announcement of the Magnuson-Stevens Fishery Convention (1976)). The literature search was undertaken using the commercial search engine Google Scholar, which indexes the full text of scholarly literature across an array of publishing formats. Combinations of the following search terms were used: ‘association’, ‘choice’, ‘connectivity’, ‘demersal’, ‘determining’, ‘distribution’, ‘ecology’, ‘EFH’, ‘essential’, ‘fish’, ‘habitat’, ‘requirement’, ‘scale’, ‘suitability’, ‘use’. Google Scholar was chosen over Web of Science and Scopus as it gives a higher number of results per general search term (on average), covers non-ISI listed journals (wider search base) and gives lower citation noise

(lower citation variation (85% unique entries compared to ISI's 60%)) (Belew, 2005, Pauly and Stergiou, 2005, Meho and Yang, 2007, Harzing and Van der Wal, 2008).

The first one hundred search results from each keyword combination were examined. From these, only peer-reviewed articles were chosen as they form the main body of literature widely available to researchers. The articles used therefore did not include any university theses, technical governmental reports or conference proceedings. Articles examining larval life stages were excluded from the analysis as they form a significant and separate body of literature. Often these early life stages also show markedly different habitat preferences to post-larval developmental stages (Gibson, 1994, Sullivan et al., 2006). Articles investigating survivorship, condition or fitness of demersal species under differing habitat conditions were included in the database when they were directly related to habitat preferences of the species. From each article fitting the above search criteria, eight categorical data variables were extracted and entered into a database (see Table 2.1 for details). The variables were publication year, location and total spatial scale of study, life stages, fish species, habitat variables and time trends analysed, and origin of data utilised. The total spatial scale (total area) of each study was calculated using ARC GIS (version 9.2) if it was not described clearly by the authors within the methods. If replicate sites were tested, the area of each was calculated and the total across all sites used. Data were categorised by their origin into stock assessment, field study and laboratory study in order to illustrate the origin of data sources within this field of research. Habitat variables investigated by authors were classified into abiotic versus biotic and further into the sub-categories listed in Table 2.1.

2.3.2 Statistical analyses and graphical outputs

Initially we focused on the distribution of journal articles across the years and spatial scales they addressed. Ordinary least squares (OLS) linear regressions were employed to analyse the relationships between i) the number of peer-reviewed journal articles published in the field and the year of publication, ii) the number of studies, and total spatial scale of each study.

Table 2.1: Table summarising the data extracted from each article fitting the search criteria and entered into the first database.

Parameter	Description of parameter	Database input categories
Year	Year of publication	1980 – 2010 (1 year intervals)
Location	Geographic location (within temperate zones) of work undertaken	N. America, Europe, Australia, New Zealand, S. America, Other
Total study scale	Total area of the study site (both laboratory and field) over which replicates were taken	$\leq 1e^{-5}km^2$ (cm^2), $\leq 1km^2$ (m^2), $\leq 10 km^2$, $\leq 100 km^2$, $\leq 1000 km^2$, $\leq 10,000 km^2$, $\leq 100,000 km^2$
Life stages analysed	Ontogenetic stage considered in the analyses	Adult, Juvenile, All
Fish order analysed	Fish species and order under study	Mixed*, Gadiformes, Pleuronectiformes, Perciformes, Scorpaeniformes, Carcharhiniformes
Study type	Origin of data used	Laboratory study, Field study, Stock assessment survey
Habitat variables analysed	Variables analysed / hypothesised to be important to the distribution / habitat requirements	Abiotic: depth, hydrography, other abiotic ¹ , salinity, substrate, temperature Biotic: competition ² , biogenic complexity ^{3,†} , predation ^{4,†}
Time trends analysed	Temporal trends formally analysed as part of the hypotheses	Not applicable, day (12hrs), day vs night (24hrs), month (30 days), season (90 days), annual (365 days)

*Mixed species are defined as studies looking at 4 or more different demersal fish species.

¹ includes dissolved oxygen / level of hypoxia and light, ² includes intra and interspecific competition,

³ 3D habitat structures of biological origin, ⁴ predation of the demersal species under investigation,

[†] often exposure to predation is a result of biogenic complexity. The distinction between the two was made by referring to the authors' hypotheses and final conclusions.

Next we examined the relationship between the number of studies conducted at particular scales and the proportion of studies that reported significant results, to understand whether the concentration of studies at particular scales was justified. Here only articles which reported results based on individual species were used since those which only reported relationships for mixed assemblages could potentially mask significant relationships at the species level. Regressions of spatial scale versus number of studies were undertaken for all of the different habitat variables plus 'Total abiotic' and 'Total biotic' categories. This process excluded geography, hydrography and predation as there were too few studies that investigated these variables. This was then repeated, except the number of studies was replaced with the proportion of these studies which showed a significant relationship.

Data were \log_{10} transformed to ensure normal distributions where required. To test if there was a significant difference between the spatial scales at which abiotic and biotic habitat variables operate, Wilcoxon rank sum t-tests were used.

2.4 Results

The literature search identified 109 peer-reviewed journal articles determining the habitat requirements of demersal fish species from the period between 1980 and 2011 (Table 2.2). The number of articles published increased significantly over time ($R^2 = 0.506$, $F_{1,29} = 29.72$, $P = <0.001$); 43% were published since 2005, with the highest number of articles published in 2001 (13), followed by 2009 (12) and 2002 / 2007 (11 each) (Fig. 2.1). North America (46%) and Europe (38%) dominated the locations where studies had been undertaken. The remaining 16% of studies were carried out in Australia, New Zealand and South America. No publications came from Africa or Asia.

Table 2.2: Table summarising separate fish species, life stages and the habitat variables analysed

Fish order	Fish species	Life stage analysed			Habitat variables analysed											Reference	
		Adult	Juvenile	All	Abiotic							Biotic					
					Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation	Prey resource		
Carcharhiniformes	<i>Scyliorhinus canicula</i>	*															Sims <i>et al.</i> (2001)
Gadiformes	<i>Gadus morhua</i>		*			*				*		*	*	*	*		Borg <i>et al.</i> (1997), Bjornstad <i>et al.</i> (1999), Fromentin <i>et al.</i> (2001), Lindholm <i>et al.</i> (2001), Blanchard <i>et al.</i> (2005), Robichaud and Rose (2006)
	<i>Gadus macrocephalus</i>		*	*	*						*		*				Laurel <i>et al.</i> (2007, 2009)
	<i>Eleginus gracilis</i>		*	*	*								*				Laurel <i>et al.</i> (2007, 2009)
	<i>Merluccius bilinearis</i>	*						*					*	*			Auster <i>et al.</i> (2003)
	<i>Merluccius merluccius</i>		*							*						*	Cartes <i>et al.</i> (2009)
Perciformes	<i>Cheilodactylus spectabilis</i>			*												*	McCormick (1998)
	<i>Micropogonius undulatus</i>		*													*	Eby <i>et al.</i> (2005)
	<i>Pagrus auratus</i>		*										*				Thrush <i>et al.</i> (2002)
	<i>Paralabrax clathratus</i>	*											*				Anderson (2001)
	<i>Sciaenops ocellatus</i>			*				*			*					*	Bachelor <i>et al.</i> (2009)
	<i>Tautoglabrus adspersus</i>		*										*				Levin (1994)
Pleuronectiformes	<i>Buglossidium luteum</i>			*			*		*	*							Amara <i>et al.</i> (2004)
	<i>Hippoglossoides platessoides</i>			*	*							*					Walsh <i>et al.</i> (2004)
	<i>Limanda ferruginea</i>			*	*				*	*		*					Simpson and Walsh (2004), Walsh <i>et al.</i> (2004)

Fish order	Fish species	Life stage analysed			Habitat variables analysed											Reference
		Adult	Juvenile	All	Abiotic							Biotic				
					Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation	Prey resource	
	<i>Hippoglossoides stenolepis</i>		*	*					*			*	*	*		Stoner and Abookire (2002), Stoner and Titgen (2003), Ryer <i>et al.</i> (2004), 2007)
	<i>Lepidopsetta polyxystra</i>	*	*	*					*			*			*	Stoner and Titgen (2003), Ryer <i>et al.</i> (2004), Stoner <i>et al.</i> (2007)
	<i>Limanda limanda</i>	*	*		*										*	Gibson and Ezzi (1987), Hinz <i>et al.</i> (2005)
	<i>Pleuronectes americanus</i>		*		*			*	*	*		*	*	*	*	Manderson <i>et al.</i> (2000), (2002), (2003), (2006), Phelan <i>et al.</i> (2001), Stoner <i>et al.</i> (2001)
	<i>Pleuronectes platessa</i>	*	*	*	*			*	*		*				*	Gibson and Robb (1992), Le Pape <i>et al.</i> (2003), Hinz <i>et al.</i> (2006), Shucksmith <i>et al.</i> (2006), Maxwell <i>et al.</i> (2009)
	<i>Solea solea</i>	*	*	*	*			*	*		*				*	Eastwood <i>et al.</i> (2003), Le Pape <i>et al.</i> (2003), Hinz <i>et al.</i> (2006), Vinagre <i>et al.</i> (2006), Nicolas <i>et al.</i> (2007), Maxwell <i>et al.</i> (2009)
	<i>Microstomus kitt</i>	*									*					Hinz <i>et al.</i> (2006)
	<i>Solea senegalensis</i>			*							*				*	Vinagre <i>et al.</i> (2006)
Scorpaenif-ormes	<i>Sebastes alutus</i>	*										*				Brodeur (2001)
	<i>Sebastes sp.</i>			*					*							Johnson <i>et al.</i> (2003)
Rajiformes	<i>Raja clavata</i>			*	*			*	*							Maxwell <i>et al.</i> (2009)

Fish order	Fish species	Life stage analysed			Habitat variables analysed										Reference	
		Adult	Juvenile	All	Abiotic							Biotic				
					Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation		Prey resource
Mixed	<i>Mixed</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	<p>Iglesias (1981), Macpherson (1981), Sedberry and Vandolah (1984), Mahon and Smith (1989), De Ben <i>et al.</i> (1990), Ekau (1990), Pihl <i>et al.</i> (1991), Gabriel (1992), Gibson (1994), Koslow <i>et al.</i> (1994), Edgar and Shaw (1995), Fujita <i>et al.</i> (1995), Syms (1995), Gutt and Ekau (1996), Farina <i>et al.</i> (1997), McClatchie <i>et al.</i> (1997), Moranta <i>et al.</i> (1998), Piet <i>et al.</i> (1998), Gaertner <i>et al.</i> (1999), Hyndes <i>et al.</i> (1999), Abookire <i>et al.</i> (2000), Dean <i>et al.</i> (2000), Demestre <i>et al.</i> (2000), Ellis <i>et al.</i> (2000), McConnaughey and Smith (2000), Amezcua and Nash (2001), Auster <i>et al.</i> (2001), Hindell <i>et al.</i> (2001), Methven <i>et al.</i> (2001), Williams and Bax (2001), Araujo <i>et al.</i> (2002), Biagi <i>et al.</i> (2002), Francis <i>et al.</i> (2002), Hughes <i>et al.</i> (2002), Lazzari and Tupper (2002), Magnussen (2002), Kaiser <i>et al.</i> (2004), Pittman <i>et al.</i> (2004), Busby <i>et al.</i> (2005), Logerwell <i>et al.</i> (2005), Massuti and Renones (2005), Perry <i>et al.</i> (2005), Leathwick <i>et al.</i> (2006), Sullivan <i>et al.</i> (2006), Wilhelmsson <i>et al.</i> (2006), Anderson and Yoklavich (2007), Medina <i>et al.</i> (2007), Stal <i>et al.</i> (2007), Bergstad <i>et al.</i> (2008), Selleslagh and Amara (2008), Anderson <i>et al.</i> (2009), Ehrich <i>et al.</i> (2009), Katsanevakis and Maravelias (2009), Katsanevakis <i>et al.</i> (2009), Laidig <i>et al.</i> (2009), Langhamer and Wilhelmsson (2009), Moore <i>et al.</i> (2009), (2011), Ordines and Massuti (2009), Persohn <i>et al.</i> (2009), Quiroga <i>et al.</i> (2009), Chatfield <i>et al.</i> (2010), Colloca <i>et al.</i> (2010), Damalas <i>et al.</i> (2010), Keller <i>et al.</i> (2010), Reiss <i>et al.</i> (2010)</p>

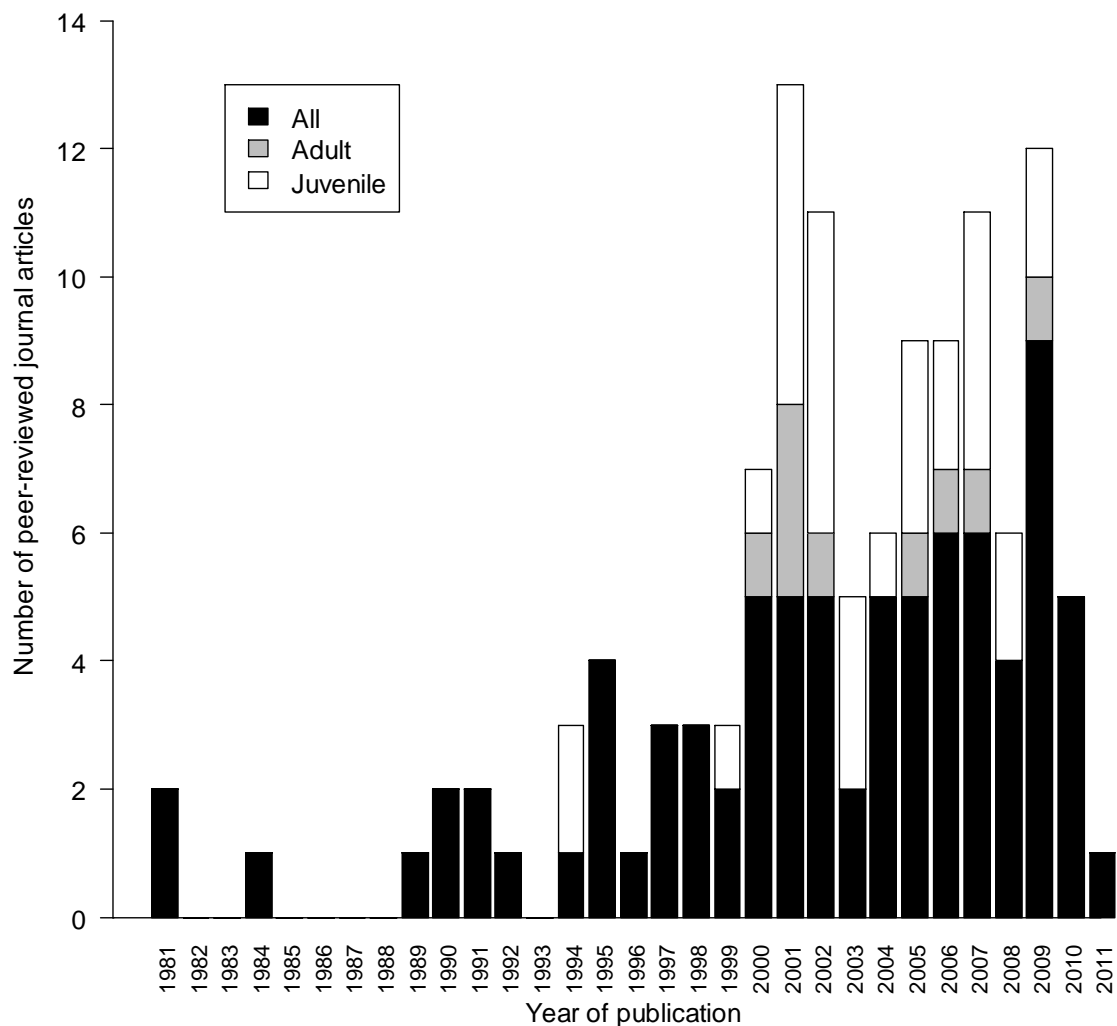


Figure 2.1 Number of peer-reviewed journal articles which have investigated the habitat requirements of temperate demersal fishes (by year of publication). Studies are separated into the major life stages analysed.

The majority of studies (67%) made no clear distinction between adult and juvenile life stages analysed. Juvenile life stages were analysed in 26% of articles whilst 7% studied only the adult life stage (Fig. 2.1). Mixed species communities were studied in 57% of the studies analysed. Of the remaining 42%, Pleuronectiformes dominated the literature (52%) followed

by Gadiformes (25%) and Perciformes (15%) (Table 2.2). The most studied single species were the Atlantic cod (*Gadus morhua*, Gadidae), Common sole (*Solea solea*, Soleidae) and Winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae). Ninety percent of all the non-mixed species studied are currently commercially exploited.

Few studies determining the habitat requirements of temperate demersal fishes came from laboratory studies (8%) with the majority originating from field and stock assessment-derived data (46% each respectively) (Fig. 2.2). Stock assessment-derived data were predominantly (98%) focussed over medium to large spatial scales of study (100s to 100,000s km²), field study-derived data (85%) over medium scales (10s to 100s km²) and laboratory scale data (100%) over the two smallest scales (cm² to m²).

Overall there was a significant difference between the scales at which abiotic and biotic habitat variables were studied ($P < 0.001$, $W_s = 5051$); abiotic variables focussed at larger spatial scales (69% at scales ≥ 100 km²) and biotic variables at low to medium spatial scales (53% at scales ≤ 100 km²) (Fig. 2.3).

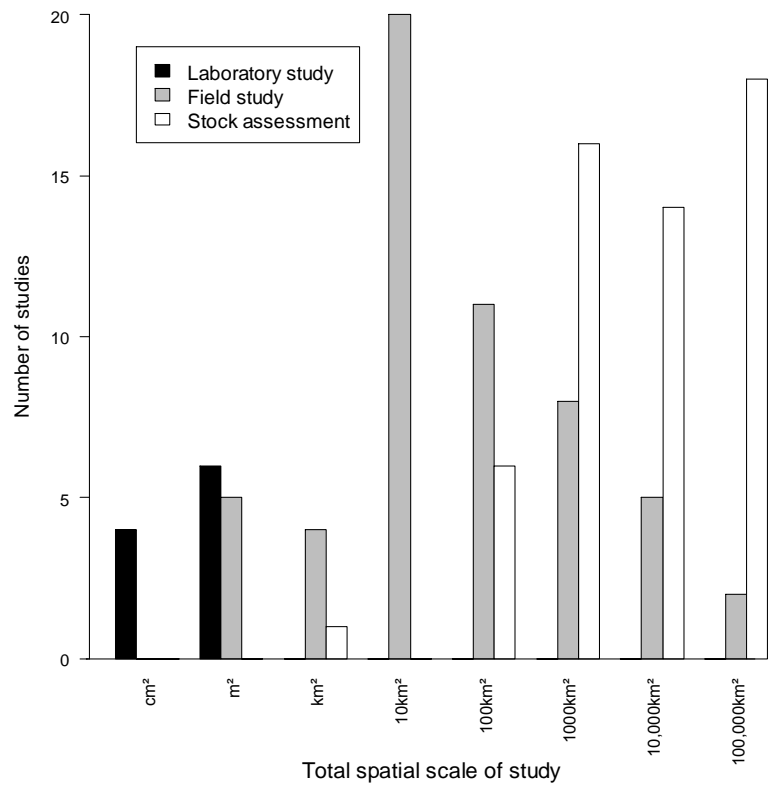


Figure 2.2 Number of studies originating from laboratory studies, field studies and stock assessments by total spatial scale of study.

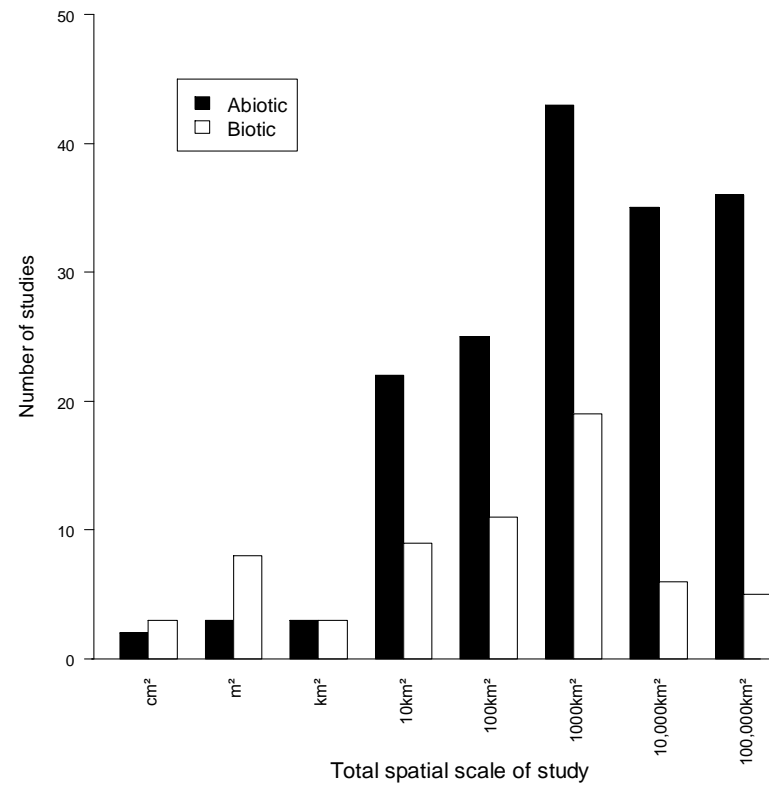


Figure 2.3 Number of studies analysing abiotic and biotic habitat variables by total spatial scale of study.

Assessment of how the proportion of studies showing significant relationships changed with spatial scale was conducted for each habitat variable separately and for the categories 'Total abiotic' and 'Total biotic' (Figures 2.4 and 2.5). For the abiotic variables there was a significant positive relationship between the spatial scale of study and the total number of studies for depth ($R^2 = 0.845$, $F_{1,5} = 35.207$, $P = 0.001$), temperature ($R^2 = 0.767$, $F_{1,4} = 19.766$, $P = 0.004$) and for all 'Total abiotic' ($R^2 = 0.846$, $F_{1,7} = 32.990$, $P = 0.001$) (Fig. 2.4). However when each of these variables and variable combinations was analysed using the proportion of studies which showed a significant relationship, rather than total number of studies, no significant regressions were found. Thus, while the total number of studies increased with spatial scale, there was no apparent increase in the proportion of studies showing significant relationships (Fig. 2.4). For the 'Total biotic' category there was no clear pattern of change in the number of studies with scale, although one biotic habitat variable (competition) showed an increase in the number of studies with increasing spatial scale ($R^2 = 0.663$, $F_{1,5} = 11.812$, $P = 0.014$) (Fig 2.5). There were no significant relationships between the proportion of significant studies and spatial scales of study for any of the individual biotic habitat variables or 'Total biotic' category.

Examination of the distribution of studies among the different habitat variables showed that depth and substrate made up more than half of the abiotic variables analysed (33% and 26% respectively) (Fig. 2.4). The most studied biotic habitat variable was biogenic complexity (48%) (Fig. 2.5). The variables of geography and hydrography, which formed 7% and 0.9% of abiotic habitat variables respectively, and competition and predation, which made up 7% and 5% of biotic habitat variables respectively, were seldom analysed.

Temporal trends were formally analysed in 46% of studies (Fig. 2.6). Annual and monthly differences in habitat requirements were the most common temporal trends analysed in studies (13% each), followed by season (11%) and day (9%).

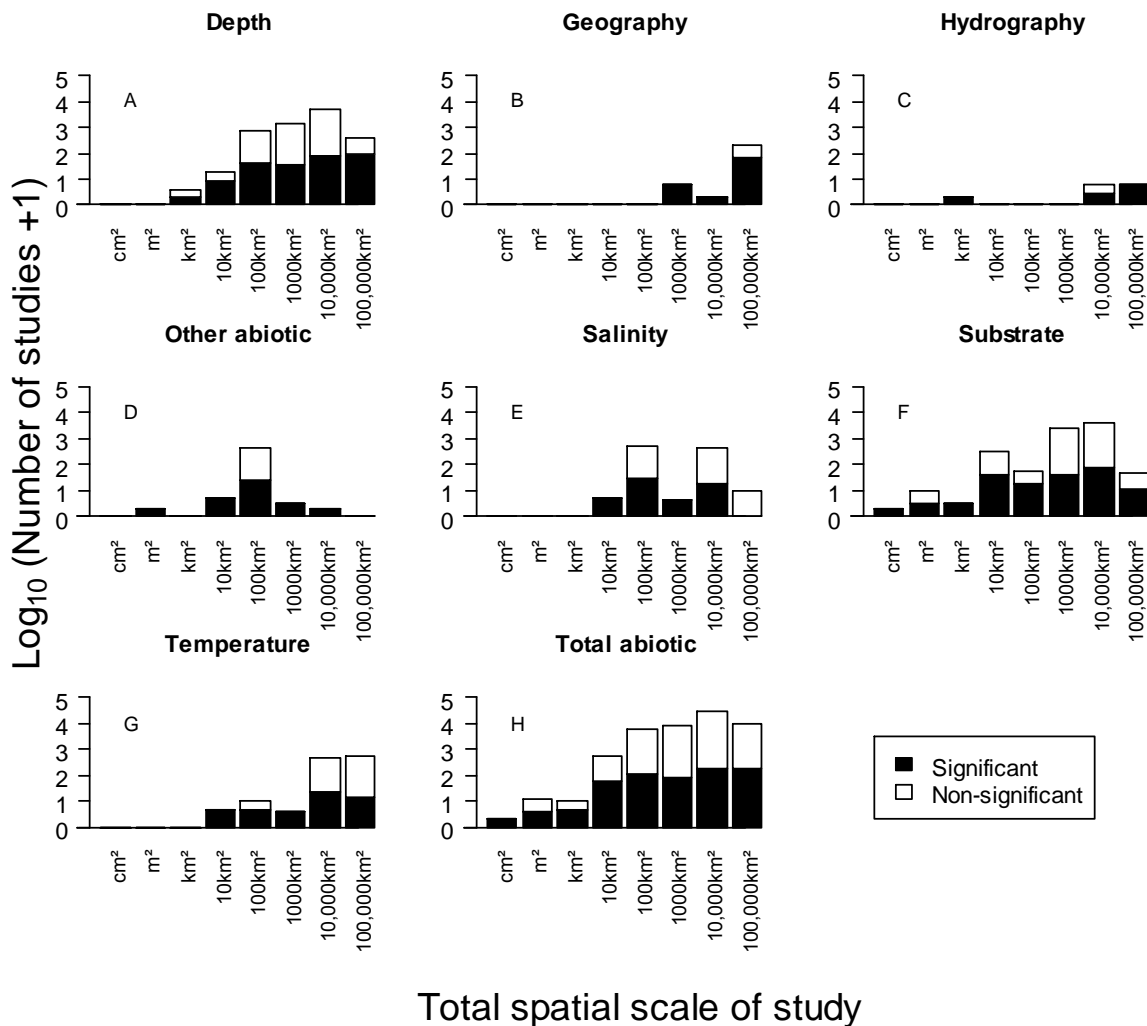


Figure 2.4 Number of non-mixed species studies (those analysing ≤ 4 species) reporting test statistics for each species and each abiotic habitat variable across the total spatial scales of study. Bars indicate the number of studies reporting significant (black) and non-significant (white) results. ‘Other abiotic’ includes the habitat variables of dissolved oxygen / level of hypoxia and light. (A) Depth, (B) Geography, (C) Hydrography, (D) Other abiotic, (E) Salinity, (F) Substrate, (G) Temperature, (H) Total abiotic (all abiotic habitat variables combined).

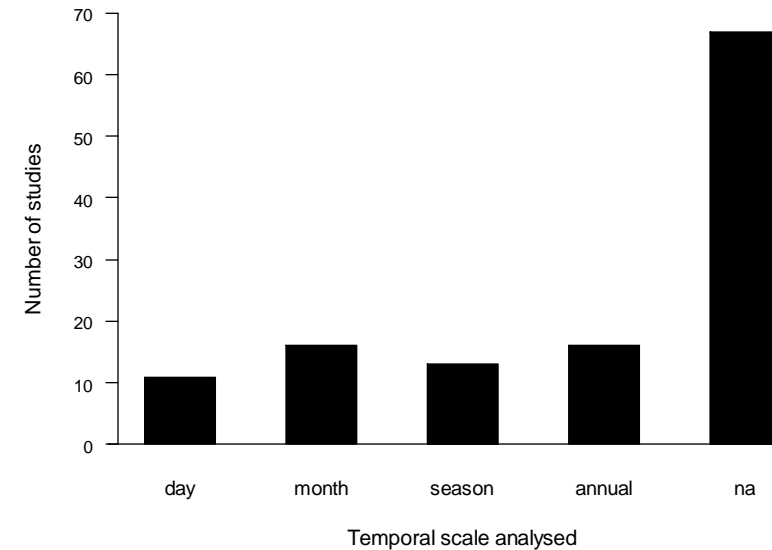
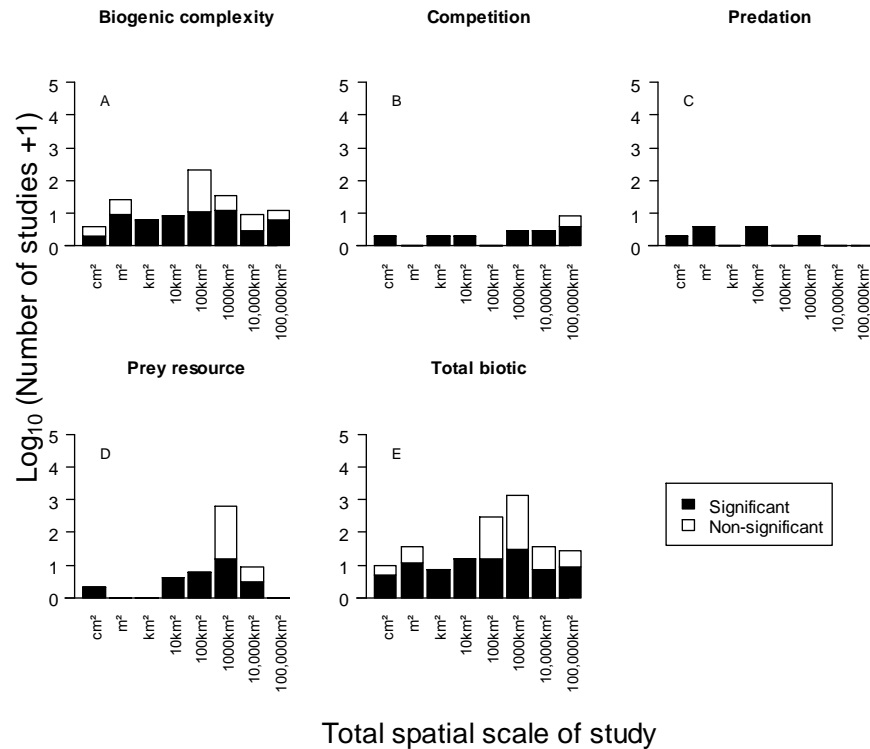


Figure 2.5 Number of non-mixed species studies (those analysing ≤ 4 species) reporting test statistics for each species and each biotic habitat variable across the total spatial scales of study. Bars indicate the number of studies reporting significant (black) and non-significant (white) results. (A) Biogenic complexity, (B) Competition, (C) Predation, (D) Prey resource, (E) Total biotic (all biotic habitat variables combined).

Figure 2.6 Number of studies carried out over different temporal scales: day = 0-24hrs, month = 30 days, season = 90 days, annual = 365 days, na represents the studies that did not analyse any temporal pattern in fish abundance and / or distribution.

2.5 Discussion

2.5.1 Data limitations and considerations

Our comprehensive literature search has allowed us to highlight some important trends and patterns in the identification of demersal fish habitat. It is however important to discuss possible limitations of our approach and the bearing they may have on our conclusions. This quantitative, systematic analysis only included peer-reviewed articles. The inclusion of dissertations, theses, government reports and conference proceedings may have added to the total number of articles reviewed. We do not however believe it would have broadened the scope of the analyses presented as only 5 non-peer-reviewed articles appeared within our search criteria, three of which are known to have been published subsequently as peer-reviewed articles which were then included in our analysis. The exclusion of non-English peer-reviewed articles may well explain the low numbers of studies coming from South America and the complete lack of work originating from Africa and Asia. Nonetheless we have no reason to believe that the patterns identified are likely to be geographically biased other than through the temperate restriction placed on the search criteria. The exclusion of articles prior to 1980 is not likely to have any significant bearing on our findings as we clearly demonstrate that work in this field did not develop substantially until post-1980, with only 4 articles published between 1980 and 1990. The tendency for authors to more readily report significant than non-significant relationships, is likely to have increased the proportion of studies reporting significance. This publication bias is however expected to operate equally across all studies and spatial scales (Brett, 1997) and therefore have little effect on our findings.

2.5.2 *Spatial scale*

The significance of scale in ecological investigations is well understood (Wiens, 1989) and many studies have demonstrated the variable habitat use of temperate demersal fishes over a range of spatial and temporal scales (Bax et al., 1999, Lindholm et al., 1999, Walsh et al., 2004). Our analysis partly supports our hypothesis that many studies focus at large spatial scales. We demonstrate that studies focusing on larger spatial scales primarily analyse abiotic habitat variables while studies addressing biotic variables typically focus at smaller spatial scales. The tendency to study abiotic habitat variables over larger spatial scales may however not be wholly justified as our analysis showed no concomitant increase in the proportion of studies reporting significance at these larger spatial scales. As a result our analyses indicate that there is no reason to limit the study of abiotic variables to large spatial scales. There was however no mismatch between the number of studies and the proportion of those studies in which biotic variables had a significant effect; both the total number of studies and the proportion of significant studies showed no pattern with spatial scale, except for the process of competition where the total number of studies was very low. Thus, although the number of studies of biotic variables is in general low compared to the number of abiotic studies, the spread across all spatial scales for biotic habitat variables is likely justified.

The preponderance of large scale abiotic studies could be a result of data availability, which will be discussed later. However we believe that this also highlights the common assumption in this field that abiotic habitat variables are inherently linked to larger spatial scales, and are most likely to influence the distribution of demersal fishes over larger spatial scales than do biotic habitat variables. This is however unlikely to be wholly the case, and numerous studies demonstrate the importance of abiotic habitat variables over small spatial scales ($\leq 100 \text{ km}^2$) (Stoner et al., 2001, Laurel et al., 2009, Moore et al., 2009) and biotic habitat variables over

larger spatial scales ($\geq 100 \text{ km}^2$) (Bjornstad et al., 1999, Vinagre et al., 2006, Le Pape et al., 2007). The lack of a relationship between the total spatial scale of study and the proportion of significant findings for the habitat variables analysed, leads to the conclusion that there is no definitive spatial scale at which each of the different habitat variables significantly affect the distribution of temperate adult demersal fishes. It is therefore appropriate to analyse the effects of each habitat variable across all of the spatial scales analysed.

As we hypothesised, the high number of studies focussing on large spatial scales may also be explained by the origin of abiotic data. Almost half of the data used in studies has originated from government-funded stock assessments and long-term, large spatial scale, scientific fish surveys. These data sources provide regular and large spatial scale information on fish abundance and local environmental variables that are directly comparable to the spatial scales of commercial fisheries. It is however important to consider that the large distances between sampling stations inherent with fishery-scale data sets means that researchers are often unable to address the processes determining fish distribution that operate at smaller spatial scales (Hinz et al., 2006, Sullivan et al., 2006). An alternative but more costly approach, the use of multi-scale, hierarchical surveys is likely to prove successful in elucidating the role of spatial scale in fish distribution (Pittman et al., 2004, Anderson and Yoklavich, 2007, Anderson et al., 2009, Monk et al., 2011). These approaches warrant further investigation and development as there is still a paucity of studies using hierarchical designs in the field of demersal fish habitat determination.

Many studies utilising large spatial scale data sets often take a 'data-mining' approach, searching for significant relationships between demersal fish abundances and measured habitat variables. This approach has been criticized for shifting our focus away from

hypothesis-driven science, and potentially ascribing coincidental correlations or indirect relationships as direct causal links (Guisan et al., 2002). Insufficient knowledge of the multiple factors influencing the population dynamics of marine species makes it difficult to form prior assumptions about causal relationships. Consequently, correlative approaches that make few or even no prior assumptions about underlying causal relationships, are considered a legitimate approach when attempting to understand the complex interactions between fish populations and their environment (see Valavanis et al., 2008). Correlations revealed from these approaches can in turn be used as the basis for subsequent hypothesis driven studies aiming to determine demersal fish habitat requirements. New statistical approaches such as Quantile Regression (QR) and Structural Equation Modelling (SEM) allow better integration of sound ecological and statistical theory as well as the possibility of testing if data are consistent with hypothesised causal pathways. Development of these approaches provides promising areas for future development (see Pittman et al., 2004, Vaz et al., 2008, Hermoso et al., 2011, Johnson et al., 2012).

2.5.3 Abiotic habitat variables

The bias towards focusing on abiotic variables analysed may be related to the ease with which abiotic data is collected. With the exception of grain size analysis to determine sediment composition, all of the abiotic variables examined require relatively low sampling effort in comparison with that needed to investigate biotic variables (see Levin, 1992). Abiotic habitat variables therefore provide a quick and often resource-effective means of collecting information on some of the habitat requirements that may determine the distribution and abundance of demersal fish species. Whether these variables and the relationships demonstrated are relevant to management strategies will likely be case

dependent, determined by the species of interest, the habitat types covered and the spatial scales over which they occur.

Of the habitat variables studied, depth and substrate have received the most attention. Both may be considered as useful proxies of other variables affecting the habitat choice of demersal fishes. Many previous studies note significant changes in community composition with depth and sediment type in benthic marine assemblages (Moranta et al., 1998, Kostylev et al., 2001, Hagberg et al., 2003). These relationships may indicate more complex associations with available prey communities and / or changes in habitat structure and complexity (Williams and Bax, 2001, Anderson and Yoklavich, 2007, Anderson et al., 2009). Although studies have successfully used depth, substrate and additional abiotic habitat variables in order to fill gaps in habitat knowledge (Last et al., 2010) and as surrogates for habitat suitability (Blanchard et al., 2005), this approach may be misleading depending on the scale of observation and the system under analysis (Chapman et al., 2010). Stevens and Connolly (2004) discuss the inadequacies of using surrogate abiotic measures to describe benthic communities at a range of spatial scales, concluding that less than 30% of the biological similarity between areas at scales covering tens of square kilometres could be explained using their abiotic proxies. Williams et al. (2009) similarly demonstrated that using a habitat characteristic describing geomorphic features over thousands of square kilometres to describe megafaunal communities, led to a misrepresentation of species' rarities. It is therefore necessary that in order to describe and classify benthic communities and habitats with accuracy using only abiotic variables, they must first be calibrated against correlated biotic variables. This has been reflected in some habitat suitability studies that find that the best predictors of habitat suitability are models combining abiotic variables with biotic ones, such as prey density (Vinagre et al., 2006) and individual organismal traits (Le Pape et al.,

2007). Planque et al. (2011) also discuss the inadequacy of expecting environmental (abiotic) habitat variables to fully explain the spatial distributions of fish populations unless their forcing effects are so strong as to over-ride all other factors driving the distribution.

