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The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*

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Abstract

The lesser sandeel *Ammodytes marinus* (Raitt, 1934) is an important component of the North Sea ecosystem and the subject of the largest single species fishery in this region. However, little is known about the distribution of this species outside the areas where they are fished. This study examines the physical characteristics of the habitat of *A. marinus* in an attempt to predict the distribution of this species. The characteristics and topography of sandeel habitat were described from video observations. Data on abundance, sediment characteristics and depth were collected from benthic sampling programmes around the Shetland Isles. These data were used in a general additive model framework (GAM) to examine the relative significance of physical factors in influencing distribution. This analysis found that *A. marinus* were absent from sediments with a silt/clay content of >10% and densities declined between fractions from 2 to 10%. The apparent dislike for fine sediments was examined further by means of sediment choice experiments. These experiments confirmed the importance of the fine particle fraction in limiting distribution and indicated that sandeels would not be expected to inhabit such areas. Given the constraints of sediment requirements, densities of sandeels in benthic samples appeared to be influenced by water depth. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: geographic distribution; habitat; sediment sorting; generalised additive model; *Ammodytes marinus*; sandeels

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1. Introduction

Sandeels are an important component of food webs in the North Atlantic (Sherman et al., 1981; Harwood and Croxall, 1988; Furness, 1990; Sparholt, 1990; Wanless et al., 1998). They also support the largest fishery in the North Sea, with recent annual landings of around a million tonnes (ICES, 1997). The magnitude of the fishery and the importance of sandeels to marine predators has led to concern over the potential impact of sandeel harvesting on the North Sea ecosystem (Monaghan, 1992). Recent expansions in the distribution of exploitation have heightened this concern and identified a need for a more detailed knowledge of sandeel distribution, particularly outside fished areas (ICES, 1997). Studies of sandeel distribution in parts of Shetland and the Firth of Forth have been useful in explaining the foraging locations of sandeel predators, such as piscivorous seabirds (Monaghan et al., 1996; Wright and Begg, 1997). However, information on sandeel distribution at a much larger scale is required in order to define where possible areas of competition between marine predators and fisheries could arise.

Of the five species of sandeels inhabiting the North

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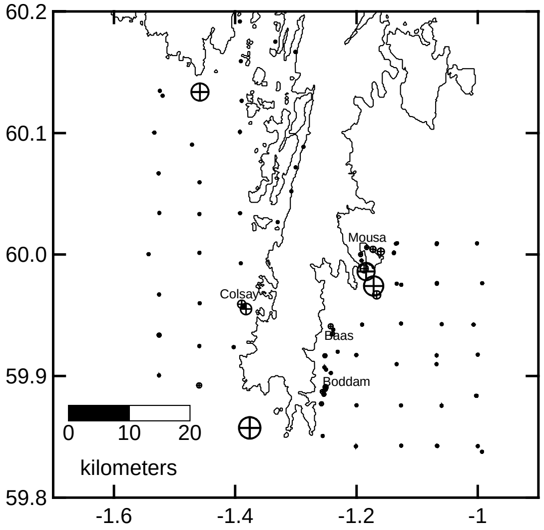

Fig. 1. Chart showing the density distribution of benthic samples around the Shetland Isles. Diameter of open circles is proportionate to catch up to a maximum of 18 sandeels per grab. Solid circles refer to zero catches. Named locations refer to fished grounds.

Sea, the lesser sandeel, *Ammodytes marinus* (Raitt, 1934) is the most abundant and comprises over 90% of sandeel fishery catches (ICES, 1997). As with other sandeel species, *A. marinus* has a close association with sandy substrates into which they burrow, following a planktonic larval phase (Macer, 1966; Reay, 1970). Observations on the availability of *A. marinus* to fisheries (Macer, 1966) and their occurrence in sediment (Cameron, 1958) suggest that this species rarely emerges from the seabed between September and March, with the exception of spawning in December and January (Macer, 1966; Gauld and Hutcheon, 1990). Even during the season when *A. marinus* is active, fish tend to emerge only during daylight hours in order to feed (Winslade, 1974) and they tend to forage over the sediments they inhabit (Macer, 1966; Reay, 1970).

The sandeel's habit of burrowing can be seen both as an anti-predator behaviour and an energy conservation strategy. Evasion by burrowing in sand has frequently been observed in response to predators foraging near the seabed (Girsa and Danilov, 1976; Pearson et al., 1984; Pinto et al., 1984), although some predators are capable of capturing buried sandeels (Hobson, 1986). The lack of both a swim-bladder and fins capable of compensatory movements means that it is energetically costly for sandeels to remain in open water when they are not feeding (Reay, 1970). Burrowing may also allow sandeels to maintain their position without being displaced by currents close to the seabed, as has been suggested for flatfish (Arnold and Weihs, 1978).

Several studies have provided descriptions of the sediment, depth and water circulation that sandeels are associated with (Macer, 1966; Reay, 1970; Scott, 1973; Pinto et al. 1984; Scott and Scott, 1988). In common with several sandeel species, *A. marinus* inhabits shallow (<150 m), turbulent sandy areas, such as the edges of sand banks (Macer, 1966; Reay, 1970). From choice experiments it is clear that sandeels prefer sandy sediments to those that are predominantly gravel or silt (Pinto et al., 1984). Interest in identifying profitable feeding areas for predators has led some to infer sandeel distribution based on this available information and maps of sediment distribution (e.g. Wanless et al., 1997). However, these studies acknowledge that the lack of detailed knowledge about the relative importance of sediment composition may lead to an over-estimate of the extent of sandeel habitat.

The present study uses information collected on sediment fraction, particle size and depth from sites where sandeels were caught in benthic samples to consider the relative significance of these physical factors in influencing distribution. A general additive model framework was used to assess which physical factors significantly contribute to explaining sandeel occurrence and abundance. Apparent sediment preferences indicated from field observations were then investigated using sediment choice experiments.

2. Methods

2.1. Benthic surveys

The bottom topography of grounds where sandeels were present was examined using a variety of underwater video systems during surveys of the waters around Shetland (1985, 1990, 1993) and the Firth of Forth (1991). Low light video cameras were deployed by means of drifting frames (1990 and 1995) and towed bodies (1985) and using a remotely operated video system (SPRINT ROV, 1991). All video cameras were deployed to within a metre of the seabed. Bottom seabed features, such as the presence of sand ripples, were recorded and, where possible, measured. In the case of the drifting frames, approximate measurements were made by reference to a metre long plumb-line attached to the frame. In the case of the ROV, metre markings on the cable were used for reference.

