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Habitat association of plaice, sole, and lemon sole in the English Channel

Hilmar Hinz, Melanie Bergmann, Richard Shucksmith,
Michel J. Kaiser, and Stuart I. Rogers

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Flatfish have been the subject of scientific research since the beginning of the 19th century, but information on specific habitat requirements of adult life stages is incomplete. This study investigates the association between benthic habitat and the adult life stage of three flatfish species (plaice, sole, and lemon sole). Data from groundfish surveys spanning nine years were used to identify three distinct site groups: sites where a species was consistently abundant, sites of variable or low abundance, and sites at which no fish were caught. We hypothesize that these three site groups should represent a gradient in habitat suitability from highly suitable to unsuitable. Habitat parameters for each site group and species are described and analysed. Besides large-scale physical parameters, the importance of structuring epifauna and prey availability was investigated. Plaice and sole showed similar trends for most abiotic parameters, whereas lemon sole was found over distinctly different habitats. Sediment associations differed between the three species. No clear association was found between flatfish abundance, structuring epifauna, and prey availability within this study. Contradictory results between prey abundance assessed by grab samples and the nutritive state of plaice suggested that the sampling scale used might have been inappropriate to determine prey availability accurately. Plaice appear to sample prey more effectively at the appropriate spatial scales, so the nutritive state of the fish might be a more reliable indicator for prey availability and thus habitat quality.

Keywords: emergent epifauna, English Channel, flatfish, habitat selection, prey availability, stomach contents.

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H. Hinz, R. Shucksmith, and M. J. Kaiser: School of Ocean Sciences, University of Wales, Bangor, Askew Street, Menai Bridge LL59 5AB, Wales, UK. M. Bergmann: School of Ocean Sciences, University of Wales, Bangor, and now Alfred Wegener Institute for Polar and Marine Research, Handelshafen 12, 27570 Bremerhaven, Germany. S. I. Rogers: The Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft NR33 0HT, Suffolk, England, UK. Correspondence to H. Hinz: current address: Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth PL1 2PB, England, UK; tel: +44 1752 633334; fax: +44 1752 633102; e-mail: hlhi@mba.ac.uk.

Introduction

Traditional fisheries management has tended to focus on the population biology of single species without considering the wider ecological requirements of target species (Link, 2002). However, there is growing acceptance that an ecosystem 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 (Jennings and Kaiser, 1998; Kaiser *et al.*, 2002). In particular, bottom fishing is one of the more 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 such habitats (Auster and Langton, 1999; Kaiser *et al.*, 2002; Ryer *et al.*, 2004). Flatfish are uniquely adapted to a benthic life style (Gibson, 1994), and alterations to the benthic habitat may therefore influence suitability and hence flatfish survivorship and distribution (Gibson, 1994; McConnaughey and Smith, 2000). Currently, sound understanding of the biotic and abiotic characteristics of critical habitats for adult flatfish is lacking, yet it is an essential requirement to locate and quantify such areas for appropriate ecosystem-based management.

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In contrast to adult flatfish, the habitat requirements of juvenile flatfish have been the focus of a number of laboratory and field-based studies (Rogers, 1992; Gibson, 1994; Gibson and Robb, 2000; Eastwood *et al.*, 2003; Le Pape *et al.*, 2003a, b; 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 because they are physically capable of burying themselves in a wider range of sediment types (Gibson and Robb, 1992). Moreover, 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 revealing the sediment types (habitats) that are used or preferred by a species (Gibson and Robb, 2000). Moreover, 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 fulfil an important function in the evasion of predators by juvenile flatfish (Stoner and Titgen, 2003; Ryer *et al.*, 2004). Benthic habitats with emergent epifauna harbour a greater abundance and diversity of epibenthic prey types, and there is a direct relationship between habitat complexity and prey diversity (Kaiser *et al.*, 1999; Bradshaw *et al.*, 2003). This increased abundance of epibenthic invertebrates could consequently represent an important food source for certain flatfish species, particularly visual predators such as plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). Flatfish species that are primarily visual predators also could utilize emergent structures as indirect cues to locate desired prey items if the habitat structure and the preferred prey types are closely linked or occur within the same environmental boundaries. Such cues are used by many animals to increase foraging efficiency (Hughes and Blight, 2000; Hill *et al.*, 2002; Kristan, 2003; 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 occur (Smale *et al.*, 1993; Albert *et al.*, 1998; Rogers *et al.*, 1998; Ellis *et al.*, 2000). Most fisheries surveys do not collect extensive habitat information (but see Freeman and Rogers, 2003), so studies that link the abundance 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 and cover large temporal and spatial scales. Such broad data sets on fish distribution offer potentially valuable opportunities to investigate the relationship between fish abundance and benthic habitat features.

Spatial variability in the distribution of a fish species may reflect differences in habitat quality that comprise a combination of different physical and biological parameters such as depth, temperature, availability of prey, or the presence of structures that provide shelter from predators. These processes operate at different scales. Habitat selection theories such as the Ideal Free Distribution (IFD; Fretwell and Lucas, 1970) or MacCall's basin theory (MacCall, 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 density, individuals will occupy the most suitable habitats, whereas individuals will occupy less suitable habitats once density increases and density-dependent effects arise (Rogers, 1994; Simpson and Walsh, 2004). Of course, decreases in overall abundance later will cause populations to contract in space and retreat once more to the most suitable habitat. Suitable benthic habitats should as a consequence reveal consistent relative abundance through time if important habitat parameters are strongly location-specific. Therefore, fish abundance data from groundfish surveys alone could indicate relative habitat quality.

Practical problems related to the sampling design for bottom-dwelling fish and overall theoretical difficulties need to be considered when consulting such data sets. The sampling grids of groundfish surveys are designed primarily to monitor fish stocks at large spatial scales, and they are restricted to locations that warrant sampling and reduce the risk of loss or damage to the sampling gear. Consequently, hard substrata deliberately may be avoided during field campaigns. 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, because sites of high fish density may not necessarily be indicative of good habitat quality or preferred habitat, because other factors may also lead to aggregation in less suitable habitats, e.g. intra- and interspecific competition may displace certain life stages or fish species from otherwise suitable areas (Kaiser *et al.*, 1999). Therefore, the non-random association of a species with a particular habitat feature does not necessarily infer preference (Underwood *et al.*, 2004), because 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. Within the present study, we have therefore attempted to describe association between the abundances of three flatfish species, plaice, sole (*Solea solea*), and lemon sole (*Microstomus kitt*), with various habitat parameters. Abundance data of groundfish surveys conducted in the English Channel were used to identify sites in which consistently high and low densities of plaice, sole, and lemon sole were found over a nine-year period (Hinz *et al.*, 2003).

For those sites, we assessed the relationship between flatfish distribution and the benthic habitat to address the following questions: (i) which sediment types and selected environmental parameters are concurrent with consistently high abundance of adult flatfish; (ii) are biotic benthic habitat structures and prey availability associated with high flatfish abundances; and (iii) are there any differences in the habitat characteristics occupied by these three flatfish species?

Methods

Delineation of site groups

Fish abundance data from groundfish surveys carried out by the Centre for Environment, Fisheries and Aquaculture Science (Cefas) of plaice, sole, and lemon sole at fixed stations in the English Channel were used for analysis. Data spanned the period 1990−1998. As adult fish were the focus of the study, only fish greater than the minimum landing size that roughly correspond with the age of maturity (MLS: plaice >26 cm, sole >23 cm, lemon sole >24 cm) were considered. Fish collected during autumn groundfish survey cruises were used in order to avoid any sampling of spawning aggregations. Overall, 133 stations were included in the analysis (Figure 1).

