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BIOLOGY AND ECOLOGY OF LARVAL LOBSTERS (*Homarus americanus*): IMPLICATIONS FOR POPULATION CONNECTIVITY AND LARVAL TRANSPORT

By

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B.A. Boston University, 1992

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A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Oceanography)

The Graduate School
The University of Maine
August, 2004

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BIOLOGY AND ECOLOGY OF LARVAL LOBSTERS (*Homarus americanus*): IMPLICATIONS FOR POPULATION CONNECTIVITY AND LARVAL TRANSPORT

By Eric R. Annis

Thesis Advisor: Dr. Robert S. Steneck

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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The connectivity of marine populations and the degree to which they are considered open or closed has important implications for the ecology, management, and resilience of commercially harvested species. Larval exchange is a primary determinant of the level of connectivity between populations, and this thesis examines the intrinsic and extrinsic factors influencing larval transport and the distribution of larvae of the American lobster (*Homarus americanus*). The potential for larval transport is directly proportional to the planktonic larval duration. Our field data suggest development times *in situ* were up to three times faster than previous laboratory development times, indicating that potential for transport is less than previously reported. Observation of postlarvae *in situ* revealed changes in vertical distribution corresponding to ontogenetic shifts in behavior and extrinsic environmental factors. Most notably, the 12°C isotherm appeared to be a temperature threshold with postlarvae remaining in warmer waters above. This suggests that settlement may be limited by bottom temperature with negligible settlement occurring below the depth of the 12° isotherm. Postlarvae spent

94% of the time above 4 m depth, reinforcing the importance of surface currents to transport of the final planktonic stage. However, only 55-80% of the time was spent in the top 0.5 m, indicating that abundance estimated from surface samples has been chronically underestimated. The quality of larvae may contribute to successful larval transport and laboratory experiments indicated that larvae from embryos of greater mass were more resistant to periods of starvation. Thus, portions of the population producing heavier eggs may contribute disproportionately to successful larval production. Patterns of larval distribution over 300 km of coast in the northern Gulf of Maine revealed high abundance of postlarvae at the downstream end of the study area suggesting a potential larval sink and two potential upstream sources of newly hatched stage I larvae. Our results are consistent with two potential source-sink models; one which is largely self-recruiting, and a second in which larvae are delivered from a distant source. The relative contribution of these larval sources to recruitment is unknown and will define the degree to which the population is open or closed.

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1. THE EFFECT OF MATERNAL SIZE AND EMBRYO SIZE ON LARVAL DEVELOPMENT AND SURVIVAL IN THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*).

Abstract

Previous studies suggest that larger lobsters (*Homarus americanus*) have greater energetic investment per embryo, and that this confers a survival advantage to the developing larvae. We present data demonstrating that advantages to larvae increase with mass per embryo, but not as a function of maternal size. We reared larvae in the laboratory and recorded body size, molt increment, stage duration, and mortality during the three larval instars and postlarval stage. Larvae were either fed continuously or subjected to starvation periods immediately after hatching. Larval mass increased with mass per embryo suggesting that energetic advantages of heavier embryos are indeed conferred to the larvae. Larvae from heavier embryos recovered faster from periods without food, and mortality decreased with increasing embryo mass in larvae subjected to periods without food. We also observed greater size increase at first molt and larger postlarval size in some treatments. The absence of maternal size effects can be attributed to a poor relationship between maternal size and mass per embryo, suggesting that other factors such as temperature and diet may be more important in determining embryo size.

Introduction

The mass of invertebrate eggs reflects the maternal energetic investment and varies both among and within species (Jaeckle 1995). Many studies have examined the inter-specific differences in egg size and their impact on larval survival with respect to

the evolution of reproductive strategy (reviewed in Havenhand 1995), but comparatively few studies have focused on the effect of intra-specific variation in egg size on the viability of crustacean larvae. Intra-specific differences in initial contribution to egg size coupled with effects of environmental conditions during embryogenesis result in variable embryo biomass at the time of hatch. In decapod crustaceans lipids are the primary source of energy during embryogenesis (Clarke et al. 1990, Pandian 1970, Petersen and Anger 1997, Wehrtmann and Graeve 1998), and greater mass at the time of hatch reflects greater yolk reserves (Sasaki et al. 1986, Sibert et al. 2004). Accordingly, it is commonly assumed that larger eggs confer a nutritional advantage to the newly hatched larvae. In studies of the intra-specific variation of egg size in decapods, larvae benefited from larger eggs through greater larval size, faster development, lower mortality rate, and increased resistance to starvation (Anger et al. 1985, Gimenez 2002, Gimenez and Anger 2003, Gimenez and Torres 2002, Hancock 1998). The influence of egg quality on larval viability could potentially play a role in the recruitment dynamics with the large egg producing members of a population making a greater contribution to the larval supply and recruitment of the population as a whole.

