Spatial variability in diet, condition and growth of juvenile plaice (*Pleuronectes platessa*) at sandy beach nursery grounds on the south-west coast of Ireland

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Characterization of suitable habitat for settlement of juvenile flatfish is important for the management of nursery areas. Food availability is one important determinant of habitat quality that can affect the condition and growth, and thus survival, of flatfish. Spatial and temporal variation in diet has been widely studied for several species of flatfish. However, levels of intraspecific variation in diet at small spatial scales are relatively unknown, with most studies focusing only on large scale variability. This study investigates how diet, growth and condition of juvenile plaice, Pleuronectes platessa*, varies over two spatial scales (10s of kilometres and 100s of metres). Juvenile plaice were collected from three beaches and from three replicate hauls on each beach using a beach seine in September 2007 and 2008. Gut content analyses of 108 juvenile plaice within the size-range of 70–90 mm were carried out. Diet composition in plaice guts differed among beaches and hauls suggesting that food abundance and availability differed at both spatial scales. A significant positive correlation was observed between a morphological condition index and the prey diversity in the gut. This suggests that fish which specialize on a limited number of prey items (perhaps due to a greater abundance of certain prey) may do better than fish which feed on a wide range of prey types. Significant differences in condition were observed between hauls and between beaches, while recent and total otolith growth varied between beaches but not between hauls. The results highlight the importance of considering small scale variation when attempting to link habitat quality to feeding, growth and condition of juvenile flatfish.*

Keywords: juvenile plaice, *Pleuronectes platessa*, diet, otolith microstructure, spatial variability, growth, condition

INTRODUCTION

Characterization of suitable habitat for juvenile flatfish is important for the management of nursery areas. The nursery value of habitat is commonly assessed by measuring growth and condition of juveniles. Higher condition and growth rate results in successive improvements in feeding (van der Veer & Witte, 1993), predator avoidance (Gibson *et al.*, 1995; Wennhage, 2000) and ultimately survival (Vethaak, 1992; Islam & Tanaka, 2005). It is the combination of several habitat variables that favour rapid growth. Physicochemical conditions (e.g. temperature, salinity and dissolved oxygen) are considered to be the primary determinants of distribution and growth in flatfish (Karakiri *et al.*, 1991; Reichert, 2003; Amara *et al.*, 2004) while food abundance and quality are also important factors affecting growth and condition of young fish (van der Veer & Witte, 1993; Burrows *et al.*, 1994; Gibson, 1994).

Some studies observed field caught juvenile fish that displayed growth rates similar to those of laboratory animals reared in excess feeding conditions. This suggested that an abundance of food and an absence of competition can occur on flatfish nursery grounds (van der Veer *et al.*, 1990; Karakiri *et al.*, 1991; Amara *et al.*, 2001) which has led to the formulation of the 'maximum growth/optimal food' hypothesis (Karakiri *et al.*, 1991; Reichert, 2003). However in other instances, differences in juvenile growth rate between regions are observed, which might reflect differences in food composition and availability (van der Veer & Witte, 1993; van der Veer *et al.*, 2001) and indicate spatial variability in the quality of nursery ground habitat. Spatial variation in growth rates and condition in juvenile flatfish has been observed across a range of spatial scales (1–100s of kilometres) (Glass *et al.*, 2008).

The diet of flatfish has been widely studied for the assessment of nursery quality. Some studies have examined how the diet of recently settled flatfish changes with size to determine if prey shifts occur during the ontogeny of the fish (Whyche & Shackley, 1986; Aarnio *et al.*, 1996). Others have addressed the issue of trophic niche width and examined dietary overlap and resource partitioning between different flatfish species (Beyst *et al.*, 1999; Cabral *et al.*, 2002; Vinagre *et al.*, 2005). However, levels of intraspecific variation in diet are relatively unknown; the few studies that address this focus on large-scale variability (100s of kilometres; Woll & Gundersen (2004), 3–10 km; Berghahn (1987)). The possible

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impact of spatial variation in diet on the growth and condition of flatfish on sandy-beach nursery areas has not yet been addressed.

This study aims to assess growth and feeding ecology of juvenile plaice (*Pleuronectes platessa* Linnaeus, 1758) within a restricted size-range of 70–90 mm in total body length. Plaice is a commercially important flatfish in the north-east Atlantic (Millner *et al.*, 2005) and juvenile plaice are widely dispersed on nursery grounds in this region. Special attention is given to the importance of studying growth, condition and diet over different spatial scales when evaluating flatfish nursery ground quality. The first objective was to investigate the intraspecific variation in diet over two spatial scales (10s of kilometres and 100s of metres). The second objective was to assess intraspecific variation in morphology, growth and condition and determine whether spatial variation in these parameters can be linked to spatial variation in diet at the above mentioned scales.

