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Ecology and habitat use of flatfishes

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Ecology and habitat use of flatfishes

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Summary

This study investigates the habitat requirements and distribution patterns of four commercially exploited flatfishes: *Pleuronectes platessa* (plaice), *Solea solea* (sole), *Microstomus kitt* (lemon sole) and *Limanda limanda* (dab). The main goal of the study was to promote species specific knowledge of habitat requirements of the adult life stage of these four flatfish species, which will be a prerequisite for the identification process of 'Essential Fish Habitats' and the integration of those into a more ecosystem based approach to fisheries management.

The first section introduces a new methodology that objectively identify sites which consistently harboured high densities of fish over considerable periods of time from large datasets such as groundfish surveys. Following assumptions of habitat selection theory these habitats should display consistent favourable conditions while other habitats with variable or low densities of flatfishes should exhibit less favourable conditions. This method was applied to groundfish survey data of roundfishes in the Irish Sea (cod, haddock and whiting) and to flatfishes in the English Channel (plaice, sole and lemon sole).

The habitat conditions of the high consistent abundance sites of the three flatfishes in the English Channel were compared to the conditions encountered at stations of variable and low flatfish abundances and with sites where no flatfishes were caught by the groundfish survey. While consistent high density plaice and sole sites showed similar habitat conditions typical of near shore environments, lemon sole was predominantly found over areas with deeper offshore conditions. Sediment associations also differed between species with plaice occurring over sand while sole was found over sediment ranging from muddy to sandy substrates. Lemon sole was found at sites with slightly higher gravel content than plaice and sole. No clear relationship was found between flatfish abundance emergent epifauna and prey availability. However, the absence of a relationship between prey availability and flatfish abundances was thought to be related to an inadequate sampling strategy.

An underwater video survey was conducted to explore the habitat characteristics of selected consistently high abundance sites of adult plaice in more detail. The sampling technique enabled exploration of habitat characteristics such as substratum morphology and heterogeneity as well as the presence of benthic macrofauna. No obvious relationships were found between substratum characteristics and plaice densities determined at these sites. Clear relationships were only observed with the presence of benthic macrofauna.

In a small scale research area in the German Bight the seasonal and interannual variability of an epifauna community was investigated to determine temporal and spatial stability of benthos important as potential flatfish prey. Fluctuations in abundance and biomass were linked to the migratory behaviour of mobile species in an out of the research area. While seasonal trends were related to temperature fluctuations, interannual changes were thought to be caused by differences in food supply to the benthic community created by changes in front formation.

The influence of changes in the benthos, in respect to prey availability, on the distribution, body condition and resource acquisition of dab was investigated. Dab abundance and prey availability followed similar decreasing trend during consecutive summer periods however during winter a steep increase in dab abundance was apparent while prey availability and body condition continued to decrease. This increase in dab abundance was linked to migratory behaviour of dab due the cold conditions in the shallow areas of the German Bight and due to spawning behaviour. The prey choice of dab was significantly influenced by the abundance of prey organisms in the environment, while the position in the environment, mobility and palatability seemed to be less important.

The main findings of these studies were discussed within a common framework and recommendations for future research were given.

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Chapter 1

General introduction

1.1 Fish habitat in the context of fisheries management

The high rates of exploitation of marine fishes globally have led to an significant decline in the population size of many commercial fish stocks over the past decades (Pauly *et al.,* 1998; Myers and Worm, 2003) and have rendered many fisheries unsustainable (Hilborn *et al.*, 2003). Such declines have been particularly marked in areas of the North Atlantic which, unlike other regions of the world, had monitoring and management regimes in place (Myers *et al.*, 1996; Jonzen *et al.*, 2002). The failure of single species management to protect and safeguard fish stocks from overexploitation, together with the growing awareness of the negative ecosystem effects of fishing activities (Jennings and Kaiser, 1998; Kaiser *et al.*, 2002), has led towards a more ecosystem orientated approach to fisheries management (Link, 2002; Sinclair *et al.,* 2002; Gell and Roberts, 2003; Christensen and Pauly, 2004).

The ecological consequences of bottom fishing extend further than the removal of the target species. The action of towed bottom fishing gear kills, damages or removes benthic organisms (Jennings and Kaiser, 1998) and modifies substratum morphology (Thrush *et al.*, 2001), ultimately leading to community and habitat change (Jennings *et al.,* 2001; Kaiser *et al.*, 2002). In particular large, structure forming emergent epifauna species which add to the complexity of habitats are regularly affected by bottom fishing (Auster,1998; Kaiser *et al.*, 2000; Kaiser *et al,.* 2002). Structured habitats fulfill a multitude of ecosystem functions. They reduce current velocities, thereby entrapping organic material (Zühlke, 2001), provide niches for small benthic organisms (Bradshaw *et al.*, 2003) which in turn are preyed upon by larger species such as fish, and thus facilitate more complex food webs. Consequently the loss of such habitat structures will have a cascading effect on food chains and in extreme cases can lead to regime shifts in whole ecosystems (Choi *et al.,* 2004). Biogenic structures have long recovery times often measured in years or decades (Collie *et al.*, 2000) and therefore the associated fauna such as certain demersal fish species also may be negatively affected for similar periods. Consequently fishing induced habitat change might also have contributed to the continuing decline in commercial fish stocks. As such future recovery plans for over-exploited stocks also need a consideration of habitat quality issues.

With the recognition of these associated consequences of fishing, management and legislation were reformed in the United States to protect fish stocks and habitats more effectively. This lead to the reauthorization of the Magnuson-Stevens Fisheries Conservation and Management Act through the Sustainable Fisheries Act (SFA) in 1996. Legislation measures of the SFA included, besides overfishing and bycatch reduction, the requirement for fisheries management councils to identify so called Essential Fish Habitats (EFH), for species within their management plans by 1998. EFH were defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (16 U.S.C. 1802(10)). In addition to locating EFH, potential threats, from fishing and non-fishing activities, also needed to be identified and actively considered in management regimes to minimize their adverse effects. This more ecosystem orientated approach to fisheries management is now recognized and integrated in the U.S. and within the new Common Fisheries Policy (CFP 2002) in Europe. The CFP does not explicitly mention Essential Fish habitats as a management concept; however it designed to protect habitats through a more ecosystem-based management framework that is intended to minimize the negative effects of fishing activities. This approach will be implemented through the adoption of recovery plans, multi-annual management plans, regional advisory committees and so called “community action plans”. One of the first action plans released under the new CFP framework advised on the conservation and sustainable exploitation of fisheries resources in the Mediterranean (COM 2002). Within this plan the protection of EFH received particular attention, and was considered an important management goal.

Although from the management point of view there is a determination with regards to EFH, the appropriate scientific knowledge required for the identification of EFH for most species and their life stages is not yet available. A fundamental understanding of the habitat requirements of fishes, as well as of the dynamics of habitats themselves, will however be a pre-requisite to locate, quantify and manage such areas within an appropriate ecosystem based framework.

1.2 Flatfish habitats

Flatfish are uniquely adapted for a benthic life style (Gibson, 1994). As a result alterations to such habitats may therefore affect flatfish survivorship and distribution (Gibson, 1994; McConnaughey and Smith, 2000). However how exactly such alterations affect flatfish populations is not fully understood. Rijnsdorp and Vingerhoed (2001) proposed that the removal of long-lived species and the consequent enhancing of smaller short lived species as a result of bottom fishing (Duplisea *et al.*, 2002) could have positive effects for flatfish species such as plaice (*Pleuronectes platessa*) and sole (*Solea solea*) by increasing prey accessibility and availability. Rijnsdorp and Vingerhoed (2001) investigated the diets of both plaice and sole in the North Sea from the beginning of the 20th century, when fishing pressure was considerably lower than present and compared them to those of the present day. In their study they found that present day diets were dominated by fast growing polychaete species while the occurrence of bivalves had decreased compared with diets at the beginning of the 20^{th} century. Bivalves have a much higher energetic value compared to polychaetes (Brey *et al.,* 1988) and are equally accessible as polychaetes (Jones, 1952). The latter finding casts doubt on the proposal that bottom fishing will have positive effects on flatfish species by increasing food availability (see above). Undoubtedly there will be a short-term benefit from trawling activity for certain flatfish species or life stages as potential prey species are killed or made more accessible by the passage of a trawl (Kaiser and Ramsay, 1997; Groenewold and Fonds, 2000) but on a long-term basis intensive fishing activities have shown to reduce overall benthic productivity and biomass (Jennings *et al.,* 2002) and hence might limit population growth and recovery of flatfish stocks.

The removal of structure-building fauna due to bottom fishing is thought to have negative effects for juvenile flatfishes, as certain species utilize such structures to avoid predator detection (Stoner and Titgen, 2003; Ryer *et al.,* 2004). Although emergent fauna and structures may play less of a crucial role in protection from predators for adult fatfish, due to their larger size and the tendency to rely on burial in sediments as means of predator evasion (Gibson,1994; Gibson and Robb, 2000; Stoner and Abookire, 2002) these structures could also serve as refuge for potential prey items for certain species (Bradshaw *et al.*, 2003). This exemplifies that no easy generalization can be made regarding flatfish ecology. Although flatfish seem very similar in a morphological sense, significant differences in body design and consequently habitat requirements and behaviour exist (Gibson, 1997; Piet *et al.*, 1998; Gibb, 2003). This demonstrates that species specific knowledge is needed for the design of management measures that achieve an ecosystem management approach. Within the context of attaining stock recovery, it is important to understand the range of conditions under which flatfish can exist, but also to determine which habitats or habitat characteristics are preferred and best promote survival. Such habitats might be candidate areas for protection and would require particular attention from fisheries managers.

1.3 Habitat selection theory and distribution patterns of flatfish

Distribution patterns of mobile biota are determined to some extent by the behavioural choices of the individual in response to its environment (Stephens and Krebs, 1986). Appropriate habitats may be selected in response to abiotic factors such as temperature and salinity, but also to ecological factors such as prey or mate availability, predation risks or the presence of competitors. Each habitat has associated energetic benefits and costs that are evaluated and together determine whether an individual remains within a habitat or relocates in search for more suitable conditions (Mittelbach, 2002). From a very simplistic viewpoint and in the absence of other influential factors, this will lead to a distribution pattern where organisms will thrive to occupy the best possible habitat to maximize their fitness (Morris, 1987), leading to higher densities over high quality habitats compared to less optimal habitats (low quality habitats). That fish are able to assess the relative quality of a habitat has been demonstrated by several experimental studies (Werner *et al.*, 1983; Werner and Hall, 1988; Abrahams, 1989; Grand and Dill, 1999) and is also thought to be a major factor that determines flatfish distribution (MacCall, 1990). As organisms interact with the environment (e.g. reduce prey availability) and with each other (e.g. intra- and inter-specific competition) habitat quality will be modified continuously and hence will be reflected in overall distribution patterns. To summarize and advance the understanding of these dynamic processes several models have been developed that have their origin in variations of the ideal free distribution theory (IFD) (Mittelbach, 2002) first described by Fretwell and Lucas (1972). The basic IFD model suggests that areas of the highest suitability attract high numbers of individuals (density-independent habitat selection) until, due to competition for food or space, suitability decreases for recently arriving individuals. These individuals may move into areas that were initially less suitable due to their lower quality or quantity of resources (density-dependant habitat selection). The lower levels of competition experienced in these areas, however, may lead to a higher resource acquisition of the individual and eventually lead to an equal resource distribution among all individuals. At the end the number of organisms within a finite area should be proportional to the total amount of resources available (Mittelbach, 2002).This basic IFD model however assumes the intrinsic quality of a habitat to be static and equal competitiveness amongst individuals. Both assumptions can rarely be upheld. The marine environment is highly dynamic in space and time and therefore habitat quality can be expected to continuously change (Shepherd and Litvak, 2004). Also equal competitiveness amongst individuals rarely exists (Tregenza and Thompson, 1998). Other studies have attempted to incorporated resource dynamics and unequal competition and are thought to describe habitat selection much more realistically (Mittelbach, 2002).

The theoretical principles of habitat selection form a framework for the interpretation of field based ecological studies that investigate the factors which influence the distribution of fish. In such studies distribution patterns and densities of free ranging fish are related to various habitat parameters (e.g. McConnaughey and Smith, 2000; Amezcua *et al.*, 2003). The argument being that, if fish are able to assess habitat quality then, fish density should be a good indicator to evaluate the strength of the association between particular fish species and a specific habitat or habitat parameter. Although the principle ideas of habitat selection are easy to understand, data on fish distributions are often highly variable and challenging to analyse and interpret. This is due to a number of factors that include the complexity of fish behaviour, multi-species interaction, multifactorial properties of habitats and the often crude ways of determining fish densities with trawls. Finding meaningful relationships with habitat parameters, which themselves undergo continuous change or are interdependent, is difficult, not the least because the spatial scales over which habitat selection occurs, and influences distribution patterns are largely unknown.

1.4 The aims of this study

The overall aim of this study was to increase the knowledge of habitat utilization of flatfish. In particular, this study focuses on the adult life stage of four species: plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), sole (*Solea solea*) and lemon sole (*Microstomus kitt*). By relating flatfish densities and habitats it was intended to identify specific habitat requirements of the respective species. The main question this thesis attempted to answer was if flatfish densities and thus distribution patterns are significantly influenced by benthic habitat parameters. In particular the thesis focused on the presence of biotic habitat structures (emergent epifauna) as well as prey availability. The H_0 hypothesis of this thesis could therefore be formulated as follows: Flatfish are distributed unrelated to benthic habitat structures and prey availability.

The study broadly presents two parts with respect to the geographical source of the data. Nevertheless both parts are conceptually integrated together in chapter 7. The first part consists of chapters 2-4 which mainly were based on data from the English Channel and covered the flatfish species plaice, sole and lemon sole. The second part consisting of chapter 5 and 6 was based on data from a predefined research area in the German Bight. Here the main focus was on specific aspects of dab ecology.

Chapter 2 introduces a new method to objectively identify sites which consistently harboured high densities of fish over considerable periods of time from large datasets such as groundfish surveys. Following supposition of habitat selection theory these habitats should display consistent favourable conditions while other habitats with variable or low densities should also exhibit less favorable conditions. This method was applied to roundfish in the Irish Sea (cod, haddock and whiting*)* and to flatfish in the English Channel (plaice, sole and lemon sole). This chapter attempts to establish if the flatfish species under investigation are randomly distributed or if certain areas exhibit higher and more stable densities of fish than others.

The habitat parameters found at stations identified by the above method (Chapter 2) as high consistent density sites of flatfishes were compared to habitat parameters found at lower or variable density flatfish sites in the English Channel (Chapter 3). Apart from abiotic parameters such as sediment type, depth, salinity, temperature, amounts of shells and stones present also the association of adult flatfish with emergent epifauna and prey availability was studied. This chapter in particular attempted to answer the question if the presence of emergent epifauna and prey densities had a significant influence on the abundance and thus distribution of the flatfishes studied (plaice, sole and lemon sole).

The habitat characteristics of stations with high consistent plaice densities during groundfish surveys (Chapter 2) were more closely investigated with video survey techniques (Chapter 4). Here the question if the heterogeneity or morphology of the sediment habitat and the presence of benthic fauna could be associated with plaice abundances was attempted to be answered. In situ observations by video allowed habitat parameters such as substratum morphology or heterogeneity to be estimated on a scale likely to be relevant for individual fish. These possibly important habitat parameters may not be quantified by traditional sampling methods such as with grabs and trawls. Besides abiotic habitat features also the relationship of plaice densities with visible benthic fauna was explored. The data for this chapter were extracted from video recordings by Richard Shucksmith and formed part of his third year undergraduate project which was conducted under my supervision. The data have been substantially reanalysed and reinterpreted for the presentation in the present thesis.

Chapter 5 and 6 are studies conducted in the German Bight. The main aim of these studies was to determine the spatial and temporal variability of benthic fauna within a small scale research area (Chapter 5 and 6) and to assess the effects of these fluctuations in form of prey availability on the local dab population (Chapter 6). Thus this chapter attempted to focus on the importance of temporal changes in prey availability and how these may effect distribution patterns of dab. In addition to density, trends in body condition, stomach fullness and diet composition of dab were recorded. Another aim of this study was to determine the underlying functional approach of prey choice in dab. Here abundances and the functional characteristics of potential prey in the environment were related to the abundances of prey types found in dab stomachs.

In Chapter 7 the general findings of this thesis are summarized and discussed. An outlook of possible future work is given.

This thesis is presented in form of papers prepared for scientific publication. As such some overlap is inevitable when common methodologies or graphic materials have been used for different components of this thesis.

The following Chapters have been published or submitted for publication. All these papers were written by the author of this thesis. Contribution of co-authors was restricted to supervision of this thesis and comments on the manuscripts before submission:

Chapter 2: Hinz H, Kaiser MJ, Bergmann M, Rogers SI, Armstrong MJ (2003). Ecological relevance of temporal stability in regional fish catches. Journal of Fish Biology 63: 1219-1234.

Chapter 3: Hinz H, Bergmann M, Shucksmith R, Kaiser MJ, Rogers S.I (submitted) The importance of sediment type and habitat features for adult flatfish in the English Channel. ICES Journal of Marine Sciences

Chapter 5: Hinz H, Kröncke I, Ehrich S (2004). Seasonal and annual variability in an epifaunal community in the German Bight. Marine Biology 144: 735-745

Chapter 6: Hinz H, Kröncke I, Ehrich S (in press) The feeding strategy of dab (*Limanda limanda*) in the southern North Sea: Linking stomach contents to prey availability in the environment. Journal of Fish Biology

Chapter 2

Ecological relevance of temporal stability in regional fish catches

2.1 Abstract

The concept of habitat selection based on 'Ideal Free Distribution' theory suggests that areas of high suitability may attract larger quantities of fishes than less suitable or unsuitable areas. Catch data were used from groundfish surveys to identify areas of consistently high densities of whiting *Merlangius merlangus*, cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* in the Irish Sea and plaice *Pleuronectes platessa*, sole *Solea solea*, lemon sole *Microstomus kitt* in the English Channel over a period of 10 and 9 years respectively. A method was introduced to delineate areas of the seabed that held consistently high numbers of fishes objectively from large datasets. These areas may constitute important habitat characteristics which may merit further scientific investigations in respect to 'Essential Fish Habitats' (EFH). In addition, the number of stations with consistently high abundances of fishes and the number of stations where no fishes were caught gave an indication of the site specificity of the fish species analysed. For the gadoids, whiting was found to be less site specific than cod and haddock, while for the flatfishes, plaice and sole were less site specific than lemon sole. The findings are discussed in the context of previously published studies on dietary specializm. The site specificity of demersal fishes has implications for the siting process for marine protected areas as fish species with a strong habitat affinity can be expected to benefit more from such management schemes.

2.2 Introduction

Marine fish stocks around the world are overexploited and many are believed to be close to or outside their 'safe biological limits' (Pauly *et al.*, 1998). Fish stocks in European waters and elsewhere have been managed traditionally by means of fishing quotas. These single species management schemes have failed to protect fish stocks and have kept them outside safe biological limits. It has been recognized that alternative approaches to fisheries management are required to ensure the viability and sustainability of fish stocks (Gislason *et al.*, 2000; Link, 2002). One alternative is thought to be the implementation of areas closed to fishing or 'Marine Protected Areas' (Garcia-Charton and Perez-Ruzafa, 1999; Auster and Shackell, 2000; Jennings, 2000; Murawski *et al.*, 2000; Roberts, 2000; Jones, 2001). The rational being that areas of seabed that are closed either entirely or temporarily to fishing may allow part of the stock to recover. As bottom fishing and aggregate extraction activities have been shown to affect the benthic fauna and habitats (Collie *et al.*, 2000; Kaiser and de Groot, 2000; Lindeboom and de Groot, 1998; Desprez, 2000), closed areas are likely to provide additional benefits for these components of the ecosystem. Many marine fishes are reliant on benthic organisms as a food source and thus a recovery of the benthic fauna could lead to an overall increase of abundance and condition in certain fish species in such areas (Badalamenti et al., 2002). As the number of individuals within a protected area increases over time some individuals are thought to spill over into adjacent areas that have remained open to fishing (Nowlis and Roberts, 1999; Jennings, 2000). The relative benefits of protected areas will depend largely on the species' biology and the size and type of area chosen for closure. If a closed area comprised habitats of high suitability for a particular species a larger positive effect could be expected than if it comprised habitats of sub-optimal or unsuitable quality. Thus, to maximise the benefit from closed areas they should include habitats essential to the survival and health of the fish stock. Such habitats have been termed 'Essential Fish Habitat' (EFH) and would comprise spawning and nursery grounds, areas that provide specific feeding resources and shelter from predators and areas of seabed that form part of a migration route (Benaka, 1999).

With the re-authorization of the Magnuson-Stevens Management Act in 1996 it has become a legal requirement in the United States to consider EFHs in fisheries management plans. Despite centuries of intensive commercial exploitation of fish in European waters, scientists know relatively little about the specific habitat requirements of most marine fish (Benaka, 1999; Coleman and Travis, 2000). While spawning grounds and nursery areas of many marine fish species are well known (Coull, 1998) little is known about areas of importance to the adult stages, namely where they are able to feed effectively and reduce their risk of predation, particularly for temperate species.

Most temperate "groundfish" species such as flatfish and gadoids do not exhibit territorial behaviour and they are able to move freely between habitats (Metcalfe and Arnold, 1997; Jennings, 2000; Righton *et al.*, 2001). Habitat selection may be underpinned by theory such as 'Ideal Free Distribution' theory (IFD) (Fretwell and Lucas, 1970) which suggests that areas of high resource value (e.g. in terms of food and shelter) attract a larger number of individuals than areas with fewer resources. Theory indicates that mobile fish are most abundant in areas with the most suitable habitat characteristics for that species. The detection of areas of the seabed where fish consistently aggregate could thus highlight areas that have a potentially important or 'essential' functional role.

In the present study, abundance data from national ground fish surveys were used to identify potential EFHs for adult whiting (*Merlangius merlangus* [L.]) cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* [L.]) in the Irish Sea and for adult plaice (*Pleuronectes platessa* L.) sole (*Solea solea* [L.]) and lemon sole (*Microstomus kitt* [Walbaum].) in the English Channel. The purpose of the present study was to develop a logical framework for the objective identification of areas of seabed which may contain EFHs and thus would merit further investigation of their biological and environmental characteristics. The areas identified by the introduced method are referred to as 'Sites of Interest' (SoI). The data were also analysed for trends that give indications on the habitat specificity of the species analysed.

2.3 Methods

2.3.1 Data preparation

For the identification of seabed that consistently harbour the highest densities of *G. morhua*, *M. aeglefinus* and *M. merlangus* in the Irish Sea (ICES division VIIa) and *P. platessa*, *S. solea* and *M. kitt* in the English Channel (ICES division VIIe and d) two databases spanning a decade of fishery-independent data from national ground fish surveys were used. The Centre for Environment, Fisheries and Aquaculture Science (CEFAS, Lowestoft) holds a complete data set from 1990 to 1998 for the English Channel. Fish were sampled using a 4-m beam trawl at fixed stations every autumn (Ellis *et al.* 2000). The Department of Agriculture and Rural Development of Northern Ireland (DARDNI, Belfast) database spans a period from 1991-2000 for the Irish Sea (Ellis *et al.*, 2002). Fish were caught by otter-trawling at fixed stations every spring or autumn. The data-sets made available by CEFAS and DARD contained abundance, biomass, and size frequencies for each fish species caught during these surveys. Only abundance data of fish above the minimum landing size (MLS) caught during summer months were included in our analysis. Accordingly, only the distributions of adult fish were analysed and spawning aggregations were avoided as the fish species subject of this study spawn during early spring. Stations that were visited less than five times during the sampling period were excluded from the analysis. Overall 133 stations were included for the English Channel and 44 stations for the Irish Sea.

The abundance data for each fish species was subject to the following procedure: for each station the percentage of fish caught relative to all other stations was determined for each year. This conversion was performed to prevent a bias in the analysis by an exceedingly high abundance of fish at a particular station in any one year. The converted data (+1) was Log_{10}-transformed to achieve a normal distribution and the mean and standard deviation over the sampling period for each station was calculated. Difficulties in converting the data to percentages were apparent as artefacts can occur if a station has consistent scores that approach either zero or 100%. The largest values of mean percentage abundance encountered, however, were approximately 20%. Hence, the distorting effects of using percentage conversion can be considered minimal. It is therefore unlikely that any trends observed for stations with high mean abundances were caused by the constraints of using the percentage conversion. It should be noted that the number of stations sampled per year varied for the Irish Sea the between 28 and 44 stations and for the English Channel survey between 118 and 133 stations (Table 2.1).

Table 2.1 Number of stations samples per year by groundfish surveys in the Irish Sea and the English Channel and the total number of stations analysed for potential 'Sol'. Stars mark years not included in the analysis

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	n Total
Irish Sea	*	28	41	44	44	35	44	44	43	42	39	44
English Channel	118	122	130	128	131	128	132	130	133	*	*	133

The percentage of the fishes caught at a station depended on the total number of fishes caught at all stations and therefore on the total number of stations sampled. Consequently, this imbalance in the sampling scheme created an increased standard deviation. To avoid this effect stations not sampled in every year would have had to be excluded from the analysis. This would have caused the loss of 21 stations for Irish Sea and 27 stations in the English Channel. Furthermore, an analysis based on the exclusion of such stations produced very similar results to those shown here. Therefore, we decided to base our results on the imbalanced dataset. To analyse the variability at each of the sampling stations over time in more detail the residuals from the mean Log_{10}-percentage for each fish species were calculated and plotted as box and whisker plots where each box represents one station and the quartiles (bars), range (the whiskers) and outliers (asterisks) give detailed information on the variability of fish abundance over time. All stations were ordered from left to right by increasing mean Log_{10}-percentage abundance. The number of catches over the sampling period with no fish was recorded for each species, as well as the number of stations that yielded no fish.

To illustrate the data and to identify hotspots of fish density which may justify further investigation our data was entered into a Geographic Information System (ArcView 3.2). Mean percentage abundance and standard deviation were interpolated between sampling sites using Inverse Distance Weighted interpolation (IDW). The IDW interpolator assumes that each input point has a local influence that diminishes with distance. It weights the points closer to the processing cell greater than those that are further away. A specified number of points, or optionally all points within a specified radius, can be used to determine the output value for each location.

2.3.2 Method used to delineate sites of interest

For each station, the mean Log_{10}-percentage abundance was plotted against the standard deviation to produce a scatter-plot for each species (Fig. 2.1 a- 2.2 a). Each point in the graph represents one sampling station with its respective mean Log_{10}-percentage and standard deviation over the respective sampling period. Stations with a high mean Log_{10}-percentage abundance and low standard deviation were considered to be the most likely areas to qualify as SoI, because they represent sites where fish continuously aggregated in high numbers compared with other stations. To overcome subjective decisions about which stations met such criteria and those that did not, a method to delineate stations from each other was developed. The mean Log_{10}-percentage abundance data were randomized over all stations within each year. Hence, within each year, every station was assigned an abundance allocated at random from within the data of that year. The mean Log_{10}-percentages and standard deviations over the whole sampling period for each station were calculated for the randomized data as outlined above for the non-randomized data.

A general linear regression model best described the relationship of the random mean Log_{10}-percentages with the standard deviation for each site (Table 2.2). The regression line and the 95% Predictive Intervals (PI) of the linear regression model based on random scores were plotted together with the observed means and standard deviations for each species (Figs 2.1 a and 2.2 a). Regression models for the randomized data were fitted using S-Plus statistical software. The PIs of the randomized data function acted as an objective demarcation line that specified which stations met our SoI criteria. Stations that lie above or below the 95% PI diverge from the random model. Stations below the lower 95% PI have a very high mean/standard deviation ratio (lower than the expected variability); stations lying above the upper 95% PI have a very low mean/standard deviation ratio compared to the random model (higher than the expected variability).

Table 2.2 Results of linear regressions preformed on randomized mean Log_{10} percentage abundance and standard deviation for the six fish species analysed

Species	Intercept	Coefficient	r^2
Whiting	0.131	0.498	0.34
Cod	0.19	0.616	0.58
Haddock	0.088	0.752	0.49
Plaice	0.034	0.954	0.6
Sole	0.067	0.567	0.41
Lemon Sole	0.086	0.135	0.74

Due to variations in the number of stations sampled in each year, the randomized linear models for each fish species were based on imbalanced data. This will have influenced the randomized data by increasing its variability which in turn will have lead to a decreased difference between the points from the random model (PI) and the observed values and ultimately to an underestimation.

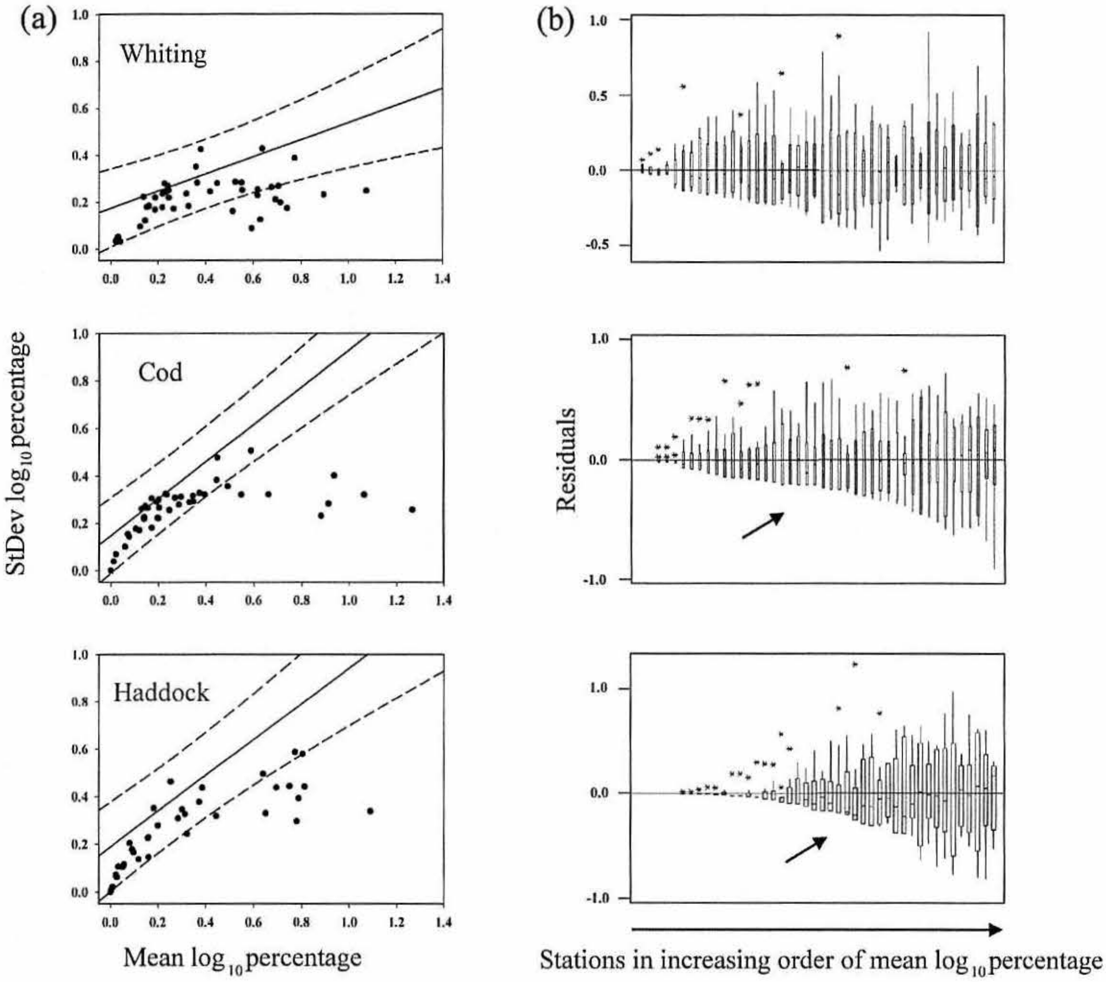

Figure 2.1 a.) Relationship between mean Log_{10}-percentage abundance and standard deviation for stations sampled over 10 years for whiting (*Merlangius merlangus*), cod (*Gadus moruha*) and haddock (*Melanogrammus aeglefinus*). Regression line (solid black line) and 95% PI (dashed line) originate from the same data after generation of random scores

b.) Box plot of residuals of the mean Log_{10}-percentage abundance of each station over 10 years for whiting, cod and haddock. Quartiles (bars), range (whiskers) and outliers (asterisks)

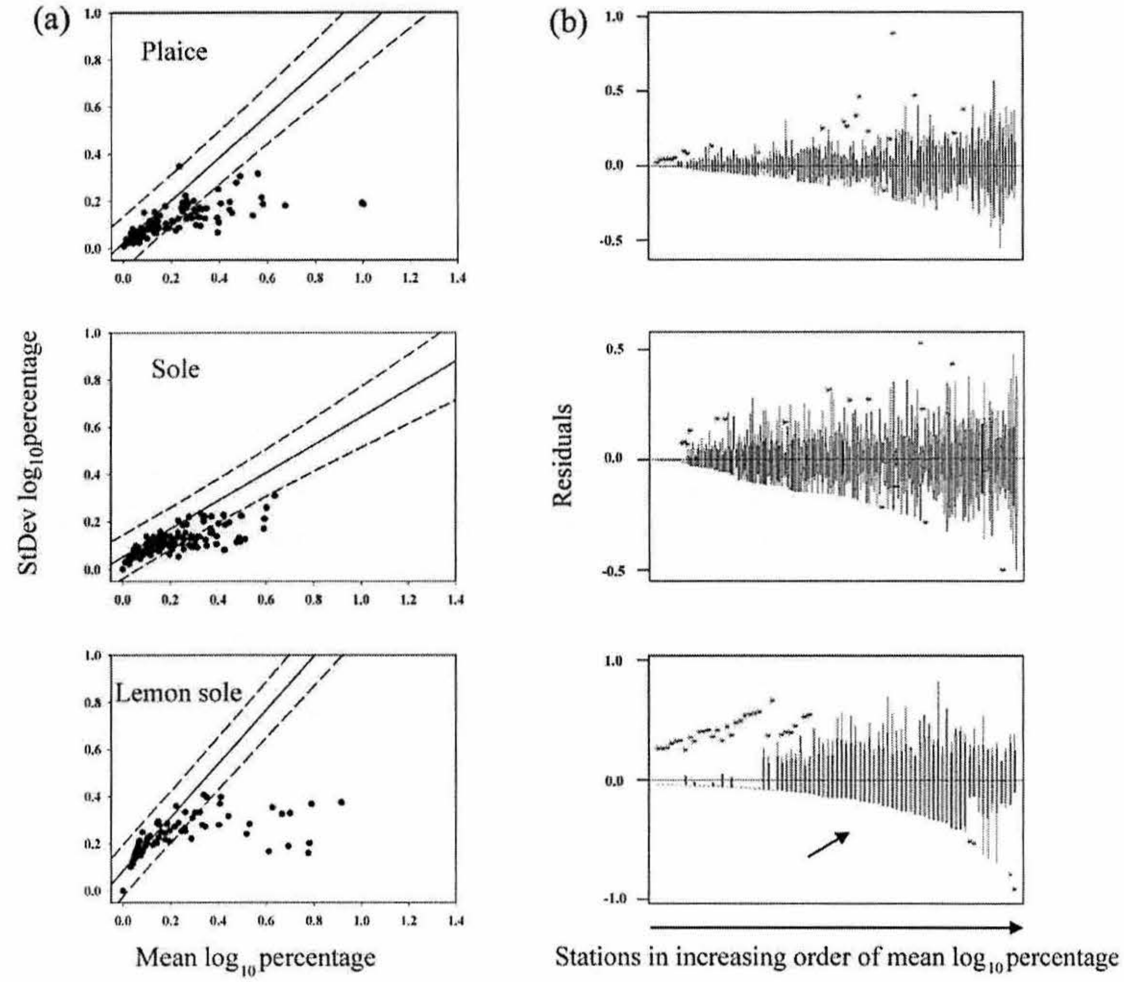

Figure 2.2 a.) Relationship between mean Log$_{10}$-percentage abundance and standard deviation for stations sampled over 10 years for plaice (*Pleuronectes Platessa*), sole (*Solea solea*) and lemon sole (*Microstomus kitt*). Regression line (solid black line) and 95% PI (dashed line) originate from the same data after generation of random scores

b.) Box plot of residuals of the mean Log$_{10}$-percentage abundance of each station over 10 years for plaice, sole and lemon sole. Quartiles (bars), range (whiskers) and outliers (asterisks)

2.4 Results

For all six fish species analysed, there were always stations below the lower 95% PI (Figs 2.1 a - 2.2 a). These stations were characterized by high means and low S.D., and were hence deemed to be stations that consistently had a relatively high abundance of fishes and met the SoI criteria.

Whiting and plaice had the highest percentage of stations with relatively high means and low standard deviations that lay below the lower 95% PI (Fig. 2.3) and hence met the criterion for SoI. Haddock and sole had an intermediate percentage of stations that qualified as EFH, while cod and lemon sole had the lowest percentage of sites that met EFH criteria (Fig. 2.3).

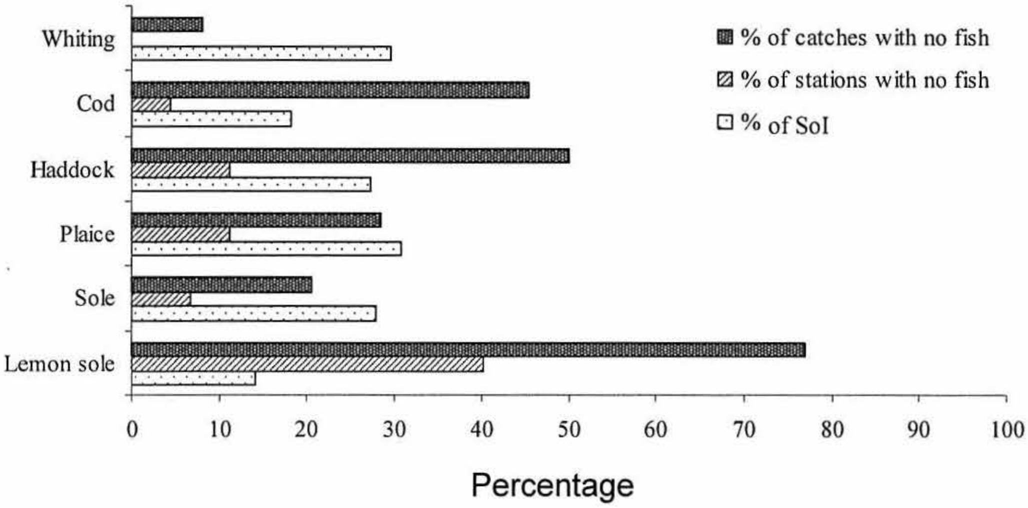

Figure 2.3 Percentage of catches and stations with no fish and percentage of stations that qualify as SoI for all six fish species analysed

2.4.1 Isopleth graphs

To illustrate the fish distribution over the sampling periods of respective surveys the mean Log_{10}-percentage abundance and standard deviations for cod and lemon sole were plotted as isopleth maps (Figs 2.4 and 2.5). The isopleths used in this paper were not meant to designate values to areas that have not been sampled but to make the existing data more accessible to the reader. Stations that were identified as SoI are highlighted as white dots. For both species it can be seen that the distribution of SoI follows a distinct spatial pattern and also that hotspots with high mean Log_{10}-perentages and low standard deviations could be identified for both species. In the Irish Sea, cod was found in consistently high abundances around Anglesey (North Wales): five out of eight potential EFHs were located in this region. The remaining potential sites were single stations situated off Burrow Head (Scotland), Ards Peninsula (Northern Ireland) and off Lambay Island (Republic of Ireland) (Fig. 2.4). In the English Channel, lemon sole aggregated consistently in three distinct regions (Fig. 2.5): five stations were identified in the Strait of Dover, two of which were positioned near the English coast off Dover and three around the French coast off Boulogne-sur-Mer. Another five stations were identified near Hastings and Brighton. The region with the highest density of stations (*n*=8) with relatively consistent lemon sole abundances was located off the south-western coastline of England between Start Point and Exmouth.

2.4.2 Residual plots

Even though the flatfish and gadoids were caught with different fishing gears and in different geographical areas, similar trends in the variability of the percentage mean abundance could be observed (Figs 2.1 b – 2.2 b). Haddock, cod and especially lemon sole showed very low variability at stations of high mean percentage abundance. For these species, the outliers and the range of the residuals were mainly negative, indicating that although most years had consistently high values, in certain years exceptionally few or no fish were caught. The variability of the mean percentage abundance was higher at intermediate stations and declined continuously with stations of decreasing mean percentage abundance. From the intermediate stations to the stations with low mean percentage abundance, the occurrence of negative residuals was constrained for haddock, cod and lemon sole which created the effect of a visual cut-off line in the graphs (Figs 2.1 b – 2.2 b). This cut-off line occurred very abruptly for haddock. Increasing numbers of zero catches occurred with decreasing mean percentage abundance, which lead to a mean close to zero and therefore constrained the occurrence of negative residuals. A similar effect was observed for whiting, plaice and sole but was restricted to stations of low mean percentage abundance. Catches of all of these species had a much higher variability at stations with a high and intermediate mean percentage abundances (Figs 2.1 b – 2.2 b) compared with haddock, cod and lemon sole (Figs 2.1 b – 2.2 b). Whiting and plaice were found at most stations with few or zero catches, which maintained the mean percentage abundances well above zero and hence did not affect the occurrence of negative residuals.

