

Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables

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Vertical distribution patterns of larval and juvenile sandeels were investigated at four locations in the North Sea. Sandeels between 6 and 65 mm were found to depths of 80 m, with vertical distributions dependent on both length and environmental factors. At one location with a stratified water column, the highest densities were found during the day in midwater where food concentration was also highest. In areas without marked vertical hydrographic gradients, larvae were relatively more abundant in surface waters during the day. At all locations, larvae of all sizes were generally more homogeneously distributed in the water column during night than during day. The extent of vertical migration, as measured by the standard deviation of the mean depth, increased generally with length. Gear avoidance was evident for larvae ≥ 20 mm. Catch efficiency generally depended on both length class and surface light intensity. A simulated drift pattern of larvae, based on ADCP current measurements from two locations, predicts that the horizontal drift trajectory would only be affected slightly by the vertical positioning of the larvae in the water column during the time of sampling. The implication of vertical migrations for dispersal of larvae away from the spawning grounds is discussed.

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Introduction

Sandeels are extremely abundant in northern European waters (Reay, 1970, 1973) and represent around 15% of the total fish biomass in the North Sea (Sparholt, 1990). Of the five species inhabiting the North Sea, the lesser sandeel, *Ammodytes marinus* (Raitt, 1934) is by far the most common species comprising over 90% of the sandeel catch.

The life history of sandeels is unusual among fish because of their association with a specific substrate type into which they burrow after settlement from the larval phase. The habitat of *A. marinus* is found at depths between 20 and 70 m where the content of silt and clay is less than 10% (Wright *et al.*, 2000). Because this habitat has a patchy distribution (Macer, 1966; Scott, 1968) and post-settlement sandeels do not move far from their habitat (Gauld, 1990; Macer, 1966), the main opportunity for large-scale horizontal movement occurs prior to settlement, during the planktonic larval

phase. In the North Sea, *A. marinus* spawn between December and January (Macer, 1966; Gauld and Hutcheon, 1990; Bergstad *et al.*, 2001) and the larvae hatch from February to May (Macer, 1965; Langham, 1971; Wright and Bailey, 1996), during which months the circulation is largely wind-driven (Turrell, 1992). Because the larval phase lasts 33–90 days (Wright and Bailey, 1996), the larvae are exposed to potentially rapid and variable transport away from the spawning grounds (Proctor *et al.*, 1998; Berntsen *et al.*, 1994), which is confirmed by the observed distribution patterns (Henderson, 1954; Macer, 1965, 1966; Munk *et al.*, 2001). Understanding the extent of larval dispersal is therefore important for understanding the population structure of this species.

Vertical migration may significantly influence the horizontal transport of those life stages of fish that are limited in their horizontal movements by their swimming ability, because it allows larvae to take advantage of vertical

gradients in water velocity, thereby either increasing or decreasing net horizontal transport (Laprise and Dodson, 1989; Heath, 1992). Also in sandeels, vertical migrations during the larval stage might have a major effect on the horizontal transport (Berntsen *et al.*, 1994).

Fish larvae may migrate vertically in response to several factors, including avoidance of poor weather conditions (Gallego *et al.*, 1999), avoidance of predators (Giske *et al.*, 1994), or to maximize food intake (Munk *et al.*, 1989). Although Monteleone and Peterson (1986) and Potter and Lough (1987) showed that migratory behaviour of sandeel larvae may occur in isothermal and isohaline water columns, in the absence of vertical gradients in water density, the influence of physical and biological factors on vertical movements is still poorly understood.

Two main types of vertical migration patterns have been identified among planktonic organisms (Neilson and Perry, 1990). In type-I (or “nocturnal” vertical migration), organisms move up at dusk and down at dawn. In type-II (or “reverse” vertical migration), they move down at dusk and up at dawn. In general, sandeel larvae do not exhibit vertical migration immediately after hatching. Yamashita *et al.* (1985) found evidence of vertical movements only in *Ammodytes personatus* larvae > 5 mm total length (TL), and Monteleone and Peterson (1986) and Potter and Lough (1987) only for *Ammodytes americanus* and *Ammodytes dubius* larvae > 8 mm TL. Larger larvae appear to move mostly down in the water column at dusk and up at dawn (type-II). Although there is evidence of inter-specific and ontogenetic differences, direct comparisons of results are difficult because of differences in larval sizes investigated, in sampling gear, and in the biotic and abiotic environment at the locations sampled. Yamashita *et al.* (1985) found that the concentration of *A. personatus* in surface waters during daylight increased with larval size from 5 to > 8 mm TL. In contrast, *Ammodytes* sp. larvae > 10 mm TL were distributed in the near-bottom layer (40–70 m) during day and in surface waters (0–20 m) during night, while juveniles of 50–81 mm TL followed the same pattern (Potter and Lough, 1987).

