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Evaluation of habitat use by adult plaice (*Pleuronectes platessa* L.) using underwater video survey techniques

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Abstract

Large-scale spatial surveys of fish species in relation to habitat have tended to focus on depth, sediment type and temperature as descriptors of fish habitats. At a smaller scale, habitat parameters such as the relief of the sea floor, the presence of structuring fauna and prey availability may have a large influence on fish distribution, but often are not considered. In the present study we used video survey techniques to study habitat components in areas of the English Channel that were known to support consistently high densities of adult plaice. Habitat features were quantified and related to the density of adult plaice caught within the same study areas. To focus the study on habitat components other than sediment type all sites chosen had sandy substrata. The scale and spatial distribution and heterogeneity of physical and biological structures were quantified for each site and correlated to plaice densities. Plaice densities correlated with the abundance of benthic fauna recorded. In particular the emergent tube-dwelling polychaetes *Lanice conchilega* and *Cheatopterus* spp., which are a valuable food source for plaice, dominated some sites. Abiotic habitat features and habitat heterogeneity showed no clear relationships with respect to plaice densities at the scale of our surveys. This indicated that prey availability might be the driving force for habitat selection of adult plaice within sandy habitats and that other habitat descriptors assume less importance at smaller spatial scales.

Keywords: *Pleuronectes platessa;* Habitat heterogeneity; Habitat selection; Food availability; Benthos; English Channel

1. Introduction

There is a current desire to move towards more ecosystem-based approaches to achieve the goal of sustainable fisheries (e.g. Link, 2002; Meester et al., 2004). While fisheries scientists have striven to understand the population dynamics of target species, knowledge of the ecological requirements of the latter are patchy in their coverage (Bigelow and Schroeder, 2002) for all but a selection of iconic species, e.g. cod *Gadus morhua*. Identification of the 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 of an ecosystem-based approach to management (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 needs to be viewed in the wider context of the ecological effects of fishing activities that have the potential to change seabed habitat structure (Jennings and Kaiser, 1998; Kaiser et al., 2002). The use of towed bottom fishing gear is known to change and alter 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).

Studies of the environmental determinants of the distribution pattern of flatfish mostly have been conducted over large geographical or regional scales and have used only the principal environmental descriptors such as depth, sediment type and temperature as predictors of these patterns (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 parameters may be important predictors of flatfish distribution at a smaller (local) scale and may influence habitat selection. The importance of some of these habitat parameters for juvenile flatfish (substratum relief and structuring fauna) has been demonstrated already (Abookire and Norcross, 1998; Norcross and Mueter, 1999; Stoner and Abookire, 2002; Stoner and Titgen, 2003; Ryer et al., 2004); however, for larger flatfish above the minimum landing size, the role of such parameters is not yet fully understood (Stoner and Titgen, 2003).

In the present study, habitat components at sites known to have consistently high densities of adult plaice (*Pleuronectes platessa* L.) were studied using underwater video surveys. Sampling benthic habitats with video transects, unlike by traditional methods such as grabs and beam trawls, permits real-time observation of the seabed and assessment of the spatial distribution and coverage/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 individually foraging fish. Although the composition of parts of the benthic assemblage can accurately be determined using grab sampling, this technique does not permit the determination and adequate quantification of other habitat descriptors, such as substratum relief and more scarcely distributed epibenthic fauna. Conversely, while beam trawls sample epifauna more efficiently covering larger areas, they pool benthic fauna over the areas sampled leading to a loss of information on small spatial scales.

The main aim of this study was to describe habitat features using video survey techniques in relation to the density of plaice of a legally landable size, sampled in the near vicinity. In this way it was possible to investigate which habitat features were correlated with catches of plaice and hence may influence habitat selection 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, the importance of spatial variability of features within sites was investigated to examine the role of habitat heterogeneity.

2. Methods

2.1. 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 sites regularly surveyed annually as part of a groundfish survey conducted by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS, Lowestoft) for fish stock assessment purposes (Rogers et al., 1998; Kaiser et al., 1999). A subset of nine of the sites that consistently had high densities of adult plaice was identified from the groundfish survey data using the method of Hinz et al. (2003). This methodology was applied as it ensures an objective selection process of such sites from large datasets rather than a choice based on subjective judgment.