Stations were divided into three distinct site groups for each species according to their trends in abundance through time: (i) sites where flatfish abundance was consistently high; (ii) sites where abundance was variable or low; and (iii) sites where no fish were caught during the survey period. To appoint objectively each station to the respective site group, the 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) were then $\log_{10}$-transformed to achieve a normal distribution. From the transformed relative abundances, the mean and the standard deviation (s.d.) of each station over the whole sampling period were calculated, and plotted to produce a scatterplot (Figure 2). To create delineation lines, the process was repeated using the same data set, but first randomizing it. Within each year, every station was assigned an abundance allocated at random from within the range of the data for that year. From the resulting random data set, the mean $\log_{10}$ percentage abundance and standard deviation were calculated. The relationship between random means and s.d. was best described by a linear model of which the 95% Predictive Intervals (PI) were used as delineation lines in the scatterplot of the original data, to divide stations into the three site groups (Figure 2). Stations below the lower 95% PI thus represented stations where fish were consistently caught at high abundance (i.e. they had a low ratio of s.d.:mean). These stations will be referred to as consistently high abundance sites (CHS). By contrast, stations found within the 95% PI boundaries corresponded to sites at which fish were caught in variable or low numbers, and are therefore referred to as variable or low abundance sites (VLS). Stations at which no fish were caught over the sampling period characterized the third site group, referred to as sites of zero catch (0-C).

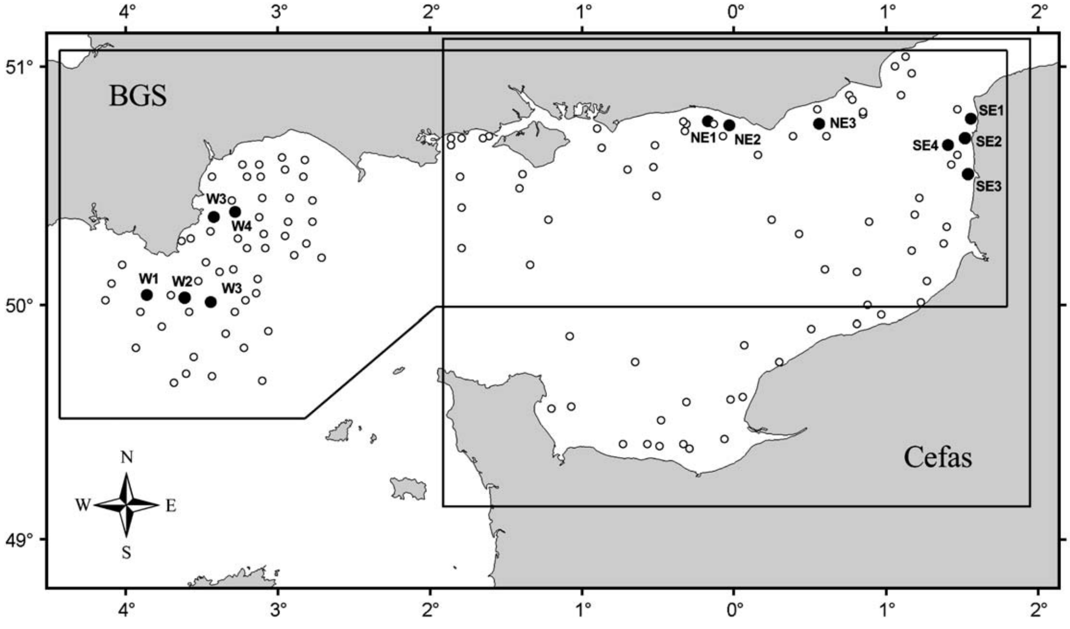

Figure 1. Map of the English Channel showing groundfish survey stations included in the analysis (black and white circles). Boxes mark the spatial coverage of the environmental data sets used for analysis (BGS and Cefas). Black circles designate survey stations revisited in 2002.

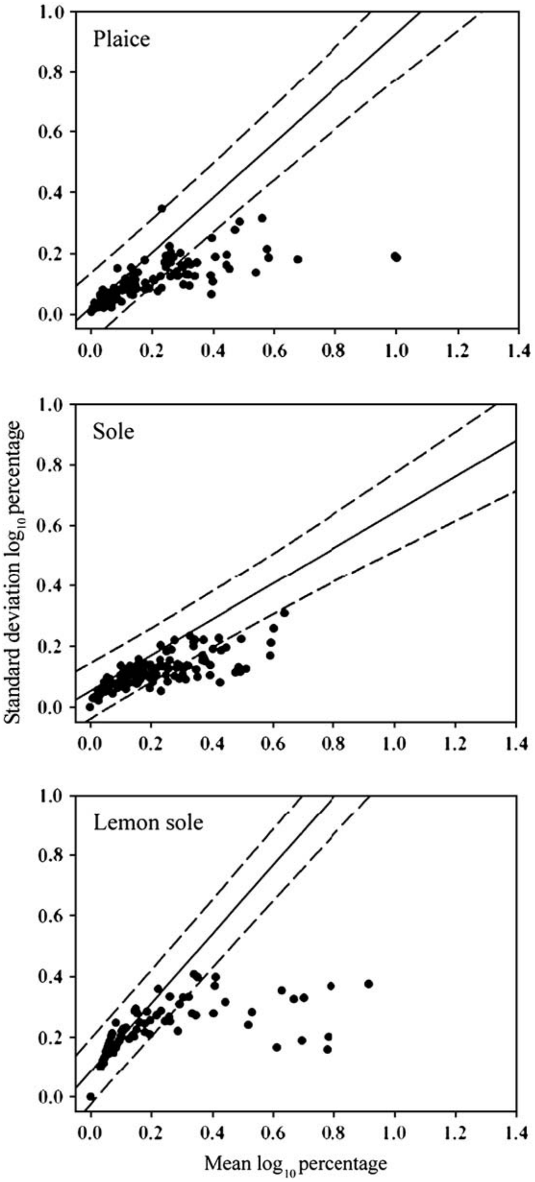

Figure 2. Relationship between mean $\log_{10}$ percentage and standard deviation for nine years of stations sampled for plaice, sole, and lemon sole. Regression lines and 95% PI originate from the same data after generation of random scores. Stations below the lower 95% PI represent stations of consistently high fish abundance. Stations within the 95% PI represent stations of variable and low abundance of fish.

British Geological Survey (BGS) sediment data

Sediment characteristics of the stations included in this analysis were extracted from digital sediment maps (British Geological Survey; BGS Licence 2003/133) using a GIS software package (ArcView 3.2). The 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 (Figure 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 do 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, so 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 data set, 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 means of a χ^2 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 χ^2 results indicate that at least one abundance category differs significantly from this assumption. Some of the nine recorded sediment classes had very few observations (Figure 3), so the data were pooled into three new sediment categories for analysis: muddy sands (muddy sand, slightly gravelly muddy sand, and gravelly muddy sand); sand (gravelly sand, slightly gravelly sand, and sand); and gravelly and hard substrata (rock and sand, gravel, sandy gravel, and muddy sandy gravel). Because of the pooling of sediment categories, detailed information about the association of sediment type and flatfish was partially lost, so visual examination of the original data was also undertaken to highlight specific trends in the data.