MATERIALS AND METHODS

Field work

Sample collection formed part of a long term annual flatfish survey which aims to assess and monitor the juvenile stages of commercially important flatfish populations on beaches in the south-west and west of Ireland. Those beaches are important nursery areas for flatfish populations like turbot and plaice (Haynes *et al.*, in press). Sampling was conducted during three consecutive days in September 2007 and during the same period in 2008. Juvenile plaice were collected during spring low tide from three beaches every year (Inch, Smerwick and Ventry in 2007 and Inch, Smerwick and Brandon in 2008) and from three replicate hauls on each beach (Figure 1). The distance between beaches ranged

from 30–80 km; the distance between hauls within the same beach ranged from 300–1000 m. A beach seine of 20 m breadth with a 12 mm square mesh size was used, covering an approximate swept area of 1380 m². Six plaice of 70–90 mm were randomly selected from each haul and kept frozen until analysis. This size-range was chosen to allow comparison of ingested food items during a specific growth stage of fully metamorphosed plaice (Ryland, 1966).

Morphology and gut content measurements

Several morphological characteristics of a total of 108 juvenile individuals were recorded after thawing; body length, eye diameter, mouth height (Braber & de Groot, 1973b) and mouth width were measured to the nearest 0.01 mm. Mouth gape (0.01mm²) was calculated by multiplying mouth width and mouth height by π (Piet *et al.*, 1998). Both stomach and intestines (guts) of all juveniles were analysed together as plaice have a rather small stomach and long alimentary tract (Beyst *et al.*, 1999). Gut content analyses of all juvenile plaice were carried out and prey items were identified under a stereomicroscope to their main taxonomic groups and counted. Total number of prey taxa and total prey abundance in the guts were measured. Stomach fullness was calculated as a percentage; length of gut containing prey divided by total gut length * 100.

Condition and growth

Fulton's condition factor (Fulton, 1911) was calculated for each fish using the formula $K = (W/L^3)*100$, where W is fresh weight (g) and L is total length (cm). This widely used morphometric index assumes that heavier fish of a given length are in better condition and it has been proven to be a good indicator of habitat quality (Gilliers *et al.*, 2004).
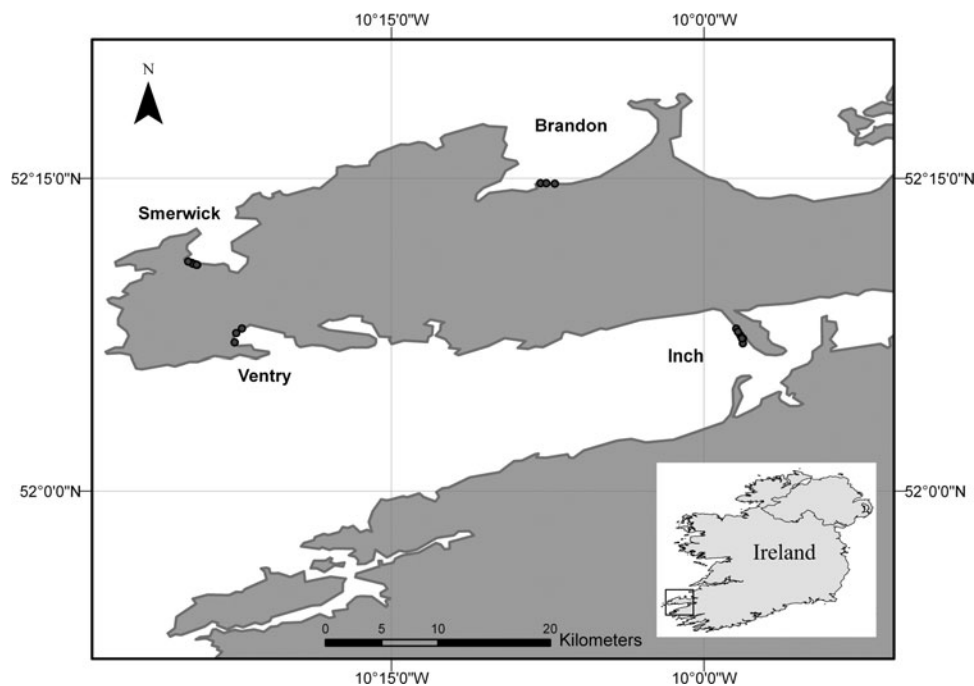

Fig. 1. Beach seine locations and position of 3 hauls per beach (per year) at nursery grounds on the south-west coast of Ireland.