Information on vertical migration in pre-settled *A. marinus* and in particular on the influence of environmental factors is largely lacking. We analyse variations in the vertical distribution of *A. marinus* larvae in relation to size, hydrography, and food distribution, to identify the factors that exert a predominant influence on their migratory behaviour and distribution.

Methods

Data on the distribution of larval and juvenile *A. marinus* were collected during two cruises of RV “DANA” that took place from 19 April to 2 May 1995 and from 23 May to 5 June 1996. Environmental parameters were measured in conjunction with sandeel sampling at three locations in 1995 (L1, L2 and L3) and at one in 1996 (L4). The locations

were chosen to represent large differences in the physical and biological environment, to allow for analyses of the relationship between environmental variables and larval vertical migration. A map of the sandeel fishing grounds in the North Sea (Jensen, 2001) was used as a proxy for sandeel habitat to relate the four locations to possible spawning sites and locations of post-settled sandeels. All samplings and measurements were carried out within a range of 0.3 nautical miles around each location (Figure 1).

During the cruises, data on position (differential GPS, accuracy ± 5 m), surface light intensity, and depth (echo sounder measurements), were logged at least every 30 s. Fluorescence, temperature and salinity were profiled at all locations, using a Seabird CTD with a mounted fluorometer. Additional CTD measurements were collected along a north–south oriented transect crossing three of the four locations (Figure 1). The CTD data were contoured and plotted by use of the PC mapping system Surfer (Golden Software Incorporated 1995). Because two different CTD systems were used in the two surveys, it was not possible to scale the fluorescence measurements to the same units.

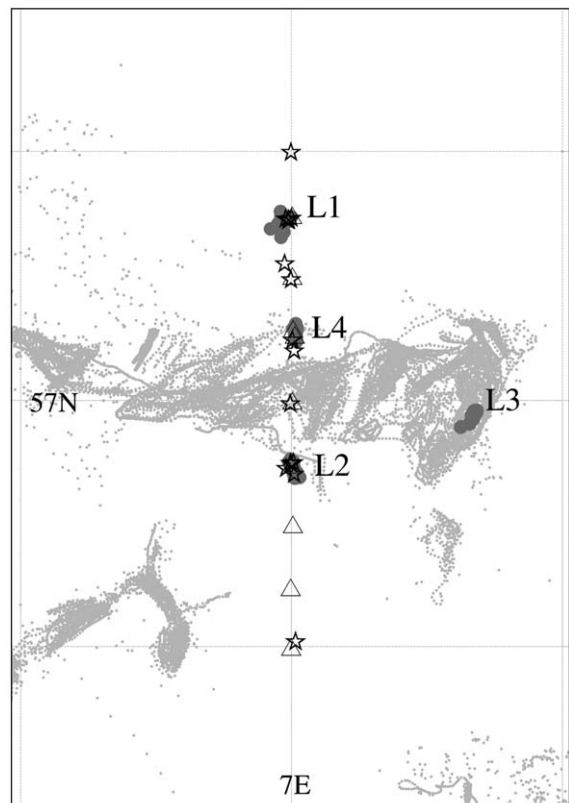


Figure 1. Map of sampling locations of sandeel larvae (filled dots, L1–L4) and CTD stations along a north–south transect (stars, 1995; triangles, 1996). Grey areas represent sandeel fishing grounds.

A submersible pump (capacity, $1.2 \text{ m}^3 \text{ min}^{-1}$), mounted in a conical net with mesh size of $30 \text{ }\mu\text{m}$, was used to collect zooplankton in 1996. The pump was lowered to 5 m above the seabed, turned on, and lifted to the surface at a speed of 10 m min^{-1} . In addition, zooplankton was collected at L4 from the depth strata specified for larval samples, by lowering the pump to the specified depth and pumping sea water through the net for 3 min. Only the size fraction of zooplankton $> 200 \text{ }\mu\text{m}$ was analysed because sandeel larvae $> 12 \text{ mm TL}$ (the dominant size class during both cruises) mainly feed on copepod nauplii, larger copepodites, and adult copepods, which are mainly $> 0.2 \text{ mm TL}$ (Covill, 1959; Monteleone and Peterson, 1986). For one sub-sample from each sample, zooplankton was sorted into three groups: (a) nauplii ($< 350 \text{ }\mu\text{m}$), (b) *Temora* sp. and (c) other species, counted and measured to the nearest micrometre, using a microscope fitted with a calibrated eyepiece. The number of animals in each size category was then raised to N m^{-3} . Total biomass (B in $\mu\text{g C m}^{-3}$) was calculated by applying the weight/length relationships used by Kjørboe and Gissel Nielsen (1990):

$$B_{\text{nauplii}} = N * 3.18 * 10^{-12} * l^{3.31}$$

$$B_{\text{other species}} = N * 2.69 * 10^{-6} * l^{2.27}$$

$$B_{\text{Temora sp.}} = N * 2.90 * 10^{-6} * l^{2.16}$$

where l is cephalothorax length in micrometres.