The American lobster, *Homarus americanus*, presents an interesting opportunity to examine intra-specific variation in egg mass because the reproductive biology is well studied (Reviewed in: Talbot and Helluy 1995, Waddy et al. 1995) but the advantages conferred by greater egg mass to newly hatched larvae have not been determined. Lobsters are the most valuable commercial fishery in the northwestern Atlantic Ocean, and there is a pressing need to understand how biological traits of the lobster contribute to the reproductive capacity of the population.

Lobsters spawn in the summer months and carry the eggs under their abdomen until they hatch in the following summer (Waddy et al. 1995). The development of embryos during this period is entirely dependent upon the reserves acquired in vitellogenesis (Talbot and Helluy 1995). The rate of embryogenesis is temperature dependant with colder temperatures resulting in longer development time and lower energetic reserves at the time of hatch (Perkins 1972, Sasaki et al. 1986). Large adult lobsters undertake a seasonal migration into deep water (>100m) where winter temperatures are warmer, thereby maximizing degree-days for developing embryos (Campbell 1986, Campbell 1990). Several studies suggest that egg size may increase with increasing maternal size (Attard and Hudon 1987, Estrella and Cadrin 1995, Ouellet et al. 2003, Plante 2001, Sibert et al. 2004) but females of all sizes exhibit high variability in egg mass.

Attard and Hudon (1987) reported that energetic investment per brood, egg mass, and caloric content (per egg) all increased with female size, and they suggested that the higher caloric content in eggs from large lobsters might impart a survival advantage to newly hatched larvae. If the additional energy were transferred to the larvae, they could potentially benefit from increased resistance to starvation (Anger et al. 1985, Sasaki 1984), larger size at time of settlement (James-Pirri and Cobb 2000), or reduced development time (Vance 1973).

Despite substantial research on egg production and larval development, little has been done to ascertain if or how egg quality actually translates into larval development and survival. Do large lobsters produce more viable larvae than small lobsters? Do eggs of greater mass confer energetic advantages to the newly hatched larvae? We collected

large and small lobsters and compared the development of their larvae with respect to size, size increase at molt, development rate, mortality, and response to starvation.

Methods

Organisms

Ovigerous lobsters were collected by local lobstermen from coastal waters of the Gulf of Maine near Boothbay, Maine (~ 43°48' N, 069°32' W) in mid-June of 1999, 2000, and 2001. Over the three years, a total of 33 lobsters ranging in size from 78-148 mm carapace length (CL) were collected and held individually in flowing seawater aquaria at ambient temperature (average 13.5-14.5°C) until hatching occurred. First hatch was observed in these lobsters on 25 June 1999, 22 June 2000, and 9 July 2001. All lobsters began hatching their larvae within three weeks of capture. Average daily bottom temperature (~25m depth) near the collection site (Ram Island; 43°48.18' N, 68°36.06' W) was provided by the Maine Department of Marine Resources. Measurements of SST (sea surface temperature) from AVHRR (Advanced Very High Resolution Radiometer) satellite images were provided by the Satellite Oceanography Data Lab at the University of Maine. Sea surface temperature anomalies were calculated by subtracting the 20-year SST climatology from monthly averages of SST (available at: www.seasurface.umaine.edu)

We used embryo mass (dry weight per embryo) as a proxy for the energetic value, because the mass of developing embryos correlates with caloric content (Attard and Hudon 1987). Hatching occurs over several days and the dry weight of newly hatched stage I larvae increases after the first day of hatching (Pandian 1970). Accordingly, we

collected unhatched embryos and stage I larvae for dry weights at the time of first hatch. Dry weight measurements were made in 2000 and 2001 (Table 1.1). Following the methods of Attard and Hudon (1987), samples were preserved in buffered (borax) formaldehyde in seawater (~5%) for two days, rinsed with distilled water, and dried at 50°C for 24 hours. The samples from 2001 were not originally intended for dry weights and were frozen at -80°C for approximately a year and a half before they were thawed and preserved in formaldehyde. The variable number of larvae in these samples (Table 1.1) resulted from efforts to select intact individuals from the thawed samples. Stage I larvae were weighed individually and averaged by replicate, while embryos were pooled by replicate and divided by the number of eggs in the sample to provide an average weight per replicate.