Cefas abiotic habitat parameters

Cefas maintains a data set of benthic habitat parameters that cover the eastern part of the English Channel (Figure 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 include: QTC VIEW™ class as a descriptor of seabed characteristics (a measure that encompasses sediment type and seabed morphology), water depth (m), near-bed tidal velocity ($\mathrm{m\,s^{-1}}$), sea surface temperature (°C), salinity, and weight of rocks and shells ($\mathrm{kg\,h^{-1}}$) caught as incidental catch with fish samples. For a more detailed description of the data collected and QTC classes, see Freeman and Rogers (2003). The parameters were all recorded during the Cefas groundfish survey of August/September 1999. Parameters such as sea surface temperature and salinity vary with season, so the figures shown should be viewed as relative values for between-site comparison. 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

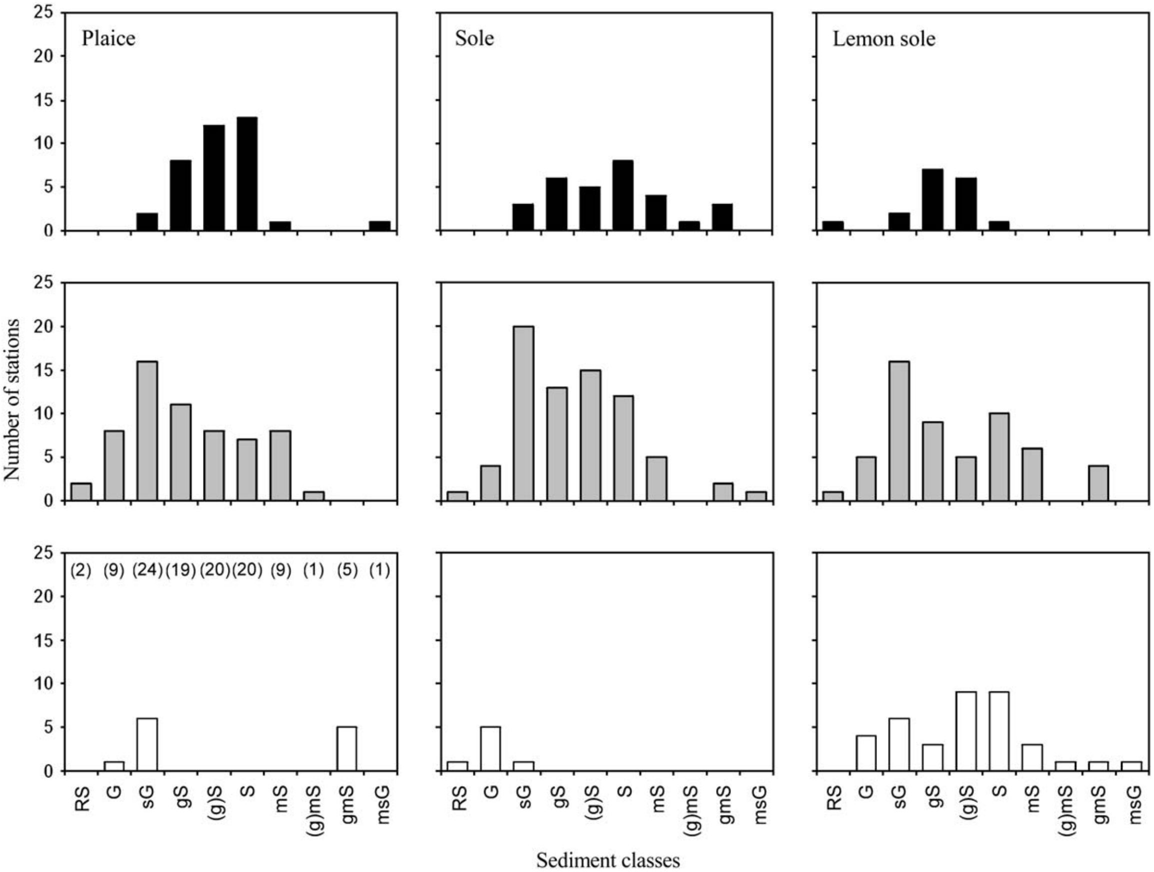

Figure 3. Sediment classes recorded for the three site groups: sites of consistently high abundance (black), sites of variable abundance (grey), and sites of zero catch (white). Numbers in parenthesis represent the total number of observations (*n*) available for each sediment class. Sediment classes: 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; and RS, rock and sand.

composition of environmental parameters between each pair of stations. Stations plotted close to each other have greater similarity in terms of their environmental parameters than those plotted farther 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 stations is explained by each principal component, the loading indicates the environmental parameter that contributes most strongly to each component. Prior to undertaking PCA, the weight of shells and rocks caught in a 4-m beam trawl were $\log_{10}$-transformed to ensure normality. Tests of significance for site-group differences for each species of fish were preformed using the ANOSIM routine (Clarke and Green, 1988) on the normalized Euclidian distance matrix. PCA plots were overlaid with the mean percentage abundance of flatfish caught over nine 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 parameter and site group were compared with means generated by a bootstrap procedure (Efron and Tibshirani, 1986) using S-Plus statistical software, because the data did not meet the assumptions for parametric analyses. Bootstrapping is a resampling technique in which new samples are repeatedly drawn at random (here, 1000 times) from the underlying data set. Each randomized 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 means imply that it is highly unlikely for the observed mean to have been a chance event ($<5\%$), so strengthening the argument that the observed trend is genuine. As QTC classes constitute categorical data, they were summarized for each station group and fish species in a separate table. The data were analysed using a χ^2 test of association. Prior to analysis, the 10 QTC classes (Table 1) were pooled into three main sediment categories to permit statistical analysis: mud and muddy sands (QTC classes 1 and 2), sand (QTC classes 3−6), and gravelly substrata (QTC classes 7−10).

Table 1. Frequency of occurrence of prey species (>5%) found in flatfish stomachs at all sites.

Prey taxon	Frequency of occurrence (%)		
	Plaice	Sole	Lemon sole
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		
Number of full stomachs analysed	166	18	5

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 was selected for more detailed site-specific investigation (Figure 1). The intensive sampling regime adopted at each site only permitted sampling 12 sites in all. This made it impossible to choose a sufficient number of sites for all three site groups (HCS, VLS, and 0-C) for each flatfish species. Therefore, sites were chosen on the basis of 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 min 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 codend with a 40 mm square-mesh liner towed at a speed of 4 knots. Catches were sorted aboard and all organisms were identified, counted, and wet-weighed. For colonial epifaunal animals such as hydroids and bryozoans, only the wet weight was recorded. Individual plaice, sole, and lemon sole were measured to the nearest centimetre below. Prior to analysis, the data were standardized to a tow length of 2 km. To evaluate whether stations followed the same trends in flatfish abundance as predicted by the long-term Cefas data set, the mean $\log_{10}$ abundance of fish caught above MLS during the "Prince Madog" cruise was correlated with the mean $\log_{10}$ percentage abundance over nine 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's correlation). Emergent epifauna included organisms from the following taxa: Anthozoa, Ascidiacea, Bryozoa, Hydrozoa, and Porifera. As many of these are colonial, making abundance estimates difficult to obtain, their wet weight was used as a measure of biomass.