The distribution of buried post-settled sandeels in the vicinity of the Shetland and Orkney Isles was examined with respect to sediment and depth during three cruises which took place in May 1985 and January and June 1993 (Fig. 1). The cruises in May 1985 and January 1993 were conducted onboard the FRV '*Clupea*'. The cruise in June 1993 was conducted onboard RRS '*Challenger*'. Depth was recorded at each sample station from an echosounder and corrected for transducer depth. Sediments and sandeels were collected using a Smith–McIntyre Grab in 1985 ($N = 12$) and a day grab in 1993 ($N = 96$). These grabs have a similar sample efficiency and cover an area of 0.1 m^2 (Tyler and Shackley, 1978). Altogether, benthic samples were taken from 108 locations around Shetland from a region of approximately 900 km^2. On the basis of a visual inspection, sediment from the grab was classified into one of seven categories: rocks, shell and gravel, coarse sand, sand, silty sand, silt and mixed (= silt, sand and gravel). Two 100-g cores were taken from the sediment for particle analysis. The remainder of the sample was sorted to determine the number of sandeels present. In both years, regional stock assessments indicated that sandeel abundance was close to the long-term average (Wright, 1996). On return to the laboratory sediment samples were dried for 24 h at 100°C and then sieved through a standard Wentworth series of sieves ranging from 2000 to 63 μm mesh, with the aid of a mechanical shaker.

2.2. Analysis of benthic data

The relationship between explanatory and response variables was examined within a generalised additive modelling framework. GAM's fit non-parametric functions to estimate the relationships between the response and the predictors, for data with error distributions other than normal or Gaussian. A detailed account of GAMs has been presented elsewhere (Hastie and Tibshirani, 1990) as has the application of GAMs to the analysis of data in a spatial framework (Swartzman et al. 1992). The data used in the model were depth, sediment median particle diameter, percentage silt and clay (fraction <0.063 mm), the presence or absence of sandeels and where present, their density (number m^{-2}). Presence/absence data were analysed by specifying a binomial distribution of errors with a logit link. A gamma error distribution was specified for abundance data and a log-link function was specified (Crawley, 1993). This choice of error structure and link function for abundance estimates is appropriate because the variance increased with the square of the mean. To overcome the problem of zero counts, only locations where sandeels were present were included in the abundance model. Minimum adequate models were derived by removing terms from the full models successively, comparing successive models with an ANOVA with χ^2 statistic for presence/absence (binomial errors) and F statistic for abundance (gamma errors). Latitude and longitude of each location were included in the model in order to account for spatial autocorrelation in abundance (Swartzman et al., 1992). Median particle diameter was treated as a factor with levels ≤ 1 mm, >1 and ≤ 2 mm and $x > 2$ mm. These factor levels were chosen to ensure each level contained at least one observation. However, the only sediments with a median diameter in excess of 2 mm were comprised of pebbles or boulders (i.e. particles >16 mm). Each of the continuous variables was initially fitted with a smooth (cubic spline) fit. The smoothed fit was removed from each term if its inclusion in the model did not reduce the residual deviance significantly. Analysis was carried out using S-Plus 3.3 for Windows.

2.3. Experimental procedures

Sandeel sediment preference was investigated by means of choice experiments using a range of sediment compositions. Live pelagic 0-group sandeels (mean total length TL = 68 range 45–110 mm) were collected in May 1996 onboard RV '*Dana*' using a 2-m pelagic ring net (MIK) with a 1.5-mm mesh. Settled sandeels between 120 and 175 mm TL were collected using an EXPO trawl fished near the seabed in July 1996. In both surveys sampling took place around the

Table 1
Percentage sediment fractions of the 11 sediment compositions used in choice experiments. For some sediment classes where the mix was made up more than once the range in percent sediment fraction is given

Class	Silt–clay	Very fine sand	Fine sand	Medium sand	Coarse sand	very coarse sand	Very fine-medium gravel	Coarse gravel
Size fraction (mm)	0.062	0.062–0.125	0.125–0.250	0.250–0.500	0.500–1.00	1.00–2.00	2.00–16.00	16–32
A	0.6	0.05		2	52	31	14	0.35
B	0.6	0.05	3.35	32	21	6	8	29
C	1	0.2	14.8	75	8	1	0	0
D	1–2	1.5–2.5	63–64	32–34	0	0	0	0
E	7–15	50–58	31–35	2–3	0.5	0.5	0	0
F	1.2	2.8	65	30.5	0.5	0	0	0
G	2	5	64	28.5	0.5	0	0	0
H	2.5	7.5	62	27.5	0.5	0	0	0
I	5–6	17–18	50–51	25.5	0.5	0	0	0
J	6.5	27.5	48–49	16–17.5	0.5	0	0	0
K	10	37–38	41–42	11.5	0.5	0	0	0

Table 2
Combinations of sediment compositions used in sediment choice experiments. The table gives number of experiments for a given combination of sediment composition, length range of fish, range in number of fish per aquarium and range of sediment compositions

Sediment trays	Mix reference	Number of experiments	Length range (mm)	Range in fish per experiment	Sediment description
A + C + D + E	1	21	55–175	19–202	Fine sand–gravel
B + C + D + E	2	4	45–85	20–78	Fine sand–pebble
C ONLY	3	4	45–85	20–55	Medium sand
D + F + G + H	4	1	45–85	49	15% Very fine sand and silt
D + I + J + K	5	4	45–85	40–119	75% Very fine sand and silt

Little Fisher Bank (57°04′N–07°07′E). On return to the laboratory the sandeels were held in 200-dm^3 (pre settled sandeels) and 800-dm^3 (post-settled sandeels) cylindrical tanks. In order to avoid confounding effects of changes in environment on burying behaviour over the course of experiments, the temperature and light conditions in the holding and experiment tanks were kept constant (10 ± 1°C; 16 h light: 8 h dark). The water in both tanks was recycled through biological filters and no sediment was provided in the holding tanks. The fish were fed frozen adult *Artemia* sp. once each day. Mortality rate over the experimental period was $<0.0015\ \mathrm{d}^{-1}$ apart from an initial 16% mortality within the first week of capture