Observations of the vertical distribution of pre-settled sandeels were made over periods of 16–24 h, corresponding to approximately two tidal periods. Densities were estimated by depth layer using a 2 m-ringnet, designed for the collection of fish larvae (Munk, 1993). The net was equipped with 13 m long black netting of 1 mm (1995) or 1.6 mm (1996) mesh size and towed at a speed of 2.5–3.5 knots. The larger mesh size was chosen in 1996 because the larvae were larger. The volume of water filtered was estimated using a calibrated flowmeter in the centre of the net opening. Sampling at each location was initiated by oblique hauls from the surface to 5 m above the seabed and back to the surface. If haul duration was $< 15 \text{ min}$, a second oblique haul was made before the gear was taken on deck. Subsequently, the net was deployed at different depth strata for 15 min each. Shooting and heaving was done in such a way that the probability of catching fish larvae on the way down to or up from the specified stratum was minimized by slowing down ship speed. A depth sensor with acoustic transmission (SCANMAR system) measured the actual depth of the net, ensuring that it was kept within $\pm 3 \text{ m}$ of the specified depth.

Larvae were identified to species, either based on the melanophore pigmentation pattern (larvae $< 20 \text{ mm TL}$), using the keys of Macer (1967) and Russell (1976), or from vertebrae counts for larger larvae. All sandeels were identified as *A. marinus*. Length was measured as total length (TL) to 1 mm below. Subsequently, larvae were combined into 5 or 10 mm length classes. Five millimetre

length classes were used to resolve changes in behaviour and distribution around the size of metamorphosis and settlement (30–50 mm; Jensen, 2001).

To investigate the effect of surface light intensity on catchability of sandeel larvae, surface light intensity was related to catch rates in the oblique hauls. The vertically stratified samples were separated into series of hauls covering the water column and carried out within periods of approximately the same surface light intensity. The relative proportion of sandeels in each depth layer was calculated for each time interval, by dividing the density of sandeels in each depth layer by the sum of densities in all depth layers sampled.

A non-parametric Pearson chi-square test was used to test the null hypothesis of no association between larval density, depth and surface light intensity (homogeneous distribution over the water column). For this purpose light intensity was split into the following five intervals: ≤ 1 , 1–30, 30–50, 50–100 and 100–200 $\text{mE s}^{-1} \text{ m}^{-2}$.

An ADCP (Research Development Cooperation) was used to measure water velocity and direction by depth at L2 and L3. ADCP data were extracted for the first 10 min of the periods of sandeel sampling in each depth layer. Mean velocity (in knots) of the water in the N/S direction ($V^{\text{N/S}}$) and in the E/W direction ($V^{\text{E/W}}$) was calculated for each depth layer and period of sampling. The distance of water movement in the N/S direction ($D^{\text{N/S}}$) and in the E/W direction ($D^{\text{E/W}}$) during a 24 h period divided by the number of hauls (k), was calculated afterwards for each depth layer (d), location (r) and haul (j) from:

$$D_{r,d,j}^{\text{N/S or E/W}} = 24 \cdot V_{r,d,j}^{\text{N/S or E/W}} / k$$

The estimates of $D^{\text{N/S}}$ and $D^{\text{E/W}}$ were used to simulate the horizontal drift of a passively drifting particle with neutral buoyancy in each depth layer with L2 and L3 as starting points. Each new position was calculated by accounting for the estimated distances travelled in each direction during each sampling interval. The simulated tracks, equivalent to a 24 h period, were plotted in a Geographical Information System (ArcView 8.2).

Results

Figure 2 provides isopleths of water density and relative fluorescence along the transect shown in Figure 1. The profiles indicate a frontal zone positioned between 57°N and $57^\circ 10' \text{N}$. L1 was positioned north of the frontal zone at depths of 92 m, L4 in the frontal zone at 59 m, and L2 and L3 south of the frontal zone at water depths of 21 and 40 m, respectively (Table 1). Figure 3 shows density and fluorescence profiles from each of the four locations. L1 and L4 had marked vertical gradients in both density and fluorescence. L4 had, in contrast to L1, a marked peak in fluorescence above the pycnocline. No pycnocline was observed at L2 and L3 because they were shallower, but fluorescence was high throughout the water column.