The groundfish survey data spanned a nine-year period from 1990 to 1998. Only plaice over the minimum landing size (>26 cm) collected during the autumn groundfish survey cruises were considered for analysis. Plaice in the English Channel spawn between February and May, hence the groundfish survey data relate to the distribution of plaice outside the spawning season. We restricted the analysis to plaice over the minimum landing size (>26 cm) because they are of greatest commercial relevance and close to maturity at this size. Male plaice tend to reach maturity at a size of approximately 24 cm, while females are mature at a size somewhat larger than the minimum landing size. For each of the 133 groundfish survey sites used for this initial analysis, the percentage of the total number of fish sampled in that year was calculated. This value was calculated for each site for every year in the dataset. This conversion was performed to prevent a bias in the analysis caused by the occurrence of an exceedingly high abundance of plaice at a particular site 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 of the sampled population was calculated for each site and plotted against its corresponding standard deviation. The resultant scatter plot was overlaid with a fitted regression and corresponding 95% Predictor Intervals (PI) generated from a regression analysis of a randomised version of the dataset. Within each year, every site was assigned a percentage of the sampled population allocated at random from within the range of the data for that year. For a more detailed description and discussion of this method see Hinz et al*.* (2003). Thus, sites that were plotted below the lower 95% PI represented sites at which plaice occurred more consistently (high mean: S.D. ratio) than predicted from the randomised data. Thirty one of the sites from the groundfish survey fell below the 95% PI of which nine had similar sediment composition (sandy substrata) and depth characteristics. The long-term mean percentage abundance of plaice varied among these sites, which enabled us to examine the relationship between habitat characteristics and plaice densities.

Previous studies of the large-scale distribution patterns of plaice have shown that they were primarily found over sandy substrata (Amezcua and Nash, 2001), so in the present study we limited our investigation to this type of habitat to increase our chances of elucidating the relationship between habitat characteristics and plaice density.

The sites sampled were distributed across three regions of the English Channel (see Fig. 1). Two sites (W1 and W2) were located off Start Point, Devon. Three sites were positioned off the English coast (NE1-NE3), between Brighton and Hastings. A further four sites were located off the east coast of France near Boulogne-sur-Mer (SE1-SE4).

2.2. Fish survey

Four daytime tows of 20 min 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 sites in August 2002. The beam trawl was fitted with a chain-matrix and an 82 mm diamond mesh cod end with a 40 mm square meshed liner. All fish were sorted into species, counted and weighed. The total length of each plaice was recorded to the nearest cm. Plaice catches were standardised to a tow length of 250 m covering an area of 1000 m^2.

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

To evaluate whether plaice abundances at the nine sites followed the same trends as those predicted by the long-term 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 concomitantly with the habitat characteristics.

2.3. 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 45° and with the lens approximately 0.7 m above the seabed. The field of view spanned an area of 0.2 m^2. Lights were mounted at 60° to the camera. The video images were recorded using a Hi-8 video cassette player.

The video sledge was towed at the speed of the current acting upon the vessel. The average video transect was 561 ±214 m and towing speeds ranged between 3.8 cm and 62.9 cm s^{-1}.

Digital images were freeze-framed and extracted from the video recordings made during individual tows at intervals of 20 s. Ninety images were extracted for each video tow. To standardise for the differences in tow length and allow analysis of images from equal distances traversed across the seabed, images were allocated into consecutive 50 m sections that were determined from the vessel speed and time of recording. Each 50 m section thus had a different number of images and was therefore sub-sampled. For each 50 m section of each tow, five images were randomly selected for detailed analysis. Five images proved to conserve sufficient habitat information for the purposes of quantifying habitat characteristics. This was determined by using cumulative sample curves calculated for habitat characteristics. The use of fewer than five images did not identify all quantifiable features within a 50 m bin interval. To make the data of each tow comparable, the overall tow length for each tow was standardised by randomly selecting an equal number of 50 m intervals for each site. As a result an equal tow length of 200 m 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 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 collected with a Day grab at each site. Sand ripples were recorded as present or absent and all other physical structures were counted (Table 1).

The habitat characteristics data were subjected to a cluster analysis to generate a dissimilarity matrix (PRIMER v.5) after calculating the standardised Euclidian distance between each pair-wise comparison of sites. Those habitat features that contributed most to the similarity among groups of sites (identified a posteriori from the cluster analysis) were determined using SIMPER analysis (PRIMER v.5).

