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Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia

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ABSTRACT: The vertical migration of lobster larvae was suspected from previous neuston collections taken off southwest Nova Scotia, Canada. An electronically-controlled Tucker trawl was developed for discrete depth sampling and used to study the diel vertical distribution of lobster larvae, together with environmental variables, over Browns Bank in late August. Significant vertical migration is demonstrated for stage I lobster, which were most frequently caught between 15 and 30 m water depth during daylight but were rarely caught below 10 m at night. Stage I lobster generally stayed below light intensities of 100 to 200 μ E m^{-2} s^{-1}. Stage II and III lobster were collected throughout the upper 20 to 30 m of the ocean but were too rare to distinguish statistically between day and night depth-abundance patterns. Stages I, II and III lobster were all confined to the upper mixed layer, above the thermocline, which varied in depth with the tidal cycle. Stage IV lobster were caught almost entirely at the surface, with no significant difference between day and night abundances. These findings are novel and have important implications for the ecology and dispersal of larval *Homarus americanus* in offshore waters.

INTRODUCTION

A long-term objective of the Department of Fisheries and Oceans, Canada, is to determine whether many of the planktonic larvae produced by large offshore lobsters settle in the inshore grounds off southwest Nova Scotia and in the proximity of the Bay of Fundy (Pringle et al. 1983). Rogers et al. (1968), working off Rhode Island, found stage I lobster offshore in the Middle Atlantic Bight while fourth-stage larvae were most abundant closer to shore, which they suggested represented an onshore drift of larvae with time, consistent with the known surface circulation. Stasko (1978) proposed that larvae produced on Browns Bank would drift towards the Nova Scotian coast where they would settle and that an offshore migration of older lobster would complete this life cycle. Stasko & Gordon (1983) subsequently undertook 2 seasonal surveys between Browns Bank and southwest Nova Scotia from which they found a prevalence of stage IV lobster in the neuston. Harding et al. (1983) attempted to explain this anomalous abundance of stage IV lobster by invoking larval drift from the northern face of Georges Bank. We undertook a preliminary neuston survey for lobster larvae between southwest Nova Scotia and Georges Bank in 1983. In these tows lobster were noticeably absent from daytime surface catches in the Gulf of Maine but appeared in the neuston shortly after dusk. However, all stages of lobster larvae were present at all times of the day over Georges Bank. Before the larger issue of inshore recruitment from offshore lobsters via larval drift can be addressed, it is necessary to accurately determine the vertical distribution of larvae in the field because current speed and direction vary with depth and position.

The vertical distribution of lobster larvae in the sea has been difficult to resolve because of both their patchy distribution (Raytheon 1979) and their relative scarcity in the plankton (Fogarty & Lawton 1983). It is therefore a logistical and technical problem to adequately sample the larval lobster population in the water column. Our approach was to sample discrete depths in one location with as large a trawl as practical, day and night, for as long as possible until a temporal pattern emerged. Here, we present the results of an intensive 2 wk field sampling program designed to

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distinguish the day and night depth preference of larval lobsters over Browns Bank.

METHODS

A Tucker trawl (see Clarke 1969) was redesigned to accept the electronic package used with our half-scale version of the BIONESS (Sameoto et al. 1979). The trawl is opened and closed at depth by electronically releasing horizontal, weighted bars which slide down lateral cables (Fig. 1). The trawl tripping electronics and release mechanism are similar in principle to BIONESS. An Applied Microsystems™ expanded CTD-12 is used to record water-flow inside and outside the net, net opening and closing events, pitch and roll of the net, depth, together with conductivity and temperature 1.5 m above the center of the net mouth. Information is sent up a conductor cable at 10 s intervals and received by a Commodore 4000 PET™, with basic 4.0 for storage (CBM 4040 dual drive floppy disk) or hard copy (Tractor Printer 4022). The effective trawl mouth opening at 1.5 m s^{-1} perpendicular to the towing path is 2.5 m wide × 1 m deep. The net material is 1.6 mm Nitex mesh, 5 m long, with a pore to mouth area ratio of greater than 3.0 (Smith et al. 1968). This ratio was sufficient to avoid clogging problems, as detected by the difference in readings of inside and outside flow meters. TSK™ flow meters, modified with magnetically actuated Hall effect sensors, are mounted in a protected encasement in the trawl mouth, beyond the effects of the trawl and bridles near the CTD (Fig. 1). Net bars are suspended from a release mechanism similar to the type described for BIONESS. The levers within the release mechanism drop through a slotted shaft which is incremented by a stepping motor. Power