The percentage of zero catches of all stations throughout the sampling period was highest for lemon sole followed by haddock and cod (Fig. 2.3). This ranking corresponded well with the percentage of stations at which no fish were caught over the sampling period. Whiting had the lowest percentage of zero catches and number of stations with no fish followed by sole and plaice (Fig. 2.3).

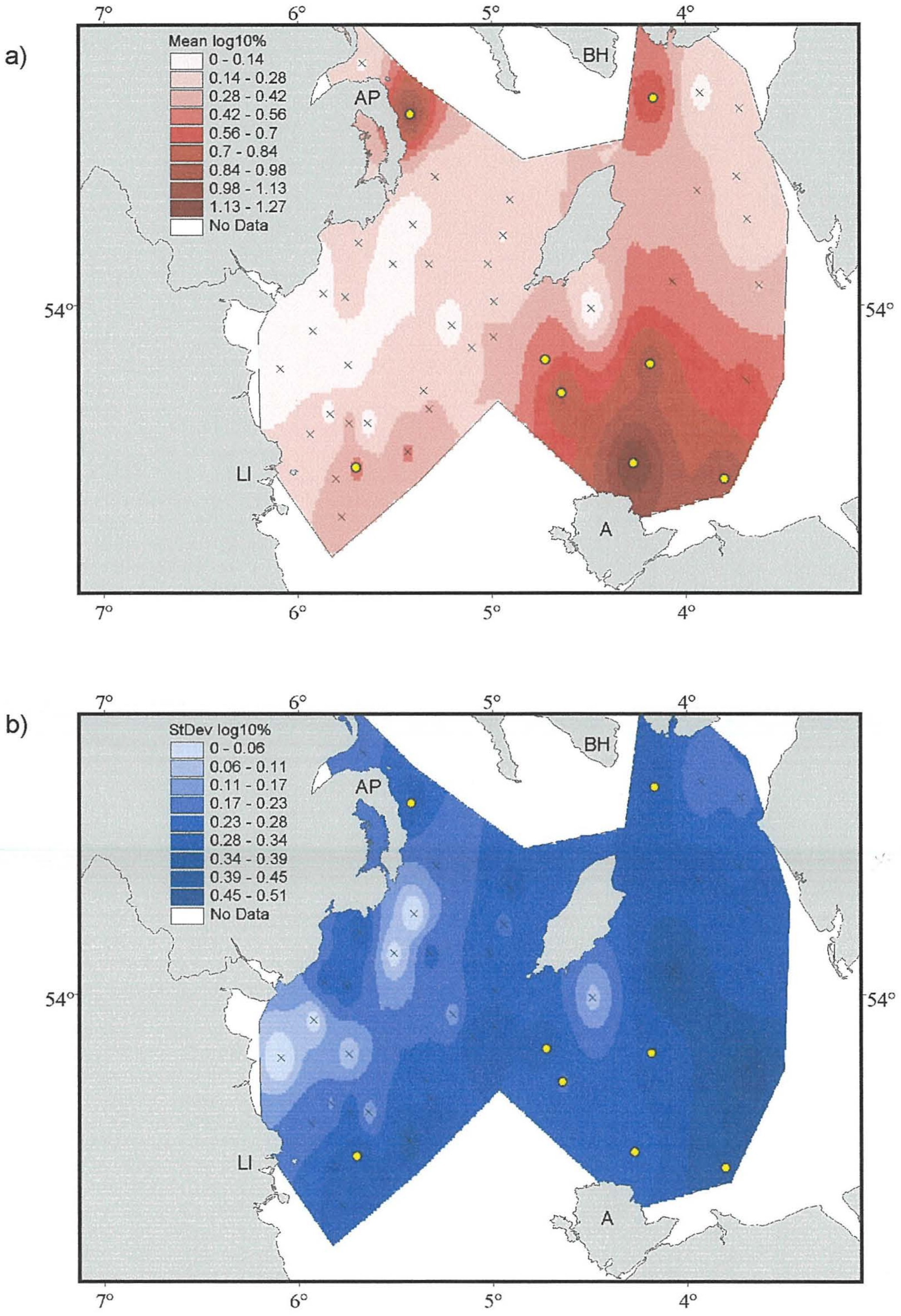

Figure 2.4. Isopleths graph of **a)** mean Log_{10}-percentage abundance and **b)** standard deviation over 10 years for cod (*Gadus morhua*) in the Irish Sea. Crosses represent sampling stations; full yellow circles mark stations which qualified as potential 'Essential Fish Habitat'. Abbreviations of locations thus A = Anglesey; BH = Burrow Head; AP = Ards Peninsula; LI = Lambay Island

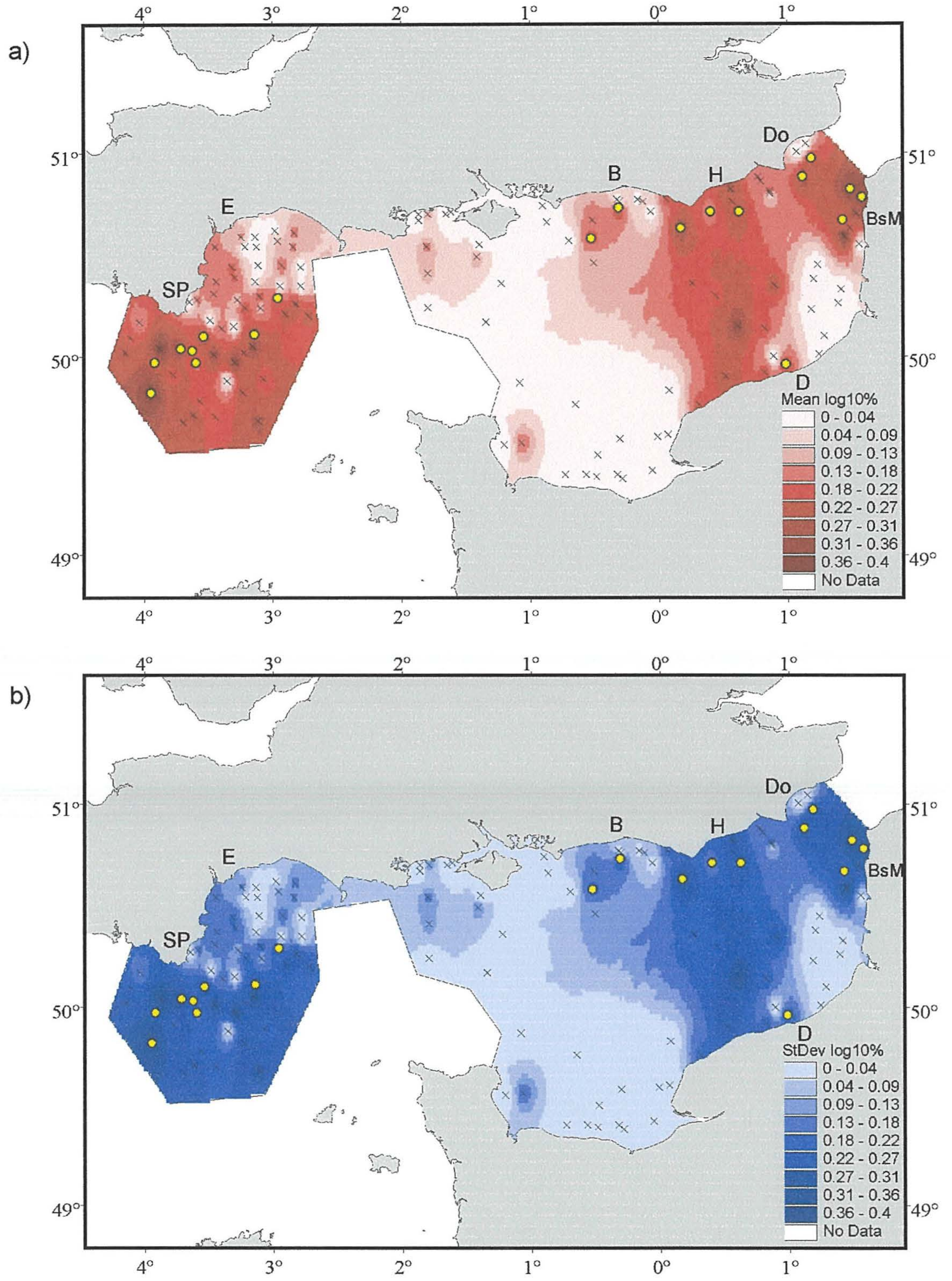

Figure 2.5 Isopleths graph of **a)** mean Log_{10}-percentage abundance and **b)** standard deviation over 9 years for lemon sole (*Microstomus kitt*) in the English Channel. Crosses represent sampling stations; full yellow circles mark stations which qualified as potential 'Essential Fish Habitat'. Abbreviations of locations thus D = Dover; BsM = Boulonge-sur-Mer; H = Hastings; B = Brighton; SP = Start Point; E = Exmouth

2.5. Discussion

The failure of conventional quota-based fisheries management to maintain European Union (EU) fish stocks at a sustainable level has required managers and scientists to consider alternative management systems. In particular, Marine Protected Areas (MPAs) have long been proposed as a tool for managing and enhancing fished populations (Jones, 2001). However to increase benefits from the reserve design MPAs should ideally incorporate essential habitats of the species that managers aim to conserve. The importance of the inclusion of highly suitable sites in MPAs becomes apparent in the context of predictions based on Ideal Free Distribution (IFD) theory (Fretwell and Lucas, 1970). The concept of habitat selection based on the IFD suggests that areas of high suitability attract high numbers of individuals until, due to competition for food or space, attractivity decreases for recently arriving individuals. These individuals may move into areas that were initially less suitable due to their lower quality or quantity of resources. The lower levels of competition experienced in these areas, however, may lead to a higher resource acquisition (Croy and Hughes, 1991). Therefore, heavily fished populations with low population densities are likely to become increasingly aggregated over high quality habitats. If an EFH was located outside a proposed MPA, density-dependant movements (relocation) from the reserve to areas of greater suitability could be expected. This scenario would permit the continuing exploitation of fish that should have been protected by the reserve and may ultimately lead to over-fishing. The management target to conserve the stock and to promote its productivity would not be met. Conversely, if the most suitable habitat was included within an MPA, then density-dependent relocation would cause the reserve to serve more effectively as a refuge especially when the abundance of the species in question becomes very low. Additionally the protection and conservation of better quality habitats can be crucial on the population level (Gross-Custard and Sutherland 1997). The loss or deterioration of such habitats e.g. due to fishing activities could after predictions from habitat selection theories lead to density dependant effects (e.g. decrease in the condition of fish or mortality) at much lower population levels.

The need to integrate EFHs in order to optimize the effectiveness of marine reserves has been addressed by many studies that deal with the theoretical approach to the design of MPAs (Nowlis and Roberts, 1999; Jennings, 2000; Rieser, 2000; Jones, 2001). However, the location of existing marine reserves has depended largely on social criteria and on opportunism rather than on scientific study (Roberts, 2000). Thus, one reason that the potential of MPAs has yet to be realized may be the lack of knowledge of marine ecosystem function (Jones, 2001) and on species ecology (Kramer and Chapman, 1999).

To manage commercial stocks successfully fisheries managers need detailed knowledge about the habitat requirements of the fish species and life stages that need to be conserved and where such habitats are located. Various authors have investigated habitat selection of demersal fish species such as juvenile cod, whiting and haddock (Lough *et al.*, 1989; Auster *et al.*, 1995; Gotceitas *et al.*, 1995; Tupper and Boutilier, 1995; Borg *et al.*, 1997; Gotceitas *et al.*, 1997; Gregory and Anderson, 1997; Swain *et al.*, 1998; Atkinson et al., submitted). A large number of these studies were undertaken in laboratories and may not be applicable to the field where a multitude of parameters may affect fish behaviour.

In this paper, we have demonstrated how fish abundance data from fixed stations collected over a decade alone provide valuable information on sites that were preferred by fish. A simple analytical framework was developed based on existing data from groundfish surveys that has enabled us to objectively detect possible EFHs for the adult stages of six fish species. The sites identified by using the objective methods outlined above only qualify as 'Sites of Interest' because they may not contain the most important habitat features for those species. The sampling grid of the surveys used was designed to monitor ground fish stocks and are thus restricted to locations that can only be sampled by bottom trawl gear. For example, hard grounds that may cause damage to the fishing gear are generally avoided. Thus, while the method presented herein provides a useful initial tool for the identification of potentially important fish habitats, it should be noted that some of the most suitable habitat may be missed out due to limitations of the underlying data.

The IFD theory predicts that fish with a density-dependant use of habitat are most abundant in areas of high suitability. Inversely, it could be expected that areas that are least suitable would harbour consistently low densities or no fish at all. According to IFD theory, fish abundance in habitats of intermediate suitability should vary in their abundances as fish spill-over from nearby 'optimal' habitats that are saturated with fish. Hence, it may be possible that the consistently high fish density at a particular station was caused by an overspill of individuals from an adjacent EFH. This station would then appear to harbour high abundances while not constituting an EFH. Stations identified in this study, however are probably valuable for directing subsequent research of the seabed characteristics.

In addition, the data has provided important ecological information about the habitat specificity of the different fish species studied. The abundance data collected over the survey periods for lemon sole, haddock and cod showed that most stations sampled over time contained a high number of zero catches, and that at some stations no fish were caught at all. A species that is very habitat-specific can be assumed to show a large number of zero catches as many areas of the seabed would be unsuitable. 'Habitat-generalists', by contrast, are likely to be found over a wider range of bottom types such that zero catches would only rarely be encountered. Whiting, plaice and sole had comparatively few stations with zero catches. Concurrently with Ellis *et al.* (2002), whiting and plaice were widely distributed over all stations sampled. The number of stations that qualified as 'Sites of Interest' generally corresponded with this trend of habitat specificity. While whiting and plaice had the highest number of SoI followed by haddock and sole, cod and lemon sole had the lowest number of SoI.

An examination of the dietary specialism of these species could shed more light on the habitat specificity implied by our analysis. Studies in European waters have shown that adult whiting are primarily piscivorous (Jones, 1954; Patterson, 1985; Gibson and Ezzi, 1987; Hislop *et al.*, 1991; Robb *et al.*, 1994; Seyhan and Grove, 1998). Predominant prey species included herring, sprat, small gadoids and sand eels (*Clupea harengus* L., *Sprattus sprattus* [L.], *Trisopterus esmarki* [Nielsson], *Trisopterus minutes* [L.], *Ammodytes* spp.) (Jones, 1954; Patterson, 1985; Gibson and Ezzi, 1987; Hislop *et al.*, 1991; Robb *et al.*, 1994; Seyhan and Grove, 1998). Collectively these prey species are highly mobile and occur over a variety of different seabed types, although some (e.g. sandeels) are very habitat-specific. The whiting's opportunistic feeding behaviour may permit them to feed on different prey as they move over different habitats. Therefore, whiting catches might vary considerably and trends that may point to a particular site as a potential EFH could be difficult to detect.

The diet of cod appears to be less confined to fish although larger size classes eat a greater proportion of fish (Kohler and Fitzgerald, 1969; Høines and Bergstad, 1999; Link and Garrison, 2002) and the species consumed are similar to those eaten by adult whiting. In addition to fish the diet includes large crustaceans like the Norway lobster *Nephrops norvegicus* [L.] (Symonds and Simpson, 1971) crabs, small crustaceans and polychaetes (Templeman, 1965; Mattson, 1990). Mattson (1990) concluded that most prey species consumed by cod were 'epibenthic' or 'hyperbenthic'. As these prey-organisms can be considered to be relatively site-specific, the same may apply to cod. The difference in the dietary preferences of cod and whiting suggests that despite an overlap in their diets cod could be associated more closely with specific benthic habitats as some of its preferred prey items have a more restricted distribution.

Haddock has been reported to feed predominantly on infaunal animals (Ritchie, 1937; Jones, 1954; Kohler and Fitzgerald, 1969; Mattson, 1992). Compared with the other two gadoid species haddock have a distinctly different feeding strategy. While adult cod and whiting feed predominantly on mobile fish or crustaceans, usually by catching one large prey item at a time, haddock feed by taking a mouthful of bottom material, sieving away the sediment particles and swallowing the remainder (Mattson, 1992). This feeding mode leads to a dietary composition of mainly small and slow-moving prey organisms (Mattson, 1992). Haddock also differs from the other two gadoids in that they use brittle stars (Ophiuroida) as an abrasive agent in their comparatively more rigid stomachs to assist digestion (Mattson, 1992). Consequently, haddock can be expected to be the most site-specific of all three gadoid species studied here, which was also reflected in our data by a high number of zero catches.

Similarly, our analysis for the three flatfish species, plaice, sole and lemon sole, suggested that plaice have the distribution pattern of a 'habitat-generalist' while lemon sole have a more habitat-specific distribution. With its wide mouth gape and large prominent eyes the plaice (Piet *et al.*, 1998) is well adapted to feed on a wide range of benthic invertebrates (Jones, 1952; Carter *et al.*, 1991; Piet *et al.*, 1998; Rijnsdorp and Vingerhoed, 2001). In contrast, lemon sole have a small mouth gape and eyes (Piet *et al.*, 1998) and feed primarily on sedentary polychaetes, many of which are associated with coarse substrata (Bennet, 1965). Plaice are capable of foraging in a variety of habitats if sufficient prey is available and hence are likely to be less habitat-specific. Lemon sole is, by virtue of its morphology, restricted to a small range of prey types that may only occur in sufficient quantities in specific habitats. Thus, the site-specificity of prey appears to be higher for lemon sole than for plaice, which concurs with its high number of zero catches at many stations in the English Channel. Sole were found over most stations and had a habitat-specificity similar to that of plaice. Although sole have a small mouth like the lemon sole, they have reduced eyes and rely on tactile and chemosensory cues to detect prey via the papillae located on the ventral area of the mouth. Thus while lemon sole is restricted to feed predominantly on small surficial fauna, sole are able to consume infaunal polychaetes and bivalves in any soft-sediment habitat in which they occur (Jones, 1952; Rogers, 1994a).

Dietary composition and the site-specificity of prey species could help to elucidate the habitat requirements of fish and are the subject of current research (Bergmann unpublished data). The distribution of prey organisms is, however, only one parameter as temperature, depth and other habitat parameters such as shelter from predators have also been shown to affect the distribution of fish (Kaiser *et al.*, 1999; Zheng *et al.*, 2001, Bergmann et al., submitted).

Valuable conclusions regarding site preference and habitat-specificity of fish species can be drawn from existing groundfish survey data. Site-specific species such as haddock and lemon sole may have benefits from the implementation of relatively small to medium scale MPAs compared to 'habitat-generalists' such as whiting and plaice which would require much large areas of protection with much greater management implications.

2.6 Supplementary information

The arrows within figure 2.1 (b) and 2.2 (b) signify the position of the cut-off lines described under 2.4.2 Residual plots page 22 line 2.

The ecological relevance of dividing stations into discrete site groups via the 95% predictive intervals (PI) was questioned during the viva. Therefore the rational behind the method used will be briefly discussed in more detail. The area within the 95% predictive intervals signifies the space in which 95% of all stations sampled would fall if fish were randomly distributed (Fig 2.1-2.2). Thus stations found below the 95% PI represent stations where fish occurred in higher consistent densities as anticipated under random conditions. There is no true ecological relevance for such a divide and the continuous nature of the variable used can be appreciated. The quantitative and rigorous divide made in this study is of a more practical nature to enable the researcher to divide stations into subunits to permit further examination. To gain insights into processes and to analyze these it might be advantageous to work with discrete groups which can be compared with more powerful statistical methods compared to correlative approaches which often have limitations of interpretation. The sites within this study were divided not arbitrary but under objectively defined criteria to compare site groups with each other. The method may however be developed further, such as to create a buffer zone around the PI in which sites close to the PI are not considered for a site group comparison. This would create more distinct cohorts of stations and may avoid bias of stations close to the 95% PI which ecologically could belong to either site group.

Chapter 3

The importance of sediment type and benthic habitat features for adult flatfish in the English Channel

3.1 Abstract

Flatfishes have been the subject of extensive scientific research but information on the specific habitat requirement of the adult life stages is largely patchy. Detailed knowledge of flatfish habitats however is a precondition for a more ecosystem orientated approach to fisheries management. Here the association between benthic habitat and the adult life stage of three flatfish species, plaice (*Pleuronectes platessa*), sole (*Solea solea*) and lemon sole (*Microstomus kitt*), was investigated in the English Channel. Data from groundfish surveys spanning a period of 9 years was used to identify three distinct site groups: sites where a species occurred in consistently high abundances, sites of variable or low abundance and sites at which none were caught. Following the supposition of habitat selection theories such as the ideal free distribution theory these three sites groups should represent a gradient in habitat suitability from highly suitable to less suitable and unsuitable respectively. Habitat parameters and features for the three site groups and species were described and analysed. In particular sediment type and the importance of structuring epifauna for adult flatfish was investigated. Overall plaice and sole showed very similar trends for abiotic environmental parameters such as depth, temperature, salinity and tidal currents while lemon sole was found over distinctly different habitats. Sediment associations differed between the three species with plaice predominantly occurring over sandy substrates with little mud and gravel content, while sole was found over a wider range of muddy to sandy substrates. Lemon sole was predominantly found over sand however containing a higher percentage of gravel than plaice. No clear association was found between flatfish abundances, structuring emergent epifauna and prey availability within this study. However opposing results between prey abundances assessed by grab samples and the nutritive state of plaice suggested that the sampling scale used might have been inappropriate to determine the true availability of prey in the environment. Plaice appeared to have sample prey organisms more effectively over the appropriate spatial scales and therefore the nutritive state of the fish might be a more reliable indicator for prey availability and thus habitat quality.

3.2 Introduction

Traditional fisheries management has tended to focus on the population biology of single species without consideration of the wider ecological requirements of the target species (Link, 2002). However, there is a growing acceptance that an ecosystem oriented approach to fisheries management is required to take into consideration not only environmental determinants of population biology, but also the wider ecological effects of fishing activities (Jennings and Kaiser, 1998; Kaiser et al. 2002). In particular, bottom fishing is one of the most important agents of seabed habitat change, altering the structure and function of habitats that fulfil an important role in the life-history of fish most closely associated with these habitats. (Auster and Langton, 1999; Kaiser et al. 2002; Ryer et al. 2004). Flatfishes are due to their morphology uniquely adapted for a benthic life style (Gibson, 1994) such that alterations to these habitats may therefore affect their suitability and hence flatfish survivorship and distribution (Gibson, 1994; McConnaughey and Smith, 2000). At present, a sound understanding of the biotic and abiotic factors that constitute critical habitats for adult flatfishes is lacking, but is an essential component to locate and quantify such areas for appropriate ecosystem based management.

In contrast to adult flatfish, the habitat requirements of juvenile flatfish have been the focus of a number of laboratory and field-based studies (Eastwood et al. 2003; Gibson, 1994; Gibson and Robb, 2000; Le Pape et al. 2003a; Le Pape et al. 2003b; Rogers, 1992; Stoner and Titgen, 2003). Sediment preferences of juvenile flatfish for burial, as a means of predator avoidance have been demonstrated for several species (Gibson and Robb, 1992; 2000; Stoner and Abookire, 2002). Sediment type has been assumed to be less important for the burial of adult flatfish as animals are physically capable of burying in a wider range of sediment types (Gibson and Robb, 1992) and cryptic predator avoidance may become less crucial as the number of potential predators decreases with increasing body size (Gibson and Robb, 1992; 2000; Stoner and Abookire, 2002). However, burial capabilities only give information about the possible sediment range that a species is able to utilize rather than to reveal which sediment types (habitats) are in fact used or preferred by a species (Gibson and Robb, 2000). Further, studies of sediment grain size preference do not take into account the influence of the associated structuring biota as determinants of flatfish habitat quality. Emergent epibenthic structures such as sponges, bryozoans and hydroids have been shown to fulfil an important function in the evasion of predator detection in juvenile flatfish (Ryer et al. 2004; Stoner and Titgen, 2003). Benthic habitats with emergent epifauna harbour a higher abundance and diversity of epibenthic prey types and there is a direct relationship between habitat complexity and prey diversity (Bradshaw et al. 2003; Kaiser et al. 1999). This increased abundance of epibenthic invertebrates could consequently represent an important food source for certain flatfish species, particularly those that are visual predators such as plaice *Pleuronectes platessa* and dab *Limanda limanda*. Flatfish species that are primarily visual predators could utilize emergent structures as indirect cues to locate desired prey-types if the habitat structure and the preferred prey item are closely linked or occur within the same environmental boundaries. Such cues are used by many animals (Hill et al. 2002; Hughes and Blight, 2000; Kristan, 2003) to increase foraging efficiency (Warburton, 2003).

Most extensive studies on fish assemblages are based on data from national fisheries surveys and often provide little information on the characteristics of the different benthic habitats in which flatfish species occur e.g. (Albert et al. 1998; Ellis et al. 2000; Rogers et al. 1998; Smale et al. 1993). Most fisheries surveys do not collect extensive habitat information, (but see Freeman and Rogers, 2003) and thus studies that link abundances of fish species to specific benthic habitat features, other than sediment type have rarely been attempted (but see Kaiser et al. 1999, McConnaughey and Smith, 2000). However, groundfish surveys are conducted on a regular basis covering large temporal and spatial scales. Such broad data on fish distributions offers a potentially valuable opportunity to investigate the relationship between fish abundances and the benthic habitat.

Spatial variability in the distribution of a fish species may reflect differences in habitat quality that comprises a combination of different physical and biological parameters such as depth, temperature prey availability or the presence of structures to hide from predators. Habitat selection theories such as the Ideal Free Distribution theory IFD (Fretwell and Lucas, 1970) or MacCall's basin theory (McCall, 1990) suggest that individuals that are free to move between habitats will select areas of high resource quality over areas of lower quality. At low population densities, individuals will occupy the most suitable habitats, while individuals will occupy less suitable habitats once densities increase and density-dependent effects emerge (Rogers, 1994; Simpson and Walsh, 2004). Decreases in overall abundance at a later time will cause populations to contract in space and retreat to the most suitable habitat. Suitable benthic habitats should as a consequence show consistent relative abundances through time if important habitat parameters are strongly linked with location. Thus fish abundance data from groundfish surveys alone could help to locate areas that would merit further research into their habitat characteristics.

Practical problems related to the sampling design for bottom dwelling fish and overall theoretical difficulties need however to be considered when consulting such datasets. The sampling grid of groundfish surveys have been designed primarily to monitor fish stocks at a large spatial scale and are restricted to locations which will allow sampling without risk of loss or damage to the sampling gear. Thus for example hard substrata may consciously be avoided while sampling. Certain habitat types may therefore be missing from the data altogether or may have received less frequent sampling that creates a bias in the overall results and their interpretation. Linking fish densities to habitat parameters to infer habitat preferences entails another major problem as sites of high fish densitiy may not necessarily be indicative of high habitat quality or the preferred habitat, as other factors may also lead to aggregation in less suitable habitats e.g. intra- and inter-specific competition may displace certain life stages or fish species from otherwise suitable areas (Kaiser *et al.* 1999). Thus the non-random association of a species with a particular habitat feature does not necessarily infer preference (Underwood *et al.* 2004) as other factors may also be responsible for the observed pattern. However if the constraints of such data are considered in the interpretation of the results, groundfish survey data may still contain valuable information about the habitat association of fish. Thus within the present study we attempted to describe the association between the abundances of three flatfish species, plaice (*Pleuronectes platessa* L.), sole (*Solea solea* [L.]) and lemon sole (*Microstomus kitt* [Walbaum]) with various habitat parameters. Abundance data of ground fish surveys conducted in the English Channel were used to identify sites in which consistently high and lower densities of plaice, sole and lemon sole occurred over a 9 year period (Hinz *et al.* 2003). For these sites, we assessed the relationship between flatfish distribution and the benthic habitat to address the following questions: 1) which sediment types and selected environmental parameters consistently harbour high abundances of adult flatfish? 2) are biotic benthic habitat structures and prey availability associated with high flatfish abundances 3) are there any differences in habitat characteristics occupied by the three flatfish species studied?

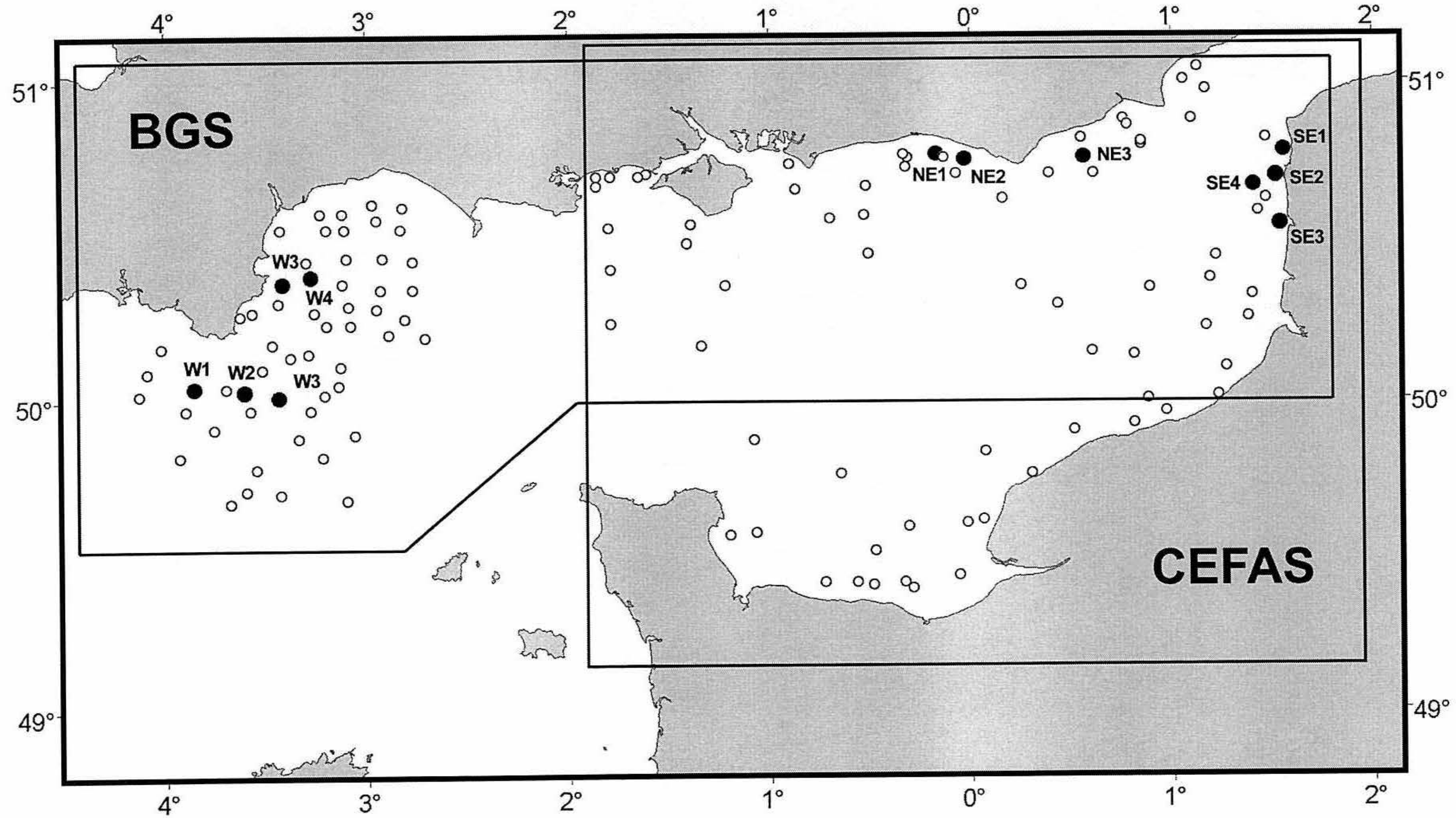

Figure 3.1. Map of the English Channel showing groundfish survey stations included in the analysis (black and white circles). Boxes mark the spatial coverage of the environmental datasets used for analysis (BGS and CEFAS). Black circles with site names designate survey stations revisited in 2002

3.3 Methods

3.3.1 Delineation of site groups

Fish abundance data from groundfish surveys (Centre for Environment, Fisheries and Aquaculture Science, CEFAS) of plaice, sole and lemon sole from fixed stations in the English Channel were used for analysis. Data spanned a period from 1990 to 1998. As adult fish were the focus of this study only fish over the minimum landing size (MLS: plaice > 26 cm; sole > 23 cm and lemon sole > 24 cm) were considered. Fish collected during the autumn groundfish survey cruises were used so as to avoid sampling spawning and nursery aggregations. Overall, 133 stations were included in the analysis (Fig. 3.1). Stations were divided into three distinct site groups for each species according to their trends in abundances through time: (1) sites where flatfish occurred in consistently high abundances (2) sites of variable or low abundance and (3) sites at which no fish were caught over the survey period. To objectively appoint each station to the respective site groups a delineation method described by Hinz et al. (2003) was used. For each station the percentage of fish relative to all other stations was determined for all years. The percentage data (+1) was then $\log_{10}$-transformed to achieve a normal distribution. From the transformed relative abundances the mean and the standard deviation (SD) of each station over the whole sampling period was calculated and plotted to produce a scatter plot (Fig. 2). For the creation of delineation lines this process was repeated using the same dataset but randomizing it first. Within each year, every station was assigned an abundance allocated at random from within the range of the data of that year. From the resulting random data set the mean $\log_{10}$-percentage abundance and standard deviation was calculated. The relationship between random means and SD was best described by a linear model of which the 95% Predictive Intervals (PI) were used as delineation lines in the scatter plot of the original data to divide stations into the three site groups (Fig. 3.2). Stations below the lower 95% PI thus represented stations where fish were consistently caught in relatively high abundances. These stations will be refereed to as consistent-high abundance sites (CHS). In contrast stations found within the 95% PI boundaries corresponded to sites at which fish were caught in variable or low numbers and thus are referred to as sites of variable abundances (VLS). Stations at which no fish were caught over the sampling period characterized the third site group referred to as sites of zero catches (0-C).

3.3.2 British Geological Survey (BGS) sediment data

Sediment characteristics of the stations included in our analysis were extracted from digital sediment maps (British Geological Survey; BGS Licence 2003/133) using a GIS software package (ArcView 3.2). These data covered 110 of the 133 sampling stations included in the analysis. The 23 remaining stations were located along the coast of Normandy (France) and were not included in the BGS data (Fig. 1). Sediment classifications used in the digital map created in ArcView were based on the classifications of Folk (1954). The data extracted from the BGS sediment maps for each station does not necessarily represent the true sediment nature of that particular site. The large spatial coverage of the BGS charts is achieved by interpolation between sampling points, thus many areas of the chart may not describe the true sediment composition at the survey stations. However, given the large number of data points in this dataset we believe that the overall estimates were adequate for the purpose of our analyses. The distribution of the three site groups over the different sediment types was compared for each flatfish species by a Chi-square test of association. The test assumes that sites within each sediment category should be equally distributed among fish abundance categories (CHS, VLS and 0-C). Significant Chi-square results show that at least one abundance category differs significantly from this assumption. Some of the nine recorded sediment classes had very few observations (Fig. 3.3) and therefore the data needed to be pooled into three new sediment categories for analysis: muddy sand (muddy sand, slightly gravely muddy sand and gravely muddy sand) sand (gravely sand, slightly gravely sand, sand) and gravely and hard substrata (rock and sand, gravel, sandy gravel and muddy sandy gravel). Due to the pooling of sediment categories, detailed information about the association of sediment type and flatfishes was partially lost and therefore visual examination of the original data was also undertaken to highlight specific trends in the data.

3.3.3 CEFAS abiotic habitat parameters

The Centre for Environment, Fisheries and Aquaculture Science (CEFAS) maintain a dataset of benthic habitat parameters that cover the eastern part of the English Channel (Fig. 3.1). These data encompass a total of 70 survey stations including the 23 stations along the coast of Normandy that were not covered by the BGS maps. The environmental data included: QTC VIEW^{TM} class as a descriptor of seabed characteristics (a measure that encompasses sediment type and seabed morphology), water depth (m), near bed tidal velocity (ms^{-1}), sea surface temperature (°C), salinity (psu) and weight of rocks and shells ($kg\ h^{-1}$) caught as incidental catch with fish samples [for a more detailed description of data collected and QTC classes see (Freeman and Rogers, 2003)]. These parameters were all recorded during the CEFAS groundfish survey between August-September 1999. To assess the environmental characteristics of the different site groups and respective species the environmental data were analysed by Principal Component Analysis (PCA). PCA is a multivariate ordination technique that allows mapping of stations in an ordination plot (Clarke and Warwick, 2001). The distance between stations represented in such a plot reflects the relative similarities in the composition of environmental parameters between each pair of stations. Stations that are plotted close to each other have greater similarity in terms of their environmental parameters than those that are plotted further apart. The PCA has two further important outputs, the 'eigenvalues' and the 'loading' of the components. While the 'eigenvalues' provide a relative measure of how much of the variation between the stations is explained by each principal component, the 'loading' indicates which environmental parameter contributes most strongly to each component. Prior to undertaking the PCA analysis, the weight of shells and rocks captured in a 4 m beam trawl were $\log_{10}$-transformed to ensure normality. Tests of significance for site group differences for each fish species were preformed using the ANOSIM randomisation test (Clarke and Green, 1988) on the normalized euclidian distance matrix. PCA plots were overlaid with the mean percentage abundance of flatfishes caught over 9 years to aid interpretation.

To demonstrate how site groups were characterized by each environmental parameter the data were plotted for each species in a series of box plots. The means of each environmental parameters and site groups were compared to means generated by a bootstrap procedure (Efron and Tibshirani, 1986) using S-Plus statistical software as the data did not meet assumptions for parametric analyses. Bootstrapping is a resampling technique in which new samples are repeatedly drawn at random (here1000 times) from the underlying dataset. Each randomised sample had the same size as the observed data. The distribution of means of each bootstrap run can be used to estimate the bootstrap mean (mean most likely to occur as a chance event) and its corresponding confidence intervals. Significant differences between observed and bootstrapped mean imply that it is highly unlikely for the observed mean to have occurred as a chance event (< 5%) and thus strengthens the argument that the observed trend is genuine. As QTC classification values constitute categorical data they were summarized for each station group and fish species in a separate table. The data was analysed using a Chi-square test of association. Prior to analysis the ten QTC classes (Table 3.1) were pooled into three main sediment categories to enable statistical analysis: mud and muddy sands (OTC classes 1 and 2), sand (QTC classes 3- 6) and gravely substrata (QTC classes 7-10).

3.3.4 Site-specific study – the role of emergent epifauna and prey availability

To investigate the association of adult flatfish densities with structuring emergent epifauna and prey availability on the same temporal scale a subset of sites drawn from the CEFAS groundfish survey were selected for a more detailed site-specific investigation (Fig 3.1). The intensive sampling regime adopted at each site only permitted sampling of twelve sites in total. This made it impossible to choose a sufficient number of sites for all three site groups (HCS, VLS and 0-C) for each of the three flatfish species. Therefore sites were chosen the basis on those that displayed a gradient in long-term mean percentage abundance based on the nine year CEFAS survey data, allowing the resulting data to be analysed in a correlative approach.

Sampling was undertaken from the RV Prince Madog in August 2002. Four tows each of 20 minutes duration were made during daylight at each site using a 4-m beam trawl fitted with a chain-matrix and an 82 mm diamond mesh cod-end with a 40 mm square meshed liner towed at a speed of 4 knots. The catches were sorted aboard and organisms caught were identified, counted and wet-weighed. For colonial epifaunal animals such as hydroids and bryozoans only the wet-weight (g) was recorded. Individual plaice, sole and lemon sole were measured to the nearest cm below. Prior to analysis, the data were standardized to a tow length of 2 km. To evaluate if stations followed the same trends in flatfish abundances predicted by the abundances of the long-term CEFAS dataset, the mean $\log_{10}$ abundance of fish caught above MLS during the Prince Madog cruise were correlated with the mean $\log_{10}$-percentage abundance over 9 years using Pearson's correlation test.

The ecological importance of emergent epifauna to adult flatfish was studied by correlating the pooled mean $\log_{10}$ biomass of emergent epifauna with the mean $\log_{10}$ abundances of each of the three flatfish species (Pearson correlation). Emergent epifauna included organisms from following taxonomic groups: Anthozoa, Ascidiacea, Bryozoa, Hydrozoa, and Porifera. As many emergent epibenthic species were colonial organisms, for which abundance estimates are difficult to attain, the wet-weight (g) of organisms was used as a measure of biomass.