Habitat heterogeneity within sites was determined to assess spatial differences in the distribution of physical features between sites (Table 1). At each site a dissimilarity matrix was calculated from the 20 video images based on Euclidean distance for each pair-wise comparison of video images. From this matrix the mean dissimilarity and its corresponding standard deviation was calculated. The mean dissimilarity of all images of one site was then used as an approximation of habitat heterogeneity. Sites with a low mean image dissimilarity indicated homogeneous substratum characteristics, while sites with high mean image dissimilarity indicated heterogeneous substratum characteristics. To test whether mean substratum dissimilarity (heterogeneity) was correlated with plaice abundance the Pearson’s product-moment correlation test was used. Both heterogeneity and plaice density were Log_{10}-transformed prior to analysis. The relationship between depth and flatfish abundance was tested in a separate correlation analysis.

From the video images, benthic organisms were identified to the lowest taxonomic level possible and counted (Table 1). The mean number of benthic animals was calculated for each 50 m section (mean of 5 images) of each tow. From this the overall mean abundance per 200 m camera tow was determined. While the larger epifauna were easily counted, smaller and hyper-abundant species were difficult to quantify. 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 well-defined areas to less defined ones.

Owing to the low number of taxa observed in six out of the nine sites, an additional analysis was performed that involved analysis of the entire video transect (90 images) for each site. The abundances of benthic species were subsequently standardised to a common transect distance of 1 km. These semi-quantitative data were included as they contained valuable information on the benthic assemblages found at each of the sites investigated that otherwise would have been lost.

The mean number of benthic animals per 50 m section for each site (200 m 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) were also correlated with plaice densities (Pearson product-moment). The abundances of benthic organisms and the number of taxa were Log_{10}-transformed prior to analysis.

3. Results

3.1. 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 sites. The median abundance of plaice per tow above the 26 cm minimum landing size (MLS) differed significantly among the nine sites sampled (K-W, $H = 27.79$, d.f. = 8, $p = 0.001$). Sites SE2 and SE1 had significantly higher median abundance of plaice above the 26 cm MLS per tow compared with all other sites. This indicated that at sites SE1 and SE2 a greater median number of larger plaice were caught than at any of the other stations (Table 1).

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. 2). This indicated that the abundance of fish sampled during the present study in general could be predicted from the long-term CEFAS groundfish survey data. However, the correlation was strongly influenced by the three sites located off the French coast: SE1, SE2 and SE4. These sites had the highest mean abundances of plaice (above MLS) in the long-term data of CEFAS, which matched with the abundances of plaice caught at these sites by the present study.

3.2. Substratum characteristics, habitat heterogeneity and depth

The analysis of the substratum characteristics showed that although the seabed at all sites was primarily composed of sand, subtle habitat differences between sites were apparent (Table 1 and Fig. 3). Sites clustered into two main groups at a dissimilarity level of 65%. Group one consisted of sites SE1, SE3, SE4 and NE3. The SIMPER analysis showed that these sites were characterised by a high mean percentage cover of sand (mean ± SD 98 ±3.6) and the presence of medium sand waves (mean percentage occurrence 36.2±47.5). The mean number (± SD) per video frame of small (1.83 ±3.4) and large stones (0.13 ±0.21) also characterised these sites. The second group consisted of sites NE1, NE2, W1, W2 and SE2. Site SE2 clustered separately from the highly similar cluster of the remaining sites and was analysed independently (Fig. 3). Sites NE1, NE2, W1 and W2 had a slightly lower percentage sand cover than group one sites (mean ± SD 95.3 ±5.7), while video images were also characterised by a low mean percentage cover of small and broken shells (4.6 ±5.7). Small sand ripples on average occurred in 81% (±22.5) of the images from these sites. Site SE2 showed sand ripples (100%) and a lower mean percentage cover of small and broken shells (11.5±27.9). Site SE2 also differed from the other sites in its mean percentage cover of sand (36±44) and it was the only site where a percentage cover of shelly gravelly sand (mean ± SD 52±49.2) was recorded. The percentage contributions of each substratum characteristic to the percentage similarity among sites in each cluster are summarised in Fig. 3. There was no clear relationship between the posterioiri defined site (habitat) groupings (Fig. 3) and plaice densities recorded during this study. Thus sites with as high and low densities of plaice occurred within both groupings of sites defined on the basis of substratum characteristics.

Calculation of the mean dissimilarity of images of each of the sites as an approximation of physical habitat heterogeneity showed that there were distinct differences in habitat heterogeneity among sites (Table 2). There was, however, no significant correlation between mean number of plaice caught and habitat heterogeneity at each site ($r = 0.504$, *d.f.* = 8, $p = 0.166$, Fig. 2).