To assess prey availability in the environment, the prey spectrum of each flatfish species was determined and linked to macrofauna abundance data obtained from grab samples collected prior to beam trawling for the assessment of flatfish abundance. Four-day grab samples (0.1 m^2) were collected 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 taxon. 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). Those fish were frozen prior to removal of their stomach contents. After washing in freshwater and dry-blotting, abundance and wet weight of prey were recorded to the highest possible taxonomic resolution. The frequency of occurrence of items ingested was calculated for each flatfish species. To calculate prey availability in the environment, only prey that had a frequency of occurrence >5% were used, thus excluding animals that could have been ingested by accident, were generally inaccessible, or were less desirable. The sum of all prey items found in grab samples therefore represented a measure of prey abundance in the environment. The species used to calculate prey abundance from prey spectra are summarized in Table 1. A Pearson's correlation test was undertaken to assess whether prey $\log_{10}$ abundance per m^2 in the environment was correlated with the mean $\log_{10}$ abundance of flatfish. Other parameters from the stomach contents analyses, such as mean abundance and biomass (wet weight, g) of prey items per fish with stomach contents, percentage of empty stomachs, and condition factor (Fulton's K), were calculated for each site, but because of the scarcity of stomachs available at most sites for sole and lemon sole, these parameters were only formally analysed for plaice. A Pearson's correlation test was undertaken to assess whether $\log_{10}$ plaice abundance was correlated with mean $\log_{10}$ abundance and biomass (wet weight, g) of prey items per fish with stomach contents. A Spearman rank correlation test was carried out to assess whether the percentage of empty stomachs and mean condition were correlated with plaice abundance (data could not be normalized).

Results

Sediment characteristics (BGS and Cefas data)

Relating fish abundance with BGS data, only plaice had a significant association ($\chi^2 = 37.831$, d.f. $= 4$, $p < 0.0001$; Figure 4). There was no such association for lemon sole ($\chi^2 = 8.96$, d.f. $= 4$, $p = 0.062$; Figure 4), whereas for sole the result proved invalid owing to expected counts below one (Figure 4). While the sites of consistently high abundance for plaice had a strong positive association with sandy habitats ($\chi^2 = 8.71$), sites of variable and low abundance showed only a weak positive association with gravelly and hard substrata ($\chi^2 = 1.85$). Sites at which no plaice were caught were most positively associated with muddy sand ($\chi^2 = 6.91$).

For the Cefas sediment data, the χ^2 test for all three species was significant (d.f. $= 4$: plaice $\chi^2 = 17.44$, $p = 0.002$; sole $\chi^2 = 13.77$, $p = 0.008$; lemon sole $\chi^2 = 11.10$, $p = 0.025$; Figure 4). For plaice, sites of consistently high abundance were negatively associated with gravelly and hard substrata ($\chi^2 = 3.82$). The variable and low abundance stations had a weak contribution to the overall χ^2, the highest value being for gravel, with a slightly positive association ($\chi^2 = 0.39$). The sites with no catches of plaice had a strong positive association with gravelly substrata ($\chi^2 = 6.26$). For sole, the sites of consistently high abundance were again negatively associated with gravelly substrata ($\chi^2 = 2.22$), whereas variable and low abundance sites had a weak negative association with mud and muddy sand ($\chi^2 = 0.09$). For the sites with no catches of sole, there was a strong positive association with gravelly and hard substrata ($\chi^2 = 6.18$). Lemon sole sites of consistently high abundance were positively associated with sand ($\chi^2 = 5.17$), and sites of variable abundance had a positive

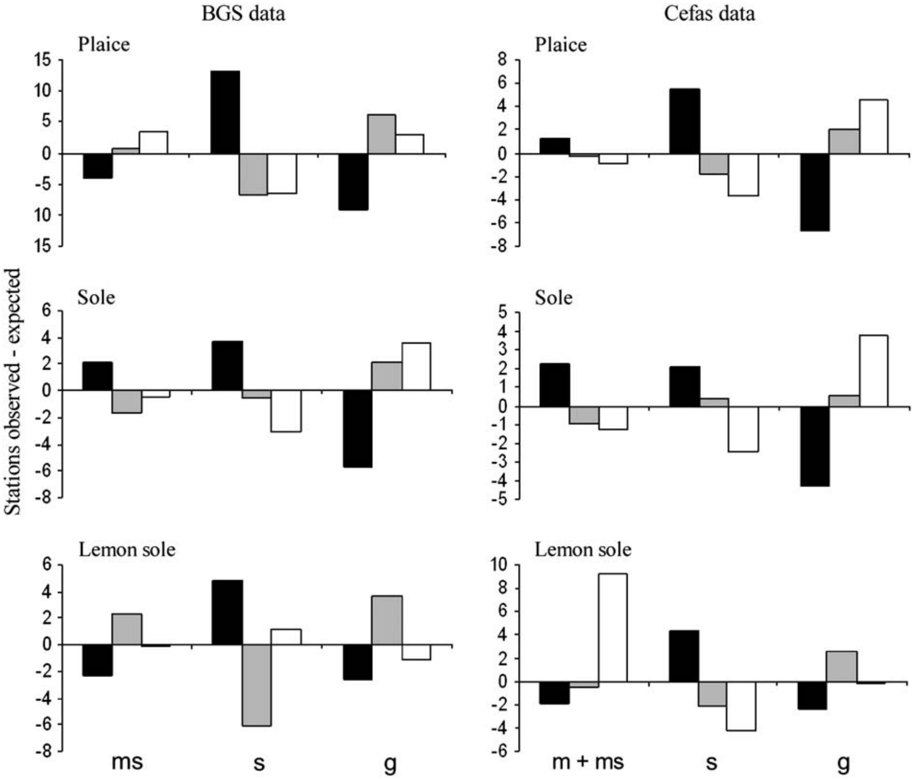

Figure 4. Observed minus expected number of stations from the χ^2 test of the three site groups for pooled sediment classes: sites of consistently high abundance (black columns), sites of variable and low abundance (grey columns), and sites of zero catch (white columns). Sediment classes for BGS – ms, muddy sand; s, sand; g, gravelly and hard substrata; for Cefas: m + ms, mud and muddy sand; s, sand; and g, gravelly and hard substrata.

association with gravelly and hard substrata ($\chi^2 = 0.7$). Sites with no lemon sole catches were positively associated with mud and muddy sand ($\chi^2 = 0.75$).

Owing to the pooling of sediment categories for the χ^2 analysis, more detailed information of the two data sets was obscured. Results of the χ^2 test indicated that plaice and lemon sole occurred consistently in abundance over sandy sediments. Visual examination of the sandy sediment categories in both unpooled data sets, however, revealed differences between the two species. Whereas sites consistently with plaice were all characterized by a high proportion of sand, sites with lemon sole had a higher gravel content (Figures 3 and 4; Table 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 <0.5.

From the bi-plots of all three species, it is apparent that environmental parameters at sites of consistently high abundance and those with low or varying abundance show considerable overlap (Figure 5). This was confirmed for plaice and sole by an ANOSIM test, which revealed no significant differences between these site groups. Hence, consistently high abundance sites were not characterized by distinctively different combinations of environmental parameters, compared with sites with varying abundance of the three species. However, there were significant differences, for both species, between consistently high abundance and 0-C (zero catch) sites (plaice: $r = 0.54$, $p < 0.05$; sole: $r = 0.53$, $p < 0.05$), and between variable abundance sites and 0-C sites (plaice: $r = 0.23$, $p < 0.05$; sole: $r = 0.5$, $p < 0.05$). This result was also reflected in the respective bi-plots for plaice and sole, sites at which no fish were caught being clustered more closely on the right side of the bi-plots. These sites generally had higher values of PC1 and lower values of PC2 than in sites where abundance was consistently high. Overall the bi-plots of plaice and sole showed many similarities (Figure 5).