To assess the prey availability in the environment the prey-spectra of each flatfish species were determined and linked to macrofauna abundance data obtained from grab samples. Four Day-grab samples 0.1 m^2 were collected during this survey at each site and sieved over a 1 mm mesh. Samples were preserved in 4% buffered formalin solution and later identified to the highest possible taxonomic resolution. Prey-spectra were determined by analysing the stomach contents of flatfish caught at each site. Stomachs complete with contents were transferred into buckets of 8% buffered formalin in individually labelled micro-mesh bags. Additional plaice were obtained during a groundfish survey in August 2002 on RV Corystes (using a 4-m beam trawl). These fish were frozen prior to removal of their stomach contents. After washing in freshwater and dry blotting the abundance and wet-weight of prey were recorded to the highest possible taxonomic resolution. The frequency of occurrence of benthic species ingested was calculated for each of the three flatfish species. To calculate prey availability in the environment only prey which had a frequency of occurrence over 5% were used thus excluding animals which could have been ingested by accident, were generally inaccessible or less desirable. The sum of all prey items found in grab samples thus represented a measure of prey abundance in the environment. The species used to calculate prey abundance form prey spectra were summarized in Table 3.2. Prey $\log_{10}$-abundance m^2 in the environment was correlated with the mean $\log_{10}$-abundance of flatfishes (Pearson correlation). Other parameters from the stomachs analysis such as the mean abundance and biomass (wet weight in g) of prey items per fish with stomach contents, the percentage of empty stomachs and condition factors (Fulton K) were calculated for each site, however due to low numbers of stomachs available at most sites for sole and lemon sole these parameters were only formally analysed for plaice. The condition factor was calculated as follows:

$$K=100(W/L^3)$$

where W is the wet-weight (g) and L is the total length (cm).

Log_{10} plaice abundances were correlated with the mean $\log_{10}$ abundance and biomass (wet weight in g) of prey items per fish with stomach contents (Pearson correlation). The percentage of empty stomachs and the mean condition was correlated with plaice abundance using Spearman rank correlation as the data could not be normalized.

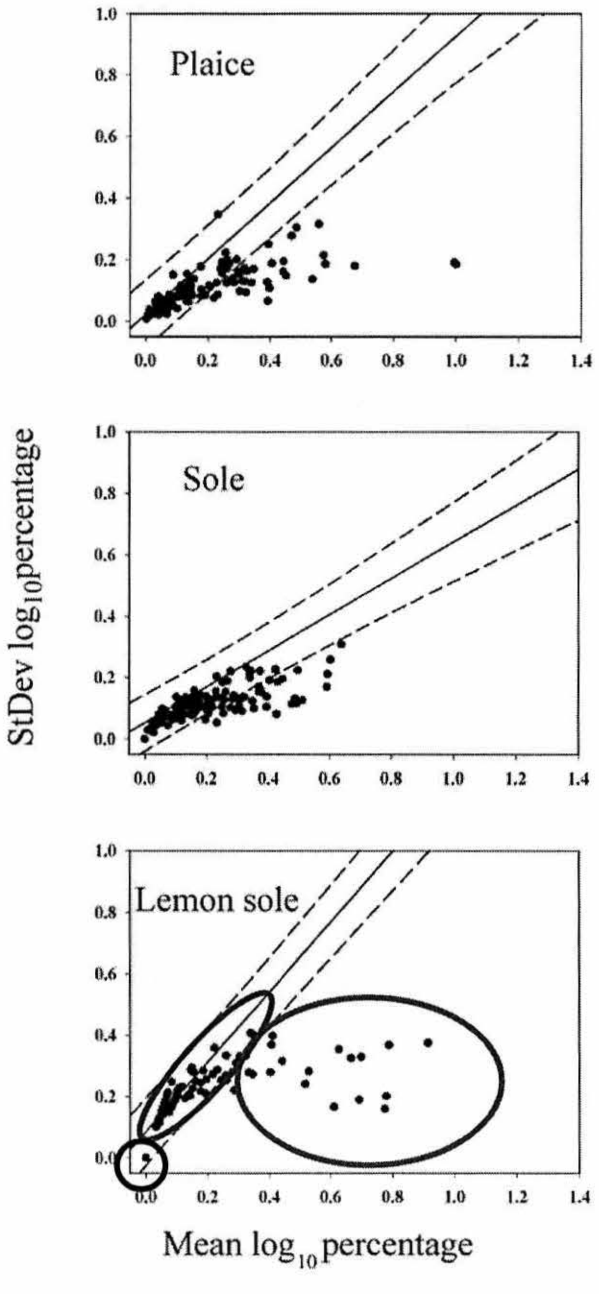

Figure 3.2. Relationship between mean Log_{10}-percentage and S.D. for stations sampled over 9 years for plaice, sole and lemon sole. Regression lines and 95% PI originate from the same data after generation of random scores. Stations below the lower 95% PI represent sites of consistent high fish abundance (CHS = red circle). Sites within the 95% PI represent sites of variable and low fish abundances (VLS = blue circle) or sites at which zero fish where caught over nine years (C-0 = black circle).

QTC Classes (substratum description)		(1) Mud	(2) Slightly muddy sand with occasional broken shell	(3) Sand with no sand waves	(4) Sand with sand waves and shell fragments	(5) Fine shelly sand with small stones and shell fragments	(6) Shelly sand	(7) Shelly sand gravel with large stones	(8) Gravelly sand	(9) Gravelly sand with large rocks	(10) Gravelly sand with cobbles and boulders
Plaice	CHS	2	6	5	3	6	4	4		1	
	VLS	5	1	1	2	4	4	3	5	4	1
	0-C	1							2	4	2
Sole	CHS	3	4	1	3	6	2	2	1	1	
	VLS	5	3	5	2	4	6	5	5	6	
	0-C								1	2	3
Lemon sole	CHS			1		3	4		1		
	VLS	4	1	3	1	2	2	4	2	5	1
	0-C	4	6	1	4	5	2	3	4	4	2

Table 3.1. Number of stations observed for each QTC class, site group and flatfish species (CEFAS survey, eastern English Channel). Consistent high abundance sites = CHS, variable and low abundance sites VLS and 0-catch sites = 0-C. Numbers in brackets signifiy QTC classes

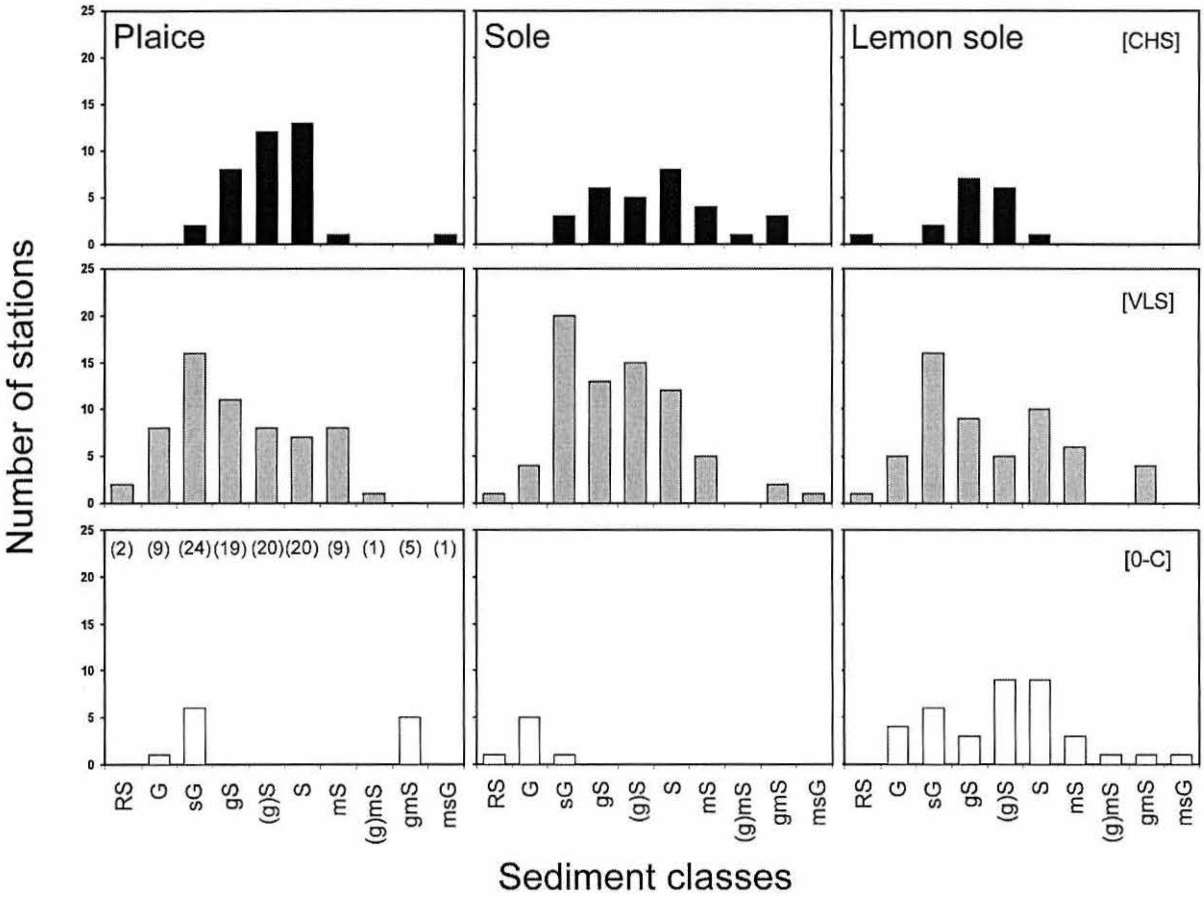

Figure 3.3 Sediment classes recorded for the three site groups: High consistent abundance sites (black columns = CHS), variable abundance sites (grey columns = VLS) and 0-Catch sites (white columns = 0-C). Numbers in brackets signifiy the total number of observations (n) available for each sediment class. Sediment classes: msG = muddy sandy gravel, gmS = gravelly muddy sand, (g)mS = slightly gravelly muddy sand, mS = muddy sand, S = sand, (g)S = slightly gravelly sand, gS = gravelly sand, sG = sandy gravel, G = gravel, RS = rock and sand

Table 3.2 Frequency of occurrence of prey species found in flatfish stomachs of all sites.

Frequency of occurrence (%)	**Plaice**	**Sole**	**Lemon sole**
Number of full stomachs analysed	166	18	5
Anthozoa			
Actinaria			20
Polychaeta			
Chaetopterus spp.	7	12	
Harmothoe spp.	6	6	
Lagis koreni	14	12	
Lanice conchilega	**34**	**29**	40
Lumbrineris spp.	6		
Nephtys spp.	25		
Nereis spp.		6	
Notomastus spp.	6	6	
Pseudopolydora spp.			20
Sabellaria spinulosa			**60**
Sigalion spp.	10		
Sthenelais spp.	6	6	
Crustacea			
Diastylis spp.	7		
Gastrosaccus spp.	15		
Phtisica marina		6	
Mollusca			
Abludomelita obtusata		6	20
Abra spp.	10		
Ensis spp.	19	6	
Venerupis senegalensis	16		
Echinodermata			
Amphiura spp.		6	
Echinocardium cordatum	17		
Echinocyamus pusillus	5		
Ophiura spp.	9		

3.4 Results

3.4.1 Sediment characteristics (BGS and CEFAS Data)

For the relationship of fish abundances with BGS data only plaice had significant Chi-square test result (χ^2 = 37.83, df = 4, p = 0.0001, Fig 3.4). The test was not significant for lemon sole (χ^2=8.96, df = 4, p = 0.062, Fig 3.4) and for sole the result proved invalid due to expected counts below one (Fig 3.4). The high consistent abundance sites for plaice had a strong positive association with sand habitats (χ^2 = 8.71) while sites of variable abundances showed only a weak positive association with gravely and hard substrata (χ^2 = 1.85). Sites at which no plaice were caught were most positively associated with muddy sands (χ^2 = 6.91).

For the CEFAS sediment data the Chi-square test for all three species was significant (df = 4: plaice χ^2 = 17.44, p=0.002; sole χ^2 = 13.77, p = 0.008; lemon sole χ^2 = 11.10, p = 0.025; Fig 3.4). High consistency sites of plaice abundance were negatively associated with gravely and hard substrata (χ^2 = 3.82). The variable abundance stations had a weak contribution to the overall Chi-square, the highest value was found for gravel with a slightly positive association (χ^2 = 0.39). The sites with no catches of plaice had a strong positive association with gravely substrata (χ^2 = 6.26). For sole, the consistent high abundance sites were again negatively associated with gravely substrata (χ^2 = 2.22) while variable abundance sites had a weak negative association with mud and muddy sands (χ^2 = 0.09). For the sites with no catches of sole a strong positive association was found for gravely and hard substrata (χ^2 = 6.18). Lemon sole sites of consistent high abundances were positively associated with sand (χ^2 = 5.17) and sites of variable abundances had a positive association with gravely and hard substrata (χ^2 = 0.7). Sites with no catches of lemon sole were positively associated with mud and muddy sands (χ^2 = 0.75).

The discrepancies in the results observed in the overall Chi-square test from the two datasets most likely derive from the underlying differences in the derivation of the datasets. The BGS data are largely based on interpolations of sediment data over large spatial areas while the QTC data was recorded directly over the CEFAS survey stations. It also needs to be recognized that both surveys covered slightly different areas and differed in their sedimentological classification. However visual examination of both unpooled and pooled datasets (Figs. 3.3 - 3.4 and Table 2) revealed that the general trends were in agreement with each other. Due to the pooling of sediment categories for the Chi-square analysis the more detailed information of the two datasets was obscured. Results of the Chi-square test showed that plaice and lemon sole occurred in high consistent abundances over sandy sediment types. Visual examination of the sandy sediment categories in both unpooled datasets however revealed that differences between the two species existed. While sites at which plaice occurred with high consistency were all characterized by a high proportion of sand, lemon sole sites had a higher gravel content (Figs. 3.3 – 3.4 and Table 3.1).

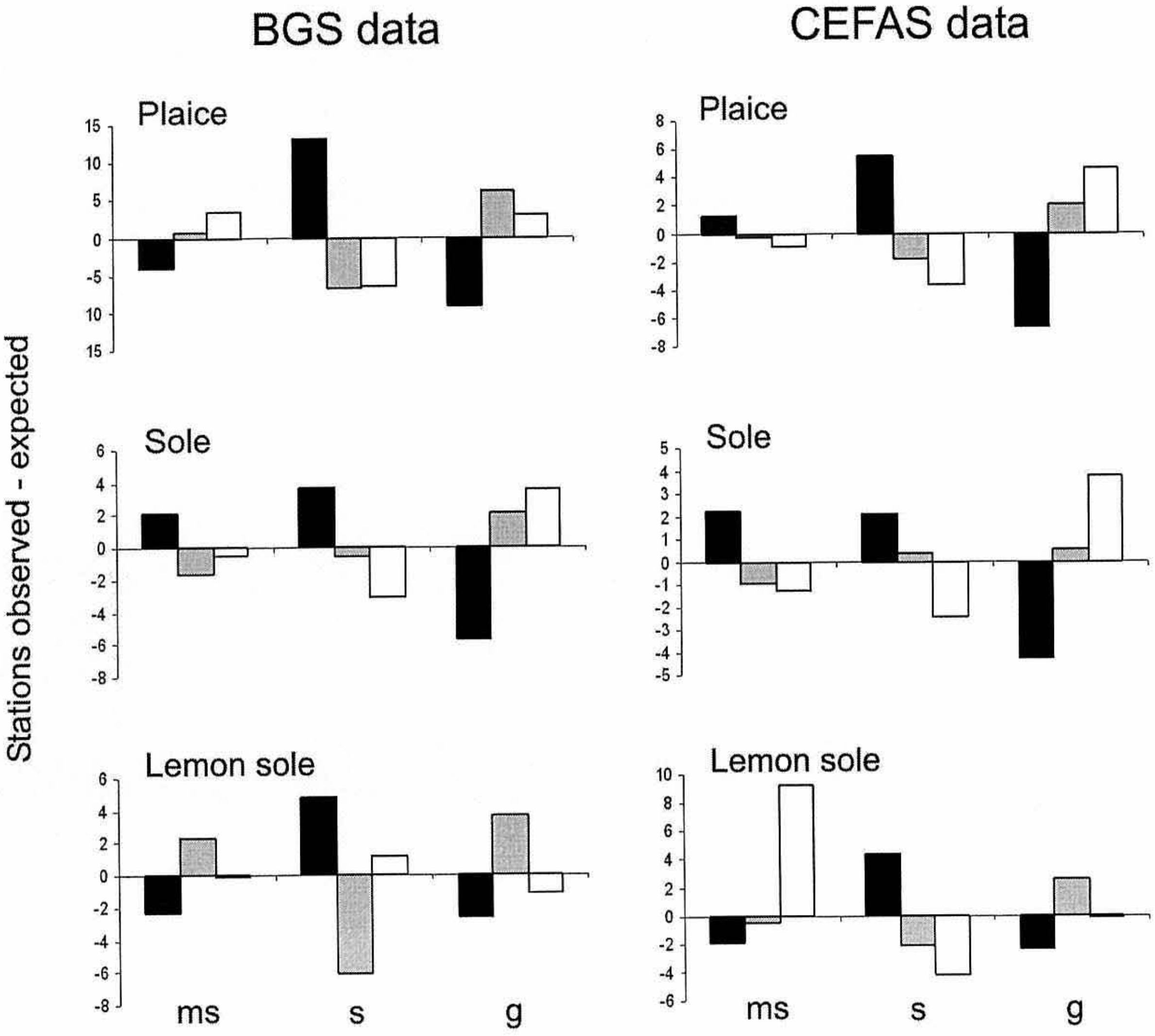

Figure 3.4. Observed – expected number stations from the chi-square test of the three site groups [high consistent abundance sites (black columns), variable and low abundance sites (grey columns) and 0-Catch sites (white columns)] for the pooled sediment classes (BGS: ms = muddy sand, s = sand, g = gravelly and hard substrates; CEFAS: ms = mud and muddy sand; s = sand, g= gravelly and hard substrates)

3.4.2 PCA analysis

The eigenvectors PC1 and PC2 described 60.2% of the observed variability. PC1 was affected to a great extent by the loading of depth ($r = 0.506$) whereas PC2 was chiefly affected by the loading of salinity ($r = 0.598$) and the weight of shells ($r = -0.593$). The other parameters had a smaller effect on the eigenvectors with loadings below 0.5.

From the biplots of all three species, it became apparent that environmental parameters of consistently high abundance sites and those with low or varying abundance showed considerable overlap (Fig 3.5). This was confirmed for plaice and sole by the ANOSIM test which showed that no significant differences could be detected between these site groups. Hence high consistent abundance sites were not characterised by distinctively different combinations of environmental parameters, compared to sites with varying abundances of these species. However there were significant differences, for both species, between high consistency versus sites where no catches were made (plaice: $R = 0.54$, $p < 0.05$; sole: $R = 0.53$, $p < 0.05$) and variable sites versus sites were no catches were made (plaice: $R = 0.23$, $p < 0.05$; sole: $R = 0.5$, $p < 0.05$). This was also reflected in the respective biplots of plaice and sole, sites at which no fish were caught clustered more closely on the right side of the biplots. These sites generally had higher values of PC1 and lower values of PC2 than the area of the consistently high abundance sites. Overall the biplots of plaice and sole showed many similarities (Fig. 3.5).

Sites of highly consistent lemon sole abundance grouped relatively close together indicating a high degree of similarity between environmental parameters (Fig. 3.5). By contrast to plaice and sole consistent high abundance sites were located more towards the right with generally higher PC1 values. Most of the sites at which no catches occurred were positioned in the area of the ordination plot that coincided with sites of highly consistent densities for plaice and sole. However differences between the three site groups of lemon sole were not significant.

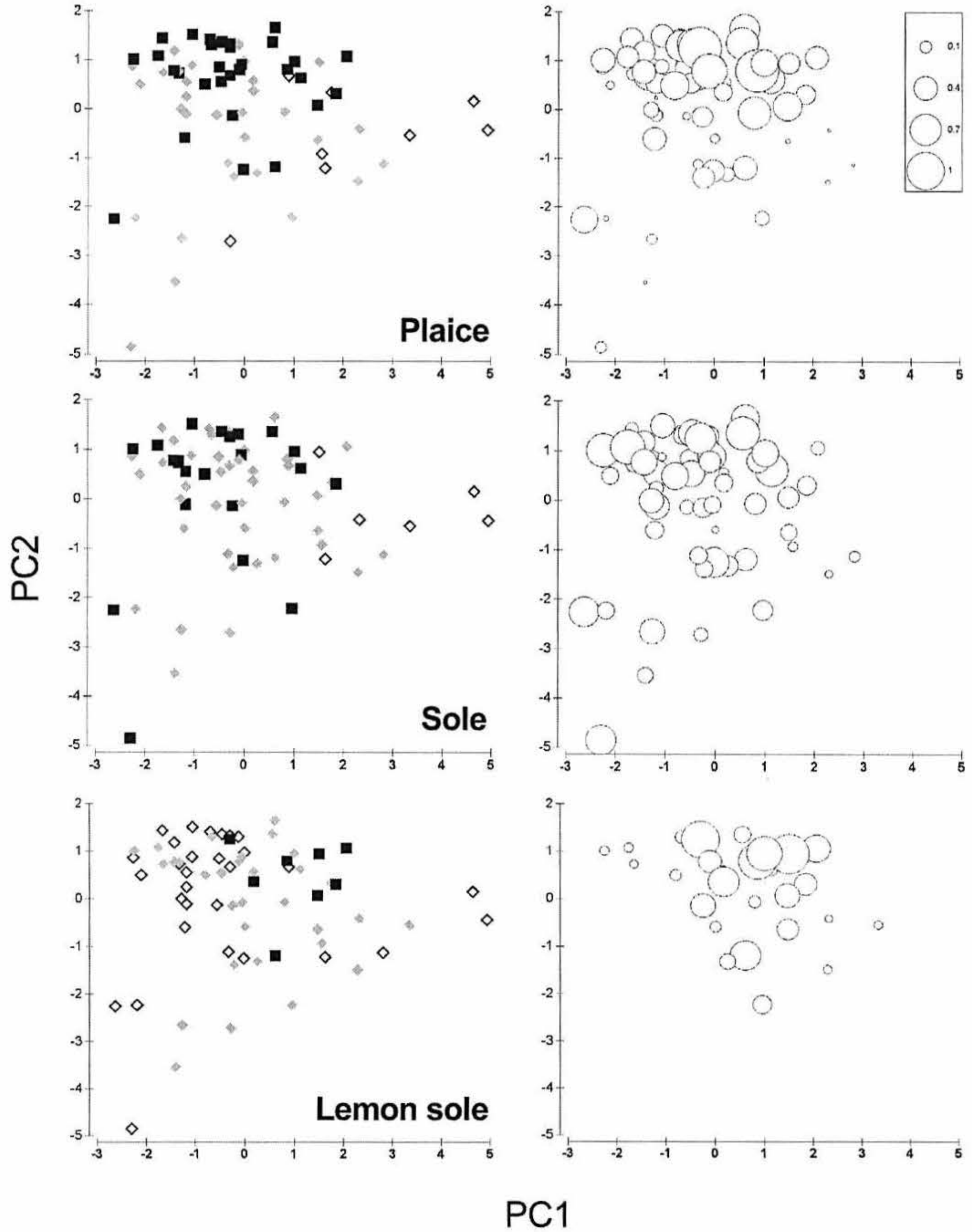

Figure 3.5 PCA biplots of environmental variables and fish abundance site groups: Consistent high abundance sites (black squares), variable and low abundance sites (grey diamonds) and 0-Catch sites (white diamonds). The PCA plot of each flatfish species were overlaid with bubble plots showing the mean $\log_{10}$-percentage abundance of respective species caught over 9 years (CEFAS).

3.4.3 Box plot bootstrap analysis

Depth (m)

For plaice and sole, consistent high and variable abundance sites had a similar depth range (25 percent quartiles around the median were referred to as the range) of ca 20-30 m (Fig. 3.6). The mean depth for both site groups and species was not significantly different from the randomly generated mean (bootstrap mean). However the sites where no catches were made had a noticeable different depth range (≈ 40-50 m) and for both species the mean depth was significantly deeper than could have been expected by chance (plaice: 43 m $p < 0.05$; sole: 50.3 m, $p < 0.05$). In contrast to the other two species, lemon sole were found in consistent high abundances in deeper water ranging from 28-50 m (39.5 m, $p < 0.05$). The depth ranges of the other two site groups were noticeably shallower (ca 20-35 m, means were not significantly differently different from the bootstrap mean).

Temperature (°C)

Plaice and sole again had similar trends for consistent high and variable abundance sites (Fig. 3.6). However plaice consistent high abundance sites had a slightly smaller and lower temperature range (18.4 C°-18.7 C°) than sole sites (18.4 C°-19.1 C°) although the means were not significantly different from random. For plaice the variable sites showed a significantly higher mean (18.9 C°, $p < 0.05$). Sites with zero catches for sole and plaice generally had lower temperatures (≈ 17.9-18.4 C°) compared to the other two site groups and the mean temperatures were significantly lower than bootstrap mean temperatures (plaice: 18.2, $p < 0.05$; sole: 17.9 C°, $p < 0.05$). High consistent abundance sites of lemon sole showed the reverse trend compared with plaice and sole. These sites had much lower temperatures (≈ 18.1-18.4 C°) compared to variable and 0-catch sites. The mean temperature of the high consistency sites was significantly lower than the random mean (18.3 C°, $\rho < 0.05$)

Salinity (psu)

Consistent high plaice abundance sites showed a slightly smaller salinity range (34.1-34.6 psu) compared to consistent high abundance sole sites (33.8-34.6 psu), while variable abundance plaice sites occupied a larger range (33.5 -34.4 psu) than variable sole sites (34.2-34.6 psu) (Fig. 3.6). 0-catch sites in both species showed a narrow range of high salinities (≈34.5-34.7 psu) however only the mean salinity of sole was significantly higher than the bootstrap mean (34.6 psu, $p < 0.05$). High density lemon sole sites were characterized by a narrow range of high salinities (34.5-34.6 psu) and the mean salinity was significantly higher than the resampled mean (34.4 psu). Variable and 0-catch sites showed generally lower salinities however the means were not significantly different from the bootstrap means.

Tidal velocity (ms^{-1})

The consistently high and variable density sites of plaice and sole had very similar tidal velocities (≈ 0.34-0.59 ms^{-1}) (Fig. 3.6). Sites of 0-catches for both species had higher tidal velocities and the mean velocities were significantly different from random (plaice: 0.74 ms^{-1}; $p < 0.05$; sole: 0.8 ms^{-1}, $p < 0.05$). No obvious trend between the three site groups was discernable for lemon sole and mean velocities were not significantly different from bootstrap means.

Stones $kg.h^{-1}$

Consistent high plaice and sole abundance stations were characterized by relatively low amounts of stones (≈ 0.6-9 $kg.h^{-1}$) while variable abundance and 0-catch sites showed larger amounts of stones (Fig. 3.6). For plaice the mean amount of stones for the variable sites was 9.7 $kg.h^{-1}$ and for 0-catch sites 52 $kg.h^{-1}$. Both means were significantly higher ($p < 0.05$) then the resampled mean. The mean amount of stones for consistently high abundance sole sites was significant (3.5 $kg.h^{-1}$, $p < 0.05$) as well as the mean of 0-catch sites (46.6 $kg.h^{-1}$, $\rho < 0.05$). Lemon sole showed the opposite trend compared to the other two flatfish species. Consistent high abundance sites showed slightly larger amounts of stones (7.3 -71 $kg.h^{-1}$) compared to the other two site groups (≈ 0-54 $kg.h^{-1}$). However, only the mean amount stones of the 0-catch sites proved to be significant (4.3 $kg.h^{-1}$).

Shells kg.h^{-1}

For all three species no obvious trends were noticeable. Plaice and sole consistent high and variable abundance sites seemed in general to contain more shells (≈ 0.4-3 kg.h^{-1}) then their respective 0-catch sites (≈ 0-1 kg.h^{-1}) (Fig. 3.6). For lemon sole 0-catch sites, this relationship was not apparent. Only the mean amount of shells for the variable abundance plaice sites proved significantly different from the randomly generated mean (55 kg.h^{-1}, $\rho < 0.05$).

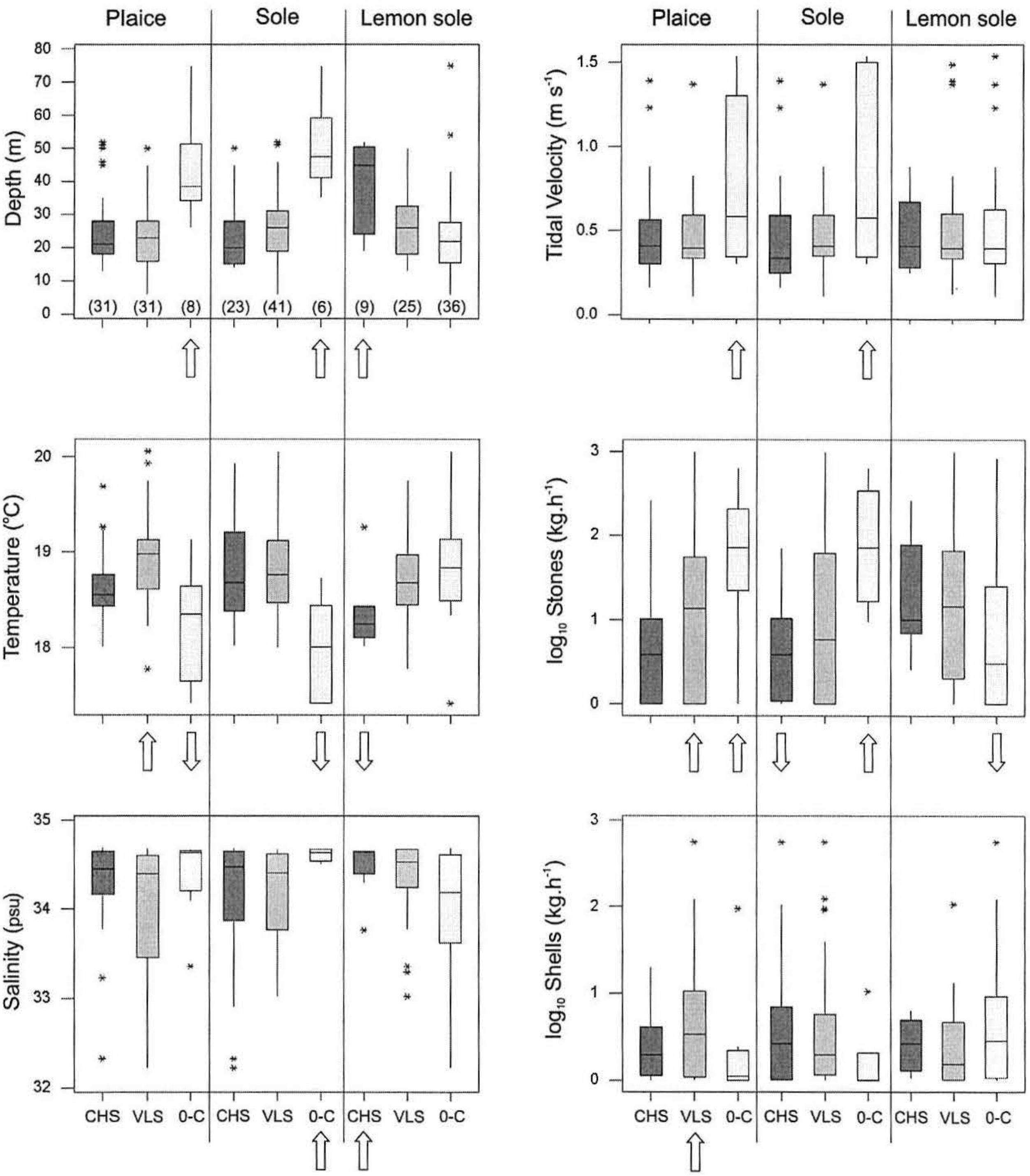

Figure 3.6 Box plots of environmental variables and site groups: Consistent high abundance sites CHS (dark grey columns), variable and low abundance sites VLS (grey columns) and 0-Catch sites 0-C (light grey columns). Columns show median and quartiles, whiskers represent the range and asterisks outliers. The arrow below a site group signifies that the group mean was significantly different ($p < 0.05$) from the random mean calculated by bootstrap procedure. Direction of arrow indicates if the observed mean was significantly higher (upward arrow) or lower (downward arrow).

3.4.4 Site specific study

Flatfish densities recorded in the long-term dataset (CEFAS) were a good predictor of the relative abundance of fish captured during our survey for plaice ($r= 0.80$, $p < 0.001$, Fig. 3.7) and sole ($r = 0.71$, $p < 0.008$, Fig. 3.7). However, lemon sole were caught at only two stations during the survey and were insufficiently abundant for meaningful analysis. However these stations were the two stations with the highest mean percentage abundance over 9 years (Fig. 3.7).

No significant correlation was found between emergent epifauna and flatfish densities (plaice, $r = 0.49$, $p = 0.1$; sole $r = -0.017$, $p = 0.958$, Fig. 3.7) using all sites sampled in the analysis. Plaice abundances did however correlate significantly with the biomass of emergent epifauna when only sites of the CHS site group were used for analysis ($r = 0.86$, $p = 0.01$). For sole the correlation of only CHS sites showed a negative, non significant trend for the relationship between sole abundance and emergent epifauna biomass.

Prey abundance in the environment did not correlate with the abundance of flatfish caught during the site-specific study (plaice, $r = 0.49$, $p = 0.1$; sole $r = 0.258$, $p = 0.418$; Fig. 7). However in the analysis of diets, for plaice a positive correlation was found between abundance of fish and the number ($r = 0.813$, $p = 0.008$) and biomass ($r = 0.77$, $p = 0.015$) of prey items ingested per fish. However the percentage of empty stomachs ($r = 0.393$, $p = 0.295$) and body condition ($r = 0.5$, $p = 0.170$) did not correlate significantly.

Habitat parameters and the results of the flatfish survey per site were summarized (Table 3.3). Analysis of the table indicated that at site SE1 the highest densities of adult plaice and lemon sole were caught. This station also had the highest biomass of emergent epifauna and plaice stomachs showed the highest number of prey and biomass levels ingested per fish. This contrasted sharply with the relatively low prey abundances observed at this station. The highest prey abundances were found at site SE3. At this site high abundances of juvenile plaice and sole were caught while abundances of adult fish were low.

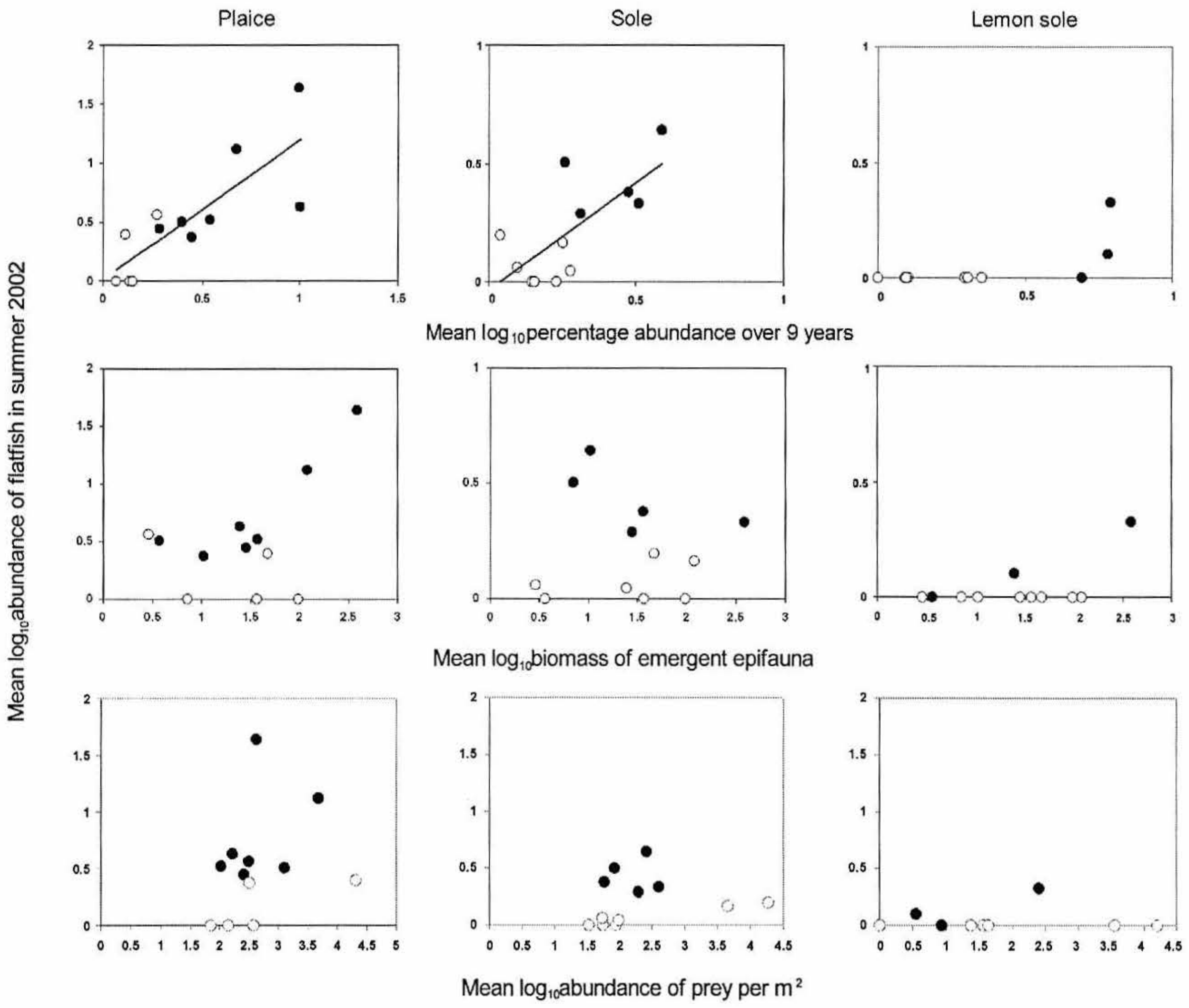

Fig. 7 Relationship between mean $\log_{10}$-abundance of flatfish caught in 2002, mean $\log_{10}$-percentage abundance of flatfish caught over 9 years (CEFS), mean log-10 biomass of emergent epifauna abundance and $\log_{10}$-abundance of prey per m^2. Black circles mark consistent high abundance sites (CHS), white circles variable abundance (VLS) and 0-catches sites (0-C).