No significant correlation could be found between the water depth (Table 2) and the abundance of plaice at each site ($r = -0.195$, *df* = 8, $p = 0.615$, Fig. 4). This is not surprising as we deliberately chose sites from within a narrow depth range to eliminate the influence of this environmental variable in the context of the present study.

3.3. Benthic fauna

There was a significant positive correlation between the mean abundance of benthic fauna recorded per 50 m at each site and plaice densities ($r = 0.75$, *d.f.* = 8, $p = 0.02$, Fig. 2). Likewise, the total abundance of benthic organisms per video tow correlated significantly with plaice abundance ($r = 0.676$, *d.f.* = 8, $p = 0.045$). The number of taxa sampled for the whole camera tow did not significantly correlate with plaice densities ($r = 0.614$, *d.f.* = 8, $p = 0.079$).

The correlations between the abundance of benthic fauna and plaice abundance were strongly influenced by the sites from the east coast of France (SE1-SE4, see Fig. 2). These sites had the highest level of community diversity and the largest quantity of benthic fauna, which corresponded well with the abundance of plaice at these sites. In particular, plaice abundance seemed to be related to the presence of high-density polychaete tube mat structures at sites SE1-SE4 (Tables 1 and 2, Fig. 5). The tube mats were composed of the polychaetes *Lanice conchilega* and a previously undescribed species of *Cheatopterus* sp. (Rees et al*.,* 2005).

Site SE1 had the highest densities of emergent polychaetes (mean ± SD, 2390 ± 470 m^{-2}, Figs. 4 and 5) and had the highest densities of plaice caught during this study (Table 1). On average 5.7 (±0.74) plaice were caught 1000 m^{-2} with the majority of individuals (5.3 ±0.72) above the MLS (Fig. 5). Densities of polychaetes were lower at site SE2 (288±575 m^{-2}) and more patchy in their distribution. Adult plaice densities also were lower at this site (1.56±0.86 m^{-2}). The density of emergent polychaetes was similar at site SE3 and site SE2 (367±185 m^{-2}). Overall densities of plaice were relatively high (3.55 ±2.08). Here, catches mainly consisted of small plaice below MLS (3.36 ±2.06, Fig. 4). No emergent tubeworms were observed at site SE4 (Fig. 5) which coincided with the lowest density of plaice encountered at any of the French coast sites (0.46, S.D. ±0.20). The majority of plaice caught were, however, above MLS (0.44±0.23). SE4 was dominated by the brittlestar *Ophiothrix fragilis* which occurred in large aggregations at the beginning of the video camera tow (Table 2). At the remaining sites (W1, W2, NE1, NE2 and NE3) benthic organisms were only rarely observed (Table 1). The only other site with a considerable abundance of benthic epifauna was site NE1, which was dominated by the common mussel *Mytilus edulis* (Table 1). Plaice densities at these sites were much lower compared to the French coast sites and ranged on average between 0.17-0.33 animals per 1000 m^2 (2-5 fish per 20 min tow, see Table 1).

4. Discussion

4.1. Site selection and plaice abundance

The results of this study demonstrated that using long-term datasets from groundfish surveys to identify sites of consistent plaice abundance in the English Channel was a relatively accurate predictor of the relative magnitude of replicated 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 across time.

4.2. Habitat descriptors and plaice densities

The present study indicated that high densities of plaice were associated with areas that had a rich benthic fauna typified by dense mats of the tube-building polychaetes *Lanice conchilega* and *Cheatopterus* spp. However, this relationship was only observed at the sites off the French coast (SE1-SE4) as all other sites 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 sites. Nevertheless, the corresponding gradient of benthic fauna and plaice densities observed within these four sites suggests the existence of a relationship between fish abundance and prey abundance beyond a critical threshold. 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). Moreover, as tubicolous polychaetes occurred in high abundances, search times when feeding will be minimal, conserving energy and ultimately yielding a higher rate of food intake. Likewise at the site with the lowest polychaete tube cover (SE3), abundances of adult plaice (>MLS) were low, while smaller plaice were found in high abundances. This aggregation of smaller size fish, on habitats of lower prey resource value could be related to intra-specific competitive exclusion by the large plaice occupying prime feeding 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. Predator avoidance is probably a more pressing issue for juvenile than adult flatfish (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, 2000; Ansell and Gibson, 1993). The open spaces left by the less dense polychaete tube mat cover at site SE3 and the sandy substratum may have fulfilled both habitat requirements (cover and food) of smaller plaice. Conversely, protection for larger flatfish is thought to be less crucial as the number of potential predators decreases with increasing body size (Gibson and Robb, 1992, 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 (Z?hlke, 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 1970s, 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 characterised by a high species richness and high abundances of *Abra alba* and *Lanice conchilega*. The 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 Contentin Peninsula that entrains these nutrient-rich and productive waters (Tappin and Reid, 2000), generate a rich food supply for the resident benthic fauna (Hoch and Garreau, 1998).

