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Vertical Distribution and Sampling Variability of Larval and Juvenile Sand Lance (*Ammodytes* sp.) on Nanutcket Shoals and Georges Bank*

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Abstract

Vertical distribution and movement of sand lance larvae and juveniles (<81 mm SL) are summarized from four cruises during winter and spring seasons in 1978, 1981 and 1983. Opening-closing nets (1-m^2 and 10-m^2 MOCNESS) were used to sample discrete strata for day and night vertical profiles and to make serial double-oblique transects for spatial variability. In December–January, recently-hatched larvae (5 mm SL) were found throughout the water column in well-mixed shelf water, with highest density usually in the 10–20 m depth range. In February–March, the larger larvae (>10 mm SL) were found throughout the water column during both day and night, but these appeared to be in transition to adult behavior, with many of them living near the bottom during the day and moving up in the water column at night. In April, premetamorphic young (20–30 mm SL) were caught mostly at night, and their abundance increased with depth. In May, postmetamorphic juveniles (50–81 mm SL) were caught mostly at night. Presumably, they were near the bottom or burrowed in the substrate during the day. Avoidance of the samplers by large larvae (>10 mm) and juveniles prevents firm conclusions on their vertical distribution and movement.

Introduction

Sand lance (*Ammodytes* sp.) larvae and juveniles occur pelagically over much of the continental shelf off northeastern United States during winter and spring (Bigelow and Schroeder, 1953; Richards and Kendall, 1973; Sherman *et al.*, 1981a). Knowledge of their vertical distribution and movement is limited. Avoidance of plankton nets, particularly in daytime, and changes in availability to nets due to behavioral changes during ontogeny have made interpretation of catches of larvae and juveniles in plankton sampling gear very difficult (Norcross *et al.*, 1961; Ryland, 1964; Richards and Kendall, 1973).

In shelf waters off Chesapeake Bay, Norcross *et al.* (1961) found mostly 10-14 mm larvae in January-March sampling and 15–19 mm larvae in April. They concluded that net avoidance was the cause of few larger larvae (>20 mm) being caught. Their data also indicated daytime net avoidance by 10–15 mm larvae. Larvae were found mainly in surface waters in January but were dispersed throughout the water column in February and April. In March, however, most of the larvae were taken near the bottom, possibly because of high winds and rough seas at the time of sampling. Richards and Kendall (1973) obtained larger catches of larval *Ammodytes* sp. at night than during the day in the Middle Atlantic Bight. In winter, they found 8–17 mm larvae to be more abundant in deep tows at night and in surface tows during the day. They also suggested that availability of larvae to the plankton net decreased for sizes greater than 25 mm. They concluded that larvae and juveniles disappear from the water column during May. Sampling at the end of March in Long Island Sound indicated that larvae were present throughout the water column during both day and night although more were collected at the surface in night tows (Wheatland, 1956).

During sand lance ontogeny, there is a transition to the bottom-burrowing life style of adults (Scott, 1973), which is described as alternating between periods of inactivity within the substrate and active feeding on zooplankton within the water column (Reay, 1970). In laboratory studies, light intensity controlled swimming activity of adult sand lance (Winslade, 1974). In the presence of food, there was a diurnal rhythm that appeared to be endogenously controlled, but, in the absence of food, swimming activity decreased. However, comparable observations have not been reported for larvae and juveniles.

Sand lance are very important in the trophodynamics of marine ecosystems. They prey on secondary consumers (Covil, 1959; Ryland, 1964; Reay, 1970; Scott, 1973; Meyer *et al.*, 1979; Sherman *et al.*, 1981b) and are preyed upon by many higher trophic level species (Scott, 1968, 1973; Bowman and Langton, 1978; Winters, 1983; Bowman, 1984; Bowman *et al.*, 1984). Biomass estimates for all life stages are required for use in ecosystem modelling. For larval and juvenile sand lance, better understanding of vertical distribution and movement, of effect of net avoidance on catches, and of changes in availability to the sampling gear is necessary before accurate biomass estimates from survey

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data are possible. To this end, data are presented on sand lance from four MARMAP (Marine Resources Monitoring, Assessment and Prediction) ichthyoplankton surveys (Sherman, 1980) on Nantucket Shoals and Georges Bank at different times during winter and spring in 1978-83.

Methods

Sand lance data for this paper were collected during four ichthyoplankton cruises of the research vessel *Albatross IV* off the northeastern United States in 1978, 1981 and 1983 (Fig. 1, Table 1). The MOCNESS (Multiple Opening/ Closing Net and Environmental Sensing System) (Wiebe *et al.*, 1976, 1982, 1985) was used to sample discrete depth intervals and for serial double-oblique tows from surface to near-bottom. The 1-m^2 MOCNESS with nine 0.333 mm mesh nets was used during three of the cruises to collect larvae, and the 1-m^2 MOCNESS with five 3.0 mm mesh nets was used during the May cruise to collect large postlarvae and juveniles. The gear was towed at about 2 knots (3.7 km/hr). Although sampling strategy varied somewhat from one cruise to the next, the 1-m^2 MOCNESS generally sampled the water column in 10 or 20 m strata from the surface to about 5–10 m off the bottom, integrating each stratum with a single net. For one tow in late February 1978, the 1-m^2 MOCNESS, consisting of nine consecutive nets, was towed in a double-oblique or towyo (symmetrical double-oblique) profile through the water column from surface to bottom and back to the surface (see Wiebe *et al.*, 1985). Each net filtered approximately 500 m^3 of water. The 10-m^2 MOCNESS was used in a similar serial double-oblique manner for nine tows in May 1983 to investigate spatial variability. In this case, each of the five nets was towed for about 30 min and filtered 10,000–15,000 m^3 of water. The 10-m^2 MOCNESS was not used to sample discrete strata.

During the cruise in late February 1978, the paired bongo sampler (Posgay and Marak, 1980) was used to sample a grid of 34 stations which were spaced 5 miles (3.7 km) apart on five west-to-east transects in the boxed area (Fig. 1) before deploying the 1-m^2 MOCNESS. The stations were sampled in a serpentine pattern beginning in the southwest corner and ending in the northeast corner of the grid. At each station, a double-oblique tow was made with the 61-cm bongo (0.333 and 0.505 mm mesh nets) from the surface to 100 m or to within 5 m of the bottom in shallower areas. Only the 0.333 mm mesh samples were used in this