2.5.4 Biotic habitat variables

There is a general paucity of studies addressing the importance of biotic habitat variables in determining the distribution of demersal fish populations. Authors investigating the importance of different abiotic habitat variables often explained their results with reference to biotic habitat variables. Few studies however formally analysed the influence of biotic habitat variables, particularly predation and competition, despite their known importance in determining the abundance and distribution of marine fishes (see Ward et al., 2006, Engelhard et al., 2008, Laurel et al., 2009). Studies addressing the importance of biotic habitat variables tended to focus at smaller total spatial scales of study compared to abiotic variables. Apart from substrate choice experiments, the two smallest spatial scale classes analysed (cm^2 and m^2) were dominated by biotic habitat variables. These spatial scales represent studies simulating environmental conditions using artificial laboratory habitat constructions. This approach provides the advantage of direct and continuous observation whilst controlling for additional habitat variables. The disadvantages however are well documented and highlighted by many authors working at this spatial scale. In an experiment aiming to investigate the role of variability in seafloor habitat structure on the survivorship of post-settlement juvenile Atlantic cod, Lindholm et al. (1999) acknowledged that limited space in such experiments does not allow for realistic foraging of predators or escape responses of prey. Manderson et al. (2000) also note that long experimental durations and small arena sizes provide increased predator-prey encounter rates in the laboratory, which are not wholly realistic for scaling up to conditions in the field.

Field validation of results from laboratory studies can help substantiate laboratory findings and may also elucidate previously overlooked variables important in determining habitat choice. Such validation may be undertaken directly by designing comparable experiments in the field or alternatively using pre-existing data to test relationships found within the laboratory. Stoner and Abookire (2002) provide an excellent example of the combination of laboratory and field experiments in their study of sediment preferences in Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae). Laboratory experiments showed detailed sediment preferences associated with fish size and burial capability. Subsequent field results overestimated the preferred sediment grain size of fish but still supported the hypothesis that sediment suitability was based on settlement capability. The authors also go on to discuss dissimilarities between laboratory and field results, highlighting discrepancies that may exist when extrapolating from small scale manipulative studies to larger spatial scales.

2.5.5 Temporal aspects of habitat

Although the dynamic nature of fish habitat is widely acknowledged (Rice, 2005), less than half of the studies reviewed looked at temporal patterns in habitat usage. Our results also support our previous suggestion that more work is needed to analyse the habitat requirements of demersal fishes temporally. Many studies utilising data from long-term, large-scale stock assessment surveys grouped annual data, meaning that between-year differences in abundance and distribution were not considered. Pooling data may give wider applicability to findings but it also reduces the accuracy and hence predictive power of the results for the specific scenario that has been analysed (Valavanis et al., 2008). Differences in habitat suitability within and between habitats as well as important additional information such as fish year class strength, variations in abundance and shifts in habitat use may be missed when

temporal data are pooled. For example, studies by Manderson et al. (2002, 2003) on the growth, habitat variation and dynamic settlement in Winter flounder demonstrated that the influence of temperature and salinity on growth varied considerably from late spring into summer. Such studies also highlight the importance of considering location when analysing temporal differences in habitat suitability. In the previous example, freshwater inputs associated with estuaries caused complex changes in temperature and salinity. This is likely to cause large variations in predator-prey dynamics and the overall suitability of habitat important to the juvenile life stage of the study species (Gibson, 1994, Manderson et al., 2006, Bacheler et al., 2009).

If researchers are to provide sound advice to managers on temporal distributions and predictions of future abundances, spatio-temporal approaches must be taken, in which temporal and spatial scales are matched *a priori*. For example, it would be impractical for a study covering thousands of square kilometres to attempt to analyse changes in habitat use over daily time scales. Similarly over very small spatial scales it would be inefficient to look at seasonal patterns in habitat use in demersal fish species, some of which are known to migrate large distances during annual spawning events (Armstrong et al., 1992, Hunter et al., 2003a). The use of data storage tags will significantly aid in identifying appropriate spatial and temporal scales of study from which to start, however such methodologies are expensive and currently rare. Such obvious examples highlight the clear need to plan sampling campaigns which incorporate appropriately matched temporal and spatial scales.

2.5.6 Ontogenetic changes in habitat use

Consideration of temporal patterns in habitat suitability is also important with respect to the ontogenetic changes which demersal fish species undergo during their development. Bacheler

et al. (2009) showed how habitat use patterns of sub-adult red drum (*Sciaenops ocellatus*, Scianidae) in estuarine environments were age-dependent as well as region-dependent at large spatial scales, whilst Laurel et al. (2007) demonstrated habitat selection in Pacific halibut and rock sole (*Lepidopsetta polyxystra*, Pleuronectidae) was mediated by the interaction between temperature, ontogeny and density under laboratory conditions. Our analysis showed that fewer than half of studies clearly defined the life stages of the fish species analysed. Although combining juvenile and adult life stages may simplify sampling strategies and increase statistical power, it prevents ontogenetic changes in sensitivity and habitat requirements from being exposed. Those studies that did define life stage were often those focussed on post-larval settlement and habitat choices of juvenile fishes. Such investigations typically operate at small spatial scales, ranging from square centimetres to tens of square kilometres, often in laboratory or estuarine and shallow coastal environments (Stoner and Titgen, 2003, Manderson et al., 2006, Laurel et al., 2007, 2009). Past studies have also shown the importance of separating analyses by sex, especially in relation to spawning events and intraspecific competition between sexes (Sims et al., 2006, Dwyer et al., 2003, Cadrin and Silva, 2005). To facilitate comparisons among studies and reduce ambiguity, there is a clear need for the specific life stages, and in certain cases, the sexes examined to be clarified. If neglected, conclusions may apply only to the dominant life stages within original samples and direct comparisons among studies may prove difficult.

2.5.7 Non-commercial and rare species

As well as a clear focus on mixed life-stages and mixed species, studies have generally concentrated on commercially targeted demersal fish species. Few studies however have attempted to define the habitat variables determining the distribution and abundance of rare species, even where these are commercially valuable. For example, skate and ray species

(Batoidea), which are known to be threatened by overfishing and habitat degradation (Hilton-Taylor, 2010) have been seldom studied, even though such species often require species-specific studies to detect declines in population numbers (Dulvy et al., 2000). Such deficiencies in data and studies of rare species distributions may hamper advice for conservation management strategies aiming to protect these or similar species.

2.5.8 Habitat suitability modelling

The number of studies in the field of demersal fish habitat associations has increased significantly over the past 20 years. This increased research effort has led to many advances in the methods and techniques used to address demersal fish habitat associations. Habitat suitability modelling has provided one attractive approach, as theoretically, results for a particular species should be applicable across systems (Rubec et al., 1999). Traditionally, many of these models assumed smooth, continuous and linear or simple polynomial relationships between habitat variables and fish populations. It is however often apparent that such functions cannot wholly predict the main processes modulating fish occurrence (see Caddy, 2007). There now exist a suite of modelling approaches that are able to deal with more complex, and biologically realistic relationships; GAMs combined with GIS platforms are generally considered the most well developed method for modelling fish habitat use (Stoner et al., 2001, Stoner et al., 2007, Valavanis et al., 2008, Bacheler et al., 2009, Katsanevakis and Maravelias, 2009).

Progress may also be made through combinations of different models that account for weaknesses of each of the constituent models used. For example, machine-learning techniques are accurate predictors of complex non-linear relationships with the additional

ability to learn using training algorithms applied to random data subsets. They are however not good predictors of habitat suitability for new or unsampled sites (Maravelias et al., 2003, Pittman et al., 2009, Knudby et al., 2010). Presence-only algorithms on the other hand are able to assess new site suitabilities defined in terms of their environmental similarity (see Monk et al., 2010). Such algorithms could therefore potentially be integrated with machine-learning techniques in order to improve shortfalls in assessments of new site suitabilities whilst accurately predicting complex non-linear relationships. Planque et al. (2011) also recommend a combinatory, multi-model approach to increase the accuracy of predictions and our overall understanding of factors controlling the spatial distribution of fish populations. This is especially important when considering the recent popularity of bioclimatic envelope models that aim to predict future distributions but include strong assumptions about the factors that determine population distributions (Cheung et al., 2009, 2011). Although an area showing promise, complex modelling approaches still need to address the numerous issues related to assumption violation, particularly with respect to spatial auto-correlation and data independence as well as model validation, evaluation and the integration of sound ecological theory (Knudby et al., 2010).

2.5.9 Technological advancements

Technological developments have also played an important role in allowing researchers to answer increasingly complex and logistically challenging questions. Direct, in-situ observations using underwater camera apparatus can inform us about patterns of distribution on small scales (Holmes et al., 2008), certain fish-habitat associations (Busby et al., 2005, Anderson and Yoklavich, 2007) as well as detailed behavioural information (Stoner et al., 2008), all of which are unattainable using trawl methodologies alone. Similarly, advances in tagging technologies, including acoustic telemetry and data storage (DST) tags, can give us

information on locations and times of residency of individual fish (Lindholm et al., 2007, Alos et al., 2011, Andrews et al., 2011) as well as additional data such as depth, temperature and information on swimming behaviours (Hunter et al., 2003a, Hunter et al., 2003b). Such precise observations can give in-depth, real-time insights into the movement and behaviour of demersal fish and differential habitat uses when analysed in conjunction with corresponding habitat maps or benthic images (Sims et al., 2001).

Only 5-10% of the world's seafloor is currently mapped at resolutions similar to terrestrial studies (see Wright and Heyman, 2008). This lack of benthic habitat maps over large scales has somewhat limited our ability to study the importance of landscape configuration and composition as well as benthic community structure on demersal fish distributions (Wright and Heyman, 2008, Moore et al., 2011). Acoustic sensing devices are now widely recommended as a method to sample large areas of the benthic marine environment (Williams and Bax, 2001). Sidescan sonars and multibeam swath bathymetry systems may now be used to produce accurate maps of seafloor substrates and bottom topography, allowing characterisation of benthic habitats across large areas with potentially increased accuracy and decreased sampling times compared to sediment surveys and fishers' interpretations (Kloser et al., 2001, Kostylev et al., 2001, Freitas et al., 2006, Van der Kooij et al., 2011). However the accuracy of a ground-truthed acoustic map, when extrapolated to larger scales, has often been debated (Bax et al., 1999, Diaz et al., 2004, Brown et al., 2011). Such an approach for large scale habitat classification has potential but will often require costly ground-truthing during field surveys (Freeman and Rogers, 2003, Roberts et al., 2005, Holmes et al., 2008). The data density mismatches between physical and biological methods will however remain unsolved unless acoustic methods can routinely resolve the elusive biological components that make a physical substrate a habitat (Diaz et al., 2004). Until then,

acoustic methods may still be used to better target benthic sampling, aid decisions regarding study scale or resolution and provide good baselines from which more detailed habitat information can be determined (Freeman and Rogers, 2003, Roberts et al., 2005).

A lot of work has been undertaken to relate acoustic maps with benthic communities, using a variety of ground-truthing methods in combination with multivariate analysis techniques (Walsh et al., 2004, Anderson and Yoklavich, 2007, Holmes et al., 2008). Moore et al. (2010, 2011) provide a good example of the ‘landscape’ approach, relating benthic habitat to demersal fish distribution using a distance based multivariate linear model (DISTLM). The authors found that a combination of depth and 6 of the 23 abiotic landscape indices explained 34.8% of the variation in the fish assemblage, demonstrating the validity of using broad scale landscape analysis along with indices of landscape configuration and composition to explain distribution patterns in temperate demersal fish assemblages. Such approaches are now considered a vital first step in unraveling ecological complexities providing improved spatial information for management of marine systems (Brown et al., 2011).

2.6 Conclusion

Determining the habitat requirements of demersal fish species is inherently difficult due to the complex nature of marine ecosystems, the multiple factors affecting fish-habitat associations, the range of scales over which they act and the general difficulties of sampling marine habitats. Defining fish-habitat relationships will however be one of the necessary steps towards the advocated ecosystem based approach to fisheries management and the sustainable exploitation of demersal fish stocks. Many developments in techniques and technologies show promise in elucidating the complex interactions between demersal fishes

and their habitat. The successful application of such developments will however strongly rely on the the quality of the data used combined with understanding of the fundamental ecology of the systems and species under study (Austin, 2007). Where possible, it will therefore be advantageous to test habitat variables under controlled experimental conditions (i.e. small-medium spatial scales), building results from such studies into larger scale models.

Our analysis highlights some important trends in the field of demersal fish habitat determination. The reasons behind the focus on larger scales are no doubt a result of a combination of factors. It is however clear that to advance the field there should be a move towards the investigation of abiotic variables at smaller spatial scales as well as increased attention to the analysis of biotic habitat variables over all spatial scales of study. This will help describe distributions determined by abiotic habitat variables that may act over small spatial scales not previously considered and allow biotic-based causal relationships to be better explained. It will therefore be necessary to invest in the implementation of more, smaller spatial scale data collections or alternatively increase the resolution of larger spatial scale data sets. Work investigating the power of monitoring surveys to detect trends in abundance (e.g. Blanchard et al., 2008) will therefore prove invaluable in the design of future studies and surveys.

Defining temporal aspects of habitat will also prove valuable in advancing ecological understanding of the species under study. The inclusion of longer time scales and the consideration of temporal differences in habitat use may also provide important information on the cumulative effects of human-induced impacts, the overall status and recovery of impacted systems and increase capabilities to predict future change of the species or system under study (Hewitt et al., 2001). We argue that through attention to the areas highlighted

herein, along with more holistic definitions of habitat, researchers are likely to be better equipped to inform management at a range of spatial and temporal scales.

CHAPTER 3

Effect of prey abundance and size on the distribution of demersal fishes

3.1 Abstract

Many demersal fish species rely on benthic prey as food sources for part of, or in some cases, all of their life history. We investigate the relationships between prey and predator abundance and prey size and predator mouth gape size for nine demersal fish species. Of the species analysed, four showed a significant positive increase in abundance with increasing prey abundance. Prey size is thought to be an important parameter for demersal fish that are limited in their feeding potential by their mouth gape size as it will influence consumption rate and energy expenditure while foraging. The relationship between prey size and mouth gape was investigated using both stomach content data and prey availability data. Stomach content analysis revealed positive relationships between maximum prey size and predator mouth gape size for six of the species. Indications of prey size selectivity were only seen in the environment for European Hake (*Merluccius merluccius*) highlighting the potential importance of prey size over prey abundance for this species. The results demonstrate that prey abundance and size are of significance for some demersal fish species feeding primarily on benthos and will help in defining habitat requirements of demersal fish species.

Key words: demersal fishes, abundance, size, predator-prey relationships

3.2 Introduction

Concerns regarding the long-term sustainability of marine fisheries and the detrimental effects of bottom trawling have led to numerous studies examining the response of benthic communities following disturbance. Many describe decreased faunal abundance, biomass and species richness (Jennings et al., 2001b, Hinz et al., 2009) as well as reduced benthic production and size structure (Hiddink et al., 2006b, Queiros et al., 2006) with increasing trawl disturbance. In order to predict the effects of decreased benthic community biomass, abundance, size structure and species richness on ecologically and commercially valuable predators, it is essential to understand the bottom-up (control through food abundance) effects on these predators.

The importance of predators and prey in regulating the size, abundance and distribution of one another has become a central tenet in marine ecology (Gilinsky, 1984, Hixon and Carr, 1997). With an ever-increasing interest in an ecosystem-based approach to fisheries management (Link, 2002), understanding such predator prey interactions is important. This is reiterated when we consider the effects of both predator removal causing trophic cascades and changes in food webs dynamics (Frank et al., 2005) and prey removal resulting in growth, condition and habitat preference implications (Booth and Alquezar, 2002).

The history of studies of predator prey relationships within fish biology is considerable yet the majority of studies have been carried out in closed (laboratory, pond or lake) or semi-closed (river) systems (Mesa et al., 1994) and few have studied demersal species. Studies that do look at broader-scale, open marine systems generally focus on large-or-mega-scale communities, often focussing on pelagic fish prey species. Consequently, there is a

comparative paucity of work within medium-scale (here defined as tens of kilometres) open marine systems, and in particular multispecies demersal fish communities.

Differences in the distributions of demersal fishes are expected to reflect variations in habitat suitability (Hinz et al., 2003). Habitat selection is likely to be determined by a combination of biotic and abiotic factors acting over different scales. These may include abiotic factors such as depth and temperature that vary over large scales (Genner et al., 2004, Moranta et al., 1998) as well as small-scale biotic interactions such as predation (Werner et al., 1983), competition (Hixon and Jones, 2005, Werner and Hall, 1979), habitat complexity (Almany, 2004, Angel and Ojeda, 2001), and prey availability (Hinz et al., 2005, Pinnegar et al., 2003). Although prey selection itself may be based on the actual abundance and availability of prey within the environment (Gill, 2003, Hinz et al., 2005), prey size is also known to be an important factor determining consumption (Juanes and Conover, 1994, Scharf et al., 2000).

The mouth gape of a fish restricts the maximum size of prey that it can consume. Many studies have demonstrated the importance of mouth gape and prey size in determining consumption and the subsequent condition and growth in the early life stages of fishes (Knutsen and Tilseth, 1985, Mittelbach and Persson, 1998). However, few consider the adult stages and how these two parameters may affect habitat preferences and the subsequent distribution of individuals. In general, habitat selection theories such as MacCall's basin theory (MacCall, 1990) or the ideal free distribution (IFD) theory (Fretwell and Lucas, 1969) predict that freely moving individuals will select areas of high resource quality over neighbouring areas of lower quality, ultimately leading to a density distribution that is proportionate to the amount and quality of the resource available.

The main objective of this study was to investigate the relationships between demersal fishes and the abundance and size of their benthic prey species. The study takes an exploratory approach and uses data collected from a standard fish stock assessment survey. First, we tested the hypothesis that over the scale of the Balearic Islands, Spain, demersal fish abundance is limited by prey abundance. Second, through stomach content analysis, we assessed the relationship between predator mouth gape and the size of prey eaten to determine whether selected species showed prey size selectivity that would be indicative of limitations in feeding potential due to mouth gape size. While prey selection is related to numerous factors in addition to prey size, such as prey handling time, capture probability and prey encounter (simultaneous vs sequential) (Gill, 2003), these parameters are largely only quantifiable through detailed experimental approaches. Owing to the accessibility of prey size data from our survey data, we focused on the relationship between predator size and prey size within this study. Using prey lists identified for each individual predator, and mean individual prey mass as a measure of individual prey size from sites around the Balearics, we tested the hypothesis that the mean mouth gape of predators showing prey size selectivity is limited by the mean prey size over an island scale.

3.3 Materials and Methods

3.3.1 Sample site

The samples used in this study were obtained on the continental shelf around the Islands of Mallorca and Menorca (Balearic Islands, western Mediterranean, Fig. 3.1). The waters surrounding the Balearics are considered a transition region between the Mediterranean Sea and the Atlantic Ocean, characterised by the convergence of large water masses, intense frontal systems and a low supply of nutrients from land run-off (Pinot et al., 1995, Vélez-

Belchí and Tintoré, 2001). The majority of vessels fishing the continental shelf are small-scale commercial and recreational boats using a diverse range of gears targeting a wide array of species predominantly between 0 and 800 m (Lleonart et al., 1999, Morales-Nin et al., 2005).

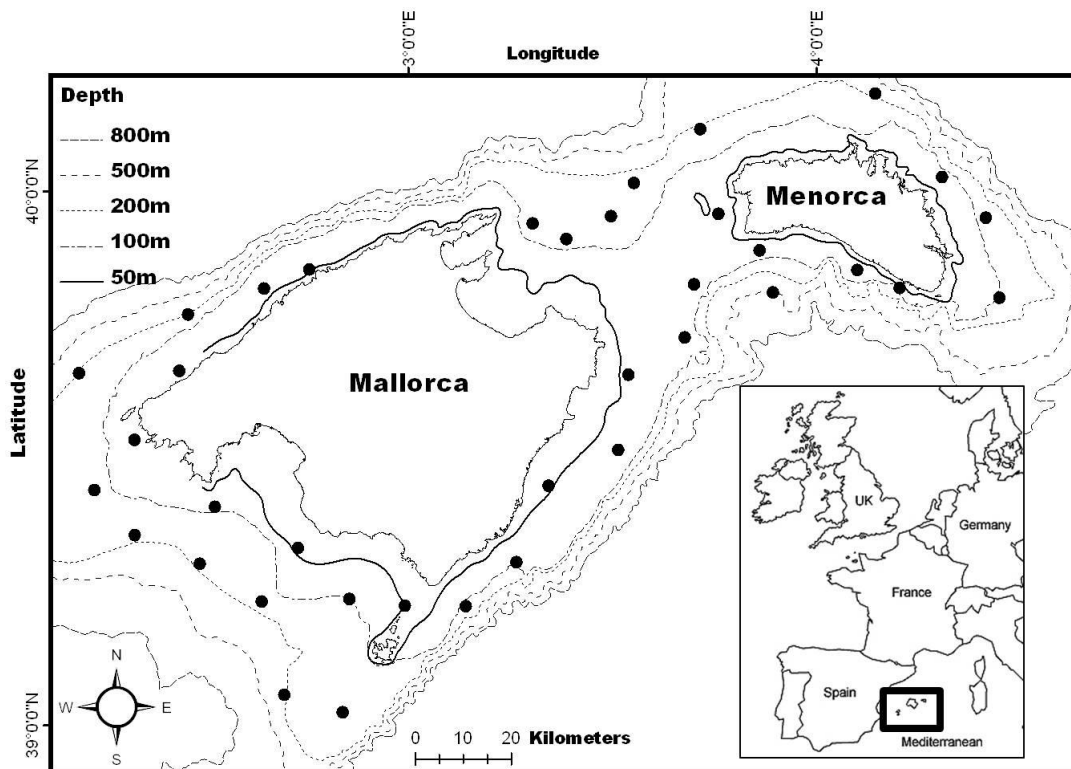


Figure 3.1 Map of the study area around Mallorca and Menorca (Balearic Islands, western Mediterranean) showing annual trawl locations (black circles).

3.3.2 Fish and epifauna data

Fish and epifaunal data from MEDITS groundfish surveys carried out by the Instituto Español de Oceanografía (IEO) in May and June from 2003 to 2009 were used for analysis. The survey used a GOC73 trawl with an aperture of approximately 17m (horizontal) x 3.2m (vertical) with a cod end mesh size of 20mm to sample both fish and epifauna. The same gear

and sampling regime has also been previously used to analyse the relationship between epifauna and demersal fishes by Ordines and Massuti (2009). Duration of tows varied from between 20 to 60 mins at a mean speed of 2.8 km per hour. All catches were standardised to 1 km². Within each haul, total abundance and biomass of all species (vertebrate and invertebrate) was recorded as well as individual length and mass of selected fish species. Owing to the origin of the data collection actual size data (lengths and widths) for individual prey items caught in each trawl were not available. Consequently the measure of mean individual prey mass (total biomass of each prey species in a haul divided by the number present) was used as a measure of prey size in the environment at each site. For a more detailed description of the MEDITS survey, including survey sites, see (Massuti and Renones, 2005).

Nine demersal fish species, making up 74% of total fish biomass and 59% abundance and caught from 2003 to 2009, were selected for the analyses. The selected species were as follows: red gurnard (*Chelidonichthys cuculus*), streaked gurnard (*Chelidonichthys lastoviza*), blue mouth (*Helicolenus dactylopterus*), four-spot megrim (*Lepidorhombus boscii*), European hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), thornback ray (*Raja clavata*), small spotted catshark (*Scyliorhinus canicula*), and greater weever (*Trachinus draco*). Only the demersal, epifaunal feeding stages of each species were included in the analysis. These stages were defined as any size classes (10 equally sized intervals from the minimum to maximum size caught in 2008) containing more than 60% benthic epifaunal prey species by abundance in their diet. Prey species included all benthic epifauna including fish species that appeared in the stomach contents of the predators more than once between 2007 and 2009. The 60% benthic prey threshold was chosen because it showed good agreement

with the literature for dominant prey types for each species' corresponding size class. Although increasing this threshold further would have ensured a more precise definition of benthic epifaunal feeders, it would also have increased the risk of unnecessarily removing predator size classes (or in extreme cases whole species) on which our hypotheses could be tested. A total of 286 hauls, from a depth of between 38 and 737 m, collected over 7 years (approximately 40 per year) were used for the analysis of fish and epifauna.

3.3.3 Stomach contents

Predator stomach contents of up to 10 individuals from each centimetre size class caught in each trawl were identified to the highest taxonomic resolution possible in order to identify the prey of the nine chosen fish species. This study was interested in prey size selectivity and used the maximum prey dimension as the measure of prey size, measured to the closest 0.1 mm using vernier calipers. Maximum prey size has previously been closely associated with gape size and allometric relationships and was therefore the best candidate for the measure of prey size (see Scharf et al 2000). In total, 750 stomachs were sampled from 29 ± 9 (standard deviation, SD) stations spread over three MEDITS surveys (2007- 2009). For details of the trophic analyses of each species, see Table 3.1.

Table 3.1 Descriptive statistics for each of the fish species analysed, including the number of different prey species of each and the number of trawl sites from which they were collected.

Predator species	n	Body Length (mm)			No. prey species	No. trawl sites
		Min.	Mean	Max.		
Red gurnard (<i>Chelidonichthys cuculus</i>)	96	120	186	300	14	33
Streaked gurnard (<i>Chelidonichthys lastoviza</i>)	110	90	178	260	10	33
Blackbelly rosefish (<i>Helicolenus dactylopterus</i>)	34	110	162	280	11	13
Four-spot megrim (<i>Lepidorhombus boscii</i>)	37	130	203	330	16	37
European hake (<i>Merluccius merluccius</i>)	87	100	243	470	7	28
Blue whiting (<i>Micromesistius poutassou</i>)	61	20	248	300	7	14
Thornback ray (<i>Raja clavata</i>)	141	50	555	910	17	32
Small spotted catshark (<i>Scyliorhinus canicula</i>)	129	130	367	510	24	43
Greater weever (<i>Trachinus draco</i>)	55	140	201	280	14	30

Table 3.1a Table highlighting all prey species and abundance in diets of the demersal fishes analysed.

Prey composition of the stomach contents of each predator from surveys in 2007 to 2009									
Prey species	<i>C. cuculus</i>	<i>C. lastoviza</i>	<i>H. dactylopterus</i>	<i>L. boscii</i>	<i>M. merluccius</i>	<i>M. poutassou</i>	<i>R. clavata</i>	<i>S. canicula</i>	<i>T. draco</i>
<i>Actiniidae</i>	0	0	0	0	0	0	0	2	0
<i>Alpheus glaber</i>	13	0	3	8	5	0	15	10	4
<i>Amphipoda</i>	17	89	3	8	2	0	13	51	19
<i>Annelida</i>	0	1	0	0	0	0	3	36	3
<i>Aphia minuta</i>	1	0	0	0	3	0	3	0	3
<i>Aphroditidae</i>	0	0	1	0	0	0	0	11	0
<i>Argentinidae</i>	0	0	0	0	1	0	0	0	0
<i>Arnoglossus laterna</i>	0	0	0	0	1	0	0	0	0
<i>Ascidia spp</i>	0	0	0	0	0	0	0	1	0
<i>A.rotundatus</i>	0	0	0	0	0	0	5	3	1
<i>Bathynectes spp.</i>	0	0	0	0	0	0	1	0	0
<i>Bivalvia</i>	0	1	0	0	0	0	1	1	1
<i>Calappa granulata</i>	0	0	0	0	0	0	3	0	0
<i>Callionymus sp</i>	5	1	0	0	0	0	1	1	1
<i>Cancer pagurus</i>	0	0	0	0	1	0	0	0	0
<i>Capros aper</i>	0	0	0	0	0	0	0	1	0
<i>Cavolinia inflexa</i>	0	0	4	0	0	0	0	0	0
<i>Centracanthus cirrus</i>	0	0	0	0	1	0	0	0	0
<i>Cephalopoda</i>	6	2	3	1	5	3	7	40	2
<i>C. macrophthalma</i>	0	0	0	0	1	0	1	3	0
<i>Chauliodus sloani</i>	0	0	1	0	0	0	0	0	0
<i>C. cuculus</i>	0	0	0	0	0	0	1	0	0
<i>C.crassicornis</i>	3	0	0	2	15	0	28	1	1
<i>Citharus linguatula</i>	0	0	0	0	0	0	1	0	0
<i>Copepoda</i>	0	0	0	2	0	0	0	0	0
<i>Crangonidae</i>	66	91	2	1	8	0	7	5	13

Prey species	<i>C. cuculus</i>	<i>C. lastoviza</i>	<i>H. dactylopterus</i>	<i>L. boscii</i>	<i>M. merluccius</i>	<i>M. poutassou</i>	<i>R. clavata</i>	<i>S. canicula</i>	<i>T. draco</i>
<i>Crustacea</i>	45	42	13	10	31	4	16	48	21
<i>C.linearis</i>	1	0	0	0	1	0	0	0	1
<i>Cymbulia peronii</i>	0	0	3	0	0	0	0	0	0
<i>C.mediterranea</i>	0	2	0	0	0	0	0	0	0
<i>Dardanus arrosor</i>	0	0	0	0	0	0	1	7	0
<i>D.quadrimaculatus</i>	4	0	0	0	0	0	0	0	7
<i>D. bimaculata</i>	0	3	0	0	0	0	0	0	1
<i>Diplodus sp.</i>	0	0	0	0	0	0	0	1	0
<i>Echinoidea</i>	0	0	0	0	0	0	3	2	0
<i>Echiodon dentatus</i>	0	0	0	0	1	0	0	0	0
<i>Esponja 110</i>	0	0	2	0	0	0	0	0	0
<i>Ethusa mascarone</i>	0	1	0	0	0	0	4	0	0
<i>Euphausiacea</i>	60	23	7	8	20	21	27	68	65
<i>Gadiculus argenteus</i>	0	0	0	3	2	4	4	0	0
<i>Galatheidae</i>	17	79	1	2	0	0	6	12	13
<i>Gobiidae</i>	22	3	0	2	3	0	8	2	14
<i>Goneplax rhomboides</i>	1	0	0	5	0	0	4	0	1
<i>H.dactylopterus</i>	1	0	0	0	0	0	2	0	0
<i>Huevos</i>	0	0	0	0	0	0	0	2	0
<i>Hygophum hygomii</i>	0	0	0	0	1	2	0	0	0
<i>Ilia nucleus</i>	0	0	0	0	0	0	0	1	0
<i>Inachus spp</i>	2	1	0	0	0	0	0	0	0
<i>Isopoda</i>	6	28	55	21	4	6	62	65	9
<i>Laetmonice hystrix</i>	0	0	0	0	0	0	0	0	1
<i>L.crocodilus</i>	0	0	0	0	1	2	0	0	0
<i>Larva crustáceo</i>	3	0	0	0	0	0	0	0	0
<i>Larva pez</i>	8	0	1	3	0	0	3	1	10
<i>Lepidopus caudatus</i>	0	0	0	0	2	0	0	0	0

Prey species	<i>C. cuculus</i>	<i>C. lastoviza</i>	<i>H. dactylopterus</i>	<i>L. boscii</i>	<i>M. merluccius</i>	<i>M. poutassou</i>	<i>R. clavata</i>	<i>S. canicula</i>	<i>T. draco</i>
<i>Liocarcinus sp.</i>	53	64	1	15	0	0	34	13	13
<i>Lophogaster typicus</i>	64	3	5	8	19	0	49	44	5
<i>M.tuberculatus</i>	6	1	2	3	0	0	23	4	3
<i>Macropodia sp.</i>	1	0	0	0	0	0	0	0	0
<i>Mauolicus sp.</i>	0	0	0	0	3	1	0	0	0
<i>M.norvegica</i>	0	0	7	1	0	25	2	33	0
<i>Merluccius merluccius</i>	1	0	0	0	25	0	3	0	0
<i>M.poutassou</i>	0	0	0	2	11	1	3	1	3
<i>Mollusca</i>	0	0	0	0	0	0	1	18	0
<i>Molva dypterygia</i>	1	0	0	0	0	0	0	0	0
<i>Monodaeus couchii</i>	0	0	0	0	0	0	1	1	0
<i>Munida intermedia</i>	0	0	1	0	0	0	0	1	0
<i>Myctophidae</i>	0	0	3	0	0	14	0	0	0
<i>Mysidacea</i>	20	17	1	16	13	0	12	39	21
<i>Natantia</i>	34	21	13	26	54	9	64	60	31
<i>Nemertea</i>	0	0	0	0	0	0	0	2	0
<i>Nephrops norvegicus</i>	0	0	0	1	0	0	0	0	0
<i>Ophichthus rufus</i>	0	0	0	0	0	0	1	3	0
<i>Ophiura spp</i>	0	0	15	0	0	0	0	0	0
<i>Ophiuroidea</i>	0	0	8	0	0	0	0	0	0
<i>Ostracoda</i>	0	0	0	0	0	0	0	1	0
<i>Paguridae</i>	2	9	0	1	2	0	18	87	5
<i>P.mauritanicus</i>	1	0	0	1	0	0	10	2	0
<i>Pandalina profunda</i>	2	10	1	0	0	0	0	0	1
<i>Parthenope massena</i>	0	1	0	0	0	0	0	1	0
<i>Pasiphaea sivado</i>	0	0	0	0	0	14	0	2	0
<i>Phronima sedentaria</i>	0	0	1	2	0	1	0	5	1
<i>Phycis blennoides</i>	0	0	0	2	0	0	1	0	0

Prey species	<i>C. cuculus</i>	<i>C. lastoviza</i>	<i>H. dactylopterus</i>	<i>L. boscii</i>	<i>M. merluccius</i>	<i>M. poutassou</i>	<i>R. clavata</i>	<i>S. canicula</i>	<i>T. draco</i>
<i>Phylocheras spp.</i>	2	0	0	0	0	0	0	1	1
<i>Plesionika antigai</i>	0	0	1	0	0	0	0	0	0
<i>Pleuronectidae</i>	2	0	1	1	0	0	4	6	1
<i>Polychaeta</i>	4	2	1	2	0	0	12	181	7
<i>P.marmoratus</i>	0	1	0	0	0	0	0	0	0
<i>P.cataphracta</i>	1	2	0	0	0	0	0	0	0
<i>Pontophilus spinosus</i>	1	0	0	0	0	0	0	0	0
<i>Porifera</i>	0	1	0	0	0	0	0	0	0
<i>Portunidae</i>	0	0	0	0	0	0	1	1	0
<i>Posidonia oceanica</i>	0	0	0	0	0	0	0	1	0
<i>Processa sp.</i>	15	19	5	27	16	0	79	76	22
<i>Processa canaliculata</i>	0	0	0	0	0	0	0	0	1
<i>Pseudaphia ferreri</i>	1	0	0	0	0	0	0	0	3
<i>Restes Posidonia</i>	0	0	0	0	0	0	0	4	0
<i>Rissoides desmaresti</i>	0	0	0	1	0	0	3	3	2
<i>Salpidae</i>	0	0	0	0	1	0	0	3	0
<i>Sardina pilchardus</i>	0	0	0	0	5	0	3	0	0
<i>Scyllaridae</i>	0	0	0	0	0	0	0	1	0
<i>Sepietta oweniana</i>	1	0	0	1	0	0	0	0	0
<i>Sepiodea</i>	0	0	0	0	0	0	0	2	0
<i>Sepiola spp.</i>	0	0	0	0	0	0	1	0	0
<i>Sepiolidae</i>	3	0	0	0	1	0	2	1	0
<i>Sergestes arcticus</i>	0	0	0	1	0	2	0	0	0
<i>Sergia robustus</i>	0	0	0	0	0	1	0	0	0
<i>Serranus cabrilla</i>	0	1	0	0	0	0	0	0	0
<i>Siphonophora</i>	0	0	0	0	0	0	0	0	1
<i>Sipunculidae</i>	0	0	0	0	0	0	0	53	0
<i>S.membranacea</i>	1	1	1	1	10	0	43	9	2

Prey species	<i>C.</i> <i>cuculus</i>	<i>C.</i> <i>lastoviza</i>	<i>H.</i> <i>dactylopterus</i>	<i>L. boscii</i>	<i>M.</i> <i>merluccius</i>	<i>M.</i> <i>poutassou</i>	<i>R.</i> <i>clavata</i>	<i>S.</i> <i>canicula</i>	<i>T. draco</i>
<i>Spicara smaris</i>	0	0	0	0	18	0	9	1	1
<i>Stomatopoda</i>	2	0	0	0	0	0	0	2	1
<i>Stomias boa boa</i>	0	0	0	0	1	0	0	1	0
<i>Sygnathidae</i>	0	0	0	0	0	0	0	1	0
<i>Symphurus ligulatus</i>	0	0	0	0	0	0	0	1	0
<i>Systellaspis debilis</i>	0	0	0	0	2	0	0	0	0
<i>Theuthoidea</i>	0	0	0	0	3	0	5	4	0
<i>Trachinus draco</i>	0	0	0	0	0	0	2	0	0
<i>T.mediterraneus</i>	0	0	0	0	3	0	0	0	0
<i>Trisopterus minutus</i>	0	0	0	0	1	0	0	0	0
<i>Xantidae</i>	0	2	0	1	0	0	3	1	0
<i>Xanto pilipes</i>	0	1	0	0	0	0	0	0	0

3.3.4 Mouth gape

Approximately 10 individuals selected from 10 predetermined size classes (based on 90% of the most common sizes for each species caught in June 2008) were selected from trawls in 2009. Maximum mouth height and mouth width (without distortion of the maxillaries on opening) were measured using digital vernier calipers to the nearest 0.01mm. Height and width alone are inaccurate descriptors of mouth gape, as they differ widely within and among species (Piet et al., 1998). Therefore, to account for the differences in mouth shape (i.e. circular, oval, etc.), mouth gape was determined from mouth height (a) and width (b) by calculating the perimeter of an ellipsoid (P) using the following equation for each individual:

$$P \approx 2\pi \sqrt{\left(\frac{a^2 + b^2}{2}\right)}$$

Fish generally display circular or oval mouth shapes, with mouth height (a) and width (b) being less than three times larger than the other (i.e. mouths do not tend to be flat or extremely squashed). All fishes sampled met this assumption. Linear regressions of body length versus mouth gape (ellipse perimeter) were plotted for each species and the slope of each regression was then used to calculate the mouth size from total body length data of all individuals used in the analysis from 2003 to 2009 (see Table 3.2 for details).