Table 1.1. Starvation experiments conducted, mass measurements, sample size (n) and number of individual larvae per replicate.

Year	Treatment	Number of Small Females (n)	Number of Large Females (n)	Number of larvae per replicate
1999	*Ad libitum* feeding	2	4	20
	1 day initial starvation period	2	4	20
	2 day initial starvation period	2	4	20
2000	*Ad libitum* feeding	6	6	10
	3 day initial starvation period	6	6	10
	4 day initial starvation period	6	6	10
	5 day initial starvation period	6	6	10
	Complete starvation	6	6	10
	Embryo mass	6	6	20
	Stage I larva mass	6	6	10
2001	*Ad libitum* feeding	6	9	5
	Embryo mass	6	9	8-20
	Stage I larva mass	4	9	4-19

For feeding experiments, we collected stage I larvae within 6 h of hatching, and maintained them individually in PVC containers with 1 mm mesh bottoms placed on a rack within two 1.0 m x 1.2 m x 0.15 m tanks. The mesh bottom allowed exchange of water and food but retained the larvae. The tanks were maintained at 17°C (1999) or 15°C (2000 and 2001) in an environmental chamber with a light:dark cycle of approximately 2:22 h. This light cycle was used in an effort to reduce mortality (Eagles et al. 1986) and to provide a more even distribution of the positively phototactic brine shrimp used for feeding. The tanks were closed systems using ~120 l filtered seawater (20μm), an aquarium pump for circulation, and two aerators. The water was replaced every 2-3 d. One tank was designated for *ad libitum* feeding treatments and contained fresh hatched brine shrimp nauplii (*Artemia* sp.) as a food source at a concentration of 5-12 ml^{-1}. A second tank was used for starvation treatments and contained only filtered seawater. We checked larvae daily for mortality and molting to determine stage duration and stage specific mortality. We measured CL following each molt and calculated the molt increment (percent increase at molt) as: $(CL_{n+1} - CL_n)/CL_n$. CL was measured from the posterior margin of the orbit to the posterior margin of the carapace at the mid-dorsal line (oblique) using a dissection microscope with an ocular scale.

Experiments

Experimental treatments varied in each of the three years (Table 1.1). Our original hypothesis examined the effect of maternal size on larval development and viability but we found no difference in the variables: size, development time, molt increment, or mortality. Variations in rearing temperature and starvation treatments

reflect our attempts to elucidate a difference in larval quality as a function of maternal size. The number of larvae used per replicate was reduced each year as we balanced the available space, number of treatments, and gained experience with the number of larvae needed to obtain results.

We grouped larvae by maternal carapace length into small (< 90mm CL) and large (> 90mm CL) lobsters and tested for between group differences in larval CL, stage duration, mortality, and molt increment. The size at maturity increases with decreasing summer water temperature (Waddy and Aiken 1991), and in the Gulf of Maine approximately 40% of the population has reached sexual maturity at 90mm CL (Fogarty 1995). Individuals below this size were likely spawning for the first time. The number of lobsters in each size class (each lobster constitutes one replicate), the number of larvae collected per replicate, and the treatments conducted are reported in Table 1.1.

We reared larvae were reared with *ad libitum* feeding to test for differences in larval development as a function of maternal size and as a control for starvation treatments. Larvae in the *ad libitum* feeding treatment were held in the feeding tank from the time of hatch until the postlarval stage. We also subjected larvae to a complete starvation treatment in which they were maintained in the tank without food from the time of hatch until they expired. The effect of initial starvation period on development was examined by starving newly hatched larvae for a period of one to five days followed by *ad libitum* feeding.