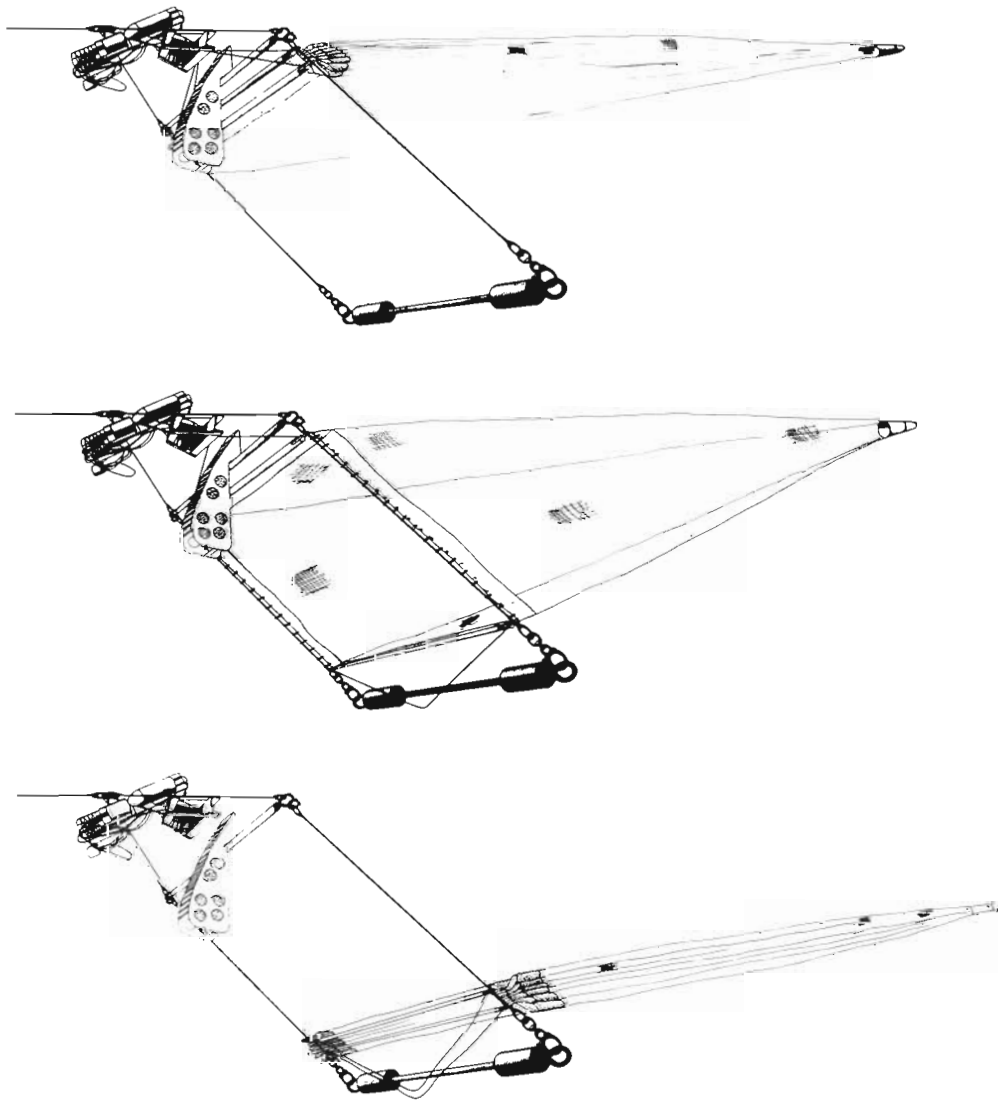

Fig. 1. Redesigned Tucker trawl for larval lobster work, showing deployment, opened, and closed positions (see text)

to drive the stepping motor is supplied by a 20 V power supply on shipboard. A 6:1 gear reduction between the stepping motor and the slotted shaft is sufficient to allow rotation of the shaft while towing.

The trawl was deployed between 16 and 30 Aug 1984, to determine the extent and timing of daily migration of lobster larvae. We trawled within 3 km of 42° 42′ N, 66° 10′ W, Browns Bank, with a bottom depth of 60 ± 2 m. Each tow was 30 min duration and tows were taken at 5 m intervals from the surface down to 30 m depth, thereafter infrequently at 10 m intervals to 50 m. Approximately 6000 m^3 of water was filtered per tow. Larval lobster abundances are reported as numbers per 5×10^3 m^3, based on flow-meter readings. Eight daylight and 7 night depth series were completed with the Tucker trawl for a total of 112 tows. Light penetration was measured in the upper 20 m at 1200 h AST with a LICOR™ model LI-185B quantum meter and L1-192 SB underwater sensor. Incident radiation was recorded on deck throughout this study with LICOR™ LI-510 integrator, set for 10 min intervals.

RESULTS

A total of 347 stage I, 43 stage II, 15 stage III and 124 stage IV lobster larvae were caught. The mean (± SE) day and night depth distributions are plotted for each larval stage, together with temperature, salinity and light intensity profiles (Fig. 2). Stage I larvae were present in 50 % of our trawls. The day and night abundances of stage I lobster clearly had divergent depth patterns (Fig. 2). More larvae resided during daylight at the 15, 20 and 30 m horizons, whereas at night stage I larvae had migrated into the surface waters with most of the larvae occurring at the surface, 5 and 10 m horizons (Fig. 2). On average, <1 % of the stage I lobster, integrated throughout the water column, occurred above 2.5 m depth during daylight, compared to ~28 % after dark (Fig. 2). Comparison of mean larval abundance and variance for each of the depth horizons by day and night showed the variance to be proportional to the mean. The large number of zeroes precluded the use of a logarithmic transform to