The experiments were carried out in four glass 100-dm^3 aquariums lit by cool-white fluorescent light-tubes giving an illumination of 300 lux m^{-2} at the water surface during the light phase (6 a.m.–8 p.m.) and less than 2 lux m^{-2} during the night phase. The aquarium water was aerated but there was no water inflow, since differences in water movement can influence sandeel distribution within a tank (Pinto et al., 1984). The fish were fed the day before the onset of each experiment but not during the experiments. Sediment was held in four trays ($0.20 \times 0.35 \times 0.06\ \mathrm{m}^3$) in each aquarium, providing sufficient volume to allow sandeels to bury completely. Due to the limited numbers of fish available for experiments, sandeels had to be used for more than one experiment. Consequently, where different sediment compositions were used in an experiment the sediments were assigned randomly to each of the four trays so that the order of the sediment compositions differed between experiments. Altogether 11 different sediment compositions were used in the experiments of which four were used in the form they were collected from the field. The rest of the sediments were either used as mixtures of these four sediments, or sediments where the smallest grains were washed out to increase mean grain size. Grain size composition of the sediments was determined by sieving the sediments through 16 standard sieves. Details of the particle size compositions are given in Table 1 and the combination of these sediments is given in Table 2. Sediments were autoclaved (120°C, 1 G′s, 30 min) and then washed in seawater before each experiment in order to ensure that sediment choice could not be confounded by the presence of food or secretions from sandeels. Before adding to the trays, the sediments were allowed to settle for about 24 h to ensure that the smallest particles were not washed out when the water was drained from them. In order to ensure that there was no confounding effect of fish having preferred areas within test aquaria a control experiment was conducted in which all four trays contained only one sediment composition C: “medium sand”. The number of sandeels was varied from 10 to 202 per aquarium in the following ranges: 10, 19–23, 30–47, 58–67, 80–84, 127–129, 202.

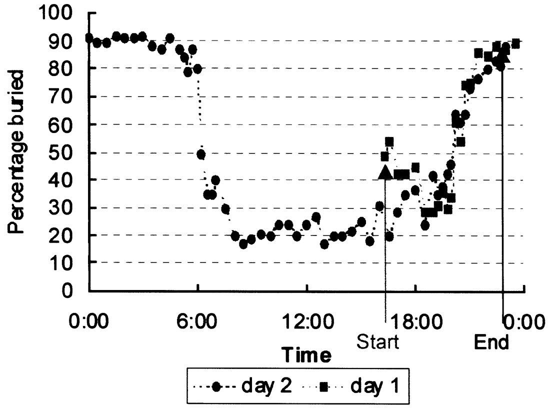

Fig. 2. An example of changes in the percentage of sandeels buried over time within a sediment choice experiment. In the example shown the sediment tray combination was the mix 1 (see Table 2) and the aquarium contained 127 sandeels. Start refers to the day on which the experiment began and end is the second day on which the experiment was terminated (as indicated by arrows).

Sandeels were introduced into the experimental aquaria within 3-dm^3 glass containers. The sandeels were held in these glass containers for an hour before release so as to mitigate handling stress and standardise release procedure. Any initial reactions to release were further mitigated by conducting the experiment over a 32-h period, during which time fish usually exhibited a diel cycle of emergence and so buried more than once (Fig. 2). Four main states of activity were recorded after the sandeels were released in the aquariums: swimming, lying on the sediment, partial emergence from the sediment (eyes and part of their head were visible) and fully buried. After the sandeels were released in the aquariums the number of sandeels in each stage of activity was recorded every half hour for each aquarium, except for one hour before and after the light was switched on and off when observations were made every 15 min. Activity was recorded either from direct observations or from photographs. As sandeels tend to be buried at night (Winslade, 1974) the experiments were terminated two to three hours after the light was switched off between 22:00 and 23:00 hours. The water was drained from the aquariums and any sandeels lying on the sediment were removed and their numbers recorded. Sandeels buried in each tray were extracted by sieving through a 2-mm mesh sieve, except for the coarsest sediments A and B (see Table 1) where the sandeels were manually sorted out because these sediments were too coarse to pass through the sieve. The numbers and lengths of sandeels buried in each sediment composition were then recorded photographically by reference to a scale.

2.4. Analysis of experimental data

To give an overall quantitative description of sediment preference in sandeels and to test hypotheses of homogeneity of preferences, i.e. that the number of sandeels buried in each of the four trays was independent of the sediment in the tray, the polynomial distribution was applied to the outcome of each experiment with sediment mix reference 1 and 2 (see Table 2):

$$(x_{1i}, x_{2i}, \ldots, x_{5i}) \propto \mathrm{poly}(N_i, (p_{1i}, \ldots, p_{5i})),$$

$$i = 1, 2 \ldots 23, \qquad \sum_{j=1}^{5} p_j = 1 \tag{1}$$

where x_{ij} denotes the number of sandeels buried in sediment j in experiment i and p_{ij} denotes the percentage of the total number of sandeels in experiment i buried in sediment j and $j = 1$ indicates “sediment composition E”, $j = 2$ indicates “sediment composition D”, $j = 3$ indicates “sediment composition C”, $j = 4$ indicates “sediment composition A or B” and $j = 5$ indicates “Not buried”.

As the experiments are assumed to be independent this implies that the numbers buried in experiment $x_{i_1 j}$ are independent of $x_{i_2 j}$ if $i_1 \neq i_2$. We assume that the sediment preferences are the same for all experiments, i.e. $p_{ji} = p_j$ for all sediment groups, j, and all experiments, i. We tested if the number of sandeels buried in each tray was the same amongst all sediments. The following hypotheses were tested:

$$H_{0_1} : p_2 = p_3 = p_4 = \tilde{p}^1$$

$$H_{0_2} : p_2 = p_3 = \tilde{p}^2$$

$$H_{0_3} : p_2 = p_4 = \tilde{p}^3$$

$$H_{0_4} : p_3 = p_4 = \tilde{p}^4$$

The hypotheses were tested using the likelihood ratio test.

The likelihood function, for the model is:

$$L(x, p) = \prod_{i=1}^{23} (\mathrm{Cons}_i) p_1^{x_{i1}} \ldots p_5^{x_{i5}} \tag{2}$$

where $x = (x_1, x_2, \ldots, x_{23})$ and $x_i = (x_{i1}, \ldots, x_{i5})$ $i = 1, 2, \ldots 23$, and $\mathrm{Cons}_i =$ a constant. The maximum likelihood estimates of the parameters in the polynomial distribution are:

$$\hat{p}_j = \frac{x_{.j}}{n_.} \tag{3}$$

where $x_{.j} = \sum_{i=3}^{i=27} x_{ij}$, denotes the number of sandeels buried in sediment j in all of the experiments, and $n. = \sum_{j=1}^{j=5} x_{.j}$, denotes the number of sandeels used in of all the experiments.