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 substrata. Heterogeneous sediments may affect burying capabilities and/or prey distribution, thus influencing overall flatfish distribution patterns. No significant relationship was apparent between plaice density and the substratum features and heterogeneity recorded by this study. However, the plaice sampled in the present study were relatively large (>26 cm) and therefore parameters important for predator avoidance may not be such 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).

4.3. Methodological evaluation and sampling scale

This study demonstrates the value of seabed imagery in the characterisation 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 sites 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 (unpubl. 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 a more restricted geographical area, so as to reduce variability due to large-scale geographical differences. This smaller-scale orientated approach seems to be supported by the data from the French coast. Sites 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 geographical 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 limited 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.

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Tables

Table 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 absence from images taken at each site (% P/A) while stones were counted (C). Epifauna was counted (C) or estimated (E). Mean abundance of epifauna per 50 m section of a 200 m tow and for the whole tow and standardised to a transect distance of 1 km. Asterisks indicate the categories 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 >26 cm per 1000 m^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 gravelly 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 0-5 cm (% P/A)	100	70	100	55			100	5	
* Medium sand waves >5 cm (% P/A)					1				0.4
* Large stones >5 cm (C)						<0.1			0.4
* Stones 0-5 cm (C)			16.8			7			0.3
* Small burrow 0-2 cm (C)					0.5				
*Large burrow 2-5 cm (C)				0.7					
Benthic fauna per 50 m 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 1 km 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

Table 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 greater the variation in physical features encountered within a transect.

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

Fig. 1. Location of study sites in the English Channel.

Fig. 2. Scatter plots of plaice abundance >26 cm per 1000 m^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 fauna, (d) Log_{10}-number of benthic taxa fauna recorded at each site.

Fig. 3. Cluster analysis of substratum characteristics showing similarities of station clusters in percentages. Characteristics of station clusters identified by SIMPER analysis were summarised below station clusters, with their corresponding percentage contribution to that cluster (contrib. %). Abundance 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).

Fig. 4. Mean abundance of two different size classes of plaice either below or above legal commercial landing size (juvenile <26 cm, adult >26 cm) per 1000 m^2 at the French coast sites SE1-SE4. Mean abundance of protruding Polychaeta tubes per 50 m section for a tow of 200 m. Error bars represent S.D.

Fig. 5. 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. Images of SE1 and SE2 showing dense tube mat cover of *Lanice conchilega* and *Chaetopterus* spp. At site SE3 the tube mat cover was less dense and the sandy sediments at this site appear to be covered with a thin layer of finer deposits. The image of SE4 shows sand waves with shell fragments and small stones deposited in the troughs.