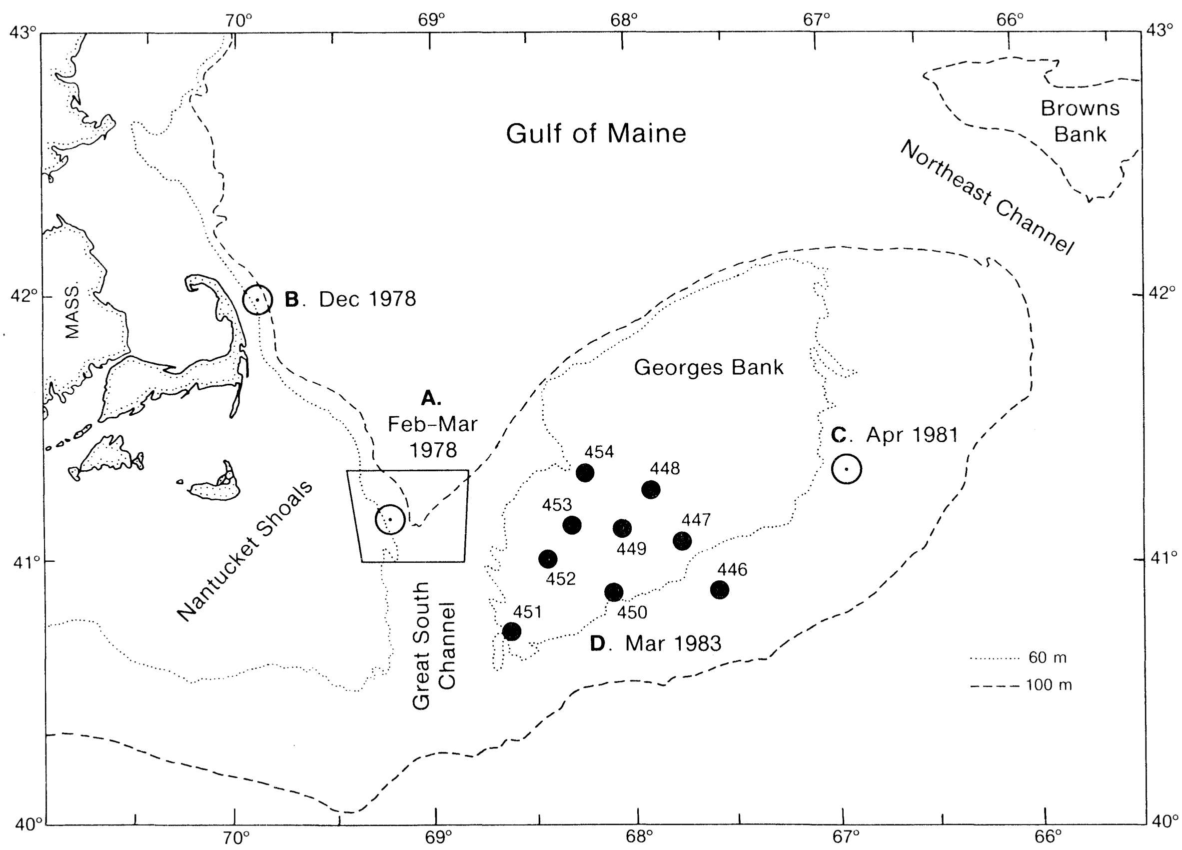

Fig. 1. The Georges Bank-Nantucket Shoals region showing locations of study areas during four cruises of *Albatross IV* in 1978-83. (Open circles indicate areas where 1-m^2 MOCNESS used, numbered dots indicate 10-m^2 MOCNESS stations, and the quadrangle represents the area covered by the grid of 34 bongo stations.

study. The bongo was deployed at 50 m/min and retrieved at 10 m/min, with the ship moving at 3.5 knots (6.5 km/hr).

Plankton samples were preserved in 5% formaldehyde-seawater solution within 20 min of retrieving the gear. Temperature and salinity data were obtained from the MOCNESS, XBT drops and/or CTD casts.

In the Northwest Atlantic, two species of sand lance (*A. americanus* and *A. dubius*) are recognized with overlapping distributions (Richards, 1982). Sand lance taxonomy is uncertain, and there is difficulty in separating these species, particularly as postlarvae. Therefore, according to the recommendation of Fahay (1983), larvae in samples from the Georges Bank-Nantucket Shoals region are designated as *Ammodytes* sp.

In the laboratory, sand lance were separated from other components of the ichthyoplankton samples, measured as standard length (SL) to the nearest 0.1 mm, and enumerated by 1 mm length groups. Catches were standardized to number of individuals per 100 m^3 of water filtered by the 1-m^2 MOCNESS and 61-cm bongo samplers and to number per 10,000 m^3 of water filtered by the 10-m^2 MOCNESS. Tows were classified as day or night and data were grouped by stratum depth for calculation of stratum mean number of fish ($\bar{X}$), standard deviation (SD), variance (VAR) and coefficient of variation (CV). These statistics were also calculated for the log-transformed data, from which 95% confidence limits (CL) of the geometric means were estimated. For the transects of serial tows (towyos), an autocorrelation function (COV/VAR) was computed (Box and Jenkins, 1976). Density-depth profiles of sand lance in day and night tows were plotted as arithmetic means, showing the integrated water column abundance as number per m^2 of surface area. Corresponding length frequencies are shown by depth stratum as mean ±1 SD, with horizontal line representing the range of observations. Differences between day and night length frequencies were tested by the Kolmogorov-Smirnov (KS) test which is appropriate for skewed distributions and sensitive to differences in location and shape (Tate and Clelland, 1957). Where appropriate, night-to-day abundance ratios were estimated for the length frequencies and a power curve was fitted to the ratios.

Tidal current amplitude and direction were calculated for each tow by the method of Moody *et al.* (1984) on the basis of the three principal semidiurnal tidal constituents: M_2 (principal lunar), N_2 (larger lunar elliptic), and S_2 (principal solar). Plots of tidal ellipses were generated and the north and east components were computed. Maximum larval abundance, presence or absence of larvae, and weighted mean depth of larvae were plotted on the tidal ellipse for each tow in the time series. Lag times of 1, 2 and 3 hr were also used in the analysis.

Results

The average temperatures and salinities in Table 1 are considered to be representative of the water column during the study periods and typical for winter and spring seasons on Georges Bank and Nantucket Shoals (Hopkins and Garfield, 1981; Limeburner and Beardsley, 1982). Strong rotary semidiurnal tides keep the water column well-mixed all year over the shallow (<60 m) parts of the bank, and strong northwest winds prevent stratification around the perimeter (60–100 m) of the bank in winter. Significant numbers of sand lance (*Ammodytes* sp.) ranging from newly-hatched larvae in December to juveniles well beyond metamorphosis in May, were collected during four cruises in different parts of the region (Table 1). No pattern was detected between sand lance abundance and tidal current speed or direction at any of the stations.

December cruise

Three daytime tows, with the 1-m^2 MOCNESS to sample discrete depth strata, were made off Cape Cod in mid-December 1978 (Table 1). The overall mean length (5.3 mm SL) and the narrow length range (3.6–7.2 mm) of sand lance larvae (Fig. 2) indicated recent hatching. Larvae were present throughout the water column to a depth of 60 m, with 77% between 10 and 40 m. Mean density of larvae was highest (175/100

TABLE 1. *Albatross IV* cruise information on collections of larval and juvenile sand lance in four areas (see Fig. 1) of the Nantucket Shoals-Georges Bank region, 1978-83.