Otolith microstructure analysis was used to provide a relative measure of recent growth for all juvenile plaice. The right sagittal otolith was extracted, mounted on a slide with the convex side facing upwards and embedded with crystalbond. Otoliths were polished and examined using transmitted light with a compound microscope (Olympus U-TV1X-2) and a $20 \times$ objective lens. Image analysis software (Image Pro Plus 6.2) was used to measure the width of the 10 most recently deposited daily increments along the core-rostrum axis. The mean daily increment width over the last 10 days before capture was calculated as an index of recent growth. The otolith diameter was measured under the $4 \times$ objective lens to obtain an index of overall fish growth.

Data analyses

Minitab 15 was used for statistical analyses. The balanced data were tested for normality and homogeneity of variances. Prior to examining variability in plaice morphology, diet descriptors, growth and condition between beaches and hauls, a two-way analysis of variance (ANOVA) with beach and year in the model was carried out to examine if any variability was attributed to year-differences. In the event a significant variation between years was found, further analyses were carried out for every year separately. Two-way nested ANOVAs were performed to examine effects of beach and haul, nested within beach, on fish morphology and diet descriptors. Beach was included as a fixed factor while haul was included as a random factor (Underwood, 1997). Significant beach effects were further explored using Tukey's *post hoc* comparisons. Analysis of covariance (ANCOVA), with fish length as a covariate, was used to investigate if relative otolith diameter differed between plaice from different beaches or hauls. Pearson's correlation was used to determine if any correlation existed between mean diversity of gut contents and mean fish condition across all hauls.

Prey assemblage composition in the stomach of fish was analysed using the non-metric multidimensional scaling (nMDS) ordination technique of the PRIMER version 5 statistical package (Clarke, 1993). From the original samples by prey matrix (108×14), abundances of prey were square root transformed and the Bray–Curtis similarity coefficient was calculated for every sample to generate a similarity matrix. Differences in diet among beaches and hauls were further analysed using two-way nested analysis of similarities (ANOSIM). Where significant differences were found, particular emphasis was placed on the R-statistic values produced by ANOSIM to identify the extent of the difference. Similarity of percentages (SIMPER) was employed to determine which prey-classes contributed the most to any similarities within beaches.

RESULTS

Spatial variation in diet composition

Diet of plaice was compared between hauls and beaches based on five different prey descriptors; numbers of prey taxa, prey abundance, prey diversity, stomach fullness and prey assemblages. Since we found variability in total prey taxa and Shannon–Wiener prey diversity between years, two-way nested ANOVA was repeated for both variables for each year separately. A two-way nested ANOVA revealed differences in gut contents on both spatial scales (Table 1). At a small spatial scale (300–1000 m), prey descriptors varied between fish from replicate hauls, except for total prey taxa and prey diversity in 2008. Prey descriptors also varied at a larger spatial scale (30–80 km) between fish collected from different beaches. A pairwise comparison revealed a significant higher prey diversity in fish from Ventry compared to Inch ($P = 0.0168$) and Smerwick ($P < 0.001$) in 2007. Differences in total prey abundance and total prey taxa in 2008 were evident across beaches but no significant differences in percentage stomach fullness were found between beaches.

The nMDS ordination plot derived from prey abundance data of the guts of fish, caught in different hauls and beaches indicated some discrete groups of prey assemblages (Figure 2). Two-way nested ANOSIM demonstrated that prey assemblages differed significantly between hauls (R = 0.200, $P < 0.001$) and beaches (R = 0.602, $P < 0.001$). The greatest difference in prey composition occurred between fish from Ventry in 2007 and fish from other beaches in both years whereas the smallest difference was found

Table 1. Results of two-way nested ANOVA, with hauls nested within beach, performed on prey descriptors in the guts of plaice, with mean and standard deviation for every beach in both years.