Sites of consistently high lemon sole abundance grouped relatively closely together, indicating a high degree of similarity between preferred environmental parameters (Figure 5). In contrast to plaice and sole, sites of consistently high abundance were located more to the right, with generally higher PC1 values. Most sites of zero catch were in the area of the ordination plot that coincided with sites of consistently high abundance of plaice and sole. However, the differences between the three site groups of lemon sole were not significant.

Box plot bootstrap analyses

Depth (m)

For plaice and sole, consistently high and variable abundance sites had a similar depth range (25% quartiles around the median are referred to as the range), ca. 20−30 m (Figure 6). The mean depth for site groups and species was not significantly different from the randomly generated mean (the bootstrap mean). However, the 0-C sites were in a noticeably different depth range (≈40−50 m), and for both species mean depth was significantly deeper than would have been expected by chance

Table 2. QTC classes observed for each site group and species (on the Cefas survey of the eastern English Channel). Sites of consistently high abundance, CHS, sites of variable and low abundance, VLS, and sites of zero catch (0-C).

QTC class (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

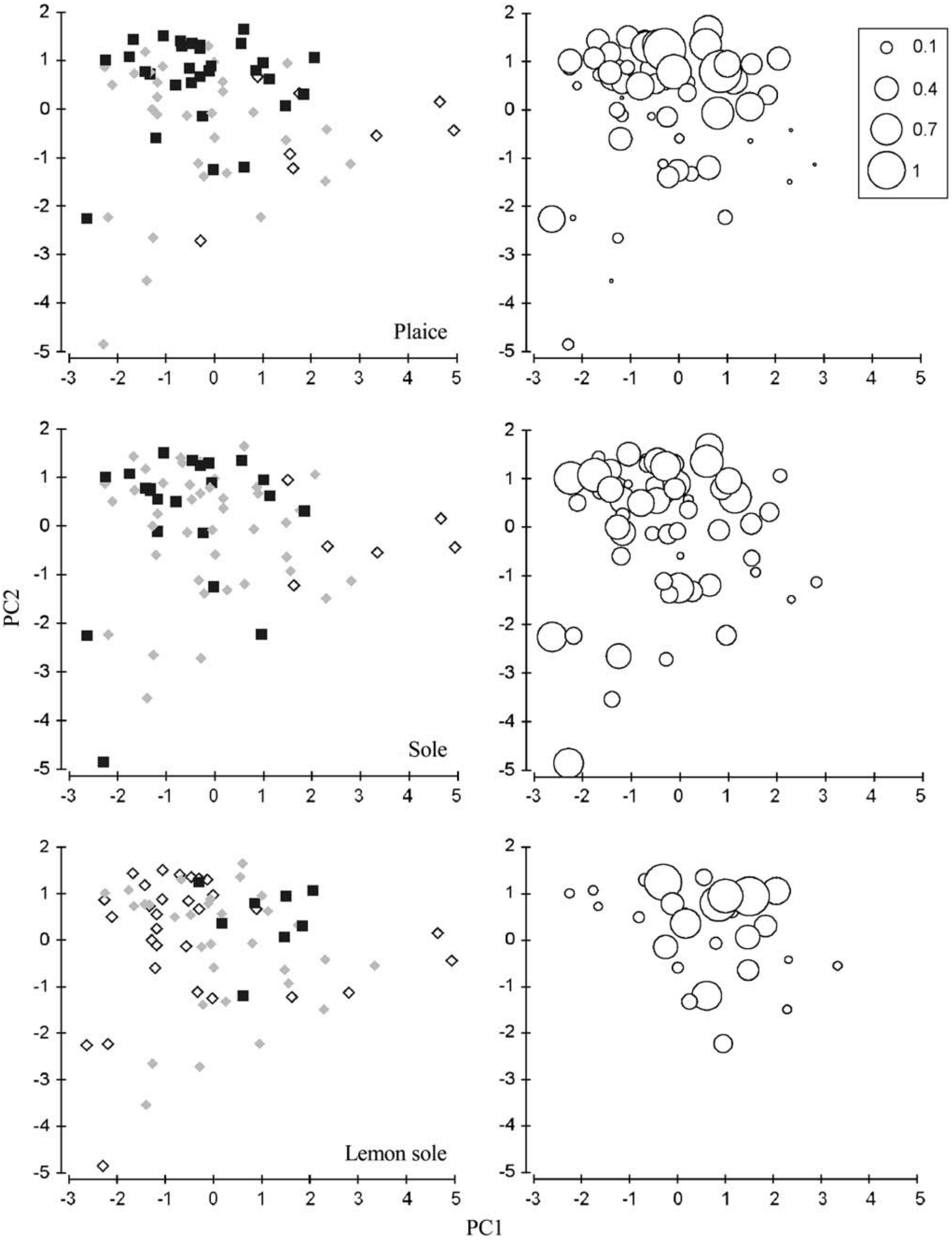

Figure 5. PCA bi-plots of environmental variables and fish abundance site groups: sites of consistently high abundance (black squares), sites of variable and low abundance (grey diamonds), and sites of zero catch (white diamonds). The PCA plot for each flatfish species is supplemented with bubble plots showing the mean $\log_{10}$ percentage abundance of each species over the nine years of the Cefas survey.

(plaice: 43 m, $p < 0.05$; sole: 50.3 m, $p < 0.05$). In contrast to the other two species, lemon sole were found at consistently high abundance in deeper water, ranging from 28 to 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 different from the bootstrap mean).

Sea surface temperature (°C) in August/September 1999
Again, plaice and sole had similar trends for consistently high and variable abundance sites (Figure 6). However, for plaice the consistently high abundance sites had a slightly narrower and lower temperature range (18.4–18.7 °C) than for sole (18.4–19.1 °C), although the means were not significantly different from random means. For