Area	Dates of study	Location (see Fig. 1)	Bottom depths (m)	Sampling gear	No. of tows	No. of sand lance	Fish length (mm SL) Mean	Range	Mean temp. (°C)	Mean sal. (‰)
A	25-26 Feb 1978	(Quadrangle)	37–157	61-cm Bongo	34	272	10.3	3–31	3.7	32.70
	28 Feb-1 Mar 1978	41°09'N, 69°12'W	55–79	1-m^2 MOCNESS	14	2,293	10.5	3–28	3.5	32.59
B	14-15 Dec 1978	42°00'N, 69°55'W	70–80	1-m^2 MOCNESS	3	7,792	5.3	4–7	8.2	32.55
C	24-29 Apr 1981	41°20'N, 66°53'W	63–72	1-m^2 MOCNESS	19	2,543	27.3	3–57	5.8	32.90
D	17-19 May 1983	(Numbered sites)	34–69	10-m^2 MOCNESS	9	2,744	57.1	32–81	9.3	33.05

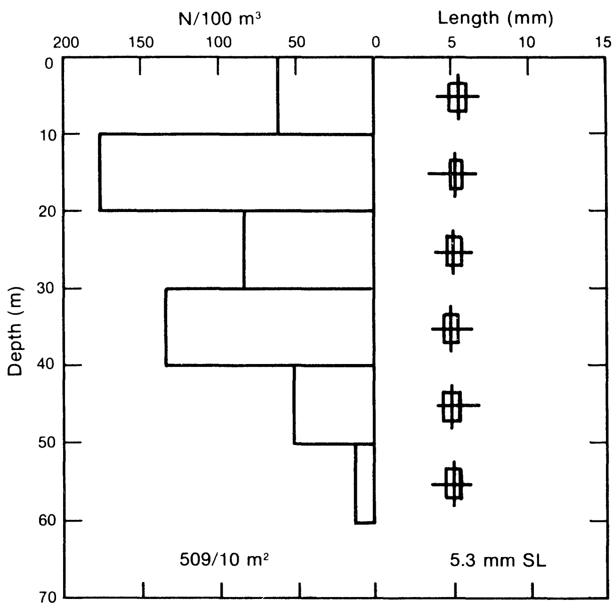

Fig. 2. Mean density and length of sand lance by depth stratum from 3 days tows with 1-m² MOCNESS on 14-15 December 1978. (Under length, vertical line on bar represents mean length, horizontal line shows the length range, and bar represents ± 1 SD. Abundance in water column and overall mean length are indicated in bottom of panel.)

m³) in the 10-20 m stratum. Densities in the upper 20 m of the water column varied among samples by more than three orders of magnitude. For discrete strata deeper than 20 m, the 95% confidence limits (CL) of the geometric mean density were 52-237%. There was no change in length composition of larvae with depth.

February-March cruise

Sampling in the northern part of the Great South Channel in late February-early March 1978 (Table 1) included (a) a day-night series of six tows with the 1-m² MOCNESS for vertical distribution of larvae, (b) a daytime serial transect of eight tows with the 1-m² MOCNESS for horizontal spatial variability, and (c) a 24-hr series of bongo tows on a grid of 34 stations in the quadrangle (Fig. 1).

For the series of vertical tows, bottom depth varied from 55 to 79 m and three strata were sampled (0-20, 20-40 and 40-70 m). At night, larvae were evenly distributed throughout the water column, with the highest mean density of larvae (10/100 m³) in the 20-40 m stratum (Fig. 3). During the day, mean density was highest (7/100 m³) in the surface (0-20 m) stratum. The 95% CL of the geometric mean density per stratum were consistently within the range of half to double the mean (CL = 46-220%) for day and night tows. Confidence limits of the geometric mean density for the surface stratum (0-20 m) were slightly wider than for the deeper strata. Larval abundance throughout the water column was higher at night (60/10 m²) than during the day (24/10 m²), implying net avoidance by larvae during daylight. Mean lengths did not vary significantly with depth for either day or night tows, and the overall mean lengths were similar (10.5 and 10.7 mm respectively). More larvae were caught at night over the entire length range (Fig. 4). Although the length compositions of the day and night samples of larvae did not differ significantly (P>0.05, KS-test), somewhat larger individuals were caught in the night tows. There was a tendency for the larger larvae to be caught in the surface (0-20 m) layer during the day and in the near-bottom (40-70 m) layer at night (Fig. 3). This may have been due to part of the larval population being in or near the bottom during the day but rising off the bottom and being more available to the sampling gear at night.

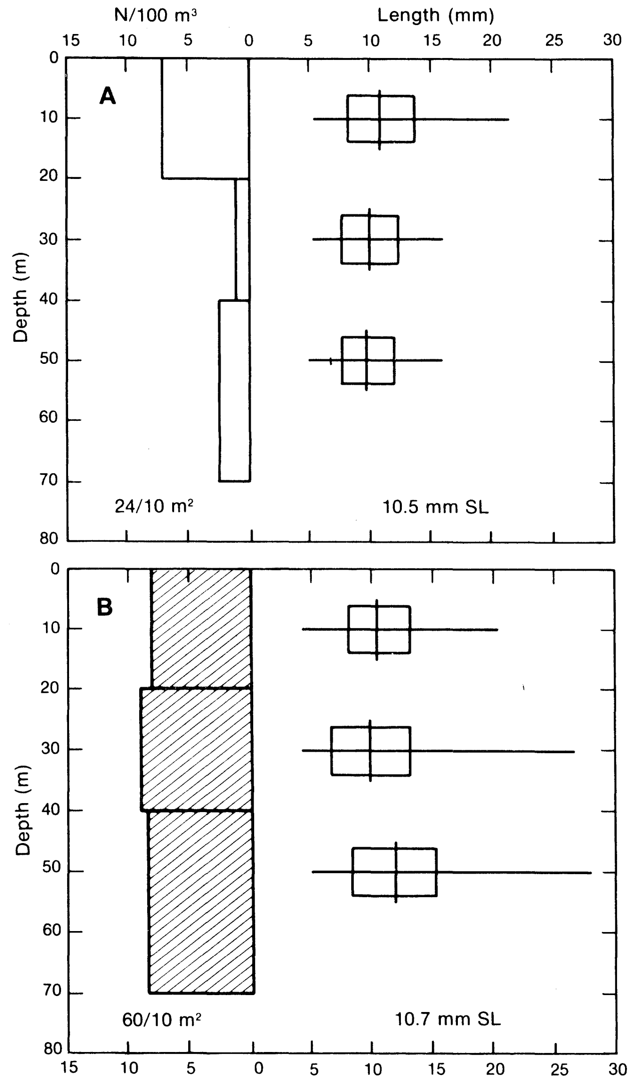

Fig. 3. Mean density and length of sand lance by depth stratum from 6 day tows (**A**) and 8 night tows (**B**) with the 1-m² MOCNESS on 28 February-1 March 1978. (Under length, vertical line on bar represents mean length, horizontal line shows the length range, and bar represents ± 1 SD. Abundance in water column and overall mean length are indicated in bottom of each panel.)