For example the likelihood under H_{0_1} is:

$$L_{H_{0_1}}(x, p_{H_{01}}) = \prod_{i=1}^{23} (\mathrm{Const}) p_1^{x_{i1}} \cdot \tilde{p}^{x_{i2} + x_{i3} + x_{i4}} \cdot p_5^{x_{i5}}$$

and the parameters under H_{0_1} are estimated as:

$$(\hat{p}_1, \tilde{p}^1, \tilde{p}^1, \tilde{p}^1, \hat{p}_5) = \left(\frac{x_{\cdot 1}}{n.}, \frac{x_{\cdot 2} + x_{\cdot 3} + x_{\cdot 4}}{3n.}, \frac{x_{\cdot 2} + x_{\cdot 3} + x_{\cdot 4}}{3n.}, \frac{x_{\cdot 2} + x_{\cdot 3} + x_{\cdot 4}}{3n.}, \frac{x_{\cdot 5}}{n.} \right) \tag{4}$$

The test statistic Q is given as:

$$Q = \frac{L_{H_{01}}(x, \hat{p}_{H_{0_1}})}{L(x, \hat{p})} \tag{5}$$

And H_{01} is tested by:

$$p_{\mathrm{val}} = p(\chi^2_{df=2} \geq -2Ln(Q)) \tag{6}$$

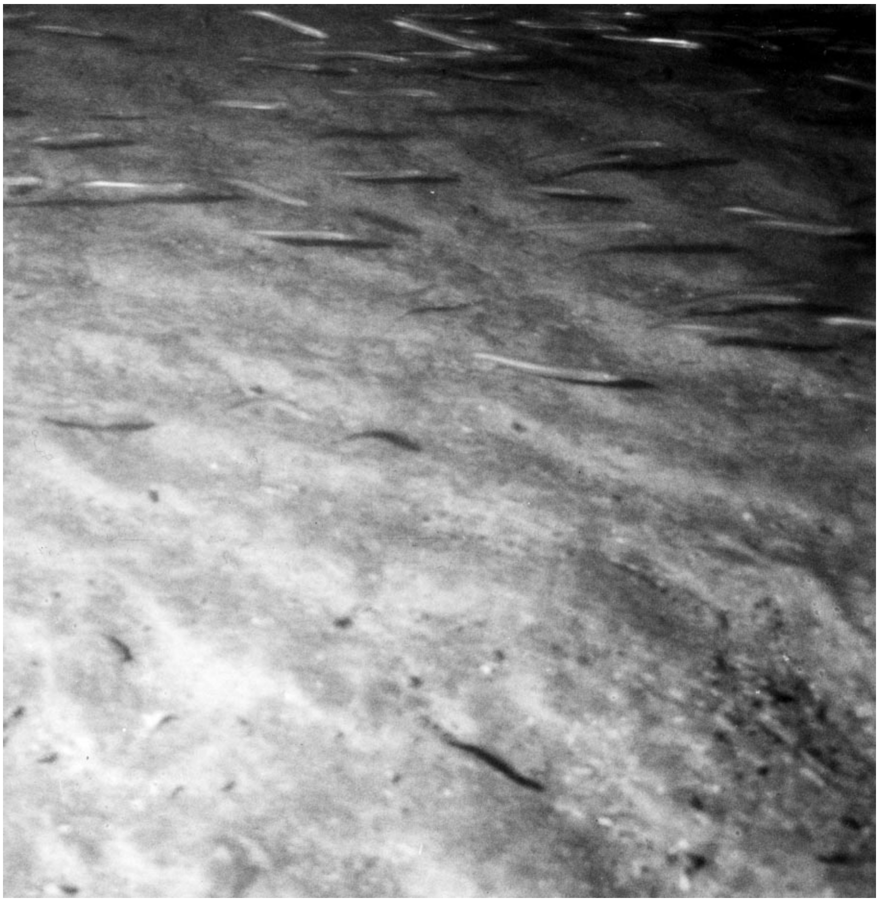

Fig. 3. Photograph of sandeel ground showing ripples in sand/shell sediment. The sandeels are approximately 12 cm total length.

with $\alpha = 0.05$, assuming that $-2Ln(Q)$ is approximately χ^2 distributed.

To evaluate if sediment choice changed with the size of the fish the four hypotheses (e.g. H_{01}–H_{04}) were tested using the results from the experiments where the mean lengths of the sandeels were either <65 mm TL, corresponding to recently metamorphosed sandeels ($N = 10$ experiments), or larger than this length ($N = 11$ experiments).

3. Results

3.1. Description of sandeel grounds

Underwater video observations at grounds around Shetland, Orkney and the Firth of Forth showed the presence of sand ripples up to approximately 1.5 m apart and with height-to-length ratios ranging from <0.1 to 0.25. In general, the ripples were tangential to the tidal stream and tended to be symmetrical, indicating bed formations produced by oscillatory flow (Fig. 3). The characteristics of these sand ripples were consistent with descriptions of rolling-grain, 2D and 3D vortex ripples (Sleath, 1982). Out of the 31 grab stations where sandeels were present, 29 were categorised as coarse sand or sand mixed with gravel or shell fragments. Video observations showed that there were differences in sediment within a ripple with gravel or shell fragments concentrated in the most hydrodynamically exposed parts.

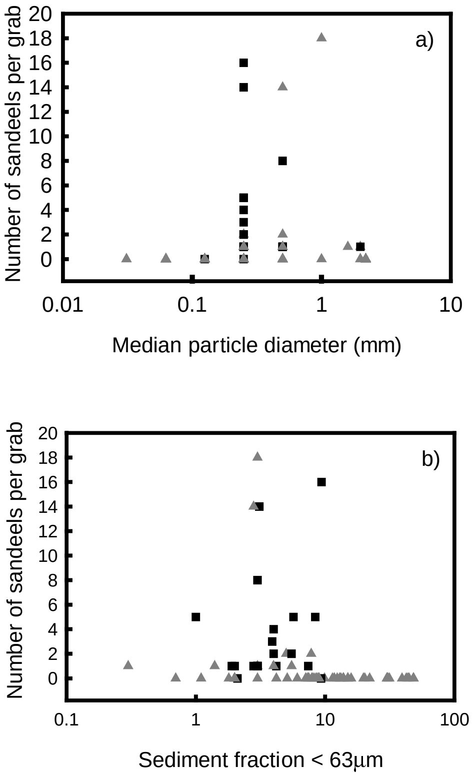

Fig. 4. Relation between the numbers of sandeels caught in grab samples and (a) median particle diameter, and (b) silt-clay fraction (<63 μm) of corresponding sediment. Squares refer to grabs within fished grounds (see Fig. 1) and triangles refer to all other sites.