Table 3.3 Summary table of habitat descriptors and flatfish parameters analyzed for each station of the site specific survey. Bold font signifies highest values for respective categories

Station	**W1**	**W2**	**W3**	**W4**	**W5**	**NE1**	**NE2**	**NE3**	**SE1**	**SE2**	**SE3**	**SE4**
Habitat descriptors												
Depth (m)	**71**	**71**	49	23	36	14	21	21	17	26	15	50
BGS classification	S	(g)mS	gmS	sM	mS	(g)S	gmS	S	(g)mS	gmS	S	S
Total stones (g m-^{2})	1	2	61	25	5	25	9	30	**213**	77	29	14
Total shells (g m^{-2})		0.8	**1.9**	0.1			0.9	0.5	0.7		0.2	0.3
Emergant epifauna mean W.w. (g m^{-2})	2	3	96	36	6	27	9	36	**383**	119	46	23
Plaice												
Site group	VLS	**CHS**	VLS	VLS	VLS	**CHS**	**CHS**	**CHS**	**CHS**	**CHS**	VLS	**CHS**
Sum of fish caught	21	14				9	22	13	**330**	76	189	26
Mean abundance >26 cm	2.7	2.2				1.8	1.4	2.3	**42.6**	12.1	1.5	3.3
Prey abundance m^{-2}	315	1273	370	70	139	255	318	104	415	4783	**20413**	165
Stomachs analysed	30	17	3			8	6	23	**42**	40	8	25
Mean prey abundance in stomachs	7	9	2			3	5	3	**25**	9	5	3
Mean prey W.w. g per stomach	0.4	1.2	1.1			0.6	0.4	0.6	**2.4**	1.1	0.7	0.1
Per cent of empty stomachs	7	12	0			13	17	9	7	13	38	**80**
Condition (K)	1.00	0.99	1.26			0.99	0.99	1.07	**1.26**	1.12	1.16	1.06
Sole												
Site groups	VLS	VLS	VLS	**CHS**	**CHS**	**CHS**	**CHS**	VLS	**CHS**	VLS	VLS	VLS
Sum of fish caught	1			8	12	4	16		9	3	**24**	1
Mean abundance >23 cm	0.1			1.4	2.2	0.9	**3.4**		1.1	0.5	0.6	0.1
Prey abundance m^{-2}	53	33	55	58	83	193	258	88	395	4468	**18420**	95
Stomachs analysed	1			6	**10**	6	**10**		6	3	3	1
Mean prey abundance in stomachs					1	1	1		10	**20**		
Mean prey W.w. g per stomach					0.1	<0.1	<0.1		1.0	**3.1**		
Per cent of empty stomachs	**100**			**100**	30	50	50		50	33	**100**	**100**
Condition (K)	0.90			0.93	0.93	0.94	1.00		**1.04**	1.03	1.03	**1.04**
Lemon sole												
Site groups	VLS	**CHS**	VLS	VLS	VLS	0-C	VLS	VLS	**CHS**	VLS	0-C	**CHS**
Sum of fish caught									**8**			2
Mean abundance >24 cm									**0.7**			0.3
Prey abundance m^{-2}		8	43	8		23	35		3533	253	**15908**	3
Stomachs analysed		1	2						**4**			3
Mean prey abundance in stomachs			1						3			**14**
Mean prey W.w. (g) per stomach			<0.1						0.5			**0.7**
Per cent of empty stomachs		100.0	50.0						**75.0**			33.3
Condition (K)		1.5	1.4						**1.4**			1.3

3.5 Discussion

3.5.1 Large scale environmental parameters

The results from the large scale environmental data indicated that all three species plaice, sole and lemon sole showed slightly different habitat associations. Sites of high consistent plaice density were generally restricted to relatively shallow areas, with low salinities indicating near shore conditions. Sediments at these sites were high in sand content and had relatively few amounts of stones and shells present. In contrary sites avoided by plaice were characterized by greater depth, higher salinities and sediments had either a high gravel or mud content. *Amezcua et al.* (2001) also found plaice prominently over sandy habitats in the Irish Sea. The association of plaice with sediments high in sand content may have several reasons related to burial and prey capture. Although flatfish might have the capabilities to bury in most sediment types as adults (Stoner and Abookire, 2002) they may still prefer substrates in which they can easily bury with relatively little energy expenditure such as loosely packed sand rather than gravely substrates. Unsuccessful burial over unsuitable substrates has been demonstrated to cause higher energy expenditure in resting soles due to continued digging in behaviour (Howell and Canario, 1987). Another factor which might be the source for this association of plaice with sand might be related to the foraging behavior. Amezcua *et al.* (2003) suggested that infaunal prey may be easier to excavate from sand compared to coarse sediments. As plaice are highly visual predators (Piet *et al.* 1998) good visibility may be an important factor for successful prey capture and increased turbidity over more muddy sediments may therefore be less favorable.

Sole sites with high consistent abundance were found over a much wider spectrum of sediment types compared to plaice ranging from muddy to sandy substrata. However sole similar to plaice seemed to avoided sediments high in gravel content. In respect to the other environmental factors analysed sole showed similar trends to plaice. Relatively shallow sites with low salinities and high temperatures showed consistent high abundances of sole while deeper sites with high salinities and low temperatures had variable low abundances or had no fish. Shells and stones were only present in small amounts at high consistent density sites. The similarity between high consistent sole and plaice sites indicted a considerable habitat overlap and over sandy substrates interspecific competition could be intense especially as also part of their prey spectrum overlaps (Hoines and Bergstad, 2002; Jones, 1952; Piet *et al.* 1998; Rijnsdorp and Vingerhoed, 2001).

Overall lemon sole was rarely caught during groundfish surveys and at many sites the species never was recorded over the whole survey period analysed. The distribution of lemon sole thus was restricted to very few specific sites. High consistent abundance sites in general showed a very different setup of environmental parameters compared to plaice and sole. Lemon sole was associated with sandy and gravely sand substrates. It was found at greater depth, higher salinities and lower temperatures then the other two flatfish species. This indicates that most stations were found in deeper offshore areas. These findings are in line with (Bennet, 1965) findings from the North Sea. Bennet (1965) also found lemon sole at high densities in relatively deep water over sediments high in gravel content. At high consistent abundance stations also larger amounts of stones were recorded compared to sites with variable or low abundances.

3.5.2 Site specific study – the role of emergent epifauna and prey availability

The results of the site specific-study investigating the association of flatfishes with emergent epifauna and prey availability sampled at the same temporal scale did not reveal any clear trends. There were some indications of a positive relationship between emergent epifauna and plaice abundances however only when high consistent abundance sites (CHS) were analysed separately. The basis for a positive relationship may be linked to the foraging strategy and analogous prey spectrum of adult plaice. With increasing size plaice have been shown to undergo an ontogenetic change in their diet (Piet *et al.* 1998), while juveniles feed predominantly on infaunal polychaetes and bivalves the diet of larger adult plaice contained a large proportion of epibenthic crustaceans, small fish and echinoderms (Carter and Grove, 1991; Piet *et al.* 1998). Some of these animals groups have shown to benefit from complex structures presented by emergent epifauna as they offer a larger number of niche spaces to epibenthic invertebrates (Bradshaw *et al.* 2003). In the present survey adult plaice almost exclusively had ingested tube building polychaetes making the functional link of emergent epifauna increasing prey availability of mobile epifauna unlikely to be an important factor for the sites analysed. Similarly a significant relationship between plaice abundance and overall prey availability could not be detected. However plaice abundances did show a significant relationship with the abundance and biomass of prey items ingested per fish. The non significant result of the relationship between adult plaice abundance and prey availability was partly caused by the mismatch of two sites SE1 and SE3. SE1 was predicted by the long term groundfish survey data (CEFAS) to show the highest abundances of adult plaice and this trend was confirmed by the highest catches of adult plaice made by the site-specific study. Stomach contents analysis and mean body condition did seem to confirm the positive habitat conditions at this site. However prey availability assessed by grab samples indicated relatively low prey abundances. These contradicting results seem to suggest that grab samples were not suitable to determine prey abundances and thus habitat quality at the appropriate spatial scales. Video and stills footage taken as supplementary information during this survey over larger spatial scales did also support this proposition as high abundances of the tube building polychaetes *Lanice conchilega* and *Chaetopterus spp.* were visible at this site (Rees *et al.* 2005, Chapter 4). Contrary to site SE1, SE3 showed the highest prey abundance recorded using grab samples by this study. High abundances of juvenile plaice and sole were recorded at this site however adult plaice and sole were almost absent.

Emergent epifauna did not appear to have a positive effect on the densities of sole. The trends in the data although not significant were negative with the highest density sole sites showing low emergent epifauna cover. Sole thus could not be associated with the presence of emergent epifauna. Sole unlike plaice have small eyes and rely on tactile and chemosensory cues to detect prey via papillae located on the ventral side of the mouth (Rogers, 1994). Sole primarily preys upon infaunal invertebrates such as polychaetes and molluscs during juvenile and adult life stages (Piet *et al.* 1998). As epibenthic invertebrates which may benefit form the presence of emergent epifauna are not an important component of sole diets this lacking relationship could have been expected. No relationship was found between prey availability and sole abundances although it should be recognized that very few soles were caught during the survey and therefore few individuals were available to determine prey spectra from stomach contents analysis which might have lead to a bias of the data.

The relationship between lemon sole, emergent epifauna and prey availability could not be analysed as lemon sole were only caught at two sites. These sites were however the stations which were predicted to have the highest lemon sole abundances from the long term CEFAS data.

3.6 Conclusion

The correlations of the large scale data survey data with the site specific study verified the approach taken to detect sites of high consistent flatfish abundances (Hinz *et al.* 2003). Abiotic habitat characteristics which operate over larger spatial scales may therefore give some indications which habitats features might be important to the three flatfish species analyzed. However, as elsewhere, this study also demonstrated the difficulty in establishing clear relationships between specific habitat components such as the presence of emergent epifauna or prey availability at the scales used for large-scale fisheries surveys (McConnaughey and Smith, 2000). Prey availability can be thought of as a principle component of habitat quality and is considered to influence fish distributions on small spatial scales (Hinz et al. 2003). However within the site-specific survey of this study this relationship could not be confirmed. The reason for the absence of a clear relationship could be related to various sources. Besides that the low number of sampling sites chosen may have been insufficient to detect such a relationship there are also more principle reasons why it will be difficult to detect such a relationships on the sampling scale adopted by this study. Under some circumstances fish densities may be unrelated to the habitat parameters which can be assessed within the area sampled. An area of low habitat quality (e.g. prey availability) could display relatively high flatfish abundances in the case where a prime habitat is found within the vicinity (not sampled by the survey) and density-dependant effects lead to an overspill of fish into the low quality area (Jennings, 2000). Fish might also aggregate over less suitable areas if the surrounding areas are even less favourable and movement towards or knowledge of prime habitats are restricted (Shepherd and Litvak, 2004). There is also the possibility that fish require more than one habitat e.g. habitat for feeding and a habitat for resting which might offer some degree of protection while digesting prey items. High fish densities may thus depend also on the habitats found in adjoining areas and their inherent habitat quality. The sampling grid of the groundfish surveys as used by this study, with their large distances between individual sampling stations, will not be able to address those processes that operate on much smaller localized spatial scales. Within this study there was good evidence that the sampling regime adopted to assess prey availability and thus habitat quality by grabs was not conducted at the appropriate scales over which flatfish in this case plaice operated. Plaice were found in high abundances and in good nutritive state over sites with relatively low prey densities suggesting that prime feeding grounds must have been within relatively close vicinity. This may point to the conclusion that fish are more efficient in sampling prey availability and that stomach contents analysis and body condition may reflect more reliable information about the true habitat quality of an area compared to point source sampling with grabs to assess prey availability.

Future field studies on habitat selection of flatfish will need to address the multifactorial causes of variability in fish densities. Point source sampling in time and space of fish abundances and selected habitat parameters will not be adequate to determine habitat requirements and explain distribution patterns. Environmental parameters and fish densities will need to be determined on a much higher spatial and temporal resolution for progress to be made within the field of fish-habitat association.

Chapter 4

Evaluation of habitat use by adult plaice (*Pleuronectes platessa* L.)

4.1 Abstract

Most routine fisheries surveys investigating the distribution pattern of flatfish only use depth, sediment type and temperature as descriptors of fish habitats. Other habitat parameters which may also influence distribution patterns such as the relief of the sea floor, the presence of structuring fauna and prey availability are often not considered. Here we used video survey techniques to study habitat components in areas which were known to support consistent high densities of adult plaice from long-term data sets in the English Channel. Habitat features were described and related to the density of adult plaice caught within the same area. To focus the study on habitat components other than sediment type all sites chosen had sandy substrata. The scale and spatial distribution of physical (sand waves, stones, broken shells etc) and biological (emergent epifauna, burrowing fauna etc) structures were measured for each site and correlated to plaice densities. The spatial variability of features within sites, habitat heterogeneity, was determined and also correlated with plaice abundances. Plaice densities correlated with the abundance of benthic fauna recorded. In particular the protruding polychaetes *Lanice conchilega* and *Cheatopterus spp,* which can be regarded as a valuable food source for plaice dominated some stations and were mainly responsible for the observed trend. Abiotic habitat features and habitat heterogeneity showed no clear relationships with respect to plaice densities. This indicated that prey availability might be the driving force for habitat selection of adult plaice in sandy habitats and that other habitat descriptors might be of lesser importance.

4.2 Introduction

There is a general consensus that fisheries management should incorporate a more ecosystem orientated approach to achieve the goal of a sustainable fishery (e.g. Link, 2002; Meester *et al.*, 2004 and others). While fisheries scientists have striven to understand the population dynamics of target species, the ecological requirements of the latter are patchy in their coverage (Biglow and Schroeder 2002) for all but a selection of iconic species e.g. cod *Gadus morhua*. Identification of key habitat requirements of key life stages and an understanding of how these affect distribution patterns on various spatial and temporal scales is a necessary component to ensure the appropriate implementation of spatial management to achieve stock conservation (McConnaughey and Smith, 2000). For demersal fish species, in particular flatfishes, that spend most of their life in close affinity with the seabed an appreciation of habitat use will be of importance and needs to be reviewed in the wider context of the ecological effects of fishing activities (Jennings and Kaiser, 1998; Kaiser *et al.*, 2002). Towed bottom fishing gear is a substantial cause for seabed habitat change and alters the structure and function of habitats that fulfil an important role in the life-history of fish most closely associated with these habitats (Auster and Langton, 1999; Kaiser *et al.*, 2002; Ryer *et al.*, 2004). Loss or fragmentation of key habitats can have detrimental effects upon the overall population dynamics and hence the viability of exploited populations.

Studies on the distribution pattern of flatfish and their environmental determinants mostly have been conducted over large geographical or regional scales and only used principle environmental descriptors such as depth, sediment type and temperature as predictors (Smale *et al.*, 1993; Albert *et al.*, 1998; Ellis *et al.*, 2000; Amezcua and Nash, 2001). Few have tried to consider and quantify other environmental components of flatfish habitats such as substratum relief, the presence of structuring epifauna, or prey availability (but see McConnaughey and Smith 2000, Stoner and Titgen, 2003). These may however be important parameters at a smaller (local) scale an may influence habitat choice in flatfish and therefore determine distribution patterns on a more localized scale. For juvenile flatfish the importance of some of these habitat parameters (substratum relief and structuring fauna) has been demonstrated (Abookire and Norcross, 1998; Norcross and Mueter, 1999; Stoner and Abookire, 2002; Stoner and Titgen, 2003; Ryer *et al.*, 2004) however, for adult flatfish their role is not yet fully understood (Stoner and Titgen, 2003, Chapter 3).

In the present study habitat components at sites that were known to harbour consistent high densities of adult plaice (*Pleuronectes platessa L.*) were studied using underwater video surveys. Sampling benthic habitats with video transects, unlike with traditional methods such as grabs and beam trawls, enables real-time observation of the seabed and assessment of the spatial distribution and density of both abiotic and biotic features. Substratum structures and habitat heterogeneity as well as the density of potential prey items can be estimated over scales most likely to be relevant for the habitat choice in individual fish. Although the composition of parts of the benthic assemblage can accurately be determined using grab sampling, it has a low spatial resolution (0.1 m^2) and lacks the ability to determine and adequately quantify other habitat descriptors, such as substratum relief and more scarcely distributed epibenthic fauna. Beam trawls on the other hand sample epifauna more efficiently covering larger areas, but here catches are pooled over larger the areas sampled that result in a loss of spatial resolution.

The main aim of this study was to describe habitat features with video survey techniques and relate those to the density of adult plaice. In this way it was possible to investigate which habitat features were correlated with adult plaice and hence may influence habitat choice and overall distribution patterns. In the analysis of video transects particular emphasis was placed on the quantification of abiotic features that add topographic structure to the seabed (e.g. sand waves, bedrock, and cobbles) and on organisms that are responsible for structuring the seabed (e.g. emergent epifauna, burrowing fauna) or may represent an important food source. Besides studying the overall relationship of habitat parameters to plaice densities among sites also the importance of spatial variability of features within sites was investigated to examine the role of habitat heterogeneity.

4.3 Methods

4.3.1 Site selection

The study was undertaken in the in the English Channel where a major fisheries for plaice (*Peuronectes platessa*) and common sole (*Solea solea*) exists. Site selection was based on a grid of stations regularly surveyed annually as part of a groundfish survey conducted by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS, Lowstoft) for fish stock assessment purposes (Kaiser *et al.*, 1999). A subset of nine of the stations that consistently held high densities of adult plaice was identified from the ground fish survey data using the method of Hinz et al. (2003)

The data spanned a nine year period from 1990 to 1998. Only adult plaice over the minimum landing size (> 26 cm) collected during the autumn groundfish survey cruises were used so as to avoid sampling spawning and nursery aggregations. For each of the 133 ground fish survey stations used for this initial analysis, the percentage of fish relative to all other stations in year was determined for all years. This conversion was performed to prevent a bias in the analysis by an exceedingly high abundance of plaice at a particular station in any one year. The percentage data (+1) was then Log_{10} transformed to achieve a normal distribution. From this, the long-term mean percentage abundance was calculated for each station and plotted against its corresponding standard deviation. The resultant scatter plot was overlaid with the regression line and corresponding 95% predictive intervals (PI) from a regression analysis performed on the same dataset but randomizing it first. Within each year, every station was assigned an abundance allocated at random from within the range of the data of that year. The relationship between random means and SD was best described by a linear model of which the 95% Predictive Intervals (PI) were used as delineation lines in the scatter plot of the original data. For a more detailed description and discussion of this method see (Hinz *et al.*, 2003). Thus, stations found below the lower 95% PI represented stations, where plaice were consistently caught in higher abundances (high mean: S.D. ratio) than predicted by the randomized data. Thirty one of the stations from the groundfish survey fell below the 95% PI of which nine were investigated by this study. For the nine sites it was possible to ascertain a gradient in the long-term mean percentage abundance, which allowed investigation into the relationship of habitat characteristics and plaice densities.

Fish distribution patterns and thus abundances are determined by fish responding to a multitude of environmental parameters which often are linked in a complex way. The investigation the relationship between fish density and only a single parameter will be extremely complicated if other parameters vary at the same time. To limit the variability of habitats to some degree, in this study the general sediment type at sites sampled was kept consistent. Areas included in the analysis had sandy substrates. Previous studies on the large scale distribution patterns of plaice showed that they were primarily found over sandy substrata (Chapter 2; Amezcua and Nash, 2001).

It should be noted that the stations chosen were partly from the same geographical region (see Figure 4.1) and therefore were not strictly independent from each other. Two stations W1 and W2 were located off near Start Point, Devon. Three stations were positioned on the English coast (NE1-NE3), between Brighton and Hastings. A further four stations were located on the east coast of France near Boulogne-sur-Mer (SE1-SE4).

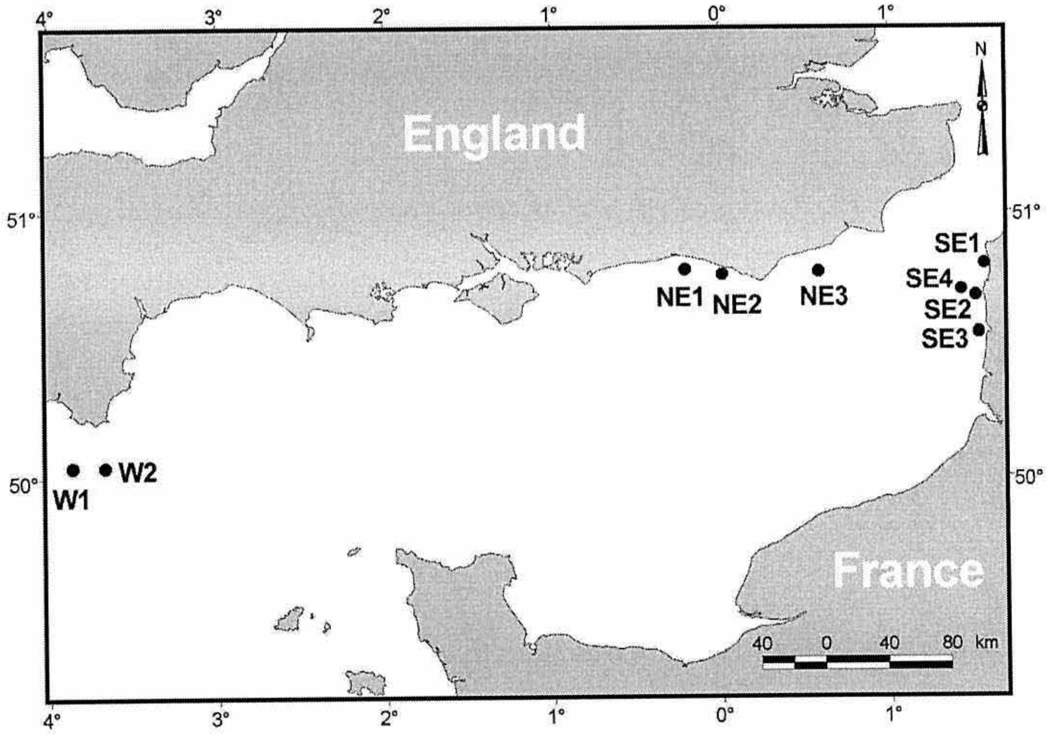

Figure 4.1 Location of study sites in the English Channel

4.3.2 Fish survey

Four daytime tows of 20 minutes duration each were made with a 4-m beam trawl, towed at a speed of approximately 4 knots, to quantify the densities of fish at each of the nine stations in August 2002. The beam trawl was fitted with a chain-matrix and an 82mm diamond mesh cod end with a 40mm square meshed liner. All fish were sorted into species, counted and weighed. The length of each plaice was recorded to the nearest cm. Plaice catches were standardized to a tow length of 250m covering an area of 1000 m^2.

Differences in plaice abundances between stations were analysed by the non-parametric Kruskal-Wallis test, as the data did not fulfil the assumptions of parametric tests. The total abundance of plaice caught, as well as the abundance of only plaice over the minimum landing size (>26cm) were analysed for differences among sites.

To evaluate if plaice abundances at the nine sites followed the same trends as those predicted by the long-term abundance groundfish survey data, the mean number of flatfish caught above the minimum landing size (MLS) was correlated with the mean Log_{10}-percentage plaice abundance sampled by CEFAS over nine years (Pearson product-moment correlation). All further analyses into the relationship of habitat characteristics identified from video tows and plaice densities, were based on fish abundance as recorded in the present study, for this data was gathered at the same spatial and temporal scale as the data on habitat-characteristics it was related to.

4.3.3 Video survey

To assess the composition of habitat structure and benthic faunal assemblages an underwater camera system was deployed prior to sampling with the 4 m beam. At each site, one 30 min camera tow along the seabed was conducted with a video sledge. The sledge was mounted with a UWTV video system Photosea 1000 arranged with the camera pointing downwards at an angle of approximately 45 degrees and with the lens approximately 0.7m above the seabed. The field of view spanned an area of $\approx 0.2m^2$. Strobes were mounted at 60 degrees to the camera. The video images were recorded using a Hi-8 video cassette player.

The video sledge was towed by the drift of the research vessel alone. Owing to the differences in the prevailing currents at each site, all approximately 30-minute tows had different lengths and were towed at different speeds. The average video transect was 561m ±214 and towing speeds ranged between 3.8 cm to 62.9 cm per second.

Digital images were frozen and extracted from the video recordings made during individual tows at intervals of 20 seconds. Thus ≈90 images were extracted in total for each video tow. To standardize for the differences in tow length and allow analysis of images from equal distances, images were allocated into respective 50m sections using distance, speed and time of recording. Each 50m section thus produced a different number of images and was therefore sub-sampled. For each 50m section of each tow, five images were randomly selected for detailed analysis. Five images proved to conserve sufficient habitat information using cumulative sample curves, while fewer images did not identify all quantifiable features within a 50m bin interval. To make the data of each tow comparable the overall tow length for each tow was standardized by randomly selecting an equal number of 50m intervals for each site. As a result an equal tow length of 200m and 20 images per site was used for analysis of physical substratum features, so that scale and sampling effort were held constant.

Extracted video images were analysed for differences in substratum type and structures by projecting the image on a screen with a grid divided into 100 equal cells. The percentage cover of sediment types per image was estimated by calculating the number of cells covered by a particular sediment type (Table 4.1). Different sediment types were identified by their colour and grain size as seen in the image and verified by grain size analysis of sediment samples taken with a Day grab at each station. Sand ripples were recorded as present or absent and all other physical structures were counted (Table 4.1).

The difference between the substratum cover and features (e.g. sand waves, shell material or burrows) between stations was determined by a Cluster analysis (Primer v.5) based on a standardized Euclidian distance dissimilarity matrix. The cluster analysis groups stations with similar substratum characteristics into distinct station clusters and the degree of similarity/dissimilarity between stations can thus be explored. Characteristic features of the resultant clusters were analysed using SIMPER analysis (Primer v.5). This program quantifies the percentage contribution that a feature makes to the similarity within a station cluster and to the differences between clusters.

Habitat heterogeneity within sites was determined to assess spatial differences in the distribution of physical features between sites. The physical parameters used to calculate habitat heterogeneity at each site were summarized in Table 4.1. At each site 20 images were used as samples for the calculation of a dissimilarity matrix (Primer v.5). The resulting dissimilarity matrix, based on Euclidian distances, summarized the dissimilarities in habitat features between all images of one station. From this matrix the mean dissimilarity and its corresponding standard deviation was calculated. The mean dissimilarity of all images of one station was then used as an approximation of habitat heterogeneity. Sites with low mean image dissimilarity indicate homogeneous substratum characteristics, while sites with high mean image dissimilarity, indicated heterogeneous substratum characteristics. To test if mean substratum dissimilarity (heterogeneity) was correlated with plaice abundance the Pearson's product-moment correlation test was used. Both heterogeneity and plaice density, had to be Log_{10}-transformed to normalize the data prior to analysis.

As depth is known to affect fish distributions and was found to vary noticeably between the stations investigated, it was tested for correlation with flatfish density using Pearson's correlation test.

Benthic organisms were identified to the lowest taxonomic level possible and if feasible counted (Table 4.1). The mean number of benthic animals was calculated for each 50m section (mean of 5 images) of each tow. From this the overall mean abundance per 200m camera tow were determined and used for further analysis. While the larger epifauna could easily be counted, smaller and hyper abundant species were difficult to quantify. Here it was attempted to estimate density as accurately as possible (Table 4.1). Due to the low quality of some images it was often difficult to count protruding worm tubes or brittle stars in all parts of an image. Therefore worm tube density was estimated for most images using the screen grid as an aid to extrapolate numbers from defined areas to less defined ones.

Owing to the low number of taxa observed in 6 out of the 9 stations additionally the entire video transect (≈90 images) for each site was analysed for benthic fauna instead of using only four 50m sections per tow. The abundances of benthic species were subsequently standardized to a common transect distance of 1km to facilitate some degree of comparison between sites. This semi-quantitative data was included as it contained valuable information of the benthic assemblages found at of each of the sites investigated that otherwise would have been lost.

The mean number of benthic animals per 50m section for each site (200m tow) was correlated with plaice densities by Pearson product-moment correlation. The total abundance of benthic animals and the number of taxa observed for the complete tow (semi-quantitative data) was also correlated with plaice densities (Pearson product-moment). The abundances of benthic organisms and the number of taxa and were Log_{10}-transformed to normalize the data prior to analysis.

Table 4.1 Plaice caught at respective sites. Substratum type cover was given as mean percentage per analysed image for each site. Sand ripples and waves were recorded as percentage presence or absent absence from images of each site = (% P/A) while stones were counted (C). Epifauna was counted (C) or estimates (E). Mean abundance of Epifauna per 50 m section of a 200m tow and for the whole tow and standardised to a transect distance of 1km. * indicate the categories, which were used to calculate the heterogeneity indices.

	English West		English East			French East			
	W1	W2	NE1	NE2	NE3	SE1	SE2	SE3	SE4
Plaice									
Total number of plaice caught	21	14	9	22	13	330	76	189	26
Mean number of plaice per tow	5.2	3.5	2.2	5.5	3.2	82.5	19	47.2	6.5
Mean number of plaice >26cm per 1000m^2	0.33	0.27	0.22	0.17	0.28	5.32	1.56	0.18	0.44
Mean length in cm	30	34	32	24	29	32	32	20	33
Min length in cm	26	28	26	18	24	22	31	12	26
Max length in cm	38	44	38	32	35	42	43	35	48
Substratum characteristics									
* Mean % cover of shelly gravely sand							52.3		1
* Mean % cover of sand	100	87	96.8	97.7	100	93	36.3	100	99
* Mean % cover of small and broken shell		13	3.2	2.2			11.4		
* Small sand ripples 0-5cm (% P/A)	100	70	100	55			100	5	
* Medium sand waves >5cm (% P/A)					1				0.4
* Large stones > 5cm (C)						<0.1			0.4
* Stones 0-5cm (C)			16.8			7			0.3
* Small burrow 0-2cm (C)					0.5				
*Large burrow 2-5cm(C)				0.7					
Benthic fauna per 50m section									
Porifera (C)						0.06			
Anthozoa (C)						0.06			
Urticina felina (C)									0.2
Polychaeta tube structures (E)				≈2.05	≈0.04	≈478	≈57.5	≈73.5	
Pagurus spp. (C)	0.05								
Asterias rubens (C)		0.05				0.23	0.2		
Ophiura spp. (C)						0.06			
Ophiothrix fragilis (E)									≈21.6
Echinocardium spp. (C)		0.05							
Benthic fauna per 1km tow									
Porifera (C)			1.3		2.2	4.2			
Anthozoa (C)						15.5	1.8		5.1
Urticina felina (C)						7.1			5.1
Polychaeta tube structures (E)				≈6	≈1	≈44886	≈16539	≈3724	
Pagurus spp. (C)	2.5			5	10.8		1.5	5.9	
Liocarcinus spp. (C)						1.4		1.9	
Goneplax rhomboides (C)									
Mytilus edulis (C)			268.8						
Asterias rubens (C)		5.7				46.5	22.8	3.9	4.1
Ophiura spp. (C)						1.4	159.4		
Ophiothrix fragilis (E)									≈2795
Echinocardium spp. (C)		1	51				3.5		
Attached epifauna (unidentified) (C)			1.3			1.4			5.1
Fish (unidentified) (C)								1.9	1.1

4.4 Results

4.4.1 Plaice densities

The median number of plaice caught at each of the nine sites differed significantly (K-W, $H = 27.06$, d.f. = 8, $p = <0.001$). Sites SE1, SE2 and SE3 off the French east coast had significantly higher median plaice densities than all other stations. The median abundance of plaice per tow above the 26cm MLS differed significantly among the 9 stations sampled (K-W, $H = 27.79$, d.f. = 8, $p = 0.001$). Stations SE2 and SE1 had significantly higher median abundance of plaice per tow compared with all other stations. This indicated that at station SE3 plaice of a length below 26cm were caught. For the number of plaice caught at each station see Table 4.1.

For each site there was a significant correlation between CEFAS long-term mean Log_{10}-percentage abundance of plaice over nine years and the mean Log_{10}-abundance of plaice caught per tow ($r = 0.68$, d.f. = 8, $p = 0.04$, Fig. 4.2). This indicates that the abundance of fish sampled during the present study in general could be predicted from the long-term CEFAS groundfish survey data. As only nine stations were investigated, which due to their geographical location could not be regarded as strictly independent, it was felt necessary to make each station identifiable in the graphical outputs of this study. This should allow the reader to follow trends of individual stations and thus make the analysis more transparent (Fig. 4.1). Here it should be noted that the correlation was strongly influenced by three sites off the French coast SE1, SE2 and SE4. These sites did show the highest mean abundances in the long term data of CEFAS, which matched with the abundances of plaice caught at these sites by the present study.

4.4.2 Substratum characteristics, habitat heterogeneity and depth

The analysis of the substratum characteristics showed that although the seabed of all sites was primarily composed of sand, subtle habitat differences between stations were apparent (Table 4.1 and Fig. 4.3). Stations clustered into two main groups at a dissimilarity level of 65.6%. Group one consisted of stations SE1, SE3, SE4 and

Station NE3. The Simper analysis showed that these stations were characterized by a high mean cover of sand (98% S.D. ±3.6) and the presence of medium sand waves (mean percentage presence=36.2%, S.D. ±47.5). The presence of small (mean no.=1.83 S.D.±3.4) and large stones (mean no.=0.13 S.D. ±0.21) also characterized these sites. The second group of sites consisted of NE1, NE2, W1, W2 and SE2. Site SE2 clustered separately from the highly similar cluster of the remaining stations and was analysed independently (Fig 3). Sites NE1, NE2, W1 and W2 had a slightly lower percentage sand cover than group one sites (mean=95.3%, S.D. ±5.7), while video images were also characterized by a low percentage cover of small and broken shells (mean=4.6% S.D. ±5.7). Small sand ripples were on average present in 81% (S.D. ±22.5) of the images from these stations. Site SE2 also showed sand ripples (100%) and a slight cover of small and broken shells (11.5% S.D. ±27.9). Site SE2 also differed, however from the other stations in its percentage cover of sand (36%, S.D. ±44) and it was the only station were a cover of shelly gravely sand (52%, S.D. ±49.2) was recorded. The substratum characteristics and their % contribution to each cluster are summarized in figure 4.3. However there was no clear relationship between these site (habitat) groupings and plaice densities recorded during this study, as stations of high and low densities occurred within both groups. SE1, the station with the highest abundance of plaice occurred within the first substratum cluster while SE2, the station with the second highest abundance, was associated with the second cluster.

Calculation of the mean dissimilarity of images of each of the sites as an approximation of physical habitat heterogeneity showed that there where distinct differences among stations (Table 4.2). There was, however, no significant correlation between mean number of plaice caught and the habitat heterogeneity calculated for each station (r= 0.504, *d.f.* = 8, p = 0.166, Fig 4.2).

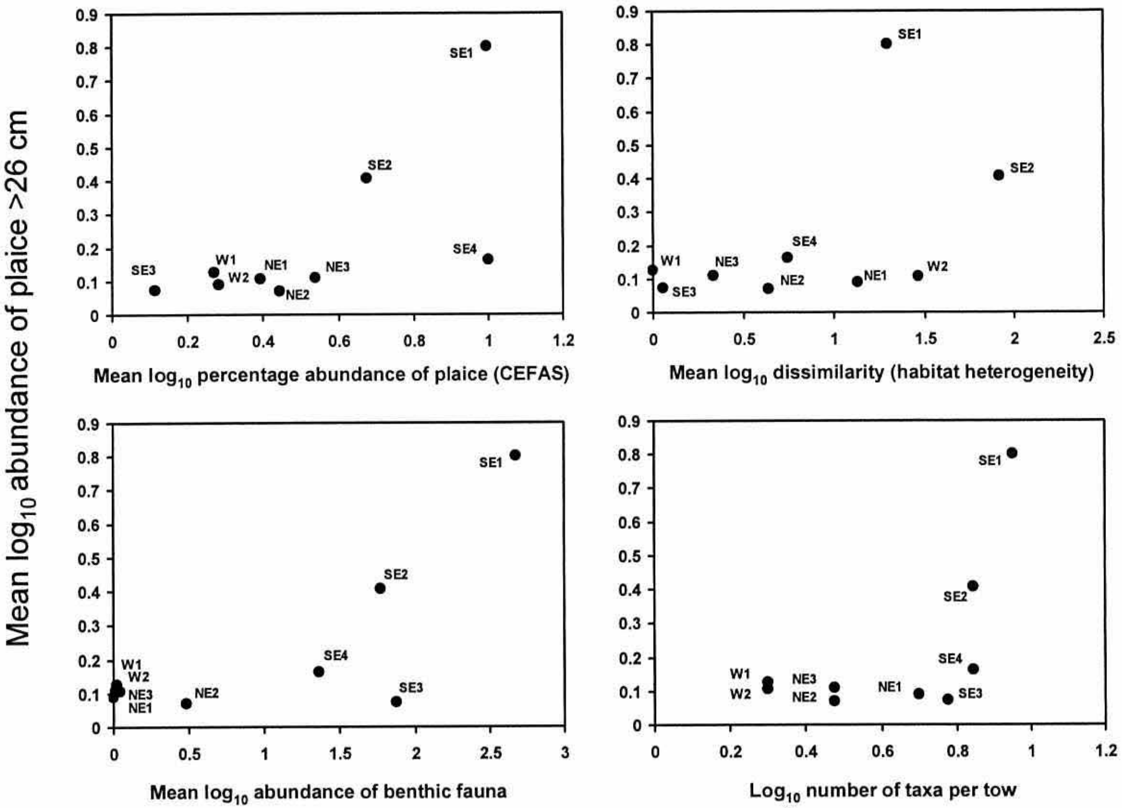

Figure 4.2 Scatter plots of plaice abundance >26cm per 1000m^2 versus: a) mean Log$_{10}$-abundance of plaice from long-term groundfish surveys (CEFAS) b) mean Log$_{10}$-dissimilarity (heterogeneity) of substratum characteristics c) mean Log$_{10}$-abundance of benthic mean d) Log$_{10}$-number of benthic taxa fauna recorded at each site

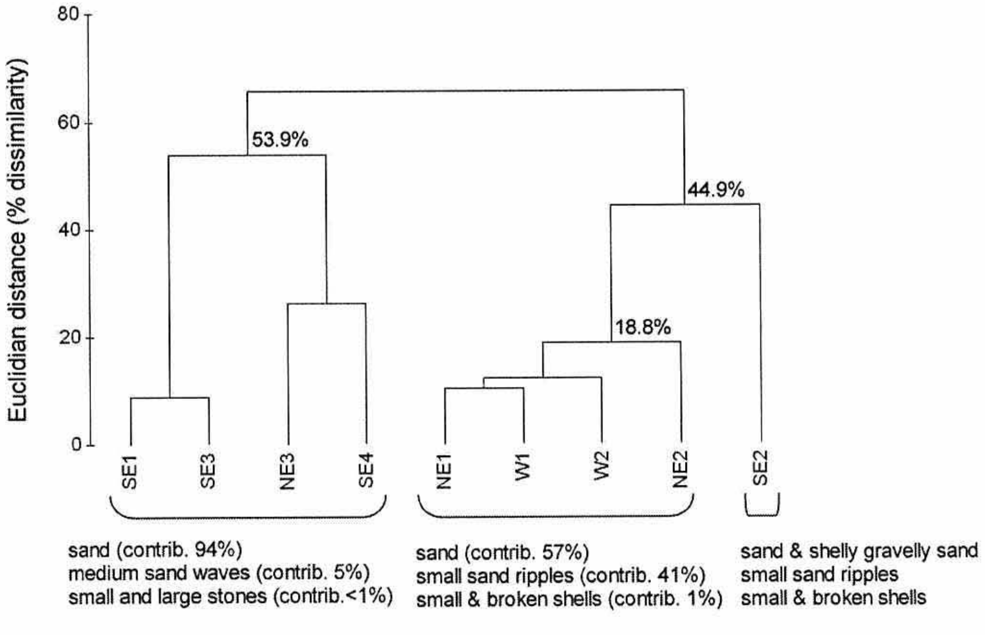

Figure 4.3 Cluster analysis of substratum characteristics showing similarities of station clusters in %. Characteristics of station clusters identified by SIMPER analysis were summarised below station clusters, signified by brackets, with their corresponding percentage contribution to that cluster (contrib.%). Abundances of plaice caught at each site per 1000 m^2: SE1 (5.32); SE3 (0.18); NE3 (0.28); SE4 (0.44); NE1 (0.22); W1 (0.33); W2 (0.27) NE2 (0.17); SE2 (1.56).

Table 4.2 Site, location, depth and a general description of the habitats recorded by video tows. Mean dissimilarity (Heterogeneity indices) and S.D. of physical factors. The higher the mean dissimilarity the more variation in physical features was encountered within a transect.

Station	Area	Dept m	Station description	Mean dissimilarity/ heterogeneity Index ± S.D.
W1	English west	70	Sand substrate, small sand ripples with detritus in the troughs.	0 ± 0
W2	English west	68	Sand substrate with small shell content. Small sand ripples.	27.93 ± 45.05
NE1	English east	16	Sand substrate with small shell and stones with sand ripples and occasional burrows. Occasional clump of *Mytilus edulis.*	12.54 ± 8.16
NE2	English east	20	Sand substrate, some broken shell, and occasional sand wave. Some burrows presents with occasional worm tubes.	3.37 ± 2.96
NE3	English east	21	Sand substrate with small sand ripples. Occasional hermit crab.	1.16 ± 1.26
SE1	French east	22	Sand substrate with some patches of stones with a tube mat cover.	18.86 ± 39.27
SE2	French east	29	Sand substrate with patchy tube mat cover. Patches of shelly gravely sand. Some small sand ripples.	81.79 ± 60.13
SE3	French east	20	Sand substrate with worm tubes at low density.	0.14 ± 0.42
SE4	French east	52	Sand substrate with *Ophiothrix frragilis* beds at the start of the tow. . Medium sand waves.	4.59 ± 7.93

No significant correlation could be found between the water depth (Table 4.2) and the abundance of adult plaice at each station (r= -0.195, *df* = 8, p = 0.615 Fig 4.4). This indicated that within the context of this study, depth had no significant effect on the abundance of plaice.