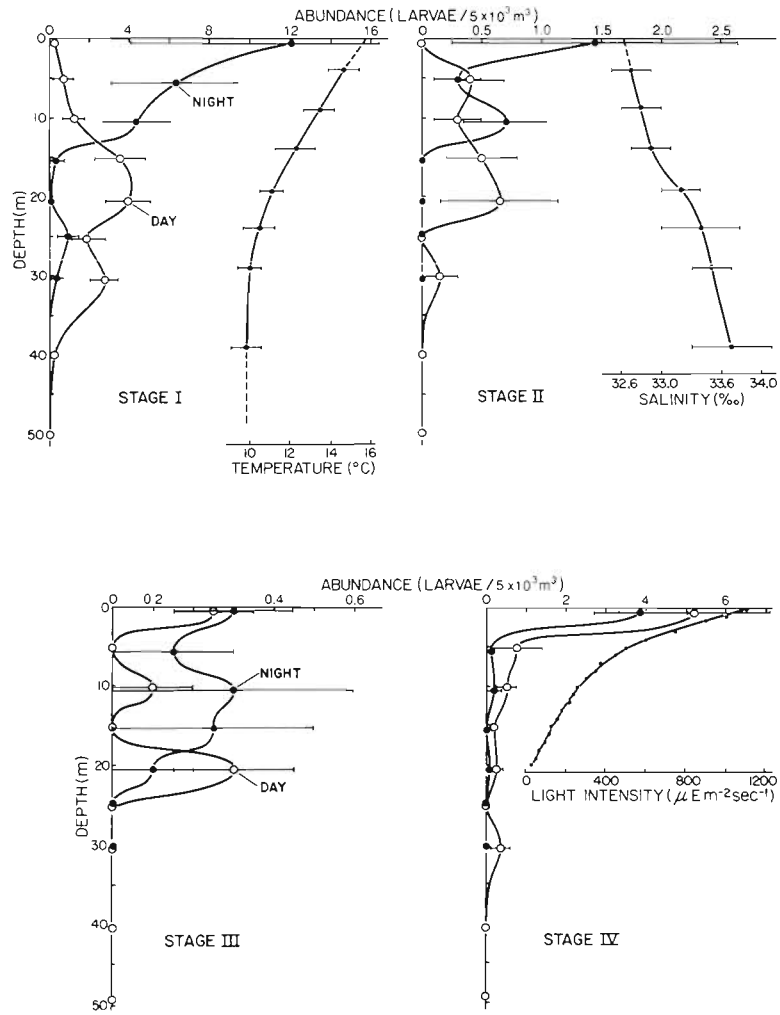

Fig. 2. Day and night-time vertical distributions of the 4 larval lobster stages ($\bar{x}$ ± SE larvae/5 × 10^3 m^3) found over Browns Bank, Aug 1984. Shown are average temperature, salinity (95 % CI) and 1200 h AST light profiles

stabilize the variances. Therefore differences between mean abundances at depth by day and night were tested using a log-linear model assuming a Poisson distribution for the abundances and the variance proportional to the mean. While standard use of the Poisson distribution assumes that the variance is equal to the mean, incorporation of the proportional relationship into the estimation and testing will give valid results (McCullagh & Nelder 1983).

Two potential outliers were identified for the stage I larvae. These were large catches made during the night, with one at the surface and the other at the 5 m horizon. These tow results were removed from the analysis. Tows from the 30 m and 40 m depth horizons were also deleted because there were only one and no positive tows, respectively, made during the night at these depths. The analysis of deviance of the log-linear model for the remaining stage I larvae data is presented in Table 1. Neither depth nor time (day/night) account for a significant proportion of the deviance. This indicates that we were sampling the entire depth range of stage I lobster and did not systematically over- or undersample the population. However, time nested within depth (designated as DEPTH.TIME in Table 1) is significant. The associated parameter estimates and their standard errors indicate that abundances at the surface, 5 m and 10 m horizons during the day are significantly less than that of the surface horizon during the night. The abundances during the day at the deeper horizons (>15 m) were not significantly different. Parameter estimates for the night show that abundances from the surface to 25 m were similar with the exception of 20 m where abundance was significantly less. The mean fitted values for the model are given at the bottom of Table 1. Note that inclusion of the 2 outliers identified earlier would not change the results in that night-time abundances are higher than daytime for the surface to 10 m depth horizons. The scale parameter for the final model of 1 + DEPTH.TIME was estimated to be greater than one (2.877) justifying our decision to incorporate it in the analysis.

Similar analyses for stage II and III larvae indicated no significant relation between abundance and depth, time or time nested within depth. Stages II and III were included in Fig. 2 to indicate that they were caught over a broad depth range above the thermocline, contrary to previous studies. Stage II larvae were caught in 16 % of the trawls and occurred mainly in the upper 20 m. Stage III were present down to 20 m depth (Fig. 2).