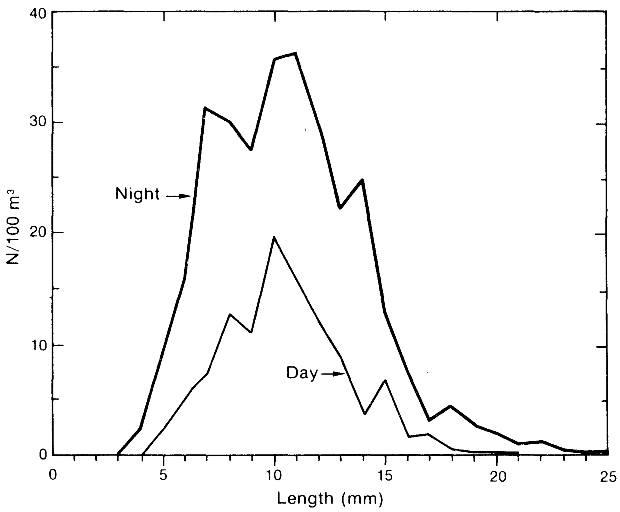

Fig. 4. Length distributions of sand lance in day and night catches with 1-m² MOCNESS on 28 February–1 March 1978.

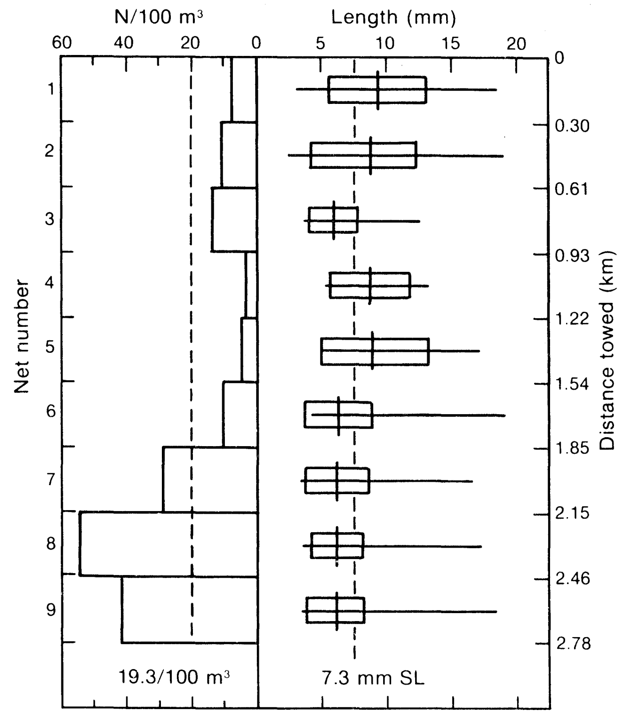

Fig. 5. Mean density and length of sand lance from nine consecutive double-oblique surface-to-near-bottom tows with 1-m² MOCNESS on 28 February 1978. (Dashed vertical lines represent mean values. Under length, vertical line on bar represents mean length, horizontal line shows length range, and bar represents ± 1 SD.)

Distance through the water for the nine consecutive double-oblique 1-m^2 MOCNESS tows averaged about 0.30 km. Mean density of larvae was 19.3/100 m^3 (Fig. 5) with a coefficient of variation of 96%. the geometric mean density was 12.8 larvae/100 m^3, with 95% CL being 47–215% of the mean. The autocorrelation function (0.52) was significantly different from zero ($P<0.05$), indicating that adjacent catches were positively correlated. The mean length of larvae was 7.3 mm (Fig. 5). The higher-than-average densities at the end of the series of nets tended to be associated with smaller-than-average larvae, but the difference was not significant ($P>0.05$).

The grid of 34 bongo stations, which were occupied in late February 1978, encompassed an area of about 2,000 km^2 (37 × 55 km) around the MOCNESS station (Fig. 1). Of these 34 stations, 16 were daytime and 18 were nighttime tows. This grid extended across the northern part of Great South Channel and included deep (>100 m) and shallow stations in an area of complex hydrography. Larval density tended to be low at the deepwater stations and much higher in the western shallow part of the grid (Table 2). The east-west stations (i.e. 1 to 7 along transects) had an average positive autocorrelation at 1 hr lag (0.15), whereas the north-south stations (i.e V to I across transects) had a slight negative autocorrelation at 1 hr lag (−0.01). The small positive trend along transects may be due to the stations being sampled closer in time (approximately 40 min between stations). If the transects are treated as a single line in the order of sampling so that more observations are included, a higher positive autocorrelation results (0.46, $P<0.05$). Additional lags were calculated but only the 1 hr lag was significant, indicating that adjacent stations tended to be positively correlated.

The length distributions of the day and night catches of larvae (Fig. 6) differed significantly ($P<0.05$, KS-test). Mean lengths were 8.3 mm (SD 3.9) and 12.3 mm (SD 4.6) for day and night catches respectively. Two modes were evident in the length frequencies, one around 6 mm representing recently-hatched larvae and another around 12 mm. Small larvae (<10 mm) were much more abundant in the day catches than in the night catches, but the day catch rate was heavily weighted by large catches at a few stations. The night-to-day catch ratios (Fig. 6) indicated light-aided avoidance of the bongo net by larvae larger than about 10 mm. A power function provided a good fit to these ratios.

April cruise

In late April 1981, 19 tows (10 day and 9 night) were made on the southeastern part of Georges Bank (Fig. 1) in 60–70 m with the 1-m^2 MOCNESS to sample discrete depth strata (10 m intervals). Night tows yielded 94% of the larvae and juveniles in contrast to 71% at night during the late February-early March cruise. Total abundance in the water column at night (106/10 m^2) was 15 times greater than during the day (7/10 m^2) (Fig. 7). Sand lance were distributed throughout the water column at night, their mean density increasing with depth from 10/100 m^3 near the surface (0–10 m) to

TABLE 2. Sand lance densities (No./100 m³) by station and transect and corresponding statistical parameters for a grid of 34 bongo stations in the Great South Channel area in late February 1978.