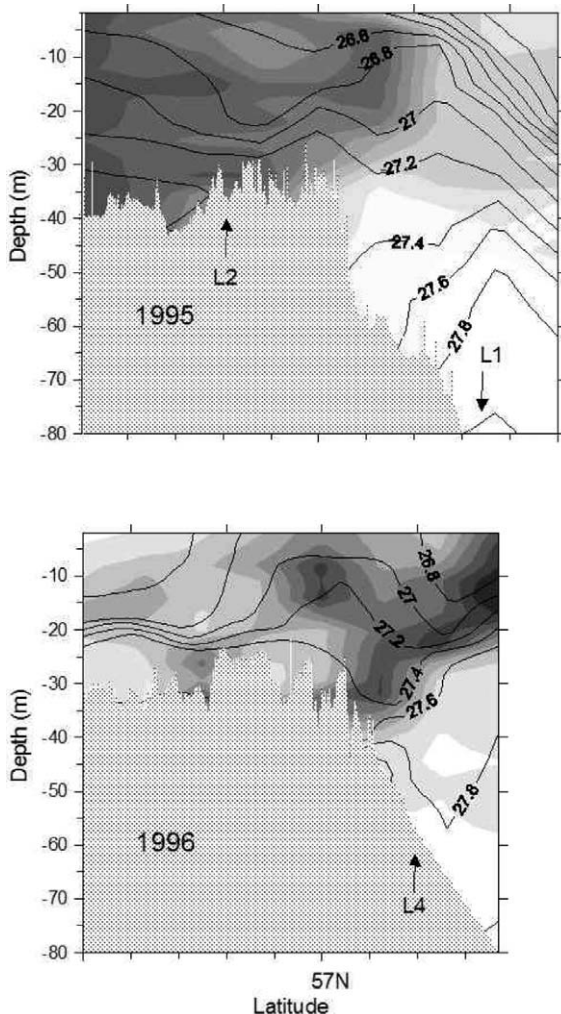


Figure 2. Isopleths of water density (0.2 kg m^{-3} intervals) and relative fluorescence (chlorophyll, scaled to the highest value observed per cruise) along the transect (0.1° intervals) shown in Figure 1, based on 12 CTD casts in 1995 and on eight casts in 1996. Positions of L1, L2 and L4 are indicated.

L3 was positioned at one of the main commercial fishing grounds in the area (Figure 1) and adult sandeels were caught in grab samples at this location. L2 and L4 were both located in the vicinity of less important fishing grounds, while L1 was positioned outside known sandeel fishing grounds.

The numbers of hauls made at each location with the 2 m-ringnet are given in Table 2 and estimates of larval density by length group are given in Table 3. Most of the larvae caught during the 1995 cruise (L1, L2 and L3) were in the range of 11–30 mm and those caught during the 1996 cruise (L4) were between 21 and 45 mm. Because larvae >35 mm in 1995 and >60 mm in 1996 were rarely caught, these size classes were excluded from the analyses.

Table 1. Mean depth (D), sandeel larval density (all sizes combined; S) and zooplankton density (Z) at four locations.

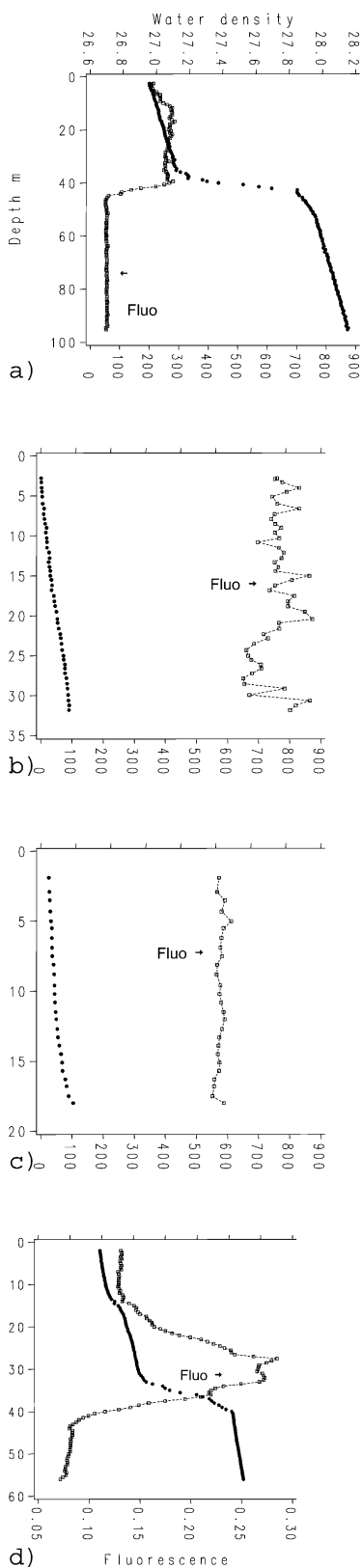
Location	D (m)	S (no. m^{-3})	Z ($\mu\text{g C m}^{-3}$)
L1	92	0.005	
L2	34	0.041	
L3	21	0.049	
L4	59	0.094	92 919