3.2. Relationship between sandeel presence and physical variables

Preliminary analysis of the data indicated that sandeels were not present in areas with sediments with median particle diameter >2 mm or percentage silt >10% (Fig. 4). To prevent these variables overriding the effects of others, it was decided to limit the analysis of the presence/absence data to locations where percentage silt and clay was <10% and median particle diameter ≤2 mm, leaving 57 of the 108 original observations. Within these limits, sandeel presence [logit(P)] was examined in relation to the following model:

$$P = \alpha_1.\text{percentage silt} + \alpha_2.\text{depth} + \alpha_3.\text{median diameter} + \alpha_4.\text{latitude} + \alpha_5.\text{longitude} + \text{constant} \qquad (7)$$

where median diameter was treated as a factor with two levels remaining.

The results from this analysis showed that only the addition of silt and clay fraction (= particles <63 μm), depth and longitude caused significant reductions in the residual deviance of the model (Table 3). Fig. 5 shows the effect of the predictor variables (i.e. silt fraction and depth) on the response. There is a significant decline in the probability of finding sandeels for sediment where the silt and clay fraction was >6%. The relationship with depth indicated that the probability of sandeels occurring increases from 20 to 45 m and then declines down to 80 m. The minimum adequate model explained 57.8% of the deviance in the data. The finding that only longitude improved the model may be related to the generally stronger tidal currents to the west of Shetland. As latitude did not improve the model this suggests that there is no significant autocorrelation between aggregations at the spatial scale investigated.

Sandeel abundance, given presence, was examined using the same model as in Eq. (7). None of the terms caused a significant reduction in the residual deviance of the model. However, whilst the

Table 3
Outcome of fitting successively more complex models up to the minimum adequate model (GAM) to sandeel presence data

Model[a]	Residual d.f.	Residual deviance	d.f.	Deviance	$p(\chi^2)$
Null	56.0	77.6			
+ s (percentage silt)	51.1	63.8	4.9	13.8	< 0.05
+ s (longitude)	47.3	54.1	3.8	9.68	< 0.05
+ s (depth)	47.2	45.2	1.3	23.4	< 0.001

[a] s (variable) indicates that a smoothed (cubic spline) fit was retained in the model since it significantly reduced the residual deviance compared to a linear fit for that variable.

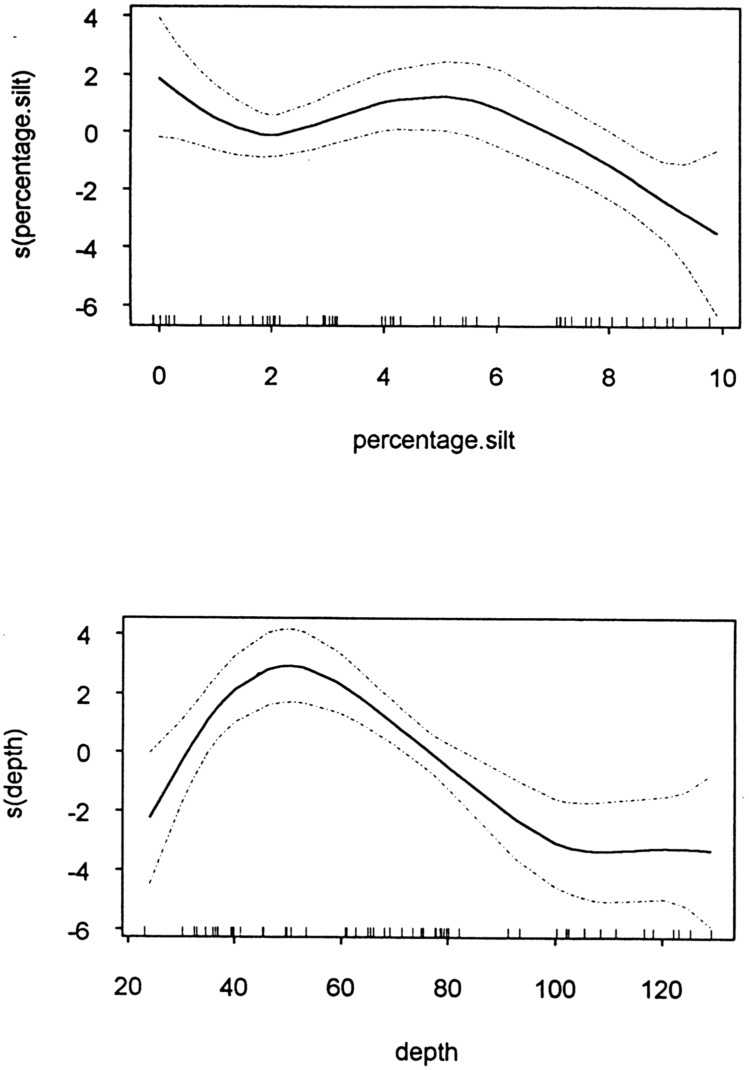

Fig. 5. Plots of the best-fitting GAM smooths (solid lines) for significant predictor variables in the minimum adequate model for presence/absence of sandeels; % silt fraction and depth (m) along with 95% confidence intervals (dotted lines).

number of sandeels per grab ranged from 1 to 18, catches of ≥2 only occurred in depths of between 30 and 80 m (Fig. 6).

3.3. Sediment choice experiments

The distribution of buried *Ammodytes marinus* was not significantly different among trays when the same sediment composition was provided, indicating that they do not have preferred areas within the test aquaria (χ^2 test; $p > 0.4$). When presented with different sediment compositions, sandeels on almost all occasions (98%) avoided trays where the fraction of particles <0.063 mm was >7% or where the particles <0.125 mm comprised >65% of the sediment. Of the 21 fish that did enter such sediment four died, whilst others did not bury but instead lay in the top 2-cm layer of the sediment–water interface. The fraction of sandeels buried in a tray differed significantly between all sediment compositions in

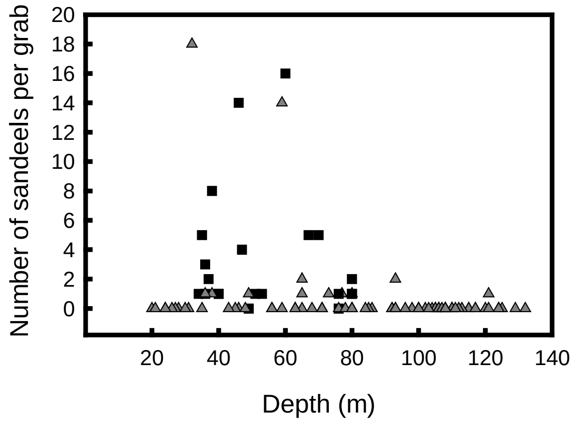

Fig. 6. Relation between the numbers of sandeels caught in grab samples and water depth. Squares refer to grabs within fished grounds (see Fig. 1) and triangles refer to all other sites.