Transects (North to South)	Stations (East to West)							Statistical parameters					
	1	2	3	4	5	6	7	$\overline{X}_A$	SD	CV	$\overline{X}_G$	95% CL	COV/VAR
V	21.9	8.1	1.0	0.3	0.5	8.6	1.7	6.0	7.9	130.6	2.3	22-445	0.23
IV	37.8	8.7	1.8	0.3	0.0	2.7	12.1	9.1	13.5	148.6	1.8	8-1,285	0.24
III	7.5	11.1	14.7	31.0	0.7	7.3	11.5	12.0	9.5	79.2	8.1	34-299	-0.22
II	21.7	15.2	16.8	26.8	0.9	2.8	3.5	12.4	10.0	81.4	7.5	30-329	0.21
I	—	32.6	47.9	20.6	12.4	15.9	5.4	22.5	15.4	68.6	19.4	51-196	0.31
$\overline{X}_A$	22.2	15.1	16.4	15.8	2.9	7.5	6.8	$\overline{X}_A$ = arithmetic mean					
SD	12.4	10.2	19.0	14.6	5.3	5.4	4.7	$\overline{X}_G$ = geometric mean					
CV	55.7	67.1	115.6	92.6	183.3	72.5	69.0	SD = standard deviation					
$\overline{X}_G$	19.1	13.1	7.4	4.4	0.5	6.0	5.4	CV = coefficient of variation					
95% CL	34-293%	50-201%	13-756%	5-2,077%	4-2,380%	39-258%	36-279%	CL = confidence limits					
								COV = covariance					
COV/VAR	-0.36	-0.24	0.30	0.28	-0.03	-0.46	-0.19	VAR = variance					

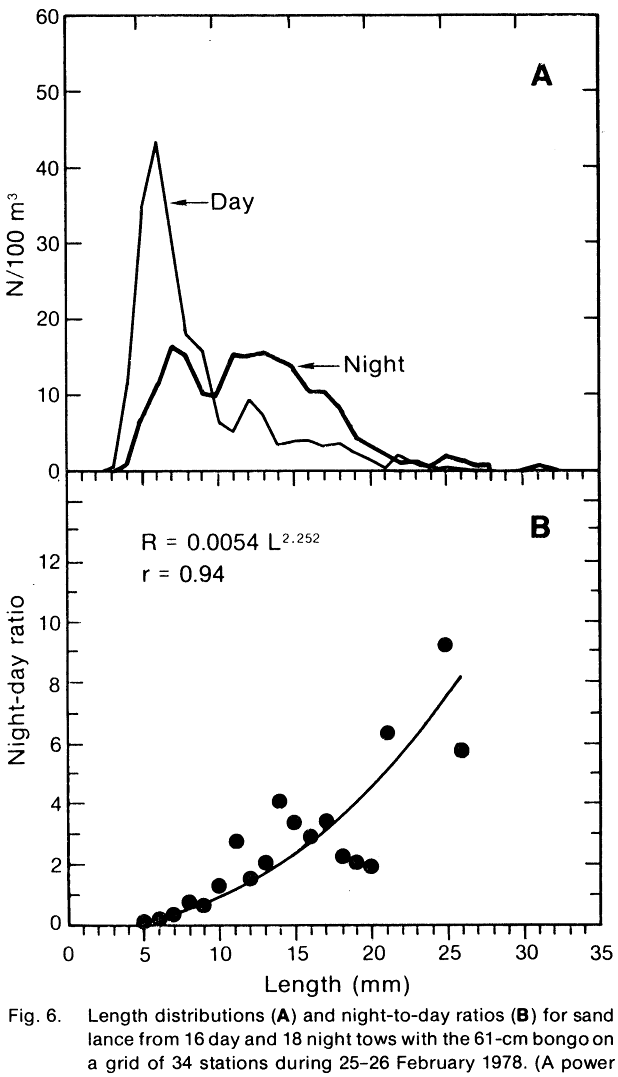

Fig. 6. Length distributions (**A**) and night-to-day ratios (**B**) for sand lance from 16 day and 18 night tows with the 61-cm bongo on a grid of 34 stations during 25-26 February 1978. (A power curve is fitted to the ratios.)

28/100 m³ near the bottom (50–60 m). During the day, density was less than 3/100 m³ in all strata, with most fish being taken in 10–30 m. The average 95% CL of the geometric mean density per stratum were similar for day (25–681%) and night (20–774%) samples. Samples from the near-surface strata (0–10 and 10–20 m) had higher average 95% CL (7–1400%) than deeper strata for both day and night tows. On the average, larger fish were collected in night than in day tows (28.4 and 24.6 mm SL respectively), although the length ranges were similar (Fig. 7). Somewhat smaller larvae were taken at night in surface (0–10 m) tows and, conversely, somewhat larger larvae were taken during the day in deep (40–50 m) tows.

The length frequencies of sand lance in the day and night catches (Fig. 8A) were significantly different ($P<0.01$, KS-test). The length distribution of night samples had modes at about 15 and 31 mm SL. The night-to-day catch ratios (Fig. 8B) indicate light-aided avoidance of the 1-m²MOCNESS by larvae and particularly by juveniles (>25 cm). A power function provided a reasonable fit to these ratios. These data indicate that juveniles were probably near bottom below the sampling depth of the net during the day and moved upward in the water column at night. However, the net avoidance capacity of juvenile sand lance precludes firm conclusions about their diel distribution.

May cruise

Postmetamorphic juveniles (50–81 mm SL) were collected at 8 of 9 stations on western Georges Bank in May 1983 (Fig. 1), the exception being station 446 where the bottom depth exceeded 60 m. Distance through the water for the five consecutive double-oblique tows with the 10-m² MOCNESS at each of the

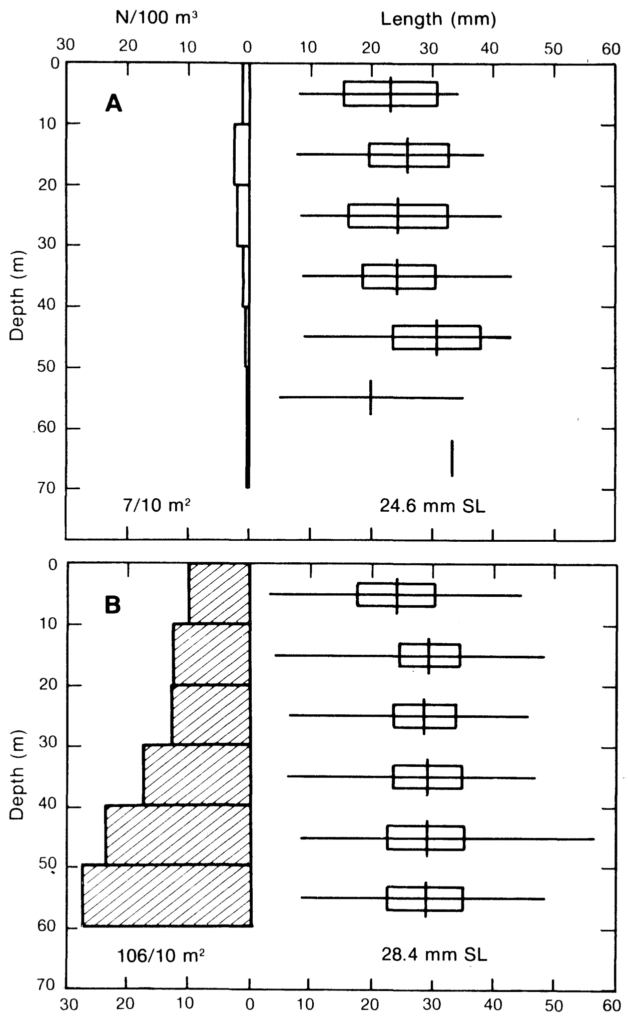

Fig. 7. Mean density and length of sand lance in 10 day tows (**A**) and 9 night tows (**B**) with 1-m^2 MOCNESS during 24–29 April 1981. (Under length, vertical line on bar represents mean length, horizontal line shows length range, and bar represents ±1 SD. Abundance in water column and overall mean length are indicated in bottom of each panel.)