3.3.5 Statistical analysis

Quantile regressions were used to test the hypotheses that *i*) predator abundance is limited by prey abundance and *ii*) the mean mouth gape of prey size selective predators is limited by the mean prey size at the scale of the Balearics. While standard regression methods use least

squares to estimate means for a response from a predictor variable, the quantile regression method estimates either the median or quantiles of the response variable. The advantage of fitting a model to statistics other than the mean of a distribution, such as the upper quantiles, is that the limiting effect of a known factor can be explored with other unknown limiting factors acting simultaneously (Cade and Noon, 2003). In the event that a measured factor limits the response variable, an upper limit can be identified above which no further change can occur. Below this upper, limit other unmeasured factors may also be limiting the response variable but will do so to a lesser extent. Therefore, quantiles >75% were considered within this analysis, as at lower quantiles the probability that the relationship is caused by additional factors increases (Scharf et al., 1998). Overall, five quantiles were selected for analysis, ranging from the 75th to the 95th (in increments of 5) to test the hypothesised limiting relationship of prey abundance and prey size respectively.

Table 3.2 Summary table of the regressions of log₁₀ body length against log₁₀ mouth ellipse perimeter for each species.

Predator Species	n	Slope	Intercept	R²	p
<i>C. cuculus</i>	85	1.002	0.576	0.803	<0.001
<i>C. lastoviza</i>	45	1.528	-4.068	0.551	<0.001
<i>H. dactylopterus</i>	39	0.877	0.069	0.961	<0.001
<i>L. boscii</i>	74	1.014	-0.971	0.982	<0.001
<i>M. merluccius</i>	83	0.909	-0.351	0.922	<0.001
<i>M. poutassou</i>	71	1.404	-3.293	0.948	<0.001
<i>R. clavata</i>	39	1.012	-1.798	0.853	<0.001
<i>S. canicula</i>	68	1.060	-2.074	0.962	<0.001
<i>T.draco</i>	73	1.072	-1.789	0.554	<0.001

In order to control the false discovery rate (FDR) associated with multiple hypothesis testing, a post hoc threshold p value was calculated as described by Benjamini and Hochberg (1995) for all fish species at all sites. This gave a conservative p value for both sets of quantile regressions undertaken. Although some authors also decrease their initial p value to reduce the probability of producing type I errors, here we felt it was more appropriate to publish only the quantiles showing significance under the FDR-corrected p value. This illustrates the significance of the relationships tested post correction without adjusting the standard probability (5%) of incorrectly rejecting the null hypothesis. Normal least-squares linear regressions were used to analyse the relationship between the maximum sizes of prey found in the stomach contents and the size of the mouth gape size of the predator. All data were \log_{10} transformed to ensure an even spread of data points and goodness of fit was estimated using standard errors calculated using a standard bootstrapping method. All statistical analyses were undertaken using the standard statistics and the `quantreg` package in R 2.10.1.

3.4 Results

3.4.1 Prey vs predator abundance

Following FDR correction, quantile regressions revealed that there was a significant ($p < 0.05$) positive relationship between prey abundance and predator abundance for *Chelidonichthys cuculus* (80th), *Chelidonichthys lastoviza* (95th), *Lepidorhombus boscii* (85th, 80th), and *Trachinus draco* (95th) (Fig.3.2). There was no significant relationship between prey abundance and predator abundance for the remaining five species (*Helicolenus dactylopterus*, *Merluccius merluccius*, *Micromesistius poutassou*, *Raja clavata*, and *Scyliorhinus canicula*).

3.4.2 Prey size and predator size

Regressions of predator mouth gape against maximum prey size (found in stomach contents) showed significant ($p < 0.05$) positive relationships for six of the nine species (*C. cuculus*, *C. lastoviza*, *L. boscii*, *M. merluccius*, *R. clavata* and *S. canicula*) (Fig. 3.3). The three remaining species (*H. dactylopterus*, *M. poutassou* and *T. draco*) showed no significant relationships ($p > 0.05$) between the maximum prey size found in the stomach and mouth gape size, suggesting that prey size was not an important limiting factor for these species.

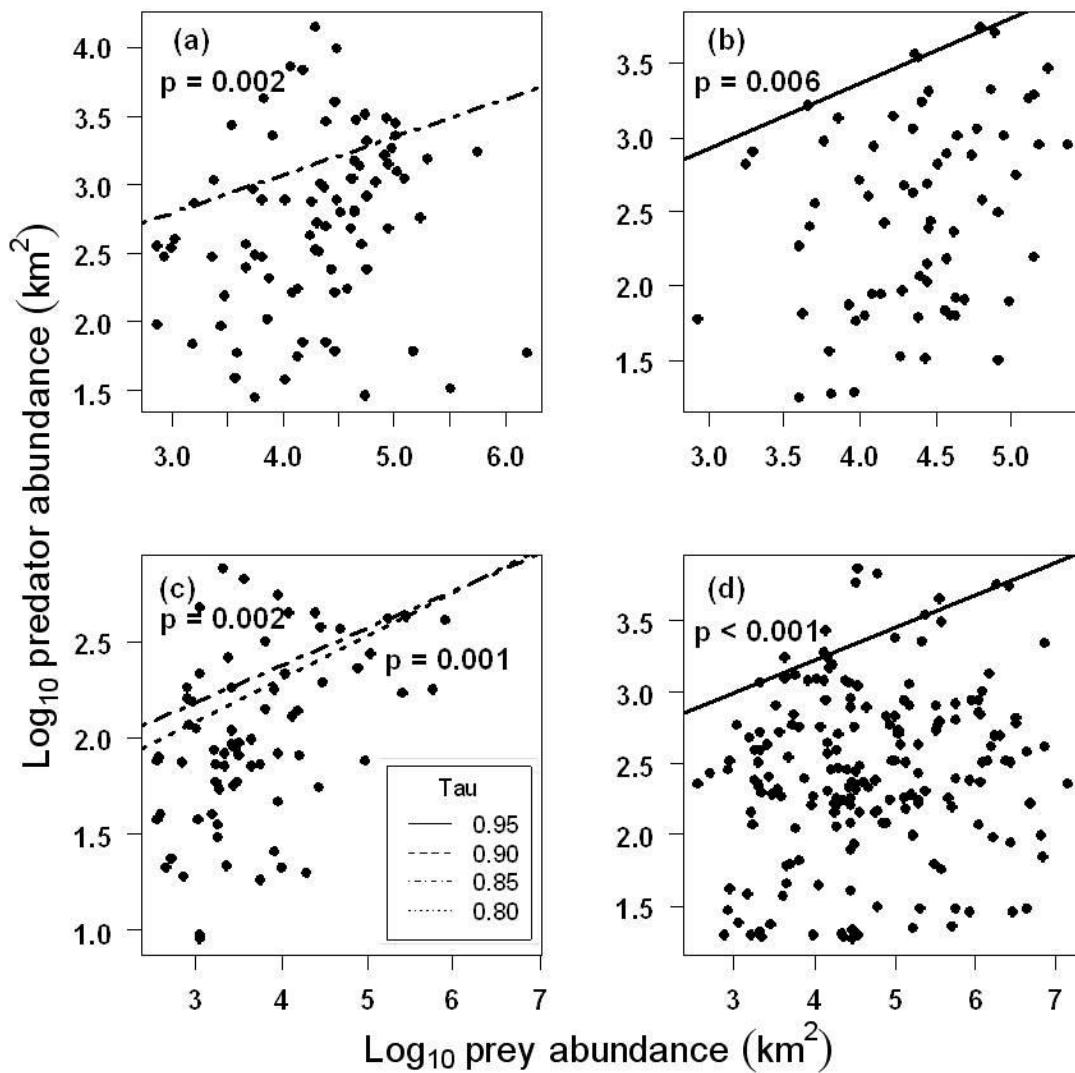


Figure 3.2 Significant linear quantile regressions (after false discovery rate correction, ($p = 0.01$)) of the relationship between prey abundance and predator abundance for *Chelidonichthys cuculus* (a), *Chelidonichthys lastoviza* (b), *Lepidorhombus boscii* (c) and *Trachinus draco* (d). Each point represents one trawl. Legend denotes quantile levels (Tau) for all four plots.

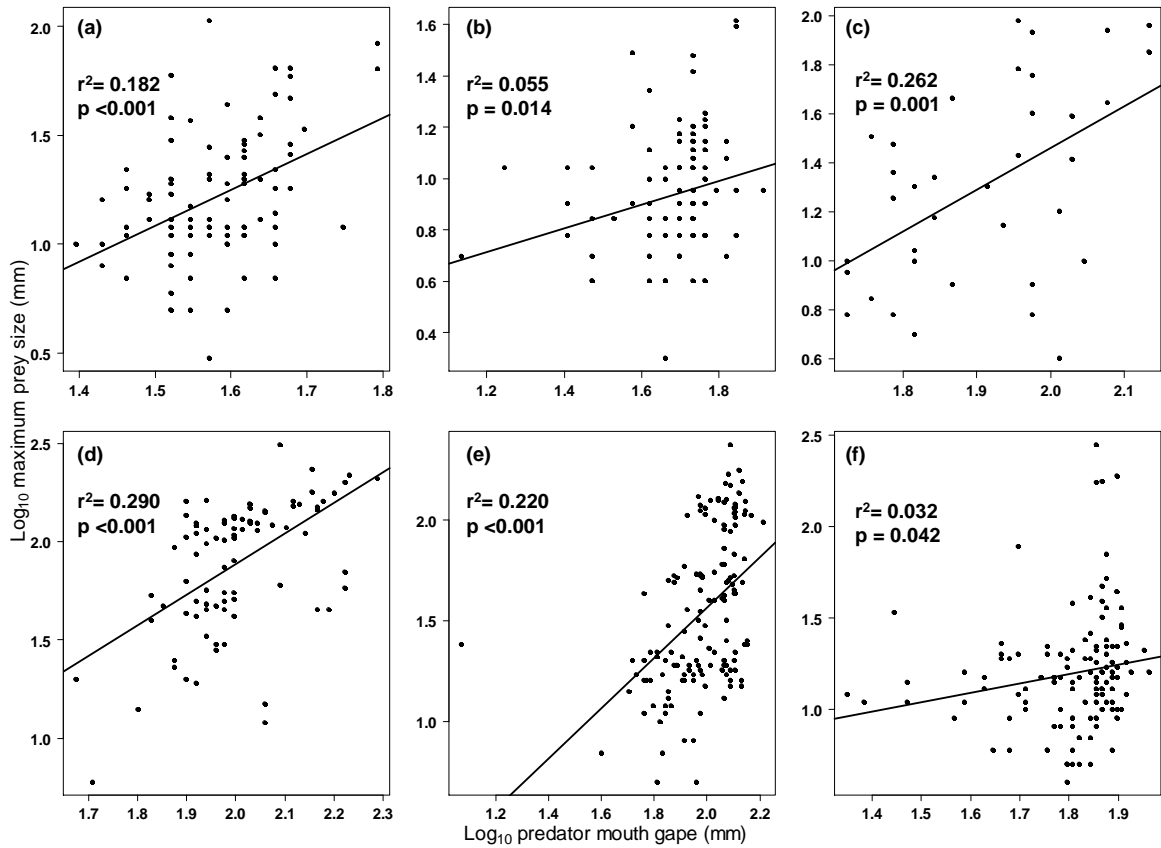


Figure 3.3 Significant linear regressions (ordinary least squares) of the relationship between maximum prey size in the stomach contents and predator mouth gape for *Chelidonichthys cuculus* (a), *Chelidonichthys lastoviza* (b), *Lepidorhombus boscii* (c), *Merluccius merluccius* (d), *Raja clavata* (e), and *Scyliorhinus canicula* (f). Each point represents a single predator.

For those species demonstrating a significant positive relationship between predator mouth gape and maximum prey size in stomach contents, it was hypothesised that the mean mouth gape of demersal fish around the Balearics would be limited by the mean prey size present in the environment for each predator. This however was not the case. Only *M. merluccius* (75th – 95th) showed significant ($p < 0.05$) positive relationships after FDR correction between mean individual prey mass and mean predator mouth gape around the Balearics (Fig. 3.4). The remaining eight species (*C. cuculus*, *C. lastoviza*, *H. dactylopterus*, *L. boscii*, *M. poutassou*, *R. clavata*, *S. canicula*, *T. draco*) showed no significant ($p > 0.05$) relationships after accounting for multiplicity (FDR correction) at any of the quantile levels tested.

3.5 Discussion

3.5.1 Prey and predator abundance

There was strong support for the hypothesis that demersal fish abundance is higher in areas of high prey abundance in *C. cuculus*, *C. lastoviza*, *L. boscii*, and *T. draco*, indicated by significant quantile regressions of predator and prey abundance after FDR correction. Many factors are known to determine habitat preference in demersal fishes, and prey abundance is expected to influence selection, but very few studies have investigated its importance (Engelhard et al., 2008, Hinz et al., 2005). Significant relationships at the quantile levels tested suggest that prey abundance is both a significant and important limiting factor affecting the aforementioned predators' abundances, and therefore habitat selections, at the scale of this study. Other parameters such as depth, bottom type, predation risk, and competition (interspecific and intraspecific) may therefore have fewer limiting effects on the

abundances of the respective species; however, the influence of these parameters lay outside the scope of the present study but warrants further investigation.

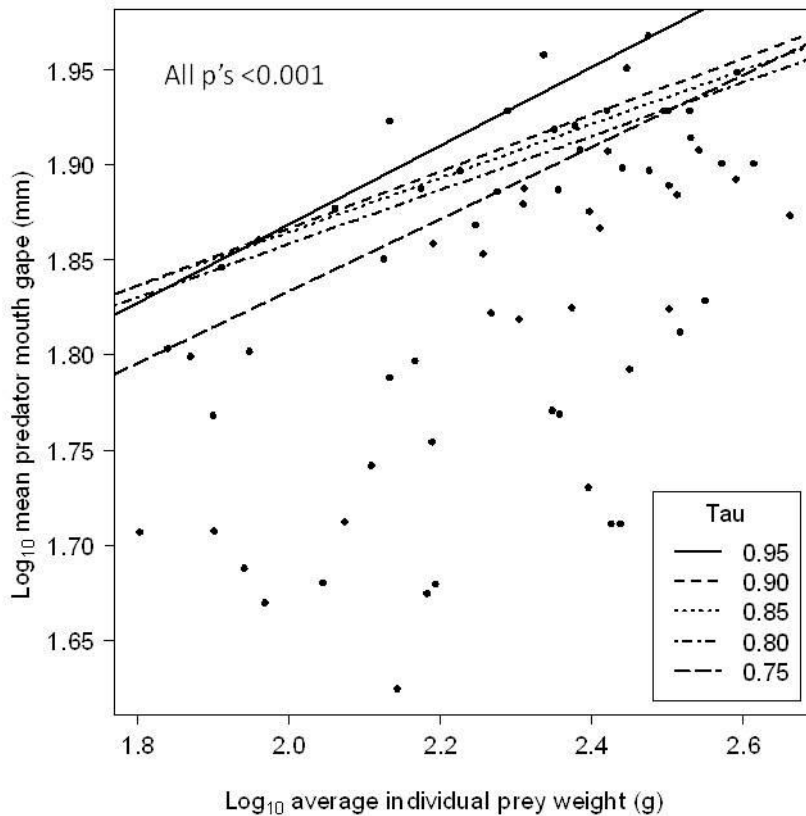


Figure 3.4 Significant linear quantile regressions (after false discovery rate correction, ($p = 0.005$)) of the relationship between mean individual prey mass at sample sites and mean predator mouth gape for *Merluccius merluccius*. Each point represents one trawl.

The lack of relationship between prey and predator abundance for the remaining species may reflect differences in feeding ecologies and the importance of additional habitat parameters in limiting predator abundance. The thornback ray (*R. clavata*) and the small spotted catshark (*S. canicula*) are well-known opportunistic, highly mobile and active predators with diverse prey ranges (Sims et al., 2006, Hunter et al., 2005). Stomach content data supported the latter

finding as both showed the largest prey diversities of all the species analysed (17 and 24 prey taxa respectively). Wide prey ranges and high mobilities are likely to mean that these predators have low habitat specificity and a wider foraging area causing a mismatch between their abundance and that of their prey. In contrast, the black belly rosefish (*H. dactylopterus*) is unlikely to be limited by prey abundances as it is known to only ingest additional prey once previous prey items have been fully digested in the stomach (Macpherson, 1985). This was supported in our data which showed that 67% of individuals of this species had only one prey item in the stomach, 62% of which was fully digested. The result for blue whiting (*M. poutassou*) is not entirely clear and necessitates further investigation, perhaps using a larger number of individuals to give a clearer picture of prey preferences and therefore potential prey abundances.

3.5.2 The importance of prey size

During foraging, a predator must make a choice between engaging in feeding on a potential prey item or continuing the search for other prey. This choice is likely to be determined by the abundance and quality (size, palatability, and ease of capture) of other viable prey species in the immediate environment (Gill, 2003). Patterns of size selectivity depend largely on the range of available prey sizes relative to that which the predator can effectively harvest. Corroborating studies demonstrate that as the abundance of prey increases, so too does size selectivity of the predator (preference for the largest prey consumable) (O'Brien et al., 1976, Werner and Hall, 1974, Ivlev, 1961). It is noteworthy, however, that previous authors have suggested that fullness can produce a switch from ecological bases (prey abundance, distribution, and prey handling) of prey selection to physiological ones (digestion, absorption, and satiation) (Whelan and Brown, 2005).

The relationship between maximum prey size in stomach contents and the mouth gape size of the predator revealed six significant positive relationships. The positive linear trends seen for these species suggest prey size selectivity and support the optimal foraging theory and basic prey model (Charnov et al., 1976). Energetic returns and profitability (potential energy gain) may be increased when optimal prey sizes are consumed. Predators will select larger prey up to a point where there exists a trade-off between energy gains (from consumption) versus time costs (from prey capture). The tendency of marine fishes to select larger prey sizes with increasing mouth gape has been demonstrated previously (Gibson and Ezzi, 1987, Pinnegar et al., 2003, Stergiou and Karpouzi, 2001), although this study is the first to focus solely on the benthic feeding stages of demersal fish species.

Traditional foraging theory predicts that predators will aim to maximise their net energy gain when selecting prey. Although this may often involve the selection of larger prey sizes (increased energy per prey capture) preferences for smaller prey items may occur as a result of a trade-off between total handling time and maximum energy intake per prey item consumed (Hoyle and Keast, 1987, Juanes and Conover, 1994). Alternative foraging strategies for which factors such as prey handling time and satiation level are more important than maximizing prey size may explain the lack of relationship seen for *H. dactylopterus* and *T. draco*. These sit-and-wait predators (Bagge, 2004, Uiblein et al., 2003) are unlikely to be adequately informed about available prey resources much beyond their immediate visual range whilst waiting for prey encounters (see also Shepherd and Litvak, 2004). Consequently, it is expected that in order to fulfil their feeding requirements, preferences for larger prey items are minimal and any passing prey that is palatable and can be sufficiently handled will

be consumed (Gill, 2003). The lack of relationship seen for *M. poutassou* is again unexpected and requires further enquiry as aforementioned.

If prey abundance is high enough to allow selective feeding but the diversity of prey species is low, a predator is more likely to select prey based on size rather than species. Moreover, if available prey types confer no advantage in terms of prey handling time, ingestion, digestion, and overall energy intake, prey size is the most likely factor to determine the selectivity (Ivlev, 1961, Gill and Hart, 1994). Consequently, the size selectivity seen in European hake (*M. merluccius*) around the Balearics may be facilitated by prey abundances that allow selectivity in combination with low prey diversities at sites. This idea is corroborated by the narrow prey ranges of the hake (seven different prey species) and the high prey abundances for this species at the sites sampled (29% higher than prey abundances of any other predator species in this study). This suggests that prey size (positive relationship between prey size and gape sizes present) and prey type (narrow prey range) rather than prey abundance (no significant relationship between prey and predator abundance) is likely to represent a constraint to the distribution of European hake of 103 – 215 mm in total length. The prey size selectivity of hake is corroborated by both Guichet (1995) and Velasco and Olaso (1998), although the latter study focussed on generally larger individuals than those analysed in this study. Additionally, Bozzano et al (1997) showed that European hake (of a similar size to those in this study) showed higher fullness indices than other size classes in the western Mediterranean. This supports our findings that the abundance of prey is not likely to be a limiting factor in the habitat choice and thus distribution of hake of this size class. The lack of significance seen for the remaining species that showed prey size selectivity from stomach contents analysis could be the result of a combination of factors. The use of mean individual prey mass as a measure of prey size may have introduced some additional variability into the

data as body mass does not account for the shape of an organism. The sampling of the benthic prey community should also be improved in future studies that aim to relate fish distributions to prey communities. Although incorporating a small mesh size aids in catching small prey items, it is likely that individuals smaller than the mesh size may have been missed and burrowing individuals not well sampled. It is important to note, however, that as previously discussed this may also illustrate that additional habitat parameters are more important in limiting predator distributions than the prey sizes present at a site.

Our analysis demonstrated that the abundance of some predator species increased at higher levels of prey abundance whilst also showing prey size selectivity in stomach contents. No species, however, showed prey size selectivity in the environment as well as an increased abundance with environmental prey abundance. Such relationships are, however, only likely to occur under certain predator prey scenarios. Different combinations of prey and predator abundances, additional habitat parameters not analysed herein, as well as differences in ontogenetic allometry, within and between species (and therefore resultant feeding ecologies) (Rodriguez-Mendoza et al., 2011), are all likely to influence the importance of prey abundance and size for demersal fish species. For instance, not accounting for competition effects, high prey abundances and wide prey size spectrums are likely to allow for increased abundances of predators and higher levels of prey size selectivity in the environment. The lack of importance of prey abundance or size in determining the distribution of certain species may, however, often be explained by certain peculiarities in their feeding ecologies. The species we analysed are representative of a large proportion (biomass and abundance) of the demersal fish assemblage of the continental shelf around the Balearic Islands. The extent to which such relationships can be generalized to the same, and other species, in different areas therefore requires additional comparative investigations. As our analyses apply to the

epifaunal-feeding life stages of each species, this would therefore have to be accounted for in any further comparisons.

For demersal fish species showing habitat selections based on the factors of prey abundance and size, failures to find areas of suitable prey abundances and the inability to optimise feeding strategies by selecting optimal prey sizes may have consequences for growth and in turn population abundance (Shephard et al., 2010). Reductions in benthic faunal abundance, production, and size structure caused by bottom-fishing disturbance could therefore have severe ramifications for demersal fish species that show strong links with benthic prey abundance and size. If sustained, these may lead to decreased condition (weight-at-length), reproductive output, and longevity of the affected species. Future studies on the importance of fish habitat characteristics, aiming to inform ecosystem-based management approaches, should therefore aim to consider prey abundance as well as size in order to describe the habitat requirements of demersal fish species.

CHAPTER 4

Indirect effects of a bottom trawl fishery on the diet and feeding ecology of two demersal fish species

4.1 Abstract

The widespread impacts of bottom trawling on benthic communities are well documented and include the reduction of faunal biomass, diversity and size structure as well as overall productivity. Little however is known about the consequences of these changes on the feeding ecology of associated demersal fishes. Within the present paper we investigated how trawling related changes in the benthos affected the diet of two demersal fishes within a commercial fishing ground. The stomach contents of plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*) from 15 stations over a gradient of chronic bottom trawling were analysed. Trawling had a significant effect on the diet composition of plaice and dab although no effect on the stomach fullness of either species was found. At higher trawl frequencies the narrow prey spectrum of plaice underwent a switch from small *Nephtys spp.*, to large *Abra alba*. It is likely that this switch allows plaice to partially compensate for the increased foraging effort associated with feeding on smaller *Nephtys spp.* at high trawl frequencies. No significant prey species shifts were noted in the diet of dab within the same sites. We suggest that the wide prey spectrum (prey taxa and prey size) of the dab gives it a more energetically favourable feeding strategy than plaice. Our results suggest that alterations in prey abundances, sizes and availabilities caused by chronic bottom trawling may lead to alterations in feeding efficiencies, particularly for species with narrow prey spectrums. This in turn could result in reduced conditions of affected fishes living in chronically disturbed areas. Understanding the effects of changing prey communities is crucial if we are to mitigate the negative, long-term impacts of benthic disturbance on demersal fish communities.

Keywords: feeding ecology, infaunal community, *Limanda limanda*, *Pleuronectes platessa*, predator-prey interaction, trawl disturbance

4.2 Introduction

The impacts of bottom trawling are now well recognised to be a major cause of anthropogenic change in benthic ecosystems globally (Kaiser et al., 2006). Past studies have demonstrated significant reductions in community biomass, abundance, size spectra and overall production in the epifaunal, infaunal and meiofaunal components of benthic ecosystems (Hiddink et al., 2006a, Queiros et al., 2006, Hinz et al., 2008, Hinz et al., 2009). These effects are however highly habitat specific with greater impacts noted in more physically complex and biogenic habitats and those with low levels of natural disturbance (Hiddink et al., 2006b, Kaiser et al., 2006)

The physical impacts of trawl gears can also lead to significant alterations in benthic community structure as species with different life traits are not equally susceptible to this types of disturbance (Kaiser et al., 2002). Large scale shifts in the functional composition of benthic communities have been demonstrated, with sessile, attached and larger animals showing significantly lower abundances in highly trawled areas than at lightly trawled sites (Tillin et al., 2006). Futhermore, in response to the increase in dead animal matter following trawl passes, high levels of chronic trawling may increase the relative availability of prey biomass for some mobile scavenging invertebrates that will as a consequence aggregate along trawl tracks (Tillin et al., 2006, Hixon and Tissot, 2007). As many demersal fish species rely on benthic, invertebrate communities for part of, or in some cases all of their life history, the changes that trawling can cause in benthic invertebrate communities can have significant consequences for associated fish communities.

The reduction of overall benthic production can have negative consequences for certain demersal fish species. Shortages in food supply may be experienced by those predators whose primary prey species show significant negative responses to trawling (reductions in biomass, abundance and size structure) and those with narrow prey spectra. Choi et al. (2004) attributed significant declines in fish condition to reduced benthic food resources in heavily trawled fishing grounds over large scales ($>10^4$ km²) off the eastern Scotian Shelf. Shephard et al. (2010) also demonstrated significant declines in length-at-age with increasing trawl frequencies of the plaice found on gravel substrates in the Celtic Sea. Combined with truncated size distributions associated with heavily trawled grounds (Wells et al., 2008) and reductions in spawning stock biomass (Fiorentino et al., 2008, Hutchings, 2000), such reductions in fish condition may exacerbate slow stock recoveries.

Some demersal fish species may however be positively affected by the changes induced by trawling activities. Scavenging fish species may benefit from the prey killed or exposed by the trawl disturbance (Groenewold and Fonds, 2000). Furthermore, changes in the size structure of the benthos towards smaller body sized species that are more resilient to trawling and have a faster reproductive cycle (Jennings et al., 2001a) may have significant positive effects on fish species or life stages that feed primarily on smaller sized benthic invertebrates. An example that demonstrates how wide ranging changes in prey communities can influence the distribution of fish is the redistribution of juvenile plaice (*Pleuronectes platessa*) to areas outside the North Sea plaice box (an effort restriction area formed in 1989). These outside areas remained intensively fished and showed higher abundances of small sized prey that juvenile plaice could better feed on (Hiddink et al., 2008). It is however noteworthy that other authors have noted that the move of juveniles offshore may also be caused by significant changes in sea temperatures (van Keeken et al., 2007). For certain fish species or ontogenetic

stages of a species, the secondary effects of trawling may therefore be temporally and / or locally advantageous (see also Kaiser and Ramsay, 1997, Groenewold and Fonds, 2000).

The objective of the present study was to thoroughly assess the feeding ecology of plaice and dab in a chronically trawled, *Nephrops norvegicus* fishing ground in the Irish Sea. This study is a follow up on previous studies by Hinz et al. (2009) and Hiddink et al. (2011) undertaken in the same area. Hinz et al. (2009) demonstrated significant reductions in benthic infaunal abundance, biomass and species richness across the trawl ground which shows large gradients in fishing frequency over a relatively small area (km²). Following on from this study, Hiddink et al. (2011) found that the condition of plaice was negatively related to chronic trawl frequency at the site, whilst the condition of dab (*Limanda limanda*) showed no such relationship. The authors suggested that the reduced condition of plaice, a relatively specialized feeder (Wyche and Shackley, 1986) with a narrow prey spectrum, was caused by a decreased availability of their specific prey at high trawling intensity sites and suggested that in contrast the opportunistic feeding strategy of dab (see Kaiser and Ramsay, 1997) allowed it to maintain its food intake despite changes in benthic community structure. The hypothesis that the difference in condition between the two species was linked to differences in their feeding ecology, is tested in the current paper.

We used detailed stomach contents data of dab and plaice from fishes used in the study of Hiddink et al. (2011) to provide information on the prey spectra and feeding ecology of these species, and assess how these changed across a gradient of trawling frequency. We hypothesized that the diet of individuals of the two fish species with overlapping mouth gapes was significantly different within the study area (H_1) and the effect of trawling on the diets of

these two species was significantly different (H_2). We also propose that these differences are the likely reason that plaice, but not dab experienced low condition at more trawled sites.

Until now few studies investigating the impacts of trawling on fish communities had progressed further than reporting declines in benthic community productivity and reduced conditions of associated fish species. This study is therefore a fundamental step towards understanding the mechanism of how bottom trawling, through alterations in prey availability and composition affect the feeding and condition of demersal fish species

4.3 Materials and Methods

4.3.1 Study area

The long-term effects of chronic trawling on the feeding ecology of the flatfishes plaice (*Pleuronectes platessa* (Pleuronectidae)) and dab (*Limanda limanda* (Pleuronectidae)) were investigated over an active fishing ground in the north-eastern Irish Sea off the Cumbrian coast (Figure 4.1). The predominant bottom-fishing activity in this fishing ground is otter trawling for *Nephrops norvegicus* (Norway lobster) and gadoid fish. The fishery operates throughout the year with a peak in activity from spring to early summer. The area is characterized by low-energy hydrodynamic conditions and consequently the substratum comprises mostly fine sand and muddy sediments. Hinz et al. (2009) demonstrated that the area displayed homogeneous habitat characteristics (depth, sediment type, bottom temperatures and tidal currents) while at the same time showing a strong spatial gradient in trawling frequency. In addition the authors showed that chronic otter trawling had a

significant, negative effect on the abundance, biomass and species richness of infaunal benthic invertebrates. More recently, Hiddink et al. (2011) found that the condition of the plaice at the study site was negatively related to trawling frequency, which was explained by a reduced production of the infaunal prey species.

4.3.2 Estimation of fishing effort

Trawl frequencies at sites were calculated using fishery protection overflight observations and Satellite Vessel Monitoring System (VMS) data. For more details of trawl frequency estimation see Hiddink et al. (2011). Trawling frequency at the sampling stations varied between 0.5 and 11.9 trawl passes year⁻¹.

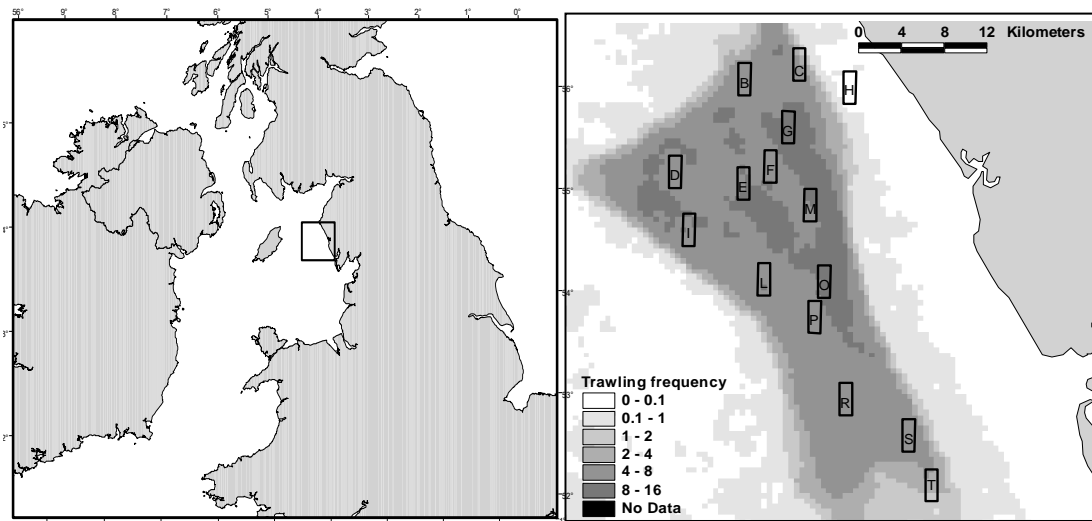


Figure 4.1 Sampling stations and the distribution of bottom trawling frequency (y⁻¹) from 2004 to 2008 in the study area.

4.3.3 Sampling fish and invertebrate populations

Fifteen stations were selected for sampling within the area, each comprising a 1 x 2 km box. Locations of each sampling site were chosen to cover the widest range of trawl frequencies

within the area. Fish and invertebrates were sampled at each station in June 2009. Two tows of 30 minute duration were made at each station using a rock hopper otter trawl (distance across mouth of the net 16 m, head line height 3 m, 82-mm diamond mesh cod-end) at 3 knots, in order to sample the bottom fish community. In order to sample fishes with similar mouth sizes, and therefore prey size potentials, only plaice and dab of a certain size (total body length (TBL)) were taken for stomach content analysis (182 – 299-mm and 168 – 274-mm respectively). These total body lengths corresponded to overlapping mouth gape ranges (calculated as ellipsoids) from 34.5 to 53.5 mm for both species, determined using fishes from the same sites, prior to the field campaign (see Appendix 4.6.1).

Stomachs were extracted from 2 individuals from each centimetre size class (within the two TBL ranges) and stored in 8% buffered formalin prior to stomach content analysis. In the laboratory, full stomach biomass and total prey contents biomass were recorded. Prey items were then separated, identified to the highest taxonomic resolution possible, counted, rated according to digestive stage (1=fresh, 2=partial, 3=well digested), blotted and wet weighed. For details of the total numbers of stomachs sampled per site see appendix 4.6.2.

The benthic invertebrate community was sampled taking five 0.1m² day grabs at haphazard locations in each station box. Samples were sorted over a 1-mm sieve and preserved in 4% formalin and later identified to the highest taxonomic resolution possible. The wet biomass of each individual organism was measured after blotting and the abundance of each infaunal species recorded per grab. Results from the five individual grabs were pooled before statistical analyses as replication within stations was aimed at increasing the accuracy and precision of our estimates of benthic production (infaunal abundance and biomass) and not at obtaining estimates of within station variability.

4.3.4 Univariate data analysis

In order to assess the effects of trawling on the infaunal community and the prey species community composition of the diets of plaice and dab, ordinary least squares (OLS) regressions of community and dietary response variables against trawl frequency were used. These response variables were total infaunal abundance, biomass and species richness per site. In the case of the whole infaunal community and respective plaice and dab prey communities both the total number of all prey species and those occurring more than ten times in the diets of each were tested (herein referred to as the “most common” in the diet).

Few demersal fish species masticate their prey items therefore generally consume their prey items whole. Prey intake is often restricted by either visual acuity or mouth gape limitations. The relationship between prey size and the mouth gape of a fish therefore has important implications in terms of energetic gain per prey capture (Gill, 2003). Past studies have shown that prey which are approximately 0.6 times the predator’s mouth width size (Prey Width : Mouth Width (PW:MW) = 0.6) are the most energetically profitable (i.e. best energetic return for the lowest cost) (Werner and Hall, 1974, Wankowski, 1979, Prejs et al., 1990). Although the fishes used in our analyses had overlapping mouth gapes and therefore prey size potentials, in order to investigate which species was feeding most optimally in terms of prey sizes within our mouth size selection, we compared the mean PW:MW and energy per g of stomach content for each (using conversion factors from Brey (2001) (see 4.6.3 Appendix)) per trawl frequency using independent samples t-tests.

Chesson’s standardised forage ratio was calculated using stomach data from across all sites for the prey species occurring more than ten times in the diets of plaice and dab. This

provided information on the preference for each common prey type across the whole fishing ground. The effect of trawling on the prey selectivity (Chesson's index), abundance and individual biomass of the most common individual prey species per fish, was then tested using OLS regressions in order to investigate the response of plaice and dab to changes in their prey community in more detail. In addition, the mean energy content per gut (accounting for all stomach contents identifiable to at least class level), Levin's niche breadth (prey diversity in stomach), Schoener's dietary overlap and mean stomach fullness (as a percentage of body biomass (Hyslop, 1980)), were also tested by the same method. The calculation of indices is described below.

For the above analysis only stations with ≥ 10 individuals of both plaice and dab were included in all analyses (see appendix 4.6.2). Only prey items of digestive stages 1 and 2 were included in analyses for total mean prey biomasses. This is because fuller digestive states mean softer bodied prey items lose structure and retain more stomach liquid making estimates of biomass inaccurate. For OLS regressions of individual prey biomasses against trawl frequency n per site was ≥ 3 . All univariate data used were \log_{10} transformed to ensure an even spread of data points and goodness of fit was estimated using standard errors calculated using a standard bootstrapping method and only significant regressions were plotted. Means herein are reported \pm standard deviation.

4.3.5 Calculation of indices

Chesson's standardised forage ratio, which describes a predator's preference for prey, was calculated using the most common species in the diets of plaice and dab respectively.

Chesson's standardised forage ratio (prey selectivity):

$$\alpha_a = r_a p_a^{-1} \left[\sum_{i=1}^2 r_i p_i^{-1} \right]^{-1} = e a_d (d a_e)^{-1} [e d^{-1} (a_d a_e^{-1} + b_d b_e^{-1})]^{-1}$$

where a_d is the number of prey animals of species a in the predator's diet, b_d is the number of all other prey animals in the diet, a_e is the number of prey animals of species a in the environment, b_e is the number of all other prey animals in the environment, d is the total number of all animals in the diet, e is the total number of all animals in the environment, r_a is the proportion of prey species a in the diet and p_a is the proportion in the environment (Chesson, 1978, 1983). This index ranges between 0 (complete avoidance) and 1 (exclusive feeding) and often outperforms similar indices (Pearre, 1982). Only principal prey species (those occurring more than ten times in the stomachs of plaice and dab) were used in the calculation of prey selectivity.

Schoener's index, and Levin's food-niche breadth were also calculated to determine the proportion of overlap and the diversity of prey species for the diets of plaice and dab.

Schoener's index (dietary overlap):

$$S = 1 - 0.5 \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right)$$

where P_{xi} is the proportion of food category i used by species x , P_{yi} is the proportion of food category i used by species y and n is the number of food categories. This index renders values from 0 to 1 and is a commonly used estimator of dietary overlap between predator species, giving the most accurate representation of true overlap compared to similar indices (see Schoener (1970) and Linton et al. (1981)).

Levins' food-niche breadth (diet diversity):

$$B = 1 / \left(\sum_{i=1}^n p_i^2 \right)$$

where p_i is the relative occurrence of prey taxon i in a given species' diet. This index renders values from 1 to n (see Levins (1968)).