Stage IV larvae were present in 75 % of the surface trawls, representing 90 % of the total catch. Stage IV were occasionally captured down to depths of 30 m (Fig. 2). Stage IV larval abundances appeared to be

Table 1. Analysis of deviance for stage I larvae assuming a log-linear model

Model	First difference in deviance	Degrees of freedom	p-level (χ^2-test)	Scale parameter
1				
+ DEPTH	10.20	5	0.779	4.080
+ TIME	5.23	1	0.257	4.066
+ TIME	6.00	1	0.217	3.944
+ DEPTH	9.35	5	0.808	4.066
+ DEPTH.TIME	130.90	11	0.000	2.877

Parameter estimates (standard errors) for model: 1 + DEPTH.TIME

Depth (m)	Day	Night
Surface	−2.787 (0.930)	0
5	−2.068 (0.790)	−0.281 (0.505)
10	−1.260 (0.607)	−0.002 (0.452)
15	−0.179 (0.445)	−2.856 (1.721)
20	−0.233 (0.440)	−3.010 (1.412)
25	−0.851 (0.574)	−1.576 (1.084)

Fitted mean values (no. per 5000 m^3) for model: 1 + DEPTH.TIME

Depth (m)	Day	Night
Surface	0.268	4.35
5	0.550	3.283
10	1.233	4.343
15	3.639	0.250
20	3.445	0.214
25	1.857	0.900

Table 2. Analysis of deviance for stage IV larvae assuming a log-linear model

Model	First difference in deviance	Degrees of freedom	p-level (χ^2-test)	Scale parameter
1				
+ DEPTH	225.80	4	0.0000	2.002
+ TIME	3.41	1	0.1898	1.984
+ TIME	8.10	1	0.1884	4.682
+ DEPTH	221.1	4	0.0000	1.984
+ DEPTH.TIME	6.30	5	0.6924	2.055

Parameter estimates (standard error) and fitted values for model: 1 + DEPTH

Depth (m)	Estimate	Mean fitted values
Surface	0	5.687
5	−2.463 (0.523)	0.484
10	−2.834 (0.625)	0.334
15	−3.834 (1.103)	0.123
20	−3.541 (0.847)	0.165

related to depth only (Table 2). The parameter estimates for the model 1+DEPTH and associated mean fitted values show that abundances at the surface horizon were significantly higher than the deeper horizons with abundances during daylight and night being similar. No outliers were identified for these data and analysis was confined to the first 5 depth horizons because no stage IV larvae were caught at 25 m.

The model discussed above for stage I larvae provides estimates of mean abundance for depth by night and day. An alternate model was fitted to the stage I data to predict depths at which larvae would be most abundant at any particular time. The response variable for this model was depth weighted by abundance (no. per 5000 m^3) and was regressed against time. A plot of stage I abundances recorded from 16 to 30 Aug is presented on a depth and 24 h time axis in Fig. 3. The size of the circles around each point reflect the size of the weight for each depth-time point. The best fit ($p < 0.001$) was given by a sine curve and this model is given on Fig. 3. The residuals from this model did not indicate any problems with the assumption of normality in this case.

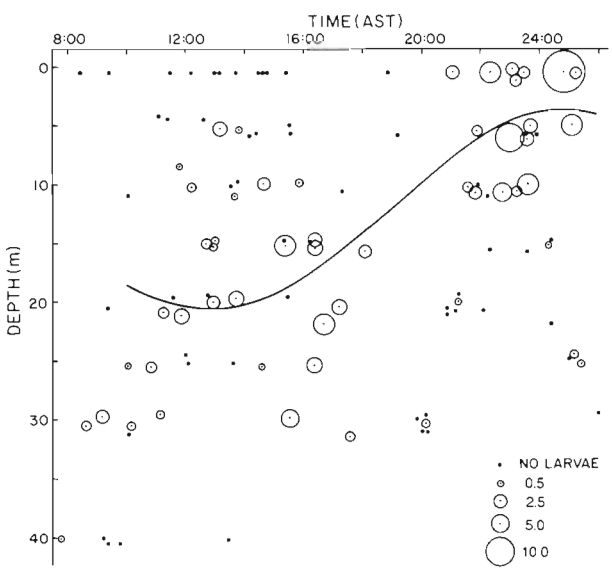

Fig. 3. Cumulative diagram of stage I lobster abundances, (no. per 5000 m^3), recorded from 16 to 30 Aug, presented on 24 h time (t) and depth (d) axes. Fitted sine curve: $d = 12.27 - 8.29 \cos \omega t - 1.89 \sin \omega t$, where $\omega = 2\pi/24$ and $r^2 = 0.55$, $F = 31.5$, $p < 0.001$

The same analysis on a continuous time basis (16 to 30 Aug) gives an almost identical equation. The sine-curve function describes a population centered around ~20 m at noon but rising to 4 m by midnight (Fig. 3). The phase of the sine curve is not significantly different from the solar cycle. On average stage I larvae stayed below a light intensity of 140 μ E m^{-2} s^{-1} at 1200 h AST. The lower limit of stage I larvae coincided with the average halocline and thermocline depths of 20 to 30 m, though there was a single larva caught at 40 m depth. This individual may represent a recent release rising towards the surface (Fig. 2). The structure and slope of the thermocline sometimes changed dramatically with the tidal cycle. Warmer water at depth, however, does not explain the presence of stage I larvae at 30 m depth. These larvae were caught in 8.5 to 11 °C water, as indicated by the average thermal profile (Fig. 2).

Lobster larvae on Browns Bank in mid to late August were therefore largely confined to the warmer, upper-mixed layer. Stage I larvae performed a typical nocturnal migration into the upper 10 m from daytime depths of 15 to 30 m. Stage IV lobster were restricted mainly to the upper metre at all times of the day.