Statistical Analysis

Differences between size groups were determined using ANOVA with repeated measures for each variable: size, molt increment, stage duration, and mortality. The results from both maternal size groups were subsequently pooled and analyzed with ANOVA to determine the effect of starvation treatments. A Pearson correlation matrix was used to examine relationships between egg mass and larval development variables. Regression analysis was used to examine the relationship between maternal CL and egg mass and other developmental parameters. A T-test assuming equal variance was used to determine differences in survival time during starvation and differences in egg mass between years.

Results

Temperature

The average daily bottom temperature for the incubation periods preceding our lobster collections in 2000 (July 16, 1999-July 15, 2000) and 2001 (July 16, 2000-June 15, 2001) are presented in Figure 1.1. Mid-July was selected as the break point between years because it approximates the timing of peak larval hatching in our study area based on the abundance of stage I larvae in plankton samples (Annis et al. in prep-b). The temperature regime differed between years with colder winter temperatures and delayed spring warming preceding the 2001 hatch. The threshold for embryo development is approximately 4°C with negligible development at lower temperatures (Sibert et al. 2004). The number of days above 4°C was 303 preceding the 2000 hatch and 263

preceding the 2001 hatch. The difference in temperature was also evident in the cumulative degree-days (above 4°C) with 1282 and 1166 degree-days in the incubation periods preceding 2000 and 2001 hatches respectively. SST anomalies based on AVHRR measurements suggest a cold anomaly in the winter months of 2001 and slightly warm anomaly in the winter of 2000. Coastal waters are vertically well mixed in the Gulf of Maine in the winter and these temperature anomalies likely reflect differences in bottom temperature between years.

Maternal Carapace Length

Embryo mass increased with maternal size in both 2000 and 2001 (Fig. 1.2), but the relationship was not statistically significant in either year. There was no relationship between stage I CL and maternal CL (Fig. 1.3). Regressions were not significant for any of the three years ($P > 0.05$) and varied between positive and negative slope between years. The stage I CL could not be pooled across years due to significant differences between years (ANOVA, $df = 2$, $P = 0.001$). Average stage I CL (mm ± S.E.) for all replicates was 2.02 ± 0.02, 1.91 ± 0.01 and 1.95 ± 0.02 in 1999, 2000 and 2001 respectively.

Larval Growth

Larvae raised with *ad libitum* feeding in 2000 and 2001 exhibited no significant difference between maternal size groups for molt increment, stage duration, or stage specific mortality (Table 1.2). Data for these years could not be pooled due to inter-annual variation in mortality and development time which could not be accounted for