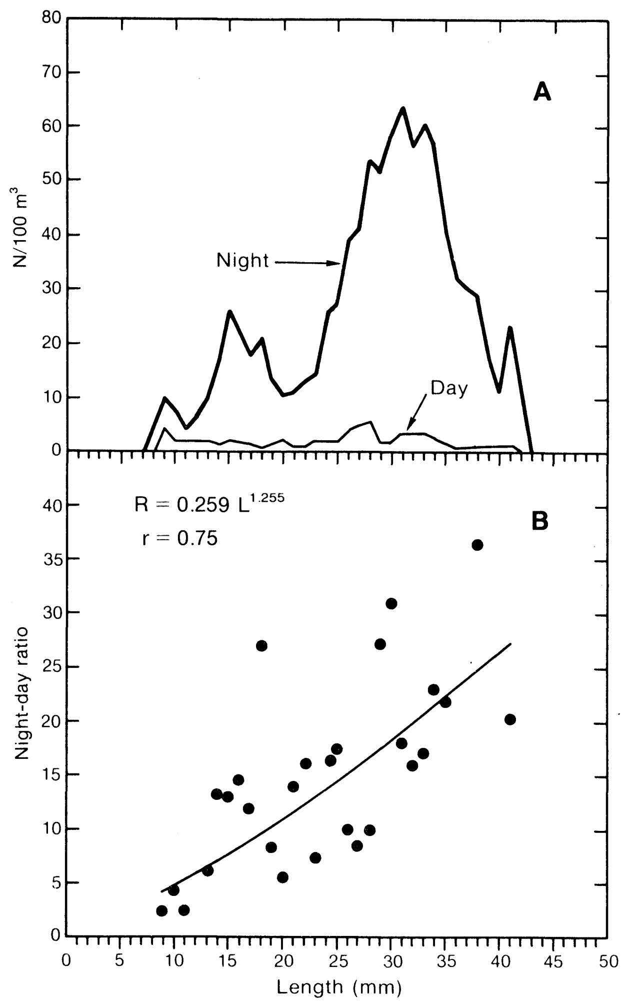

Fig. 8. Length distribution (**A**) and night-to-day ratios (**B**) for sand lance in 10 day and 9 night tows with 1-m^2 MOCNESS during 24–29 April 1981. (A power curve is fitted to the ratios.)

nine stations averaged 1.4 km. On the average, significantly greater numbers of juveniles were caught at night (110.1/10,000 m^3) than during the day (9.8/10,000 m^3), but the coefficients of variation were large (121 and 209% respectively) (Table 3). Average 95% CL were 46–775% of the geometric mean for night tows and 28–355% for the one day tow in which a significant number of sand lance was caught. The positive autocorrelation values (1-hr lag) for stations 447 and 451 indicate that catches in consecutive tows may be correlated, whereas the negative autocorrelation for station 450 may indicate a more contagious distribution.

The night and day length distributions (Fig. 9) were significantly different ($P<0.01$, KS-test) although the length ranges were similar. Mean lengths were 58.3 and 62.3 mm SL in the night and day samples respectively. There was no clear relationship between the night-to-day rations of catch and fish length, presumably because all sizes of juveniles were capable of avoiding the 10-m^2 MOCNESS. In fact, the data imply that the juveniles may live near the bottom or in the substrate during the day and rise into the water column at night.

Discussion

Larvae, which had recently hatched from demersal eggs, were found to be dispersed throughout the well-mixed water column in December and January. Most of the larvae were located in the mid-depth (10–40 m) with highest density usually between 10 and 20 m. In February–March, larvae with a mean length of 10 mm SL were found from surface to bottom during both day and night tows, but there was some indication that part of the population resided near the bottom during the

TABLE 3. Sand lance mean densities (No./10,000 m^3) and statistical parameters for five consecutive double-oblique 10-m^2 MOCNESS tows (surface to near-bottom) at nine stations on western Georges Bank, May 1983. (See Table 2 for definitions of abbreviations.)

Time	Station	$\overline{X}_A$	SD	CV	$\overline{X}_G$	95% CL	COV/VAR
Night	446	0.0	—	—	—	—	—
	447	48.5	58.7	121.2	11.5	5-2,016	0.38
	450	19.5	3.7	18.7	19.2	79-127	-0.28
	451	262.4	124.8	47.5	238.8	55-183	0.19
	Combined	110.1	132.7	120.5	89.8	46-775	0.10
Day	448	2.0	2.2	112.0	—	—	—
	449	0.2	0.4	201.3	—	—	—
	452	46.4	46.0	99.1	30.6	28-355	0.09
	453	0.2	0.4	201.3	—	—	—
	454	0.2	0.4	201.3	—	—	—
	Combined	9.8	20.5	208.9	(30.6)	(28-355)	(0.09)

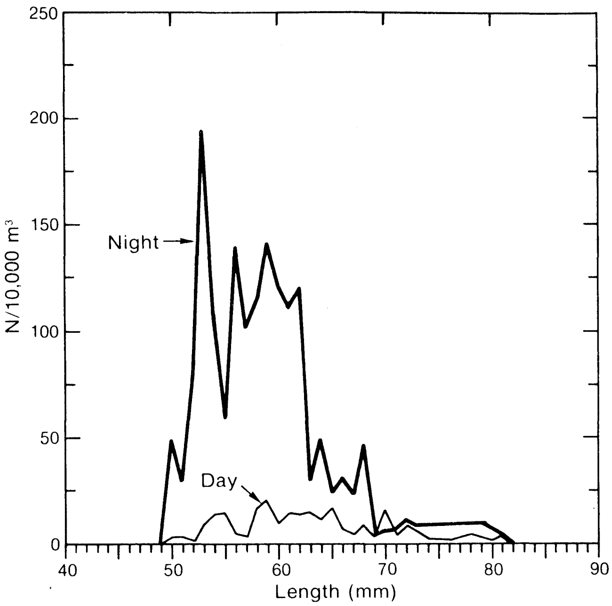

Fig. 9. Length distributions of sand lance in 5 day and 4 night tows with the 10-m^2 MOCNESS during 17-19 May 1983.

day and migrated upward in the water column at night. The swimming capability of 10 mm and larger sand lance is such that avoidance of the nets was a major sampling problem. By April, when they were 20-30 mm SL, they were caught in significant numbers only in night tows. The few individuals in the day catches were still distributed in the mid-depth range, but their abundance increased with depth at night, especially the larger fish. Avoidance of 1-m^2 MOCNESS and the 61-cm bongo nets by 10-30 mm SL sand lance was evident, but, because of their daytime bottom-seeking behavior, many were probably distributed below the maximum sampling depth of the nets during the day. In May, 50-81 mm SL juveniles were collected almost entirely at night in the 10-m^2 MOCNESS tows. Despite the problem of net avoidance, it was evident that juveniles were distributed near or on the bottom during the day.