DISCUSSION

The earliest observations on record of lobster larvae in the wild were made by Smith (1873) in mid-summer from Vineyard Sound and Buzzards Bay, off Massachusetts, USA. Smith frequently collected stage I and stage IV larvae at the surface during the day in dip and plankton nets. The literature since then on the depth distribution of lobster larvae is both diverse and fragmentary. The details of earlier studies are therefore collated, more or less chronologically, in Table 3 to facilitate a reappraisal of the vertical distribution and movements of lobster larvae in the wild.

Inshore studies

There have been numerous distributional studies of larval lobsters in inshore regions yet extensive vertical migrations, such as the daily 20 m migrations reported here in offshore waters, have not been observed. Most inshore investigators, however, were not looking for vertical migrations because they assumed that lobster larvae live continuously near the sea surface. This assumption was based on observations of aggregations of larvae near the surface when simultaneous surface and subsurface sampling was carried out (Table 3). This reasoning can be fallacious if the larval population is aggregated near the surface and either at some depth beneath the surface or diffusely spread throughout the subsurface waters.

The most detailed studies, to date, of the vertical distribution of lobster larvae in inshore waters have found that the early stages were present throughout the water column with aggregations at the surface in the southern Gulf of St. Lawrence (Scarratt 1973), in the upper 3 m (Collings et al. 1981) and at 3 m depth in the southern Gulf of Maine (Matthiessen & Scherer 1983). The fourth and final planktonic stage is more restricted to near-surface waters (Templeman 1939, Bibb et al. 1983, Collings et al. 1983, Hudon et al. 1986), similar to our offshore results (Fig. 2).

There are conflicting accounts on whether lobster larvae undergo vertical migrations in inshore regions. Previous investigators have observed all larval stages of the lobster near the sea surface both day and night (Table 3). However, more larvae per tow were caught during daylight when the results of day and night sampling could be compared (Scarratt 1973, Bibb et al. 1983). Scarratt also found that early stage larval lobsters disappeared from the upper 1.2 m of the water column just after sunset and before sunrise, reminiscent of Smith's (1937) preliminary findings yet contrary to those of Hudon et al. (1986). During daylight, several investigators have observed increased surface catches of larvae under overcast skies, as opposed to sunny conditions, from simultaneous surface and subsurface plankton tows (Templeman & Tibbo 1945, Harding et al. 1982, Hudon et al. 1986) and from seasonal surveys (Collings et al. 1983, Greenstein et al. 1983). There are reports also of lobster larvae progressively descending beneath the surface layer as dusk proceeds to night (Templeman & Tibbo 1945, Lux et al. 1983). Harding et al. (1979) observed that lobster larvae disappeared completely from the sea surface at night under rainy skies during a seasonal neuston survey done after dark. Conversely, Templeman (1939) found, using paired surface and subsurface plankton tows, that moonlight attracted lobster larvae to the surface.

Most of the inshore observations can be explained by the light hypothesis proposed by Templeman and Tibbo (1945) which states that a minimum light intensity is required to attract larvae near the sea surface but above some intensity larvae seek lower light levels. This also agrees with the earlier laboratory findings of Hadley (1908) on the light response of stage I larvae older than 2 d, stage II and III lobster; except for a few hours before each moult. This hypothesis does not, however, explain the observed difference between the small-scale vertical movements observed inshore and the 20 m migrations observed offshore. Summer light attenuation inshore in the Gulf of St. Lawrence (Harding et al. 1987) and offshore over Browns Bank (Fig. 2) are similar with 1 % of surface radiation reaching 18 to 20 m depth. Other factors than light intensity and penetration, such as prey or predator interactions, may be responsible for the observed differences in the scale of vertical distribution and movements for inshore and offshore populations.

Offshore studies

Little was previously known about the depth distribution of lobster larvae in deep water over the continental shelf. Stasko (1977) reported that 12 stage I, 12 stage II, 28 stage III and 90 stage IV lobster were collected from 76 stations on the Scotian Shelf at which both surface and deep oblique tows were taken (Table 3). Only 1 stage I and 2 stage IV lobster were captured in gear towed beneath the surface (1 m) and these could have been captured as the nets passed through the surface water open (J. Reid pers. comm.). Stasko & Gordon (1983) followed this study with a 2 yr, seasonal survey for lobster larvae using a variety of gear types in the most promising continental waters, specifically the Browns Bank region off southwest Nova Scotia (Table 3). They collected 3.5, 1.9 and 1.2 lobster larvae per tow at 0 to 0.2, 0.2 to 1.3 and 1 to 2 m depth, respectively (Table 3). Only 12 larvae (<0.1 per