4.3.6 Multivariate data analysis

To investigate species composition changes in the diets of plaice and dab with increasing trawl frequency data were analysed using the PRIMER (v.6) software package. The dominant factor determining prey availability and the outcome of the sequence of prey encounter, selection, capture and consumption is prey density (Gill, 2003). Prey abundance was therefore favoured over prey biomass as the response variable used in all multivariate data analyses. Mean abundance at sites and in stomach contents was calculated for each station for each prey species. Data were analysed using cluster analysis in conjunction with the SIMPROF routine based on Bray-Curtis similarity matrices (Bray and Curtis, 1957). Clusters identified by the SIMPROF test were visualized using a multi-dimensional scaling (MDS) plot which was overlaid with bubble plots that displayed relative trawling frequency.

The PRIMER (version 6) DISTLM (PERMANOVA) extension package was used to investigate the effects of trawl frequency on the separate responses of the infaunal community composition and on the diets of plaice and dab respectively. DISTLM (Distance-based Linear Models) tests the relationship between multiple variables (in this case infaunal and prey species) to one or more factors based on a Bray-Curtis resemblance matrix. Data was tested for resemblance patterns using the RELATE routine (PRIMER v.6) to test the relationship between environmental prey availability and prey items ingested, and therefore to highlight any potential likelihood that fish were foraging outside stations in which they were caught. All multivariate data was square root transformed to reduce the influence of highly dominant species and multivariate dispersion was checked using PERMDISP.

4.4 Results

4.4.1 Univariate analyses

The abundance, biomass and species richness of the infaunal community and the prey species of plaice and dab showed significant negative relationships with increasing trawl frequency as did the abundance and biomass of the most common (those occurring more than ten times in the diets) prey species of plaice and dab (Table 4.1).

Table 4.1 Results of linear regressions (OLS) describing the relationship between the univariate infaunal and prey species (any species occurring in the diet of plaice or dab respectively (*)) and those more than ten times in the stomachs (≥ 10)) community descriptors (total abundance, total biomass, species richness) and trawling frequency.

Data	Descriptors	Slope	Intercept	r ²	df	F	P
Infauna	Log ₁₀ (abundance)	-0.114	2.468	0.601	1,13	19.601	≤ 0.001
	Log ₁₀ (biomass)	-0.113	0.993	0.624	1,13	21.56	≤ 0.001
	Species richness	-1.804	33.617	0.659	1,13	25.166	≤ 0.001
Plaice	Log ₁₀ (abundance*)	-0.12	2.064	0.570	1,13	17.25	≤ 0.001
	Log ₁₀ (abundance ≥10)	-0.217	5.674	0.53	1,13	14.67	0.002
	Log ₁₀ (biomass*)	-0.559	5.61	0.490	1,13	12.48	≤ 0.001
	Log ₁₀ (biomass ≥10)	-0.18	2.879	0.513	1,13	14.18	<0.002
	Species richness	-0.615	12.414	0.265	1,13	4.687	0.002
Dab	Log ₁₀ (abundance*)	-0.121	2.412	0.580	1,13	17.98	≤ 0.001
	Log ₁₀ (abundance ≥10)	-0.206	5.533	0.507	1,13	13.38	0.003
	Log ₁₀ (biomass*)	-0.612	5.819	0.446	1,13	10.47	≤ 0.001
	Log ₁₀ (biomass ≥10)	-0.187	2.877	0.552	1,13	16.05	0.001
	Species richness	-1.086	18.732	0.402	1,13	8.744	0.011

The total abundance of 13 of the 23 infaunal prey species showed a significant negative relationship with trawling frequency. Only the deeply burrowing mud shrimp, *Jaxea nocturna* (Laomediidae), showed an increase in total abundance with increasing trawl frequency. The remaining 9 infaunal species all showed negative, but non-significant relationships with trawl frequency (Table 4.2). The total biomass of 6 of the 23 infaunal prey species showed a significant negative relationship with trawling frequency. Only the basket shell, *Corbulla gibba* (Corbulidae) and the Amphiurid, *Amphiura filiformis* (Amphiuridae) showed significant increases in total biomass with increasing trawl frequency. Of the remaining 15 infaunal species, 10 showed positive and 5 negative non-significant relationships with trawl frequency (Table 4.3).

Table 4.2 Results of OLS regression analyses (total abundance against trawl frequency ($n \geq 8$ trawl frequencies)) for the most important (90% by abundance) individual infaunal species. \emptyset denotes occurrence in diet, \S denotes occurs ≥ 10 times in diet, numbers in parentheses denote order of preference (calculated as Chesson's standardised forage ratio see figure 4.2; those in bold are positively selected for).

Species	Plaice	Dab	Slope	Intercept	r ²	df	F	P
<i>Abra alba</i>	\S (1)	\S (4)	-0.006	0.164	0.032	1,14	0.433	0.522
<i>Ampelisca</i> sp.	\emptyset	\S (5)	-0.018	0.320	0.246	1,14	4.246	0.060
<i>Amphiura filiformis</i>	\S (8)	\S (8)	-0.0197	1.911	0.633	1,14	22.456	0.001***
<i>Callianassa subterranea</i>	\emptyset	\S (2)	-0.003	0.118	0.014	1,14	0.187	0.673
<i>Corbula gibba</i>			-0.039	0.367	0.403	1,14	8.789	0.011*
<i>Cylichna cylindracea</i>			-0.027	0.295	0.366	1,14	7.519	0.017*
<i>Edwardsia clapparedii</i>		\emptyset	-0.029	0.279	0.342	1,14	6.768	0.022*
<i>Glycera</i> sp.	\S (2)	\S (6)	-0.048	0.591	0.444	1,14	10.381	0.007**
<i>Golfingia</i> sp.	\S (6)	\emptyset	-0.046	0.491	0.619	1,14	21.117	0.001**
<i>Goneplax rhomboides</i>		\S (1)	-	-	-	-	-	-
<i>Jaxea nocturna</i>	\S (7)	\S (3)	0.015	0.086	0.277	1,14	4.991	0.044*
<i>Lagis koreni</i>	\S (5)	\emptyset	-0.051	0.476	0.525	1,14	14.972	0.002**
<i>Lumbrineris gracilis</i>	\S (4)	\emptyset	-0.051	0.666	0.508	1,14	13.404	0.003**
<i>Magelona alleni</i>	\emptyset		-0.054	0.589	0.353	1,14	7.104	0.019*
<i>Melinna elisabethae</i>	\emptyset	\emptyset	-0.034	0.340	0.346	1,14	6.883	0.021*
<i>Mysella bidentata</i>			-0.083	0.731	0.542	1,14	15.381	0.002**
<i>Mysia undata</i>			-0.021	0.219	0.283	1,14	5.127	0.041*
<i>Nephtys</i> sp.	\S (3)	\S (7)	0.015	0.726	0.093	1,14	1.336	0.269
<i>Notomastus</i> sp.			-0.014	0.412	0.042	1,14	0.564	0.466
<i>Phoronis</i> sp.		\emptyset	-0.103	1.845	0.448	1,14	10.546	0.006**
<i>Polydora</i> sp.			-0.014	0.344	0.018	1,14	0.237	0.634
<i>Prionospio</i> sp.			-0.004	0.564	0.002	1,14	0.030	0.865
<i>Scalibregma inflatum</i>		\emptyset	-0.119	1.397	0.308	1,14	5.797	0.032
<i>Spisula subtruncata</i>			-0.024	0.264	0.20.4	1,14	3.339	0.091

Note: Significant correlation results are indicated by asterisks * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Low occurrences of *G. rhomboides* in infaunal samples mean OLS regression was not possible for this species.

Table 4.3 Results of OLS regression analyses (total biomass against trawl frequency ($n \geq 8$ trawl frequencies)) for the most important (90% by abundance) individual infaunal species. θ denotes occurrence in diet, \S denotes occurs ≥ 10 times in diet, numbers in parentheses denote order of preference (calculated as Chesson standardised forage ratio see figure 4.2; those in bold are positively selected for).

Species	Plaice	Dab	Slope	Intercept	r ²	df	F	P
<i>Abra alba</i>	\S(1)	\S(4)	0.000	0.005	0.004	1,14	0.046	0.833
<i>Ampelisca sp.</i>	θ	\S(5)	0.000	0.003	0.049	1,14	0.664	0.430
<i>Amphiura filiformis</i>	\S(8)	\S(8)	0.059	0.522	0.528	1,14	14.534	0.002**
<i>Callianassa subterranea</i>	θ	\S(2)	0.000	0.009	0.032	1,14	0.432	0.522
<i>Corbula gibba</i>			0.000	0.015	0.374	1,14	7.754	0.015*
<i>Cylichna cylindracea</i>			0.000	0.004	0.206	1,14	3.364	0.090
<i>Edwardsia clapparedii</i>		θ	-0.002	0.016	0.572	1,14	17.385	0.001**
<i>Glycera sp.</i>	\S(2)	\S(6)	-0.016	0.186	0.394	1,14	8.464	0.012*
<i>Golfingia sp.</i>	\S(6)	θ	0.000	0.019	0.001	1,14	0.008	0.932
<i>Goneplax rhomboides</i>		\S (1)	-	-	-	-	-	-
<i>Jaxea nocturna</i>	\S(7)	\S(3)	0.005	0.007	0.188	1,14	3.008	0.106
<i>Lagis koreni</i>	\S(5)	θ	-0.004	0.036	0.539	1,14	15.211	0.002**
<i>Lumbrineris gracilis</i>	\S(4)	θ	0.000	0.007	0.083	1,14	1.178	0.298
<i>Magelona alleni</i>	θ		-0.001	0.015	0.188	1,14	3.001	0.107
<i>Melinna elisabethae</i>	θ	θ	-0.002	0.002	0.391	1,14	8.298	0.013*
<i>Mysella bidentata</i>			-0.001	0.009	0.397	1,14	8.554	0.012
<i>Mysia undata</i>			-0.006	0.059	0.205	1,14	3.359	0.090
<i>Nephtys sp.</i>	\S(3)	\S(7)	-0.003	0.110	0.041	1,14	0.562	0.467
<i>Notomastus sp.</i>			0.003	0.007	0.043	1,14	0.585	0.458
<i>Phoronis sp.</i>		θ	-0.003	0.031	0.527	1,14	14.508	0.002**
<i>Polydora sp.</i>			0.000	0.003	0.043	1,14	0.589	0.456
<i>Prionospio sp.</i>			0.000	0.003	0.016	1,14	0.206	0.657
<i>Scalibregma inflatum</i>		θ	-0.007	0.103	0.061	1,14	0.844	0.375
<i>Spisula subtruncata</i>			-0.017	0.153	0.377	1,14	7.864	0.045*

Note: Significant correlation results are indicated by asterisks * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Low occurrences of *G. rhomboides* in infaunal samples mean OLS regression was not possible for this species.

Chesson's standardised forage ratios (α_a) calculated from stomach content data from all trawl sites indicated that plaice selected positively for bivalve, *Abra alba* (Semelidae) and the polychaeta, *Glycera sp.* (Glyceridae). Dab selected positively for the angular crab, *Goneplax rhomboides* (Goneplacidae) and the mud shrimp, *Callianassa subterranea* (Callianassidae) (see Fig. 4.2). These species were therefore the main target prey species that are actively searched for by plaice and dab.

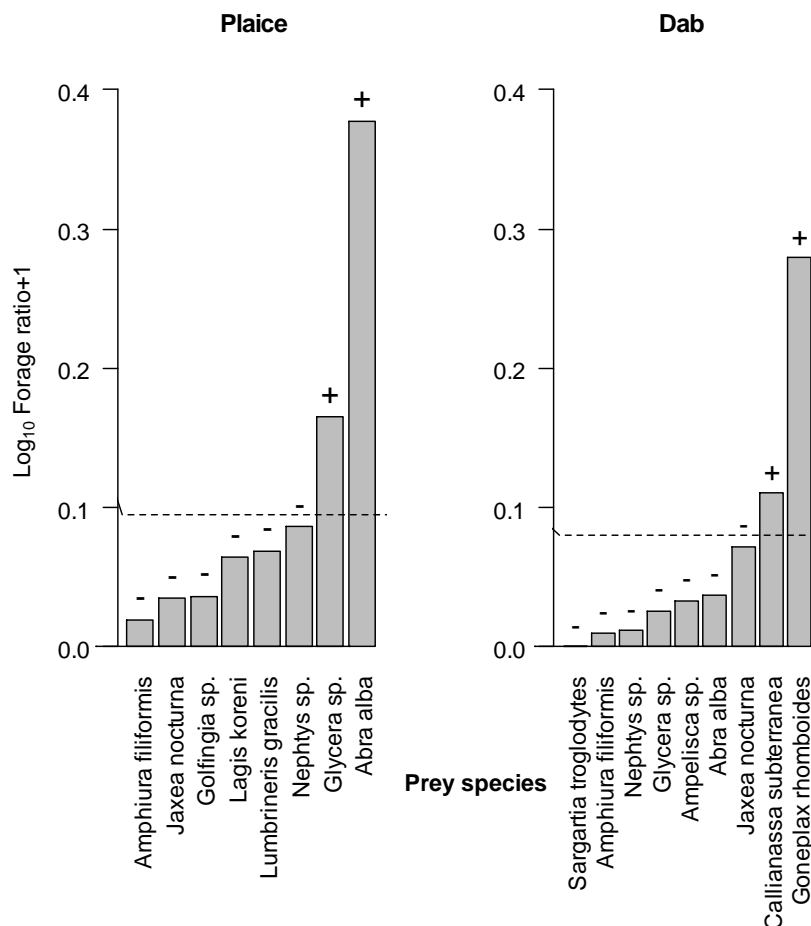


Figure 4.2 Bar charts of Chesson's standardised forage ratio (prey selectivity) for prey species occurring more than ten times in the stomachs of dab and plaice combining data from all sites. Broken lines mark $\alpha_a = m^{-1}$, random feeding i.e. level at which a prey item is taken

by the predator in exactly the same proportion as in the environment. Positive (+) therefore denotes active selection and negative (-) denotes prey items not preferentially selected for.

Combining data from all trawl frequencies, the calculation of Schoener's index demonstrated that the prey species composition of plaice and dab diets overlapped by 41.6% when considering all prey species that occurred in the diet of both species. Plaice had a much narrower prey spectrum (Levin's niche breadth (B)) both in terms of prey species (5.16) and compared to dab (8.87).

Dab had a significantly higher prey width to mouth width (PW:MW) ratio ($t = -5.821$, $df = 18.08$, $P = <0.001$) across trawl sites than plaice ($0.519 \text{ mm} \pm 0.126$ versus $0.319 \text{ mm} \pm 0.043$ respectively) (Fig. 4.3). The stomach contents of dab also contained significantly more ($t = -11.089$, $df = 400.83$, $P = <0.001$) energy content per gram of fish than plaice gut contents ($2.12e^{-7}$ KJ per g of fish $\pm 0.34e^{-7}$ vs $3.59e^{-8}$ KJ per g of fish $\pm 0.067e^{-8}$ respectively) (Fig. 4.3).

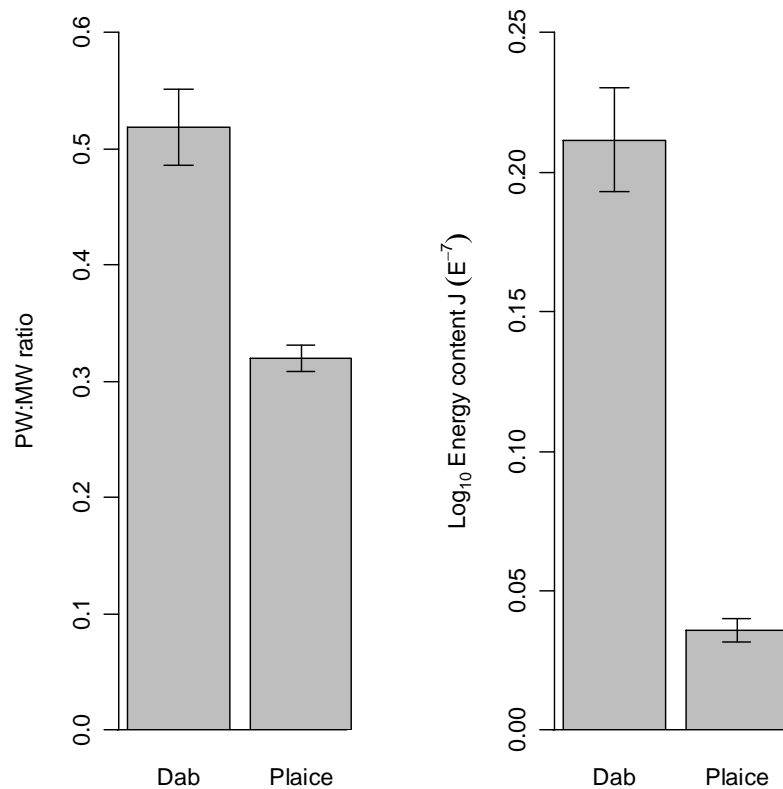


Figure 4.3 Bar charts of mean PW:MW ratio (calculated as mean per site) and mean energy content of stomach contents (calculated as mean per stomach). Error bars denote \pm S.D.

There was a significant positive relationship between the number of *Abra alba* in the stomach contents of plaice (per fish) and trawling intensity ($R^2 = 0.292$, $F_{1,13} = 6.357$, $P = 0.027$) whilst a negative relationship was found for number of *Nephtys sp.* ($R^2 = 0.333$, $F_{1,13} = 7.477$, $P = 0.018$) was detected (Fig. 4.4). No other relationships were found for the other prey species in plaice stomach. No significant relationship between trawling and the abundance of any prey species in the stomach contents of dab was detected even for the three most selected prey species (*G. rhomboides* ($R^2 = 0.017$, $F_{1,13} = 0.23$, $P = 0.639$), *C. subterranea* ($R^2 = 0.091$, $F_{1,13}$

= 1.296, $P = 0.275$) and ($R^2 = 0.1354$, $F_{1,13} = 2.036$, $P = 0.1772$), indicating that trawling had no significant effect on the feeding of dab (Fig. 4.5).

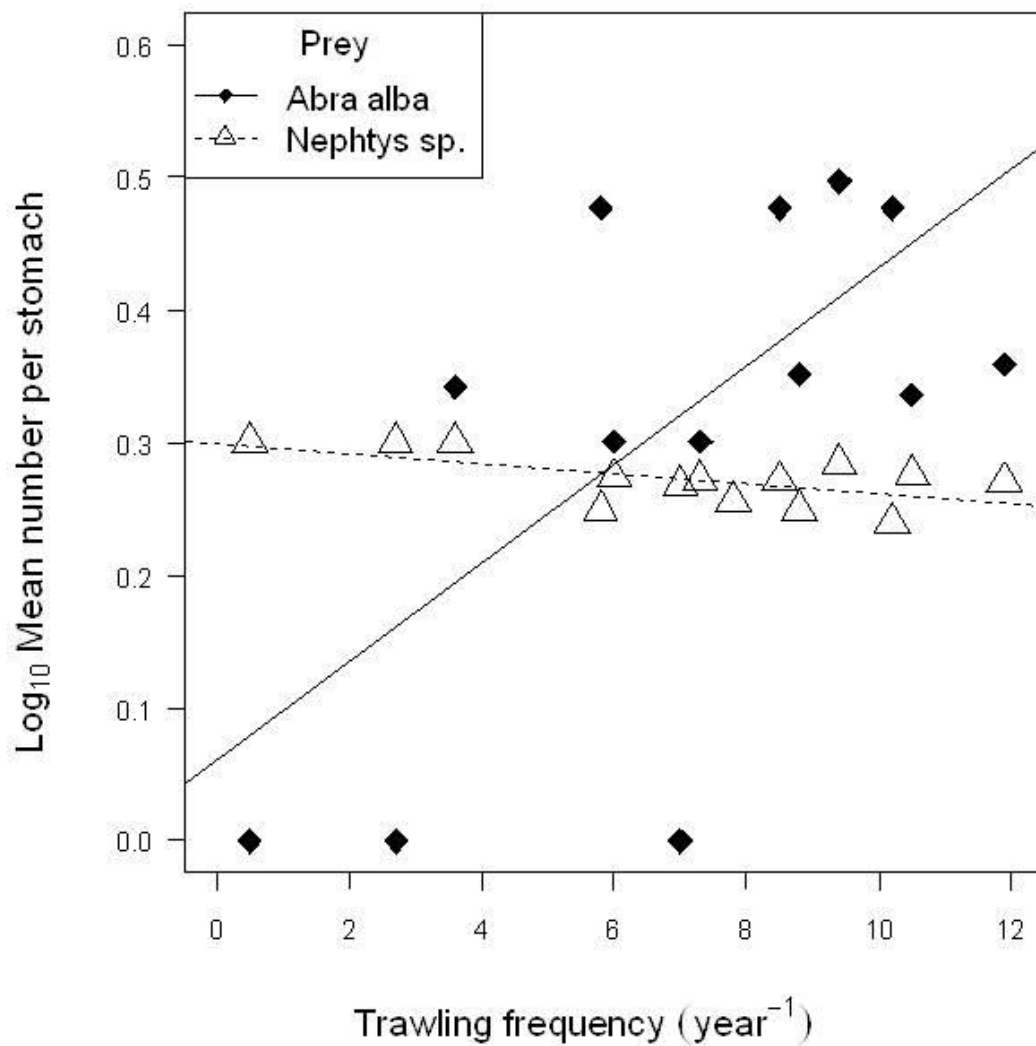


Figure 4.4 OLS regressions of trawl frequency against mean prey abundance in the stomach contents of plaice. Each point represents a mean value of abundance per fish.

With increasing trawl frequency there was a decrease in the mean individual biomass of *Nephtys sp.* ($R^2 = 0.477$, $F_{1,13} = 12.83$, $P = 0.004$) and an increase in the mean individual biomass of *Abra alba* ($R^2 = 0.341$, $F_{1,11} = 7.204$, $P = 0.0213$) found in the stomachs of plaice (Fig. 4.6), however no such relationships were detected for any of the prey species of dab.

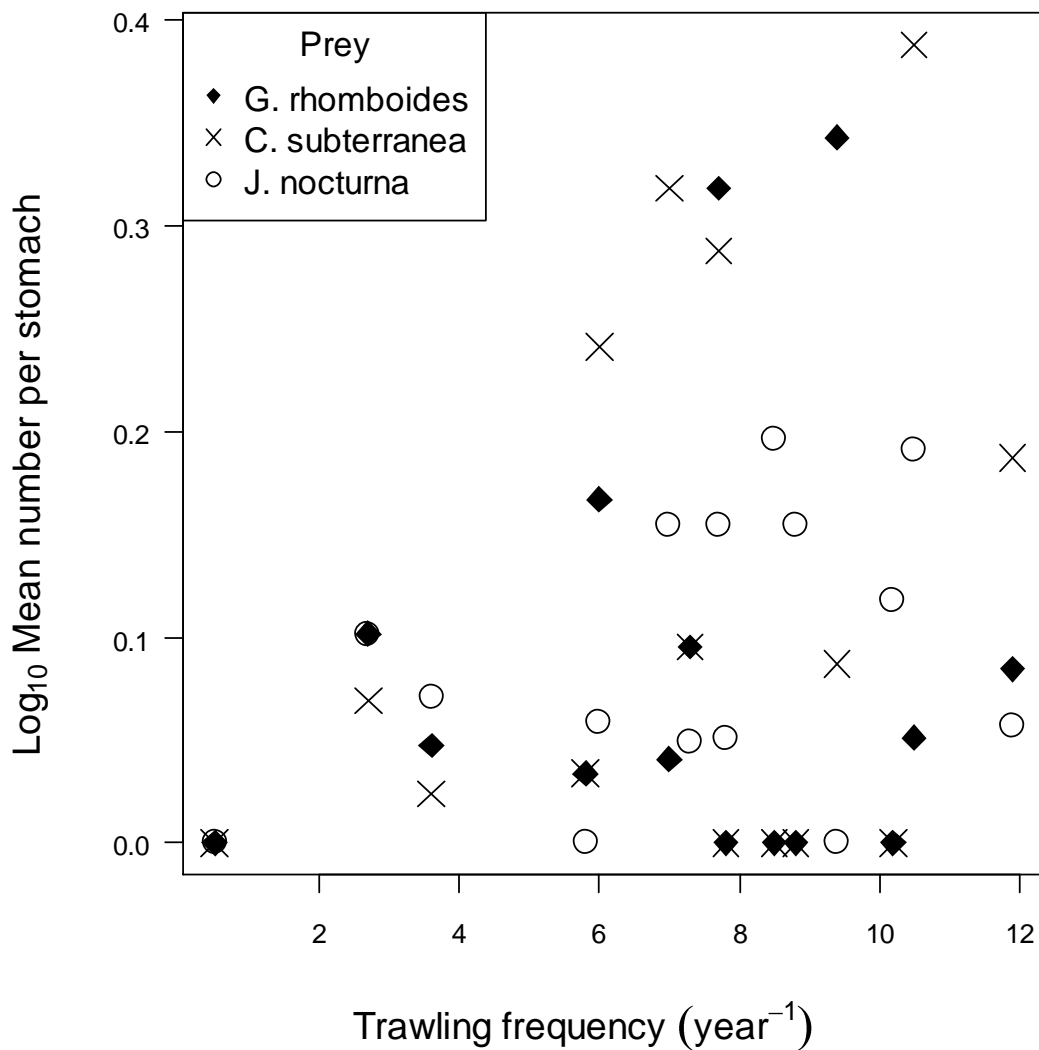


Figure 4.5 OLS regression of trawl frequency against mean prey abundance of the three most important prey species in the stomach contents of dab. Each point represents a mean value of abundance per fish.

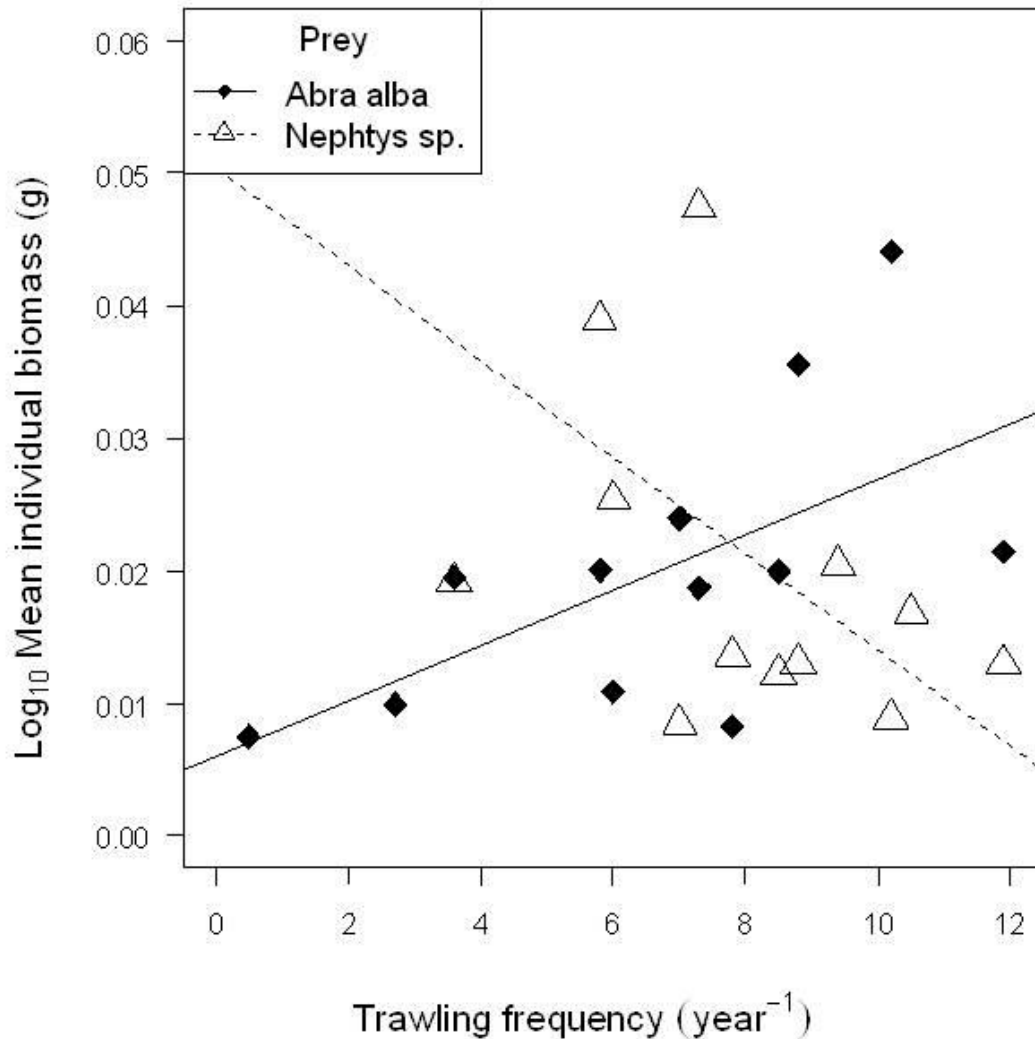


Figure 4.6 OLS regressions of trawl frequency against mean biomass (g) of *Bivalve sp.* ($n \geq 3$ stomachs per station) and *Nephtys sp.* ($n \geq 8$ stomachs per station) in the stomach contents of plaice. Each point represents a mean value of wet biomass per site.

There was a change in preference of prey species by plaice with increasing trawl frequency indicated by a significant decrease in the prey selectivity (Chesson's index) of plaice for *Nephtys sp.* ($R^2 = 0.328$, $F_{1,13} = 7.347$, $P = 0.0189$) and an increase for *Abra alba* ($R^2 = 0.396$, $F_{1,11} = 7.204$, $P = 0.0213$) (Fig. 4.7).

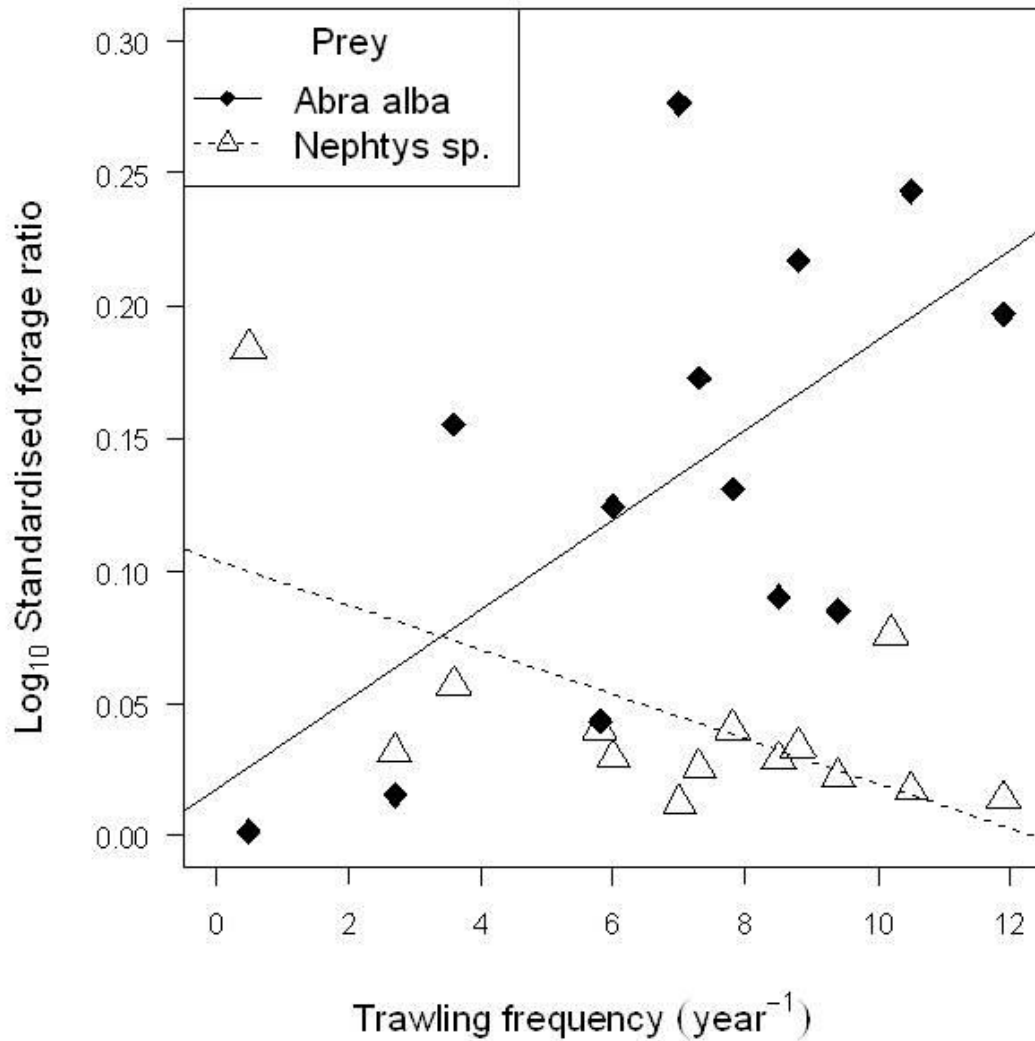


Figure 4.7 OLS regressions of trawl frequency against prey selectivity (α_a) of plaice (*Nephtys sp.* and *Abra alba*). Each point represents a mean value of selectivity per site.

No significant relationships between the mean amount of energy contained in stomachs and trawl frequency was detected for plaice ($R^2 = 0.009$, $F_{1,13} = 0.113$, $P = 0.743$) or dab ($R^2 = 0.009$, $F_{1,14} = 0.199$, $P = 0.735$).

Trawling frequency had no significant effect on the niche breadth (i.e. the number of prey species found in the diet at each trawl frequency) of dab ($R^2 = 0.038$, $F_{1,14} = 0.470$, $P = 0.506$) but did increase the niche breadth of plaice ($R^2 = 0.367$, $F_{1,13} = 6.595$, $P = 0.022$). A negative but non-significant relationship between trawl frequency and dietary overlap of plaice and dab was detected for prey species composition ($R^2 = 0.211$, $F_{1,13} = 4.144$, $P = 0.064$). Trawling also had no significant effect on the stomach fullness of plaice ($R^2 = 0.001$, $F_{1,13} = 0.04$, $P = 0.899$) or dab ($R^2 = 0.003$, $F_{1,14} = 0.017$, $P = 0.844$).

4.4.2 Multivariate analyses

The cluster analysis and SIMPROF test identified three statistically significant clusters (A and B and C) for the stomach contents data. There was a clear separation of station clusters by species between cluster A and B (A exclusively containing plaice stomach data and B dab data). Cluster C contained stations of both species. All three separated at a similarity level of 40% (Fig 4.8). Cluster A and B had mean trawl frequencies of 8.16 ± 2.28 and 8.05 ± 2.09 respectively, while cluster D showed lower mean trawl frequencies of 4.87 ± 3.78 .

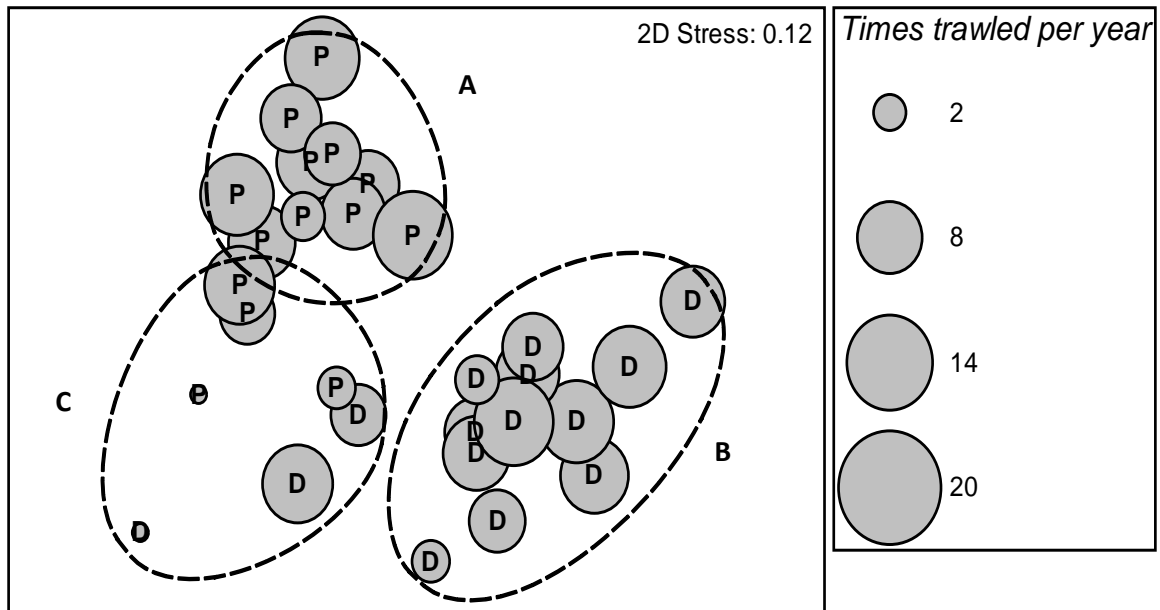


Figure 4.8 Multidimensional scaling plot of stomach contents of Plaice (P) and Dab (D) with fishing frequency overlaid as bubble plots. Broken lines denote clusters of 40% resemblance.

DISTLM indicated that trawl frequency had a significant effect on the whole infaunal community and the diet composition of both fish species. This effect was however stronger for plaice than dab (Table 4.4).

Table 4.4 Results of DISTLM for whole infaunal community and prey species in the stomach contents of plaice and dab.

Data	df	SS	Pseudo-F	P (perm)
Infauna	13	4835.2	5.5969	0.001
Plaice	12	3220.8	3.5266	0.003
Dab	13	4196.2	2.6697	0.022

The RELATE routine rejected the null hypothesis of no relationship between the infaunal prey availability matrix and the prey species found in the stomachs of plaice and dab. It is therefore unlikely that that fish were foraging outside the sites at which they were caught ($\rho = 0.488, P < 0.001$).

4.5 Discussion

Our results indicate that the diets of plaice and dab were significantly different within the study area and the overall effect of trawling frequency on their diets differed significantly. The dietary differences between plaice and dab and the subsequent alterations in foraging behaviours are likely to explain the reduced condition of plaice found by Hiddink et al. (2011) at more frequently trawled sites within the study area.

Trawling significantly reduced the abundance, biomass and species richness of the infaunal community as well as the prey species community of plaice and dab. From low to high trawl frequencies plaice switched from feeding on small *Nephtys sp.* to larger *Abra alba*. Trawl frequency had no significant effect on the feeding of dab as no changes in prey selectivity, abundance or individual biomass of prey species were detected in stomach contents. Trawl frequency also had no effect on the energy content per stomach or fullness for either fish species. This therefore supports our hypothesis that that the reduced condition of plaice found by Hiddink et al. (2011) in high trawl sites was not caused by reductions in feeding but may be attributed to reduced feeding efficiencies caused by changes in its available prey community.