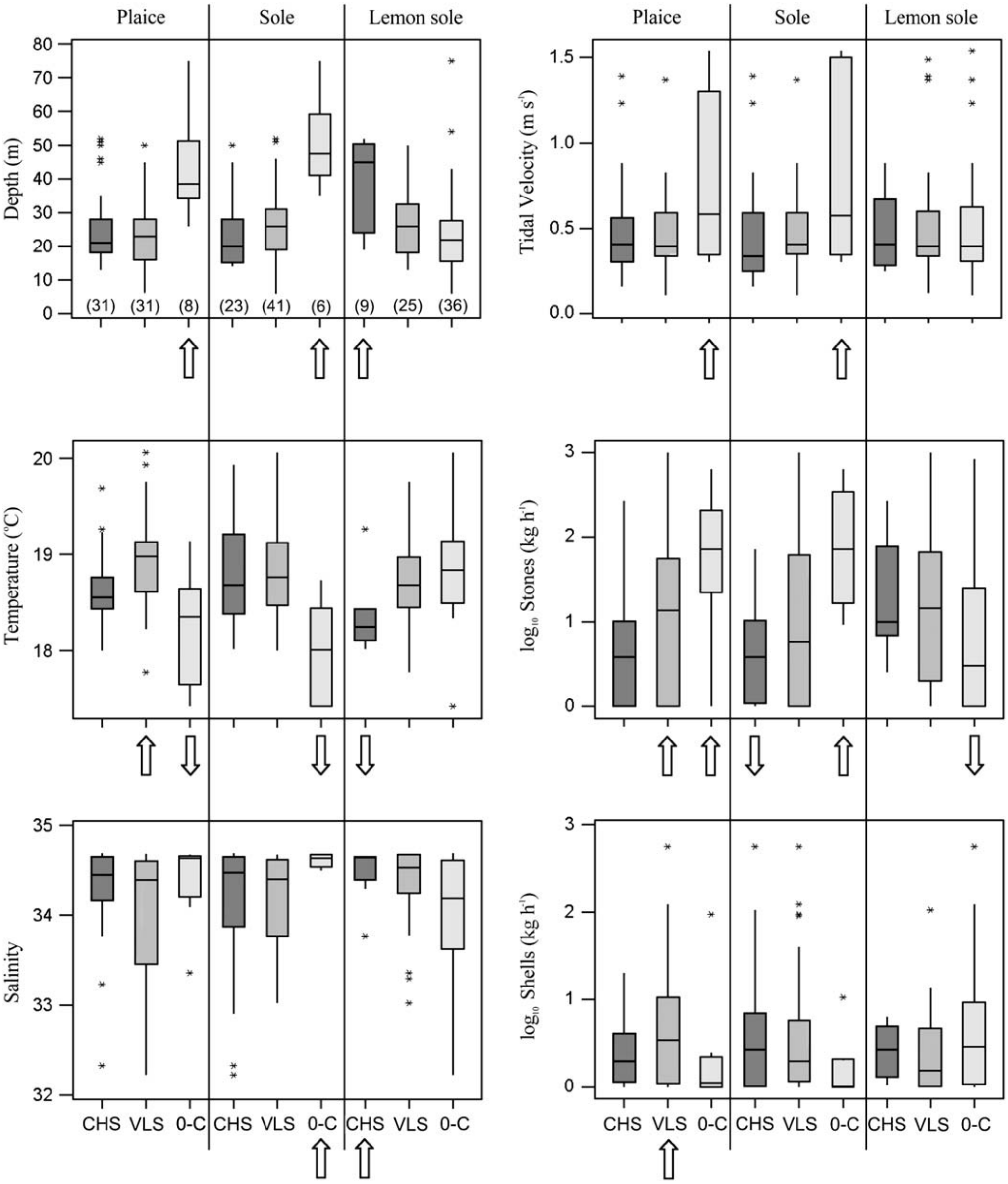

Figure 6. Box plots of environmental variables and site groups: sites of consistently high abundance, CHS (dark grey), sites of variable and low abundance, VLS (grey), and sites of zero catch, 0-C (light grey). Boxes represent median and quartiles, whiskers represent the range, and asterisks are outliers. 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. The direction of the arrow indicates whether the observed mean was significantly higher (upward arrow) or lower (downward arrow).

plaice the variable abundance sites showed a significantly higher mean (18.9°C, $p < 0.05$). Sites with zero catches for sole and plaice were characterized by generally lower temperatures (≈17.9−18.4°C) than the other two site groups, and the mean temperatures were significantly lower than bootstrap means (plaice: 18.2°C, $p < 0.05$; sole: 17.9°C, $p < 0.05$). Consistently high abundance sites of lemon sole showed the reverse trend. These sites were characterized by much lower temperatures (≈18.1−18.4°C) than variable abundance and 0-C sites. The mean temperature of the consistently high abundance sites was significantly lower than the random mean (18.3°C, $p < 0.05$).

Salinity

Consistently high abundance plaice sites showed a slightly narrower salinity range (34.18−34.6) than did similar sole sites (33.8−34.6), whereas variable abundance plaice sites occupied a larger range (33.5−34.4) than similar sole sites (34.2−34.6; Figure 6). 0-C sites in both species showed a narrow range of high salinity (≈34.5−34.7), but only the mean salinity of sole was significantly higher than the bootstrap mean (34.6, $p < 0.05$). Lemon sole sites of consistently high abundance were characterized by a narrow range of high salinity (34.5−34.6), and the mean salinity was significantly higher than the re-sampled mean (34.4). Variable abundance and 0-C sites were characterized by generally lower salinity, but the means were not significantly different from the bootstrap means.

Tidal velocity (m s^{-1})

For plaice and sole, the consistently high and variable abundance sites were characterized by similar tidal velocities (≈0.34−0.59 m s^{-1}; Figure 6). 0-C sites for both species were distinguished by higher tidal velocities, and the mean velocities were significantly different from random means (plaice: 0.74 m s^{-1}, $p < 0.05$; sole: 0.8 m s^{-1}, $p < 0.05$). No obvious trend between the three site groups was discernible for lemon sole, and the mean velocities were not significantly different from bootstrap means.

Stones (kg h^{-1})

Consistently high abundance plaice and sole sites were characterized by relatively low quantities of stone (≈0.6−9 kg h^{-1}), whereas variable abundance and 0-C sites contained more stones (Figure 6). For plaice the mean quantity of stones for the variable sites was 9.7 kg h^{-1}, and for 0-C sites it was 52 kg h^{-1}. Both means were significantly higher ($p < 0.05$) than the re-sampled mean. The mean quantity of stones for sole sites of consistently high abundance was significant (3.5 kg h^{-1}, $p < 0.05$), as was the mean quantity at 0-C sites (46.6 kg h^{-1}, $p < 0.05$). Lemon sole showed the opposite trend. Consistently high abundance sites had slightly larger quantities of stones (7.3−71 kg h^{-1}) than the other two site groups (≈0−54 kg h^{-1}). However, only the mean quantity of stones at 0-C sites proved to be significant (4.3 kg h^{-1}).

Shells (kg h^{-1})

For all three species there were no obvious trends. Plaice and sole sites of consistently high and variable abundance seemed in general to contain more shells (≈0.4−3 kg h^{-1}) than their respective 0-C sites (≈0−1 kg h^{-1}; Figure 6). For lemon sole 0-C sites, this relationship was not apparent. Only the mean quantity of shells for plaice sites of variable abundance proved significantly different from the randomly generated mean (55 kg h^{-1}, $p < 0.05$).

Site-specific study: emergent epifauna and prey availability

Flatfish densities recorded in the Cefas long-term data set were a good predictor of the relative abundance of fish captured during our survey for plaice ($r = 0.80$, $p < 0.001$; Figure 7) and sole ($r = 0.71$, $p < 0.008$; Figure 7). However, lemon sole were caught at only two stations during the survey, and were insufficiently abundant for a meaningful analysis. Those two stations were the ones with the highest mean percentage abundance over the nine years of the data set (Figure 7).

No significant correlation was found between emergent epifauna and flatfish density (plaice: $r = 0.49$, $p = 0.1$; sole: $r = -0.02$, $p = 0.96$; Figure 7) using all sites sampled in the analysis. Plaice abundances, however, did correlate significantly with the biomass of emergent epifauna when only consistently high abundance sites were used for analysis ($r = 0.86$, $p = 0.01$). For sole, only the correlation of consistently high abundance sites showed a negative, non-significant trend for the relationship between abundance and emergent epifauna.

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: $r = 0.26$, $p = 0.42$; Figure 7). However, from the analysis of diets, there was a positive correlation between abundance of plaice and the number ($r = 0.81$, $p = 0.008$) and biomass ($r = 0.77$, $p = 0.01$) of prey items ingested per fish. Yet, the percentage of empty stomachs ($r = 0.39$, $p = 0.3$) and condition did not correlate significantly ($r = 0.5$, $p = 0.17$).