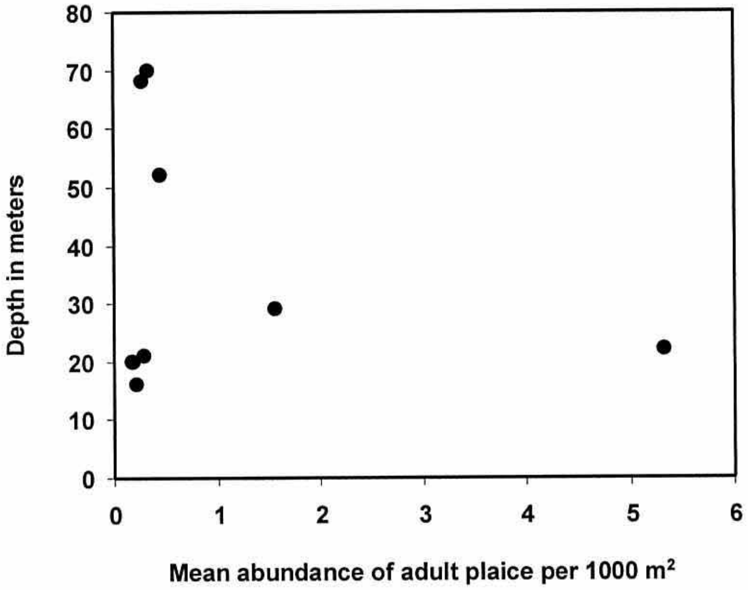

Figure 4.4 Relationship between water depth and mean abundance of plaice per 1000 m^2

4.4.3 Benthic fauna

There was a significant positive correlation between the mean abundances of benthic fauna recorded per 50m at each site and plaice densities (r = 0.750, *d.f.* = 8, p = 0.02, Fig. 4.2). Likewise the total abundance of benthic organisms per video tow also correlated with plaice densities (r = 0.676, *d.f.* = 8, p = 0.045). The number of taxa of the whole camera tow did not significantly correlate with plaice desities (r = 0.614, *d.f.* = 8, p = 0.079).

The correlations between the abundances of benthic fauna and plaice abundances present were greatly influenced by the sites from the east coast of France (SE1-SE4, see Fig 4.2). These sites were the most diverse and largest quantity of benthic fauna was observed, which corresponded well with the numbers of plaice caught. In particular, plaice abundances seemed to be related to the presence of the polychaete tube mat structures, which were found in large patches of high abundance at these sites (Table 1 and 2, Fig 4.5 and 4.6). The species were identified as *Lanice conchilega* and a yet not described species of *Cheatopterus* spp, (Rees *et al.*, 2005).

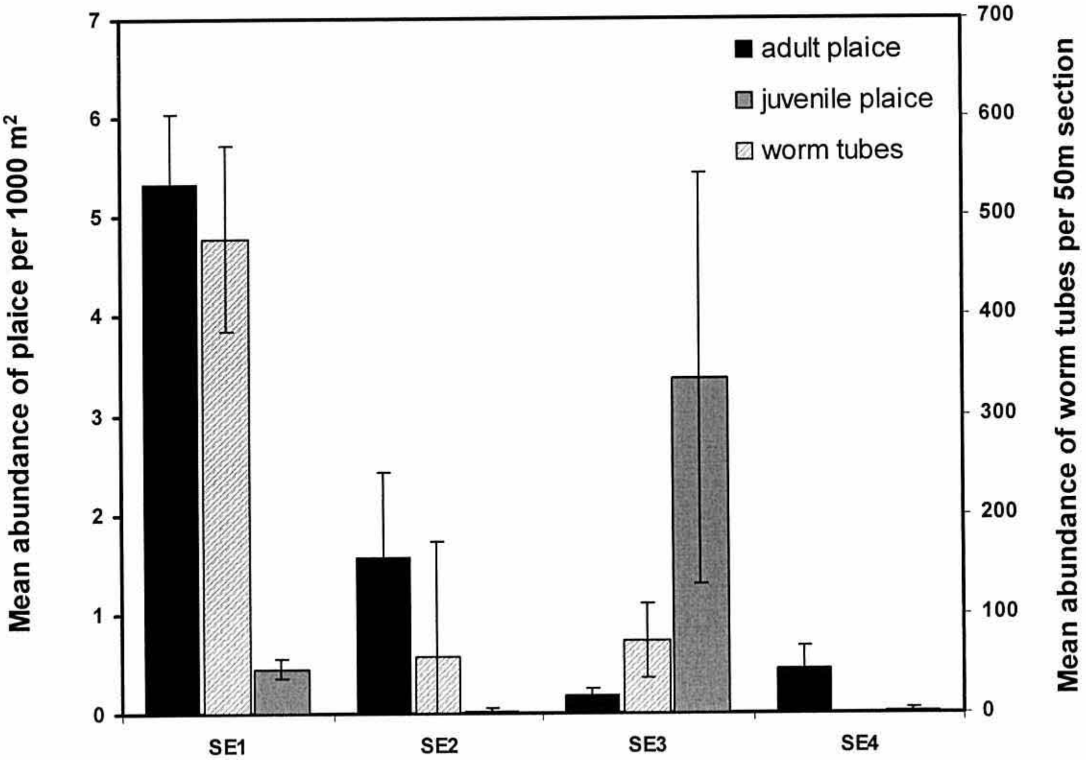

Figure 4.5 Mean abundance of juvenile (<26 cm) and adult plaice (>26 cm) per 1000 m^2 at the French coast sites SE1-SE4. Mean abundance of protruding polychaeta tubes per 50m section for a tow of 200m. Error bars represent S.D.

Station SE1 had the highest densities of protruding polychaetes (≈2390 m^2 S.D. ±470, Fig 4.4 and 4.5) and it also had the highest densities of plaice caught during this study (Table 4.1). On average 5.7 (S.D. ±0.74) plaice were caught per 1000m^2 with the majority of individuals (5.3, S.D. ±0.72) above the MLS (Fig 4.5). Densities of polychaetes were lower at site SE2 (≈287.5 per m^2, S.D. ±575) and more patchy in their distribution. Adult plaice densities also decreased at this site (1.56, S.D. ±0.86). At site SE3 similar mean density levels of protruding polychaetes (≈367 m^2 S.D. ±185) to SE2 were found. However here the distribution was less patchy and if the whole trawl was considered abundances tended to be much lower compared to SE1 and SE2 (Table 4.1). Overall densities of plaice were relatively high (3.55, S.D. ±2.08). Here, catches mainly consisted of small plaice below MLS (3.36, S.D. ±2.06 Fig 4.4). No protruding tubeworms were observed at station SE4 (Fig 4.5 and Fig 4.6) concurring with the lowest density of plaice of all the French coast stations (0.46, S.D. ±0.20). The majority of plaice caught were, however, above MLS (0.44, S.D. ±0.23). SE4 was dominated by the brittlestar *Ophiothrix fragilis* which occurred in large aggregations at the beginning of the tow (Table 4.2). At the remaining sites (W1, W2, NE1, NE2 and NE3) benthic organisms were only rarely caught (Table 4.1). The only other station with a considerable abundance of benthic fauna was station NE1, which was dominated by the common mussel *Mytilus edulis* (Table 4.1). Plaice densities at these sites were much lower compared to the French coast stations and ranged on average between 0.17-0.33 animals per 1000m^2 (2-5 animals per 20 minute tow see Table 4.1).

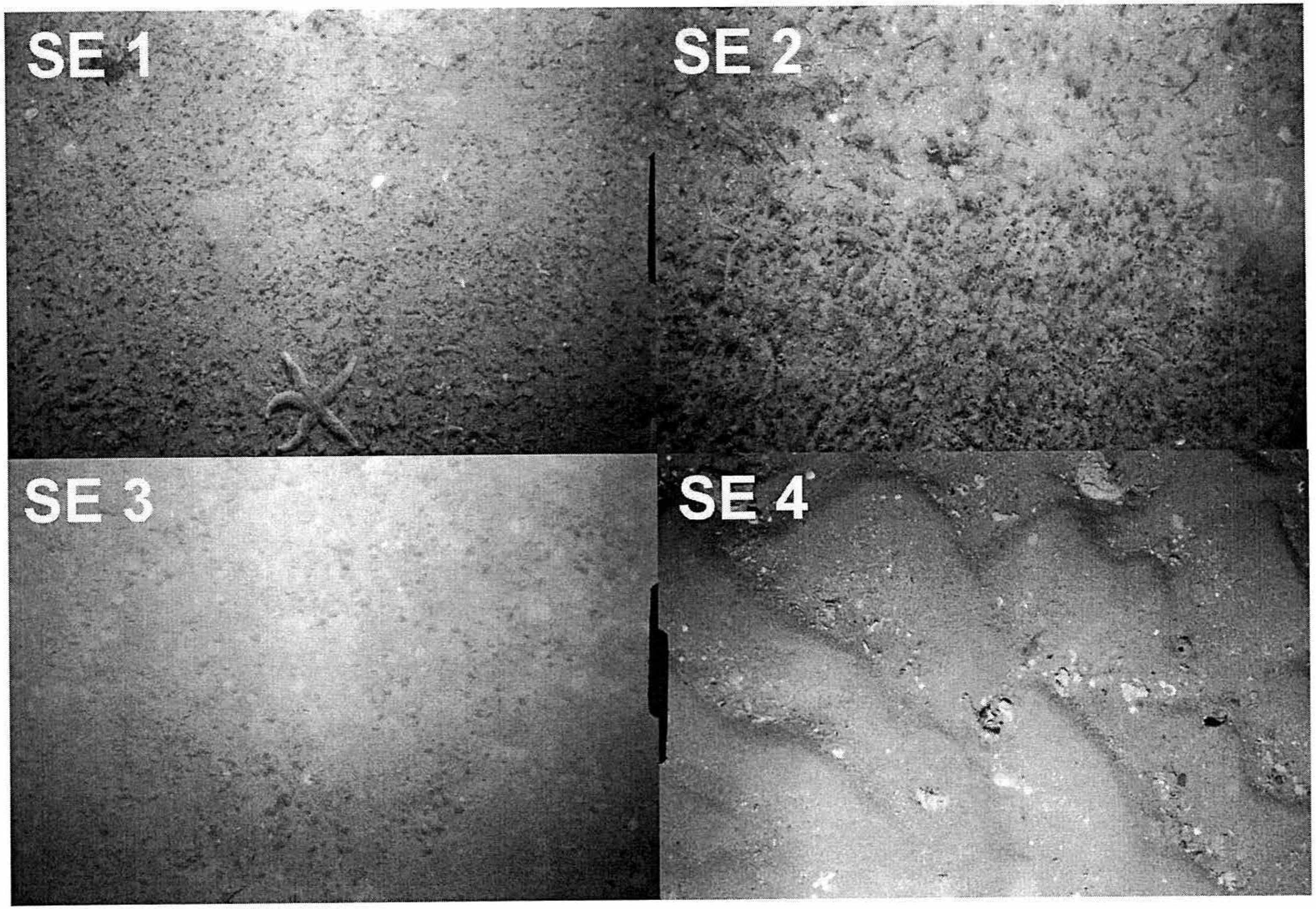

Figure 4.6 Selected representative images from the French coast stations SE1-SE4 taken with a stills camera mounted together with the underwater camera on the video sledge.

4.5 Discussion

4.5.1 Site selection and plaice densities

The results of this study demonstrated that using long-term data sets from groundfish surveys to identify sites of consistent plaice abundances in the English Channel was a relatively accurate predictor of the relative magnitude of fish catches among different sites. Thus it would appear that some environmental component or habitat feature at these sites or behaviour of flatfish in relation to these habitats is relatively consistent. However, relatively few fish were caught at some of the sites which that had lower long-term mean abundances. As all the sites surveyed by this study were apparently consistently utilized by plaice, mean catches of 2-5 individuals per 20 min tow were surprisingly low. This could have been related to low population levels of plaice during the year of sampling. When fish are at low densities, habitat selection theory e.g. Ideal Free Distribution theory (Fretwell and Lucas, 1970) predicts that habitat of highest quality will be occupied first, until density dependant effects (population increase leading to competition) cause them to also occupy less favourable habitats. Consequently if fish densities remain low, fish will be found aggregated over prime habitats (Jennings, 2000) possibly without density dependant effects forcing them into less favourable habitats. Another explanation for the low numbers of fish caught over these sites might be that habitat parameters which attracted fish in previous years had changed due to natural variability or due to the effects of bottom fishing.

4.5.2 Habitat descriptors and plaice densities

The findings of this study suggested that high densities of plaice could be associated with areas that had a rich benthic fauna. In particular, the presence of dense mats of the tube building polychaetes *Lanice conchilega* and *Cheatopterus spp.* seemed to be related to high abundances of plaice. However this relationship was only observed at the stations off the French coast (SE1-SE4) as all other stations had generally low abundances of tubicolous polychaetes and other benthic organisms. Therefore it should be noted that the interpretation of these results relied profoundly on these stations. Nevertheless, the corresponding gradient of benthic fauna and plaice densities observed within these four stations seems to suggest a relationship, which could be explained by the predictions of habitat selection theories e.g. ideal free distribution theory (Fretwell and Lucas, 1970)or MacCall's basin theory (McCall, 1990). Habitat selection theory predicts that areas of high quality (here food resources) will attract larger abundances of fish than habitats of a lesser quality. The abundances of adult plaice observed at the French coast stations followed these theoretical principles when polychaetes tube structures were used as a proxy for habitat quality. Tube building polychaetes are known to be an important component of plaice diet (Jones, 1952; Wyche and Shackley, 1986; Piet *et al.*, 1998; Rijnsdorp and Vingerhoed, 2001) and thus the polychaete mats found in this study can be regarded as a high quality food resource. Moreover, as polychaetes occurred in high abundances, search times when feeding will be minimal, conserving energy and ultimately yielding a higher rate of food intake. It was also interesting to note that at the station with the lowest polychaete tube cover (SE3), abundances of adult plaice (>MLS) were low, while smaller size plaice were found in high abundances. This aggregation of smaller size fish, on habitats of lesser resource value could be related to intra-specific competitive exclusion by the large plaice occupying prime habitats (such as SE1 and SE2). The presence of mainly small plaice could also be due to different habitat requirements between juvenile and adult flatfish. Juvenile flatfish need besides food, protection from predation (Gibson, 1994), since a variety of crustaceans and fish prey upon them leading to high mortality rates (Ansell and Gibson, 1993). Protection from predators is achieved by the cryptic body colouration and the ability to bury into the sediment (Gibson and Robb, 1992; Ansell and Gibson, 1993; Gibson and Robb, 2000). The open spaces left by the less dense polychaete tube mat cover at station SE3 and the entirely sandy substrate may thus have fulfilled both habitat requirements of smaller size plaice. On the contrary protection for larger size flatfish is thought to be less crucial as the number of potential predators decreases with increasing body size (Gibson and Robb, 1992; Gibson and Robb, 2000; Stoner and Abookire, 2002).

Using density of worm tubes, recorded at one point in time as a prognostic tool to predict distribution patterns of plaice for longer time periods may prove to be difficult. Populations of *Lanice conchilega* for example have an ephemeral and patchy distribution (Zühlke, 2001) and densities are likely to change through time. However, there is evidence that the area off the French coast had a similar faunal composition in the early 1970's, indicating some degree of long-term faunal stability. Sanvicente-

Anorve *et al.* (2002) analysed dredge samples collected in 1971-1975 in the eastern English Channel and reported a distinct *Abra alba* assemblage which was characterized by a high species richness and high abundances of *Abra alba* and *Lanice conchilega* (Sanvicente-Anorve *et al.*, 2002). This long-term benthic productivity within the area is likely to be linked to local hydrodynamic regimes. The nutrient rich discharges from the rivers Seine and Somme, together with the eddy caused by the Contentine Peninsula entrapping these nutrient rich waters (Tappin and Reid, 2000), strongly affect primary production (Hoch and Garreau, 1998), thus creating a rich food supply for the resident benthic fauna.

Other habitat parameters besides food availability have been suggested as important for flatfish in particular structuring components such as certain bed forms e.g. sand waves (Norcross and Mueter, 1999) or emergent epifauna e.g. Porifera, Anthozoa or Bryozoa (Stoner and Titgen, 2003) which are thought to give additional protection from predators. Norcross and Mueter (1999) showed that juvenile flatfish were often associated with structures such as biogenic depressions and troughs between sand waves. They also showed that flatfish were randomly distributed over a uniform seabed but had a clustered distribution on heterogeneous substratum. This may indicate that heterogeneous sediments may affect burying capabilities and or prey distribution thus influencing overall flatfish distribution patterns. No significant relationship was apparent between plaice densities and the substratum features and heterogeneity recorded by this study. Although it should be noted that plaice caught by this study were mainly of relatively large size (<26cm) and therefore parameters important for predator avoidance may not be an important factor influencing their distribution (see above). Similar conclusions for adult plaice may hold true for the protective function of structuring epibenthic fauna. Nevertheless this habitat component may still be important for adult plaice as it may provide habitat niche spaces for potential prey organisms. The diet of larger adult plaice besides polychaetes, also contains a large proportion of epibenthic crustaceans and small fish (Carter and Grove, 1991; Piet *et al.*, 1998) which may benefit from the habitat provided by emergent epibenthic fauna (Bradshaw *et al.*, 2003). Thus adult flatfish are more likely to use emergent structures as cues for prey availability. In this study, besides station SE1 (with the highest plaice and faunal densities), few structuring epibenthic species were recorded. Possibly associated prey fauna e.g. small crustaceans or fish could not be detected on images as a consequence of too poor image quality for such mostly small and fast moving animals. Therefore a clear relationship between emergent benthic fauna and plaice abundances could not be established by this study.

4.5.2 Methodological evaluation and sampling scale

This study demonstrates the value of seabed imagery in the characterization of habitat preferences of fish. Unlike other sampling methods video transects allow real-time sampling of the seabed and observation of the spatial distribution and density of both abiotic and biotic features. However, the low resolution of the digital camera makes the detection and identification of small organisms such as amphipods, shrimps and protruding worms sometimes difficult or impossible. Burrowing and small fauna may remain undetected amongst other benthic fauna. Video imagery can therefore not substitute samples taken by trawls and grabs, which sample cryptic fauna more efficiently. However larger areas can be covered by this method and this study demonstrated that meaningful relationships between flatfish and habitat parameters could be established. As the location of the stations sampled were partly separated by considerable geographical distances differences in flatfish density observed may not necessarily reflect differences in habitat quality but indicate differences in populations within regional geographical areas. Indeed CEFAS (unpublished data) assumes the presence of two distinct sub-stocks of plaice in the western and eastern English Channel. These two stocks may vary in their population size and give rise to natural variation in the density of flatfish. One way to reduce the confounding variables would be to compare areas of high and lower flatfish density in more restricted geographical area, so as to reduce variability due to large scale geographical differences. This more small scale orientated approach seems to be supported by the data from the French coast. Stations were positioned in relatively close vicinity to each other and the trends observed here between plaice and benthic fauna may indicate that a sampling regime on a smaller grographical scale may be more successful in studying distribution patterns and thus habitat requirements of plaice than the sea basin scale. However, the results of such a smaller-scale study would have little power as the conclusions would only be applicable to a very restricted area. To date it is unclear at what scale the mechanisms of habitat selection operate (Tyler and Hargrove, 1997). This demonstrates one of the inherent difficulties in the identification of essential fish habitats and habitat requirements of fish in the field and needs further scientific attention.

Chapter 5

Seasonal and annual variability in an epifaunal community in the German Bight

5.1 Abstract

While the benthic infauna of the North Sea has been studied intensively over the past decades, few studies have focused on the larger mobile epifauna. Studies carried out to date have described the distribution of epifaunal communities over the whole of the North Sea but variability within the identified communities, which occurs on a much smaller scale, has so far remained unstudied. This is the first study to describe seasonal and annual variability of an epifaunal assemblage in the German Bight area where environmental conditions are highly variable. The benthic community was sampled with a 2-m beam trawl from 1998-2001. The echinoderms *Ophiura albida, Asterias rubens* and the crustacean *Pagurus bernhardus* were the dominant species caught throughout the study period. Overall the species composition of the catches was relatively consistent while abundances of dominant species fluctuated considerably between sampling periods. Differences between sampling periods were not only influenced by the abundances of dominant species but also by less dominant species such as *Ophiura ophiura*, *Astropecten irregularis, Corystes cassivelaunus, Crangon crangon* and *Aphorrahis pespelicani.* The abundances of these species varied annually and seasonally in the assemblage. Clear differences between summer and winter in the species composition, abundance and biomass were identified. Annual and seasonal changes were most likely linked to migratory movements of epifauna into and out of the area under investigation. Temporal changes in species composition and abundance correlated best with water temperatures while the spatial distribution of the total biomass over the whole sampling period was correlated with sediment characteristics. Anthropogenic influences such as fishing activity and chronic large scale eutrophication are thought to have influenced the community on a long term basis but have been considered unlikely causes for the short term variability described by this study.

5.2 Introduction

Benthic organisms play a key role in the marine ecosystem. They contribute to the biogeochemical cycling of nutrients (Marcus and Boero, 1998; Lilleboe *et al.*, 1999; Levin *et al.*, 2001), provide habitat structures for other organisms (Botto and Iribarne, 1999; Reise, 2002) and serve as an important food source for fish (Jones 1952; Mattson, 1990; Mattson, 1992; Ntiba and Harding, 1993; Du Buit, 1995; Piet *et al*,. 1998). While the benthic infauna of the North Sea has been studied intensively over the last few decades (e.g. Salzwedel *et al*,. 1985; Künitzer, 1990; Kröncke and Rachor, 1992; Kühne and Rachor, 1996) very few studies have systematically investigated the standing stock or variability of benthic epifaunal communities (Jennings *et al.*, 1999).

Due to the lack of contemporary information on the distribution of benthic epifauna in the North Sea research efforts have intensified to monitor their distribution. These studies have mainly focused on the large-scale distribution of the epifauna (Jennings *et al.*, 1999; Ellis *et al.*, 2000; Callaway *et al.*, 2002) in which the distribution patterns of epifaunal assemblages were essentially related to large-scale hydrodynamic features of the North Sea and the results were consistent with those in earlier studies (Glemarec, 1973; Dyer *et al.*, 1983; Frauenheim *et al.*, 1989; Duineveld *et al.*, 1991).

Most of these existing analyses comprise single large scale surveys, only Frauenheim *et al.*, (1989) investigated temporal changes in the distribution pattern of epifauna by comparing epifauna catches made in the summer of 1986 and the winter of 1987 in the whole North Sea. The large-scale studies of epifaunal communities thus far have been limited in their spatial and temporal resolution usually as a result of logistical constraints placed by huge survey areas, a limited amount of time at sea and financial constraints. The sampling grids tended to be very coarse with large distances between individual sampling points. Hence, while these studies captured the large-scale spatial variability of epibenthic assemblages, they did not provide any insight into processes that occur at smaller spatial and temporal scales. However to gain a fuller understanding of the natural variability within the wider epifaunal assemblage, it is necessary to ascertain variability at a range of scales. Without this knowledge it will be difficult to distinguish between the natural variability within an assemblage and long-term changes that might be caused by anthropogenic effects such as pollution, fishing and climate change, or responses to management measures such as the implementation of marine reserves.

This study describes the seasonal and annual variability of an epifaunal assemblage within a mesoscale area of the seabed in the North Sea. At the study site located in the German Bight, the epifaunal biota is exposed to highly variable environmental conditions. Due to the shallow nature of the German Bight the coastal water masses tend to be mixed all year round which causes large seasonal and annual temperature fluctuations compared to the deeper central parts of the North Sea which show much more stable seawater temperature throughout the year (Otto *et al.,* 1990). Additionally, the discharges of Weser and Elbe lead to large fluctuations in salinity and nutrients over a yearly cycle (Otto *et al.,* 1990; Becker *et al,.* 1992), while frontal systems and eddy currents add to the dynamical complexitiy of this region. The position and extent of these frontal systems within the German Bight is mainly driven by variable meteorological conditions (Dippner, 1991). Frontal systems and eddy currents coincide with areas of high primary and secondary productivity (Josefson and Conley, 1997; Skov and Prins, 2001; Dewicke *et al.,* 2002). Changes in the extent and position of frontal systems and eddies can be expected to cause variability in food supply to the benthos and, thus, affect epifaunal community structure along with intensive bottom-fishing activities (Philippart, 1998; Rijnsdorp *et al.,* 1998; Rumohr and Kujawski, 2000; Callaway *et al.,* 2002) and chronic large-scale eutophication .(Hickel *et al.,* 1993; Colijn *et al.,* 2002).

In the present study, we quantify the seasonal and annual variability in an epifaunal assemblage in the German Bight between 1998-2001 and attempt to identify the factors which are accounted for the observed temporal changes and spatial patterns.

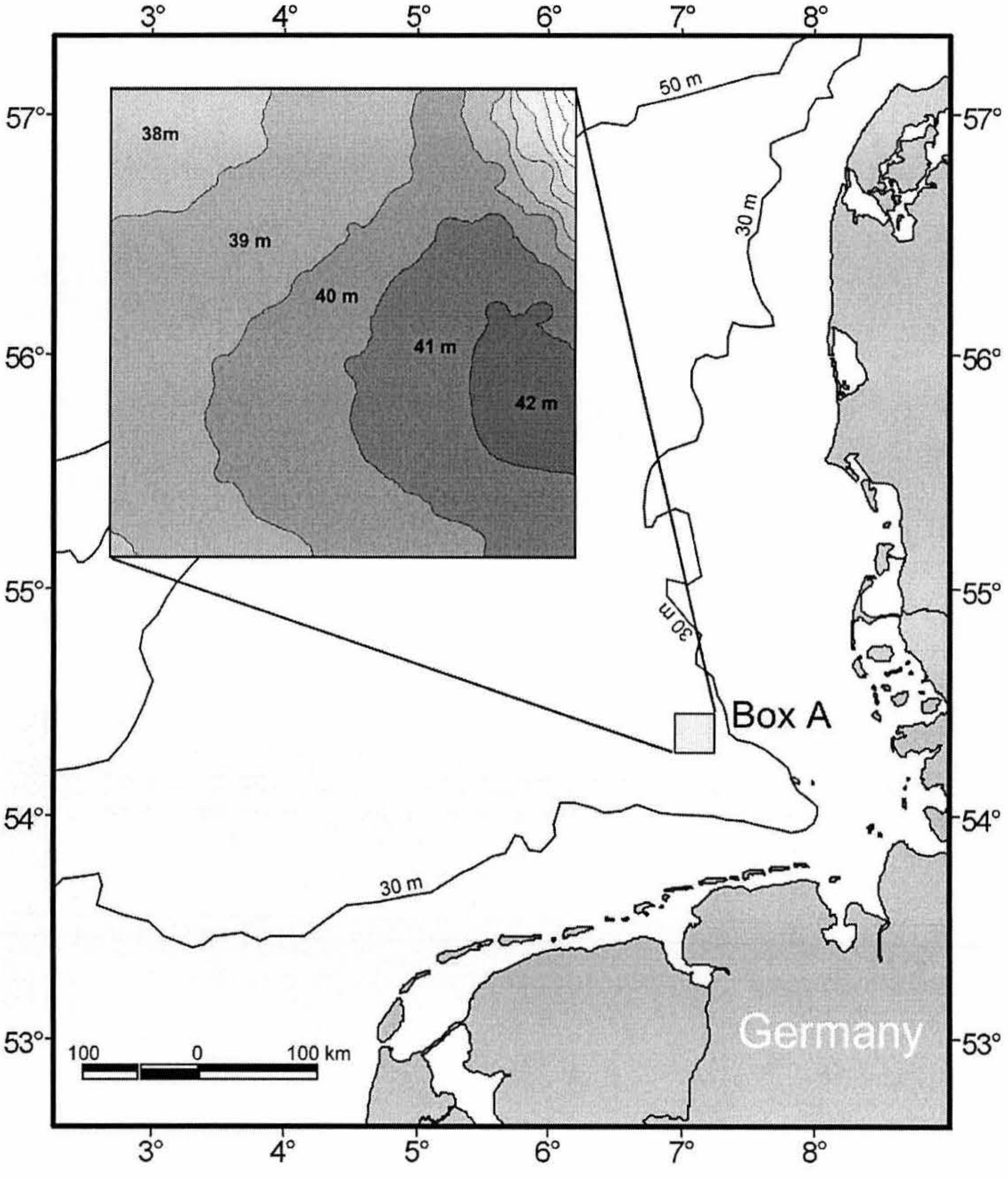

Figure 5.1. Location of the study area Box A in the German Bight and the bathymetry of Box A. Bathymetry isopleths presented in greyscale intervals of 1 meter.

5.3 Methods

5.3.1 Study area

The study area (10 x 10 nautical miles) was located about 30 nautical miles north west of the Island of Helgoland in close proximity of the 30 m-isobath off the old Elbe glacial valley (Fig. 5.1). The mean depth of this area was 39 m with the shallowest area lying in the northeast corner at 33 m and the deepest area in the southeast corner at 43 m (Fig 5.1). The study area (Box A) was setup by Ehrich in 1987, and has been under intensive research effort over the past 15 years (Ehrich and Stransky, 2001). Box A is one of 10 similar survey boxes located around the North Sea. The purpose of studying these boxes was to assess the mesoscale variability of fish assemblages and their changes in relation to fishing effort and climatic changes. Since 1998, quantification of the benthic assemblage has become part of the GSBTS (German Small-scale Bottom Trawl Survey) programme. At Box A, sampling is carried out twice a year, in January and between July-August. The present study examines the spatial, seasonal and annual trends in the epifauna community of Box A between summer 1998 and summer 2001.

5.3.2 Beam trawl sampling

Samples were obtained from the FRV 'Walther Herwig III'. Box A was sampled with a standard 2-m beam trawl (Jennings *et al.*, 1999) using a randomised stratified sampling protocol. The mesh-size of the codend was 4 mm with an outer net with a mesh-size of 1 cm. The beam-trawl was fitted with a Scanmar depth-finding sonar attached to the top of the net just behind the steel beam. The depth sonar was used to monitor the descent of the 2 m beam trawl to the sea floor and to determine the exact time and position of contact with the ground. From the moment of contact with the ground the beam was towed with a speed of about 1 knot for 5 minutes noting the starting and ending positions of each haul. Towing speed and the distance fished over the ground varied according to local currents and wind conditions. The average tow length was 426 m ranging between 205 m to 865 m. Altogether 46 beam trawls were taken during the study period. On average 8 samples where taken in a sampling season. During winter 2000 only 3 samples could be taken due to adverse weather conditions. Sampling did not take place during winter 1999.

Samples were sieved over a 5 mm mesh and then sorted. Most epibenthic fauna was identified and counted onboard ship. Problematic specimens were fixed in 4% buffered formalin for later identification. Wet weight biomass was determined using a motion compensated marine scale. Colonial species, which were difficult to count e.g. *Flustra foliacea,* were noted as absent/present and if possible were weighed.

5.3.3 Sediment characteristics

Sediment samples were obtained during the summer cruise in 1999 to describe the sediment characteristics of the substratum within Box A. Samples were sieved with a 1000 µm sieve to remove shell particles and macroalgae. The fine fraction was then separated by wet sieving over 63 µm mesh size.

Samples for the analyses of total sediment organic carbon (TOC) and nitrogen contents (TN) were stored at –20 °C. Prior to analysis the samples were freeze-dried, powdered and homogenized. An aliquot of 10-30 mg was combusted at 1010 °C in a C/N analyser (vario el) following acidification of the samples with concentrated HCl in silver sample cups to remove inorganic carbonates.

To visualize the distribution of mud content within Box A the sediment data was entered into a Geographic Information System (Arc View 3.3) and interpolated over the whole study area (Fig. 5.2 b-d). The percentage mud content of the sediment was interpolated using Inverse Weighted Distance interpolation (IDW). The IDW interpolator assumes that each input point has a local influence that diminishes with distance. It weights the points closer to the processing cell greater than those that are further away. A specified number of points, or optionally all points within a specified radius, can be used to determine the output value for each location.

The results of this interpolation were compared to an earlier study on the sediment characteristics in this region (Figge, 1981) (Fig. 5.2 a). Although the two sampling events were separated in time by approximately 18 years the spatial distribution of mud within Box A was very similar (Fig. 5.2 a, b). From the similarity between the results of these studies it would appear that sediment distributions in Box A are relatively stable. The distribution of TOC and TN and mud content are usually a refection of prevailing hydrodynamic conditions. Highly mobile sediments within the

German Bight predominantly occur in the near shore area around the 10-20 m isobath (Zeiler *et al.*, 2000) while the deeper areas below 30 m are depositional sites. Due to this sign of stability, and the absence of sedimentlogical data for the other sampling periods it was decided to apply the interpolated sediment data collected in 1999 to all stations sampled during different sampling periods. The derived values were used as environmental factors in the BIOENV analysis described below.

5.3.4 Data treatment and analysis

Invertebrate catches where standardized to a tow length of 200 m (area sampled = 400 m²) and multivariate community analyses were carried out using the Primer v.5 analytical software. Multidimensional scaling analysis (MDS) were undertaken on fourth root-transformed data (semi quantitative) and on presence and absence data (purely qualitative) to separate groups of stations with similar species composition. Both transformed and presence/absence data were used in the analysis as a comparison between quantitative and qualitative data permits an evaluation of how strongly the observed patterns in the quantitative data are influence by species abundance data. Multidimensional scaling were based on calculations of Bray-Curtis similarity matrices (Bray and Curtis, 1957). Significance tests for temporal differences in the composition of the assemblage were preformed using the ANOSIM randomisation test (Clarke and Green, 1988). Characteristic species for each sampling season were identified using SIMPER analysis. This programme quantifies the percentage contribution that each species makes to the similarity within each each group of samples (in the present study a specific sampling period) and to the difference (dissimilarity) between different groups of samples.

To identify which underlying environmental factor best correlated with the observed community patterns the BIOENV analysis was used. The BIOENV analysis compares the agreement between the biotic similarity matrix and the Euclidian environmental matrix using the Spearman rank correlation coefficient. In the BIOENV analysis following parameters were used: depth, average seasonal sea surface temperature, percentage mud (<63 µm), percentage TOC, percentage TN and the distance covered by individual tows. Seasonal sea surface temperatures were used as a proxy for bottom temperature as the water column is generally well mixed throughout the year in this area of the North Sea (Otto *et al.*, 1990).

To investigate spatial trends in the distribution of the total epifauna biomass within the area of Box A, the biomass values of each station were standardized by conversion to percentage biomass per sampling period. This conversion was preformed to prevent bias in the analysis by exceedingly high biomass levels in any one sampling period. It should be noted that the number of stations per sampling event varied from 3-11 and that the data therefore were slightly imbalanced. This imbalance was tolerated for all sampling periods to avoid loss of spatial coverage except for winter 2000. In winter 2000 only three samples were taken and the sampling period was therefore excluded from the analysis. The percentage biomass was correlated with percentage mud (<63 µm), percentage TOC, percentage TN using Spearmann's rank correlation.

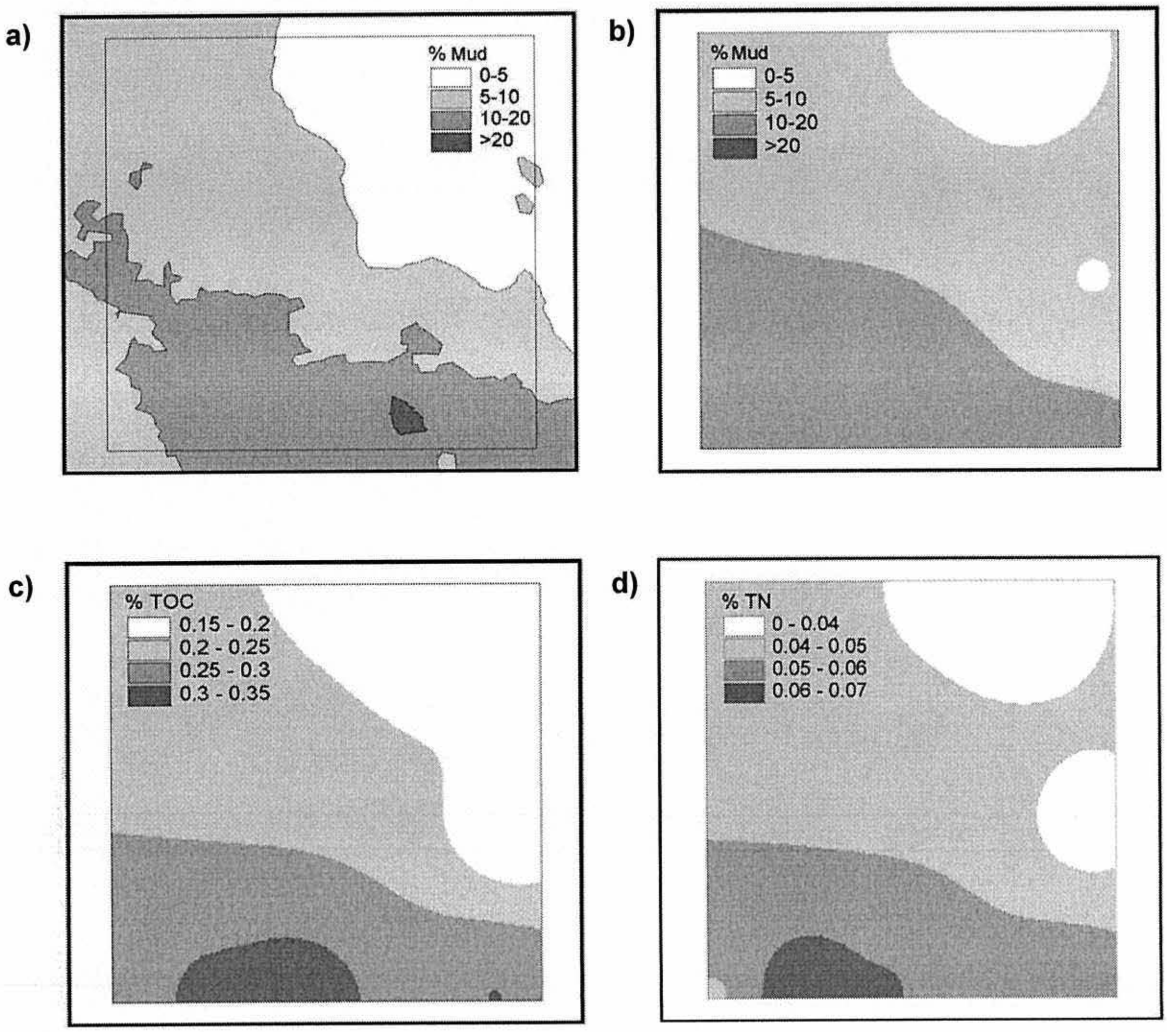

Figure 5.2. Sediment characteristics within the study area Box A **a** Percentage mud content modified after Figge (1981) **b** Percentage mud content in 1999 **c** Percentage of total organic carbon **d** Percentage of total nitrogen

5.4 Results

5.4.1 Sampling effort

The number of samples obtained during each sampling period varied between 3 in winter 2000 and 11 in summer 1998 (Fig. 5.3 a). The distribution of sampling sites within Box A was haphazard (Fig. 5.4 a). The number of samples taken in any sampling period depended on suitable weather conditions and available sampling time.

5.4.2 Sediment characteristics

The isopleths of the mud content of the sediments of Box A showed a clear pattern with high mud content in the south west corner gradually decreasing towards the north east corner (Fig. 5.2 b). This pattern was consistent with findings from an earlier study (Figge 1986, Fig 5.2 a). Variation in TOC and TN percentage was consistent with variation in the mud content, with high values in the south west corner of Box A decreasing towards the north east corner (Fig 5.2 c, d).

5.4.3 Biomass

Across all years the highest mean biomass was recorded in summer 1998 when catches ranged from 2.1 to 7.6 kg wet weight per 400 m^2 (5.2-19 g m^2). Not surprisingly the biomass of winter catches was always lower than summer catches. The lowest mean biomass was recorded in winter 2001, which ranged between 0.05 to 0.4 kg per 400 m^2 (0.12-1 g m^2). Six months later, in summer 2001, biomass rose to 0.5-2.7 kg per 400 m^2 (1,25-6.75 g m^2, Fig. 5.3 a).