|		Total taxa	Total abundance	Shannon–Wiener diversity	% Stomach fullness
Differences between beaches					
	Inch 2007	3.78 ± 1.59	28.39 ± 17.18	0.83 ± 0.38	56.48 ± 21.93
	Inch 2008	2.61 ± 0.70	24.39 ± 15.69	0.63 ± 0.32	59.45 ± 16.60
	Ventry 2007	4.11 ± 1.08	9.89 ± 6.09	1.21 ± 0.32	51.51 ± 29.21
	Smerwick 2007	2.39 ± 1.33	13.72 ± 9.56	0.54 ± 0.47	64.72 ± 18.13
	Smerwick 2008	1.72 ± 0.96	9.06 ± 7.25	0.32 ± 0.45	53.55 ± 17.59
	Brandon 2008	2.50 ± 0.96	20.22 ± 18.05	0.50 ± 0.40	61.16 ± 10.27
	2007	3.51^{ns}		6.77^{*}	
F ratio	2008	5.33^{**}		2.81^{ns}	
	2007 + 2008		3.40^{*}		0.37^{ns}
Differences between hauls					
	2007	2.85^{*}		3.05^{*}	
F ratio	2008	1.28^{ns}		2.09^{ns}	
	2007 + 2008		2.19^{*}		4.12^{***}
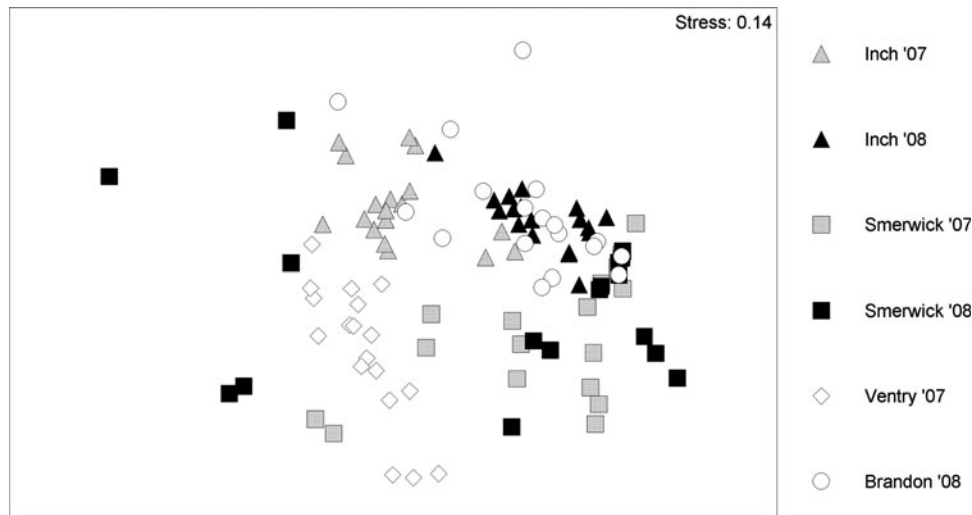
Fig. 2. Non-metric multidimensional scaling ordination plot of the prey abundance data in the guts of 108 juvenile plaice. Sampling was carried out during 6 sampling occasions divided over 4 beaches and 2 years.

between fish from Inch and Brandon in 2008 and between fish from Smerwick in 2007 and 2008 (Table 2).

SIMPER analysis performed on prey data in the fish guts detected an average similarity within beaches between 26% and 52% (Table 3). Diet of plaice from Inch is in both years characterized by a high abundance of amphipods and cumaceans; similarly to diet of fish from Brandon in 2008 but very different from diet of plaice from the other beaches. Diet of plaice from Smerwick is dominated by a high abundance of one prey item, bivalve siphons, and a small amount of decapods. Fish from Ventry in 2007 were feeding on a large variety of prey from different taxonomic classes. Pie charts in Figure 3 graphically represent both small and large scale differences.

Intraspecific variability in plaice morphology

All fish were within the size-range of 70–90 mm in total length. A two-way nested ANOVA (Table 4) showed no significant differences in fish body length between beaches or

Table 2. Results of ANOSIM pairwise test with R-statistic values close to unity indicating a high difference in composition of gut samples between sampling occasions and vice versa.

Pairwise comparison	R values
Inch 2008, Brandon 2008	0.015
Smerwick 2007, Smerwick 2008	0.030
Smerwick 2008, Brandon 2008	0.193
Smerwick 2007, Brandon 2008	0.275
Smerwick 2008, Inch 2008	0.305
Smerwick 2007, Inch 2008	0.390
Inch 2007, Brandon 2008	0.484
Inch 2007, Ventry 2007	0.583
Ventry 2007, Smerwick 2008	0.603
Inch 2007, Inch 2008	0.620
Inch 2007, Smerwick 2008	0.622
Ventry 2007, Smerwick 2007	0.710
Inch 2007, Smerwick 2007	0.753
Ventry 2007, Brandon 2008	0.794
Ventry 2007, Inch 2008	0.931

between hauls within each beach. Similarly, eye diameter (which was only measured from 2007 fish) was not significantly different between beaches or hauls. Mouth gape, standardized for fish length, differed significantly between hauls and between beaches. A pairwise comparison test showed that mouth gape was significantly larger in fish from Smerwick in 2007 compared to fish from Smerwick in 2008 ($P = 0.008$), Ventry in 2007 ($P < 0.001$), Brandon in 2008 ($P = 0.006$) and Inch in 2007 ($P < 0.001$). Fish from Inch