To describe catchability changes in relation to surface light intensity and larval size, the ratio of average density in day and night oblique hauls (defined as periods with mean surface light intensity >3 and $<1 \mu\text{E s}^{-1} \text{m}^{-2}$, respectively) by length class is plotted in Figure 4. In general, catchability during the night tends to increase relative to the day with length of the larvae, especially for larvae >20 mm TL, with the exception of larvae <31 mm at L2 for which day catches were larger than the night catches.

A graphical presentation of the vertical distribution pattern of sandeel larvae is given in Figure 5. The null hypothesis that there is no association between larval density, depth, and surface light intensity, was rejected for all length groups at all locations ($p > 0.05$), i.e. larvae were never evenly distributed in the water column. The vertical distribution changed in relation to both light and size. Larvae had generally a more patchy distribution during the day than during the night. In most cases, the highest concentrations were found in surface waters during the day, whereas the larvae were more homogeneously distributed throughout the water column during the night. However, there were deviations from this general pattern. At L2, a higher fraction of 11–20 mm larvae at 18 m depth and of 21–30 mm larvae at 30 m depth was found than near the surface from about 11:00 GMT to the end of the sampling period (Figure 5b). At L4, larvae seemed to congregate at 30 m depth during the day, concurrent with declining densities in surface and bottom waters, followed by a gradual movement away from 30 m depth towards both surface and bottom when light intensity decreased from about 15:00 GMT onwards (Figure 5d).

Although all length groups undertook vertical migrations, the extent depended on length. To further investigate this topic, the standard deviation of the position of the centre of mass Z_{cm} (as an index of the extent of the vertical movements) was plotted against larval length (Figure 6). The standard deviation generally increases with length for all locations, with a few exceptions at the lower end of the size range (notably larvae <10 mm at L1 and L2 and 11–20 mm larvae at L4).

At L4, one zooplankton sample was collected during daytime and one during night at each depth fished by the 2 m-ringnet (Figure 7). The highest density was observed at 30 m depth (around the thermocline) during both day and night. Thus, sandeel larvae at this location concentrated



during daytime in the water layers where zooplankton density was highest, whereas no association was observed during the night.

Figure 8 shows the simulated drift pattern of larvae based on the ADCP current measurements. The analysis predicts that the horizontal drift trajectory would be affected only slightly by the vertical positioning of the larvae in the water column at both locations. The larvae would, independently of vertical position and migration, be dispersed from their original locations. Only those that had stayed close to the bottom at L2 would have ended up at their starting position 24 h later. Potential advection away from L3 (at a sandeel ground) should have been larger (6–11 nm in 24 h) than from L2 (3–4 nm in 24 h).

Discussion

The observations of vertical distribution patterns of sandeel larvae across a range of different environmental conditions suggest a strong influence of light conditions, hydrography and prey distribution. At the frontal station L4, the sandeel larvae congregated at daytime in midwater above the pycnocline, where there was a peak in the abundance of zooplankton (>200 μm). Although only a few hauls were made here during the night, the available data suggest that the larvae were more concentrated in both surface and bottom waters. At stations with only weak stratification (L2 and L3), the larvae apparently exhibited type-II (reverse) vertical migration behaviour, consistent with the findings of Ryland (1964) and Yamashita *et al.* (1985) for 5–20 mm larvae in the absence of vertical gradients in hydrography or plankton abundance.

The patterns observed in *A. marinus* larvae are comparable to those seen in herring. Herring larvae moved to depths where light was sufficient for feeding, and the distribution within that zone was refined to reach a compromise between optimal light conditions for feeding and optimal prey densities (Munk *et al.*, 1989). This may apply to pre-settled *A. marinus* as well. Larvae of both sandeel and herring are visual feeders and feed only during the day (Covill, 1959; Ryland, 1964; Yamashita *et al.*, 1985; Monteleone and Peterson, 1986).