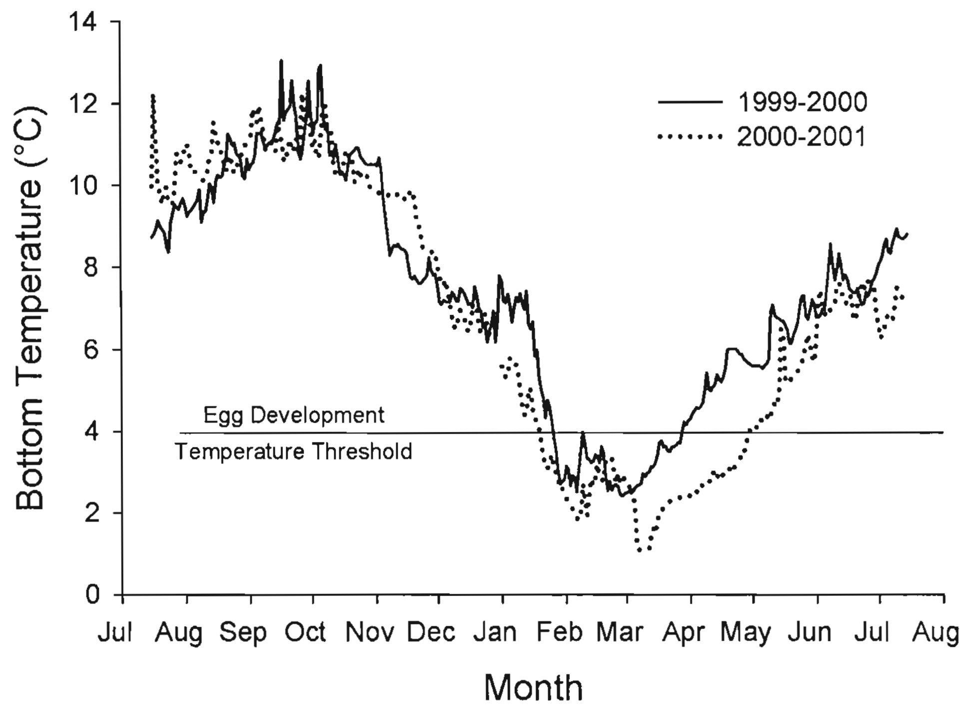


Figure 1.1. Bottom temperatures near Boothbay, Maine during the incubation periods preceding larval hatches in 2000 (1999-2000) and 2001 (2000-2001). The daily average temperature from ~25 m depth at Ram Island was provided by the Maine Department of Marine Resources. The horizontal line makes the 4°C threshold below which larval development is negligible.

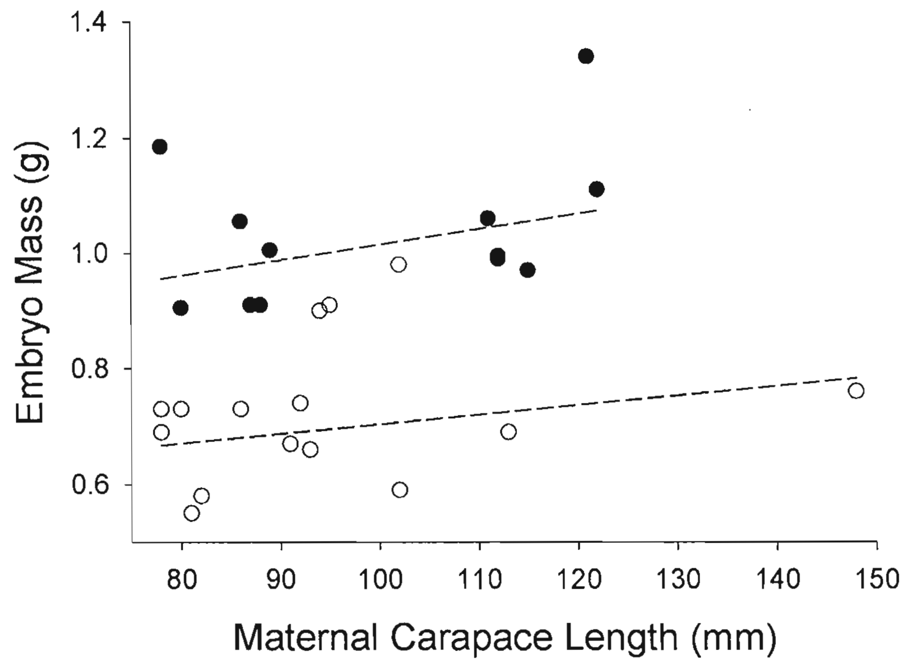


Figure 1.2. Average mass per embryo (dry weight) as a function of maternal size in 2000(●) and 2001(○). The regressions were not significant in either year. 2001 Data: $Y = 0.0016X + 0.540$, $r^2 = 0.07$, $n = 15$, $P = 0.606$. 2000 Data: $Y = 0.0027X + 0.747$, $r^2 = 0.15$, $n = 12$, $P = 0.217$. Variance was not calculated because eggs were pooled for weighing and divided by the sample size.