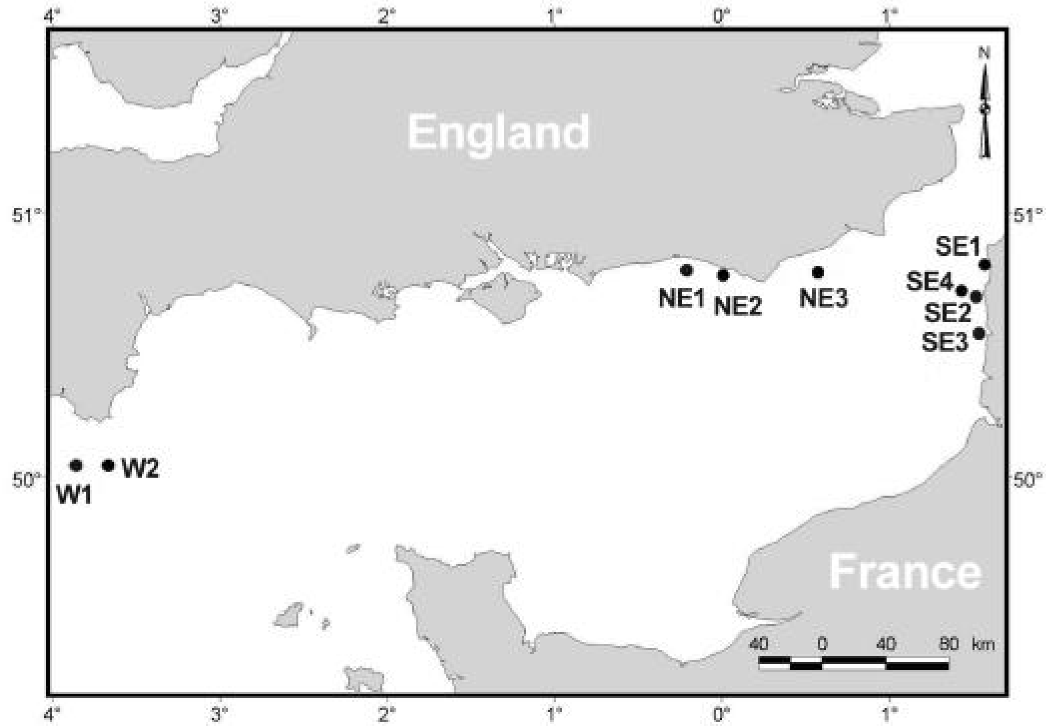
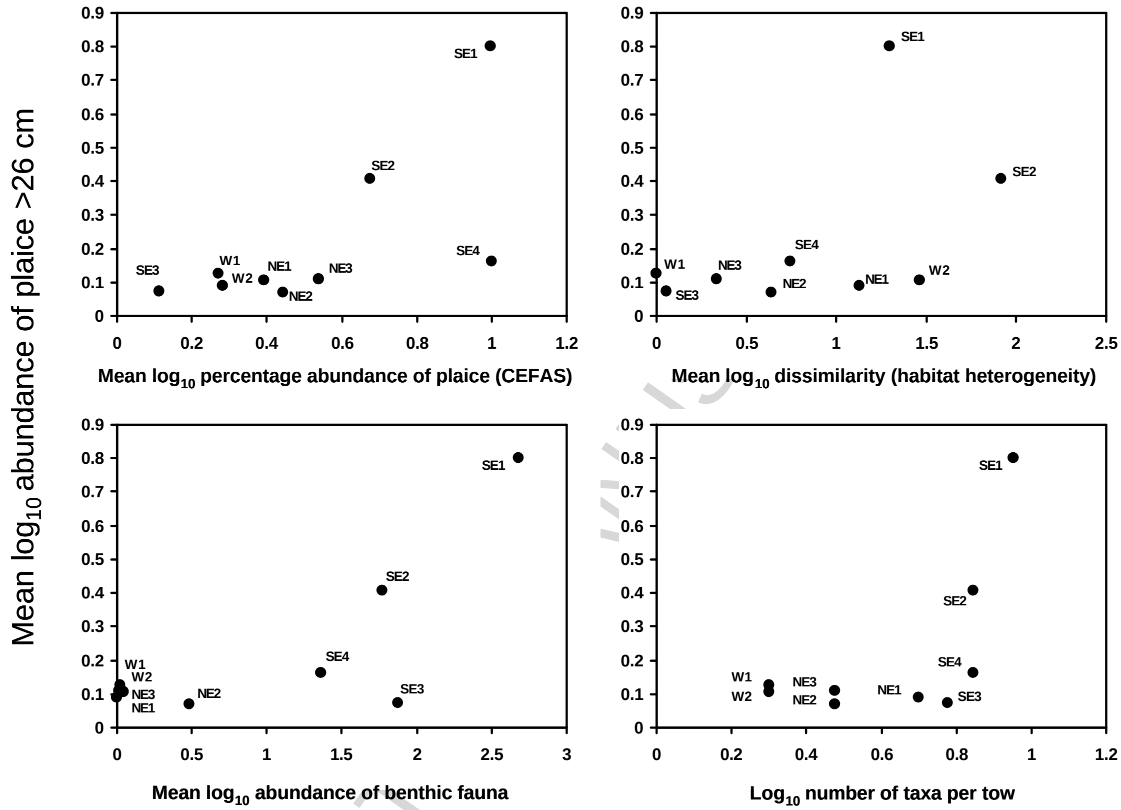

England
France
N
SE1
SE4
SE2
SE3
NE1
NE2
NE3
W1
W2
40 0 40 80 km
4° 3° 2° 1° 0° 1°
51°
50°

Fig. 1.