mix 1 and most in mix 2 (Table 4). Based on the level of significance the sandeels showed a lower degree of preference in the mix 2 containing coarse sand with a high proportion of gravel than in the mix 1 where the coarse sand had a low gravel fraction. Size-related differences in sediment preference were found from a comparison between sandeels <65 and >65 mm TL in sediment mix 1 (Table 5). The smaller sandeels did not prefer the coarsest sand (sediment A) over medium sand (sediment C) suggesting that the preference for coarse sands may increase with fish size. A higher proportion of the sandeels buried in sediment A, coarse sand/fine gravel, than in the other sediment compositions (median = 0.44; range = 0.27–0.73; $N = 11$ experiments). The coarse sand sediment containing a large coarse gravel fraction (sediment B) was less preferred than sediment A (median proportion in sediment B based on experiments with >30 fish = 0.24; range = 0.08–0.39; $N = 4$ experiments).

Table 4

The experiments are assumed to be independent, which implies that the numbers buried in experiment i and k are independent with j sediment of x_{kj} if $i \neq k$. Test of hypotheses of homogeneity of preferences for sediment mixes 1 and 2 (see Table 2) based on likelihood ratio test (Q) for sandeels of all lengths. The null hypothesis was rejected in all but one case indicating significant differences in the numbers buried between sediment compositions E, D and C (p_1–p_3). p_4 refers to sediment composition A in mix 1 and B in mix 2 (NSD — no significant difference)

H_0	Q	p
Sediment mix 1		
H_{01}: $p_2 = p_3 = p_4$	89.6	< 0.0001
H_{02}: $p_2 = p_3$	24.9	< 0.0001
H_{03}: $p_2 = p_4$	89.5	< 0.0001
H_{04}: $p_3 = p_4$	20.3	< 0.0001
Sediment mix 2		
H_{01}: $p_2 = p_3 = p_4$	13.7	0.001
H_{02}: $p_2 = p_3$	1.7	0.19 NSD
H_{03}: $p_2 = p_4$	13.5	0.0002
H_{04}: $p_3 = p_4$	5.7	0.017

Table 5

Test of hypotheses of homogeneity of preferences for sediment mix 1 based on likelihood ratio test (Q) for sandeels (a) < 65 and (b) >65 mm TL. The null hypothesis was rejected in all but one case indicating significant differences in the numbers buried between sediment compositions E,D,C and A (p_1–p_4, respectively) (N.S.D. — no significant difference) (H_0 is rejected)

H_0	Q	p
(a) <65		
H_{01}: $p_2 = p_3 = p_4$	41.7	< 0.0001
H_{02}: $p_2 = p_3$	23.0	< 0.0001
H_{03}: $p_2 = p_4$	39.8	< 0.0001
H_{04}: $p_3 = p_4$	2.36	0.12 N.S.D.
(b) >65		
H_{01}: $p_2 = p_3 = p_4$	54.0	< 0.0001
H_{02}: $p_2 = p_3$	8.3	0.004
H_{03}: $p_2 = p_4$	52.5	< 0.0001
H_{04}: $p_3 = p_4$	19.3	< 0.0001

In order to obtain an index of relative carrying capacity of different sediment compositions, we examined the relationship between the maximum number of sandeels within a tray and sediment composition for all experiments combined (Fig. 7). In all cases the number of sandeels in a tray was not limited by the total number of sandeels in the aquarium. With the exception of the high gravel sediment B, the maximum sandeel densities declined in relation with both the silt/clay (<0.062 mm) and very fine sand (<0.125 mm) fractions when these accounted for more than 2 or 10% of the sediment, respectively.

4. Discussion

In common with previous investigations, the present study indicates that post-settled sandeels

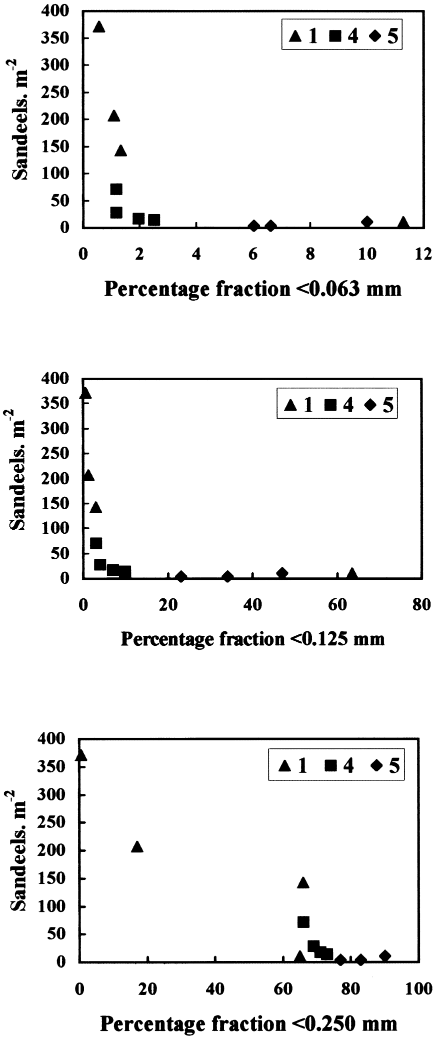

Fig. 7. Maximum densities of buried sandeels recorded in sediment choice experiments (see Table 1 for sediment classification). The numbers 1, 4 and 5 refer to densities in the sediment mixes given in Table 2.

actively select specific substrates for burying. Around Shetland, *A. marinus* appears to have a strong preference for medium to very coarse sands (median particle size 0.25–2 mm). This range is slightly broader than the 0.35–1.35 mm particle range reported by Reay (1970) for sandeel grounds in the English Channel. The present study also provides direct evidence for such a preference based on the proportion sandeels buried in sediment choice experiments. Other studies have reported that sandeels occur in areas of coarse sand, although they do not give information on particle size (Macer, 1966; Scott, 1973; Scott and Scott, 1988). However, despite its importance, the presence of sand does not appear to be the only factor influencing sediment choice in *A. marinus*.