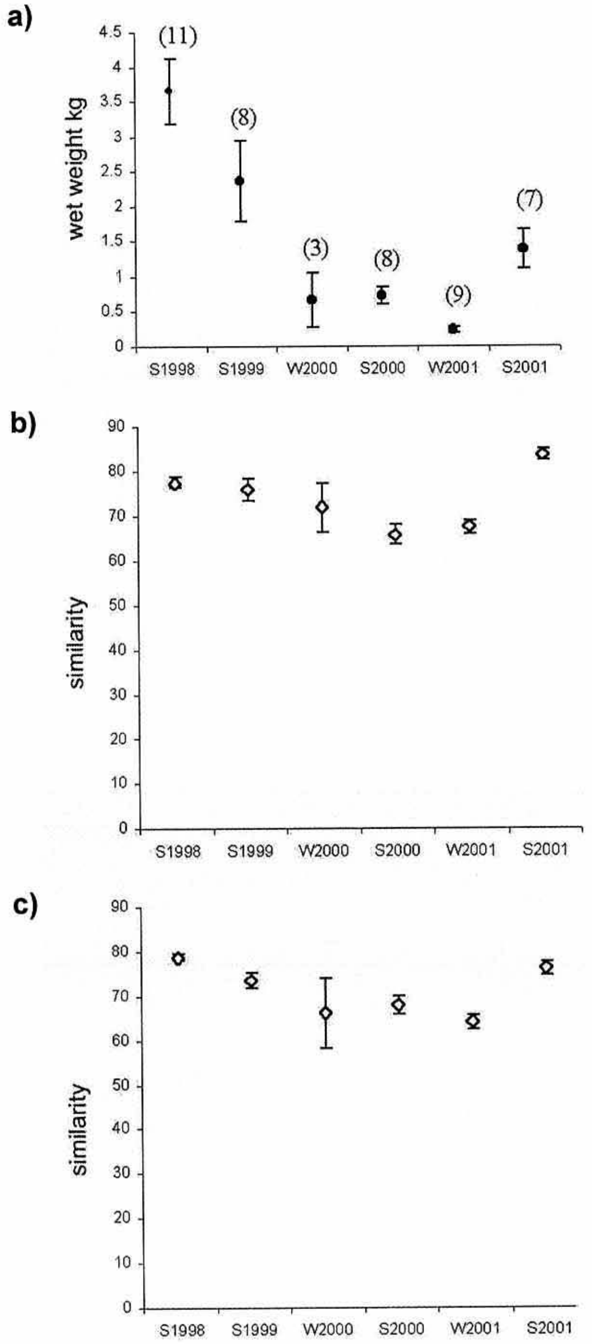

Figure 5.3 Temporal changes in biomass and community similarity **a** Biomass expressed as mean wet weight (± S.E). The number of trawls conducted in each sampling period is given in brackets **b** Mean Bray Curtis similarity presence/absence data (± S.E.) **c** Mean Bray Curtis similarity fourth root transformed data (± S.E.).

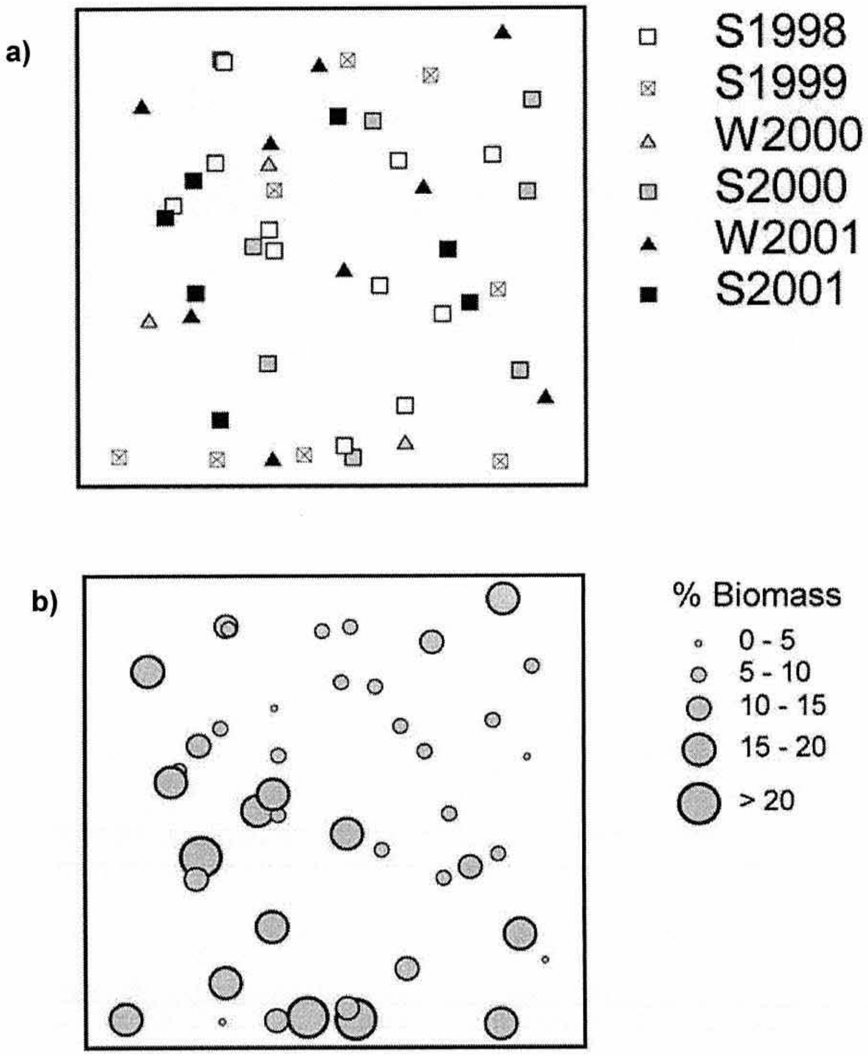

Figure 5.4. Tow location and relative biomass distribution in different sampling periods within Box A **a** Position of individual tows **b** standardized percentage biomass of each tow.

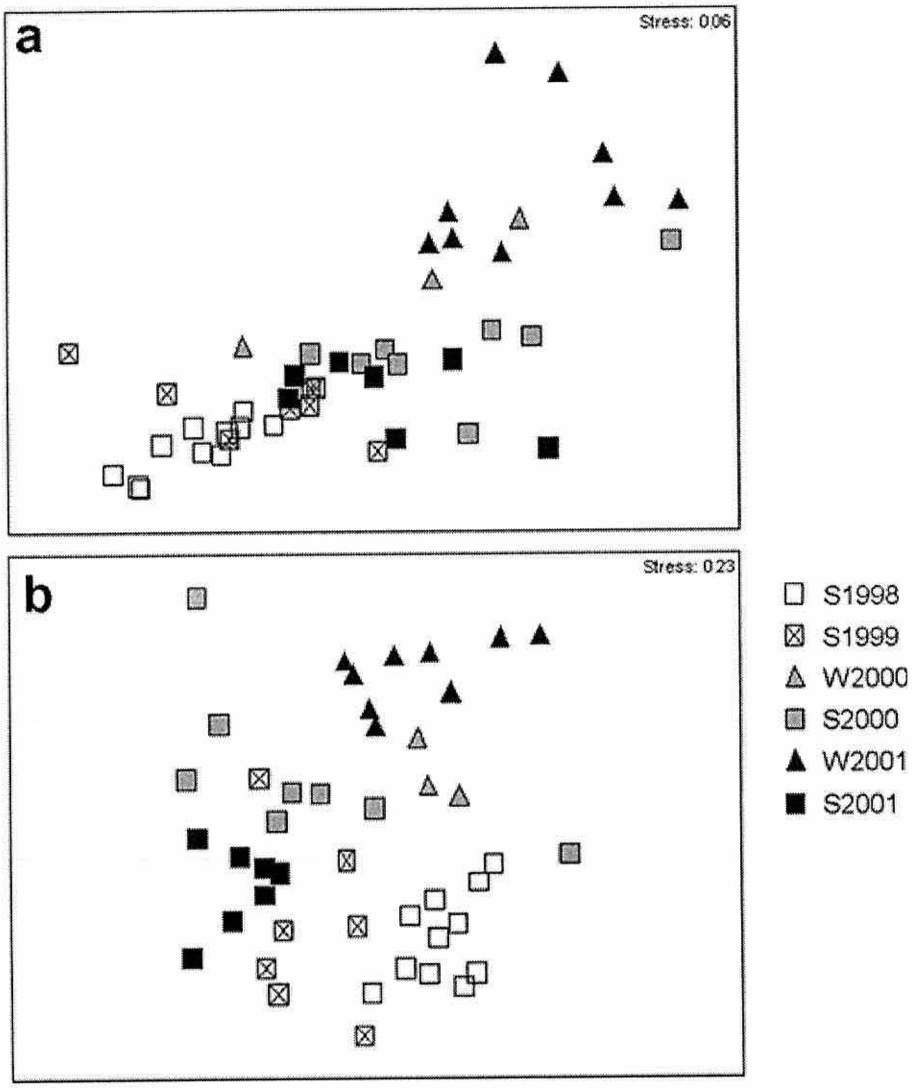

Figure 5.5 Multivariate community analysis of animals collected during different sampling periods **a** MDS plot of fourth root transformed abundance data **b** MDS plot of presence and absence data

5.3.4 Community analysis

The overall similarity of all samples taken throughout this study was 47% for the fourth root transformed data and 48% for the presence and absence data. The similarity of catches within each sampling season was very high. The highest similarity was found in summer 1998 with a mean of 76% for the fourth root transformed data and in summer 2001 with a mean similarity of 84% for the presence and absence data. The lowest similarity of catches was observed in winter 2001 with a mean of 64% similarity between catches for the fourth root transformed data and in summer 2000 with a mean of 66% similarity for the presence/absence (Fig. 5.3 b, c).

The MDS plot of the fourth root transformed data showed winter and summer samples well separated (Fig. 5.5). However samples from the summers 2000 and 2001 did not show significant differences with either previous winter sampling period (Table 5.1). The separation of samples collected during the summer periods between 1998-2001 was less prominent but statistically significant except for the summers 2000 and 2001 which did also not differ significantly from each other (Table 5.1). 1998 was the most distinct sampling period with all 11 tows clustering very close together, which indicated the low inter-sample variability in that year. All other years showed a much greater dissimilarity between replicate tows. The MDS plot showed a clear directional trend in the summer samples from 1998 onwards. Summer sampling periods following 1998 were found shifted towards the right side of the MDS plot closer towards samples collected during the winter periods (see Fig. 5.5 a). Presence and absence data showed a greater overall similarity between samples from different sampling periods compared to fourth root transformed data and the separation of sampling periods was also much clearer (see Fig. 5.5 b). The clear directional trend between summer sampling periods observed in the fourth root transformed data was not apparent in the presence and absence data (Fig. 5.5 a, b). The ANOSIM results of the presence/absence data (qualitative) showed that station groups from different sampling periods differed significantly from each other except samples collected during winter 2000 and winter 2001 (Table 5.2).

Table 5.1 Anosim results of the fourth root transformed abundance data. Significant differences at P < 0.05 were made noticeable by a star (*)

	S1998	S1999	W2000	S2000	W2001
S1999	0.429*				
W2000	0.837*	0.543*			
S2000	0.845*	0.339*	0.191		
W2001	0.994*	0.916*	0.121	0.428	
S2001	0.783*	0.196*	0.413	0.092	0.759*

Table 5.2 Anosim results of the presence and absence data. Significant differences at P < 0.05 were made noticeable by a star (*)

	S1998	S1999	W2000	S2000	W2001
S1999	0.829*				
W2000	0.842*	0.745*			
S2000	0.84*	0.431*	0.401*		
W2001	0.953*	0.761*	-0.086	0.656*	
S2001	0.886*	0.76*	0.994*	0.478*	0.912*

Table 5.3 Results of the Simper analysis for the fourth root transformed abundance data. Contribution (%) of epifauna caught from 1998 to 2001. Cut-off point 90% (S summer; W winter)

	S1998	S1999	W2000	S2000	W2001	S2001
Ophiura albida	39	38	31	37	26	33
Asterias rubens	25	20	22	27	22	21
Astropecten irregularis		7		17	11	5
Psammechinus miliaris						8
Pagurus bernhardus	8	8	7	6	4	10
Corystes cassivelaunus	4	6				10
Liocarcinus holsatus	8	8		4	8	
Liocarcinus depurator						6
Crangon allmani	7		16		11	
Crangon crangon			8		11	
Nucula nitidosa		7				
Total number of species	6	7	5	5	7	7

5.4.5 Species variability

Samples during all periods were consistently dominated by the brittle star *Ophiura albida* and the sea star *Asterias rubens. O. albida* was the most dominant species in numerical and biomass terms. The SIMPER analysis on the quantitative data showed that together both species contributed to over 48 % to the similarity within each sampling period (Table 5.3). The hermit crab *Pagurus bernhardus* was found to consistently contribute to the similarity within each sampling period. All other species varied in their contribution to the similarity in each of the sampling periods.

In Summer 1998 the abundances of *Ophiura albida* (Fig. 5.6 a), *Asterias rubens* (Fig. 5.6 c), *Pagurus bernhardus* and the swimming crab *Liocarcinus holsatus* were higher then observed during any other sampling period. In addition the masked crab *Corystes cassivelaunus* (Fig. 5.6 d) and the shrimp *Crangon allmanni* (Fig. 5.6 b) were found in high abundances and contributed to the overall similarity of summer 1998 (Table 5.3). Between summer 1998 and summer 1999 the abundances of the dominant species decreased and other species such as *Ophiura ophiura* and the gastropod *Aphorrhais pespelecani,* which were present in summer 1998, did not occur in catches in summer 1999. However the sea star *Astropecten irregularis* (Fig 5.6 e), of which only a few individuals were caught in summer 1998, occurred in high abundances in summer 1999. Individuals caught in 1999 were adult animals with a diameter of 5-8 cm. In summer 2000 the abundance of the dominant species *O. albida, A. rubens* and *P. bernhardus* were the lowest abundances recorded for the summer seasons, In 2001 abundances of these dominant species rose again as did abundances of *Astropecten irregularis.* .

Winter samples were characterized by very low abundances of dominant species compared to summer samples. The samples from winter 2000 showed slightly higher abundances than in winter 2001; however, in 2000 only three samples could be obtained compared to nine samples in 2001. *Crangon crangon* (Fig. 5.6 f), which was only present in the summer samples of 1998, occurred frequently in the winter samples 2000 and 2001 together with *C. allmanni* (Fig. 5.6 b). The abundance of *A. irregularis* decreased in the winter samples compared to abundances of the previous summer samples (Fig 5.6 e).

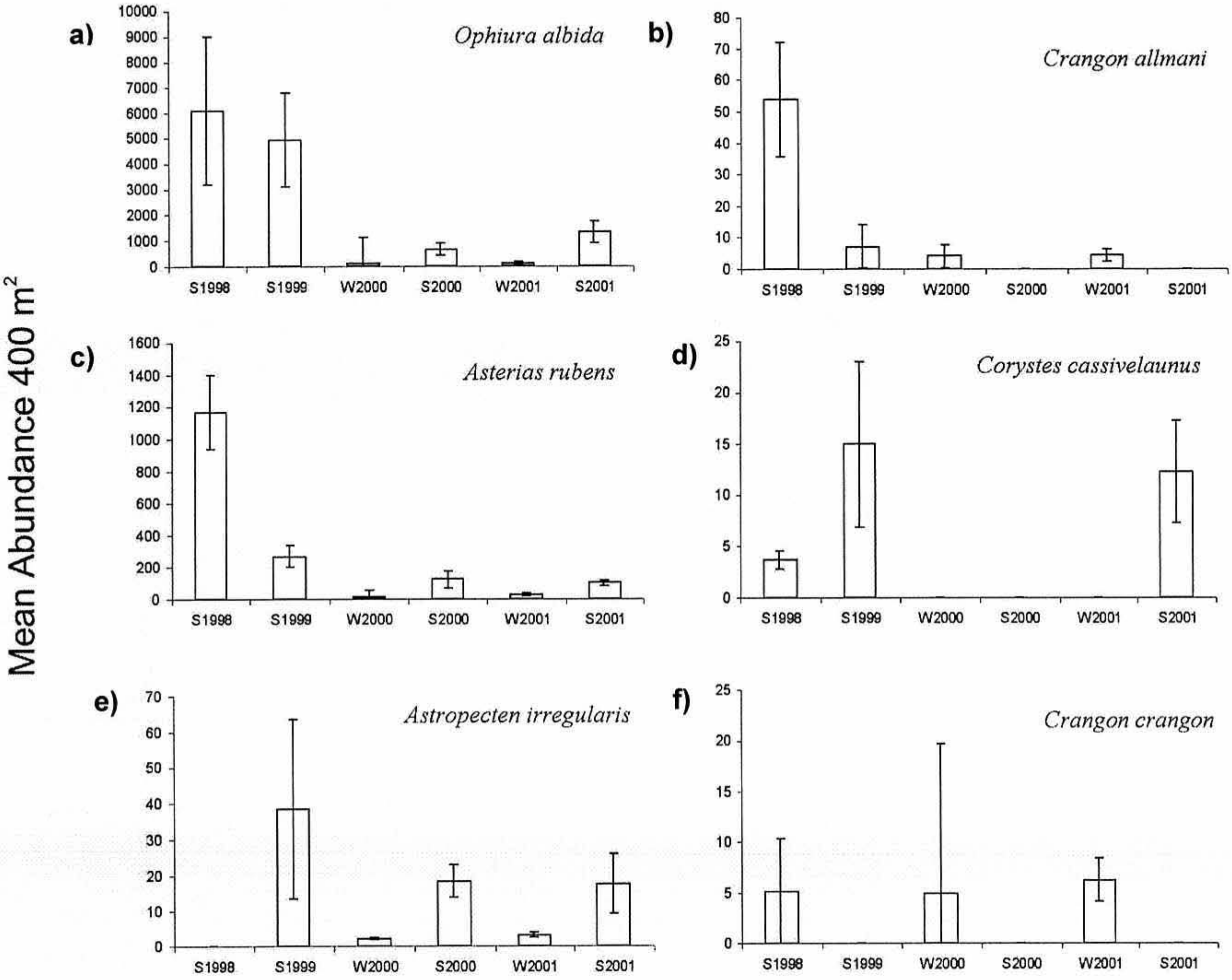

Figure 5.6 Mean abundance + S.E. of selected species collected during different sampling periods **a** Abundances of *Ophiura albida* **b** *Crangon allmanni* **c** *Asterias rubens* **d** *Corystes cassivelaunus* **e** *Astropecten irregularis* **f** *Crangon crangon* within Box A

5.4.6 Environmental factors

The correlation of the quantitative biotic data with environmental factors (BIOENV) showed that the observed assemblage pattern was best correlated with the average seasonal sea surface temperature ($p = 0.51$). The combination of all environmental factors had a Spearman rank correlation factor of $p = 0.34$. Percentage mud content alone showed a weak correlation with the observed assemblage pattern ($p = 0.04$).

The distribution of the standardized percentage total biomass of the different sampling periods showed a clear gradient within Box A with high biomass levels occurring in the south west corner decreasing towards the north east corner (Fig. 5.4). This trend corresponded with the spatial distribution of percentage mud, percentage TOC and percentage TN (Fig. 5.2 c-d). Correlation of percentage biomass with percentage mud (Spearman rank $R = 0.507$; $p < 0.001$), percentage TOC (Spearman rank $R = 0.457$; $p < 0.001$) and percentage TN (Spearman rank $R = 0.515$; $P < 0.000$) proved to be positive and statistically significant. The biomass was composed in the main of two species *Asterias rubens* and *Ophiura albida*. These occurred in large abundances in all sampling periods and contributed on average to 84% of the total biomass ranging from 65% in winter 2001 to 91% in summer 1998. Data of the total abundance of fauna followed the same spatial and seasonal trends as described here for the biomass.

5.5 Discussion

5.5.1 Temporal and spatial community structure

The epifauna assemblage encountered in the study area northwest of Helgoland (Box A) was composed of species that are typical for the southern parts of the German Bight as described by many authors (Künitzer, 1990; Duineveld *et al,*. 1991; Kühne and Rachor, 1996; Jennings *et al.,* 1999; Rees et al. 1999; Callaway *et al.*, 2002). The echinoderms *Ophiura albida, Asterias rubens* together with the hermit crab *Pagurus bernhardus* were the dominant species caught throughout the study period between 1998-2001. Over all, the species composition of the catches was relatively consistent over the whole sampling period. This was reflected in the proportional importance of the dominant species in terms of their contribution to the assemblage, which remained stably high throughout the whole sampling period. However, abundances of these species fluctuated considerably between sampling periods. This variability in abundance largely influenced the results of the multivariate analysis as a comparison of MDS plots based on fourth root-transformed data and from presence/absence data clearly indicated. However, differences between sampling periods were not only influenced by the abundances of dominant species but also by less numerically dominant species such as *Ophiura ophiura, Astropecten irregularis, Corystes cassivelaunus, Crangon crangon* and *Aphorrahis pespelicani.* These less dominant species varied annually and seasonally in their importance in structuring the assemblage.

The overall similarity of replicate tows within any one sampling period was high. This indicated that replicate tows taken at random within the area of Box A had relatively homogenous catch compositions. The replicate tows of the winter 2000 and 2001 had the lowest within sampling-period similarities which indicated that catch composition was more heterogeneous compared to the summer sampling periods. As the similarity of replicate tows collected during the winter periods were still considered as being relatively high (minimum 64 %) this suggested that spatial patterns in the species composition within Box A had a relatively weak influence on the overall similarity within sampling periods. Spatial patterns did however exist in Box A and these became apparent when the distribution of total biomass was considered, biomass values decreased from the northeast corner to the southwest corner of Box A. Thus this spatial pattern seemed to be consistent through time. The spatial pattern was positively correlated with sediment characteristics (percentage mud content, TOC and TN). High numbers of the dominant species *O. albida* and *A. rubens* in Box A thus appear to be associated with a high mud content, TOC and TN levels in the sediment. A positive correlation of high benthic biomass levels and sediment characteristics is also well documented for infauna communities in the North Sea (Heip and Craeymeersch 1995).

The temporal changes noted in the species composition between sampling periods were most influenced by water temperature. These results correspond well with recent findings on the distribution of epifauna communities in the North Sea (Callaway *et al.*, 2002) which also showed that water temperature was the major factor in influencing community structure and abundances.

5.5.2 Abundance and biomass variability

Biomass of the assemblage continually decreased from relatively high levels in summer 1998 until winter 2001 when the lowest biomass levels were observed. The decrease in biomass was mainly caused by the decrease in abundance of the dominant species *Ophiura albida* and *Asterias rubens.* In summer 2001 a sharp increase in abundance of *O. albida* and *A. rubens* led again to higher levels in biomass but these remained at lower levels than occurred in summer 1998 and summer 1999. The question now is what causes these large fluctuations in biomass levels over this relatively short period of time?

O. albida and *A. rubens* are both mobile species able to react to favourable and unfavourable conditions. In 1998 favourable conditions might have attracted or sustained high abundances of these two species. High organic matter input caused by a frontal system which may have occurred in the area of Box A or in its proximity around 1998 could be one explanation. Fronts occur in areas where water masses of different physical properties such as salinity, temperature or nutrients come into contact with each other. They have been shown to be sites of increased primary productivity with concomitant higher productivity in the benthos (Josefson and Conley, 1997) and hyperbenthos (Dewicke *et al.,* 2002). Box A lies in close proximity to the main catchments areas of fronts which occur in the German Bight (Fig. 5.7). Three types of fronts can be observed within this area of the German Bight, which have been classified by Krause *et al.* (1988). The seasonal thermal fronts, which occurs between the boundaries of stratified and mixed water, the River Elbe plume front and the upwelling front caused by easterly wind conditions. There is some evidence that in 1997 weather conditions prevailed that could have influenced frontal systems in the German Bight. "Strong easterly winds at the beginning of 1997 might have caused the frontal plume of the river Elbe to shift offshore in westerly direction towards Helgoland" (Weigelt, 1997). Easterly wind conditions are also thought to cause upwelling fronts where the southern North Sea bottom water of the Old Elbe glacial valley estuary is brought to the surface causing a "temperature anomaly" (Scherhag, 1963). Although the area of Box A does not lie directly in the catchments areas of the frontal systems described by Krause (1988) infra red satellite images of thermal fronts have been recorded for the area of Box A by Harding between 1978 to 1980 (Otto *et al.,* 1990) (Fig. 5.7). Josefson and Conley (1997) studying the frontal system in the area of the Skagerrak–Kattegat reported high abundances of the ophiurid *Amphiura filiformis* (maximum density > 3000 ind. m^2) that were explained by the high sedimentation rate of primary production in the frontal area. *Ophiura albida* in 1998 showed proportionally to its size high abundances of a similar magnitude (maximum density 30 ind. m^2). *O. albida* and *A. filiformis* both can feed and benefit from particulate organic matter settling from the water column. While *A. filiformis* is an interface feeder actively selecting particles with its arms from the water column (Loo *et al.*, 1996), *O. albida* is able to feed on already settled particles on the sediment surface. *Ophiura albida* may also benefit indirectly from the increased organic matter by feeding predatory on the increase secondary benthic production as it is generally classified as an omnivore (Ambrose, 1993). *O. albida* being the larger and more mobile species may in contrast to *A. filiformis* be able to react more flexible to varying environmental conditions. *O. albida* may thus be able to move in respond to the changing front. *Asterias rubens* has a mainly scavenging and predatory mode of life and may therefore respond to the general trends in biomass levels and food availability.

The continuous decrease in overall abundance and biomass from summer 1999 to winter 2001 might suggest that favourable conditions ceased which led to a mass migration out of Box A into more favourable areas. Other alternative explanations could be hypoxia events leading to mass mortality or low new recruitment following summer 1998 leading to a continuous decrease in abundances over time. However no hypoxia event has been recorded for this area of the North Sea during the study period. Failed recruitment could be a possible scenario leading to low abundance levels if a high mortality rate of the adult population of the dominant echinoderms is assumed. But this does not explain the sharp increase in abundances in summer 2001 following the lowest abundances and biomass levels recorded by this study six month earlier (winter 2001). *Ophiura albida* and *Asterias rubens* found in the trawls of summer 2001 were of adult size and therefore mass migratory movements seems the only plausible explanation for the observed increase in summer 2001.

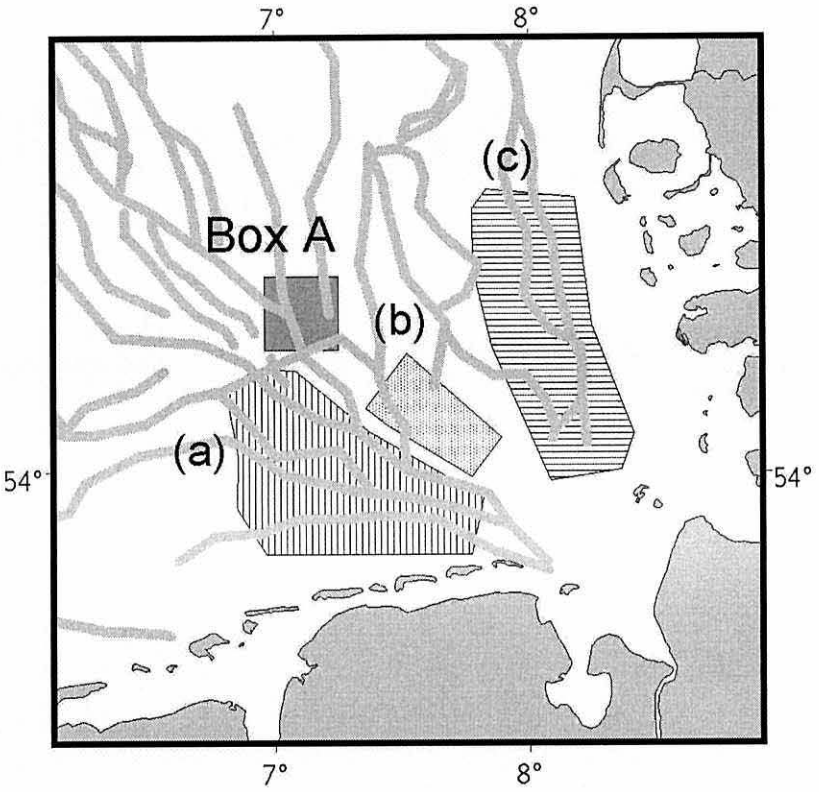

Figure 5.7 Location of Box A in relation to frontal areas in the German Bight. Area block (a) thermal (b) up welling (c) river plume modified after Krause et al (1988). Grey lines represent the positions of thermal fronts recorded via infra red satellite from 1978 to 1980 by Harding (Otto et al. 1990)

5.5.3 Seasonal variability

From the multivariate community analysis it became obvious that winter and summer samples had a distinct composition. *Astropecten irregularis, Crangon crangon* and *Crangon allmanni*, which occurred in proportionally higher abundances in the winter samples were responsible for the main differences between seasons. *A. irregularis* showed seasonal fluctuations in abundance after it was first caught in high abundances in summer 1999. The reason why it was almost absent in summer 1998 could be explained by the previously severe winters in 1995-1996 and 1996-1997. Similarly *A. irregularis* was absent from samples collected near Helgoland after the severe winter of 1962-1963 (Ziegelmeier, 1964). *A. irregularis* is thought to be affected by seawater temperature below 3°C limiting its distribution (Ursin, 1960). The 3°C isothermal border is likely to have shifted further offshore during these cold winters inducing *A. irregularis* to migrate into deeper water. Seasonal migration of *A. irregularis* triggered by cold temperatures was described by Freeman *et al.* (1999)

for a shallow area in the Irish Sea, where seasonal migration patterns were revealed. The mild winter temperature after 1997 might have allowed *A. irregularis* to migrate into the area of Box A in 1999 shifting the extend of its distribution border further inshore. In particular, the influx of exceptionally warm water masses into the North Sea in 1998 associated with a positive NAO Index (Reid *et al.*, 2001), could be linked to the changes in distribution of temperature limited species. As the specimens of *A. irregularis* found in 1999 were adult animals with a diameter of 7-8 cm migration seems the only plausible explanation for the observed increase in 1999. After 1999 a slight seasonal trend with higher abundances during summer and lower abundances in the winter was observed which could suggest a trend similar to that observed by Freeman *et al.* (1999) in the Irish Sea.

Crangon crangon followed a similar seasonal pattern to *A. irregularis* after summer 1998. Between 1999-2001 it occurred in high abundances in the winter samples and absence in the summer samples. The seasonal migration patterns of the brown shrimp *C. crangon* are well known (Boddecke 1976; Spaargaren 2000; Temming and Damm, 2002). During autumn shrimp migrate from the shallow areas of the Wadden Sea to areas offshore and then return in spring with the onset of warmer water temperatures. The pattern of migration depends largely on the weather conditions while during mild winters there may be nearly no migration offshore, under moderate to severe winter conditions *C. crangon* is reported to migrate from 1 to 90 km offshore (Boddecke, 1976). *C. crangon* distribution is thus largely dependant on relatively warm water conditions. The reason why in 1998 *C. crangon* was also present in the summer samples in the offshore area of Box A could be related to the influence of the warm water masses entering the North Sea in 1998 (Reid *et al.*, 2001) leading to similar temperature conditions as in the Wadden Sea resulting in a shift of the distribution border this time further offshore.

5.5.4 Anthropogenic influences on community structures

Box A lies within an area of the German Bight which is exposed to a high level of bottom fishing activities (Rijnsdorp *et al.*, 1998). The species composition found here was similar to the species composition reported by other studies in this area (Künitzer, 1990; Dewarumez *et al.*, 1992; Kühne and Rachor, 1996; Rees *et al.*, 1999; Callaway *et al.*, 2002) some of which have linked the occurrence of large numbers of scavenging and opportunistic species such as *A. rubens, O. albia* and *P. bernhardus* and the lack of sedentary species to fishing activities (Rumohr and Kujawski, 2000; Callaway *et al.,* 2002). Scavenging and opportunistic species are thought to benefit from fishing activities as these may lead to an increase in suitable food items such as dead or damaged animals in the trawl track or from discards (Ramsay *et al.*, 1998; Groenewold and Fonds, 2000). While the overall composition found in Box A might be influenced by decades of intensive fishing, changes observed in Box A in this study were thought to be unrelated to this activity. Fishing intensity within the ICES Rectangle has remained fairly consistent over the sampling period (unpublished data S. Ehrich) and observed changes are more likely to be linked to climatic conditions and food supply leading to redistribution of animals rather then to fishing activities. The same was considered for chronic large scale costal eutrophication (Colijn *et al.,* 2002) which may also had an influence on the species composition and biomass levels found within the German Bight. While long term surveys in the German Bight have been showing an increase in benthic biomass following increased nutrient input over the past decades (Rachor, 1990) changes occurring on a very short time period as reported by this study are not thought to be linked to eutrophication events.

5.5.5 Sampling scale

The mesoscale sampling scale chosen by this study was sufficient to describe assemblage structure and its variability in time and space.. However, the sampling scale was too small and too infrequent to demonstrate conclusively how large-scale fluctuations between sampling periods in abundance and biomass were accomplished. Recognition of spatial scaling is vital for the design of benthic ecological studies (Armonies, 2000). The scale at which local epifauna assemblages should be studied largely depends on the size and mobility of species within the assemblage and by the spatial and temporal distribution of environmental factors in the area under investigation. Most epifauna species are highly mobile and are able to react to changing environmental conditions (Ursin, 1960; Boddecke, 1976; Ramsay *et al.*, 1998; Groenewold and Fonds, 2000; Freeman *et al.*, 2001) thus in an areas with highly variable environmental conditions the spatial scale of sampling will have to be larger and more frequent compared to areas with very stable environmental conditions.

The mobility of most epifauna species suggests that the scale at which they are sampled will have to be much larger than for the relative sedentary infauna. Is the scale small it may be possible to detect changes but it will be difficult to distinguish if the observed changes are fundamental long term changes or if they are caused by the spatial discontinuity derived from redistribution of organisms e.g. drifting or migration.

Chapter 6

The feeding strategy of dab (*Limanda limanda*) in the southern North Sea: Linking stomach contents to prey availability in the environment

6.1 Abstract

The feeding strategy of dabs (*Limanda limanda*) was investigated within a predefined research area in the southern North Sea for 2 years. The aims were: i) to establish the relationship between prey availability and dab abundance, distribution, body condition and prey selection ii) to determine the underlying functional processes of prey choice in dab. Temporal and spatial trends of prey availability in relation to dab abundances, distribution, condition and prey selection were analysed. Temporal trends in dab condition, percentage of empty stomachs and numbers of ingested prey were apparent. In particular in the winter period 2000-2001 dabs were in poor condition and prey items were only rarely found in stomachs. Similarly prey availability decreased in the environment while the abundance of dabs increased. Thus, temporal changes were partly thought to be attributed to density-dependent effects. The stomach composition of dabs during the two consecutive summers was mainly dominated by *Pariambus typicus* and *Ophiura albida* while in the winter period only *O. albida* made a significant contribution to the stomach content. Analysis of prey characteristics indicated that only prey densities in the environment significantly influenced prey choice in dabs, while other characteristics such as the position of the prey in the habitat, its palatability or mobility did not have significant effects. The feeding strategy of dab thus was highly opportunistic, although trends were apparent that suggested that buried living fauna was less likely to be ingested, which was also observed in previous studies.

6.2 Introduction

Anthropogenic threats to the marine environment such as bottom trawl fisheries, climate change and the invasion of alien species all have the potential to change benthic and fish communities (Jennings and Kaiser, 1998; Reise *et al.*, 1998; Frid *et al.*, 1999; Wieking and Kröncke, 2003; Schiel *et al.*, 2004 and others). The consequences such changes may have on individual fish species are not fully understood. Nevertheless, there is an increasing need and will to manage fish stocks within a more ecosystem orientated framework (Link, 2002). Consequently a sounder understanding of the habitat requirements of fish and habitat quality are highly relevant. Prey availability can be regarded as a major component to habitat quality and might be one of the most important factors influencing fish distributions on small and regional scales (Hinz *et al.*, 2003). However, to determine the true availability of prey species within habitats, detailed knowledge about suitability, accessibility and preference of potential prey items in the environment is a prerequisite. Here it is not only important to identify individual prey species, but to understand the underlying functional processes of prey choice, as only these will allow to access consequences of habitat and ecosystem change. Dietary studies of fishes have been a central part of fisheries science since its early beginnings. Countless studies have been conducted on various fish species (e.g. Steven, 1930; Wyche and Shackley, 1986; Molinero and Flos, 1991; Beare and Moore, 1997; Serrano *et al.*, 2003a and many others) in an attempt to establish and categorize prey spectra, prey preferences and feeding strategies. Most studies have been based on prey items found in stomachs, but few have tried to simultaneously establish the actual prey availability in the environment (e.g. Jones, 1952; Wyche and Shackley, 1986) and analysed both in a consistent approach (e.g. Serrano *et al.*, 2003b). The use of stomach content analysis alone to establish the feeding ecology of flatfishes limits the possibility of drawing firm conclusions about prey preferences and feeding strategy as the potential prey choices encountered by the predator in the environment are unknown. Knowledge of those prey species ingested are of importance, but it is equally important to know those species not ingested, yet that are present in the environment.

Detailed knowledge about the feeding ecology of fish species is also needed since stomach contents analysis have been suggested as a tool for monitoring changes in benthic communities (Frid and Hall, 1999; Link, 2004). For such studies it is essential to have a sound understanding of the principles underlying prey choice in the species used for such investigations. Only with this knowledge will scientists be able to interpret and assess the bias that exists in such data sets.

Limanda limanda (L.) is one of the most abundant flatfish species in the North Sea (Daan *et al.*, 1990) and has an extensive geographical distribution range with the vast majority of its population living in the southern North Sea (Rijnsdorp *et al.*, 1996). Despite high rates of exploitation as a target species, but mainly as a by-catch species in mixed flatfish fisheries, the population levels have remained relatively stable or have in some parts even increased in comparison with other flatfish species such as plaice *Pleuronectes platessa,* L. and sole *Solea solea* (L.) (Heessen and Daan, 1996). The reasons behind this resilience to fishing pressure are not fully understood as exploitation levels are similar for all three flatfish species (Pope *et al.*, 2000). Several explanations have been put forward to clarify this phenomena: the reduction of predatory species such as *Gadus morhua* L. which feed on dab (Daan *et al.*, 1990; Greenstreet and Hall, 1996), eutrophication and the effects of trawling disturbance increasing prey availability or accessibility (Duineveld and Vannoort, 1986; Kaiser and Ramsay, 1997), and the early maturity of dabs allowing them to spawn before they recruit to the fishery (Pope *et al.*, 2000). In addition the general feeding strategy of dab may also be an important component that contributed to the resilience of dab populations in the North Sea. To investigate the feeding strategy of dab in more detail, dabs were studied within a predefined small scale research area in the southern North Sea over three consecutive seasons (summer 1999, 2000 and winter 2000-2001). By linking dab catches and stomach contents with macrofauna samples collected over comparable spatial and temporal scales the prey availability could be determined and its effects on distribution, body condition and feeding behaviour investigated. This sampling strategy contrasts with traditional dietary studies which often pool data on fish diets over the large scales adopted by groundfish surveys. Furthermore the aim of this study is to establish the underlying functional processes of prey choice in dab using detailed information about characteristics of prey items ingested and animals not found in stomachs but which were present in the environment. The results are discussed in respect to the regional population dynamics of dab.

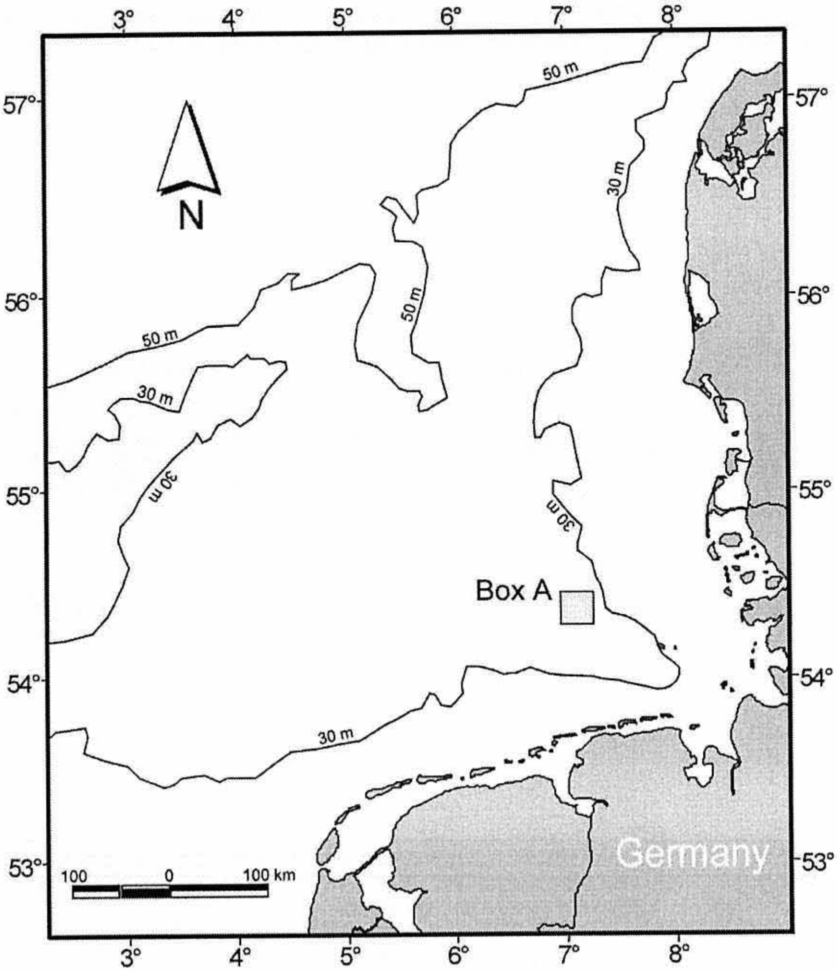

Figure 6.1 The research area (box a) in the southern North Sea

6.3 Methods

6.3.1 Sampling protocol

Samples were collected randomly within the predefined research area (Box A) (Ehrich and Stransky, 2001; Hinz *et al.*, 2004) situated in the south-eastern German Bight near Helgoland (see Fig 6.1). Dabs, dab stomachs and infauna were sampled during three cruises of the German small-scale bottom trawl survey (Ehrich and Stransky, 2001): i) in summer (July-August) 1999, ii) in summer 2000 and iii) in winter 2000-2001 (February). Dabs were sampled by the GOV, the standard otter trawl in the North Sea (ICES 1999) and a standard 0.1 m^2 Van Veen Grab was used to sample the benthic fauna. All gears were deployed in close proximity to each other at each station to limit spatial variability and enable comparison of dab stomach composition with the composition of potential benthic prey organisms in the environment. Four stations were sampled during each sampling period. At each station one 30 min otter trawl sample was taken. From these catches dab abundances were determined and 30 dabs were taken from the respective catches for condition and stomach analysis. Only adult fish >15 cm length were used for analysis. Dabs reach maturity at a size of approximately 11-12 cm (Rijnsdorp *et al.*, 1992). At each station three Van Veen grabs were taken to determine abundances of benthic fauna. Macrofauna samples were sieved over 1 mm and subsequently fixed in 4% buffered formalin solution for later identification. All animals were identified to the highest taxonomic separation possible and counted in the laboratory.