Mean log10 abundance of plaice >26 cm
SE1
SE2
SE4
SE3
W1
W2
NE1
NE2
NE3
Mean log10 percentage abundance of plaice (CEFAS)
Mean log10 dissimilarity (habitat heterogeneity)
Mean log10 abundance of benthic fauna
Log10 number of taxa per tow

Fig. 2.

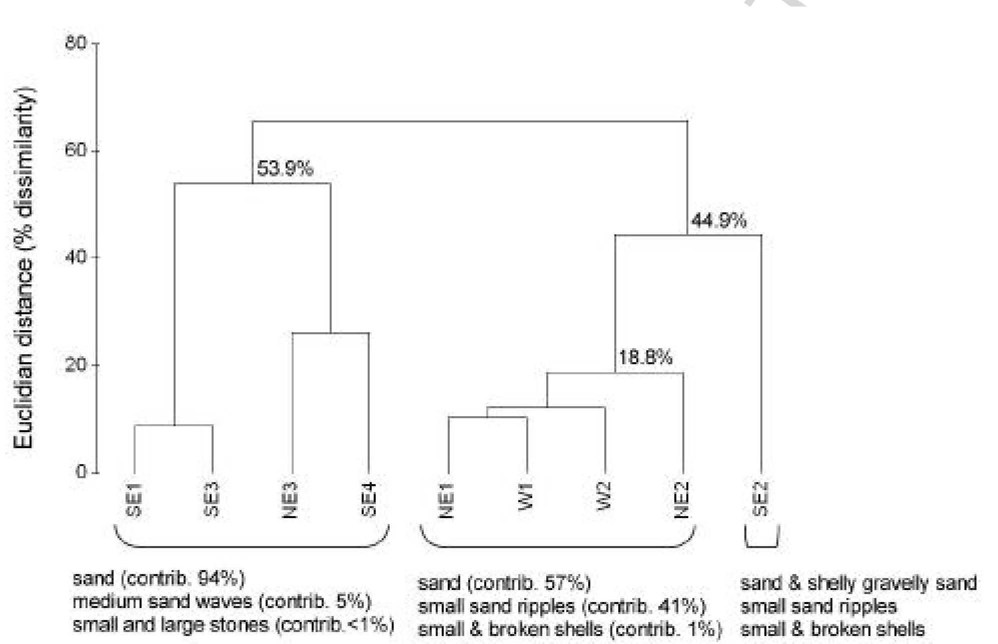
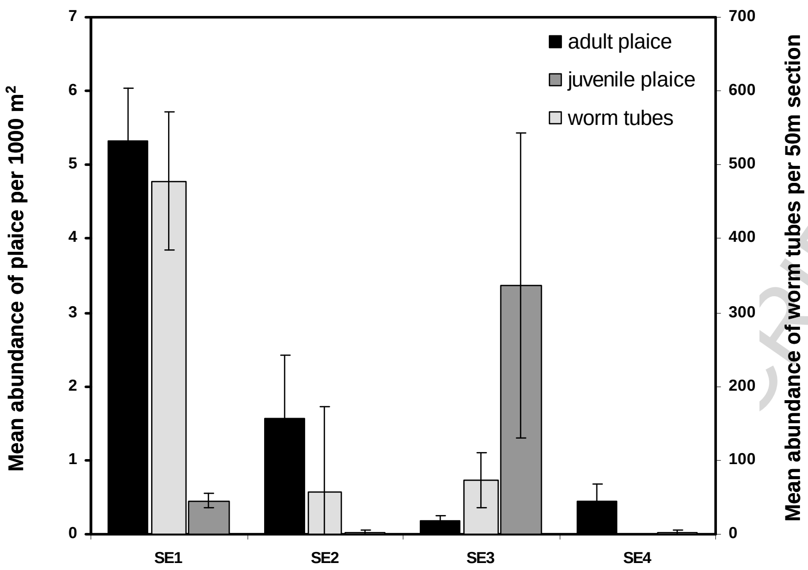

80
60
40
20
0
Euclidian distance (% dissimilarity)
53.9%
44.9%
18.8%
SE1
SE3
NE3
SE4
NE1
W1
W2
NE2
SE2
sand (contrib. 94%)
medium sand waves (contrib. 5%)
small and large stones (contrib.<1%)
sand (contrib. 57%)
small sand ripples (contrib. 41%)
small & broken shells (contrib. 1%)
sand & shelly gravelly sand
small sand ripples
small & broken shells

Fig. 3.