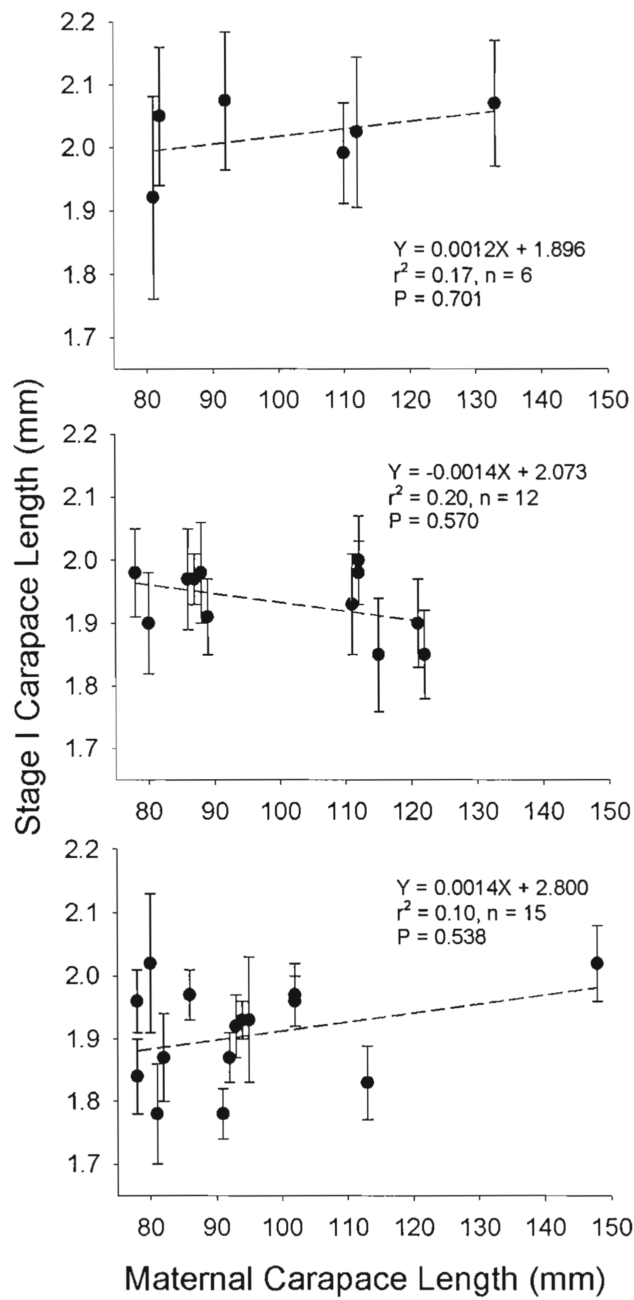


Figure 1.3. Average size (± 1 S.D.) of newly hatched stage I larvae as a function of maternal size in 1999 (top), 2000 (middle), and 2001 (bottom). Regressions were not significant in any of the three years sampled.

Table 1.2. Larval development under *ad libitum* feeding conditions in 2000 (left) and 2001 (right). Development variables (mean ± 1 S.E.) for stages I-III and postlarvae (PL) were pooled by maternal size (small < 90 mm CL, large > 90 mm CL) and tested for differences with ANOVA (P values are reported at the right).

Year		2000					2001				
	Female Size	Stage I	Stage II	Stage III	PL	P	Stage I	Stage II	Stage III	PL	P
Carapace Length (mm)	Small	1.96± 0.02	2.75± 0.04	3.36 ± 0.02	4.00 ± 0.02	0.701	1.90 ± 0.04	2.65 ± 0.04	3.26 ± 0.07	3.81± 0.09	0.223
	Large	1.93± 0.02	2.77± 0.02	3.37 ± 0.01	4.03 ± 0.02		1.91 ± 0.02	2.71 ± 0.04	3.36 ± 0.06	3.95± 0.04	
Molt Increment (%)	Small	40.64± 2.28	22.00± 1.16	19.24 ± 0.99	-	0.179	39.2 ± 2.7	22.9 ± 1.7	17.0 ± 2.1	-	0.212
	Large	43.71± 1.41	21.34± 0.61	19.63 ± 0.79	-		41.7 ± 2.4	24.4 ± 1.9	17.4 ± 1.6	-	
Stage Duration (d)	Small	5.78± 0.27	5.77± 0.43	8.41 ± 0.23	-	0.225	6.96 ± 0.27	7.94 ± 0.37	11.53 ± 1.00	-	0.165
	Large	5.99± 0.05	6.08± 0.11	8.55 ± 0.19	-		6.84 ± 0.23	7.49 ± 0.24	10.46 ± 0.35	-	
Mortality (stage specific)	Small	0.02± 0.04	0.03± 0.05	0.12 ± 0.07	-	0.226	0.17 ± 0.20	0.14 ± 0.17	0.39 ± 0.33	-	0.870
	Large	0.05± 0.09	0.02± 0.06	0.02 ± 0.04	-		0.00 ± 0.00	0.18 ± 0.23	0.36 ± 0.36	-	

with the variables measured. We observed no obvious differences between the larvae from the two maternal size groups in 1999, although statistical analyses were not conducted due to a sample size of two in the small lobster group.