6.3.2 Dab abundance, condition and prey availability

Differences trends in dab abundance and condition between sampling seasons were investigated using one way ANOVAs. The abundances of dabs per station had to be $\log_{10}$ (n+1) transformed prior to analysis to normalize the data and were subsequently tested for homogenity of variances. *Post hoc* multiple comparisons were carried out using the Tukey test. For each sampling period 120 fish were measured to the nearest cm and weighed wet (±1g) prior to the removal of stomachs. The condition factor was calculated as follows:

$$K=100(W/L^3)$$

where W is the wet-weight (g) and L is the total length (cm).

To assess differences in prey availability in the environment between sampling seasons, the macrofauna data were sorted as follows: species not found in the stomach contents during the entire study period were omitted from the analysis as they were deemed undesirable or inaccessible to dab and would otherwise have had a strong bias on the resources truly available. Similarly, two species, the polychaete *Owenia fusiformis* and the phoronid *Phoronis* sp. were excluded as they were only rarely found in dab stomachs but occurred in high abundances in the environment (see result section, prey selectivity index). Differences in prey availability per sampling period were also investigated by a one-way ANOVA. Prey abundances per station were $\log_{10}$ (n+1) transformed prior to analysis and tested for normality and homogenity of variances. *Post hoc* multiple comparisons were carried out using the Tukey test.

6.3.3 Small scale spatial distribution and prey availability

The small scale distribution of fishes may be influenced by prey availability such that areas of higher food availability attract a larger number of fishes than areas of lower food availability (Hinz *et al.*, 2003). Thus, to determine if prey availability influences dab distribution at the spatial sampling scale adopted in the current survey, dab abundances were correlated (Spearman rank correlation) with prey abundances in the environment for each sampling season.

6.3.4 Stomach content analysis

Dab stomachs were removed immediately after sorting of the otter trawl catches aboard the research vessel. Subsequently they were transferred into labelled fine-mesh paper bags (teabags for loose tea) and stored in buckets containing 8% buffered formalin solution for detailed analysis on land. In the laboratory the stomach contents were rinsed in fresh water and the food items contained counted and identified to the nearest taxonomic level. The total number of ingested animals was determined per station as well as the percentage of empty stomachs. Temporal changes in the number of ingested prey and the percentage of empty stomachs between sampling seasons were statistically examined using one way ANOVA. Prior to analysis the abundance of ingested animals was $\log_{10}$ (n+1) transformed and tested for normality and homogeneity of variances.

To investigate possible density-dependent food limitation, dab abundances and the percentage of empty stomachs were correlated for each sampling season using Spearman rank correlation analysis.

6.3.5 Temporal changes in prey importance and feeding pattern

The modified Costello method was used to investigate temporal changes in prey importance between sampling seasons, feeding pattern and niche width components over the sampling period. The analysis developed by Costello (1990) and later modified by Amundsen *et al.* (1996) is based on a plot of prey-specific abundance versus the frequency of occurrence of respective prey types in stomach samples. Prey-specific abundance is defined as the percentage a prey taxon comprises of all prey items in only those predators in which this prey type occurred:

$$P_i = (\sum S_i / \sum St_i)100$$

where P_i= prey-specific abundance of prey i; S_i= stomach contents comprised of prey i, St_i = total stomach contents in only those individuals containing prey i. The frequency of occurrence of a prey item is defined as the number of stomachs in which that prey occurs, expressed as a frequency of the total number of stomachs in which prey are present. To ease the understanding of the resulting plots Amundsen *et al.* (1996) defined three axis of interpretation which will briefly be described here (see Fig. 6.4a) For a more detailed description of the method see Amundsen *et al.* (1996). The diagonal axis running from the lower left to the upper right of the graph represents a measure of prey importance as a function of prey-specific abundance and frequency of occurence with dominant prey at the upper and rare or less important prey at the lower end. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization. Predators have specialized on prey items found in the upper part of the graph while prey items in the lower part have been ingested occasionally and indicate generalization. Thus, prey items located in the upper left would represent specialization of individual predators while prey items in the upper right represent population specialization. The axis running from the upper left to the lower right describes the contribution of between- and within-individual components to the niche width. In a population in which individuals feed nearly exclusively on one particular prey type different to the prey types chosen by other individuals (prey points found in the upper left corner) the population displays a high in between- individual component. Particular prey items are only found in a few individuals but in relative high abundances in comparison to other prey items also present in the stomachs. This differs to populations in which almost all individuals utilize most of the prey types in relatively low abundances (prey points mostly in the lower right corner). Here the population displays a high within-individual component. In the original describtion of the modified Costello method Amundsen *et al.* (1996) named these as between- and within-'phenotype' components to the niche width. However the term 'phenotype' can unintentinally be misleading, implying a genetic component to prey choice, while Amundsen *et al.* (1996) intending to describe the inherent variability in individual feeding behaviour. To avoid misunderstandings the term 'phenotype' was replaced by 'individual' by this study.

The Shannon-Wiener diversity index was calculated for each season as univariate indicator of nich breadth (Krebs 1999).

6.3.6 Prey selectivity index

To assess the relationship between stomach contents and the abundance of potential prey organisms in the environment obtained from grab samples Ivlev's selection index (E) (Ivlev, 1961) was calculated for prey types in different seasons:

$$E = (r_i - p_i) / (r_i + p_i)$$

where r_i is the relative abundance of prey i (% stomach contents by number) in the stomachs of plaice from one station, and p_i is the abundance of that prey in grab and trawl samples (% of the total number). E ranges from –1 to +1, such that negative values indicate avoidance or inaccessibility of prey. Positive values imply selection for a prey type (or very low abundances in grab and trawl samples), whereas a value of E = -1 indicates that a species was absent in stomachs but present in grab samples. Non-selective feeding is indicated by zero values.

6.3.7 Functional analysis of prey selection

Although the Costello method and Ivlev index deal with certain aspects of the feeding strategy of fishes they are not able to determine the functional mechanism that underpins prey selection in dabs. To establish if dab predominantly forage on macrofauna species that show a specific set of characteristics a generalized linear model (GLM) was performed on assigned prey species characteristics as independent variables and abundances of prey species found in dab stomachs as the dependant variable. Species were characterized by three categorical factors: i) position of prey in the environment ii.) prey mobility and iii) prey palatability and one continuous factor iv) density in the environment. Within each categorical factor prey species were grouped according to displayed traits. For the position of potential prey species in the environment, species were subdivided into three groups. (1) Species predominantly buried in sediment (e.g. many polychaete species), (2) partially buried species that protrude in part from the surface (e.g. bivalves with siphons or tube building polychaetes) and (3) animals which live predominantly on the surface (e.g. brittle stars like *Ophiura albida* or amphipods). For the category mobility, only two characteristics were assigned, either species were classified as (1) mobile or (2) relatively immobile. Animals capable of fast movements and therefore possibly able to escape dab attacks were classified as mobile, while slow moving or sedentary species were classified as relatively immobile. The third category was termed palatability describing the hardness of prey bodies, shells or cuticles. Potential prey species were classified according into three classes (1) hard shells, cuticles or calcareous bodies (e.g. certain bivalves such as *Nucula nitidosa* or brittle stars), (2) animals with thin shells or cuticles (e.g. the bivalve *Abra spp.*, amphiods or tube building polychaetes) and (3) soft bodied animals (e.g. most infaunal polychaetes). The analysis was performed on the total abundance of all three sampling seasons for stomach contents and macrofauna samples. The pooled data were $\log_{10}$ (+1) transformed prior to analysis. Due to the large amount of zero values in the data on the species level the assumptions for variance analysis (normality and homogeneity of variances) could not be met. The data was therefore pooled into taxonomic functional groups prior to analysis. Species of the same taxonomic group displaying similar characteristics according to the predefined categories were pooled together. Thus all scale worms which live on the surface, for example, were grouped together as were all thin shelled bivalves. Due to this reduction of the data it was not possible to run a full model with interaction terms and therefore only the main effects were analysed.

6.4 Results

6.4.1 Dab abundance, condition, prey availability and small scale distribution

Dab condition decreased throughout the time of the study (Fig. 6.2a). Dabs in the winter period had significantly lower conditions compared to the previous summer periods (Table 6.1, Fig. 6.2a). The number of prey items in the environment (prey availability) showed a similar trend as dab condition (Fig. 6.2c) however differences between seasons were not statistically significant (Table 6.1). Mean dab abundances however differed significantly between sampling seasons (Table 6.1). There was only a slight decrease in mean dab abundance from summer 1999 to summer 2000 (not significant, Fig. 6.2b) while in the winter period of 2000-2001 a sharp increase in dab abundance was noted (Fig. 2b).

Correlations of the number of prey items in the environment with the abundance of dab caught within each sampling season were not significant (Table 6.2). However it should be noted that only four stations where sampled during each sampling season which will have lowered the possibility of detecting a statistically significant relationship. The general trends within the two summer periods indicated a positive relationship between prey abundances in the environment and dab abundance (Fig. 6.3a), while during the winter period when dab abundances within the research area were the highest recorded by this study (Fig. 6.2d), the relationship was negative (Fig. 6.3a).

6.4.2 Percentage of empty stomachs and number of ingested prey

The mean percentage of empty stomachs per season followed a similar trend to the mean dab abundance (Fig. 6.2d, Table 6.1). A slight non-significant decrease in the percentage of empty stomachs occurred from summer 1999 to summer 2000 which increased markedly in the winter period of 2000-2001. The mean number of ingested prey items per season followed the trends observed for dab condition and prey availability (Fig. 6.2e). The mean number of ingested prey items per station decreased significantly (Table 6.1) throughout the sampling period.

During summer 2000 a significant negative relationship was found between dab abundance and the percentage of empty stomachs (Table 6.2). This together with the trends observed between dab abundance and prey availability (Fig. 6.3b) may indicate that dabs were aggregated over areas of high food availability during this period. No significant correlation was found for the other sampling periods. During summer 1999 a very slight negative trend was detected while in the winter period 2000-2001 a clear positive trend between dab abundance and the percentage of empty stomachs was apparent (Fig. 6.3b). This clear positive trend, together with the negative trend observed between dab abundance and prey availability during the winter period seems to indicate that prey availability was limited and possibly was further reduced by dab aggregations.

6.4.3 Temporal changes in prey importance and feeding pattern

Visual examination of the Costello plots of the three sampling periods showed that the overall distribution of prey species changed over time and suggested a fundamental change in the feeding pattern of dab (Fig. 6.4b-c). During summer 1999 most prey species found in stomachs showed low prey-specific abundances with low to medium levels in the frequency of occurrence. This suggested a non-specific generalized feeding pattern for most prey species. Two species, the caprellid *Pariambus typicus,* and the small razor shell *Phaxas pellucidus,* proved to be the dominant species ingested in summer 1999. Both species showed relatively high values in terms of their prey-specific abundance and their frequency of occurrence which indicated some degree of population specialization for these species. In summer 2000 most ingested prey had higher prey-specific abundances and lower frequency of occurrences than in the previous season (Fig. 6.4b-c). At this time, dabs displayed a more specialized feeding behaviour with a high between-individual component; individuals feed nearly exclusively on one particular prey type different to the prey types chosen by other individuals. *P. typicus* was also the dominant species in summer 2000 and again had high values of prey-specific abundance and frequency of occurrence which indicated population specialization. The brittle star *Ophiura albida* showed very high frequency of occurrence in summer 2000 and was found in 86 % of stomachs that had stomach contents. However, their low prey specific abundance indicated that few individuals were ingested which is most likely related to the relatively large size of *O. albida* that limit the amount which can be ingested by an individual fish at any one time. During winter 2000-2001 a further shift in feeding pattern towards a higher degree of specialization and a high between-individual component was apparent. Most prey species had higher values of prey specific-abundance and low values of the frequency of occurrence. Only *O. albida* had a high frequency of occurrence and it was the dominante prey species ingested in this sampling period. The observed changes in feeding patterns between seasons that altered from generalized feeding to an increasing specialization of the individual can be linked to the decrease in prey availability for the individual fish through time. In particular during the winter period 2000-2001 when prey availability was at its lowest (Fig. 6.2e) single prey species were found in stomachs of only one or two individuals leading to prey-specific abundances of 100% e.g. *Abra alba* (Fig. 6.4b-c). Thus the paucity of prey species during this period is the most likely explanation for this apparent trend in specialization.

The Shannon-Wiener Index indicated that the diversity of the diet was increasing leading to the highest diversity in the winter sampling period (Fig. 6.4b-c). The reason for this again was related to the low levels of prey availability limiting feeding patterns and causing a more even distribution among ingested prey species thus increasing overall diversity.

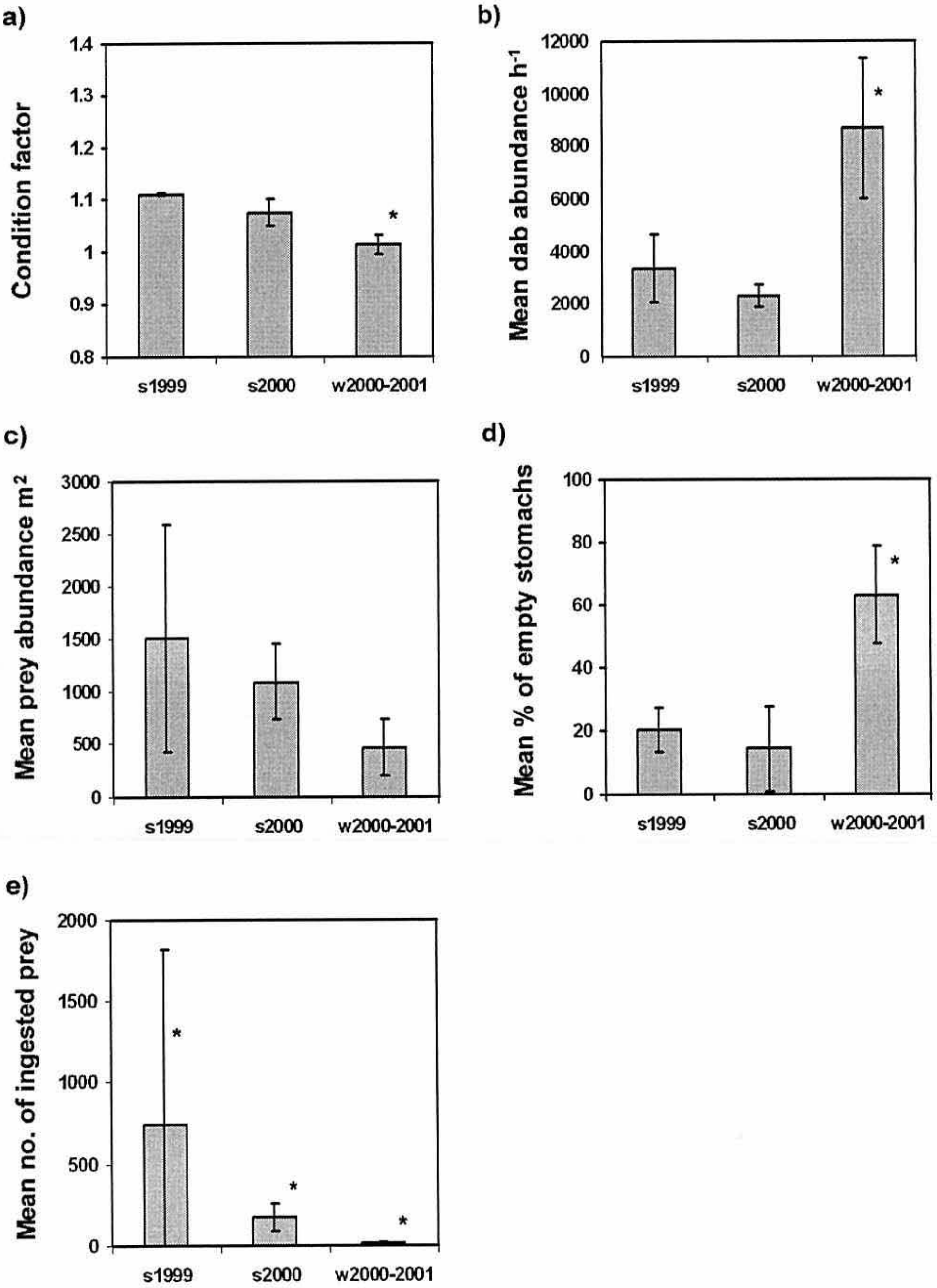

Figure 6.2 Temporal changes in a) mean dab condition b) mean dab abundance per h^{-1} c) mean abundance of prey items in the environment m^2 d) mean percentage of empty stomachs e) mean number of ingested prey items per station. The error bars given in graphs represent the ±S.D. Untransformed data is shown. Significant different means identified by multiple comparison Tukey test ($p < 0.05$) were signified by a star

Table 6.1 Results of Anova tests conducted on temporal parameters analysed

	df	f	P
Condition factor	2, 9	26.95	**0.000**
Log_{10} dab abundance h^{-1}	2, 9	11.8	**0.003**
Log_{10} prey abundance m^2 in the environment	2, 9	2.65	0.141
Percentage of empty stomachs	2, 9	18.06	**0.001**
Log_{10} abundance of ingested prey	2, 9	34.87	**0.000**

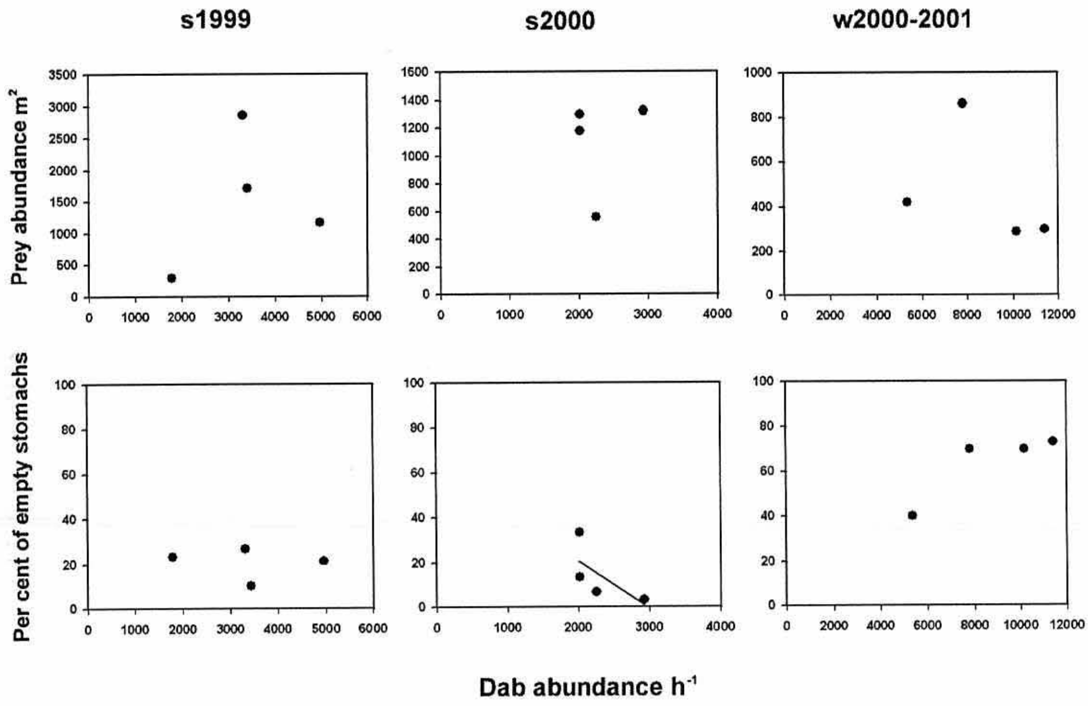

Figure 6.3 Correlation analysis of dab abundance versus a) prey abundance in the environment per station and b) percentage of empty stomachs for each sampling season.

Table 6.2 Results of the Spearman rank correlation analysis per season of dab abundances with prey abundances and the percentage of empty stomachs. S = summer, w = winter

	s1999	**s2000**	**w2000-2001**
Dab abundance vs. prey availability	r=0.6; p=0.4	r=0.6; p=0.4	r=-0.2; p=0.8
Dab abundance vs. percentage of empty stomachs	r=-0.6; p=0.4	**r=-1**	r=0.94; p=0.051

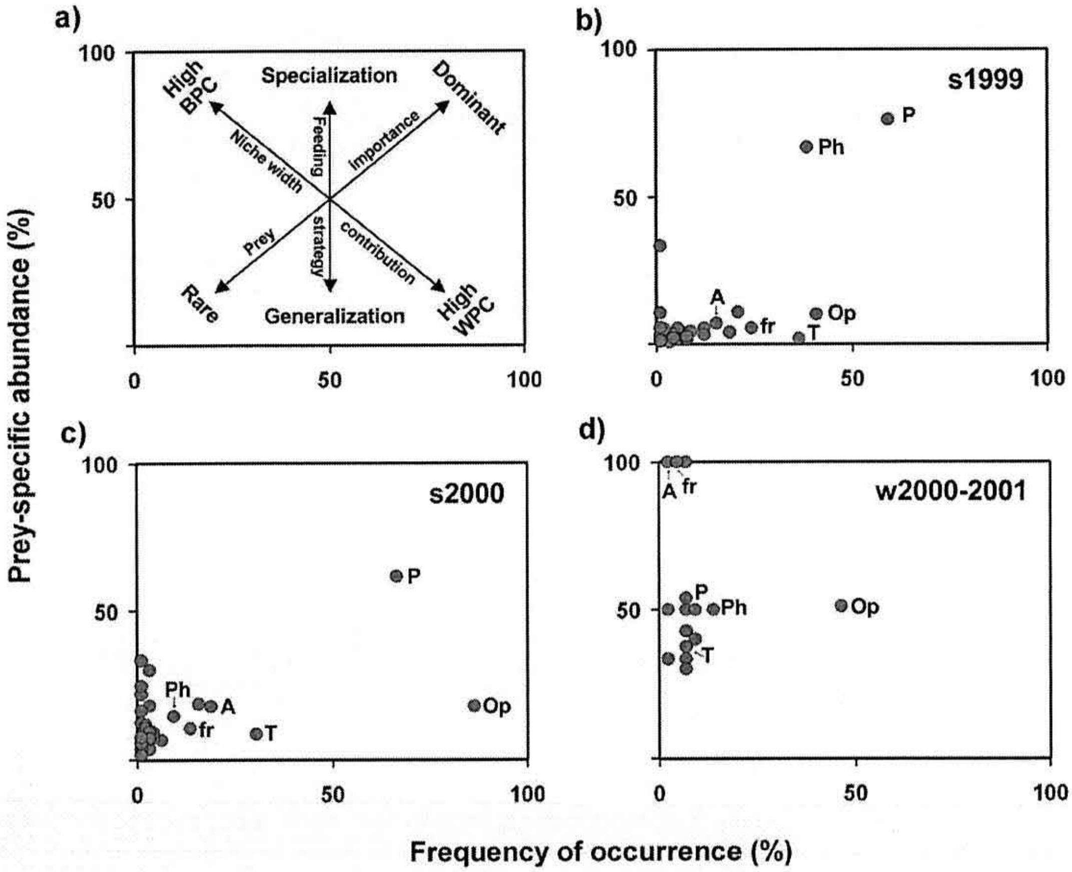

Figure 6.4 Modified Costello graphs showing axes of interpretation a) and feeding patterns of dab for each sampling period summer 1999 b) summer 2000 c)and winter 2000-2001 d). Selected species were made noticeable by abbreviations: P = *Pariambus typicus*, Ph = *Phaxas pellucidus* ., Op = *Ophiura albida*, A = *Abra alba*,T = *Tubularia indivisa*, fr = fish remains

6.4.4 Prey selectivity index

The Ivlev index was calculated for all macrofauna species found in grab samples. However, due to the large amount of information this analysis produced only the results of the most relevant species will be discussed here. Species which had an overall relative contribution to the stomach content of >1% within all sampling seasons were selected as well as two species, the tube building bamboo worm *Owenia fusiformis* and a species of Phoronidae, which occurred in high abundances in the environment (Fig. 6.5). The most dominant prey species in the stomachs during summer 1999 and 2000 was the caprellid *Pariambus typicus*. This species was rarely found in grab samples and therefore had high Ivlev index scores (Fig. 6.5). This might suggest strong positive selection and possible dietary preference behaviour for *P. typicus*. However it is very likely that the sampling technique was not very efficient for this species. *P. typicus* lives clinging onto hydroids or the arms of ophiuroids (Volbehr and Rachor, 1997) and the pressure wave created by the grab as it descends to the seabed might have been sufficient to displace them. In the winter period 2000-2001 the relative abundance of *P. typicus* in dab stomachs decreased substantially while the Ivlev index remained high (+1). *Phaxas pellucidus* was the overall second most abundant prey species found in dab stomachs (Fig. 6.5). In summer 1999 it was found in similar relative abundances in the environment and in stomach contents (Ivlev index -0.08) while in summer 2000 relative abundances in the stomach contents were very low (Ivlev index -0.61). In the winter period 2000-2001 *P. pellucidus* showed high positive selection scores (Ivlev index 0.85). The brittle star *Ophiura albida* had positive selection values during all three periods (Fig. 6.5). This trend might again suggests a strong preferential selection for this species, but due to the species' size and distribution patterns, the abundances quantified from grab samples might not be representative of the abundances in the environment. Other important prey species were the bivalves *Abra sp.*, *Nucula nitidosa*, the tube building polychaeta *Lanice conchilega*, the brittle star *Amphiura* sp., Cumacea, and the hydroid *Tubularia indivisa* (Fig. 6.5). During most periods these species had positive selection scores or scores close to zero except for *Nucula nitidosa* which showed negative selection throughout the sampling period (Fig. 6.5). The hydroid *T. indivisa* occurred in most instances together with the caprellid *P. typicus* which suggests that the former species was only accidentally ingested while dabs were feeding on caprellids clinging onto its stolon. The tube building bamboo worm *O. fusiformis* and a species of Phoronidae occurred in relatively high abundances in the environment but these species were only rarely ingested by dab (Fig. 6.5). This seems to indicate that of dabs avoid or can not utilize these prey species. Both species build tubes which protrude from the seafloor, similar to *L. conchilega* which in contrast was ingested in greater numbers (Fig. 6.5). Thus, it seems that accessibility can not have been a problem and that other underlying factors such as the composition of the tube or possibly chemical deterrents might make these species less desirable as prey items.

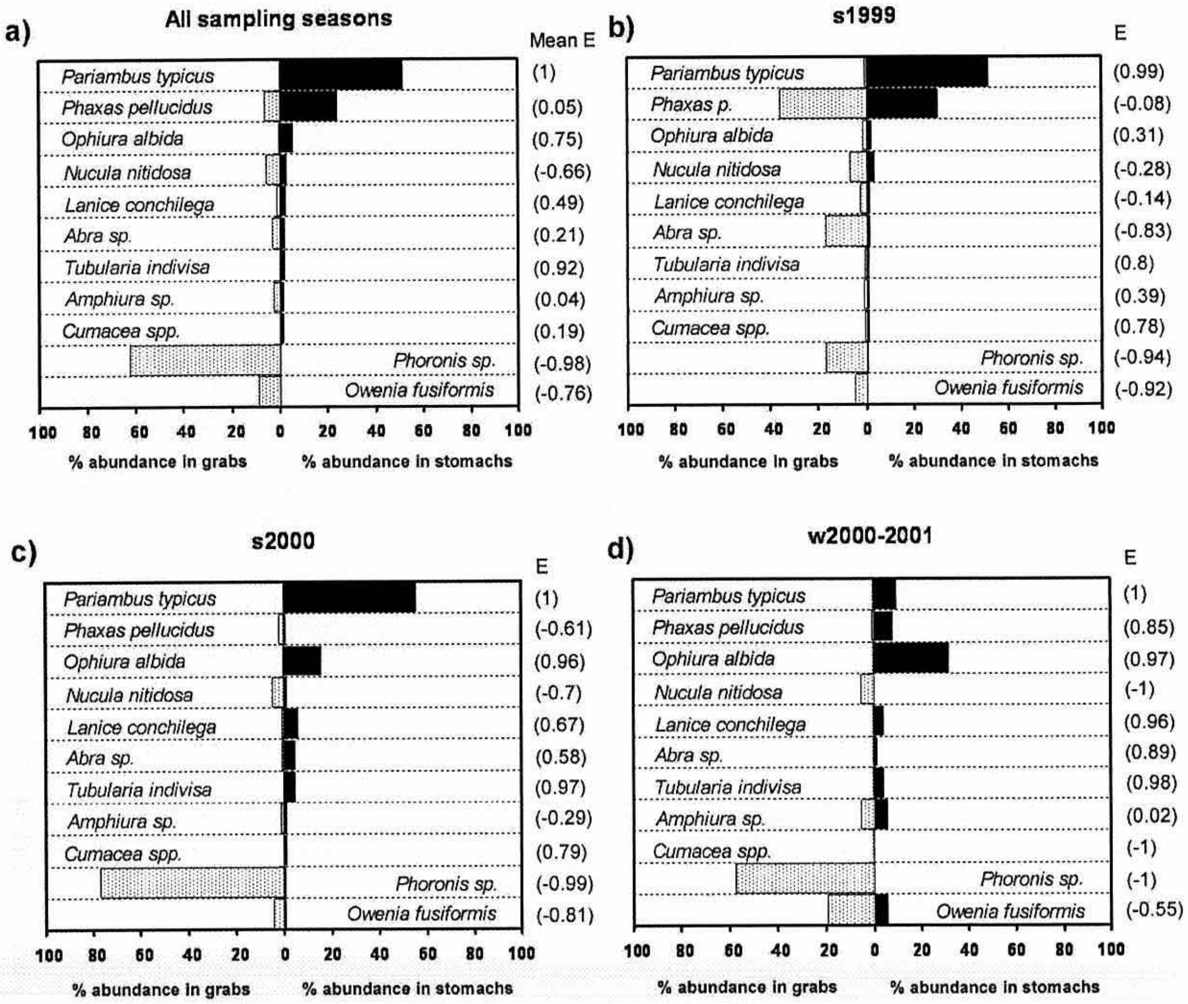

Figure 6.5 Relative abundances of selected macrofauna species in the environment and in the stomach contents a) for all seasons pooled b) summer 1999 c) summer 2000 and d) winter 2000-2001. The Ivlev selection index score per species was displayed in brackets

6.4.5 Functional Analysis of prey selection

The results of generalized linear model (GLM) showed that only the $\log_{10}$ abundance of macrofauna species in the environment had a significant effect (Table 6.3) on the log10 abundance of prey species found in dab stomachs. Trends for the categorical factors position in the environment and palatability were visible when exploring the means (Fig. 6.6). In general buried living, soft bodied prey species which comprised mainly infaunal polychaetes, showed lower abundances in dab stomachs, while harder bodied animals living at the interface or at the surface showed higher means.

Table 6.3. Results of the GLM analysis preformed on macrofauna characteristics and abundances in the environment with abundances found in stomachs as a dependant variable

	df	ss	ms	f	p
Intercept	1	0.43	0.43	0.63	0.436
Position	2	1.34	0.67	0.97	0.394
Mobility	1	0.41	0.41	0.60	0.446
Palatability	2	0.86	0.43	0.62	0.545
Log_{10} abundance of macrofauna in the environment	1	3.53	3.53	5.13	**0.035**
Error	20	13.77	0.68		

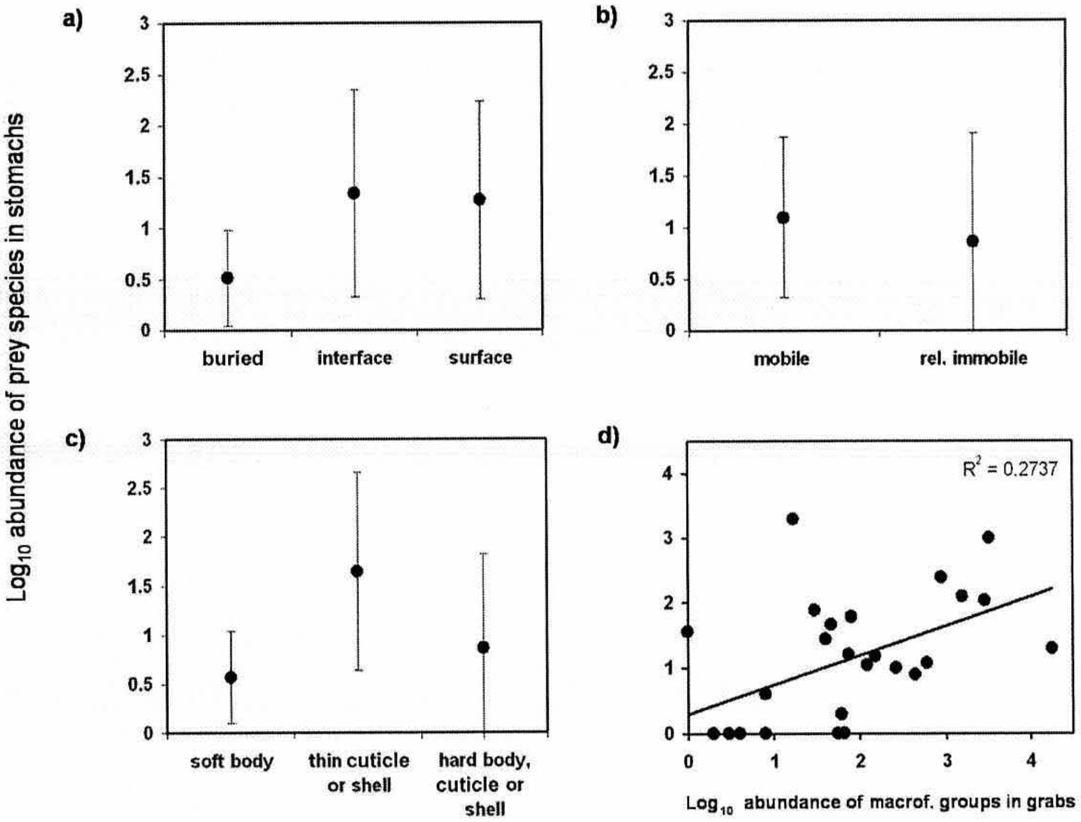

Figure 6.6 Mean Log_{10} abundance of prey species found in stomachs for the three categorical macrofauna characteristics a) position in the environment b) mobility c) palatability. d) Relationship between macrofauna Log_{10}-abundance in the environment and Log_{10} abundance in dab stomachs. The error bars given in graphs represent the ±S.D.

6.5 Discussion

6.5.1 Population dynamics of dab in the German Bight

Dabs in the southern North Sea, in particular mature females, are known to display migratory movement on the onset of winter from the relatively shallow Wadden Sea regions towards the deeper areas of the central German Bight (Rijnsdorp *et al.*, 1992; Saborowski and Buchholz, 1997) which corresponds with the area investigated by this study. This region, besides being a refuge from the cold coastal water masses during winter, also serves as the major spawning ground of dabs in the southern North Sea (Rijnsdorp *et al.*, 1992; Saborowski and Buchholz, 1997) and is thought to be also utilized by dabs from further offshore regions, such as the Dogger Bank (Rijnsdorp *et al.*, 1992). The spawning period of dab runs from January to September with a broad peak in February (van der Land, 1991). After spawning at the onset of spring the spawning aggregation is thought to disperse and females return to their original feeding grounds. The abundances observed in the present study from summer to winter were most likely a reflection of the migratory movements of dabs into the study area. Reductions in condition, the high percentage of empty stomachs and the low amount of prey ingested during winter periods were also reported by other authors for this area (Knust, 1996; Saborowski and Buchholz, 1996). However, none of the previous studies clearly associated these changes in the nutritive state of dab with the possible density-dependent effects such as intraspecific competition for food which may occur in these winter-spawning aggregations. Female dabs which are the dominant sex encountered in these aggregations (Saborowski and Buchholz, 1997) continue to feed during the winter period to maintain their gonado-somatic growth while male dabs were reported to feed less during this period (Saborowski and Buchholz, 1996; 1997). Here, indications were found that the percentage of empty stomachs was positively related to the abundance of dabs during the winter period, while dab abundance showed a negative relationship with prey availability in the environment. These findings increase the likelihood that the seasonal differences in the nutritional state of dab observed by this study are, at least in part, related to density -dependent effects caused by the spawning aggregation. This conclusion was also supported by the fact that seasonality in the nutritive state of dab observed in the German Bight by Knust (1996) was not detected on the Dogger Bank. Here food uptake by dab and condition were reported to remain nearly constant throughout the year (Knust, 1996). However, the reduced prey availability in winter may not be attributed to density-dependent effects alone as seasonal fluctuations in prey availability may also play an important role in the observed difference between summer and the winter periods. Winter conditions in the southern North Sea are characterized by low temperatures and reduced primary productivity (Otto *et al.*, 1990) and populations of benthic invertebrates may be at seasonally low levels unrelated to dab predation. It also has to be noted that for the relevant time period a decrease in the abundance of and biomass of epibenthic species (Hinz *et al.*, 2004) was observed within the research area. The decreasing trend in epibenthic biomass was thought to be related to mass migratory movement of large epibenthic animals out of the area due to less favourable food conditions. This trend corresponded well with the decreasing infaunal prey abundance over the whole sampling period reported here thus the low prey availability in winter 2000-2001 could not be attributed to density dependent effects of dab alone. To establish if predation pressure during winter aggregations is a reoccurring event that influences overall macrofauna abundances would therefore require further research.

The hypothesis that the small scale distribution of fishes is mainly influenced by prey availability with areas of higher food availability and thus quality attracting a larger number of fishes than areas of lower food availability (Hinz *et al.*, 2003) could not be fully supported by the results of this study. During the summer periods a positive relationship between prey availability and dabs was apparent, indicating that fish aggregated over areas of higher prey abundance. This aggregation effect was also supported by the negative trends between dab abundance and and the percentage of empty stomachs during summer periods. These results contrast with the winter period in which dab abundance were at its highest and prey availability at its lowest level observed during this study. The relationship between dab abundances and prey availability was negative possibly implying density-dependent effects of dabs on prey abundance. This again was supported by the positive trend between dab abundance and the percentage of empty stomachs indicating that food was limited when dab abundances were high. These trends demonstrate that prey availability can not be viewed as a good predictor of fish distributions in all instances and that the nature of the relationshiop will ultimately depend on the amount of resources available and fish density. Thus aggregation effects on a small scale may only be possible to detect if population levels of the predator are low and the rate of prey intake has relatively little effect on the standing stock of prey. While during periods of high fish abundances the rate of food intake might reverse the relationship and dab abundances may then influence prey avaialbility.. The results and conclusions drawn should be viewed with caution as only four data points where available for analysis during each sampling period however, the consistent trends between the relationships of dab abundance with prey availability and the percentage of empty stomachs during sampling periods may strengthen the argument for these trends to be genuine.