Mean abundance of plaice per 1000 m²
Mean abundance of worm tubes per 50m section
adult plaice
juvenile plaice
worm tubes
0
1
2
3
4
5
6
7
0
100
200
300
400
500
600
700
SE1
SE2
SE3
SE4

Fig. 4.

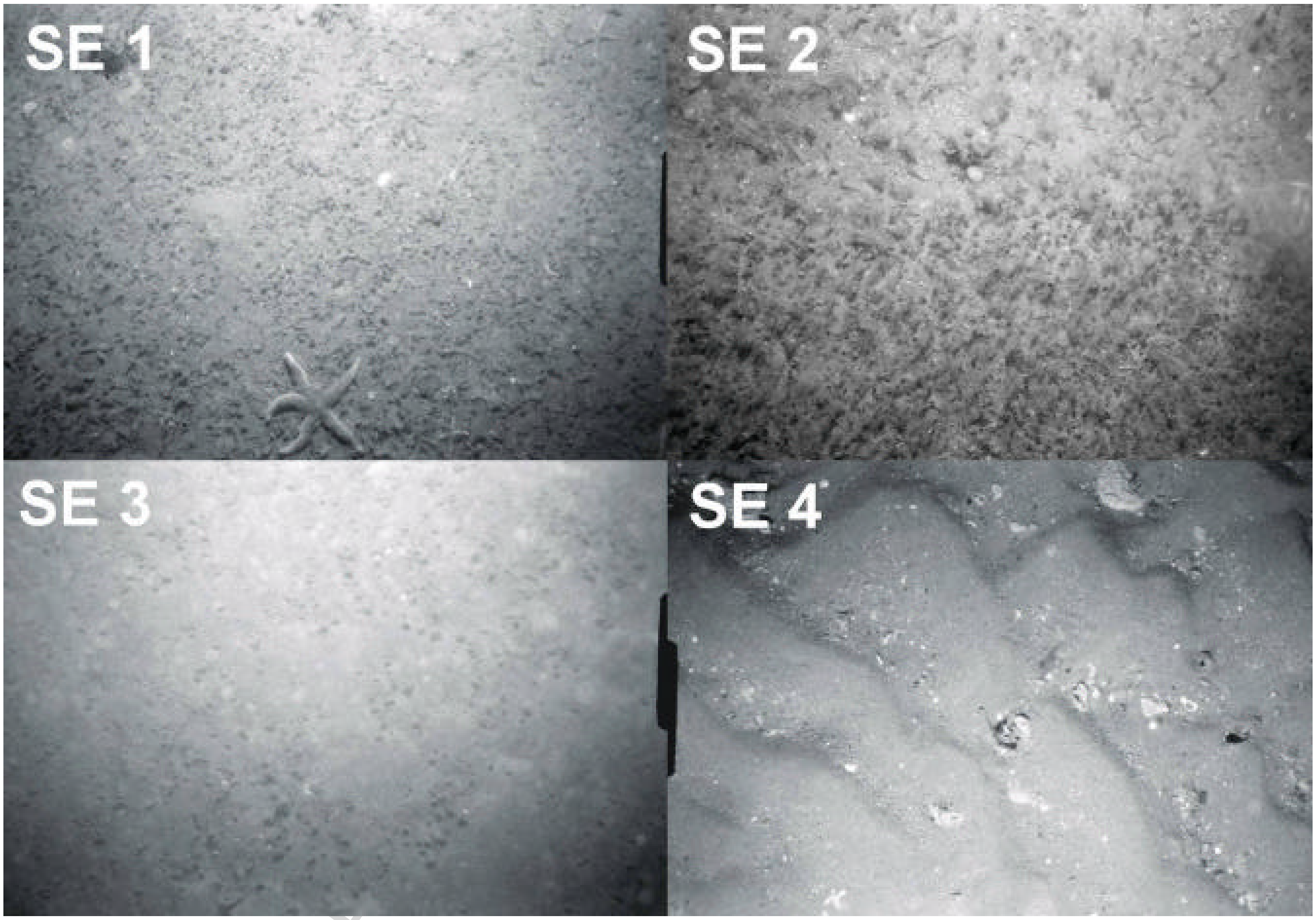


Fig. 5.