Response to Starvation

We recorded survival time of newly hatched stage I larvae maintained without feeding. The average survival time in response to complete starvation was slightly greater in larvae from large females (17.2 ± 0.4 d for larvae from large females and 16.1 ± 0.6 d from small females) but the difference was not statistically significant (Fig. 1.4).

In 2001 we recorded the growth of newly hatched larvae that were subjected to initial starvation periods of 3, 4, and 5 d. There were no statistically significant differences between larvae from large and small females with respect to size, molt increase, development time, or mortality (Table 1.3). Data from both size groups were pooled and analyzed for treatment effects. The initial starvation periods delayed the first molt, and stage I duration was significantly longer in the starvation treatments (ANOVA, $df = 3$, $P < 0.001$). The relationship between the length of starvation period and development time was linear (Fig. 1.5). Stage I duration in starved treatments is expressed as a multiple of the development time of larvae fed *ad libitum* (*sensu* Anger et al. 1981a), and accordingly all values were greater than 1.0. Reporting the developmental delay as a multiple of a fed treatment development time permitted the inclusion of 1- and 2-d starvation treatments (1999 data) which were conducted at a higher temperature resulting in shorter development times. The dotted line in Figure 1.5

indicates the expected value if the delay in development were equal to the initial starvation period. A treatment effect also occurred in stage I mortality where larvae subjected to a 5 d initial starvation period had significantly higher mortality than the other treatments (ANOVA, df = 3, $P < 0.05$) (Fig. 1.6). Size and molt increment did not vary significantly with treatment ($P > 0.05$ in all cases).

Embryo Mass

In 2000 and 2001 we observed significant positive correlations between embryo mass and subsequent stage I larval mass (Pearson correlation matrix, $P < 0.05$, Table 1.4). The relationship between embryo mass and stage I mass was linear in both years (Fig. 1.7). Average embryo mass (mg ± S.D.) for all replicates was 1.04 ± 0.12 in 2000, 0.74 ± 0.13 in 2001, and was significantly different between years (t-test, df = 25, $P < 0.001$). The difference between years prevented the pooling of embryo mass data for

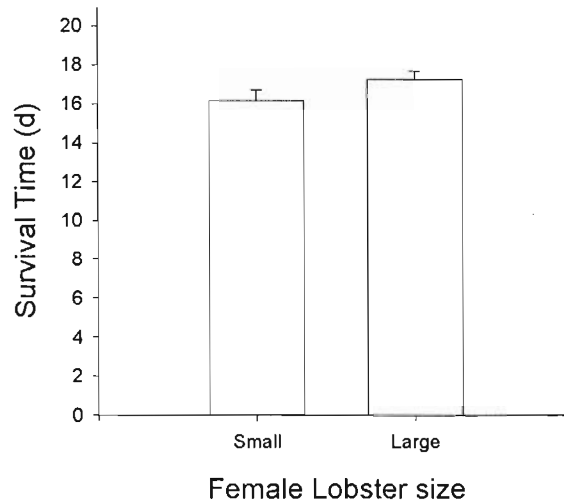


Figure 1.4. Average survival time of stage I larvae starved from time of hatch grouped by maternal size (small < 90 mm CL, large > 90 mm CL) . There was no significant difference between maternal sizes (t-test; P = 0.08, n = 6). Bars are mean + 1 S.E.