Hiddink et al. (2011) concluded that density dependent changes in competition over prey resources could not explain the reduced condition of plaice found at more trawled sites as fishes of reduced condition were present at sites with low abundances of conspecifics. Although it may be intuitive that morphometrically similar fish species experience increased levels of food competition with diminishing prey resources in a shared area, significant differences in the diet composition (low dietary overlap) and no effect of trawling on the dietary overlap of plaice and dab would suggest this is not the case. The partitioning of prey resources by plaice and dab was also reflected in the respective overall Chesson prey selectivity values and Schoeners dietary overlap index as well as the mean energy content per stomach and the PW:MW of each species.

The greater number of prey species and the larger PW:MW ratio of dab is supported by past studies that classify it as an opportunistic, generalist feeder (Kaiser and Ramsay, 1997, Hinz et al., 2005) compared to plaice which is known to be more specialised in its prey choice (Wyche and Shackley, 1986). Differences in the morphology and feeding strategy of these species can readily explain the differences in their diets. Russo et al. (2008) found that plaice was well suited to preying on buried, rather than motile prey, due to its superior suction capability and horizontal mouth, head-down foraging position and well developed olfactory bulb (Degroot, 1969, Basimi and Grove, 1985). Previous studies describe dab as a better accelerator (well developed tail peduncle) with larger eyes than plaice making it more adept at preying on mobile species such as crustacea (Degroot, 1969, Batty and Hoyt, 1995, Piet et al., 1998). Our results support these findings as the dominant prey species of plaice and dab can be broadly categorised as small buried infaunal species and mobile crustacean species respectively.

Feeding on larger individuals often involves increased prey handling time and therefore increases overall foraging costs of a predator (Charnov, 1976). Dab stomachs contained a high number of crustacean chelipeds, which were almost totally absent in plaice stomachs. The partial utilisation (appendages only) of large crustacean prey means that dab can exploit a very energy rich prey resource (4.047 KJ g^{-1}) (Brey, 2001), which is predominantly unavailable to plaice due to differences in feeding morphology, without incurring high prey handling costs.

Plaice generally fed on lower energy value prey species than dab (bivalves < polychaetes < crustaceans) (Brey, 2001) across all trawl frequencies, leading to a significantly lower energy gain per gram of prey captured. Although the preference for less energy rich prey by plaice is likely to contribute to its reduced condition with bottom trawling, it cannot fully explain the findings of Hiddink et al. (2011) as no significant relationship between gut energy content and trawling was detected. Instead, differences in the overall energy gain per prey capture (net energy gain after accounting for energy spent during prey handling) are more likely to explain these results.

Stomach fullness did not change significantly across trawl frequencies in dab or plaice suggesting that individuals of both species were unlikely to be significantly food limited across trawl frequencies. Fullness is however likely to vary considerably over short time scales and gives only a snapshot view of feeding history. This interpretation should therefore be taken with caution, especially considering evacuation rates of plaice and dab have been shown to be between 14h at 15°C and 9.28h at 16.4°C respectively (Jobling et al., 1977, Jobling, 1980). The idea that bottom trawling did not reduce the overall feeding potential of

the fishes is however corroborated considering there was an increase in the number of prey species options (niche breadth) of plaice.

Past studies have shown that very low levels of bottom trawl disturbance (0 to 1 trawls year⁻¹) are likely to enhance the condition of juvenile plaice over soft sediment habitat types through an increased production (Jennings et al., 2001b, Hiddink et al., 2008) and availability (Groenewold and Fonds, 2000, Shephard et al., 2010) of polychaeta prey. Our results however demonstrate no significant relationships between the abundance and biomass of *Nephtys sp.* with trawl frequency however the majority of our sites were much more heavily trawled than previous studies (0.5 to 11.9 trawls year⁻¹). Stomach content data however showed that increasing trawl frequency caused an increase in the mean abundance of *Nephtys sp.* but a decrease in mean biomass in the stomachs of plaice, suggesting a decrease in the individual size of this species at more trawled sites. We also show that the mean biomass of *A. alba* increased whilst their abundance decreased in the stomach of plaice suggesting larger individuals are being targetted at higher trawl frequencies.

The switch observed in the diet of plaice may well allow it to compensate for the increased foraging costs / times associated with smaller sized *Nephtys sp.* at more trawled sites, which are likely to be more difficult to detect (Breck and Gitter, 1983). Although prey mass per capture may be sufficiently compensated for or even exceeded with this adaptive prey shift, it is important to note the low energy content of *Abra alba* (1.494 kJ⁻¹) compared to *Nephtys sp.* (3.272 kJ⁻¹). This means that although plaice are likely to adapt their prey choice to reduce foraging efforts and increase the ease with which they can become satiated, reflected from our stomach fullness calculations, energy capture per prey item is reduced. Therefore in order for an individual plaice to gain the same energy at highly trawled sites as at low trawled sites,

increased effort must be spent foraging for fewer, but larger, less energy rich prey items (in this case *Abra alba*). The data further supports this hypothesis as trawl frequency had no effect on the amount of energy contained in the stomachs of plaice.

In addition to increasing the numbers and reducing the sizes of certain infaunal species, trawl disturbances may increase the proportion of annual, secondary production available to the scavenger food chain (1 beam pass = 6.2 – 13% (Groenewold and Fonds, 2000)). Specifically, previous studies have noted that bottom trawl disturbances can increase the potential feeding opportunities of the opportunistic, scavenging dab (Kaiser and Ramsay, 1997, Groenewold and Fonds, 2000). This is highlighted by our results which show that the three most important prey species of dab, either increased (*J. nocturna*) or showed no relationship (*C. subterranea*, *G. rhomboides*) to trawl frequency. All of these species are burrowing and are likely to be largely unavailable to dab when concealed within their burrows. Although we did not detect an increase in abundance of these species in the stomachs of dab, it is likely that passing trawls uncover previously concealed individuals for dab to forage on. This was reflected in the infaunal data for *J. nocturna*. It is also noteworthy that *G. rhomboides* is a highly mobile species that may not have been well sampled in the grab samples. This may also account for the high selectivity of this species by the dab. It is however difficult to quantify this discrepancy between numbers actually present and those sampled without analysing the effectiveness of the grab for this species specifically.

The lack of relationship between trawling and the abundance and mean individual biomass of species found in the stomach contents of dab is likely to reflect its wide prey spectrum and subsequent ability to adapt and perhaps even profit from benthic disturbances and changing prey spectrums as a result of trawling. Our study therefore supports the idea that dab is an

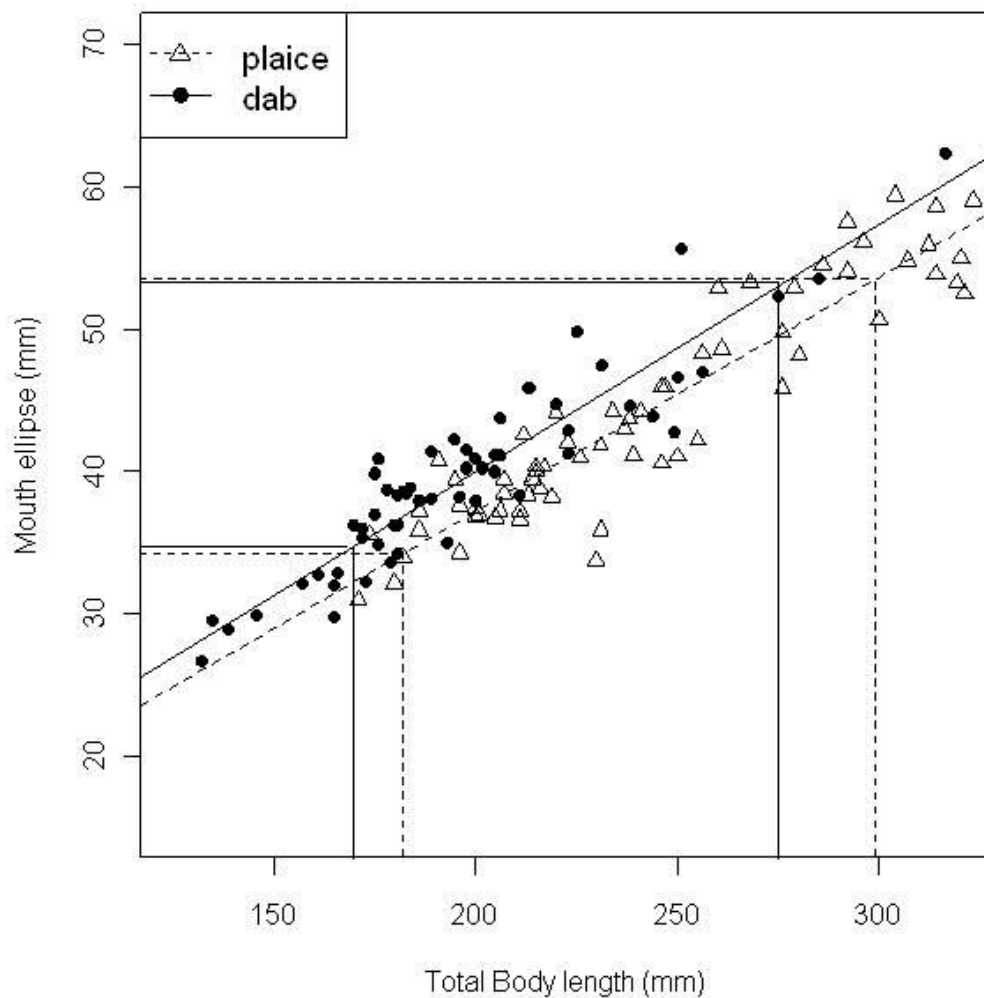
opportunistic generalist able to easily adapt and perhaps even benefit from bottom trawl disturbances. Prey selection based on the most readily available items and the ability to feed with a larger PW:MW theoretically gives dab a more energetically favourable feeding strategy than plaice (Charnov, 1976, Gill, 2003). This is also reiterated when considering the energy per gram of the dominant prey species of plaice and dab. The wide geographic distribution of dab in the NE Atlantic and stable population numbers (Heessen and Daan, 1996, Rogers et al., 1998) despite high levels of exploitation and by-catch mortality (Kaiser and Spencer, 1995) may in part reflect this ready adaptability.

Our study indicates that the negative effect of bottom trawling on the condition of plaice found by Hiddink et al. (2011) is likely to be caused by perturbations in its prey resource and subsequent changes in foraging behaviour and reductions in feeding efficiencies. The condition of the opportunistic, generalist feeder dab is however unaffected as it can readily adapt its diet to the bottom disturbances caused by trawling without subsequent reductions in feeding efficiency. Demersal fish species with limited prey spectra and low adaptabilities to changes in benthic prey resources may experience population-level consequences through potential decreases in condition, growth and recruitment from bottom trawl disturbances. In order to predict and mitigate such long-term, chain reaction responses of populations adversely affected by human activities it is essential that we thoroughly understand the secondary effects of such activities as well as the trophic linkages connecting prey and predator communities.

4.6 Appendices

4.6.1 Appendix

OLS regression displaying mouth gape ellipse sizes against total body length used to ensure all mouth gapes of plaice and dab used in analyses overlapped (see reference lines) (plaice: $R^2 = 0.857$, $F_{1,64} = 384.3$, $P < 0.001$. dab: $R^2 = 0.894$, $F_{1,57} = 477.6$, $P < 0.001$).



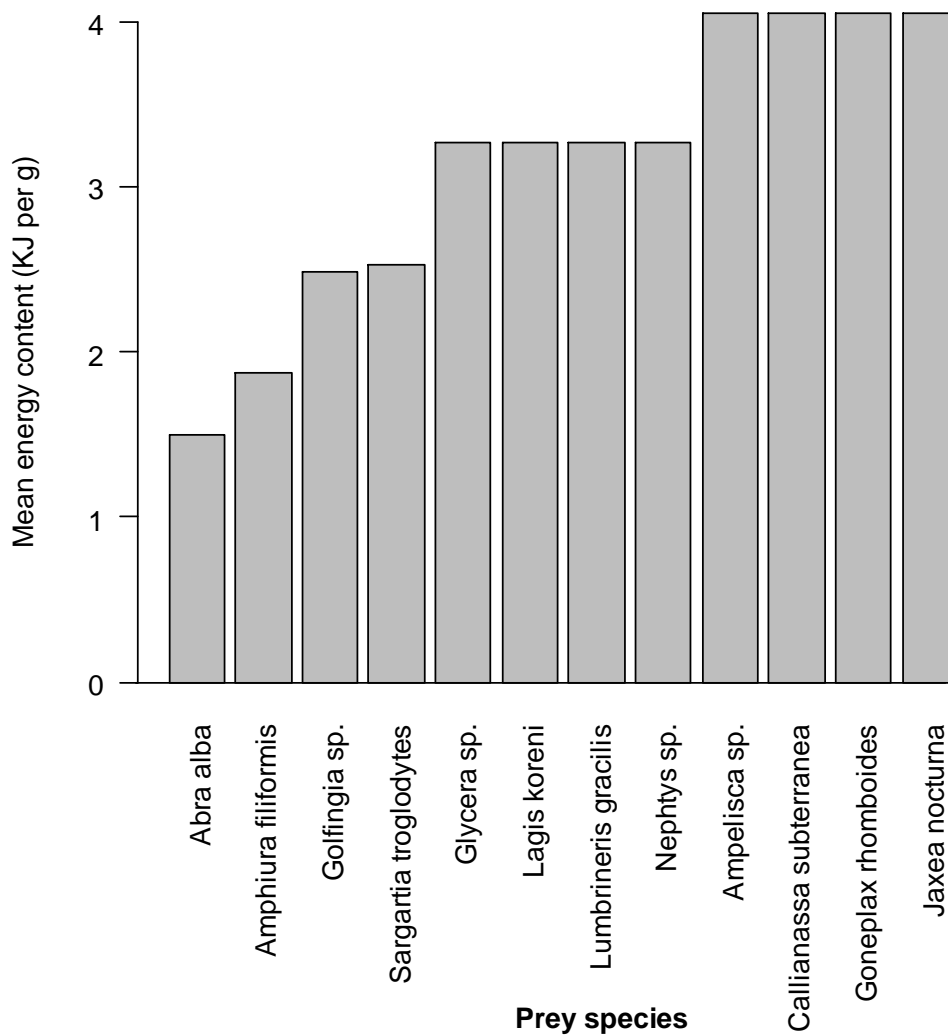
4.6.2 Appendix

Table showing the total numbers of plaice and dab stomach sampled per trawl frequency with corresponding site letters.

Station	Trawl yr ⁻¹	Dab n°	Plaice n°
H	0.5	32	55
T	2.7	50	47
R	3.6	28	19
C	5.8	33	13
S	6	35	17
P	7	41	28
B	7.3	40	38
L	7.7	28	28
I	7.8	36	1
F	8.5	15	11
D	8.8	47	27
G	9.4	47	15
M	10.2	52	25
E	10.5	46	40
O	11.9	45	50

4.6.3 Appendix

Bar chart of mean energy content (KJ per g) of prey species occurring more than ten times in the diets of plaice and dab respectively calculated from Brey (2001) conversions. Number of individuals animals used to calculated Brey conversion value ≥ 10 .



CHAPTER 5

Habitat requirements of demersal fishes – a small scale perspective

5.1 Abstract

The habitats of demersal fish species have traditionally been characterised by the abiotic habitat variables of depth and sediment. It may however be argued that habitat cannot be described by either of these parameters alone without accounting for the biotic habitat components that may be determined by them. In this investigation we tested the hypothesis that the distribution of the common dragonette (*Callionymus lyra*) was determined by its prey community across different sediment types, over small spatial scales (100's m²). Detailed stomach content analysis revealed significant changes in the diet of *C. lyra* with development, in terms of prey taxa and prey size. Fullness and energetic values of stomach contents also demonstrated a clear bioenergetic / optimal feeding strategy with small individuals eating high numbers of small, low energy prey and larger individuals consuming few large, energy rich prey items. Although strong prey preferences were demonstrated across body length size classes, we found no significant relationship between the prey community (whether defined as prey taxa or prey size distribution) and the stomach contents of *C. lyra*. This may indicate that home ranges exceeded the size of the different habitat types tested or that other habitat variables such as sediment type and predation risk are more important than prey resources in determining the distribution of *C. lyra*. Significant temporal differences in the size class distribution of *C. lyra* were driven by the abundance of juveniles in autumn samples that are likely to be linked to the previous spring spawning events. This study highlights the importance of considering predator size when relating the distribution of demersal fish species to their environment and briefly discusses the use of benthic maps to pre-define habitats based on sediment type.

Keywords: *Callionymus lyra*, habitat map, ontogeny, prey distribution

5.2 Introduction

The link between habitat and sustainable fisheries management is now well understood (Schmitt, 1999). Understanding what makes a habitat suitable for the successful growth and development of a fish species is however no easy task when considering the multiple facets making up a habitat (see Johnson et al., 2012). This is further complicated when considering the numerous spatial and temporal scales over which different habitat variables may act. Untangling this complex web is however necessary if we are to clearly understand what drives a fish to inhabit an area in preference to its neighbouring surroundings.

The complexity of describing marine habitats is not helped by the difficulty and expense of sampling aquatic environments (Diaz et al., 2004). Descriptions of biotic communities in benthic marine habitats often involve laborious sampling and high levels of replication (Chapman et al., 2010). Advances in mapping technologies, such as side scan sonar and multi-beam swath bathymetry now allow relatively fast, high resolution, large spatial scale, abiotic descriptions of sea beds (Kenny et al., 2003, Brown and Blondel, 2009). In turn these may be used to predict the distribution of biotic assemblages and to direct smaller spatial scale sampling (Brown and Collier, 2008, Monk et al., 2010). Many believe that such advances have the potential to revolutionise spatial management strategies (Kaplan et al., 2010) and the success of using acoustic habitat maps in the design of marine protected areas (MPAs) has already shown promise in tropical and temperate systems (Ortiz and Tissot, 2008, Copeland et al., 2011). Stevens and Connolly (2004) however warn that MPAs designed on the basis of abiotic surrogates in certain cases may have questionable benefits for conservation. One thing that remains clear however is that the data density mismatches between abiotic and biotic community descriptions will remain unsolved until acoustic

methods can routinely resolve the biological components of benthic systems (Diaz et al., 2004).

The influence of biotic habitat variables in determining the habitat choice and distribution of demersal fish species is an area that is generally lacking and the parameter of prey resource is no exception (Johnson et al., 2012). Small spatial scale studies that have addressed its importance are often undertaken in laboratory settings that attempt to simulate natural environmental conditions and extrapolate findings to the field. The disadvantages of this approach, such as unrealistic encounter rates and escape responses of prey, are well known and readily highlighted by the authors of such studies (Lindholm et al., 1999, Manderson et al., 2000). The few studies that do investigate the importance of prey resource in the field usually look at correlations between prey and predator abundance over large spatial scales ($\geq 10 \text{ km}^2$) using broad / low resolution definitions of prey preferences and communities of the species under analysis. These studies often do not account for changes in predator size or habitat type (see Toole et al., 2011 - consideration of pseudo-species based on ontogeny). Those that do account for the predator size differences in diets and the resulting distributions of the predator fishes generally focus on the vertical migrations of pelagic juvenile stages only (e.g. Pillar and Barange, 1995, Bozzano et al., 2005).

The aim of this study was to: 1) accurately describe the feeding ecology of *C. lyra*, accounting for dietary changes as a result of predator size, 2) describe the community of *C. lyra* over three different habitat (sediment) types classified using a detailed multi-beam swath bathymetry habitat map, 3) describe the prey community of *C. lyra* over these habitats and 4) examine whether differences in the distribution of *C. lyra* were related to differences in the prey community between these sites. Overall, I hypothesise that prey choice will change

significantly with predator size and the distribution of *C. lyra* will be related to the distribution of its prey community. *C. lyra* was selected as it is a useful model species that appears in high numbers allowing the rigorous investigation of the above aims. It is a benthivorous species with a flat underside and downward facing mouth aperture meaning it has a strong link with the benthic community where it is found. Such investigations are necessary to understand the role prey communities play in demersal fish distributions over small spatial scales and the use of such habitat variables to define areas for spatial management strategies.

5.3 Materials and Methods

5.3.1 Study site

This research was conducted within Plymouth Sound, located in the south-west of England (Latitude 50 20 06 N, Longitude 04 08 51 W), south of Plymouth which is a designated Special Area of Conservation (UK0013111) (Fig. 5.1). The subtidal environment comprises soft sediment, gravel and cobble beds as well as granite reefs. The inner part of the Sound is protected by a 1.6 km long breakwater which shelters much of the area from prevailing south / south-west winds and swells carried in by the Atlantic. The sheltered nature of the area gives rise to a number of habitat types from beds of *Zostera marina* to rocky bottomed red algae communities as well as fine sediment bottoms.

Qualitative and quantitative descriptions of the marine flora and fauna of Plymouth Sound have to our knowledge been restricted to localised SCUBA, ROV and dredge surveys (see Johnson, 1890, Somerfield and Clarke, 1997, Parry et al., 2003). The study site of this work is composed of three distinct bottom types of coarse sand, coarse boulder gravel and shingle / shell gravel running from SW to NE at the western entrance of the breakwater. This area has

previously been mapped by Pike et al. (2008) using a multibeam bathymetry system in conjunction with thorough ground truthing. In order to provide a larger area to work within, these areas were extended considerably to include more of each of the three bottom types. The habitat map produced from this site extension was used to clearly define the separate bottom types and allow isolated sampling within each.

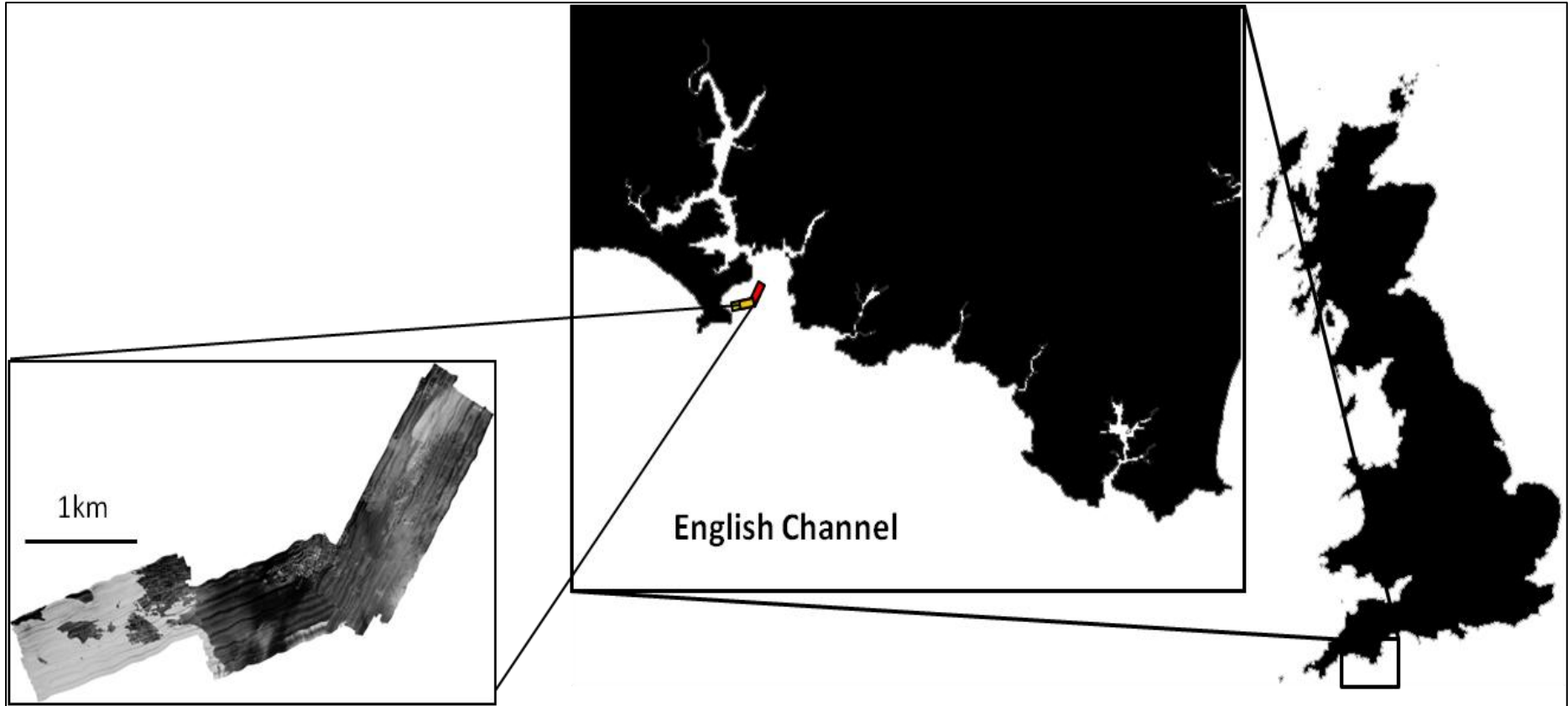


Figure 5.1 Location of the research area, Plymouth Sound, Plymouth, south-west England, (Latitude 50 20 06 N, Longitude 04 08 51 W). Inset shows texture map of study area.

5.3.2 Site description

We used the same v-plate mounted Geoacoustics GeoSwath Plus (GS+) swath bathymetry system as Pike et al. (2008) to collect additional bathymetry and texture data of the sites previously described. In order to provide a high resolution ‘image’ of the seabed types, we used 250 KHz transducers along with a grid bin size of 1.6m when processing the multibeam data. Prior to all mapping, the system was calibrated for yaw, pitch and latency over a distinct, deep channel and for roll over a sheltered, flat area of sea bed. The mean tow speed during data acquisition was 4 knots (± 0.7 knots). All Multibeam data was collected during August 2008.

In order to ground-truth the sediment maps and allow an accurate habitat classification of the texture map, a total of 50 sediment samples were taken using a Van Veen grab across the whole mapped area using an approximate square grid pattern (Fig.5.2), the positional accuracy of which was estimated to be ± 5 m. All sediment samples (approximately 1kg each) were frozen at -20°C within 6 hours of collection. A series of sieves from $2000\mu\text{m}$ to $63\mu\text{m}$ were used to quantify the percentage composition of the sediment across the study site. The side-scan mosaics produced using the Geoswath system were classified using Geotexture software (version 3.16c) to create the final habitat maps. This process consists of selecting the locations on a side-scan mosaic where the ground truthing sediment samples were collected and specifying the classification of the sediment for that location. The shade and texture of the side-scan mosaic at the ground-truthed location is then used by the software to classify the rest of the mosaic (Fig.5.3).

It should be noted that the term ‘habitat map’ is somewhat inaccurate as we are really only referring to sediment type of each site and we do not account for the numerous other abiotic

and biotic components making up a habitat (see also Whittaker et al., 1973, Hall et al., 1997, Naiman and Latterell, 2005 for more detailed discussions of the term ‘habitat’). We do however use the term habitat map as this follows convention within the scientific literature and allows for ease of description. Table 5.1 provides information on some of the additional abiotic characteristics of each site.

Table 5.1 Physical characteristics of each site classified from the habitat map. Depth is measured as maximum height above chart datum. Tidal velocities are calculated from a grid of 10 equally spaced points across each site. Phi is a measure of sediment size (calculated on a log base 2 scale).

Site	Mean Phi	St.Dev Phi	Mean Depth (m)	Tidal velocities (knts)		
				min	mean	max
1	-0.8	3.06	6.23 ± 1.21	0.1	0.81	1.53
2	-0.4	4.44	11.31 ± 1.92	0.1	0.72	1.3
3	1.89	0.65	9.30 ± 1.90	0.2	0.70	1.25

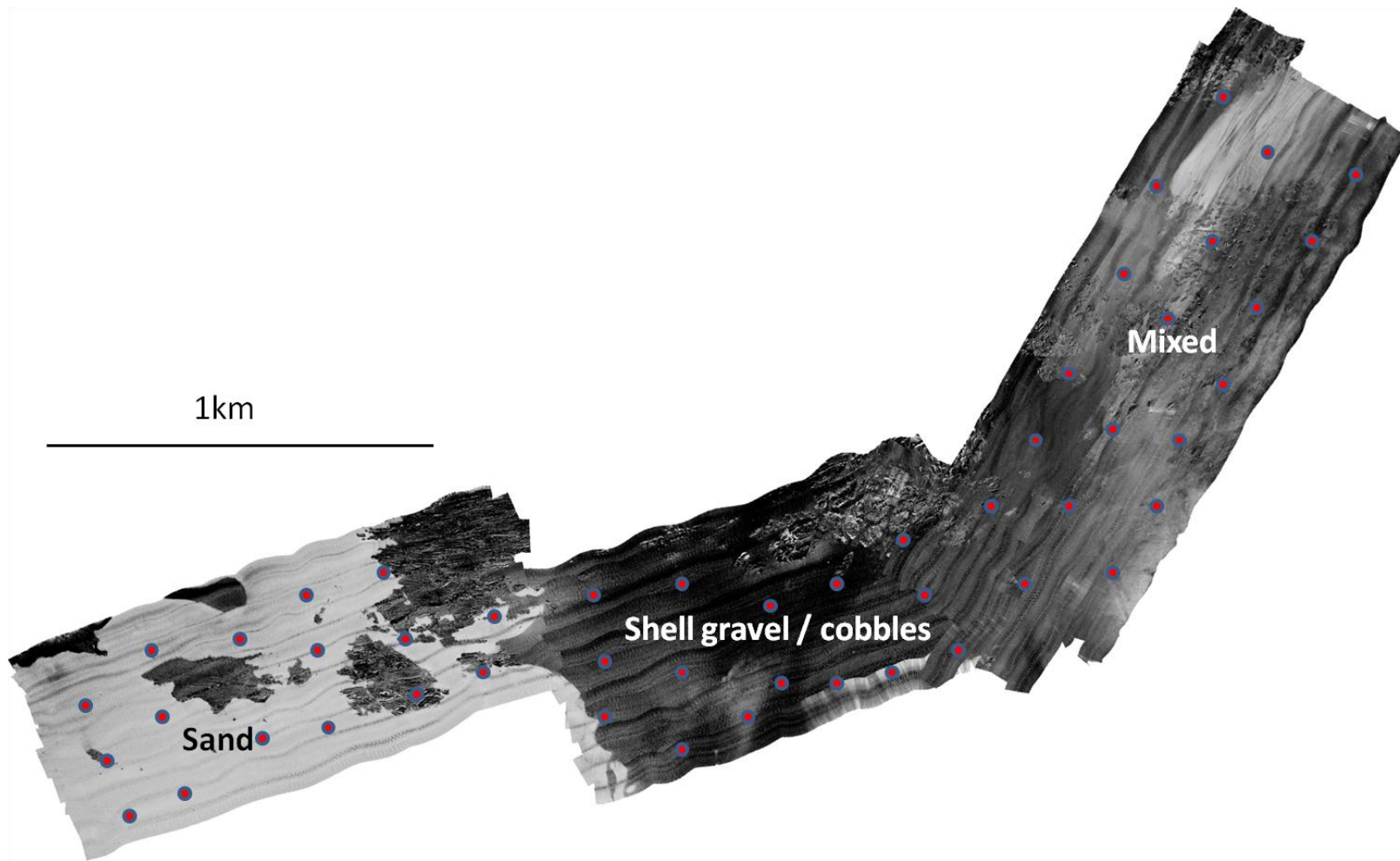


Figure 5.2 Final texture map of study site. Red dots mark approximate grab locations used for sediment-sample ground truthing.

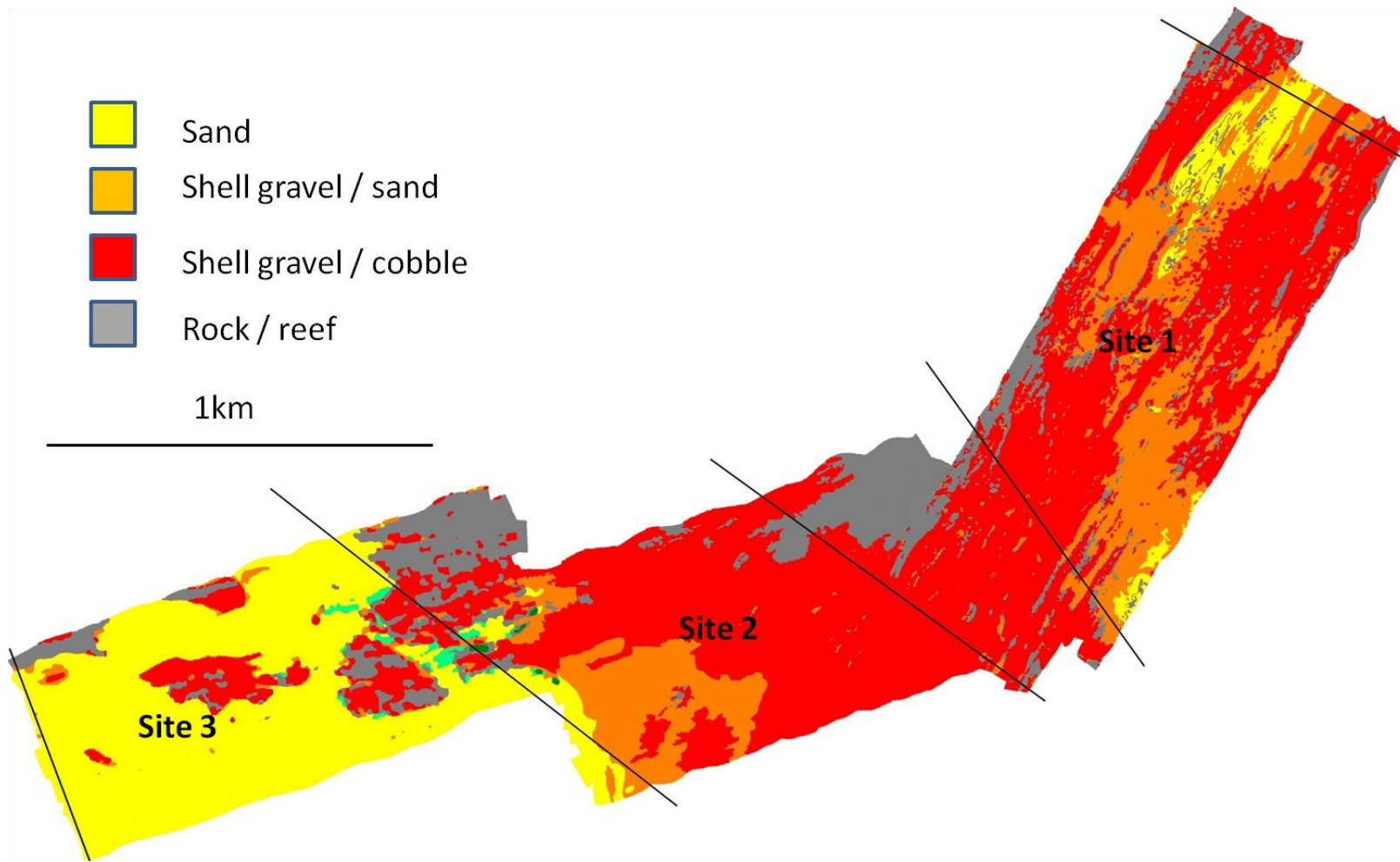


Figure 5.3 Final classified (using ground truthing) habitat map of study site. Lines mark boundaries between ‘different’ sites.

5.3.3 Sampling design

We collected data on the relative abundance and biomass of *Callionymus lyra*, and its prey community for each of the three sites classified in our ‘habitat’ map. We were interested in differences in the distributions of *C. lyra* and its prey community between sites and seasons (spring *versus* autumn). We sampled each site on four different occasions (2 springs, 2 autumns). Our spring samples were taken between the 15th of April and the 7th of May and the autumn samples between the 21st of September and the 10th of October.

As individual tows tended to vary in length, resulting abundance and biomass data for *C. lyra* were corrected for tow length and standardized to per km². Abundance and biomass data of the prey species was standardised to per m², as the amount per grab varied between grabs and sites. All sample collections and habitat mapping were carried out from the RV Sepia of the Marine Biological Association (Plymouth, UK).

5.3.3.1 The *C.lyra* community

The community of *C. lyra* at each site was sampled using a 4 m beam trawl (0.4 m height), fitted with a chain matrix and 15 mm square meshed net with a 5 mm cod-end liner. This was towed at a speed of approximately 2.5 knots for 5 minutes from the moment the trawl landed on the seabed to the moment its retrieval began. A total of 24 tows were undertaken at each site, located randomly within each of the 3 sites although sampling was directed towards the centre of each site to ensure only one bottom type was sampled at a time. All *C.lyra* were frozen and kept for processing in the laboratory. The total body length ($\pm 1\text{mm}$), full stomach weight, ($\pm 0.001\text{g}$) and stomach contents ($\pm 0.001\text{g}$) were measured in the laboratory. The stomach contents were then identified to the highest taxonomic resolution possible, counted, weighed ($\pm 0.001\text{g}$) and measured ($\pm 0.5\text{mm}$) (using a series of circular holes of known size

±0.5 mm). Using a calibration graph of length versus age of *C. lyra* caught within Plymouth Sound (Chang, 1951), we calculated the approximate age and year class of every individual caught (see Appendix 5.7.1).

5.3.3.2 *The Prey community*

The prey community was defined as any taxa that occurred more than 10 times in the stomachs of all of the *C. lyra* sampled (total of 1997 individuals). In order to describe the abundance of available prey accurately, each site was sampled using a 0.1m², Van-Veen grab (approx. 10 per site, per season sampling) and sieved over a 0.5 mm mesh to remove excess sediments. Sieved material was retained and stored in 4% formalin within 6 hours for post-processing in the laboratory. In the laboratory, prey species were identified, counted and each taxon weighed (±0.001g) and measured (±0.5 mm).

5.3.4 *Data analysis*

5.3.4.1 *The feeding ecology of C. lyra*

In order to accurately describe the feeding ecology of *C. lyra* across a range of different body sizes we combined data from all seasons and sites into one large dataset. Ordinary Least Squares (OLS) regression models were then used to relate body size to a number of different dietary variables, the mean of which was calculated per five mm size class (of total body length) from the stomach content analysis. These variables included: the abundance and biomass as a percentage of the total diet and the mean size (mm) for each prey taxa, the Levin's food niche breadth (prey diversity in stomach – see Chapter 4 methods – 4.3.5 *Calculation of indices*), the number of prey items found in the stomach, the fullness of the stomach (calculated as Hyslop's index (1980) – see Chapter 4 methods - 4.3.4 *Univariate*

data analysis), the biomass of individual prey items in the stomachs and the total energy of stomach contents calculated using conversion factors from Brey (2001) (see Appendix 5.7.2). These variables were selected as we believed they would give an accurate overall description of how the feeding and prey species of *C. lyra* changes with body length. Empty stomachs were removed from the analysis as were any of the five mm size classes with less than ten fishes. Only females were analysed as few males were caught and they show significantly different allometry to females (see Chang, 1951, Gibson and Ezzi, 1979). Only significant regressions are plotted throughout ($P < 0.05$). Akaike information criterion (AIC) (Akaike, 1974) was used to measure the relative goodness of fit when both a linear and a quadratic regression model gave P values ≤ 0.05 .