Habitat parameters and the results of the flatfish survey per site are summarized in Table 3. Inspection of the table indicates that at site SE1, adult plaice and lemon sole were most dense. This station also had the largest biomass of emergent epifauna, and plaice stomachs showed the greatest number of prey and biomass levels ingested per fish. This contrasted sharply with the relatively low prey abundance observed at this station. Greatest prey abundance was at site SE3; there, catches of juvenile plaice and sole were large, but abundance of adults was apparently low.

Discussion

Large-scale environmental parameters

Overall, analysis of flatfish abundance data and habitat parameters demonstrated a difficulty in determining distinctive habitat features associated with consistently high abundance of flatfish. For many habitat parameters analysed, except for some limitation in terms of sediment composition, no significant difference between sites of consistently high abundance of flatfish and sites of variable or low abundance could be detected. This was particularly apparent for plaice and sole. By contrast, sites that had no plaice or sole over the nine-year period analysed had a more distinctive set-up of environmental parameters. The findings therefore indicate that whereas the large-scale environmental parameters were associated with the presence or absence of flatfish at specific sites, there was no obvious relationship in respect of relative flatfish abundance. Hence, it was possible to identify unfavourable

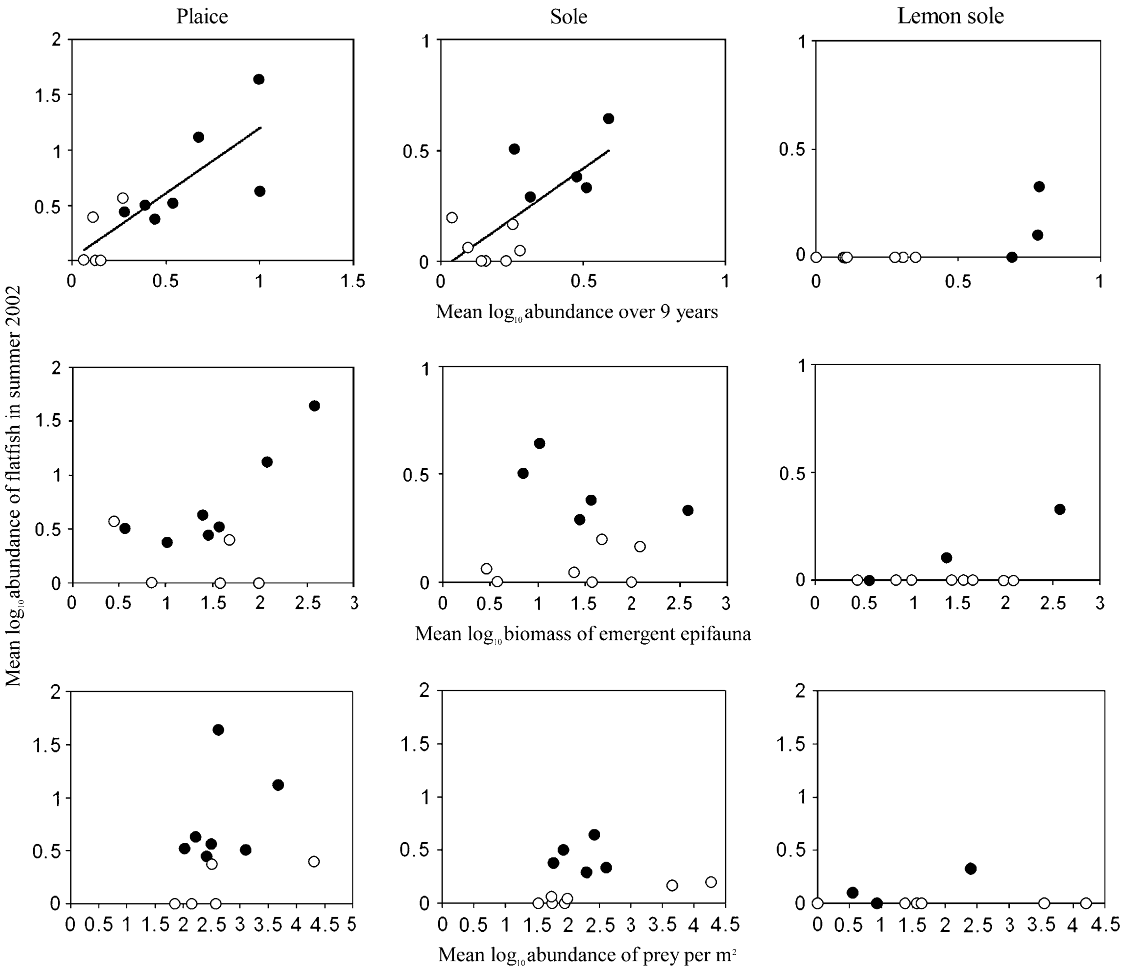

Figure 7. Relationship between mean $\log_{10}$ abundance of flatfish caught in 2002, mean $\log_{10}$ percentage abundance of flatfish caught over nine years in the Cefas survey, mean $\log_{10}$ biomass of emergent epifauna, and mean $\log_{10}$ abundance of prey per m^2. Black circles mark sites of consistently high abundance, and white circles sites of variable or low abundance or of zero catch.

environmental conditions, but no differentiation could be made between the overall range of conditions tolerated by respective flatfish species and favoured habitat. These results may be a reflection of the broad range of environmental conditions that these flatfish are able to occupy (Munroe, 2005), but they also highlight the fact that other factors not accounted for in the large-scale physical data set available to us may be more important in influencing relative abundance of flatfish in the English Channel.

Nevertheless, the results did provide indications of specific habitat associations for all three flatfish species, as well as differences between them. Sites of consistently high abundance of plaice were generally restricted to relatively shallow areas, with low salinity indicating nearshore conditions. Sediments at such stations were high in sand content and had relatively small quantities of stones or shells. By contrast, stations avoided by plaice were characterized by being deeper, and having a higher salinity, and sediments with either a high gravel or mud content. Amezcua and Nash (2001) found plaice to be prominent in sandy habitat in the Irish Sea, so the association of plaice with sediments high in sand content may have reasons related to burial potential and prey capture. Although flatfish might have the capability to bury themselves in most sediment types (Stoner and Abookire, 2002), they may still prefer substrata in which they can bury themselves easily with less energy expenditure; examples would be loosely packed sand rather than gravelly substrata. Unsuccessful burial in unsuitable substrata has been demonstrated to result in greater energy expenditure by resting sole, as a consequence of continued digging behaviour (Howell and Canario, 1987). Another factor that might account for this association of plaice with sand might be related to their foraging behaviour. Amezcua *et al.* (2003) suggested that infaunal prey may be easier to excavate from sand than from coarse sediments. As plaice are visual predators (Piet *et al.*, 1998),

Table 3. Summary table of habitat descriptors and flatfish parameters analysed at each station (BGS classification codes are also given).