Whilst the avoidance of sediments composed almost entirely of silt (i.e. >90%) has previously been demonstrated experimentally (Pinto et al., 1984) and earlier field studies have reported that sandeels tend to inhabit areas of “clean sand” (Macer, 1966; Reay, 1970; Meyer et al., 1979), the present study is the first to quantify the effect of fine sediments. Sandeels were not found in field samples where the silt content of sediments was greater than 10% and densities decreased for silt/clay fractions of between 2 and 10%. Sediment choice experiments indicate that the absence of sandeels from silt-rich sands observed in the field was related to the avoidance of such sediments. Indeed, even small fractions of 2% silt/clay or 10% very fine sand influenced where sandeels chose to bury. A limitation to the approach used in the experiments is that they could not distinguish between the effect of increasing content of “silt/clay” (particles <0.062 mm) and “very fine sand” (particles <0.125 mm), on sediment preference, as the relative proportions of these sediment grade classes were correlated.

Two factors may explain the absence of *A. marinus* from silt-rich sediments. Sandeels do not maintain permanent burrow openings so they have to ventilate their gills with interstitial water. This means that fine particles could clog their gills (Scott, 1973; Meyer et al., 1979; Pinto et al., 1984). Consequently, oxygen tension and the rate of exchange of interstitial water could be important factors influencing sediment choice. Although sandeels appear to have a metabolic compensatory mechanism that enables them to cope with oxygen tensions as low as 16 μmol dm^{-3} during their overwintering phase (Quinn and Schneider, 1991), they have been observed to move out of substrates when exposed to low oxygen tensions (Girsa and Danilov, 1976; Quinn and Schneider, 1991). Further, a preference for well-flushed sediments has been seen in laboratory experiments (Pinto et al., 1984). Field observations also indicate that sandeels prefer tidally active areas (Macer, 1966; Meyer et al., 1979; Pinto et al., 1984). The sand ripples observed in the present study support this view, since these seabed structures are generally associated with an abundant supply of sand and with maximum current flows of around 1 m s^{-1} (Stride, 1982).

Field measurements show that oxygen concentrations and sediment–water diffusion rates differ markedly between sand and silt-rich sediments in the North Sea (Lohse et al., 1996). In the sandy sediments that Lohse et al. (1996) measured, oxygen concentrations in the top 15 mm were very similar to those found in the water column and the oxic zone of these sediments extended down to 45 mm. In contrast, the depth of the oxic zones of sediments with a silt fraction of >10% was generally so small (<10 mm) as to make them uninhabitable for sandeels. Permeability and the characteristics of the boundary layer flow affect the rate of water percolation through sediments (Huettel et al., 1996). As permeability of sediments is a function of grain size and porosity (Chilingar, 1964), silt-rich sediments tend to have small interstitial water volumes and low rates of water exchange. Even small amounts of fine particles can clog the pores and reduce permeability. Ripples affect the boundary layer flow by deflecting bottom currents and creating small horizontal pressure gradients that force water into the seabed upstream and downstream of protruding surface structures (Thibodeaux and Boyle, 1987; Huettel and Rusch, 2000). Consequently, the preference of sandeels for areas of coarse and rippled sands may be explained by the importance of both sediment permeability and bottom roughness for interstitial water movements. Further experimental investigations into sediment permeability and the relation between ripple geometry and water percolation might help to better characterise sandeel habitat preferences.

In addition to a requirement for well-flushed sediments, the ease of penetration is generally regarded as a key determinant of sediment choice in sandeels (Macer, 1966; Reay, 1970; Meyer et al., 1979; Pinto et al., 1984). In the present study, only 1 of the 31 sediment samples containing sandeels was predominantly fine gravel (i.e. had a median particle size of 2 mm). Pinto et al. (1984) considered sediment penetrability by comparing shear stress in coarse sand and 16-mm gravel. Based on their measurements they found no reason why sandeels should be deterred from entering gravel. However, they found that sandeels showed a preference for sand compared with gravel in sediment choice experiments. In the present study, sandeels appeared to favour a coarse sand with fine to medium gravel (2–16 mm) sediments more than a coarse sand with coarse gravel (>16 mm). Moreover, recently metamorphosed sandeels showed similar preferences for medium and coarse sand sediments. Clearly, further research is needed to understand the avoidance of gravel /pebble sediments and particularly in relation to fish size. As has previously been reported, *A. marinus* were frequently associated with sandy sediments containing gravel or shell debris. This mixture of sediments is likely to result in a sediment with less compaction relative to a well-sorted sand. As such the use of such substrates may reflect a trade-off between ease of penetration and a preference for well-flushed sediments.

Within the limitations of preferred sediment, depth also appears to be an important explanatory variable influencing both sandeel occurrence and density. The optimal depth range of 30–70 m determined from the model fit is consistent with the recorded depth distribution in other regions of the North Sea, as well as that at which most North Sea sandeel fisheries operate (Macer, 1966). The low abundance of sandeels in deeper waters may be related to the decline in water movement with depth.

The sediment preferences reported here indicate that sandeels inhabit a narrower range of 'sand' sediments than could be surmised from previous studies. As such, attempts to predict sandeel distribution from maps of all types of sand will have over-estimated the extent of sandeel habitat (see Wanless et al., 1997). Based on the evidence presented in this study it should be possible to make inferences about the distribution and quality of potential *A. marinus* habitat in the North Sea from information on sediment fractions and depth, since these factors will limit the extent of distribution. Data on sediment composition have been collected for large areas of the North Sea, although the scale of sampling would only allow an indication of the extent of sandeel habitat to be made.

The preference of sandeels for specific sediment types may help explain the nature of observed changes in distribution associated with stock size. In a study of stock changes around the Shetland Isles, Wright (1996) demonstrated a contraction of sandeel distribution into certain fished grounds at low stock sizes. On the basis of our grab sampling, Shetland fished grounds appear to be characterised by the coarse sand sediments (Fig. 4) most preferred by sandeels in choice experiments. This would suggest that the contraction and expansion of sandeel distribution is centred around sites of preferred sediment type. Given the relatively persistent nature of sediment distribution, this contraction into preferred areas could have consequences for both predators and the fishery. A number of both fish and mammalian predators are known to be able to catch sandeels in the sediment (Hobson, 1986) and so certain predators may aggregate over such areas of preferred sandeel habitat. Evidence for such a concentration of predators around sandeel habitat has been seen in diving seabirds during a period when the regional prey density was low (Monaghan et al., 1996). The present study indicates that sandeel fishing is targeted at the areas of coarse sand sediments sandeels prefer. The movement of sandeels into such habitats could allow fishermen to maintain high catch rates up to a level where densities in less preferred sediments had severely declined. As such, the fishery may have the potential to remain economic even when the overall abundance of a regional sandeel stock is low. Clearly, further work is needed outside of Shetland to examine the relationship between physical habitat preferences and distributional responses in relation to fishing effort.