5.3.4.2 *The distribution of C. lyra and its prey community*

We used two-sample Kolmogorov Smirnov test tests to compare the five mm size class distributions of *C. lyra* between sites (per season) and between seasons (per site) . This is a non-parametric test that looks for differences between two independent samples. That is, it tests whether the populations from which two samples are drawn have the same location. In order to analyse the effects of site and season on the total abundance, biomass, species richness and diversity (Shannon - Weiner index) of the prey community, we used two-way analysis of variance (ANOVA) with Tukey HSD post-hoc analyses. All data were Log_{10} transformed to ensure an even spread of data points (except the Shannon-Weiner index) and Bartlett's test was used to examine for homogeneity of variance.

A permutational resemblance-based approach was used to analyse the year class abundance of *C. lyra*, and the abundance and biomass data of the prey community (using the PRIMER (v.6) and software package and the extension package PERMANOVA). PERMANOVA is a

routine for testing the simultaneous response of one or more variables (*C. lyra* and its prey community) to one or more factors (site and season) in an ANOVA experimental design on the basis of any resemblance matrix, using permutation methods (Anderson et al., 2008). Analyses were conducted using Bray-Curtis resemblance matrices (Bray and Curtis, 1957) with square-root transformed data to reduce the influence of highly dominant species in the prey community data. As permutational multivariate analyses of variance can be sensitive to dispersion, data was tested for dispersion using the PERMDISP routine before running each PERMANOVA model. PERMDISP may detect differences in dispersion that, in many cases are not substantial enough to inflate error rates of the PERMANOVA output. Therefore non-significant results from this routine are not implicit (see Anderson et al., 2008). Results from the routine are however included in outputs in order that conclusions drawn from the results are conservative, accounting for possibilities of type one errors occurring from heterogeneity of dispersions.

Data were (also) analysed using cluster analysis based on the resemblance matrices and were visualised using multi-dimensional scaling (MDS) plots. The SIMPER routine was used to quantify the percentage contribution that each five mm size class and year class made to the similarity within clusters (site or season groups) and to the dissimilarity between different clusters (90% most abundant groups reported herein).

5.3.4.3 Linking the C.lyra community with its prey community

We used the RELATE function in Primer (v.6) to relate the abundance of prey in the environment with the abundance found in the stomachs of *C. lyra*. RELATE measures how closely related two sets of multivariate data are, for a matching set of samples (in this case per site, per season) by calculating a rank correlation coefficient (Spearman's rho) between

all the elements of their respective (dis)similarity matrices. This analysis is based on the results from the feeding ecology of *C. lyra* (see 5.4.1) and our exact approach is explained in more detail in the results section (see section 5.4.4).

5.4 Results

5.4.1 The feeding ecology of *C. lyra*

With increasing size of *C. lyra* there was a significant decrease in the relative abundance of the small crustaceans; ostracods, caprellids and hydroids found in the stomachs of *C. lyra* (Fig. 5.4 and Appendix 5.7.3). Cumaceans showed a similar pattern with higher numbers found in the smaller size classes of *C. lyra* and none found in size classes over 115 mm. However, no significant relationship was detected for this prey taxa. Mid-size classes (approximately 70 – 125 mm) fed on higher numbers of amphipods and ophiuroids resulting in significant negative quadratic regressions for these prey taxa. With increasing size class there was a significant increase in the percentage abundance of algae, bivalvia, echinoidea, gastropoda, paguridae and polychaeta found in the stomachs of *C. lyra*. A similar, but non-significant pattern was seen for oligochaeta.

The above patterns in abundance were reflected in the biomass of the prey taxa (Fig. 5.5 and Appendix 5.7.4). Those taxa showing different relationships to those of the abundance data were the hydroid (negative quadratic), amphipoda (no significant relationship) and oligochaete taxa (positive linear).

Figures 5.6 and 5.7 allow a useful comparative representation of the contribution to the diet of the different prey taxa in terms of percentage abundance and biomass per 5 mm size class. Overall the bivalvia, polychaeta, amphipoda and ostracoda, were the largest prey taxa groups (by abundance and biomass) in the diet of the *C. lyra* size classes analysed (see Table 5.2).

Table. 5.2 The four highest contributing taxa, by abundance and biomass, to the diet of *C. lyra* between 35 and 170 mm total body length.

Prey taxa	% contribution to total diet	
	Abundance	Biomass
Bivalvia	28.3	28.9
Polychaeta	18.2	20.1
Amphipoda	15.5	10.4
Ostracoda	10.9	13.6

In order to examine the diversity of prey taxa in the stomachs the mean Levin's food niche breadth was calculated for each size class. This showed that the prey diversity of *C. lyra* was highest for mid-sized individuals, with a peak of 5.71 for individuals of the 100 mm size class, and then decreased with increasing size class ($R^2 = 0.343$, $F_{2,24} = 6.257$, $P = 0.002$) (Fig. 5.8).

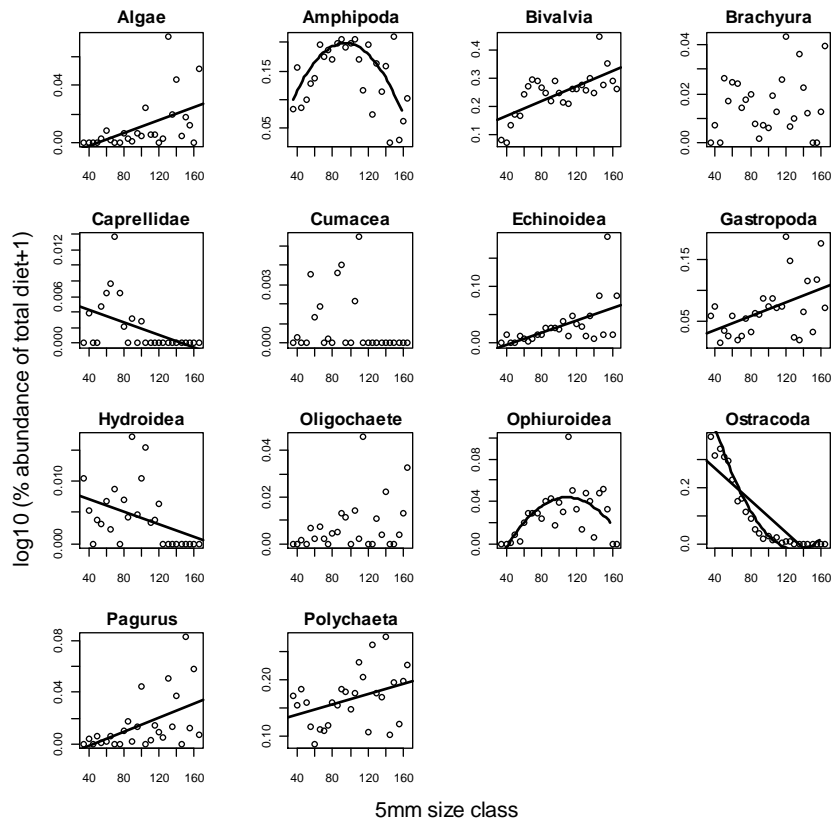


Figure 5.4 Scatter plots showing the change in percentage abundance of total diet for each prey taxa per 5 mm size class.

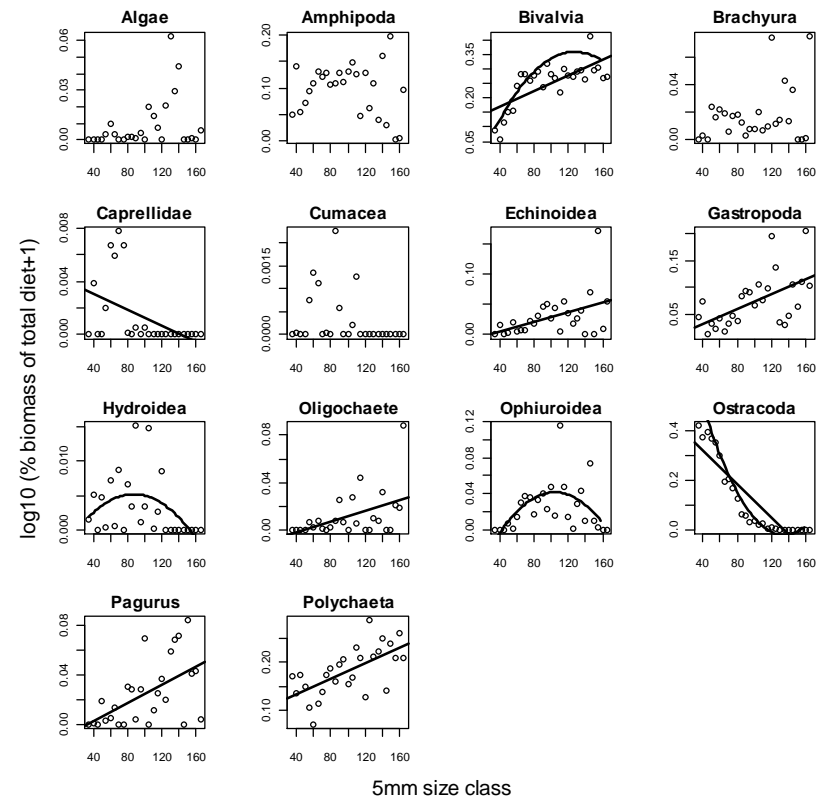


Figure 5.5 Scatter plots showing the change in percentage biomass of total diet for each prey taxa per 5 mm size class.

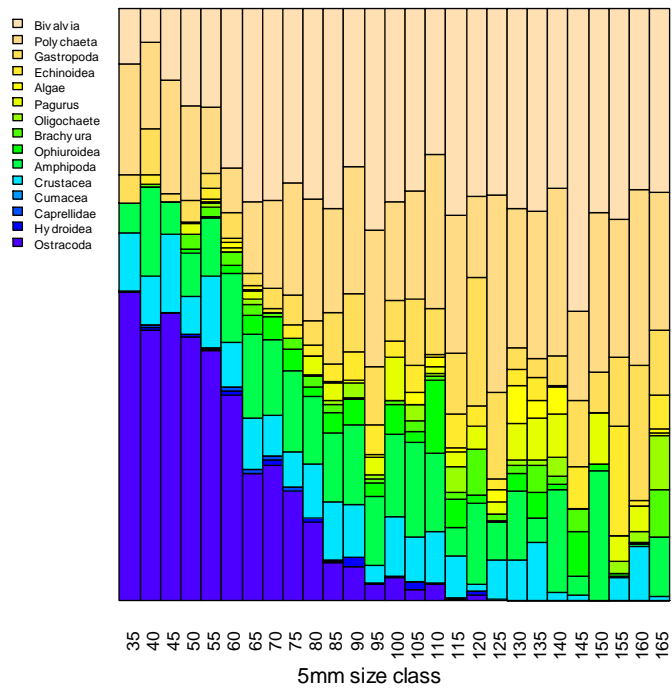


Figure 5.6 Stacked bar plot showing the change in percentage abundance of total diet for each prey taxa per 5 mm size class.

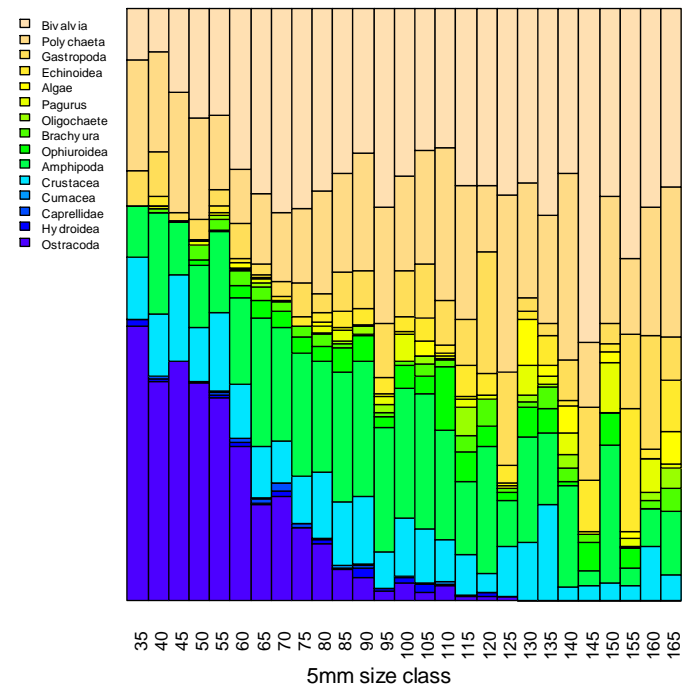


Figure 5.7 Stacked bar plot showing the change in percentage biomass of total diet for each prey taxa per 5 mm size class

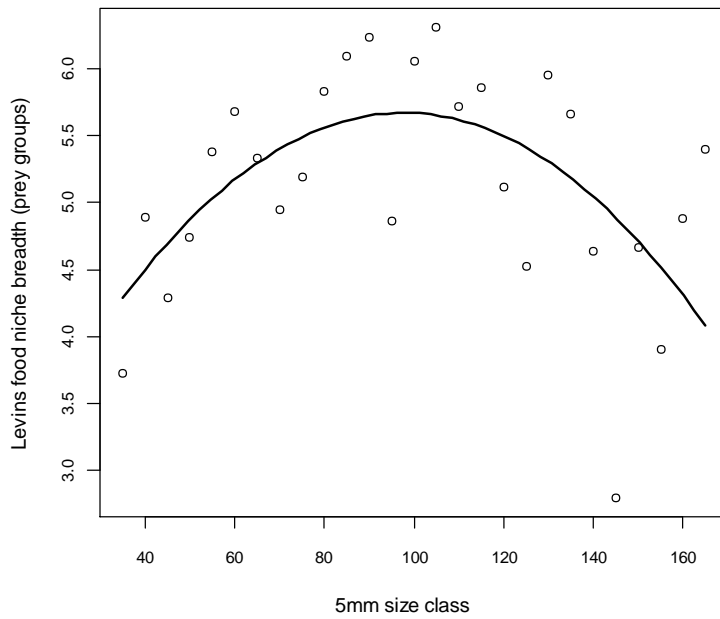


Figure 5.8 Levins food niche breadth (prey diversity in stomachs) for each 5mm size class.

There was a significant decrease in the number of prey items found in the stomachs of *C. lyra* with increasing size (linear: $R^2 = 0.35$, $F_{1,25} = 8.366$, $P = 0.001$, $AIC = 2.96$ / quadratic $R^2 = 0.393$, $F_{2,24} = 7.763$, $P < 0.001$, $AIC = 3.1$) (Fig. 5.9). This indicates that smaller individuals were feeding on more prey items than larger fishes. The calculation of stomach fullness showed that smaller *C. lyra* were feeding to a higher level of satiation than larger fishes (linear: $R^2 = 0.58$, $F_{1,25} = 34.496$, $P < 0.001$, $AIC = -171.61$ / quadratic: $R^2 = 0.822$, $F_{2,24} = 55.53$, $P < 0.001$, $AIC = -192.85$) (Fig. 5.10). There was a significant positive relationship between the size class of fish and the mean biomass of individual prey items found in the stomachs ($R^2 = 0.467$, $F_{1,25} = 21.894$, $P < 0.001$) (Fig. 5.11). This suggests that as *C. lyra* gets larger (and its mouth gape and therefore prey size potential increases), so does its preference for eating larger prey items (its prey size selectivity). This prey size selectivity was reflected when we examined the same relationship for the actual size (mm) of each prey taxa (Fig. 5.13 and Appendix 5.7.5).

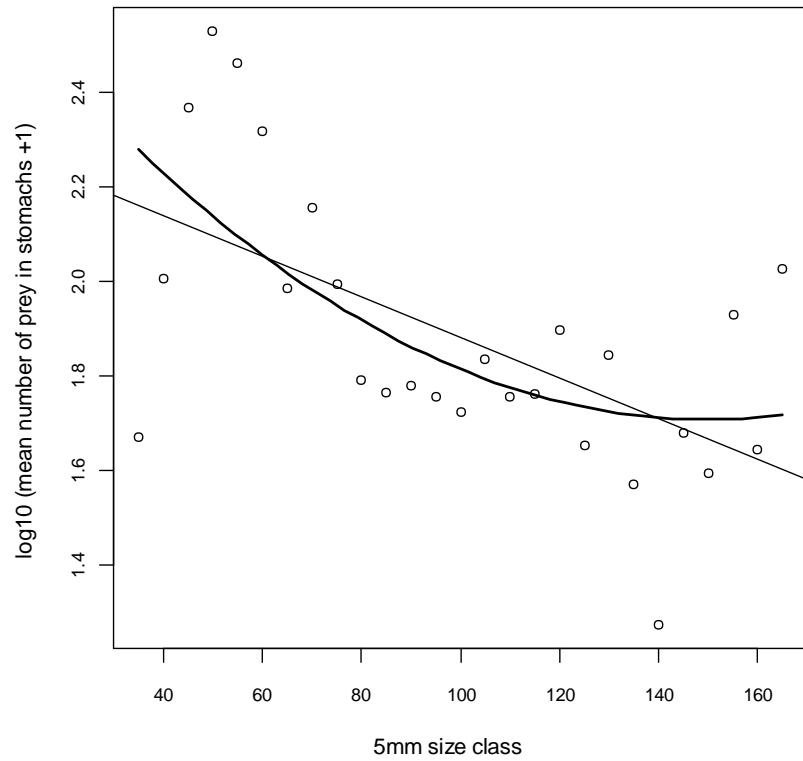


Figure 5.9 OLS regression of 5 mm size class against mean number of prey found in the stomachs of *C. lyra*.

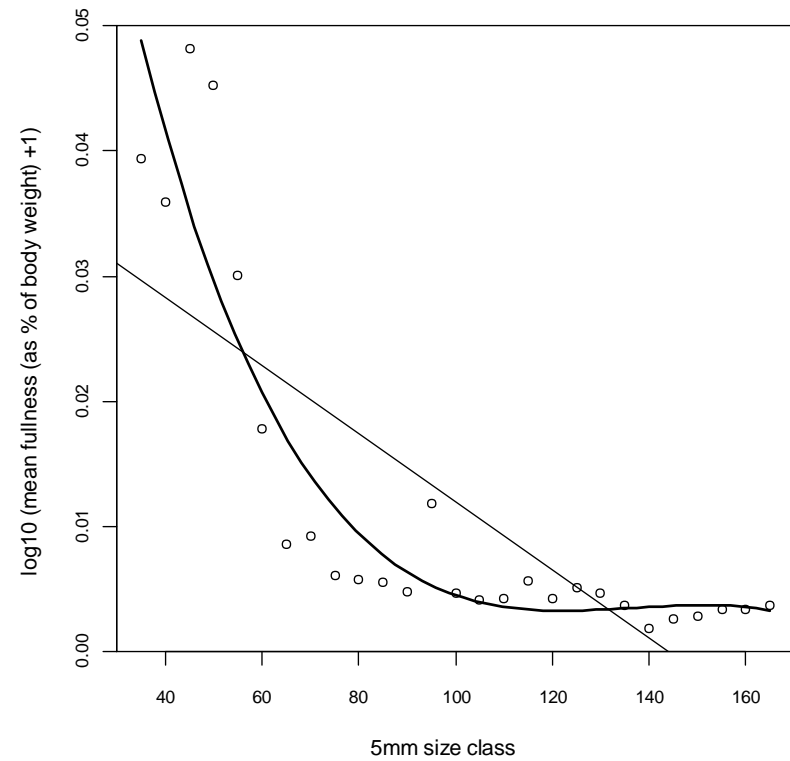


Figure 5.10 OLS regression of 5 mm size class against mean fullness of the stomachs, calculated as a percentage of body mass (see Hyslop, 1980).

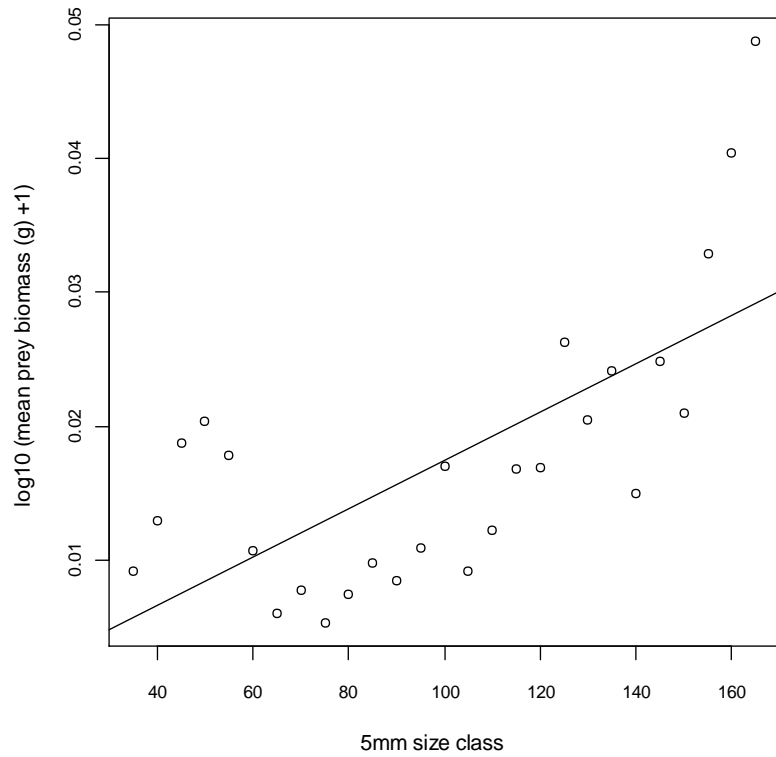


Figure 5.11 OLS regression of 5mm size class against mean biomass of prey items found in the stomachs of *C. lyra*.

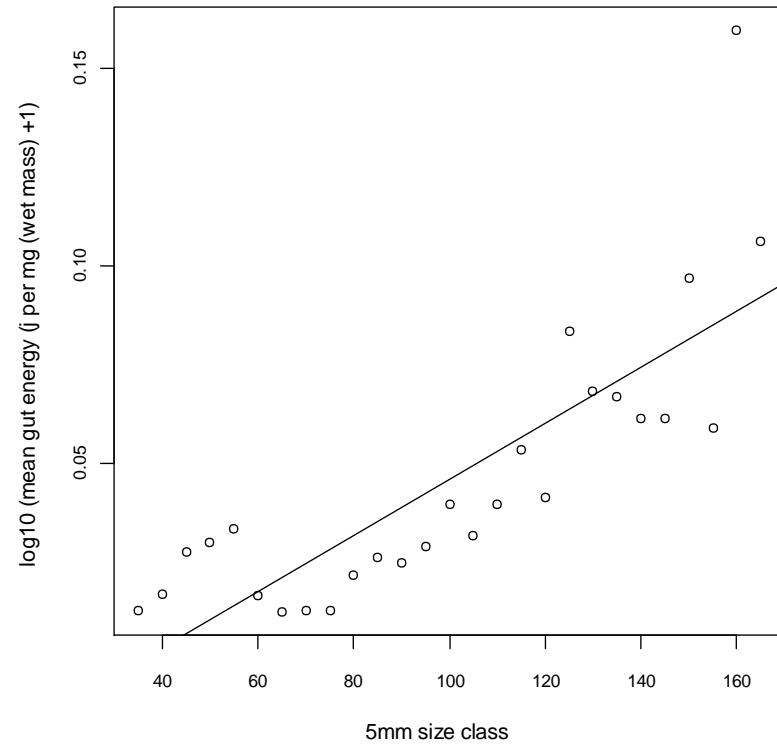


Figure 5.12 OLS regression of 5 mm size class against mean energy content of prey items found in the stomachs (calculated per gram of each prey item from Brey energy conversions (2001) (see Appendix 5.7.2)).

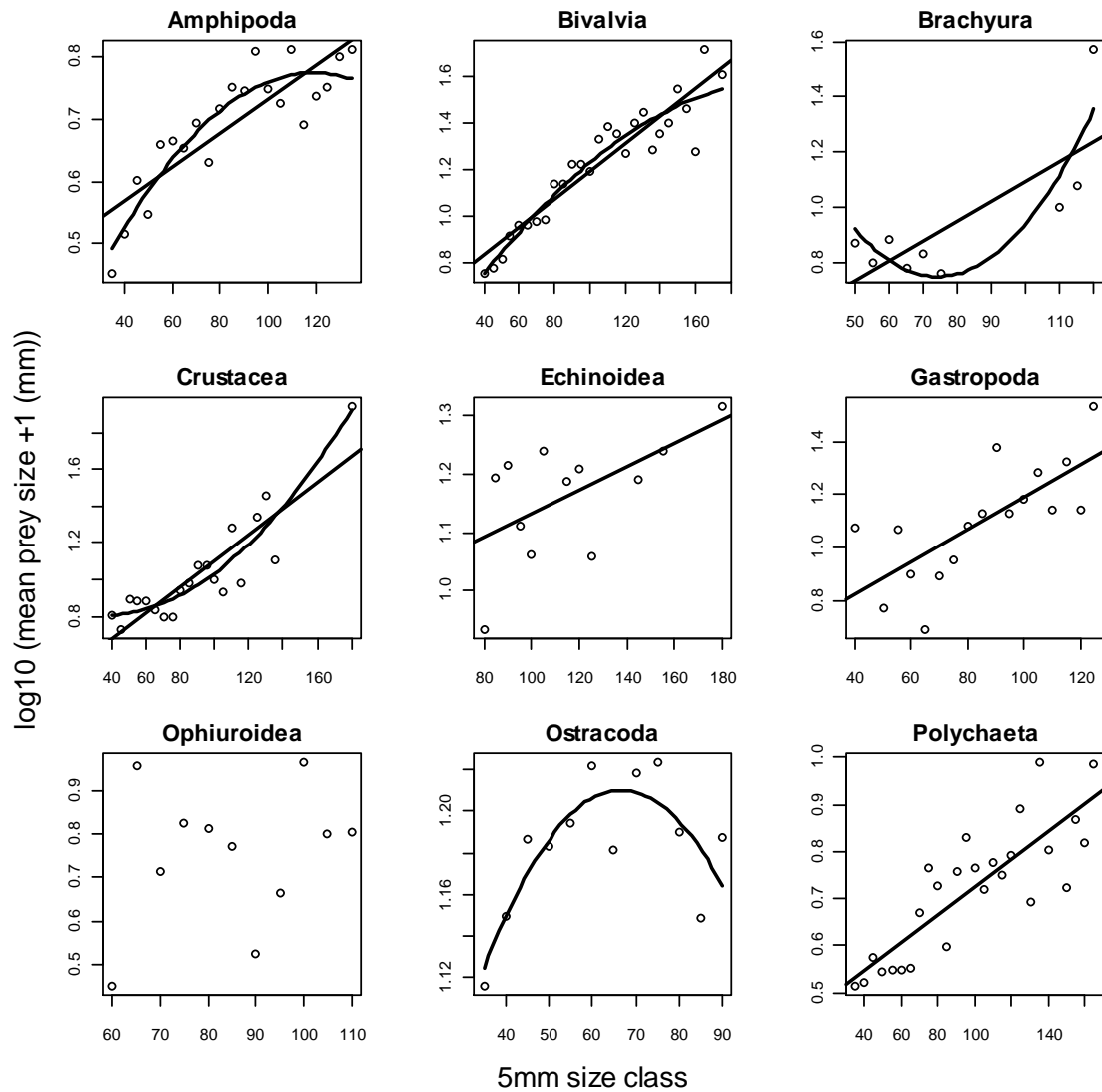


Figure 5.13. OLS regressions of 5 mm size class against mean ($n \geq 7$) prey size for each prey taxa found in the stomachs.

Using Brey energy conversions (see Appendix 5.7.2) to calculate the energy content of the identifiable prey items (from their biomass) shows that smaller *C.lyra* ate less energy rich prey than larger fishes ($R^2 = 0.663$, $F_{1,25} = 49.222$, $P < 0.001$) (Fig. 5.12).

All of the prey taxa, except ophiuroidea and ostracoda, showed significant positive relationships between size of *C. lyra* and mean size of prey items found in stomachs (see Appendix 5.7.5). *C. lyra* was not prey size selective for ophiuroidea because no relationship was detected. The mean size of ostracods increased with increasing 5 mm *C. lyra* size class up to the 65 mm size class at which point they decreased with further increases in *C. lyra* body length size class (negative quadratic).

5.4.2 *The distribution of C. lyra*

Permutational resemblance analysis (PERMANOVA) shows that both season and site had a significant effect on the year class distribution of *C. lyra* (Table 5.3). There was also a significant interaction between site and season. Pairwise comparisons (Table 5.4) show that the distributions of *C. lyra* in the autumn in sites 1 and 2 was not significantly different ($P = 0.154$) however in the spring they were ($P = 0.003$). The PERMDISP routine highlighted homogeneity of dispersion for the effect of site and season on the year class distribution of *C. lyra*.

Table 5.3 PERMANOVA and PERMDISP outputs testing the effect of site and season on the distribution of *C. lyra* year classes.

Factor	Num.df	Den.df	Pseudo F	PERMANOVA <i>P</i>	PERMDISP	Pair-wise PERMDISP violations
Season	1	69	5.71	0.002	0.701	-
Site	2	69	7.37	0.001	0.464	-
Season*Site	2	69	2.39	0.021	-	-

Table 5.4 Pairwise comparisons for the interaction between site and season for the year class distribution of *C. lyra* (see Table 5.3)

Season	Site comparison	<i>t</i>	<i>P</i>
Autumn	1 vs 2	1.289	0.154
	1 vs 3	2.765	0.001
	2 vs 3	2.481	0.001
Spring	1 vs 2	2.361	0.003
	1 vs 3	2.527	0.004
	2 vs 3	1.721	0.022

MDS plots (Figure 5.14 (a)) shows a grouping of points for site 3 for the year class distribution of *C. lyra*. This is separated from site 1 and site 2 *C. lyra* year class distributions. There were no visible groupings between seasons as there was a large overlap in points in the MDS plot (Figure 5.14 (b)).

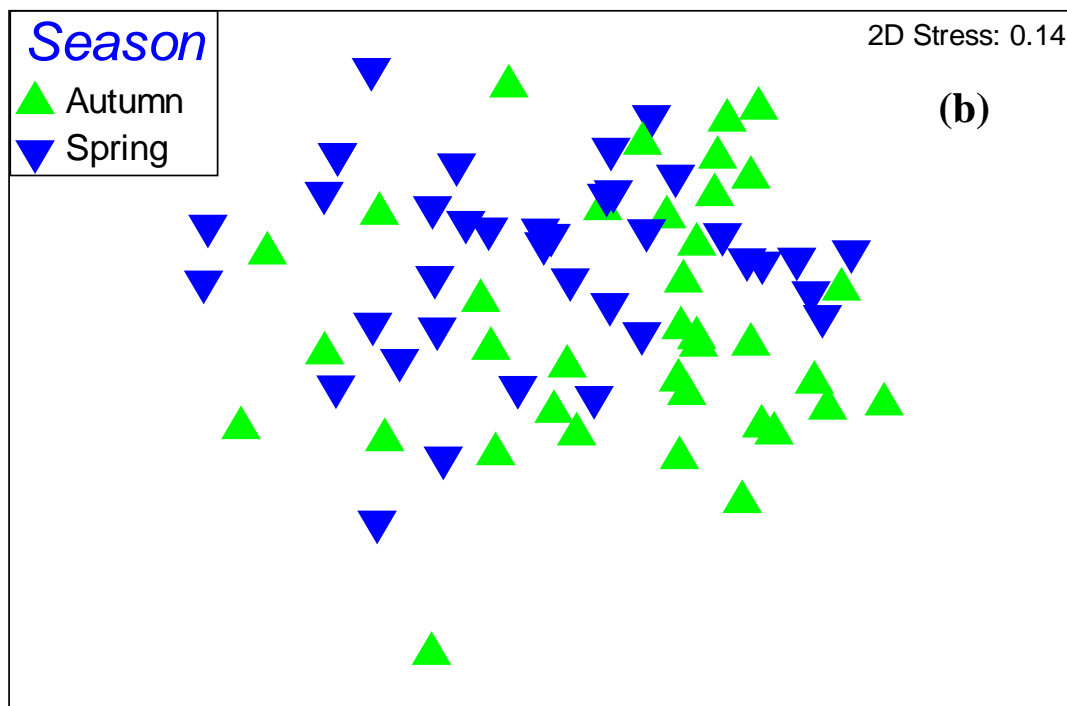
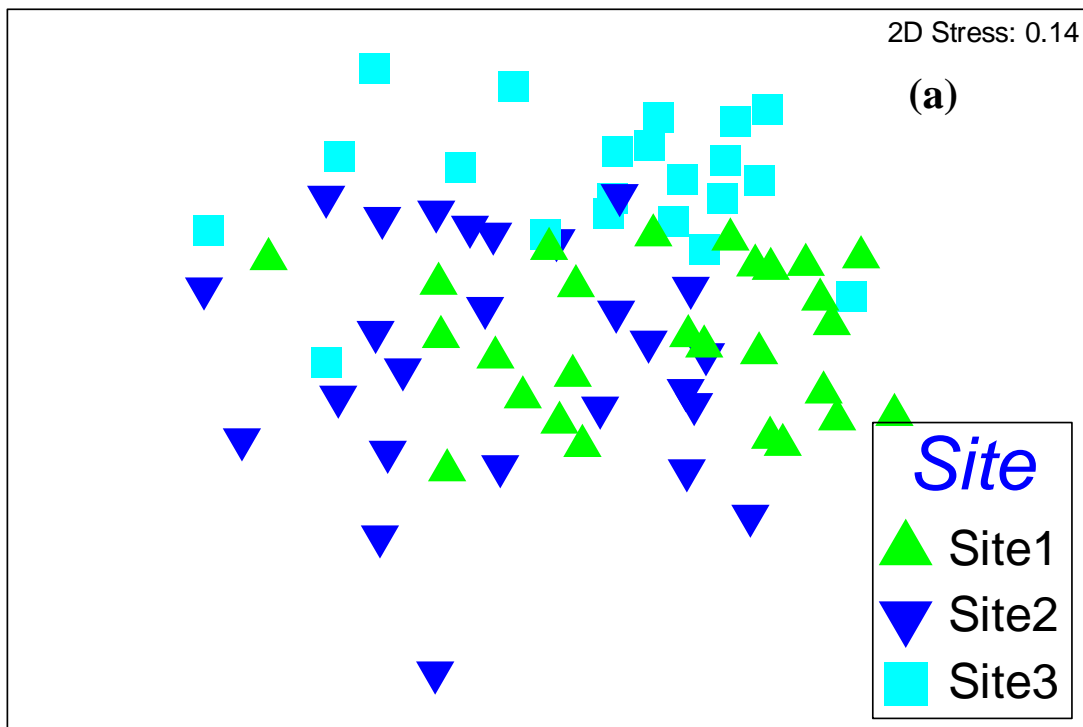


Figure 5.14 MDS plots of the year class distribution of *C. lyra* displayed by site (a) and season (b).

SIMPER analysis of the year class distribution of *C. lyra* showed that both the sites and seasons were dominated by the year 1-2 and year 2-3 classes. These groups also accounted for the largest dissimilarities between sites and seasons (see Tables 5.5 and 5.6 and Figures 5.15 and 5.16).

Table 5.5. The percentage contribution made to the differences between sites for the top ranked 5 year classes of *C.lyra*.

Measure	Site combination	Overall dissimilarity (%)	Top ranking year classes contributing to dissimilarity				
			1 st	2 nd	3 rd	4 th	5 th
<i>C. lyra</i> year class distribution	1 vs 2	59.21	2-3	1-2	3-4	0-1	4-5
	1 vs 3	63.31	1-2	2-3	3-4	0-1	4-5
	2 vs 3	62.93	1-2	2-3	3-4	4-5	0-1

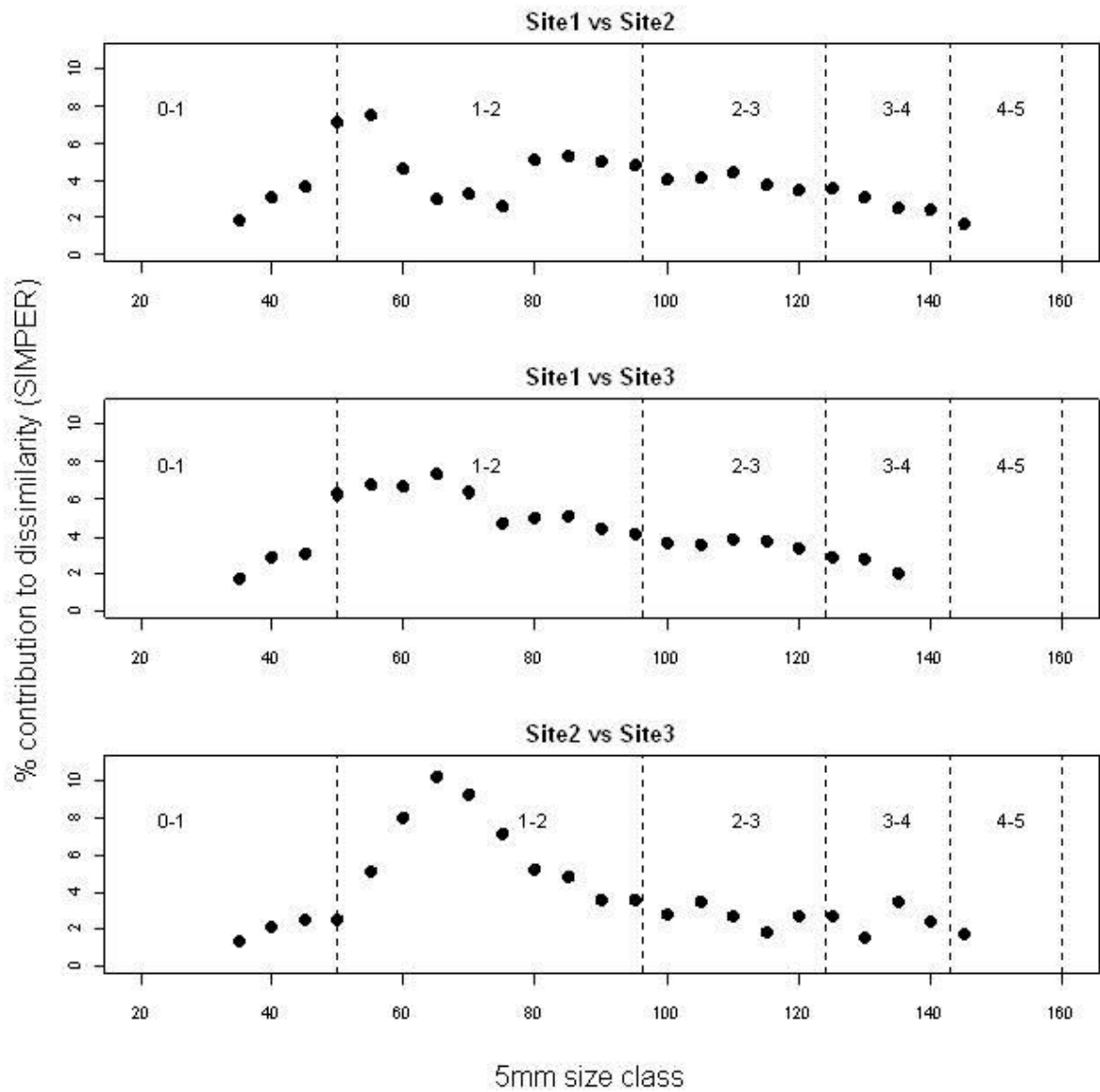


Figure 5.15 Plots of the percentage contribution of each 5 mm size class of *C. lyra* to dissimilarity between sites. Broken lines mark divisions between year classes.