	W1	W2	W3	W4	W5	NE1	NE2	NE3	SE1	SE2	SE3	SE4
Habitat descriptor												
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
Emergent epifauna mean wet weight (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 per m^2	315	1 273	370	70	139	255	318	104	415	4 783	20 413	165
Number of 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 wet weight (g) per stomach	0.4	1.2	1.1			0.6	0.4	0.6	2.4	1.1	0.7	0.1
Percentage 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
Sole mean abundance >23 cm	0.1			1.4	2.2	0.9	3.4		1.1	0.5	0.6	0.1
Prey abundance per m^2	53	33	55	58	83	193	258	88	395	4 468	18 420	95
Number of stomachs analysed	1			6	10	6	10		6	3	3	1
Mean prey abundance in stomachs					1	1	1		10	20		
Mean prey wet weight (g) per stomach					0.1	<0.1	<0.1		1.0	3.1		
Percentage 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
Lemon sole mean abundance >24 cm									0.7			0.3
Prey abundance per m^2		8	43	8		23	35		253	3 533	15 908	3
Number of stomachs analysed		1	2						4			3
Mean prey abundance in stomachs			1						3			14
Mean prey wet weight (g) per stomach			<0.1						0.5			0.7
Percentage of empty stomachs		100.0	50.0						75.0			33.3
Condition (*K*)		1.5	1.4						1.4			1.3

good visibility would be important for successful prey capture, and the increased turbidity over muddy sediments might therefore be less favoured by the fish. Sites with consistently high abundance of sole were over a much wider spectrum of sediment types than plaice, ranging from muddy to sandy substrata. However, as with plaice, sole seemed to avoid sediments high in gravel content. With respect to the other environmental factors considered, sole trends were similar to those of plaice. Relatively shallow stations with low salinity and higher temperature seemed to be preferred, whereas deeper stations with high salinity and low temperature appear to be less favoured or avoided. Shells and stones were only present in small quantities at sites of consistently high abundance. The similarity detected between consistently high abundance sites for plaice and sole indicated considerable habitat overlap. Over sandy habitats, interspecific competition could therefore be intense because part of the prey spectrum of the two species overlaps (Jones, 1952; Piet *et al.*, 1998; Rijnsdorp and Vingerhoed, 2001; Hoines and Bergstad, 2002).

Lemon sole are rarely caught during groundfish surveys, and at many stations the species was not recorded once during the whole survey period. The distribution of lemon sole was therefore restricted to very few specific sites. In general, sites of consistently high abundance of lemon sole had a very different suite of environmental parameters from that of plaice and sole. Lemon sole seemed to prefer sandy and gravelly sand substrata, living deeper, at higher salinity and lower temperature than the other two flatfish species. Therefore, most positive stations for lemon sole were in deeper offshore water, in accord with the findings of Bennet (1965) for the North Sea. Bennet (1965) also found lemon sole to be abundant in relatively deep water over sediments high in gravel. At consistently high abundance sites too, more stones were recorded than at sites with variable or low abundance.

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

The results of the site-specific study investigating the association of flatfish 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 abundance, but only when consistently high abundance sites were analysed separately. The basis for a positive relationship may be linked to the foraging strategy and the analogous prey spectrum of adult plaice. With increasing size, plaice undergo an ontogenetic change in diet (Piet *et al.*, 1998), juveniles feeding mainly on infaunal polychaetes and bivalves, and larger adult plaice taking a large proportion of epibenthic crustaceans, small fish, and echinoderms (Carter and Grove, 1991; Piet *et al.*, 1998). Some fish species living in such regions benefit from the complex structures presented by emergent epifauna, because they offer a larger number of niche spaces to epibenthic invertebrates (Bradshaw *et al.*, 2003). In the present survey, adult plaice almost exclusively consumed tube-building polychaetes, which themselves are emergent from the seabed (the worm tubes protrude from the seabed). Similarly, there was no significant relationship between plaice abundance and overall prey availability. However, plaice abundance was significantly related to 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 a mismatch at the two sites, SE1 and SE3. SE1 was predicted to show the greatest abundance of adult plaice by the long-term data, and this trend was confirmed by the largest catches there of adult plaice during this study. Stomach contents analysis and mean body condition did seem to confirm positive habitat conditions at the site, but prey availability assessed by grab samples indicated a relatively scarcity of prey. These contradictory results may suggest that grab samples were not a suitable sampling device for determining prey abundance and habitat quality at the appropriate spatial scale. Video and still footage taken as supplementary information during this survey over larger spatial scales supported this theory, because tube-building polychaetes *Lanice conchilega* and *Chaetopterus* spp. were clearly visible in great numbers at site SE1 (Rees *et al.*, 2005; Shucksmith *et al.*, in press). In contrast to the situation at site SE1, SE3 had the greatest prey abundance recorded during the study. Juvenile plaice and sole were very abundant there, but adult plaice and sole were virtually absent.

Emergent epifauna did not appear to have a positive effect on the abundance of sole. The trends in the data, although not significant, were negative, the consistently high abundance sole sites showing low percentage cover of emergent epifauna. Therefore, sole did not appear to be associated with the presence of emergent epifauna. Unlike plaice, sole 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 prey on infaunal invertebrates such as polychaetes and molluscs during their juvenile and adult phases (Piet *et al.*, 1998). As epibenthic invertebrates that may benefit from the presence of emergent epifauna are not an important component of sole diet, this lack of a relationship between emergent epifauna and sole abundance was expected. There was no relationship between prey availability and sole abundance, but very few sole were available to determine prey spectra from stomach contents analysis, possibly leading to a bias in the data. Because of the scarcity of adult sole and lemon sole in survey catches, it was not possible to analyse the results of the stomach contents analysis and condition.

Evaluation of the research approach adopted and recommendations for future studies

The correlations between the large-scale survey data and the information from the site-specific study verified the approach taken to detect sites of consistently high abundance of flatfish (Hinz *et al.*, 2003). Abiotic habitat characteristics that operate over large spatial scales may therefore give some indications as to which habitat features are important to the three flatfish species analysed. However, as elsewhere, this study demonstrated a difficulty in establishing clear relationships between specific habitat components, such as the presence of emergent epifauna and 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 probably influence fish distributions at small spatial scales (Hinz *et al.*, 2003). However, this hypothesis was not supported by the results from the site-specific study. The reason for the absence of a clear relationship could be related to various factors. The few sampling sites may have been insufficient to detect such a relationship, but there may also be other principle reasons why it would be difficult to detect such a relationship on the sampling scale adopted here. Under some circumstances, fish density may be unrelated to the habitat parameters that can be assessed within the area sampled. An area of low quality habitat (e.g. in terms of prey availability) could have relatively abundant flatfish in the case where prime habitat is nearby (and not sampled by the survey), leading density-dependent effects to overspill fish into the area of lesser quality (Jennings, 2000). Fish might also aggregate temporarily over unsuitable areas if the surrounding areas are even less favourable and if movement towards or knowledge of prime habitats are restricted (Shepherd and Litvak, 2004). Moreover, fish may require more than one habitat type, e.g. feeding and resting habitats that offer some degree of protection while digesting prey. Consequently, abundance of fish and habitat quality may depend also on adjoining habitat. The sampling grid of groundfish surveys, with large distance between sampling stations, cannot address processes that operate on smaller spatial scales. Our study indicates that the sampling regime adopted to assess prey availability and thus habitat quality by grabs was not conducted at the appropriate scales over which fish, in this case plaice, operate. Plaice were abundant and in good nutritive state at sites with relatively low prey density, suggesting that prime feeding grounds were probably relatively nearby. We conclude that fish are more efficient at assessing prey availability and that the results from stomach contents analysis and condition may therefore be better indicators of true habitat quality than, for example, results from point-source sampling with grabs.

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

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