Table 3. SIMPER analysis showing average similarity percentages of prey composition in guts of fish within different sampling occasions. The average abundance and percentage contribution of typifying prey classes contributing >5% to within-group similarity for the fish in the six sampling occasions are shown.

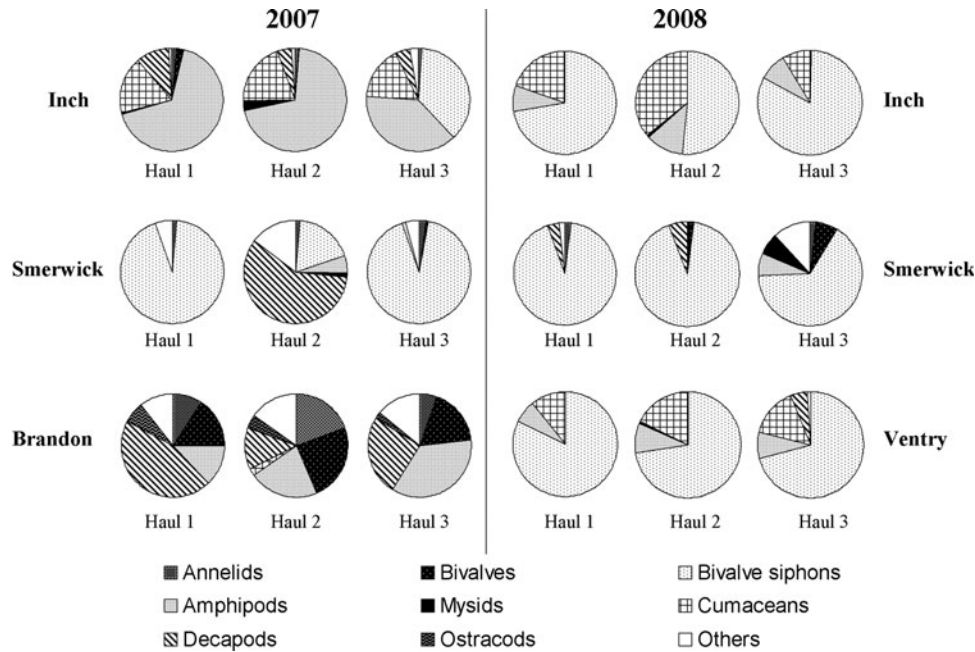| Beach—year	Average similarity (%)	Typifying prey-classes	Average abundance	Contributing %
Inch 2007	46.76	Amphipods	17.94	73.54
		Cumaceans	5.22	17.08
		Decapods	2.06	6.18
Inch 2008	51.94	Siphons Bivalves	17.28	73.24
		Cumaceans	4.67	18.69
		Amphipods	2.33	8.07
Ventry 2007	36.74	Amphipods	2.22	30.51
		Bivalves	1.83	29.30
		Decapods	3.00	19.13
		Annelids	1.06	12.28
		Ostracods	0.44	5.15
Smerwick 2007	32.87	Siphons Bivalves	9.61	78.60
		Decapods	2.44	12.12
Smerwick 2008	25.73	Siphons Bivalves	7.50	92.16
		Decapods	0.28	4.73
Brandon 2008	37.09	Siphons Bivalves	15.11	71.57
		Cumaceans	3.06	17.29
		Amphipods	1.69	10.79

Fig. 3. Pie charts showing the taxonomic breakdown of prey items in the guts of juvenile plaice across 3 replicate hauls on 3 beaches over 2 years. Flatworms, gastropods, copepods, echinoderms and arachnids were rarely found in some guts and pooled in the group 'others'.

in 2008 also showed a significantly larger mouth gape compared to fish from Inch in 2007 ($P = 0.010$) and Ventry in 2007 ($P = 0.030$).