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References

Arnold, G.P., Weihs, D., 1978. The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa* L.). J. Exp. Biol. 75, 147–169.

Cameron, J., 1958. Studies on the Ammodytidae of Isle of Man waters. PhD thesis, Univ. of Liverpool, unpublished.

Chilingar, G.V., 1964. Relation between porosity, permeability and grain size distribution of sands and sandstones. In: Van Straaten, L.M.J.U. (Ed.). Deltaic and Shallow Marine Deposits. Elsevier, Amsterdam, pp. 71–75.

Crawley, M.J., 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford.

Furness, R.W., 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981–83. Ibis 132, 205–217.

Gauld, J.A., Hutcheon, R., 1990. Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* (Raitt), in the north-western North Sea. J. Fish Biol. 36, 611–613.

Girsa, I.I., Danilov, A.N., 1976. Defensive behaviour in sand lance, *Ammodytes hexapterus* of the White Sea. J. Ichthyol. 16, 862–865.

Harwood, J., Croxall, J.P., 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Mar. Mamm. Sci. 4, 13–33.

Hastie, T.J., Tibshirani, R.J., 1990. Generalised Additive Models. Chapman and Hall, London (335 pp.).

Hobson, E.S., 1986. Predation on the Pacific sand lance, *A. hexapterus* (Pisces:Ammodytidae) during the transition between day and night in southeastern Alaska. Copeia 1, 223–226.

Huettel, M., Rusch, A., 2000. Transport and degredation of phytoplankton in permeable sediment. Limnol. Oceanogr. 45, 534–549.

Huettel, M., Ziebis, W., Forster, S., 1996. Flow induced uptake of particulate matter in permeable sediments. Limnol. Oceanogr. 41, 309–322.

ICES, 1997. ICES working group on the assessment of demersal stocks in the North Sea and Skagerrak ICES, Doc. C.M. 1997/Assess:6.

Lohse, L., Epping, E.H.G., Helder, W., Van Raaphorst, W., 1996. Oxygen pore water profiles in continental shelf sediments in the North Sea: turbulent diffusion versus molecular diffusion. Mar. Ecol. Prog. Ser. 145, 63–75.

Macer, C.T., 1966. Sandeels (Ammodytidae) in the south-western North Sea: their biology and fishery. MAFF Fish. Investig. Lond. 2 24 (6), 1–55.

Meyer, T.L., Cooper, R.A., Langstone, R.W., 1979. Relative abundance, behaviour and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. Fish. Bull. 77, 243–254.

Monaghan, P., 1992. Seabirds and sandeels: The conflict between exploitation and conservation in the northern North Sea. Biodiv. Conserv. 1, 98–111.

Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., Walton, P., 1996. The influence of changes in food abundance on diving and surface feeding seabirds. In: Montevecchi, W.D. (Ed.). Studies of High-Latitude Seabirds. 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems. Can. Wildlife Serv. Occ. Paper, No. 91Can. Wildlife Serv. Occ. Paper, pp. 10–19.

Pearson, W.H., Woodruff, D.L., Sugarman, P.C., Olla, B.L., 1984. The burrowing behavior of sand lance, *Ammodytes hexpterus*:

effects of oil-contaminated sediment. Mar. Environ. Res. 11, 17–32.

Pinto, J.M., Pearson, W.H., Anderson, J.W., 1984. Sediment preferences and oil contamination in the Pacific sand lance *Ammodytes hexapterus*. Mar. Biol. 83, 193–204.

Quinn, T., Schneider, D.E., 1991. Respiration of the teleost fish *Ammodytes hexapterus* in relation to its burrowing behavior. Comp. Biochem. Physiol. 89A, 71–75.

Reay, P.J., 1970. Synopsis of biological data on north Atlantic sandeels of the genus *Ammodytes*. FAO Fish. Synop. No.82.

Raitt, D.S., 1934. A preliminary account of sandeel of Scottish waters. J. Cons. Int. Explor. Mer 9, 365–372.

Scott, J.S., 1973. Food and inferred feeding behaviour of northern sand lance, *Ammodytes dubius*. J. Fish. Res. Bd Can. 30, 451–454.

Scott, W.B., Scott, M.G., 1988. Atlantic Fishes of Canada. University of Toronto Press, Toronto (pp. 438–442).

Sherman, K., Jones, C., Sullivan, L., Smith, W., Berrien, P., Ejsymont, L., 1981. Congruent shifts on sand eel abundance in western and eastern North Atlantic ecosystems. Nat. Lond. 291, 486–489.

Sleath, J.F.A., 1982. Sea Bed Mechanics. Wiley, NewYork (330 pp.).

Stride, A.H. (Ed.), 1982. Offshore Tidal Sands, Processes and Deposits Chapman and Hall, London (222 pp.).

Sparholt, H., 1990. An estimate of the total biomass of fish in the North Sea. J. Cons. Int. Explor. Mer 46, 200–210.

Swartzman, G., Huang, C., Kaluzny, S., 1992. Spatial analysis of Bering Sea groundfish survey data using generalized additive models. Can. J. Fish. Aquat. Sci. 49, 1366–1378.

Thibodeaux, L.J., Boyle, J.D., 1987. Bedform-generated convective transport in bottom sediment. Nature 325, 341–343.

Tyler, P., Shackley, S.E., 1978. Comparative efficiency of the Day and Smith-McIntyre grab. Estuar. Coast. Mar. Sci. 6, 439–445.

Wanless, S., Bacon, P.J., Harris, M.P., Webb, A.D., Greenstreet, S.P.R., Webb, A., 1997. Modelling environmental and energetic effects on feeding performance and distribution of shags (*Phalacrocorax aristotelis*): integrating telemetry, geographic information systems and modelling techniques. ICES J. Mar. Sci. 54, 524–544.

Wanless, S., Harris, M.P., Greenstreet, S.P.R., 1998. Summer sandeel consumption by seabirds breeding in the Firth of Forth, southeast Scotland. ICES J. Mar. Sci. 55, 1141–1151.

Winslade, P., 1974. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. J. Fish Biol. 6, 577–586.

Wright, P.J., 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Greenstreet, S.P.R., Tasker, M.L. (Eds.). Aquatic Predators and their Prey. Fishing News Books. Blackwell Science, Oxford, pp. 154–165.

Wright, P.J., Begg, G.S., 1997. A spatial comparison of common guillemots and sandeels in Scottish waters, ICES seabirds in the marine environment symposium. ICES J. Mar. Sci. 54, 578–592.