6.5.2 The feeding strategy of dab

According to its morphology dabs can be classified as visual feeders with relatively large eyes, small mouth gapes and the ability for fast acceleration (transient thrust) in comparison to other common flatfish species found in the southern North Sea (Piet *et al.*, 1998). With these characteristics it is morphologically similar to the scaldfish *Arnoglossus laterna* (Walbaum) and the long rough dab *Hippoglossoides platessoides* (Fabricius) (Piet *et al.*, 1998). Most dietary studies of dab conducted so far have classified the species as a general feeder with a relatively wide prey spectrum (Steven, 1930; Jones, 1952; Braber and De Groot, 1973; Wyche and Shackley, 1986; Knust, 1996; Saborowski and Buchholz, 1996; Beare and Moore, 1997). This classification was strongly supported by the results of this study which revealed that the main factors that influenced prey choice seemed to be the relative abundance of prey species in the environment. Although not significant the results also seem to indicate that buried soft-bodied animals, principally polychaetes, were found less often in stomach contents. This could to some extent be explained by the faster digestion rate of this animal group compared with organisms with cuticles or shells. Nevertheless the the scarcity of polychaetes in dab stomachs compared to other flatfish species has been noticed by several authors (Steven, 1930; Wyche and Shackley, 1986; Beare and Moore, 1997). Other evidence comes from a field experiment in which dabs were caged in various densities to see if predation pressure or disturbance by burial behaviour had a significant effect on the benthic fauna (Hall *et al.*, 1990). No significant effect was found for any of the polychaetes analysed and caged dabs were found to be in a poorer nutritive state at the end of the experiment. Only mobile crustaceans were found to be significantly reduced. The authors concluded that dab did not appear to have a significant negative effect on the benthic fauna. This observation might hold true for benthic communities which are dominated by polychaetes, but other communities which have a rich epibenthic fauna as in this study are very likely to show density-dependent effects. Another interesting fact reported by Hall *et al.* (1990) was that *Owenia fusiformis* although present in cages were left untouched by dabs. This finding was in line with the observation of the apparent avoidance of this species by dab as indicated by the present study. The reason for the lack of infaunal polychaetes in the dab diet could be related to the visual more surface orientated hunting strategy adopted by dab, which can be supported by observations made on dabs feeding on the brittle star *Amphiura filiformis.* This brittle star lives buried in the sediment with only its arms protruding to the surface. Under normal circumstances dabs will mainly feed on *A. filiformis* arms and only rarely ingest whole animals (Duineveld and Vannoort, 1986; Kaiser and Ramsay, 1997). After a trawling event however, in which whole animals are exposed at the surface, the amount of body disks of *A. filiformis* have been shown to increase significantly in dab stomachs (Kaiser and Ramsay, 1997). Another reason for the absence of infaunal animals could be related to morphological constraints. Dabs have been reported to exhibit a lower pressure gradient while opening the mouth during feeding (Bels and Davenport, 1996) compared with plaice which feeds to a greater extent on polychaetes (Jones, 1952; Braber and De Groot, 1973; Wyche and Shackley, 1986; Rijnsdorp and Vingerhoed, 2001and others). A low pressure gradient implies less suction which might be a disadvantage when foraging on infaunal polychaetes.

In this study the caprellid *Pariambus typicus* was numerically the most abundant prey species in the two summer periods (1999 and 2000). Records of caprellids or tubiculous crustaceans associated with hydroids being ingested by dabs have also been mentioned by other studies (Braber and De Groot, 1973; Wyche and Shackley, 1986). *P. typicus* not only lives clinging onto hydroids but has also been found living on the arms of ophiuroids in the German Bight (Volbehr and Rachor, 1997). Accidental ingestion due to foraging on *Ophiura albida* which was numerically the third most dominant species in the stomach recorded can however be disregarded because individuals were very abundant in the stomachs; one individual for example in summer 1999 was found to have ingested 371 individuals of *P. typicus.* Although *P. typicus* is a relatively small species, with respect to volume, it might still have made a considerable contribution to the energy demands of dabs due to the large numbers ingested. With respect to volume or weight, however, other species were more important although not directly recorded by this study. Other studies conducted in this area of the German Bight showed that *O. albida* was the dominant stomach content by weight (Knust, 1996; Saborowski and Buchholz, 1996). For the period between January 1993 to December 1994 (Saborowski and Buchholz, 1996) found that around 50 % of the weight in dab stomach content was attributed to *O. albida* while other groups such as polychaetes (8-13%), bivalves and crustaceans (<5%) made lesser contributions. The ingestion of ophiuroid species by dabs was also reported from other regions such as the central North Sea (Duineveld and Vannoort, 1986), Irish sea (Jones, 1952; Wyche and Shackley, 1986; Kaiser and Ramsay, 1997) and Dogger Bank (Knust, 1996) and seems to be a relatively common occurrence in dab stomachs. The energy content of this species can be expected to be very low compared with to other taxa such as polychaetes or bivalves. Brey *et al.* (1988) reported energy content of echinoderms of 9.46 J mg^{-1} DW while polychaetes had values of 14.1-16.8 J mg^{-1} DW and bivalves 18.8 J mg^{-1} shell free DW. Nevertheless although ophiuroids may not have a very high energy content they might still be a nutritively beneficial food source for dabs. Ophiuroids tend to occur in high density beds on the sea floor which would allow dab to capture this prey type with relatively little effort. Search times when feeding on ophiuroids are minimal, conserving energy and ultimately yielding a higher rate of food intake. Both factors might, as a result, compensate for the relatively low energy content of the ophiuroid body tissue. This opportunistic foraging strategy, focusing efforts on quantity rather than on specific prey items was supported by the results of this study investigating the underlying mechanisms of prey choice in dab. Overall, this foraging strategy might also help to explain the scavenging behaviour observed in dab (Kaiser and Ramsay, 1997; Groenewold and Fonds, 2000).

6.6 Conclusion

The feeding strategy of dab was demonstrated to be truly opportunistic. The main factor for prey choice in dab was prey density. Other factors such as the position of the prey, its palatability or mobility did not have a significant effect on prey choice. Also, the nutritive value of prey items seems to have little influence on prey selection, as animals such as brittle stars, which have a low energetic value, often represent the bulk of the diet. Although not statistically significant there were trends within the GLM analysis that suggested that buried living fauna was less likely to be ingested than fauna found near the surface of the seafloor. This more surface-orientated feeding behaviour was supported by observations made by previous studies. Due to the opportunistic feeding strategy of dab this species can be expected to be highly adaptable in respect to habitat and ecosystem change. This, along with other factors (see above), may have contributed to the stable population levels of dabs observed in the North Sea, despite high levels of exploitation and to its wide geographical distribution throughout the North East Atlantic.

6.7 Supplementary information

Within appendix 1 the prey characteristic identified for macrofauna species found during the whole sampling period are presented. Appendix 2 summarizes the functional taxonomic groupings macrofauna species were pooled in for GLM analysis. Appendix 3 gives Ivlev index scores per season of species ingested by dabs while Appendix 4 lists all species which were found in the environment but were not ingested by the dab during this study. Appendix 4 also reports on the relative abundances above <0.1 % of these species in the environment for each sampling season.

Chapter 7

General discussion

7.1 Identification of specific habitat requirements for flatfishes

7.1.1 Site selection and habitat parameters (Chapter 2 and 3)

Using the delineation method introduced in Chapter 2 it was possible to identify areas that consistently harboured high densities of flatfish from long-term datasets derived from fisheries surveys. Areas for all three flatfish species (plaice, sole and lemon sole) could be identified for the English Channel. Thus flatfishes were not randomly distributed and a clear pattern of sites which had consistently high abundance of flatfishes could be recognized. The number of sites that met the criteria of 'Sites of Interest' (SoI) (areas that would merit further research) gave a good indication of the general ecological traits exhibited by these species. While lemon sole was classified as a habitat specialist, plaice and sole were classed as more habitat generalistic. These trends seemed to be in general agreement with other studies (Jones, 1952; Bennet, 1965, Carter *et al.*, 1991; Piet *et al.*, 1998; Rijnsdorp and Vingerhoed, 2001) and were explained with respect to prey distributions and feeding strategies.

Nonetheless other habitat parameters also determine flatfish distributions and these were examined in more detail in Chapter 3. Within this study general habitat descriptors (sediment type, depth, temperature, salinity, tidal velocity and the amount of shells and stones) of SoI were compared to areas which had shown either variable densities or no flatfish during groundfish surveys. The trends in these abiotic parameters which mainly operate over relatively large spatial scales gave indications of the habitat conditions that supported high abundances of fish. According to habitat selection theory (e.g. McCall, 1990; Fretwell and Lucas, 1970) these sites should be classed as more suitable. While sites with consistently high densities of plaice and sole had similar habitat conditions that were typical of near shore environments, lemon sole was predominantly found in areas with deeper offshore conditions. Sediment associations also differed between species, plaice predominantly occurred over sand while sole were found over a wider spectrum of sediment types ranging from muddy to sandy substrata. Lemon sole were found at sites with slightly higher gravel content than either plaice or sole.

Although some tendencies were apparent when the trends of the three different flatfish species were compared, a clear relationship between flatfish abundances and emergent epifauna biomass could not be established. The data seemed to indicate a positive relationship for plaice with emergent epifauna. Plaice are visual predators (Piet *et al.*, 1998) and thus could benefit from the potentially more complex food webs offered by these structures (Kaiser *et al.* 1999; Bradshaw *et al.*, 2003). However as mainly polychaetes were found in plaice stomachs which do not benefit from such structures (Bradshaw *et al.*, 2003) the observed relationship of adult plaice and emergent epifauna remained unexplained. Sole did not display such a trend but is a tactile feeder (Rogers, 1994a) as opposed to a visual predator like the other two species, preying predominantly on infaunal animals (Jones, 1952; Rogers, 1994a). No relationship was found between flatfish abundances and prey availability assessed by grab samples. This may indicate that flatfish abundances were unrelated to the resource availability at the sites sampled. However there were strong indications that the grab samples taken were not representative for the actual resource situation at some of the sites sampled. At the site with the highest plaice abundances fishes were in a very good nutritive state and showed the highest percentage of full stomachs as well as the highest abundance and biomass of prey items per stomach. This contrasted with the relatively low prey abundances assessed by grab samples. On the basis of these opposing results it was concluded that fishes may be more efficient at sampling prey availability over the relevant spatial scales and therefore stomach content analysis and body condition might be a more reliable source of information to assess the true habitat quality (prey availability) of an area compared to point source grab sampling.

The variability of the relationship between flatfish densities, emergent epifauna, and prey availability highlights the inherent problems of field studies that attempt to relate fish densities from fisheries surveys to particular habitat parameters. Many studies, including the one presented here have difficulties in establishing clear relationships, due to a high degree of variability within the underlying data (see McConnaughey and Smith, 2000; Eastwood *et al.*, 2001; Amezcua *et al.*, 2003). The sources of variability within this study were related i) to the sampling regime adopted by the groundfish survey and, ii) to the fact that relative densities are in some cases not necessarily indicative of habitat quality and can therefore not be linked in a causal manner to specific habitat parameters.

In this study we have used data and sampled at stations originating from the groundfish surveys conducted on a regular basis by CEFAS (Kaiser *et al.,* 1999). These surveys were intended for stock assessments on a sea basin scale and therefore incorporate mostly stations which can easily be fished without the danger of damaging or losing sampling gear. This inevitably has lead to a very unbalanced design with certain habitats being rarely or never sampled while others are over-represented (see sediment types chapter 2). This consequently will have lead to some inevitable bias in the results.

Although fish catches of the ground fish survey were supposedly taken from fixed stations a considerable variation in starting points and bearings of individual tows existed, possibly related to the tidal conditions at the time of sampling or other constraints such as fixed gear deployed in the proposed tow path. As these tows were of considerable length, potentially distinctly different areas were sampled which possibly incorporated fish from different habitats. Thus stations identified as consistently high density sites refer more probably to small local areas rather than to specific sites. While this inconsistency might not create a problem for the analysis of habitat conditions which operate over larger scales, such as abiotic factors (e.g. temperature, salinity etc.), it might be for biotic parameters (e.g. emergent epifauna) which can be expected to have a patchy and more site-specific distribution.

Another source of variability within the ground fish survey data is that each station was only sampled once during a survey. As fish are able to move freely within areas they may aggregate or disperse on a scale where the element of chance increases that they are caught at disproportionately high or low abundances, than could otherwise be anticipated from the existing habitat parameters.

Under some circumstances fish densities may be unrelated to the habitat parameters which can be assessed within an area. Such situations consequently add to the variability when attempting to establish relationships between specific habitat parameters and flatfish. An area of low habitat quality could display relatively high flatfish abundances in the case where a prime habitat within the vicinity (not sampled by the survey) experiences density-dependant effects leading to an overspill of fish into low quality area (Jennings, 2000). Fish might also aggregate over less suitable areas if the surrounding areas are even less favourable and movement towards or knowledge of prime habitats are restricted (Shepherd and Litvak, 2004). High fish densities and habitat quality might also thus depend on the habitats found in adjoining areas. The sampling grid of the groundfish surveys, with their large distances between individual sampling stations, will not be able to address those processes that operate on much smaller localized spatial scales. While the processes described so far will tend to overestimate the importance of certain habitat parameters found within certain areas the reverse scenario is also imaginable. Due to high fishing pressure highly suitable habitats may show lower abundances than otherwise would have been expected from the prevailing habitat conditions.

Another factor that complicates analysis into relationships between habitats and fish density is the complexity of habitat-fish interactions. Habitat can be described by a multitude of environmental parameters, which can occur in a multitude of combinations. The relative importance of one parameter to a fish may change according to changes in another or in combination with other parameters. For example a habitat maybe desirable due to its high prey availability while temperatures are favourable however when temperatures become unfavourable this factor may override the positive aspects of food availability leading to a decline in fish densities. This fact makes it difficult, if not impossible, to detect clear relationship with more subtle habitat parameters, which might add positive attributes to habitats but are not strictly limiting. Thus for example in the case of emergent epifauna and adult plaice it is easily imaginable that it might have a positive effect under some circumstances e.g. by increasing prey availability, while in others it might not be detectable due to the presence of a more important factor (negative or positive) such as unfavourable temperatures, presence of competitors etc.

Due to this cumulative variability and the complexity of habitat, fish interactions, results on species specific habitat requirements and preferences of flatfishes should be interpreted with caution. One might argue that the way to reduce at least some of this variability and thus enhance statistical power might be to increase the number of data points. The groundfish survey data upon which this study was based is however already one of the largest datasets available within European waters. More data on the same spatial scale would not necessarily deal with issues discussed above. The ground survey data and the analysis presented in Chapter 1 and 2 are thus the best existing initial tools to explore habitats requirements. While their use for habitat parameters on small scales was found to be limited, results of habitat parameters that operate over wider geographical scales should be valid and useful.

7.1.2 Limiting the multifactorial characteristics of benthic habitats (Chapter 4)

One mechanism to overcome some of the problems related to the multifactorial characteristics of habitats and to allow investigations into more subtle habitat parameters is to limit the analysis to one particular type of habitat which is known to be suitable for the species under study. This knowledge could be established from the type of analysis outlined in chapter 2 and 3. With the main constituents of habitats (e.g. sediment type) kept relatively similar over all study sites and only one or two habitat parameters varying, relationships between these particular habitat components and fish densities may become more apparent.

This approach was used in Chapter 4. Nine sites out of the original 12 sites of the 'site-specific survey' (see Chapter 3) were investigated using video survey techniques. The substratum of all nine sites chosen for analysis was primarily composed of sand. Of the remaining sites two were omitted from the analysis as they comprised muddy substrates which are known to represent less suitable habitats for adult plaice (Amezcua *et al.*, 2003 and Chapter 3) and the third station was not sampled due to bad weather conditions. The main aim of this study was to determine which other habitat constituents might be important to adult plaice other than the general substratum type. Substratum morphology and heterogeneity as well as the abundances of benthic biota were determined and correlated with plaice densities. No correlation could be found with substratum morphology or heterogeneity. Correlations were found with benthic biota, in particular the presence of the tube worms *Lanice conchilega* and *Chaetopterus* spp. Sites near Boulogne-sur-Mer were considered responsible for this trend. As these polychaetes form part of the diet of adult plaice (e.g. Jones, 1952; Wyche and Shackley, 1986; Rijnsdorp and Vingerhoed, 2001, Chapter 3) prey availability might be the driving factor for habitat selection over sandy substrata. The trends of plaice abundances and prey availability observed here contrast the findings of chapter 3 where grab samples were used to assess prey availability and no relationship between the two variables was found. The video data on macrofauna abundances did however correspond with results of the stomach sample analysis and the condition of plaice for the relevant stations (Chapter 3). These results suggested that the video data was collected at a larger and more appropriate spatial scale which was probably more comparable to the spatial scales over which plaice operated during the time of the survey. The fact that the clear trend between plaice abundances and macrofauna abundances was observed between sites from the same geographic location might be an indication that habitat selection processes are only detectable on a more localized scale (Shepherd and Litvak, 2004), rather than on the sea basin scale adopted by this study. The role of emergent epifauna could not be properly explored by this study as the resolution of the images were not detailed enough to estimate more subtle structures such as hydrozoans and their associated fauna. Emergent epifauna biomass was however already addressed in Chapter 3 ('site specific study') for the same sites.

The question now is whether the approach taken to identify specific areas in the English Channel using temporal stability of fish catches as a potential proxy for habitat quality was valid. In the case of plaice, in particular the sites near Boulogne-sur-Mer were predicted to have potentially high habitat quality from CEFAS long term data sets. The rich benthic communities and the high plaice densities found during the 'site specific study' (Chapter 3 and 4) seemed to vindicate these predictions. The area near Boulonge-sur-Mer is however known to display consistently high primary and secondary production, due consistent hydrodynamic conditions (Hoch and Garreau, 1998; Sanvicente-Anorve *et al.*, 2002). This finding focuses on the fact that the approach taken will have emphasised sites with temporally more stable habitat conditions. Stability in fish catches and habitats may be brought about by specific local environmental conditions as indicated, but may also be a result of low fishing activity. Conversely, sites with high fluctuations in fish densities do not necessarily indicate unsuitable habitat conditions. This demonstrates that the method introduced might be a good tool to locate productive stable environments or areas of low fishing activity, but that it is of limited use in quantifying relative habitat quality for specific sites. On the other hand, knowledge of stably productive areas will be beneficial from a management point of view. Due to the dynamic nature of marine environments it might be more sensible to protect and manage areas which offer some degree of predictability rather than protecting specific habitat features found within an area at any particular time.

7.2 Benthic community dynamics, prey availability and dab distribution

Benthic communities show large temporal fluctuations in abundance and composition as demonstrated for an epifauna community in the German Bight (Chapter 5). Prominent seasonal and inter-annual trends in composition, abundance and biomass of epifauna were apparent throughout the study period. Fluctuations in the epibenthic community were probably related to the migratory behaviour of mobile species in and out of the research area. While seasonal trends were linked to temperature fluctuations, inter-annual changes were thought to be related to differences in food supply to the benthic community caused by changes in front formation. While temporal trends were highly dynamic some degree of spatial stability was found within the research area for the period of the study for the distribution of epibenthic biomass.

The aim of chapter 6 was to investigate the influence of these changes in the benthos on the distribution, condition and resource acquisition of dab. Benthic prey availability, the abundance of ingested food items as well as the body condition showed the same decreasing trends throughout the study period. Dab abundance within the research area did follow a similar trend during the two consecutive summer periods sampled however during winter a steep increase in dab abundance was apparent. This increase in abundance was most likely linked to the local migratory movements of dab using the area as a refuge from low water temperatures experienced in the more shallow areas of the German Bight during winter, and as a spawning ground (Rijnsdorp *et al.*, 1992; Saborowski and Buchholz, 1997). The abundance and species composition within dab stomachs closely reflected the trends of prey availability within the area. A spatial relationship between prey availability and dab densities were not apparent as the statistical power may have been limited for this analysis.

The findings of this study demonstrate again that fish density and habitat parameters measured at the same time are not necessarily related in a simple causal manner. In the present case temporal density changes in dab, within the research area were partly related to the low temperatures within other areas and to behavioural patterns related to spawning activity. This highlights that if we want to study and understand distribution patterns of fish in relation to specific habitat parameters (e.g. prey availability) we need to take a much more holistic approach.

Knowledge of the local environmental patterns and population dynamics on the relevant spatial scales will be a prerequisite before fish densities and habitat parameters can be linked in a meaningful way. Chapter 5 and 6 also highlight how dynamic habitat components such as prey availability can be and that substantial changes can occur in relative short time scales. These changes can be induced by environmental processes as well as by predation pressure. Habitat quality (here with respect to prey availability) even within the benthic environment can therefore not be viewed as a static component inherent to a specific area. With reference to the siting process of 'essential fish habitats' and marine protected areas this implies that repeated sampling over considerable time will be necessary to quantify the habitat quality of an area.

7.3 Recommendations for future research

Future field studies on habitat selection of flatfish will need to address the multifactorial causes of variability in fish densities. Point source sampling in time and space of fish abundances and selected habitat parameters will not be adequate to determine habitat requirements and explain distribution patterns. Thus the large spatial and temporal scales at which fish have been studied so far (mostly ground fish surveys) will not be sufficient to address questions of habitat suitability and distribution patterns adequately. Environmental parameters and fish densities will need to be determined on a much higher spatial and temporal resolution. The spatial scales that will be required for sampling will need to be on the one hand small enough to be relevant for the individual fish, on the other hand large enough to capture the overall distribution patterns of the local fish population. This could be achieved with a dense sampling grid incorporating various different habitats and environmental gradients. The temporal scale would at least need to be adequate to follow seasonal changes. Overall a cohesive understanding of the environmental processes within the research area will need to be established against which the distribution of fish could be monitored. In this way it might be possible to establish which habitats are selected over others within the research area and possibly under changing environmental conditions. Shepard and Litvak (2004) suggested that only with such a relatively small scale approach the existence of density-dependant habitat selection (IFD) could be proven. They argue that individual fish will not be able to make informed decisions about optimal suitability of habitats beyond their immediate perceptual range and even if they could travelling to these habitats my outweigh any benefits. Thus Ideal Free Habitat selection or density dependant selection, will not be applicable to the large scale sampling grids used to study fish distributions so far. The understanding of fish distribution gained from small scale area may however not be readily applicable to any other area, as each area will tend to have its own specific environmental set-up. The resulting data from such a sampling design would be challenging to analyse, but this might be the only way to gain a deeper understanding of the underlying factors determining flatfish distribution in the field.

7.4 Summary of main findings

H_0 hypothesis = flatfish are distributed unrelated to benthic habitat structures and prey availability

- Flatfish were not randomly distributed and sites of stably high abundances could be identified from long term data sets for plaice, sole and lemon sole (Chapter 2).

- Consistently high abundance sites of flatfish could be associated with specific sediment types and environmental parameters which operate on larger spatial scales such as depth, temperature and salinity. The association between flatfish and emergent epifauna could not clearly be established. For plaice a positive relationship between abundance and emergent epifauna biomass was found however the underlying functional importance of emergent epifauna to plaice could not be clarified. Prey availability and flatfish abundance could not be associated by this study possibly due to inadequate sampling methods and the overall sampling scale adopted by this survey. (Chapter 3)

- Video surveys of sandy habitats showed that prey availability could be an important factor in determining distribution patterns of plaice over relatively small spatial scales. Sediment morphology and habitat heterogeneity were found to have no significant effect on plaice abundances within the context of this study (Chapter 4).

- Flatfish abundances (dab) can be unrelated to benthic habitat parameters such as prey availability within small scale areas if large scale processes control distribution patterns such as seasonal migration or spawning aggregations. The study also indicated that high flatfish densities might have a significant negative influence on prey abundances (Chapter 6).

The null hypothesis in most cases could not be rejected by the results presented in this thesis. However this does not imply that flatfish distributions are unrelated to the presence of emergent epifauna or prey availability. Within this thesis it became clear that the sampling regimes adopted were not appropriate to clarify the importance of these habitat components in influencing flatfish distribution patterns. Future research will need to adopt more sophisticated sampling designs on smaller spatial scales to clarify the role benthic habitat structures and prey availability in shaping flatfish distributions.

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Appendix 1 Benthic fauna and their prey characteristics

ID	Taxa	Position in the envioment	Mobility	Palatability
	Cnidaria			
	Hydrozoa			
1	*Bougainvillia ramosa*	surface	rel. immobile	thin cuticle/shell
2	*Obelia longissima*	surface	rel. immobile	thin cuticle/shell
3	*Tubularia indivisa*	surface	rel. immobile	thin cuticle/shell
	Anthozoa			
4	*Anthozoa spp.*	surface	rel. immobile	thin cuticle/shell
5	*Cerianthus lloydii*	interface	rel. immobile	thin cuticle/shell
6	*Edwardsia sp.*	interface	rel. immobile	thin cuticle/shell
	Nemertea			
7	*Nemertea spp.*	buried	rel. immobile	soft bodied
	Platyhelmintes			
8	*Turbularria spp.*	buried	rel. immobile	soft bodied
	Annelida			
	Polychaeta			
9	*Anaitides maculata*	buried	rel. immobile	soft bodied
10	*Antinoella sarsi*	buried	rel. immobile	soft bodied
11	*Aphrodita aculeata*	surface	rel. immobile	thin cuticle/shell
12	*Chaetopterus variopedatus*	buried	rel. immobile	soft bodied
13	*Chaetozone f. group*	buried	rel. immobile	soft bodied
14	*Eteone spp.*	buried	rel. immobile	soft bodied
15	*Eumida sanguinea*	buried	rel. immobile	soft bodied
16	*Eunoe nodosa*	buried	rel. immobile	soft bodied
17	*Glycinde nordmanni*	buried	rel. immobile	soft bodied
18	*Goniada maculata*	buried	rel. immobile	soft bodied
19	*Harmothoe spp.*	surface	rel. immobile	thin cuticle/shell
20	*Lagis koreni*	interface	rel. immobile	thin cuticle/shell
21	*Lanice conchilega*	interface	rel. immobile	thin cuticle/shell
22	*Magelona spp.*	buried	rel. immobile	soft bodied
23	*Malmgeniella sp.*	surface	rel. immobile	thin cuticle/shell
24	*Nephtys sp.*	interface	rel. immobile	soft bodied
25	*Nereis juv.*	interface	rel. immobile	soft bodied
26	*Nereis longissima*	interface	rel. immobile	soft bodied
27	*Ophelina acuminata*	buried	rel. immobile	soft bodied
28	*Ophiodromus flexuosus*	surface	rel. immobile	thin cuticle/shell
29	*Owenia fusiformis*	interface	rel. immobile	thin cuticle/shell
30	*Pholoe baltica*	surface	rel. immobile	thin cuticle/shell
31	*Phyllodocidae*	buried	rel. immobile	soft bodied
32	*Poecilochaetus serpens*	buried	rel. immobile	soft bodied
33	*Scalibregma inflatum*	buried	rel. immobile	soft bodied
34	*Scolelepis bonnieri*	buried	rel. immobile	soft bodied
35	*Scoloplos armiger*	buried	rel. immobile	soft bodied
36	*Sigalionidae*	surface	rel. immobile	thin cuticle/shell
37	*Spio spp.*	buried	rel. immobile	soft bodied
38	*Spiophanes bombyx*	buried	rel. immobile	soft bodied
39	*Sthenelais limicola*	surface	rel. immobile	thin cuticle/shell
	Oligochaeta			
40	*Oligochaeta spp.*	buried	rel. immobile	soft bodied
	Crustacea			
	Amphipoda			
41	*Ampelisca brevicornis*	surface	mobile	thin cuticle/shell
42	*Amphipoda spp.*	surface	mobile	thin cuticle/shell
43	*Aora typica*	surface	mobile	thin cuticle/shell
44	*Apherusa spp.*	surface	mobile	thin cuticle/shell
45	*Argissa hamatipes*	surface	mobile	thin cuticle/shell
46	*Bathyporeia spp.*	surface	mobile	thin cuticle/shell
47	*Corophium insidiosum*	surface	rel. immobile	thin cuticle/shell
48	*Gammaropsis nitida*	surface	mobile	thin cuticle/shell
49	*Gammerus oceanicus*	surface	mobile	thin cuticle/shell
50	*Isaeidae spp.*	surface	mobile	thin cuticle/shell
51	*Lembos websteri*	surface	mobile	thin cuticle/shell
52	*Liljeborgia pallida*	surface	mobile	thin cuticle/shell
53	*Lysinassidae*	surface	mobile	thin cuticle/shell
54	*Melita obtusata*	surface	mobile	thin cuticle/shell
55	*Mysidacea spp.*	surface	mobile	thin cuticle/shell
56	*Pariambus typicus*	surface	rel. immobile	thin cuticle/shell
57	*Perioculodes longimanus*	surface	mobile	thin cuticle/shell
58	*Photis longicaudata*	surface	mobile	thin cuticle/shell

ID	Taxa	Position in the envioment	Mobility	Palatability
59	*Stenothoe monoculoides*	surface	mobile	thin cuticle/shell
60	*Urothoe elegans*	surface	mobile	thin cuticle/shell
	Cumacea			
61	*Cumacea spp.*	interface	rel. immobile	thin cuticle/shell
	Decapoda			
62	*Callianassa juv.*	interface	rel. immobile	thin cuticle/shell
63	*Corystes cassivelaunus*	surface	mobile	hard bodied
64	*Crangon sp.*	surface	mobile	thin cuticle/shell
65	*Decapoda sp.*	surface	mobile	thin cuticle/shell
66	*Liocarcinus juv.*	surface	mobile	hard bodied
67	*Pagurus bernhardus*	surface	mobile	thin cuticle/shell
68	*Philoceras bispinosus*	surface	mobile	thin cuticle/shell
69	*Processa sp.*	surface	mobile	thin cuticle/shell
70	*Upogebia deltaura*	buried	mobile	hard bodied
	Mollusca			
	Gastropoda			
71	*Acteon tornatilis*	surface	rel. immobile	hard bodied
72	*Cylichna cylindracea*	surface	rel. immobile	hard bodied
73	*Eulimidae spp.*	surface	rel. immobile	hard bodied
74	*Nudibranchia spp.*	surface	rel. immobile	soft bodied
75	*Polinices pulchellus*	surface	rel. immobile	hard bodied
	Bivalvia			
76	*Abra sp.*	interface	rel. immobile	thin cuticle/shell
77	*Acanthocardia*	interface	rel. immobile	hard bodied
78	*Chamelea gallina*	interface	rel. immobile	hard bodied
79	*Clausinella fasciata*	interface	rel. immobile	hard bodied
80	*Corbula gibba*	interface	rel. immobile	hard bodied
81	*Fabulina fabula*	interface	rel. immobile	thin cuticle/shell
82	*Mactra glauca*	interface	rel. immobile	thin cuticle/shell
83	*Mysella bidentata*	interface	rel. immobile	thin cuticle/shell
84	*Nucula nitidosa*	interface	rel. immobile	hard bodied
85	*Phaxas pellucidus*	interface	rel. immobile	thin cuticle/shell
86	*Spisula sp.*	interface	rel. immobile	hard bodied
87	*Tellimya ferruginosa*	interface	rel. immobile	thin cuticle/shell
88	*Thracia sp.*	interface	rel. immobile	thin cuticle/shell
89	*Thyasira flexuosa*	interface	rel. immobile	thin cuticle/shell
90	*Tritaeta gibbosa*	interface	rel. immobile	thin cuticle/shell
	Phoronidae			
91	*Phoronis sp.*	interface	rel. immobile	thin cuticle/shell
	Bryozoa			
92	*Electra pilosa*	interface	rel. immobile	hard bodied
	Echinodermata			
	Asteroidea			
93	*Asterias juv.*	surface	rel. immobile	thin cuticle/shell
94	*Astropecten irregularis*	surface	rel. immobile	hard bodied
	Ophiuroidea			
95	*Amphiura sp.*	interface	rel. immobile	hard bodied
96	*Ophiura albida*	surface	rel. immobile	hard bodied
	Echinoidea			
97	*Echinocardium cordatum*	interface	rel. immobile	hard bodied
98	*Echinocardium flavescens*	interface	rel. immobile	hard bodied
99	*Echinocardium juv.*	interface	rel. immobile	thin cuticle/shell
100	*Echinocyamus pusillus*	interface	rel. immobile	thin cuticle/shell
101	*Psammechinus miliaris*	surface	rel. immobile	hard bodied
	Cephalochordata			
102	*Branchiostoma lanceolatum*	interface	mobile	soft bodied
	Pisces			
103	fish remains	surface	mobile	soft bodied

Appendix 2 Taxonomic groupings and prey characteristics

Taxonomic functionl groups	Position in the environment	Mobility	Palitability
Cnidaria			
Hydrozoa	surface	rel. immobile	thin cuitical
Anthozoa	interface	rel. immobile	thin cuitical
Platyhelmintes			
Platyhelmintes	buried	rel. immobile	soft bodied
Nemertea			
Nemertea	buried	rel. immobile	soft bodied

Annelida			
Polychaeta (tube building)	interface	rel. immobile	thin cuticle/shell
Polychaeta (scale worms)	surface	rel. immobile	thin cuticle/shell
Polychaeta (errant predatory)	interface	rel. immobile	soft bodied
Polychaeta (mostly buried living)	buried	rel. immobile	soft bodied
Oligochaeta	buried	rel. immobile	soft bodied
Crustacea			
Amphipoda (mobile)	surface	mobile	thin cuticle/shell
Amphipoda (relativelt immobile)	surface	rel. immobile	thin cuticle/shell
Cumacea	interface	rel. immobile	thin cuticle/shell
Decapoda (large buried)	soft	mobile	thin cuticle/shell
Decapoda (large surface)	surface	mobile	hard bodied
Decapoda (shrimp like)	surface	mobile	thin cuticle/shell
Mollusca			
Bivalves (hard shelled)	interface	rel. immobile	hard bodied
Bivalves (soft shelled)	interface	rel. immobile	thin cuticle/shell
Gastropoda (shelled)	surface	rel. immobile	hard bodied
Nudibranchia	surface	rel. immobile	soft bodied
Phoronidae			
Phoronidae	interface	rel. immobile	thin cuticle/shell
Bryozoa			
Bryozoa	interface	rel. immobile	hard bodied
Echinodermata			
Asteroidea	surface	rel. immobile	hard bodied
Echinoidea (large)	surface	rel. immobile	hard bodied
Echinoidea (small)	surface	rel. immobile	thin cuticle/shell
Ophiuroidea	surface	rel. immobile	hard bodied
Cephalochordata			
Cephalochordata	interface	mobile	soft bodied
Pisces			
Fish remains	surface	mobile	soft bodied

Appendix 3 Ivlev's selectivity Index

Taxonomic group	S1999	s2000	w2000-2001	Average E
Cnidaria				
Hydrozoa				
Obelia longissima	0.88	0.64	-1	0.17
Tubularia indivisa	**0.80**	**0.97**	**0.98**	**0.92**
Nemertea				
Nemertea spp.	-1	0.05	-1	-0.65
Annelida				
Polychaeta				
Chaetopterus variopedatus	-	0.92	-1	-0.04
Harmothoe spp.	-0.36	0.49	-1	-0.29
Lanice conchilega	**-0.14**	**0.67**	**0.96**	**0.49**
Malmgeniella sp.	-1	1	-1	-0.33
Nephtys sp.	-0.91	-0.02	**0.58**	-0.12
Owenia fusiformis	-0.92	-0.81	**-0.55**	-0.76
Phyllodocidae	0.70	0.94	-1	0.21
Scoloplos armiger	-1.00	0.59	-	-0.21
Sigalionidae	-	1	-	1
Sthenelais limicola	-1.00	0.05	**0.74**	-0.07
Crustacea				
Amphipoda				
Amphipoda spp.	1	1	-	1
Aora typica	1	1	-1	0.33
Apherusa spp.	1	-	-	1
Argissa hamatipes	-0.03	0.94	-1	-0.03
Gammaropsis nitida	-1	1	-	0
Isaeidae spp.	1	-	-	1
Liljeborgia pallida	1	-	-	1
Lysinassidae	0.42	0.53	-	0.48
Melita obtusata	-1	0.84	-	-0.08
Pariambus typicus	**0.99**	**1**	**1**	**1**
Perioculodes longimanus	-0.36	0.92	-1	-0.15
Photis longicaudata	1	1	-	1
Stenothoe monoculoides	-1	1	-	0
Urothoe elegans	1	-	-	1
Cumacea				
Cumacea spp.	**0.78**	0.79	-1	**0.19**
Decapoda				
Callianassa juv.	-0.18	0.70	-1	-0.16
Corystes cassivelaunus	-1	0.44	0.99	0.14
Crangon sp.	-0.56	0.84	0.99	0.42
Liocarcinus juv.	0.52	**0.88**	-1	0.13
Pagurus bernhardus	-1	0.84	-	-0.08
Processa sp.	-0.77	0.21	**0.96**	0.13
Mollusca				
Gastropoda				
Eulimidae spp.	1	-1	-1	-0.33
Polinices pulchellus	-0.08	-0.22	**0.23**	-0.02
Bivalvia				
Abra sp.	-0.83	0.58	**0.89**	**0.21**
Acanthocardia	-0.48	-	-	-0.48
Chamelea gallina	0.89	-1.00	-1	-0.37
Fabulina fabula	-0.92	-1.00	-1	-0.97
Mactra glauca	-	0.84	-	0.84
Mysella bidentata	-0.36	-1	-1	-0.79
Nucula nitidosa	**-0.28**	-0.70	-1	**-0.66**
Phaxas pellucidus	**-0.08**	-0.61	**0.85**	**0.05**
Tellimya ferruginosa	-0.89	-1	-1	-0.96
Tritaeta gibbosa	1	-	-	1
Phoronidae				
Phoronis sp.	-0.94	-0.99	-1	-0.98
Bryozoa				
Electra pilosa	-	1	**0.89**	0.95
Echinodermata				
Ophiuroidea				
Amphiura sp.	**0.39**	-0.29	**0.02**	0.04
Ophiura albida	**0.31**	**0.96**	**0.97**	**0.75**
Echinoidea				
Echinocardium juv.	-1	-0.67	**0.73**	-0.31
Pisces				
fish remains	1	**1**	**1**	1

Appendix 4 Species not found in dab stomachs. Percentage abundance in the environment.

	S1999	**s2000**	**w2000-2001**
Cnidaria			
Hydozoa			
Bougainvillia ramosa	<0.1	<0.1	<0.1
Anthozoa			
Anthozoa spp.	<0.1	<0.1	<0.1
Edwardsia sp.	<0.1	**0.2**	**0.1**
Cerianthus lloydii	<0.1	<0.1	<0.1
Platyhelmintes			
Turbularria spp.	<0.1	<0.1	<0.1
Annelida			
Polycheata			
Anaitides maculata	<0.1	<0.1	<0.1
Antinoella sarsi	<0.1	<0.1	<0.1
Aphrodita aculeata	<0.1	<0.1	<0.1
Chaetozone f. group	<0.1	<0.1	<0.1
Eteone spp.	<0.1	<0.1	<0.1
Eumida sanguinea	**0.1**	**0.2**	**0.2**
Eunoe nodosa	<0.1	<0.1	<0.1
Glycinde nordmanni	<0.1	<0.1	<0.1
Goniada maculata	**0.2**	<0.1	**0.1**
Lagis koreni	**0.6**	<0.1	**0.1**
Magelona	**1.8**	**0.2**	**0.6**
Nereis juv.	<0.1	<0.1	<0.1
Nereis longissima	<0.1	<0.1	<0.1
Ophelina acuminata	<0.1	<0.1	<0.1
Ophiodromus flexuosus	<0.1	<0.1	<0.1
Pholoe baltica	<0.1	<0.1	**0.2**
Poecilochaetus serpens	**0.5**	**0.1**	<0.1
Scalibregma inflatum	<0.1	0.4	<0.1
Scolelepis bonnieri	<0.1	<0.1	<0.1
Spio spp.	**0.1**	<0.1	<0.1
Spiophanes bombyx	**2.3**	**0.5**	**0.4**
Oligochaeta			
Oligochaeta spp.	<0.1	<0.1	<0.1
Crustacea			
Amphipoda			
Ampelisca brevicornis	<0.1	<0.1	**0.2**
Bathyporeia spp.	<0.1	<0.1	<0.1
Corophium insidiosum	<0.1	<0.1	<0.1
Gammerus oceanicus	<0.1	<0.1	<0.1
Lembos websteri	<0.1	<0.1	<0.1
Mysidacea spp.	<0.1	<0.1	<0.1
Decapoda	**0.5**	<0.1	<0.1
Philoceras bispinosus	<0.1	<0.1	<0.1
Upogebia deltaura	<0.1	<0.1	<0.1
Mollusca			
Gastropoda			
Acteon tornatilis	<0.1	<0.1	<0.1
Cylichna cylindracea	<0.1	<0.1	<0.1
Nudibranchia spp.	<0.1	<0.1	<0.1
Bivalvia			
Clausinella fasciata	<0.1	<0.1	<0.1
Corbula gibba	**0.1**	<0.1	<0.1
Spisula sp.	**0.2**	<0.1	<0.1
Thracia sp.	**0.4**	**0.1**	**0.6**
Thyasira flexuosa	**0.8**	**0.4**	**0.5**
Echinodermata			
Asteroidea			
Asterias juv.	<0.1	<0.1	<0.1
Astropecten irregularis	<0.1	<0.1	<0.1
Echinoidae			
Echinocardium cordatum	**0.1**	<0.1	**0.5**
Echinocardium flavescens	<0.1	<0.1	<0.1
Echinocyamus pusillus	<0.1	<0.1	<0.1
Psammechinus miliaris	<0.1	<0.1	<0.1
Cephalochordata			
Branchiostoma lanceolatum	<0.1	<0.1	<0.1