Spatial variation in condition and growth

In this study, Fulton's K condition index of juvenile plaice ranged between 0.86 and 1.20 g cm^{-3} in 2007 and between 0.96 and 1.40 g cm^{-3} in 2008. Fish from 2008 were in significantly better condition than those from 2007 (two-way ANOVA, $F = 98.52$, $P < 0.001$). Two-way nested ANOVA revealed significant differences in condition between beaches within both years and between hauls in 2007 but no variation between hauls was found in 2008 (Table 5). In 2007, fish with lowest condition were found in Ventry and were significantly lower compared to fish from Inch ($P < 0.001$) and Smerwick ($P = 0.001$). In 2008, fish with lowest condition were found in Smerwick, and were significantly lower than fish from Brandon ($P < 0.001$) and Inch ($P = 0.038$).

Otolith diameter showed a linear increase with fish length ($F = 84.40$, $P < 0.0001$) confirming that otolith growth reflects somatic growth. ANCOVA did not detect differences in otolith diameter, corrected for fish length, between hauls ($F = 1.42$, $P = 0.172$) but otolith diameter differed between beaches ($F = 4.19$, $P = 0.002$). Pairwise comparisons showed that fish from Ventry in 2007 had larger otoliths than fish from Inch in 2007 ($P < 0.001$) (Figure 4). This indicates slower growth rates over the life of fish on Ventry compared to fish on Inch. This finding corresponds with observed variation in recent growth. A two-way nested ANOVA showed that mean peripheral increment width, which ranged between 3.62 μm and 9.82 μm, was not different between hauls but differed significantly between beaches (Table 5). Recent growth was lower for fish from Ventry in 2007 compared to fish from all other beaches in both years ($P < 0.05$). In contrast to fish condition, recent growth did not differ between years, suggesting that differences in recent growth were not large enough to contribute to differences in overall condition of plaice between beaches.

Table 4. Results of two-way nested ANOVA, with hauls nested within beach, performed on morphological characteristics of plaice, with mean and standard deviation for every beach in both years.

		Body length (mm)	Eye diameter (mm)	Mouth gape (mm²)
Differences between beaches				
	Inch 2007	83.06 ± 4.92	5.30 ± 0.43	54.58 ± 9.06
	Inch 2008	81.01 ± 4.66		68.56 ± 13.50
	Ventry 2007	80.22 ± 4.52	5.33 ± 0.42	53.91 ± 13.88
	Smerwick 2007	80.39 ± 4.65	5.03 ± 0.31	78.40 ± 13.73
	Smerwick 2008	78.49 ± 4.46		60.38 ± 12.59
	Brandon 2008	78.26 ± 3.33		59.92 ± 17.29
F ratio	2007		2.19[ns]	
	2007 + 2008	2.82[ns]		11.39[***]
Differences between hauls				
F ratio	2007		1.50[ns]	
	2007 + 2008	0.77[ns]		3.71[***]

Levels of significance;[ns], not significant; *, $P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 5. Results of two-way nested ANOVA, with hauls nested within beach, performed on condition (Fulton's K) and recent growth (otoliths' average increment width over last 10 days) of plaice, with mean and standard deviation for every beach in both years.

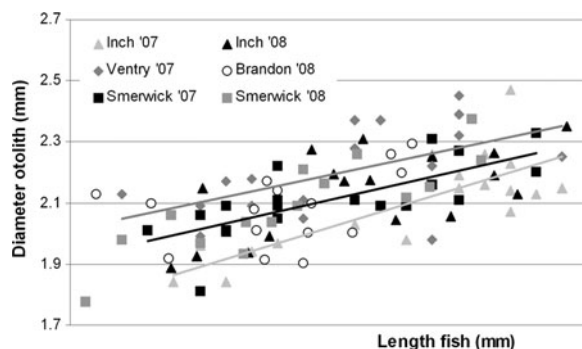|		Fulton's K condition (g/cm³)	Increment width last 10 days (µm)
Differences between beaches			
	Inch 2007	1.02 ± 0.07	6.65 ± 1.47
	Inch 2008	1.23 ± 0.05	6.86 ± 1.02
	Ventry 2007	0.94 ± 0.06	5.19 ± 0.89
	Smerwick 2007	1.02 ± 0.06	5.94 ± 1.07
	Smerwick 2008	1.16 ± 0.11	6.28 ± 0.77
	Brandon 2008	1.27 ± 0.06	6.67 ± 0.92
	2007	13.88***	
F ratio	2008	8.54***	
	2007 + 2008		6.33***
Differences between hauls			
	2007	4.04**	
F ratio	2008	1.59[ns]	
	2007 + 2008		1.67[ns]

Levels of significance;[ns], not significant; *, $P<0.05$; **$P < 0.01$; ***$P < 0.001$.