The size-related differences in vertical migration may be explained by the gradual development of fins (Blaxter, 1986) and swimming ability (Monteleone and Peterson, 1986) and the differential vertical distribution patterns of their preferred copepod prey (Fransz *et al.*, 1991; Frost and Bollens, 1992). In *A. marinus*, the caudal, anal and dorsal fin rays are fully developed at a length of 20 mm TL (Macer, 1967). With increasing size, food preference moves from eggs to nauplii (8–12 mm larvae), to copepodites

Figure 3. Vertical profiles of water density (kg m^{-3}) and fluorescence (chlorophyll, arbitrary scaled by cruise) by sampling location: (a) L1, (b) L2, (c) L3, and (d) L4.

Table 2. Number of hauls by location, sample depth and time of day.

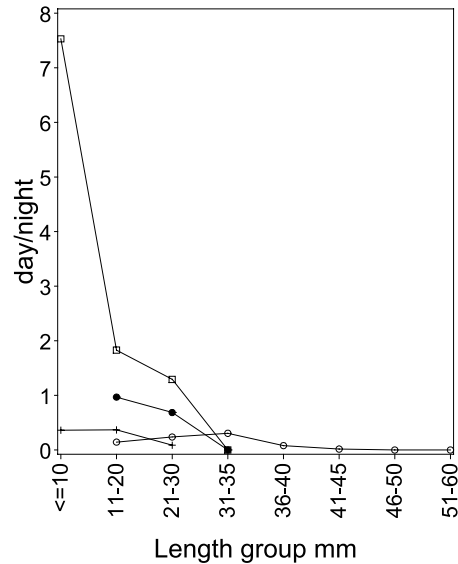
Location	Depth (m)	Day	Dusk	Night	Total
L1	7	1	0	3	4
	35	1	0	3	4
	55	1	1	3	5
	91	2	0	2	4
	Oblique	1	0	1	2
L2	7	5	0	5	10
	18	6	0	4	9
	30	5	1	4	10
	Oblique	2	0	1	3
L3	7	5	1	5	11
	16	5	0	6	11
	Oblique	3	0	1	4
L4	7	8	0	2	10
	30	8	1	1	10
	50	8	0	2	10
	Oblique	2	0	2	4

(12–20 mm) and finally to larger copepodites and adult copepods, the same prey as consumed by adult sandeels (Covill, 1959; Monteleone and Peterson, 1986).

The more homogeneous distribution observed during night may be related to a reduced swimming activity. Yamashita *et al.* (1985) observed in the laboratory that *A. personatus* larvae ceased swimming during night and sank to the bottom. Such inactivity may reduce detection by predators (Neilson and Perry, 1990) or simply save on energetic expenditure.

Table 3. Minimum, maximum and median densities (1000 m^{-3}) of sandeels in oblique and vertical stratified hauls, by location and length group (mm).

	Length group	Minimum	Maximum	Median
L1	≤10	0.0	2.6	0.5
	11–20	0.0	24.8	4.2
	21–30	0.0	11.3	3.0
	31–35	0.0	0.7	0.0
L2	≤10	0.1	29.2	1.5
	11–20	0.4	33.5	9.4
	21–30	0.2	42.5	4.6
	31–35	0.0	2.4	0.3
L3	≤10	0.0	5.7	1.0
	11–20	0.7	103.8	35.3
	21–30	0.0	15.2	1.9
	31–35	0.0	1.0	0.0
L4	11–20	0.0	22.1	1.1
	21–30	1.8	39.6	6.5
	31–35	0.0	30.7	2.5
	36–40	0.0	54.2	2.5
	41–45	0.0	77.6	0.7
	46–50	0.0	17.4	0.0
	51–60	0.0	14.6	0.0



● L1 □ L2 + L3 ○ L4

Figure 4. Ratio of mean day and night densities of sandeel larvae in oblique hauls with the 2 m-ringnet, by location and length group. At location 1, sandeels ≤10 mm were caught during night but not during day.

Gear avoidance was particularly evident in larvae >20 mm and appeared to be related to surface light intensity. During the day, zero catches of larvae >45 mm from all depth layers were frequently observed, whereas this never occurred during the night. Similar signs of gear avoidance have been reported for larvae of other fish (Bridger, 1956; Lenarz, 1973; Munk, 1988; McGurk, 1992) as well as other sandeel species (Richards and Kendall, 1973; Potter and Lough, 1987).