Table 3. Field studies relevant to vertical distribution of lobster larvae

Region	Gear	Date	No. stations	No. net tows	Tow duration (min)	Depths sampled	Sampling period	No. larvae					Source
								I	II	III	IV	Tot.	
E. Northumberland Str., Caribou to Havre Bouche, NS	1 m conical 569 or 1024 µm	18/7–7/8/36	6	28	60	surface and deep (1.5–11 m), paired*	day	319	10	2	2	333	Templeman (1937)
E. Northumberland Str., Pictou, NS	0.76 m conical 752 µm	22/7–5/8/37	5	30	60	surface and deep (4, 6 or 8 m), paired	day and night	80	2	1	2	85	Smith (1937)
St. George's Bay and Bay of Islands, Nfld	0.91 m conical 1024 µm	9–10/8/38	2	13	30	surface and deep (0.5 to 3.3 m)	day and night	7	2	28	13	50	Templeman (1939)
Placentia Bay, Nfld	0.91 m conical 1024 µm	26–28/8/39	2	18	15	surface and deep (3.8 or 4.3 m), paired	day	9	16	10	0	35	Templeman & Tibbo (1945)
		11–12/8/40	1	14	15	surface and 2.9–3.8 m, paired	day and night	269	0	1	0	270	
Notre Dame Bay, Nfld	0.30 m conical 1024 µm	9–13/8/40	1	20	15	surface and deep (0.4–4 m), paired	day and night	8	3	9	10	30	
Port au Port Bay, Nfld	0.50 m conical 1024 µm	?/62	3+	81	15?	surface	day		**			616	Squires (1970)
Bay of Islands, Nfld		24/7/–7/9/64	14	49	15	surface	day					61	Squires et al. (1971)
Bonavista Bay, Nfld	0.50 m conical 366 µm, diver operated	6/71–7/71	1	70	5	surface, 3, 6, 9 m	day					?	Ennis (1983)
W. Northumberland Str., N.B.–P.E.I.	Rectangular 0.9 × 3.7 m, 1364 µm	6–8/63, 8/65	?	72	30	0–0.6 m	day and night	259	125	67	18	469	Scarratt (1973)
		7–8/62	?	34		0–0.6 m and 0.6–1.2 m, paired	day and night	925	44	2	0	971	
		22–23/8/62	?	13		4 to 13 m	day	11	3	0	0	14	
			?	17	15	btm; 5 to 13 m	day	0	0	0	0	0	
E. Northumberland Str., St. Georges Bay, NS	Square 0.4 × 0.4 m, 520 µm	21/6–7/9/76	9	74	15	0–0.3 m	night	91	2	0	1	94	Harding et al. (1979)
	Tricompartment 0.4 × 1.2 m, 520 µm	22/6–6/9/78	15	79	15	0–0.3 m, 0.3–0.7 m, 0.7–1.1 m	day	794	92	15	24	922	Harding et al. (1982)

Table 3 (continued)

Region	Gear	Date	No. stations	No. net tows	Tow duration (min)	Depths sampled	Sampling period	No. larvae					Source
								I	II	III	IV	Tot.	
Penobscot Bay, Maine	Rectangular 0.9 × 3.7 m, 1000 µm	24/5–20/9/76	3	210	30	0–0.75 m	day	52	1	0	5	58	Greenstein et al. (1983)
Cape Cod Canal, Mass.	Rectangular 1 × 2 m, 1050 µm	25/5–19/7/76	3	43	30	0–0.8 m	day	498	308	477	145	1428	Collings et al. (1981, 1983)
		27/5–22/7/77		50				310	89	60	195	654	
		26/5–14/9/78		58				207	44	69	110	430	
Buzzards Bay, Mass.		20/5–28/7/76	3	31				389	110	123	65	687	
		25/5–3/8/77	10	103				1161	888	1040	946	4035	
		26/5–14/9/78	5	90				575	237	233	518	1563	
Cape Cod Bay, Mass.		12/5–19/7/76	1	14				32	1	3	11	47	
		25/5–11/8/77	3	36				544	30	23	75	672	
		2/6–3/10/78	2	34				60	6	11	38	115	
Buzzards Bay, Mass.	Rectangular 1 × 2 m, 970 µm	9/6/76	3	6	30	0–0.7 m	day and night	259	137	95	0	491	Lux et al. (1983)
Block Island Sd, R.I.	Tucker, 2 × 2 m, 950 µm	31/5–2/8/77	4	107	12+12 +12	0–1.2 m	day and night	1047	349	199	66	1661	Bibb et al. (1983)
		6/6–30/8/78		132		btm		175	106	84	396	761	
Cape Cod Bay, Mass.	Tucker, 1 × 1.5 m, 1050 µm	9/6–1/8/77	2	48	20	0,3, 5.5, 7.6 m	day	1	0	0	1	2	Lawton et al. (1983)
Cape Cod Bay	Tucker, 1 × 1.5 m, 1050 µm	25/5–11/8/77	3	41	20	0,3, 5.5, 7.6 m	day	85	29	103	57	274	Collings et al. (1981, 1983)
Buzzards Bay, Cape Cod Canal, Mass.			3	25				191	105	61	29	386	
Cape Cod Bay, Mass.	Tucker, 2 × 2 m, 1000 µm	7/6–8/7/76	1	115	30	0, 3, 6, 9, 12 m	day and night	2106	?	?	?	2290	Matthiessen & Scherer (1983), Matthiessen (1984)
Scotian Shelf, NS	Rectangular 0.18 × 1 m, 1180 µm	13–23/8/76	76	76	30	0–0.2 m	day or night	10	9	19	72	110	Stasko (1977)
	1 m conical, 1180 µm					0–0.7 m		1	3	9	16	29	
	0.6 m bongo, 1180 µm					oblique from bottom		0	0	0	1	1	
	1.2 m Isaacs Kidd, 7.6 cm + 471 µm							1	0	0	1	2	