Correlation between diet and condition

As described above, prey diversity in juvenile plaice guts varied between hauls within beaches. For each haul, mean condition and mean prey diversity were calculated. Pearson's correlation analysis detected significant decreases in condition with higher prey diversity ($r = -0.630$, $P = 0.005$). This significant inverse linear relationship showed that fish feeding on greater prey diversity also displayed the poorest condition (Figure 5).
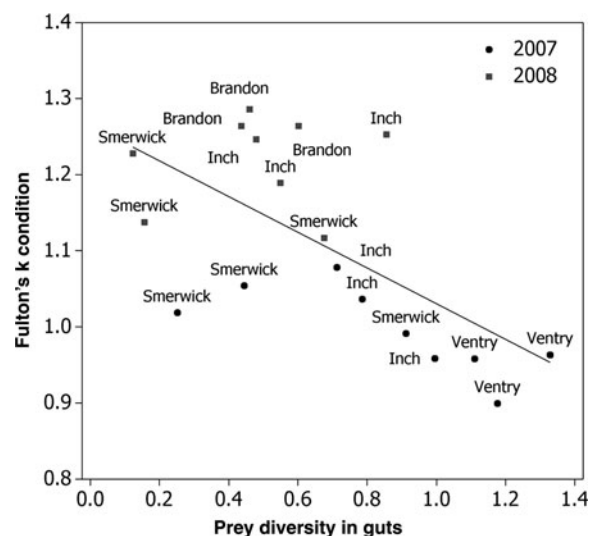
DISCUSSION

Our results on food composition in plaice guts are in agreement with earlier findings. Polychaetes, molluscs and crustaceans are major food items in diet of juvenile plaice on sandy beach nursery areas (Braber & de Groot, 1973a), with an ontogenetic shift occurring in larger fish from polychaetes towards crustaceans (Edwards & Steele, 1968; Rijnsdorp & Vingerhoed, 2001). Whyche & Shackley (1986) found this change in diet occurring at a fish length of 35–40 mm, probably because at this size plaice move to deeper parts of the littoral zone where wave action is strong and food organisms

such as amphipods, harpacticoids and young bivalves are more exposed. Major taxonomic groups dominating plaice diet in our study, revealed by multivariate analyses, differed among beaches. Variation in stomach fullness and prey abundance was also observed at a smaller spatial scale (between hauls) within beaches. This spatial variability in diet suggests a high degree of trophic adaptability to different prey.

Without information on the benthic fauna, it is unclear if differences in diet are the result of selective feeding behaviour and/or differences in prey distribution and availability between locations. The observed variation in the quantity and diversity of prey items occurred at a scale of 100s of metres (300 m was the smallest distance between hauls). Following the observations of Burrows *et al.* (2004) that plaice have a very high probability of remaining in a 100 m wide zone for at least one day, we can assume that plaice caught in one haul were also feeding in distinct areas compared to each other. As it is unlikely that plaice from adjacent hauls have different

Fig. 4. Ratio of otolith diameter by total fish length for every individual with trendlines displaying the different beaches over both years. Trendlines are presented for 2007 fish data.

Fig. 5. Scatterplot of prey diversity in plaice guts against Fulton's K condition of plaice. Every point represents the averages of all studied plaice pooled per haul.

feeding preferences, we hypothesize that food abundance and availability differs between the haul locations.

Small-scale variation between hauls within beaches was found in Fulton's condition of plaice. Condition indices are indicative of short term fish growth and are directly linked with food (Ferron & Leggett, 1994). As discussed above, we hypothesize that food abundance and availability differed between haul locations, affecting plaice condition. The correlation between prey diversity and condition of plaice from different hauls suggested that a varied diet leads to poorer condition whereas a feeding strategy which is based on a high degree of specialization on a few prey types results in good condition. Plaice were generally in better condition in 2008 compared to 2007 and large-scale variation between beaches was found within both years. Plaice from Inch and Brandon had a better than average condition and a low prey diversity in their gut, compared to plaice from Ventry and Smerwick. Abundant food resources might be available here in combination with selective feeding (of amphipods in Inch and bivalve siphons in Smerwick) to obtain the best nutritional status. Plaice caught in some hauls in Smerwick and in all hauls of Ventry did not grow up under optimal food conditions and had a lower condition as a result. We assume that prey are less abundant in this area. Another plausible suggestion for this diet difference (maybe as a result of lower prey availability) is that fish feeding on Ventry are exploiting less mobile prey because they are in poorer condition. We observed a higher stone content in the guts of plaice from Ventry and this might indicate they have a rather endobenthic feeding behaviour.