Larger catches of fish larvae in night than in daytime tows have been noted for many species (Bridger, 1956; Lenarz, 1973), and this phenomenon has been attributed to net avoidance by the larvae during daylight. In our study, the night-to-day catch ratios increased with fish size. Apparently, as the larvae develop, improved sensory and swimming abilities enhance detection and avoidance of the gear. Wheatland (1956), from sampling *A. americanus* in Long Island Sound, concluded that net avoidance rather than diurnal migration accounted for most of the decrease in catches of larvae (>9 mm) from night to day tows. Larval fish are capable of "burst" speeds of about 10 body lengths per second for a few seconds (Blaxter, 1969). Therefore, 10-90 mm sand lance would likely be capable of speeds of 10-90 cm/sec. Meyer *et al*. (1979), during diving operations on Stellwagon Bank in Massachusetts Bay in daylight, observed 12-17 cm sand lance making avoidance maneuvers at speeds of 70-120 cm/sec and even greater. The success or failure of an avoidance reaction depends on the perception distance. This distance is unknown for sand lance larvae, but, with their "burst" speed capability, only a few seconds warning would enable them to avoid a towed net. Comparison of data from towing different nets at the same station is not available, but the night-to-day catch (10-25 mm fish) ratios for the 1-m^2 MOCNESS towed at 3.7 km/hr (Fig. 8) were about double those for the 61-cm bongo towed at 6.5 km/hr (fig. 6), indicating that these fish were better able to avoid the slower net. Small differences in perception distance or escape speed between day and night can account for high night/day catch ratios. The similarity of length frequencies of the day and night samples in this study implies that avoidance swimming speeds during day and night were also similar. Perception distance may be the main factor responsible for the smaller day catches of sand lance larvae. Further gear comparisons are needed to more fully evaluate avoidance of towed nets by sand lance larvae. It is clear, however, that net avoidance, as well as diel changes in availability to the nets, should be considered in any attempt to estimate larval abundance.

During each of the four cruises, the water column was isothermal and isohaline. Strong rotary semidiurnal tidal currents (up to 3.5 km/hr) were present in each sampling area. However, contrary to Scott's (1973) observation of larger catches of sand lance during times of the weakest currents and Madsen's (1963) observation of best catches during periods of maximum current, no correlation between tidal phase or amplitude and catch of *Ammodytes* sp. was found with lag periods of 0, 1, 2 or 3 hr.

Sampling variability at sea is usually large, whatever gear is used or organism studied. Even for log-transformed data, coefficients of variation from 20 to 100% are common. With such variability, averaging of data from multiple observations on suitable time and space scales is necessary to detect trends. The autocorrelation technique that was used in this study was instructive, even though statistical comparisons were weakened by the few observations. The positive correlation between adjacent samples at various distances from 0.3 to 9.3 km appears to be consistent with the hydrographic regime on the shallow areas of Nantucket Shoals and Georges Bank, where the strong (>3.5 km/hr) rotary tidal currents (10–20 km in diameter) keep the water column well-mixed. Thus, after demersal hatching, sand lance larvae are quickly dispersed throughout the water column and over much of the continental shelf. Norcross *et al.* (1961) found that length frequencies of larvae collected in January, when combined by 10-mile (18.5 km) intervals, were statistically different. That observation and the results from the present study indicate that the minimum spatial scale for surveys of the sand lance population in the Nantucket Shoals-Georges Bank region should be in the range of 5–10 nautical miles (9.3–18.5 km) between stations.

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References

BIGELOW, H. B., and W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *Fish. Bull. U.S.*, **53**: 577 p.

BLAXTER, J. H. S. 1969. Development: eggs and larvae. *In*: Fish physiology, Vol. 3 (p. 177–252), W. S. Hoar and D. J. Randall (ed.), Academic Press, New York, 485 p.

BRIDGER, J. P. 1956. On day and night variation in catches of fish larvae. *ICES J. Cons.*, **22**: 42–57.

BOWMAN, R. E. 1984. Food of silver hake, *Merluccius bilinearis*. *Fish. Bull. U.S.*, **82**: 21–35.

BOWMAN, R. E., and R. W. LANGTON. 1978. Fish predation on oil-contaminated prey from the region of the *Argo Merchant* oil spill. *In*: The wake of the *Argo Merchant* (p. 137–141), Center Ocean. Manag. Studies, Univ. Rhode Island, Kingston, R. I., 181 p.

BOWMAN, R., R. EPPI, and M. GROSSLEIN. MS 1984. Diet and consumption of spiny dogfish in the Northwest Atlantic. *ICES C. M. Doc.*, No. G:27, 16 p.

BOX, G. E. P., and G. M. JENKINS. 1976. Time series analysis forecasting and control (revised edition). Holden-Day, San Francisco, Calif., 575 p.

COVIL, R. W. 1959. Food and feeding habits of larvae and postlarvae of *Ammodytes americanus*, 1952–55. *Bull. Bingham Oceanogr. Coll.*, **17**: 125–146.

FAHAY, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic, Cape Hatteras to the southern Scotian Shelf. *J. Northw. Atl. Fish. Sci.*, **4**: 1–423.

HOPKINS, T. S., and N. GARFIELD III. 1981. Physical origins of Georges Bank water. *J. Mar. Res.*, **39**: 46–500.

LENARZ, W. H. 1973. Dependence of catch rates on size of fish larvae. *ICES Rapp. Proc.-Verb.*, **164**: 270–275.

LIMEBURNER, R., and R. C. BEARDSLEY. 1982. The seasonal hydrography and circulation over Nantucket Shoals. *J. Mar. Res.*, **40**(suppl.): 371–406.

MADSEN, K. P. 1963. Tides and the sand eel fishery. *Skr. Danm. Fisk. Havunders.*, **23**: 45–48.

MEYER, T. L., R. A. COOPER, and R. W. LANGTON. 1979. Relative abundance, behaviour, and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. *Fish. Bull. U.S.*, **77**: 243–253.