The large vertical range inhabited by *A. marinus* larvae and their migration behaviour could have important implications for their horizontal transport. Published simulations of larval transport have been of limited value because of lack of direct information. For example, the results of Berntsen *et al.* (1994) may overestimate the extent of transport of sandeel larvae away from the spawning locations, because the larvae were assumed to remain close to the surface. The simulations of the drift trajectory of larvae (Figure 8) suggest that vertical movements would not have affected the horizontal dispersal to a great extent in either of the two locations. Still, the higher advection from L3 compared to L2 may explain why the density of larvae <10 mm was much higher at the latter location. However, as the available information on drift trajectories came from two snapshots

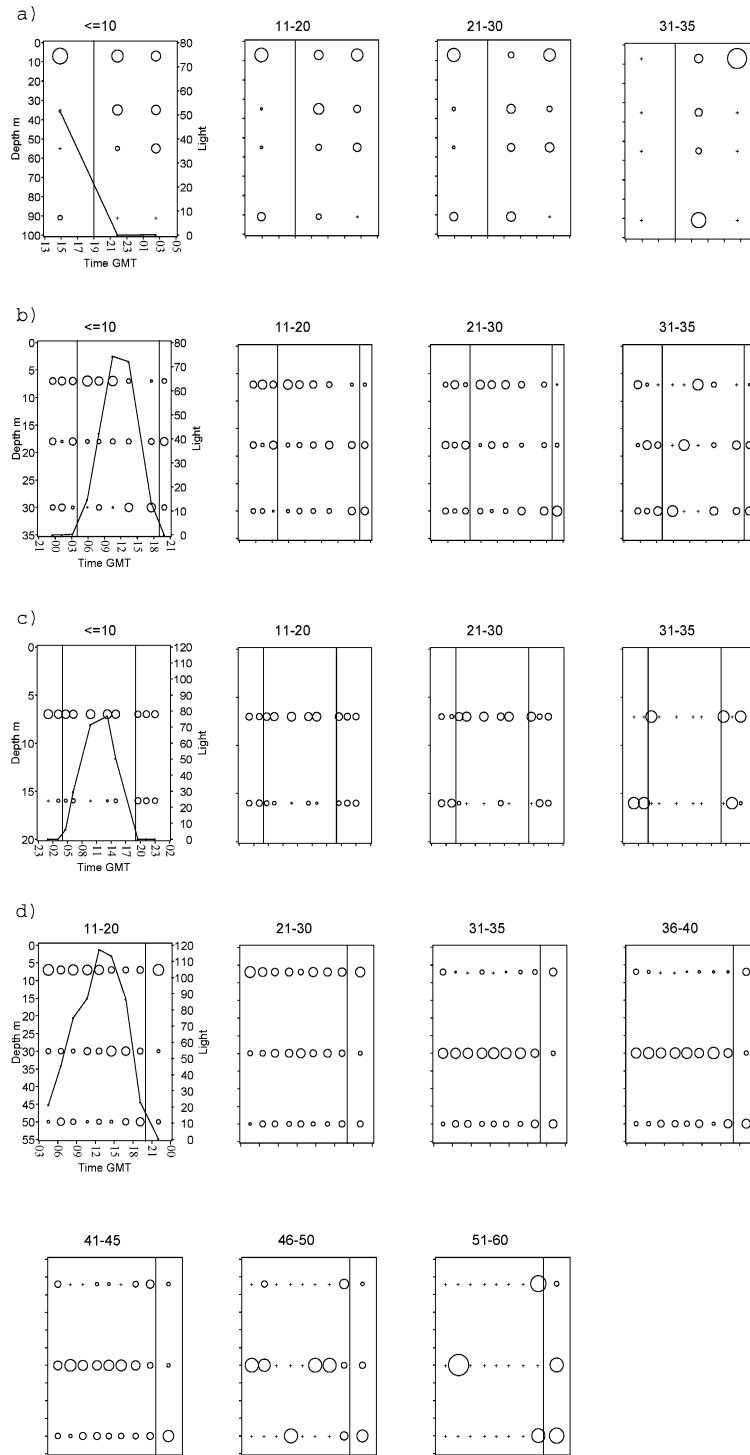


Figure 5. Relative densities of sandeels by depth (circles sum up to 100% by time interval), and surface light intensity (line; $\mu\text{E s}^{-1} \text{m}^{-2}$) plotted against depth and time, by location (a, L1; b, L2; c, L3; and d, L4) and length group (vertical lines represent dawn and dusk; +, no sandeels caught).

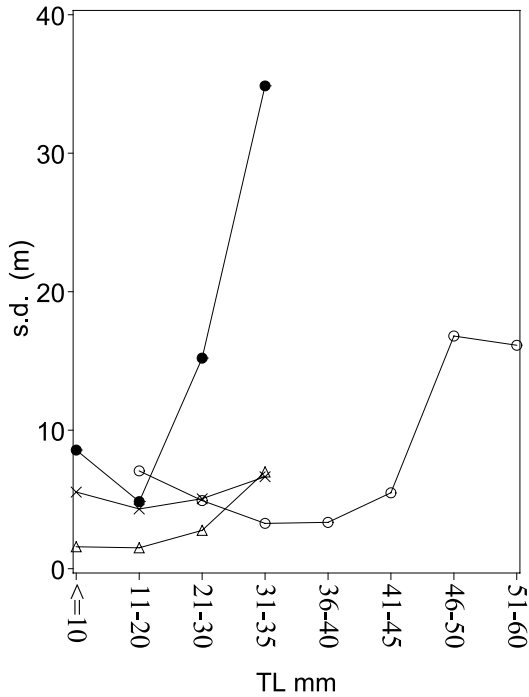


Figure 6. Standard deviation of mean larval depth plotted against length group by location.