While diet very likely caused condition and growth differences of plaice between hauls and between beaches in this study, we cannot exclude possible additional factors (working in combination) that could be driving large-scale spatial variation. The physical environment is known to affect nursery quality and subsequently fish growth. Variation in temperature between beaches might occur as there is a river inflow in Ventry beach but no freshwater input in Smerwick and Inch beaches. Optimal growth temperature for juvenile plaice is around 20°C when abundant food is available (Fonds et al., 1992). At this temperature, the high assimilated energy from a faster ingestion is still exceeding the energy losses for metabolism which increases with temperature (Yamashita et al., 2001). Sediment type also influences a fish's ability to bury itself in the substrate in order to escape predators (Gibson & Robb, 1992). The beach in Inch is more exposed than in Smerwick and Ventry, therefore, differences in sediment type are likely. However, more research is needed to investigate if differences in burying effort, and subsequently fish growth, occur between beaches. Amezcua et al. (2003) found significant differences in flatfish diet between sediment types. This highlights the direct influence of beach structure and exposure on composition of benthic communities. The biotic environment can affect the growth rate of plaice. Previous studies have linked spatial patterns in growth and abundance of plaice with the availability of food. Karakiri et al. (1989) and Berghahn (1987) reported higher growth rates of plaice in the tidal flats of a nursery area compared to plaice in the tidal channels and concluded that food limitation occurred in the channels. Poxton et al. (1982) found a higher abundance of juveniles in areas with an abundant benthic food supply in the Clyde Sea area. Van der Veer & Witte (1993), showed a positive relationship between food abundance and growth of plaice in the Dutch Wadden Sea. In our study, prey abundance in some haul locations could have been reduced by predator foraging (Berghahn, 1987) or other disturbances which lead to different food availabilities; e.g. beam trawling enhances the abundance of small opportunistic benthic species such as polychaetes (Rijnsdorp & Vingerhoed, 2001). Lower growth rates might also be ascribed to density dependent growth as demonstrated by Modin & Pihl (1994). In the absence of more biological or environmental data on the studied sites, we can only speculate about possible additional factors influencing variation in juvenile plaice growth and condition.

Condition indices in larval and juvenile fish respond quickly to changes in food availability and can give a good indication of the growing conditions over the previous 24 hours (Ferron & Leggett, 1994). On the other hand, otolith growth responds more gradually to changes in feeding conditions and metabolic rate and represents a running average of fish growth rather than an instantaneous measure (Campana & Neilson, 1985). This could explain why variation between hauls was observed in fish condition, but not in otolith growth rate. While patchy distribution of prey items may produce small scale variation in fish condition, over a longer time period the movement of plaice between sites within a beach would produce a more homogeneous pattern of otolith growth. Moreover, diet differences between hauls do not override diet differences between beaches, as shown by a clear separation on the nMDS plot. This may reflect overall differences in habitat quality between beaches, contributing to variation in plaice growth.

In this study, dissimilarity in mouth morphology was observed; mean mouth gape differed between hauls and was higher in plaice from Smerwick compared to plaice from Inch and Ventry. No other citing of intraspecific differences in mouth gape was found in the literature and the reason for this difference here can only be speculated upon. The mouth gape has been identified by Piet et al. (1998) as the most important morphological characteristic affecting prey selection. As such, the observed larger mouth gape in Smerwick might be related to the high level of predation on bivalves. The jaws of plaice are well modified to biting off parts of bivalve molluscs (Yazdani, 1969). Different flatfish species adapt their behaviour to the behaviour of the prey (Holmes & Gibson, 1983) but the question remains whether juvenile plaice morphology can adapt depending on the available prey items. In stock identification studies two-dimensional measurements of the head can be useful for distinguishing fish from different areas. Further experimental work could help to establish how the availability of prey and feeding preferences influence mouth morphology.

Variation in growth and condition across replicate hauls within beaches highlights the importance of adequate replicate sampling. As juvenile plaice are active and mobile feeders but with a strong sense for site fidelity (Burrows et al., 2004), studies which attempt to link the composition of the benthic fauna to flatfish dietary preferences should consider small scale variation in these parameters. There is a danger of misinterpretation if assessments of nursery ground quality are based only on broad descriptors of the benthic community and average condition or growth across a beach. Also, closer examination of how diet and condition varies within a nursery area can help to elucidate how habitat characteristics influence growth and survival of juvenile fish.

ACKNOWLEDGEMENTS

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