Table 5.6 The percentage contribution made to the differences between seasons for the top ranked 5 year classes of *C.lyra*

Measure	Season combination	Overall dissimilarity (%)	Top ranking year classes contributing to dissimilarity				
			1 st	2 nd	3 rd	4 th	5 th
<i>C. lyra</i> year class distribution	Autumn vs Spring	58.27	1-2	2-3	0-1	3-4	4-5

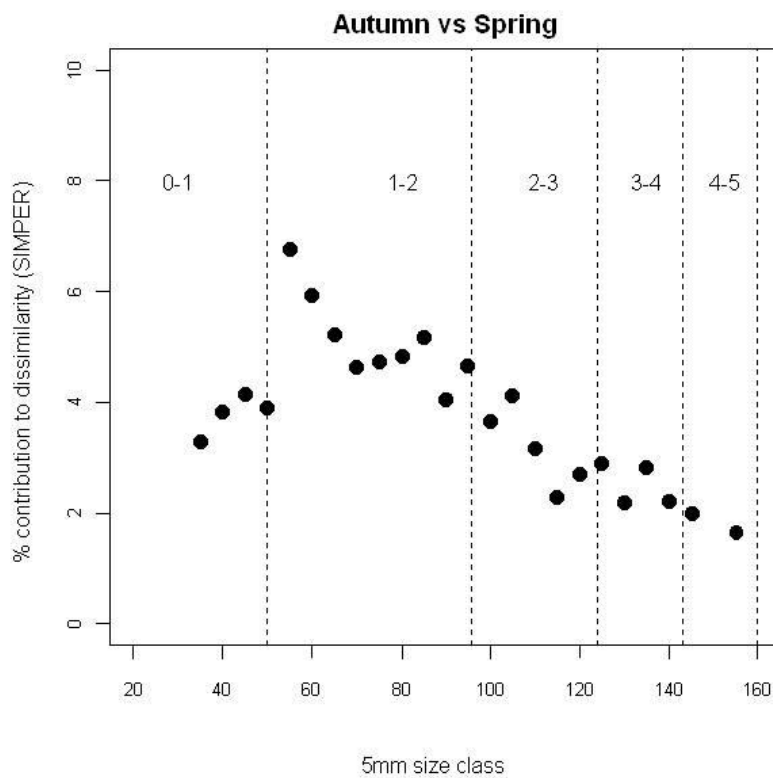


Figure 5.16 Plots of the percentage contribution of each 5 mm size class to dissimilarity between seasons. Broken lines mark divisions between year classes.

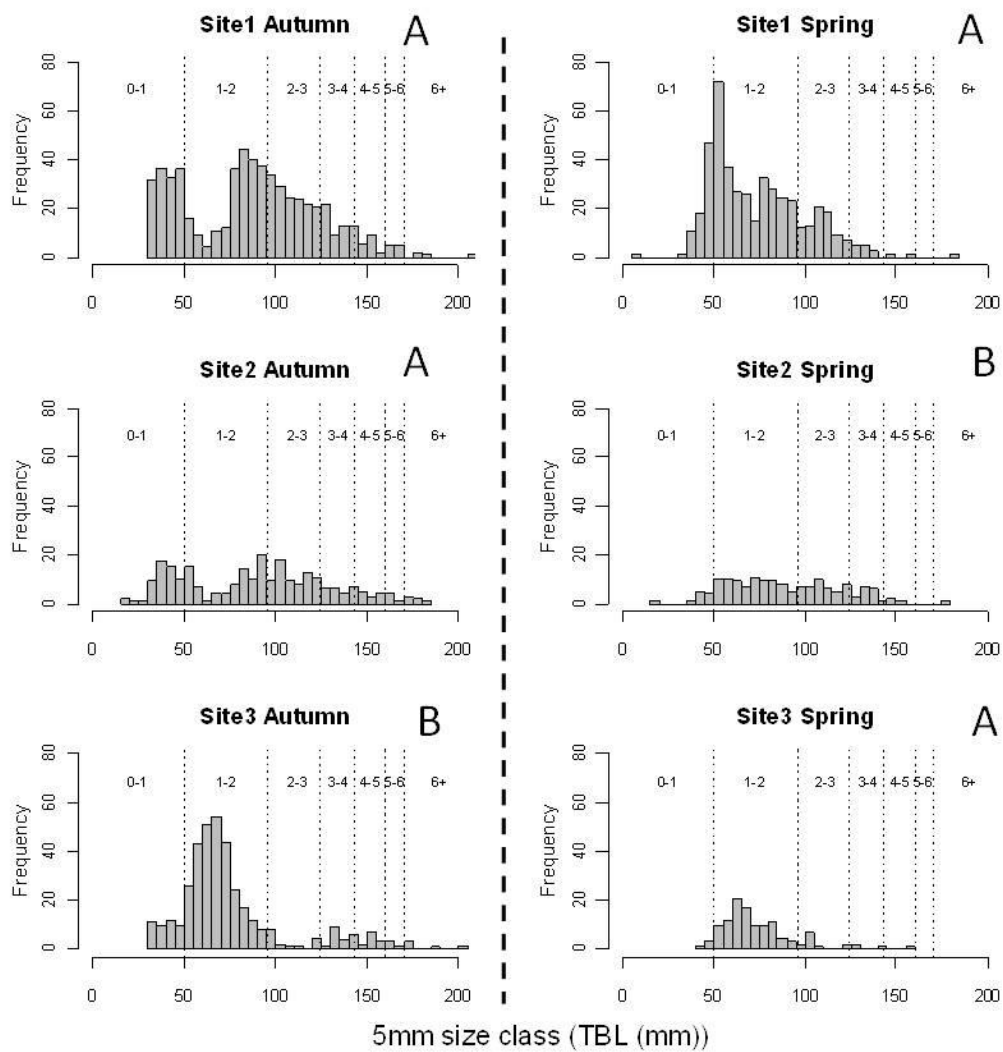


Figure. 5.17 Histograms of the size distributions of *C. lyra* for each site per season. The large broken line marks the division between autumn and spring. The small broken lines mark divisions between year classes. Distributions in plots sharing capital letters (within the same season) are not significantly different from one another (see also Table 5.7).

Table 5.7. Results from two-sample Kolmogorov Smirnov test comparisons between the size class distributions of *C. lyra* between sites for each season.

Season	Site comparison	Total N	Z	P
Autumn	1 vs 2	842	-0.031	0.497
	1 vs 3	970	5.605	<0.001
	2 vs 3	632	4.640	<0.001
Spring	1 vs 2	614	2.287	<0.001
	1 vs 3	580	2.020	0.001
	2 vs 3	272	2.467	<0.001

Table 5.8. Results from two-sample Kolmogorov Smirnov test comparisons between the size class distributions of *C. lyra* between seasons (autumn versus spring) for each site.

Site	Total N	Z	P
1	1051	3.915	<0.001
2	405	1.428	0.034
3	499	0.842	0.477

The histograms in figure 5.17 show differences in the distribution of the 5 mm size classes of *C.lyra* between sites and seasons. Although all different in terms of the number of individuals from the different 5 mm size classes (and therefore year) classes, the results of the Mann-Whitney U test demonstrate the significant differences in distributions between sites for each season (Table 5.7) and differences in distributions between seasons for each site (Table 5.8). In the autumn the distributions of *C. lyra* size classes did not differ significantly between site 1 and site 2. The difference between these sites and site 3 however was significant in the

autumn. In the autumn both sites 1 and 2 showed a bi-modal distribution with high numbers of *C. lyra* in the 0-1 (all 5 mm size classes in this year class) and 1-2 (80-100 mm size classes). Site 3 on the other hand showed a uni-modal distribution with high numbers of individuals in year class 1-2. Another difference between site 3 versus sites 1 and 2 was the low numbers of larger individuals in site 3 during the autumn. Interestingly the differences between sites changed in the spring and the distribution of *C. lyra* size classes was not significantly different between sites 1 and 3, but these sites differed significantly from site 2. In the spring, site 2 showed a very flat distribution with no obvious peak in numbers of *C. lyra*. Sites 1 and 3 in the spring however showed clear uni-modal distributions, both peaking in the 2-1 year class group.

Overall site 1 showed the highest population numbers of *C.lyra* followed by site 3 then site 2 in the autumn (Table 5.9). There was however an overall higher abundance of *C. lyra* at site 2 in the spring than site 3. Autumn showed higher abundances of *C. lyra* than spring for all sites.

Table 5.9 The number of *C. lyra* of each year class for each site per season.

Season	Site	Year class							Mean	Total
		0-1	1-2	2-3	3-4	4-5	5-6	6+	5 mm	number
Autumn	1	137	210	134	65	28	12	4	89.9	590
	2	55	83	57	27	15	15	6	92.6	252
	3	43	279	12	19	15	7	5	77.7	380
Spring	1	78	286	74	20	1	1	1	76.4	461
	2	11	78	35	24	4	0	1	91.4	153
	3	4	99	10	4	1	1	0	76.4	119

5.4.3 Distribution of *C. lyra*'s prey community

Two-way ANOVAs indicate that site had a significant effect on the biomass ($F_{2,112} = 19.07$, $P < 0.001$), species richness ($F_{2,112} = 16.87$, $P < 0.001$) and Shannon-Weiner diversity ($F_{2,112} = 25.66$, $P < 0.001$) of the prey community of *C. lyra* (Fig. 5.18). The results for species richness and Shannon-Weiner diversity should however be taken with caution as Bartlett's test indicates heterogenous variances, therefore violating the assumptions of the two-way ANOVA, increasing the probability of a type I error (see Underwood, 1981). Season had a significant effect on the abundance ($F_{2,112} = 14.16$, $P < 0.001$) and biomass ($F_{2,112} = 4.3$, $P = 0.04$) of the prey community. Figure 5.18 shows that there was a higher abundance and biomass of prey species in the spring compared to the autumn. These seasonal effects on abundance were particularly noticeable for site two which showed almost double the amount of prey items in the spring compared to the autumn. From the results of prey biomass, abundance and species richness the data suggests that the prey community at site 3 was larger in size (in terms of individual prey items – higher biomass but no difference in abundance) but less diverse than sites 1 and 2. Sites 1 and 2 had a much higher diversity of prey species than site 3.

PERMANOVA results show that season had a significant effect on both the abundance and biomass of the species composition of the prey community (Table 5.10). There was also a significant interaction between site and season for the abundance and biomass of prey taxa. Pairwise comparisons (Table 5.11) show that the abundance of the *C. lyra* prey community in the autumn and spring was not significantly different between sites 1 and 2 ($P = 0.108$ and 0.352 respectively). Similarly, the biomass of the prey community in sites 1 and 2 was not significantly different in the autumn ($P = 0.009$) but did show significant differences in

community structure in the spring ($P = 0.026$). The PERMDISP routine highlighted heterogeneity of dispersion for the effect of site and season on the abundance and season on the biomass of the prey community. Although it is not strictly necessary to obtain a non-significant result for the PERMDISP routine, it is important to note that significant effects may in some cases be caused by heterogeneous dispersion (see Anderson et al., 2008).

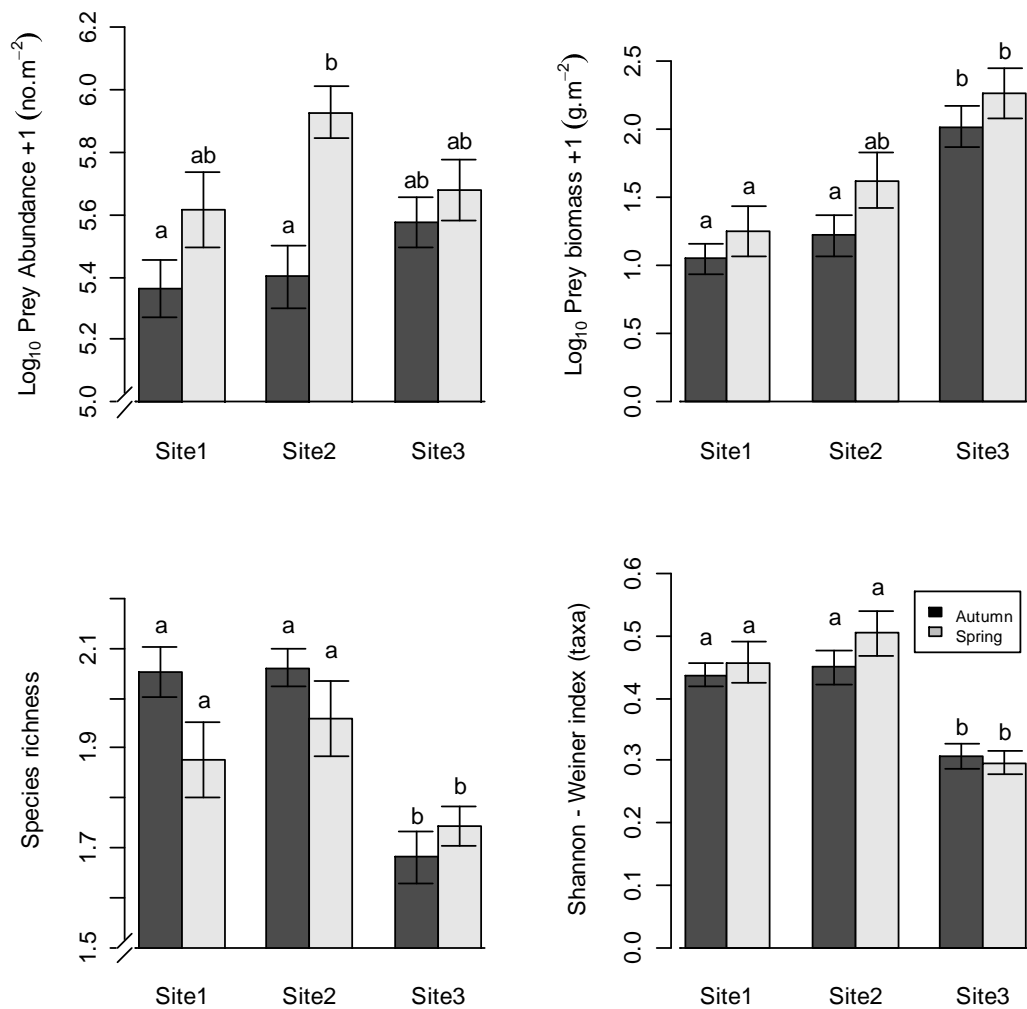


Figure 5.18 Total abundance, biomass, species richness and Shannon-Weiner index of the prey community of *C. lyra*, for each site. Dark bars represent autumn and light bars represent spring. Data are presented as mean \pm S.E.M. ($n \geq 20$). Points sharing a letter are not significantly different from one another (ANOVA post hoc: Tukey HSD).

Table 5.10: PERMANOVA and PERMDISP outputs for the abundance and biomass of the *C. lyra* prey community.

Measure	Factor	Num.df	Den.df	Pseudo F	PERMANOVA P	PERMDISP	Pair-wise PERMDISP violations
Abundance	Season	1	112	7.32	0.001	0.006	Spring vs Autumn
	Site	2	112	13.86	0.001	0.019	Site1 vs Site3 Site2 vs Site3
	Season *Site	2	112	2.65	0.008	-	-
Biomass	Season	1	112	4.43	0.001	0.008	Spring vs Autumn
	Site	2	112	8.77	0.001	0.347	-
	Season *Site	2	112	2.09	0.012	-	-

Table 5.11 Pairwise comparisons for the interaction between site and season for the abundance and biomass of the prey community of *C. lyra* (see Table 5.10).

Measure	Season	Site comparison	t	P
Abundance	Autumn	1 vs 2	1.355	0.108
		1 vs 3	4.349	0.001
		2 vs 3	4.095	0.001
	Spring	1 vs 2	1.856	0.009
		1 vs 3	2.372	0.001
		2 vs 3	3.217	0.001
Biomass	Autumn	1 vs 2	1.061	0.352
		1 vs 3	3.732	0.001
		2 vs 3	3.079	0.001
	Spring	1 vs 2	1.646	0.026
		1 vs 3	2.185	0.001
		2 vs 3	1.947	0.004

MDS plots show a clear grouping of points for both prey abundance and biomass for site 3 which is separated from site 1 or site 2 (Figure 5.19 (b) and 5.20 (b)). There were no visible differences between seasons as there is a large overlap in points from each in the MDS plot (Figure 5.19 (a) and 5.20 (a)). This reiterates the PERMDISP results in Table 5.10 of heterogeneous dispersion (more variation / noise in spring than autumn). Again this highlights the fact that a significant effect of season from the PERMANOVA may not be wholly valid.

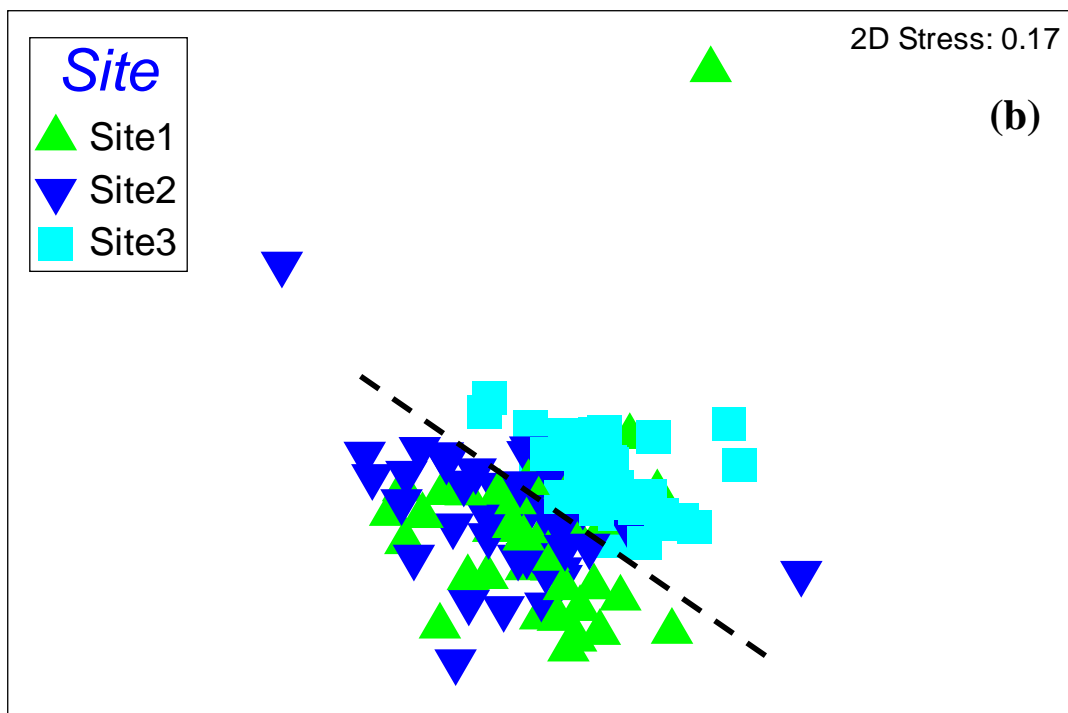
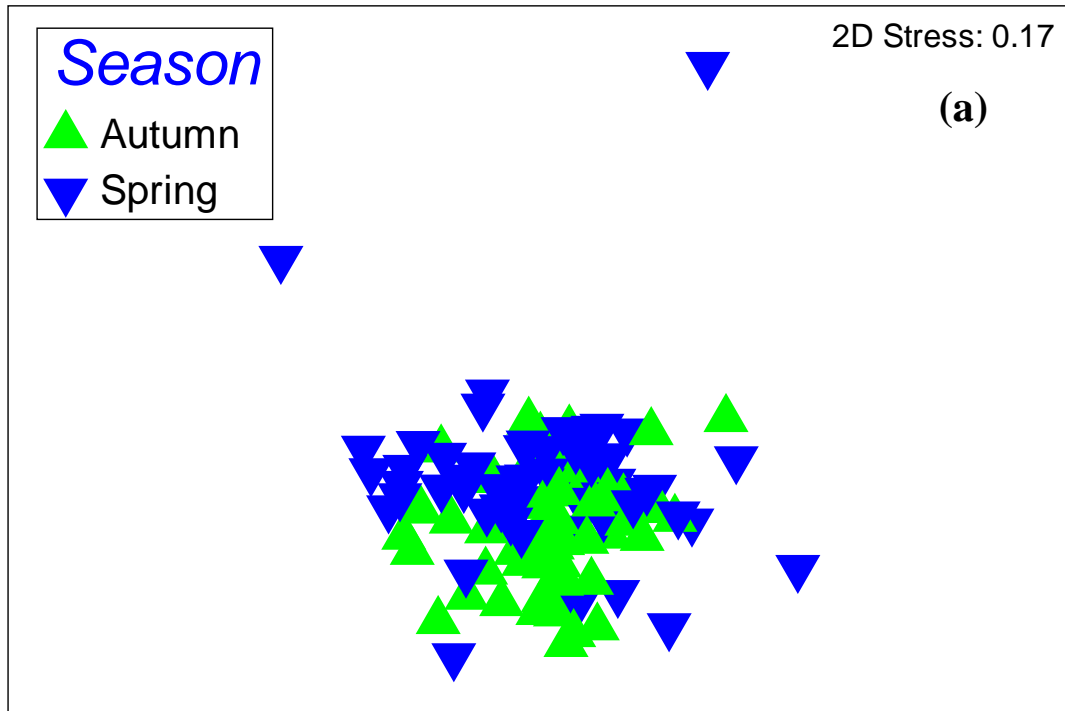


Figure 5.19 MDS plots of abundance of the *C. lyra* prey community displayed by season (a) and site (b). Broken lines mark approximate divisions between groups of points.

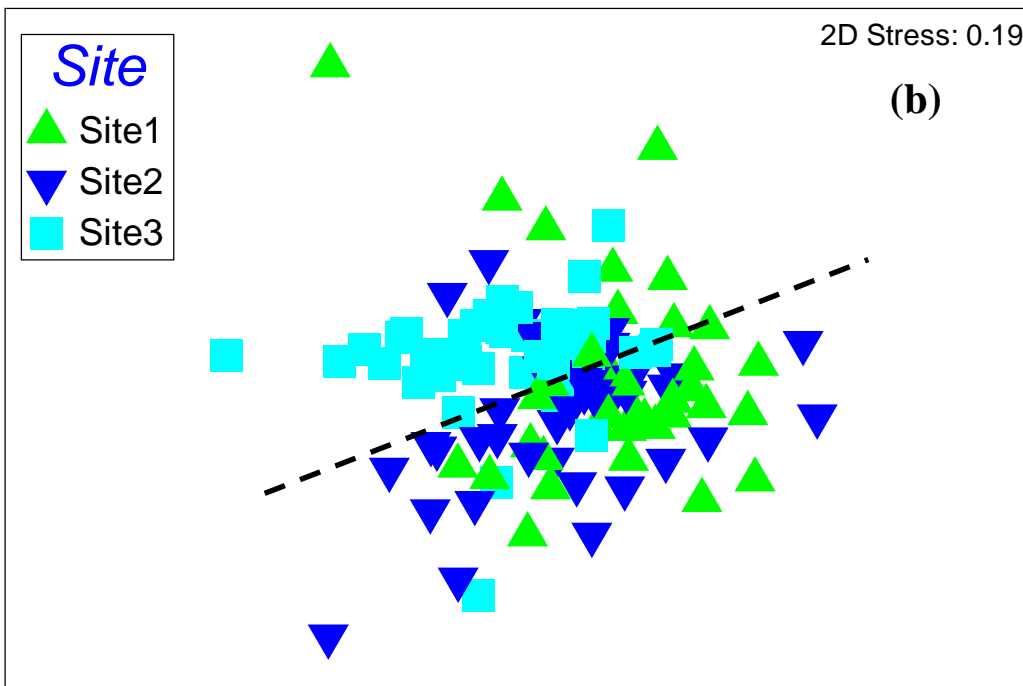
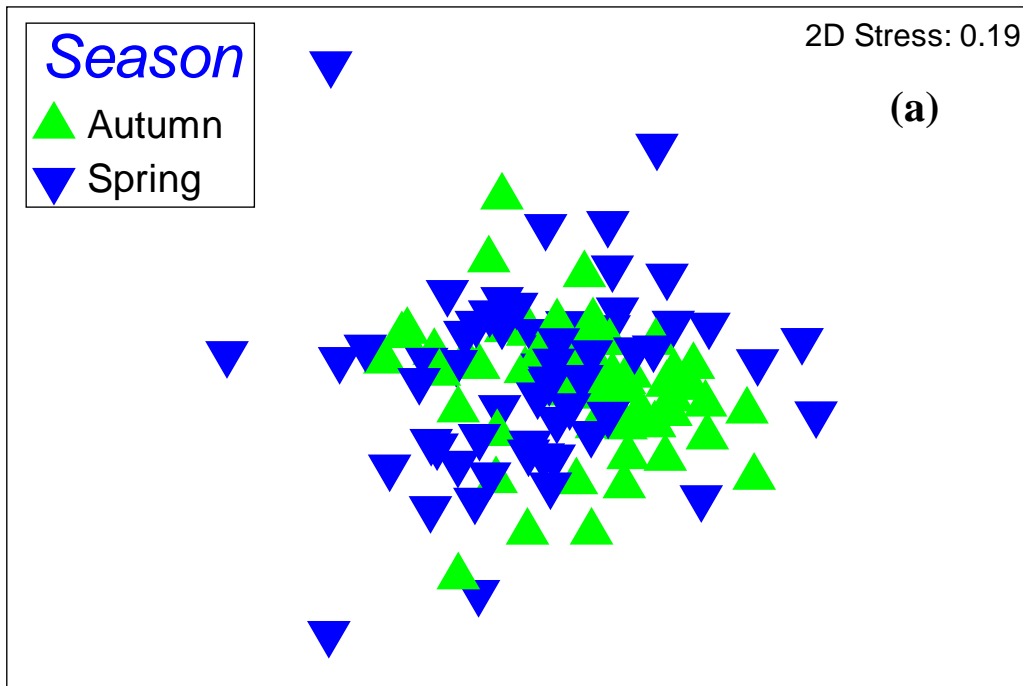


Figure 5.20 MDS plots of biomass of the *C. lyra* prey community displayed by season (a) and site (b). Broken lines mark approximate divisions between groups of points.

SIMPER analysis of prey community abundance and biomass data showed that all sites were dominated by the taxa *Polychaeta sp.* (60 to 65 individuals per m² / 1.75 to 2.5 g per m²). *Amphipoda sp.* was consistently the next most dominant prey taxa across the three sites in terms of abundance (17 to 40 individuals per m²). The next most dominant taxa in terms of biomass varied across the sites (Site1 - *Amphipoda sp.*, Site2 - *Ophiuroidea sp.*, Site3 - *Bivalvia sp.*). The largest dissimilarities between sites were caused by *Polychaeta sp.* and *Amphipoda sp.* followed by a mixture of *Ophiuroidea sp.*, *Brachyura sp.*, *Echinoidea sp.*, *Bivalvia sp.*, and *Gastropoda sp.* for both abundance and biomass (see Table 5.12). Overall, the SIMPER analysis did not highlight any noteworthy compositional differences in the prey species communities between any of the sites (i.e. it is not obvious that one site is characterised by a certain prey species over another).

Overall the above results were mirrored when defining the community per season with *Polychaeta sp.* again dominating both the autumn and spring prey communities in terms of abundance (autumn - 63, spring - 67 individuals per m²) followed by *Amphipoda sp.* (autumn - 34, spring - 28 individuals per m²). *Polychaeta sp.* also dominated the biomass of each season (autumn - 2.5, Spring - 3 g per m²) followed by *Amphipoda sp.* in the autumn and *Bivalvia sp.* in the spring (1.76 g per m²). The largest dissimilarities between seasons were caused by *Polychaeta sp.* for both abundance and biomass (see Table 5.13).

Table 5.12 The percentage contribution made to the differences between sites for the top ranked 5 prey species of *C. lyra*.

Site combination	Overall dissimilarity (%)	Measure	Top ranking taxa contributing to dissimilarity				
			1 st	2 nd	3 rd	4 th	5 th
1 vs 2	32.86	Abundance	<i>Polychaeta sp.</i>	<i>Amphipoda sp.</i>	<i>Brachyura sp.</i>	<i>Ophiuroidea sp.</i>	<i>Bivalvia sp.</i>
	51.79	Biomass	<i>Bivalvia sp.</i>	<i>Polychaeta sp.</i>	<i>Brachyura sp.</i>	<i>Ophiuroidea sp.</i>	<i>Amphipoda sp.</i>
1 vs 3	36.67	Abundance	<i>Amphipoda sp.</i>	<i>Polychaeta sp.</i>	<i>Ophiuroidea sp.</i>	<i>Echinoidea sp.</i>	<i>Bivalvia sp.</i>
	58.23	Biomass	<i>Polychaeta sp.</i>	<i>Ophiuroidea sp.</i>	<i>Bivalvia sp.</i>	<i>Brachyura sp.</i>	<i>Amphipoda sp.</i>
2 vs 3	36.37	Abundance	<i>Polychaeta sp.</i>	<i>Amphipoda sp.</i>	<i>Brachyura sp.</i>	<i>Ophiuroidea sp.</i>	<i>Bivalvia sp.</i>
	54.18	Biomass	<i>Polychaeta sp.</i>	<i>Ophiuroidea sp.</i>	<i>Brachyura sp.</i>	<i>Bivalvia sp.</i>	<i>Gastropoda sp.</i>

Table 5.13 The percentage contribution made to the differences between seasons for the top ranked 5 prey species of *C. lyra*.

Season combination	Overall dissimilarity (%)	Measure	Top ranking taxa contributing to dissimilarity				
			1 st	2 nd	3 rd	4 th	5 th
Spring vs Autumn	32.05	Abundance	<i>Polychaeta sp.</i>	<i>Amphipoda sp.</i>	<i>Ophiuroidea sp.</i>	<i>Bivalvia sp.</i>	<i>Brachyura sp.</i>
	51.81	Biomass	<i>Polychaeta sp.</i>	<i>Ophiuroidea sp.</i>	<i>Bivalvia sp.</i>	<i>Brachyura sp.</i>	<i>Amphipoda sp.</i>

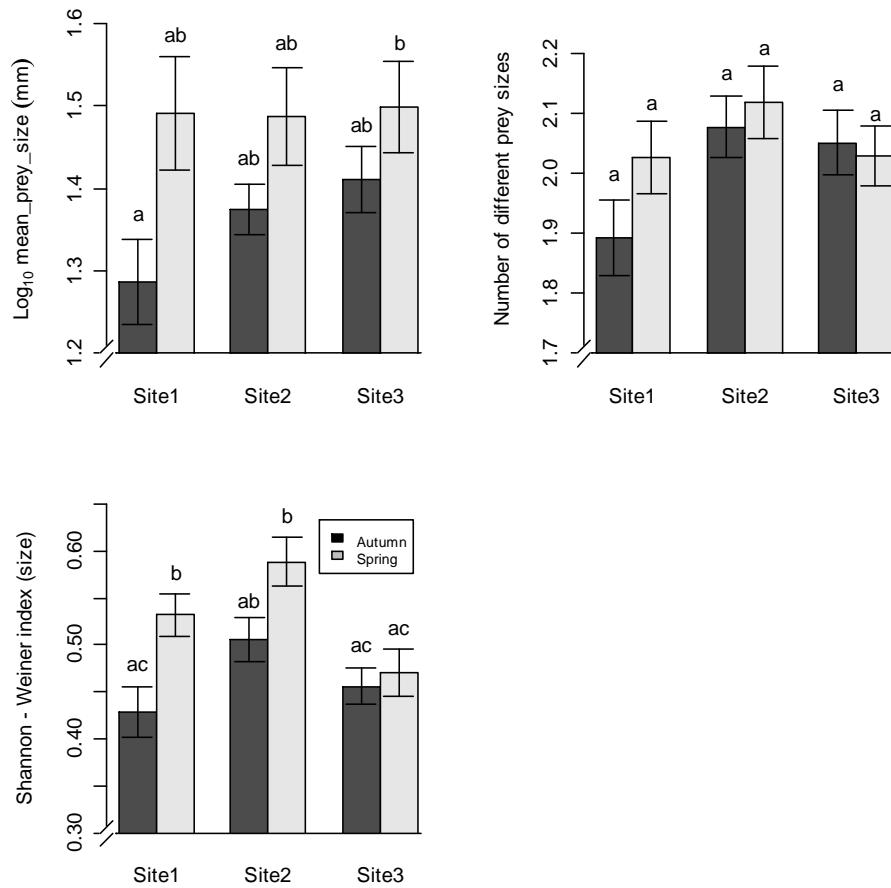


Figure 5.21 Mean prey size (mm), species richness (prey sizes), and Shannon-Weiner index of the prey sizes of *C. lyra*, for each site. Dark bars represent autumn and light bars represent spring. Data are presented as mean \pm S.E.M. ($n \geq 5$). Points sharing a letter are not significantly different from one another (ANOVA post hoc: Tukey HSD).

Two-way ANOVAs indicate that site had no significant effect on the mean prey size of the prey community of *C. lyra* ($F_{2,112} = 0.89$, $P = 0.413$) (Fig. 5.21). Season however did have a significant effect on the mean prey size of the prey community of *C. lyra* ($F_{2,112} = 10.018$, $P = 0.002$) with mean prey sizes in the spring larger than in the autumn. Site and season had no significant effect on the prey size species richness ($F_{2,112} = 3.052$, $P = 0.051$, $F_{2,112} = 1.217$, $P = 0.272$ respectively) of the prey community of *C. lyra*. Site ($F_{2,112} = 6.744$, $P = 0.002$) and season ($F_{2,112} = 11.523$, $P < 0.001$) did however have significant effects on the Shannon-Weiner diversity of prey sizes of the *C. lyra* prey community.

5.4.4 Linking the *C. lyra* community with it's prey community

We used the RELATE routine in Primer (v.6) to look at the relationship between the prey in the environment and the prey found in the stomachs of *C. lyra*. Matrices of the abundance of the environmental prey community of *C. lyra* per sampling site and sampling time and the abundance of prey in the stomachs of *C. lyra* were analysed for significant correlations between the two. As we found that the prey choice of *C. lyra* changes significantly with body length (see section 5.4.1) we separated the RELATE analysis so matrix relationships were tested per year class of *C. lyra*. In addition, as we found that *C. lyra* shows prey size selectivity in its prey choice (see Fig. 5.12 and 5.13) we undertook the above analysis using abundance data of prey taxa and prey size classes.

RELATE uses a Spearman's rank correlation and outputs a rho value which denotes how related the matrices. Under the null hypothesis that there is no relationship between the matrices, rho will be approximately 0. A rho value of 1 therefore means a perfect match between matrices and under the current scenario would signify that the stomach contents of

the *C. lyra* year class tested exactly matched the environmental prey community of the year class. This in turn would allow us to infer that these fishes had been feeding at the sites at which they were caught. High rho values may also signify that their distribution was likely a result of the prey community distribution.

All of the rho outputs for each year class were very close to zero demonstrating there was very little relationship between the abundance of prey taxa and prey size in the environment and the prey abundance in the stomachs of any of the *C. lyra* year groups (Table 5.14).

Table 5.14 Results from the RELATE function used to relate environmental prey matrices to stomach content matrices of each *C. lyra* year class for both prey taxa and prey size.

Year class	Prey Size			Prey Taxa		
	Rho	Sig. level	No. Stats >Rho	Rho	Sig. level	No. Stats > Rho
0-1	0.197	11.6	115	0.334	4.3	42
1-2	0.171	10.1	100	0.153	18.4	183
2-3	-0.028	49.4	493	0.082	32.4	323
3-4	0.153	19.7	169	0.065	32.3	322
4-5	0.323	2.3	22	0.38	0.6	5
5-6	-0.012	51.5	514	0.076	24.7	246
6-7	0.057	31.2	311	-0.12	73.4	733

Plotting year class rho values from the RELATE routine against prey abundance (taxa and size) allows a comparison of year classes to see if the relationship between stomach contents and prey community was related to size / age of fish. We expected to see higher rho values for the younger year classes of fish (an overall negative linear relationship) using prey size data as these are the fish whose distribution were most likely to be restricted by the prey sizes available to them. In addition we expected to see a negative quadratic relationship between the rho values (using the prey taxa matrices rho values) and year class. This is because our previous analysis of the feeding ecology demonstrated that medium sizes of *C. lyra* demonstrated the most diverse prey spectra (Fig. 5.8). These fishes would therefore be the least likely to be restricted in their feeding by prey taxa available at sites, thus showing lower values of rho compared to the younger and older fishes. Figure 5.22 however shows that there was no relationship between rho value and year class for prey taxa ($R^2 = 0.059$, $F_{1,5} = 0.313$, $P = 0.6$) or prey size ($R^2 = 0.049$, $F_{1,5} = 0.262$, $P = 0.6304$) demonstrating no significant shifts in the relationship between prey found in the stomachs and the environmental prey community with increasing body length size class. It is however important to note that a lack of relationship between the two matrices may well be caused unrepresentative sampling of the prey community with the gear type (Van-veen) used, this is discussed below.

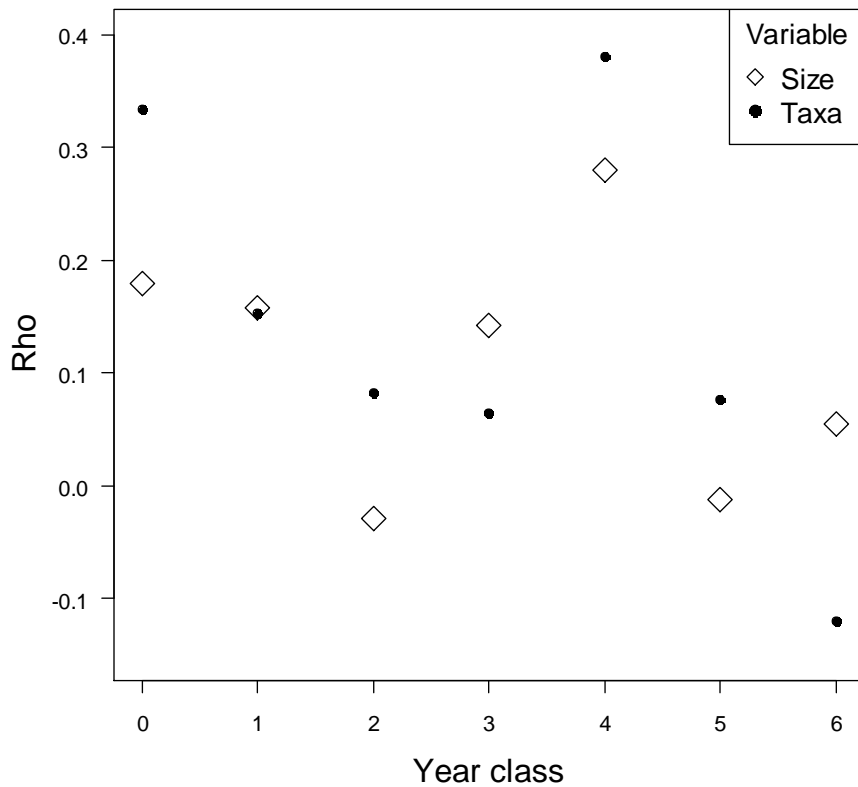


Figure 5.22 Scatter plot of rho value outputs from the RELATE routine (relating stomach content prey abundance data to environmental prey abundance data) and year class of *C. lyra*.