Table 3 (continued)

Region	Gear	Date	No. stations	No. net tows	Tow duration (min)	Depths sampled	Sampling period	No. larvae I	II	III	IV	Tot.	Source
S.W. Nova Scotia, incl. Browns Bank region, NS	Rectangular 0.18 × 1m, 1180 µm	5/7–16/9/77	140	140	30	0–0.2 m	day or night	206	35	12	268	521	Stasko & Gordon (1983)
	1 m conical, 1180 µm					0.3–1.3 m		60	15	0	110	185	
	1.2 m Isaacs-Kidd, 7.6 cm + 471 µm			160		20–0 m		8	1	0	2	11	
	Rectangular, 0.18 × 1 m, 1180 µm	12/7–24/8/78	117	117		0–0.2 m	day	12	12	12	329	365	
	1 m conical, 1180 µm					0.2–1.2 m		32	5	7	260	304	
						1–2 m		44	6	6	78	134	
Iles-de-la-Madelaine, Québec	Rectangular, 0.31 × 1 m and 1 m conical 1000 µm	18/6–17/9/78	20	160	30	0–0.2 m	day	3964	453	100	68	4584	Hudon et al. (1986)
						1–2 m							
		8/6–30/8/80	23	153		0–0.2 m	day	519	700	451	587	2257	
						0–1 m							
	Tricompartment 0.8 × 2.4 m, 1000 µm	9/7–28/8/81	2	66		0–0.8 m	day and night	874	295	89	376	1634	
						0.8–1.6 m							
						1.6–2.4 m							

* Surface and deep nets towed simultaneously
** Mainly stage II

tow) were collected in 160 stepped oblique tows (20 to 10 to 2 m) with an Isaacs-Kidd trawl; however, most lobster larvae would have passed through the 76 mm mesh of the main section of this net. Stage IV lobster larvae made up 66 % of the total offshore catch (Stasko & Gordon 1983) which is similar to the skewed distribution of developmental stages found off New England in coastal surface waters (Table 3). In 1977 when offshore sampling was done both day and night, 38 % and 54 % of the surface catch (0 to 1.2 m) were stage I and IV, respectively, whereas 7 % and 83 % were stage I and IV the following year when all sampling was done during daylight. This discrepancy in the proportion of developmental stages between years can be explained readily by our findings of a migration of most of the stage I population into the surface waters at night combined with the persistence of fourth stage larvae in the surface waters (Fig. 2). Similarly, our results could also explain the greater proportion of stage IV larvae found in New England surface waters (Collings et al. 1981, 1983, Bibb et al. 1983, Fogarty et al. 1983, Grabe et al. 1983, Lawton et al. 1983, Lux et al. 1983, Matthiessen & Scherer 1983) compared to that expected from estimates of natural mortality (Scarratt 1964, 1973, Harding et al. 1982). Another explanation is that larvae could be advected away from the 'spawning' sites so that the developmental stages are segregated from each other by drift and dilution. As we have seen, the preponderance of stage IV lobster in New England is such a widespread phenomena that this explanation is not considered tenable. It is more likely that the first 3 developmental stages of the lobster spend proportionately more time beneath the surface waters as we have found in offshore waters (Fig. 2).

Laboratory studies and ecological implications

The vertical extent of stage I lobster migration reported here, daily traversing as much as 30 m depth over Browns Bank, was not expected from the results of previous field studies. However, the early laboratory studies of Hadley (1905, 1908) hinted that this would be the case. Hadley noted that the larval response to the intensity and direction of light changed as the lobster developed. In the first hours after hatching, experimental larvae were most attracted to a light source of high intensity but this response reversed by the second day into a negative reaction to bright daylight, although stage I lobster were still positive to reduced light (Hadley 1908). These results anticipated not only a vertical migration cued to light intensity but the presence of some stage I larvae at the surface throughout the day. Hours before moulting into stage II, III or IV larval lobster were strongly attracted to bright light again (Hadley 1908). This response could also explain the presence of some stage II and III larvae in the surface waters over Browns Bank during daylight. Lobster larvae had a negative response to daylight after moulting into the second and third developmental stages, and actively sought regions of reduced light (Hadley 1908). Stage II and III lobster larvae were too rare in our collections to statistically detect any day-night depth differences. Hadley (1908) found early stage IV larvae actively choose greater light intensities although this response reversed later in the larval stage. These results agree with our finding of 90 % of the stage IV larvae being caught in the upper metre (81 % of surface tows were positive) over Browns Bank. Early experimental stage IV lobster were characterized also by continuous swimming near the surface which was more active and superficial in the presence of food (Hadley 1908). Unfortunately light intensity was never quantified in these behavioural studies of Hadley.

Later experimental studies indicated that the depth regulating activities of the first 3 larval stages were most responsive to pressure changes but that the presence of overhead light substantially reduced the reaction time at low pressures (Ennis 1975). As Hadley had found, early stage I lobster reacted more positively to overhead light intensities than 3 d old stage I, 6 to 8 d old stage II and 15 d old stage III larvae (Ennis 1975). However, the responses of larval lobsters, over a range of light intensities, were not consistent in this experimental design.