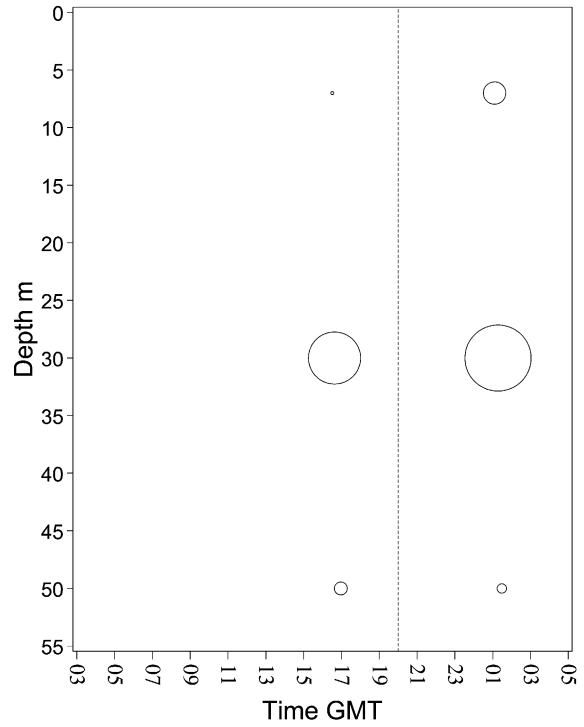


Figure 7. Relative densities of zooplankton > 200 μ m (circles) plotted against time and depth (vertical line, dusk).

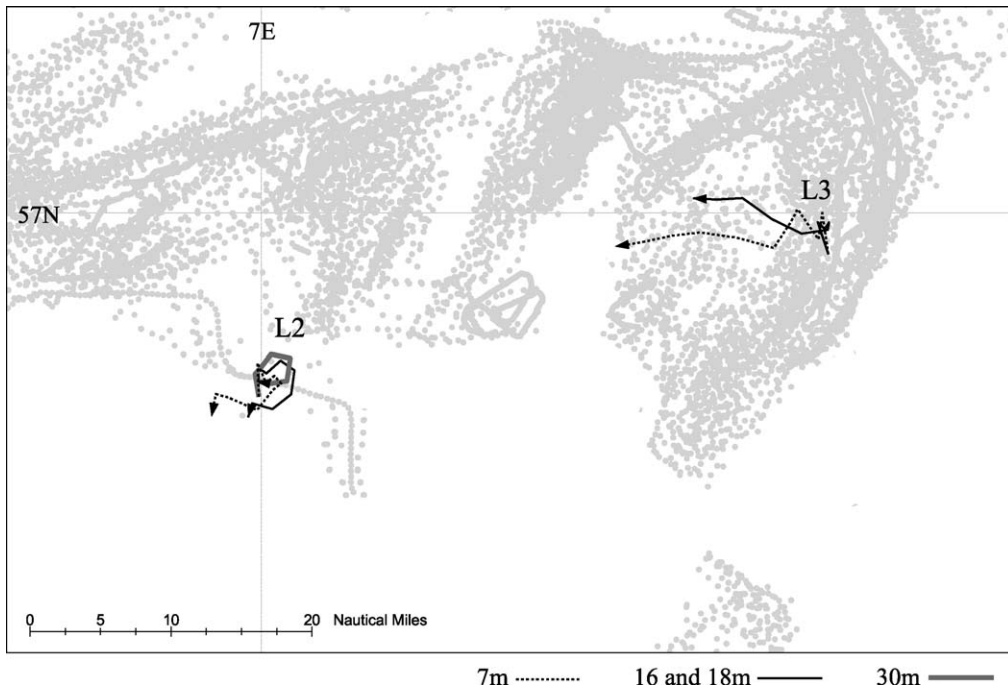


Figure 8. Simulated 24 h drift trajectories of sandeel larvae (lines, arrows indicate drift direction), by location and depth based on ADCP measurements. Grey areas represent sandeel fishing grounds.

of a duration less than a 24 h cycle, the results must be considered as preliminary.

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