MOODY, J. A., B. BUTMAN, R. BEARDSLEY, W. S. BROWN, P. DAIFUKU, J. D. IRISH, D. A. MAYER, H. O. MOFJELD, B. PETRIE, S. RAMP, P. SMITH, and W. R. WRIGHT. 1984. Atlas of tidal elevation and current observations on the northeast American continental shelf and slope. *Bull. U.S. Geol. Surv.*, **1611**: 122 p.

NORCROSS, J. J., W. H. MASSMAN, and E. B. JOSEPH. 1961. Investigations of inner continental shelf waters off lower Chesapeake Bay. Part II. Sand lance larvae, *Ammodytes americanus*. *Chesapeake Sci.*, **2**: 49–59.

POSGAY, J. A., and R. R. MARAK. 1980. The MARMAP bongo zooplankton sampler. *J. Northw. Atl. Fish. Sci.*, **1**: 91–99.

REAY, R. J. 1970. Synopsis of the biological data on North Atlantic sand eels of the genus *Ammodytes* (*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*.) *FAO Fish. Synop.*, **82**: 42 p.

RICHARDS, S. W. 1982. Aspects of the biology of *Ammodytes americanus* from the St. Lawrence River to Chesapeake Bay, 1972–75, including a comparison of the Long Island Sound postlarvae with *Ammodytes dubius*. *J. Northw. Atl. Fish. Sci.*, **3**: 93–104.

RICHARDS, S. W., and A. W. KENDALL Jr. 1973. Distribution of sand lance, *Ammodytes* sp., larvae on the continental shelf from Cape Cod to Cape Hatteras from *R/V Dolphin* surveys in 1966. *Fish. Bull. US.*, **71**: 371–386.

RYLAND, J. S. 1964. The feeding of plaice and sand eel larvae in the southern North Sea. *J. Mar. Biol. Assoc. U.K.*, **44**: 343–364.

SCOTT, J. S. 1968. Morphometrics, distribution, growth and maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia banks. *J. Fish. Res. Board Can.*, **25**: 1775–1785.

1973. Food and inferred feeding behaviour of northern sand lance (*Ammodytes dubius*). *J. Fish. Res. Board Can.*, **30**: 451-454.

SHERMAN, K. 1980. MARMAP, a fisheries ecosystem study in the Northwest Atlantic: fluctuations in ichthyoplankton-zooplankton components and their potential impact on the system. *In*: Advanced concepts in ocean measurements for marine biology (p. 9-37), F. P. Diemer, F. J. Vernberg and D. Z. Mirkes (ed.), Univ. S. Carolina Press, Columbia, S. C., 572 p.

SHERMAN, K., C. JONES, L. SULLIVAN, W. SMITH, P. BERRIEN, and L. EJSYMONT. 1981a. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature*, **291**: 486-489.

SHERMAN, K., R. MAURER, R. BRYON, and J. GREEN. 1981b. Relationship between larval fish communities and zooplankton prey species in an offshore spawning ground. *ICES Rapp. Proc.-Verb.*, **178**: 289-294.

TATE, M. W., and R. C. CLELLAND. 1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Danville, Ill., 171 p.

WHEATLAND, S. B. 1956. Oceanography of Long Island Sound, 1952-54. VII. Pelagic fish eggs and larvae. *Bull. Bingham Oceanogr. Coll.*, **15**: 234-314.

WIEBE, P. H., S. H. BOYD, B. M. DAVIS, and J. L. COX. 1982. Avoidance of towed nets by the euphausiid *Nematoscelis megalops*. *Fish. Bull. U. S.*, **80**: 75-91.

WIEBE, P. H., K. H. BURT, S. H. BOYD, and A. W. MORTON. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J. Mar. Res.* **34**: 313-326.

WIEBE, P. H., A. W. MORTON, A. M. BRADLEY, R. H. BACKUS, J. E. CRADDOCK, V. BARBER, T. J. COWLES, and G. R. FLIERI. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and microplankton. *Mar. Biol.*, **87**: 313-323.

WINSLADE, P. 1974. Behavioral studies on the lesser sand eel, *Ammodytes marinus* (Raitt). I. The effects of food availability on activity and the role of olfaction in food detection. II. The effect of light intensity on activity. III. The effect of temperature on activity and the environmental control of the annual cycle of activity. *J. Fish. Biol.* **6**: 565-599.

WINTERS, G. H. 1983. Analysis of the biological and demographic parameters of northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. *Can. J. Fish. Aquat. Sci.*, **40**: 409-419.

1973. Food and inferred feeding behaviour of northern sand lance (*Ammodytes dubius*). *J. Fish. Res. Board Can.*, **30**: 451-454.

SHERMAN, K. 1980. MARMAP, a fisheries ecosystem study in the Northwest Atlantic: fluctuations in ichthyoplankton-zooplankton components and their potential impact on the system. *In*: Advanced concepts in ocean measurements for marine biology (p. 9-37), F. P. Diemer, F. J. Vernberg and D. Z. Mirkes (ed.), Univ. S. Carolina Press, Columbia, S. C., 572 p.

SHERMAN, K., C. JONES, L. SULLIVAN, W. SMITH, P. BERRIEN, and L. EJSYMONT. 1981a. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature*, **291**: 486-489.

SHERMAN, K., R. MAURER, R. BRYON, and J. GREEN. 1981b. Relationship between larval fish communities and zooplankton prey species in an offshore spawning ground. *ICES Rapp. Proc.-Verb.*, **178**: 289-294.

TATE, M. W., and R. C. CLELLAND. 1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Danville, Ill., 171 p.

WHEATLAND, S. B. 1956. Oceanography of Long Island Sound, 1952-54. VII. Pelagic fish eggs and larvae. *Bull. Bingham Oceanogr. Coll.*, **15**: 234-314.

WIEBE, P. H., S. H. BOYD, B. M. DAVIS, and J. L. COX. 1982. Avoidance of towed nets by the euphausiid *Nematoscelis megalops*. *Fish. Bull. U. S.*, **80**: 75-91.

WIEBE, P. H., K. H. BURT, S. H. BOYD, and A. W. MORTON. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J. Mar. Res.* **34**: 313-326.

WIEBE, P. H., A. W. MORTON, A. M. BRADLEY, R. H. BACKUS, J. E. CRADDOCK, V. BARBER, T. J. COWLES, and G. R. FLIERI. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and microplankton. *Mar. Biol.*, **87**: 313-323.

WINSLADE, P. 1974. Behavioral studies on the lesser sand eel, *Ammodytes marinus* (Raitt). I. The effects of food availability on activity and the role of olfaction in food detection. II. The effect of light intensity on activity. III. The effect of temperature on activity and the environmental control of the annual cycle of activity. *J. Fish. Biol.* **6**: 565-599.

WINTERS, G. H. 1983. Analysis of the biological and demographic parameters of northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. *Can. J. Fish. Aquat. Sci.*, **40**: 409-419.