Templeman (1936) found that salinities as low as 21 ‰ were only slightly less favourable to lobster larvae than seawater for their survival to stage IV. Scarratt & Raine (1967) showed that early stage I lobster avoided an experimental surface layer of 21.4 ‰ but not 26.7 ‰ salinity. Obviously salinity is of little importance in the ecology of lobster larvae except in the immediate vicinity of freshwater runoff, where larvae would be expected to select deeper more saline waters.

Templeman (1936) demonstrated that lobster larvae could be reared in the laboratory through the fifth stage at 10 to 20 °C in the ample presence of prey over approximately 109 to 29 d, respectively. MacKenzie (1985) found that over a range of 10 to 22 °C there was no effect on larval survival in the laboratory up to the end of the second developmental stage, however, larvae reared at 10 °C suffered significantly higher mortality (>90 %) before reaching the fifth or settled stage. It would appear that there is a considerable advantage to the species for individuals, at least stage III and IV larvae, to maintain themselves above the thermocline. In our Browns Bank study only one stage I larvae was caught below the ~10 °C thermocline at 30 m depth and most larvae were collected above the 20 m halocline (Fig. 2).

The upper mixed layer over Browns Bank contains a species assemblage and size composition of prey previously found suitable for the larval lobster (Harding et al. 1983). We have not yet investigated this possibility in our Browns Bank study but it is almost certain that the vertical migrations of zooplankters, such as lobster larvae, are influenced by the changing depth distributions of their predators and prey as shown in other regions (Janssen & Bradt 1980, Ohman et al. 1983, Harding et al. 1986).

Templeman (1936) has shown that a reduction in prey abundance from that considered optimal can effect both the duration of the larval stages and their survival. Reduction of prey levels to half optimal concentrations almost doubles the time needed to reach stage III (Templeman 1936). Hunger was found to postpone the final development of a strong negative response to light in late stage IV larvae whereas continual satiation favoured earlier settlement in laboratory conditions (Hadley 1908).

The advantages and disadvantages of a feeding planktonic larval phase, such as that evolved in many marine benthic macrofauna, has aroused scientific interest over the decades (Thorson 1950, Mileikovsky 1971, Sastry 1983, Olive 1985). The evolution of a planktotrophic larva offers more numerous progeny, though necessarily smaller because of the finite energy cost that can be allocated to reproduction (Vance 1973), with higher mortality than direct development of large eggs to juveniles in protective brood pouches. The lobster has evolved an intermediate course with the mother carrying and protecting yolky eggs over the winter, which then hatch in the spring into carnivorous plankters of 4 to 6 wk duration. The release of planktonic larvae serves to remove benthic organisms from the bottom at a critical size and stage in their development. It has been judged from both the lack of species and the predictable gaps present at certain sizes in the biomass spectrum of the benthos that the bottom is least favourable for survival due to either phylogenetic limitations inherent in meio- and macrofauna (Warwick 1984) or to physical constraints of grain size in the environment (Schwinghamer 1981). A bottom dwelling existence compresses a species habitat very nearly into 2 dimensions such that if the organisms are of a size which is too large to live interstitially but too small to effectively burrow into the sediments, they would be restricted to the surface and therefore be extremely vulnerable to predators. Schwinghamer (1985) believes that the usually low biomass of benthic organisms around the 1 mm ESD size category, which corresponds to the planktonic phase of most benthic organisms, is evidence for strong negative selection forces.

It is widely believed, however, that a planktonic existence in surface waters also makes larger organisms more vulnerable, but to visual predators during daylight (Hrbáček 1958, Brooks & Dodson 1965, Iwasa 1982). The chances of a larval lobster surviving to the bottom-living stage are believed to be reduced by prolonging this phase of the life cycle (Templeman 1936, Harding et al. 1983). It is perhaps not fortuitous that larval lobsters are hatched to coincide with the warmest season (Harding et al. 1983) which would enhance growth and hasten settlement (Templeman 1936, Mackenzie 1985). One of the recognized benefits of a planktonic phase is that it serves to spread relatively immobile benthic species which are often habitat specific (Strathmann 1974, Ayal and Safriel 1982) and increases genetic exchange over longer geographic distances (Scheltema 1971, Underwood 1974, Crisp 1976). Adult lobsters are known to travel long distances on the bottom (Fogarty et al. 1980, Campbell & Stasko 1985) and some portion of the offshore population is known to migrate seasonally onto banks (Uzmann et al. 1977, Pezzack & Duggan 1986) which makes a planktonic stage less essential for dispersion. More importantly a planktonic existence brings the lobster into the photosynthetic zone of the ocean at a time when the surface water is warmest and small-copepod prey production is highest (Dagg & Turner 1982, Davis 1984) which would result in rapid growth through a vulnerable size in its life history. A widely evolved compromise, considering the opposing forces of natural selection operating on a large planktonic predator, is for vertical migration to occur to take advantage of the prey and fast growth supported in the warm sunlit waters yet descend during daylight to avoid visual predators (Gliwicz 1986).

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