5.5 Discussion

Traditionally the habitats of demersal fishes have been characterised based on the abiotic habitat parameters of depth and sediment. Biotic habitat variables have been analysed less commonly (Johnson et al., in press). Although numerous studies describe clear ontogenetic patterns in the diets of many demersal fish species (Gibson and Ezzi, 1987, Lowe et al., 1996, McCormick, 1998), few describe these in conjunction with population distribution patterns. Here we used detailed stomach content and prey community analysis to test if the distribution of a common temperate demersal fish, *C. lyra* was related to prey abundance over small

spatial scales (100's m²), accounting for changes in predator body length, across three different sites characterised by their sediment.

Stomach content analysis showed clear differences in the feeding ecology of *C. lyra* for both prey taxa and prey sizes with body length. Our results indicate that *C. lyra* is a size selective predator feeding on small prey items when young and eating generally larger prey items with increasing body length. Although, patterns of prey size and prey taxa selectivity in the feeding of demersal fishes are reiterated elsewhere in the literature for both large and small fish species (Lowe et al., 1996, Labropoulou et al., 1997, Pinnegar et al., 2003, Moore et al., 2010), few go on to analyse the number and relative energy content of prey items in stomachs and relate this to the foraging ecology of the individual.

With increasing size, the number of prey items decreased in the stomachs of fishes in our study and the relative energy content per prey item increased. This indicates that small *C. lyra* individuals, limited by mouth gape size, consume high numbers of energy poor prey items in order to meet the stringent energy requirements associated with the early stages of development (Fonds et al., 1992, Von Herbing and White, 2002). As mouth gape size increased, and therefore the number of potential prey options increased, fish ate fewer but larger, more energy rich prey items. The balance between prey quality and quantity seen from our analyses support the optimal foraging theory (OFT) that individuals will aim to maximise their energy intake whilst foraging (Charnov, 1976).

A bioenergetic feeding strategy that changes with body length is further supported if we consider how the functional type of prey items changed with fish size. Younger individuals fed on small crustacean species, which corroborates one other study of individuals of the

same genus (Gibson and Ezzi, 1979). Many of these prey taxa are closely associated with branching hydroids and bryozoa species, where they often aggregate in high numbers (Caine, 1980). This is likely to explain the abundance of these associated hydroids and bryozoans in the diets of the younger fishes. These prey aggregations provide a high density prey resource that can be readily consumed by resident juveniles without high costs of foraging associated with searching and prey handling (see Caine, 1989). Low costs and high abundances of prey likely allow juveniles to feed to high levels of satiation on a relatively low energy source whilst still maintaining the levels of energy intake required during juvenile development. Conversely, the largest fishes in the study fed almost solely on either large, infaunal prey items (polychaetes and bivalves) or large, mobile crustaceans, all of which are likely to be costly in terms of search times, prey handling or digestibility (Gill, 2003). Although the costs of somatic growth are likely to be lower for more mature fishes, past studies have highlighted the importance of feeding on energy rich prey items (namely the shift to piscivory) in the development to sexual maturity, and to a size refuge from predators (Bromley et al., 2000, Huskey and Turingan, 2001). The shifts seen in the diet of *C. lyra* support the idea of an optimal feeding strategy, individuals feeding as efficiently as possible within their abilities (based on morphology).

Changes in the diet of demersal fishes have been related to their ability to forage in different sediment types, and their ability to directly consume available prey as a function of mouth gape limitation (McCormick, 1998, Lukoschek and McCormick, 2001). For example, small fishes that feed on infaunal prey items are likely to find foraging harder on tightly packed sediments of larger grain size than larger fishes better capable of penetrating and burrowing into the sediment. Previous studies have shown both significant (e.g. Byron and Link, 2010) and non-significant (e.g. Hinz et al., 2006) relationships between demersal fish communities

and their prey over large spatial scales ($\geq 10 \text{ km}^2$). Recently, Toole et al. (2011) found that shifts in the distributions of juvenile demersal fishes were a function of settlement and ontogenetic changes in nursery habitat suitabilities over 10 km^2 spatial scales. Jenkins et al. (2011) also found that the diet of *Sillaginodes punctatus* recruits were significantly correlated to habitat utilization over similar spatial scales. In the current study we found that the distribution of *C.lyra* year classes was significantly affected both by site and season. These differences were apriori hypothesised to be related to the prey community present at each of the sites. We did not however find any significant relationships between the prey contents (taxa or size) of the stomachs of *C. lyra* and the prey communities present at each of the three sites in the autumn or spring.

The lack of relationship between the predator and prey community in our study may have been caused by certain data limitations which require discussion in order that they are addressed in future studies. Although we sampled high numbers of fishes, many of these were from one year class only (year 1-2). The overall, positively skewed population distribution seen is fairly typical and has been noted for this species in the North Sea (see Van der veer et al., 1990 and Appendix 1). It does however mean that we had low numbers of individuals in the 0-1 year and >3 year classes when splitting analyses by ontogeny. The level of replication was further reduced by separating analyses per site and per season. This may have reduced our ability to detect significant relationships as our estimates of prey stomach contents may not be wholly accurate. If we consider that the greatest affinity between a fish and its prey in the environment should exist for individuals most restricted by their prey options, the above point is particularly pertinent as the feeding ecology results show small fish will be restricted by prey size and taxa and large fishes by taxa (see Fig. 5.8, 5.11, 5.13).

Past studies within the same area have shown significant vertical migrations of juvenile *C. lyra* in response to pelagic prey species (namely *Calanus sp.*) (Russell, 1928, see also Sabates, 1990). This may mean that our population descriptions of the year 0-1 class may be inaccurate and again reiterates the fact that our prey community for this class may be an underestimate. This inadequate sampling may also have been exacerbated if we consider our method of sampling the benthic prey community. Stomach content analysis revealed a high number of small, relatively light epibenthic crustaceans in the diets of the younger fishes. The use of a Van Veen grab to sample the whole prey community is however not likely to be conducive to sampling these faunas. On contact with the sediment such grab devices create a pressure wave which is likely to dislodge such animals from the path of the grab. Future studies would therefore benefit from using additional gears to sample the primary prey species of the younger fishes as well as the vertical and horizontal, benthic distributions of these individuals.

Although the above limitations may reduce our ability to detect significant relationships between the prey in stomachs and the environment, ecological theory may well also support the lack of relationship. Considering the broad differences between the three sites in this study it is clear that sites 1 and 2 did not differ extensively in terms of their prey community or their habitat type. Although the habitat map classifies sites 1 and 2 differently, both contain the same range of sediment types within their boundaries but exhibit differences in patch sizes of these sediments. Over the spatial scales of this study, these dissimilarities may not be sufficient to drive differences in the distributions of species (prey or predator communities), especially if *C. lyra* individuals are moving freely between sites. Understanding the home range of the study species when attempting to explain distribution

patterns is clearly important, however to our knowledge no studies exist investigating the small scale movements of *C. lyra*.

Our results may also indicate that over the small spatial scales of this study the prey community is not a significant habitat variable driving the distribution of any of the year classes of *C. lyra*. It is therefore interesting to address other habitat variables, albeit speculatively, that may have led to the differences in the shape of size distributions of *C. lyra* between sites. The sediment preferences of demersal fishes are generally well documented in the literature for demersal fish species (Scott, 1982, Phelan et al., 2001, Stoner and Abookire, 2002). These preferences are however most often linked to levels of predation rather than prey availability, a preferred sediment making burial or camouflage easier, thus reducing the risk of predation (see Manderson et al., 2000). In one case predation risk has been shown to be more important than prey availability for group 0 demersal fishes in the field (Lough et al., 1989). The bimodal distribution of *C. lyra* size classes seen in the autumn at sites 1 and 2 could potentially reflect differences in predation risk between these sites which were of a much higher complexity (in terms of abiotic and biotic 3 dimensional structure) compared to site 3. Ryer et al. (2004) and Stoner and Titgen (2003), both demonstrated the importance of emergent epifauna in the predation risk experienced by juvenile demersal fishes. In the same study Stoner and Titgen (2003) noted significantly higher numbers of demersal fish juveniles in habitats containing high abundances of structuring epifauna than less complex habitats as did Martin et al. (1995) for numerous small, demersal fishes. Sites 1 and 2 may therefore provide more adequate shelter for the smallest size classes of *C. lyra* compared to the bare sand of site 3. The low number of medium size classes (year 2-3) at site 3 may also be related to predation risk as older *C. lyra* show darker colorations with maturity (author observation) increasing the difficulty of hiding from potential predators on a pure sand bottom. Both of the

above suggestions would require a thorough investigation of the predation risks experienced by different size classes over different sediment types as well as a quantification of the potential predators present within the study area.

Seasonal differences in the distribution of demersal fishes are well documented (Chen et al., 2009, Damalas et al., 2010, Ribiero et al., 2012) and some have been described as a response to the prey availability of the demersal fish community (Byron and Link, 2010, Jenkins et al., 2011). Although the distribution of *C. lyra* may not be related to the prey community, higher numbers of *C. lyra* in the autumn than the spring is likely to be a result of increased numbers of juveniles following spring spawning events, (see King et al., 1994). This is supported by Svedang (2003) who described similar patterns in a mixed demersal fish assemblage, however this was over much larger spatial scales (>100's km²) (see also Hyndes et al., 1999, Machias et al., 1998). Further confirmation of this pattern would require higher replication to see if the patterns seen in this study were consistent over a number of years. A more adequate sampling of pre-settlement and new post-settlement *C. lyra* individuals would also be beneficial.

5.6 Conclusion

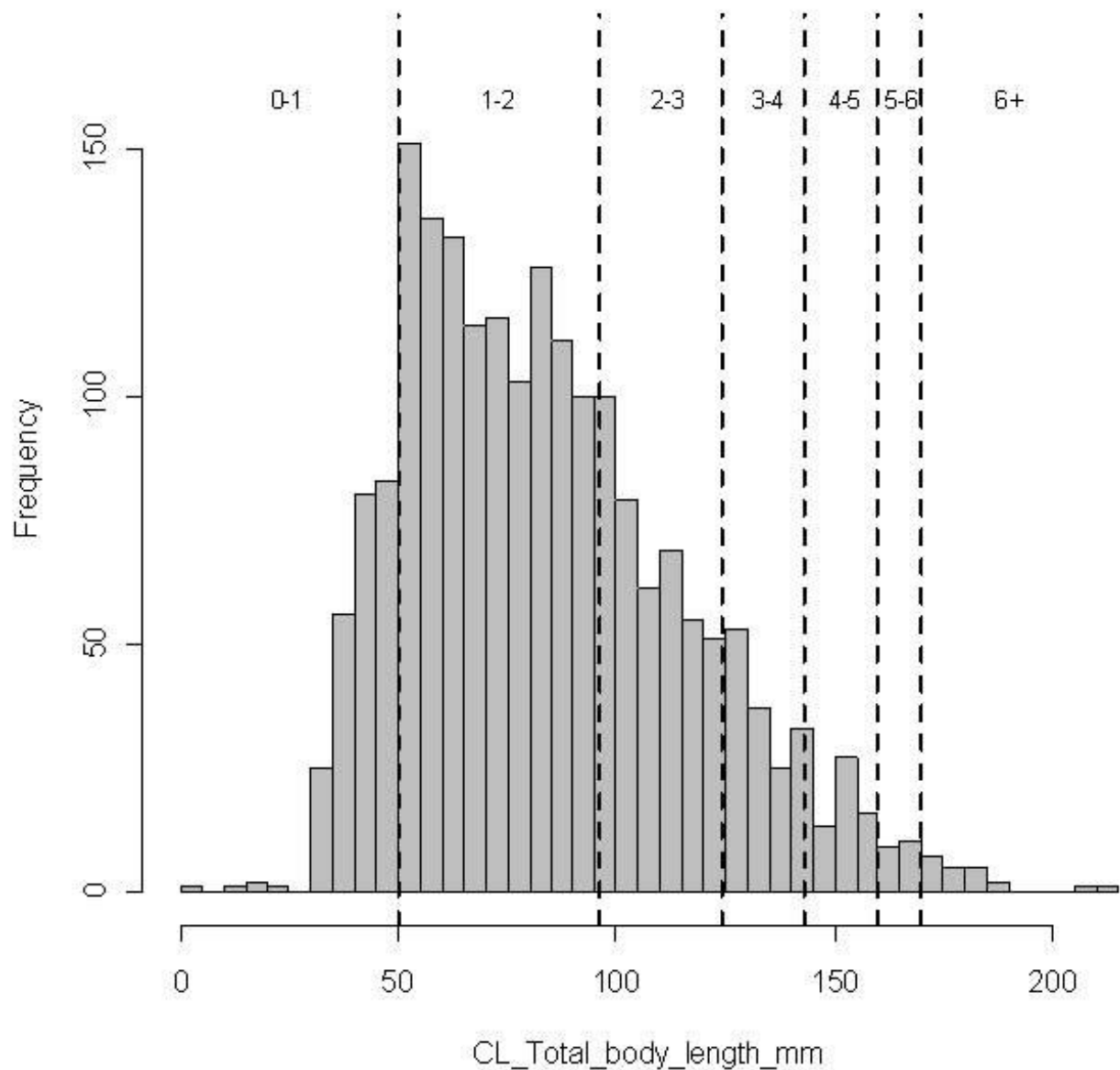
Clearly understanding the distribution patterns of marine species is one prerequisite for the successful implementation of spatial management strategies. Our study highlights the importance of addressing predator size when relating the distribution of demersal fishes to their environment. If left unconsidered, conclusions regarding the habitat variables determining distribution may only apply to the most dominant life stages sampled and may neglect particularly sensitive or important life stages (e.g. young of the year juveniles or

spawning adults). This study also highlights the potential problems of using habitat maps based on the sediment characteristics of sites to delineate sampling stations and the theoretical differences in habitats, even over small spatial scales; a “fundamental” *versus* “realised” niche argument. Extensions of this work will benefit from accounting for the data limitations discussed and measuring more habitat variables that may potentially determine the size class distributions of *C. lyra* (predation, competition, habitat complexity etc.) In addition, increasing the spatial scale of study whilst maintaining a high resolution approach would allow a detailed hierarchical design, testing the importance of spatial scale in determining the strength of any relationships between predators, their prey community and additional habitat variables.

5.7 Appendices

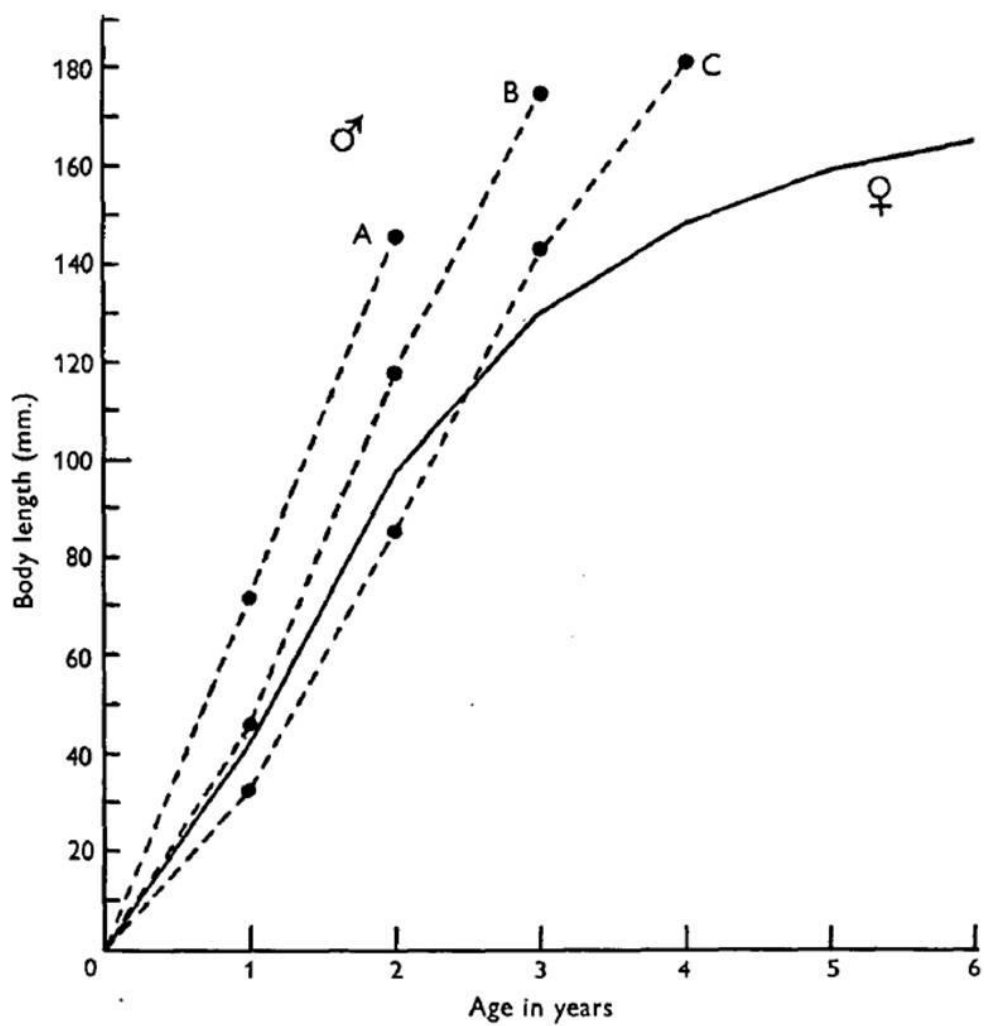
Appendix 5.7.1a

Histogram showing size class distribution of all *C. lyra* used in the study with year classes calculated from Chang (1951) (Appendix 5.7.1b), marked by broken lines.



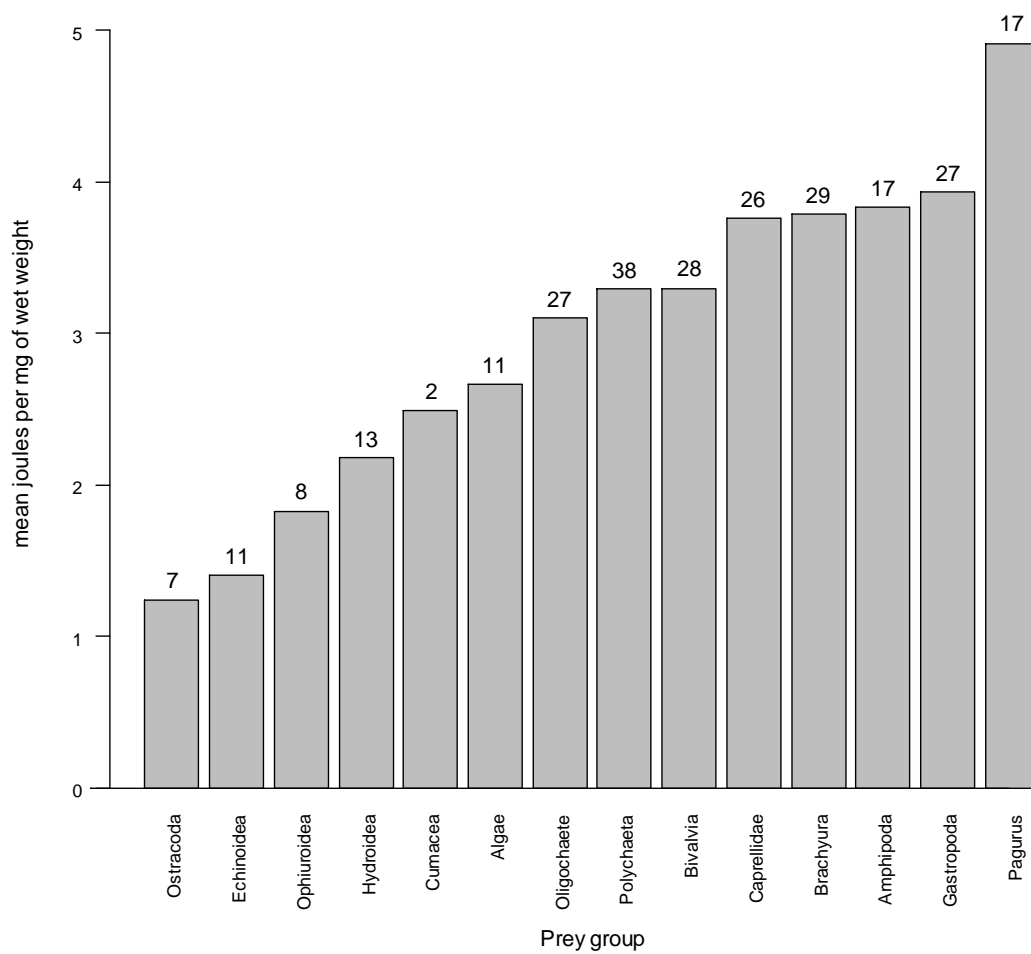
Appendix 5.7.1b

Age versus body length graph from Chang (1951) used to approximate year classes, based on size of females *C. lyra*.



Text-fig. 4. Growth of *Callionymus lyra*. ♂ (broken line), A, third-year breeder; B, fourth-year breeder; C, fifth-year breeder. ♀ (continuous line), mixed.

Appendix 5.7.2 Bar plot showing prey energy conversion values for the prey taxa groups of *C. lyra*. Numbers above bars denote number of values used to form Brey approximation.



Appendix 5.7.3 OLS regression results for the relationship between 5 mm size class of *C. lyra* and the mean percentage abundance of total diet for each prey taxa found in stomachs. Bold highlights the best fitting model as determined by the AIC criteria.

Prey taxa	<i>Linear</i>					<i>Quadratic</i>				
	<i>R</i> ²	F	<i>df</i>	<i>P</i>	<i>AIC</i>	<i>R</i> ²	F	<i>df</i>	<i>P</i>	<i>AIC</i>
<i>Algae</i>	0.251	8.366	25	0.008	-142.6	0.252	4.052	24	0.687	-138.97
<i>Amphipoda</i>	0.049	1.294	25	0.266	-75.12	0.422	8.771	24	0.001	-79.7
<i>Bivalvia</i>	0.47	22.147	25	0	-74.36	0.518	12.882	24	0.089	-61.65
<i>Brachyura</i>	0.03	0.781	25	0.385	-157.52	0.041	0.514	24	0.617	-154.78
<i>Caprellidae</i>	0.219	7.019	25	0.014	-232.52	0.238	3.741	24	0.447	-230.89
<i>Cumacea</i>	0.043	1.129	25	0.298	-268.89	0.165	2.378	24	0.073	-270.46
<i>Echinoidea</i>	0.318	11.645	25	0.002	-104.85	0.335	6.041	24	0.311	-98.92
<i>Gastropoda</i>	0.227	7.328	25	0.012	-92	0.226	3.501	24	0.953	-84.84
<i>Hydroidea</i>	0.166	4.962	25	0.035	-211.17	0.29	4.892	24	0.051	-213.13
<i>Oligochaete</i>	0.132	3.812	25	0.062	-165.8	0.132	1.833	24	0.866	-162.78
<i>Ophiuroidea</i>	0.089	2.452	25	0.13	-124.88	0.423	8.79	24	0.001	-133.06
<i>Ostracoda</i>	0.767	82.074	25	0	-68.66	0.966	337.024	24	0	-109.25
<i>Pagurus</i>	0.273	9.383	25	0.005	-135.66	0.277	4.602	24	0.65	-131.98
<i>Polychaeta</i>	0.146	4.281	25	0.049	-86.82	0.15	2.126	24	0.866	-75.40

Appendix 5.7.4 OLS regression results for the relationship between 5 mm size class of *C. lyra* and the mean percentage biomass of total diet for each prey taxa found in stomachs. Bold highlights the best fitting model as determined by the AIC criteria.

Prey taxa	<i>Linear</i>					<i>Quadratic</i>				
	<i>R</i> ²	F	<i>df</i>	<i>P</i>	<i>AIC</i>	<i>R</i> ²	F	<i>df</i>	<i>P</i>	<i>AIC</i>
<i>Algae</i>	0.111	3.131	25	0.089	-147.35	0.154	2.18	24	0.28	-145.27
<i>Amphipoda</i>	0.026	0.67	25	0.421	-83	0.15	2.113	24	0.069	-79.7
<i>Bivalvia</i>	0.493	24.348	25	0	-75.56	0.686	26.187	24	0.001	-74.53
<i>Brachyura</i>	0.094	2.58	25	0.121	-132.63	0.095	1.264	24	0.92	-128.73
<i>Caprellidae</i>	0.22	7.066	25	0.014	-248.75	0.223	3.438	24	0.783	-246.65
<i>Cumacea</i>	0.069	1.846	25	0.186	-323.12	0.144	2.019	24	0.159	-323.35
<i>Echinoidea</i>	0.212	6.734	25	0.016	-106.58	0.208	3.155	24	0.885	-100.35
<i>Gastropoda</i>	0.316	11.563	25	0.002	-91.86	0.31	5.391	24	0.999	-84
<i>Hydroidea</i>	0.078	2.12	25	0.158	-212.66	0.22	3.381	24	0.047	-214.82
<i>Oligochaete</i>	0.23	7.477	25	0.011	-138.91	0.272	4.488	24	0.24	-136.43
<i>Ophiuroidea</i>	0.018	0.456	25	0.506	-114.4	0.309	5.356	24	0.004	-119.36
<i>Ostracoda</i>	0.792	95.032	25	0	-62.98	0.968	363.951	24	0	-101.16
<i>Pagurus</i>	0.308	11.119	25	0.003	-124.78	0.321	5.672	24	0.484	-121.34
<i>Polychaeta</i>	0.41	17.373	25	0	-93.87	0.412	8.424	24	0.933	-82.12

Appendix 5.7.5 OLS regression results for the relationship between 5 mm size class of *C. lyra* and the mean size (mm) of each prey taxa found in stomachs. Bold highlights the best fitting model as determined by the AIC criteria.

<i>Prey taxa</i>	<i>Linear</i>					<i>Quadratic</i>				
	<i>R</i> ²	<i>df</i>	<i>F</i>	<i>P</i>	<i>AIC</i>	<i>R</i> ²	<i>df</i>	<i>F</i>	<i>P</i>	<i>AIC</i>
<i>Amphipoda</i>	0.721	19	49.158	<0.001	-59.39	0.833	18	44.938	0.003	-68.17
<i>Bivalvia</i>	0.873	25	172.614	<0.001	-47.68	0.898	24	105.956	0.024	-51.57
<i>Brachyura</i>	0.597	7	10.352	0.015	-2.24	0.802	6	12.128	0.047	-6.63
<i>Crustacea</i>	0.775	18	61.933	<0.001	-18.03	0.858	17	51.375	0.006	-25.26
<i>Echinoidea</i>	0.351	10	5.416	0.042	-20.60	0.352	9	2.440	0.956	-18.61
<i>Gastropoda</i>	0.530	15	16.939	0.001	-11.71	0.568	14	9.206	0.287	-11.13
<i>Ophiuroidea</i>	0.058	9	0.559	0.474	-4.64	0.063	8	0.269	0.847	-2.70
<i>Ostracoda</i>	0.163	10	1.954	0.192	-45.56	0.687	9	9.898	0.004	-55.38
<i>Polychaeta</i>	0.699	24	55.843	<0.001	-55.41	0.723	23	29.962	0.178	-55.51

CHAPTER 6

General discussion

6.1 Introduction

The preceding chapters documented 4 separate studies that differ in terms of the fish species analysed, the approaches used, and the geographic areas studied. All however share a common theme: the link between demersal fishes and their habitat in particular, the relationship between these fishes and their prey communities. In Chapter 2 I used a literature review to evaluate work that has already been carried out in the field of demersal fish habitat determination and suggest areas for future development. This work supported the hypothesis that research in the field of demersal fish habitat determination will benefit from a change in focus increasing the number of studies focussing on biotic parameters and those studying long temporal scales. It also highlights a need to reduce the spatial scale over which abiotics are generally analysed. In chapters 3, 4 and 5 I investigated the importance of prey resources for demersal fish communities under different scenarios. Results from these chapters supported the hypotheses that prey abundance, and in fewer cases, prey sizes are important factors determining the distribution and perhaps the condition of some demersal fish species over small to medium spatial scales (1 – 100s km²). They also highlight the importance of defining fish sizes / developmental stages when attempting to describe the prey communities of demersal fishes. In this general discussion I bring the findings of these previous chapters together and discuss areas for future development emerging from them.

6.2 Taking new approaches

6.2.1 Reviewing past work

Science often relies on technological development to open new windows of opportunity for novel research approaches to be taken. A good example in marine science is the recent

advancement in acoustic technologies which can now give us high resolution images of sea floor habitats across large spatial scales (Freitas et al., 2011), and even describe complex behaviours of schooling fish species (Fielding et al., 2012). It is however important to remember that thorough evaluations of past studies can be just as helpful in pointing research in new directions. Such approaches can therefore help us to think “outside the box” taking more exploratory approaches than following common research trends.

The review used in Chapter 2 is useful in that it gives a good introduction to the background of demersal fish habitat determination whilst quantifying patterns and evaluating research trends. One important finding was the propensity for research to focus on easily measured abiotic variables that may be used to describe demersal fish habitat. Also, significantly fewer studies investigated the influence of biotic variables on the distribution of demersal fishes. All three field studies presented in this thesis primarily analysed demersal fish prey resources, an important biotic habitat variable which is often neglected at spatial scales between metres and tens of kilometres.

6.2.2 Prey resources – taxa and size

A sufficient amount of food resource is essential for any animal to survive. It is therefore intuitive that the habitat of an organism is to some extent determined by the levels of these resources. Chapter 3 introduces the idea of mouth gape limitation in demersal fishes and the importance of considering prey size as a habitat variable in addition to the commonly analysed prey taxa and functional type classifications. Although the importance of prey size has been thoroughly investigated in juvenile fishes in the laboratory and piscivorous adult fishes in the field, this is the first time it has been analysed solely for the benthic feeding stages of demersal fishes in the field. Chapters 4 and 5 reiterate the importance of prey size

considerations when measuring prey resource as a habitat variable. In chapter 4 we see how two morphometrically similar flatfish species have variable prey spectra based on differences in their mouth gapes which determine their foraging capabilities. Feeding limitations as a result of mouth gape size mean significant differences in the size and type of prey they are able to consume and ultimately the efficiency with which each can feed. This is an important consideration for populations in anthropogenically impacted prey environments.

Chapter 5 also discusses optimal foraging theory and ontogenetic shifts in prey size selectivity of a common UK demersal fish species. The efficiency of feeding strategies are discussed in terms of the number of prey items consumed, energy contents of preys and changes in prey taxa and size with predator size.

Future studies aiming to relate the distribution of demersal fishes to prey resource should aim to analyse both prey taxa and prey size because the size of a prey item may be just as important in determining consumption, especially for opportunistic predators in areas of high prey diversity and density. This however is not an easy task. The measurement of exact prey sizes is laborious and adds considerable time to the collection of taxonomic data, a point highlighted by my use of mean prey biomass as a surrogate for mean prey size in chapter 3. If numbers of individuals and the mean biomass of prey species are known, species specific biomass-size calibration graphs could potentially be used to convert total prey biomass and number to mean prey size per haul. However, the accuracy of such extrapolation requires rigorous testing.

6.2.3 Ontogenetic differences in habitat suitability

In Chapter 2 I also discuss the utility of separating analyses by ontogeny, acknowledging how relationships between demersal fishes and their habitat are likely to change with development. The results presented in the last field chapter reiterate this point well. Through a detailed analysis of stomach contents, accounting for differences in the size of the study species, I demonstrate significant changes in the diet of demersal fishes with size. If all of these predator size classes had been grouped to produce an overall description of the species feeding ecology, significant differences in prey taxa and sizes in the diets would have been overlooked. Fish distributions evaluated using such general descriptions would likely give inaccurate estimates of habitat suitability and potential distributions. The consideration of ontogenetic differences is not only relevant to prey resources but to all habitat variables determining demersal fish distribution.

Although the separation of life stages will give more detailed descriptions of habitat preferences and a better understanding of fish distributions, it is likely to require additional sampling effort. Different life stages in hauls require separation, and replication needs to be increased to account for reduced numbers of fishes within each replicate after separating per life stage. It is likely that for this reason, many studies neglect ontogenetic changes in demersal fish habitat preferences, especially over large spatial scales. Toole et al. (2011) discuss the idea of “pseudo-species” classifications to separate species by ontogeny and differences in depth distributions. Such classifications however were not deemed possible in this study as life histories were not sufficiently accounted for in field observations and variations in depth preferences were too variable at the spatial scale of the study. Unless specific objectives to study ontogenetic variations in habitat suitability are defined, such within-species variations are likely to remain unconsidered. Acoustic approaches are now

showing promise, providing relatively quick in-situ censuses of pelagic fishes, enabling the numeration of juveniles and adults separately (Horne, 2003, Mann et al., 2009). Such applications for demersal fish species however do not currently exist.

6.2.4 Anthropogenic impacts on demersal fish habitat

The impacts of human activities on benthic systems are now well understood. However, the consequences of anthropogenic-induced change for demersal fish species associated with these systems are not. Chapter 4 studies the impacts of bottom trawling on benthic communities and more specifically what the changes in the benthos mean for the fish species present in impacted areas. Here I demonstrate that the well known consequences of benthic disturbance caused by bottom fishing have the ability to significantly alter the feeding ecology of two demersal fish species. This brings us full circle in understanding the impacts of bottom fishing on demersal fishes as it makes a link between changes in the benthos and the reduced condition of fishes associated with impacted areas, presenting clear ecological reasoning why this is likely to occur. With the ongoing problem of “shifting baselines” (see Pinnegar and Engelhard, 2008) and the necessity to study human-induced impacts in marine systems, I believe that studies analysing the condition of species in impacted areas should be adopted across other systems, especially potential areas for the implementation of spatial management strategies.

6.2.5 Condition versus abundance

As aforementioned in this thesis, the determination of fish habitat often involves relating the abundance of a species to measured habitat variables hypothesised to be important to the species distribution. Essentially this is the approach that has been taken within this thesis. Early on, I do however note that determinations of demersal fish habitat should ideally

address the growth and survival of individuals to give us true measures of habitat quality. Chapter 4 builds on work that takes this approach. As a general extension of chapters 3 and 5, I believe it would be valuable to look at the same relationships switching abundance for condition (e.g. weight-at-length). This would tell us if areas of high abundances correlate to areas of high condition and allow an interesting test of the ideal free distribution – Is the condition of fish similar between areas of differing abundance? Measurements of fish condition related to habitat variables and population distributions is an area that I would like to develop and one that although mentioned by authors, has remained almost untouched in the literature.

6.2.6 Implications for modelling and fisheries management

In recent years many advances in the field of demersal fish habitat determination have come from the development of statistical models. It is therefore important to note how the results from the previous chapters could be used in future modelling procedures. A now-popular modelling approach is that of Dynamic energy budget (DEB) theory. DEB offers a systematic way of describing how organisms acquire and use energy for physiological processes and how their physiological processes are influenced by environmental variables such as food density and temperature (Nisbet et al., 2000). DEB models generally describe the performance (growth, development, reproduction, respiration etc.) of the different life stages of the animal and predict differences in physiological rates with changes in environmental conditions (Pecquerie et al., 2009, Nisbet et al., 2000). Work from this thesis will prove useful in elucidating the importance of prey communities, and in some cases individual prey species, to some of the demersal fish species analysed. It will however be beneficial to incorporate ideas from each chapter in order to make these results more readily usable for such applications. For example, Chapter 4 looks at the diet of adult fishes and how prey choice and availability may affect overall condition but neglects the juvenile life stages of the

fishes. Chapter 5 on the other hand analyses the dietary differences between fish sizes but does not analyse the effects of prey choice on condition. If combined these approaches will account for both changes in development and the influence of prey communities on the condition and ultimately potential habitat suitabilities of the fish species analysed.

Another modelling method which has received a lot of recent attention is that of bioclimatic envelope modelling (see Pearson and Dawson, 2003). This offers an attractive method of using numerous data layers to predict future fish distributions as a result of climate change and different management scenarios. However, these models have been criticised as they are based on a correlative / data-mining approach which has the potential to ascribe coincidental or indirect relationships as direct causal links (Guisan et al., 2002, Jennings and Brander, 2010). The results presented in thesis could benefit such approaches by providing extra biotic data layers which are rarely included in such approaches, although advocated, particularly the use of prey field information of fish species modelled (see Cheung et al., 2011).

Broadly, an increased knowledge of where fishes live and the reasons for their distributions will help towards a more ecosystem based approach to fisheries management as long as it is used at the appropriate spatial scales (see Chapter 2). If management is based across small to medium scales then it will prove more difficult to confidently apply results from larger spatial scale studies as the importance of relationships between demersal fishes and their habitats are likely to change with spatial scale. Specifically, this thesis could potentially benefit the EU's current MSFD. The focus on the relationship between demersal fishes and their prey items may prove useful for quality descriptor number 4 of the EU's MSFD which states "*All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the*

species and the retention of their full reproductive capacity”(see Heslenfeld and Enserink, 2008). In order to incorporate ideas from this thesis into management it will be necessary to first understand if patterns persist between geographic regions, species and spatial scales, it is therefore essential to analyse more, different areas and species at a number of spatial scales.

6.3 Concluding remarks

Despite the known importance of understanding the distribution of species for the use of spatial management strategies, still many unknowns remain in the field of marine fish habitat identification. Research presented in this thesis sheds light on several poorly studied areas. In order that we can better manage exploited demersal fish resources, there are numerous areas that can be developed in the field of demersal fish habitat determination. These include further investigations attempting to understand the role of competition, prey resources and predation in determining fish distributions (see Link et al., 2011). This field will also benefit from increasing the number of spatial scales over which fish-habitat relationships are studied. Developing ways to scale up laboratory experiments to field scales, the adoption of more multi-scale / hierarchical approaches will benefit management aiming to conserve demersal fish stocks through the use of spatial management strategies. Likewise, more approaches accounting for temporal changes in distributions, particularly over long time scales will help us evaluate current management strategies and our capabilities of predicting future fish distributions. Ultimately fisheries managers need a tool box primed with studies covering many spatial and temporal scales, species and habitats in order that research from the field of demersal fish habitat determination can be used effectively in the implementation of EBFM, particularly the designation of MPAs.

Chapter 7

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