Variable	Starvation Treatment (d)	Female Size	Larval Stage I	II	III	PL	*P*
Carapace Length (mm)	3	Small	1.89 ± 0.03	2.70 ± 0.04	3.30 ± 0.06	3.80 ± 0.07	0.318
		Large	1.93 ± 0.03	2.70 ± 0.03	3.36 ± 0.04	3.86 ± 0.04	
	4	Small	1.90 ± 0.02	2.63 ± 0.04	3.26 ± 0.06	3.78 ± 0.07	0.170
		Large	1.93 ± 0.02	2.70 ± 0.03	3.30 ± 0.05	3.80 ± 0.03	
	5	Small	1.91 ± 0.03	2.66 ± 0.04	3.26 ± 0.06	3.76 ± 0.07	0.692
		Large	1.93 ± 0.02	2.72 ± 0.03	3.32 ± 0.04	3.79 ± 0.06	
Molt Increment (%)	3	Small	42.99 ± 2.77	22.36 ± 1.56	15.32 ± 1.69	-	0.867
		Large	40.13 ± 1.41	24.86 ± 1.83	14.97 ± 0.96	-	
	4	Small	38.50 ± 3.32	23.83 ± 0.90	16.19 ± 1.16	-	0.725
		Large	40.23 ± 1.03	22.23 ± 2.06	13.69 ± 1.00	-	
	5	Small	39.50 ± 2.93	22.45 ± 0.85	14.09 ± 2.20	-	0.869
		Large	41.07 ± 1.41	22.20 ± 1.24	14.33 ± 1.58	-	
Stage Duration (d)	3	Small	10.13 ± 0.29	8.41 ± 0.52	12.83 ± 0.68	-	0.352
		Large	9.97 ± 0.30	7.15 ± 0.36	13.10 ± 0.52	-	
	4	Small	11.45 ± 0.18	8.18 ± 0.44	13.60 ± 0.63	-	0.352
		Large	11.28 ± 0.32	8.01 ± 0.46	13.29 ± 0.56	-	
	5	Small	13.38 ± 0.56	8.14 ± 0.41	12.77 ± 0.41	-	0.782
		Large	13.15 ± 0.68	8.49 ± 0.53	13.07 ± 0.54	-	
Mortality (stage specific)	3	Small	0.13 ± 0.16	0.23 ± 0.20	0.45 ± 0.27	-	0.211
		Large	0.07 ± 0.14	0.07 ± 0.10	0.44 ± 0.31	-	
	4	Small	0.03 ± 0.08	0.29 ± 0.18	0.29 ± 0.26	-	0.896
		Large	0.09 ± 0.11	0.21 ± 0.26	0.46 ± 0.28	-	
	5	Small	0.23 ± 0.29	0.03 ± 0.08	0.45 ± 0.35	-	0.530
		Large	0.21 ± 0.19	0.24 ± 0.25	0.43 ± 0.41	-	

Table 1.3. Larval development after initial starvation periods of 3, 4, and 5 d in 2001. Development variables (mean ± 1 S.E.) for stages I-III and postlarvae (PL) were pooled by maternal size (small < 90 mm CL, large > 90 mm CL) and tested for differences with A (P values are reported at the right).

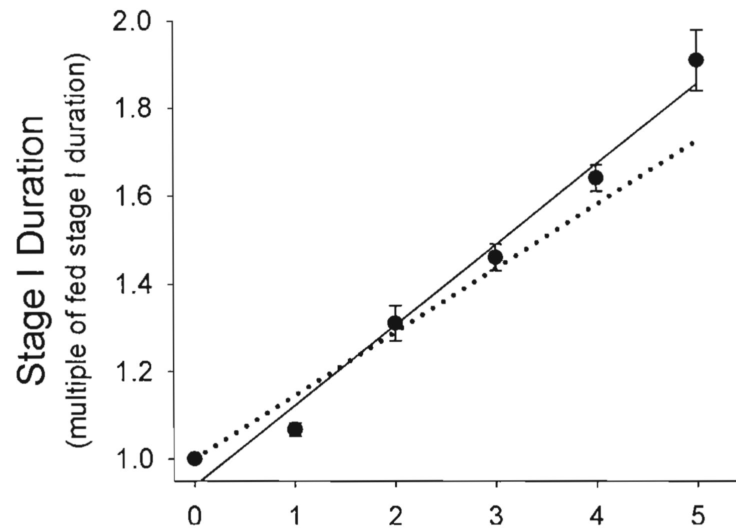


Figure 1.5. Mean (± 1 S.E.) duration of stage I as a function of initial starvation period ($y = 0.183x + 0.939$, $r^2 = 0.97$, $n = 6$, $P < 0.001$) Stage I duration is expressed as a multiple of the mean stage I duration of larvae fed *ad libitum*. Data are from 1999 (1 and 2 d starvation) and 2000 (3, 4, and 5 d starvation). Dotted line depicts predicted delay in development if delay in development were equal to starvation period.

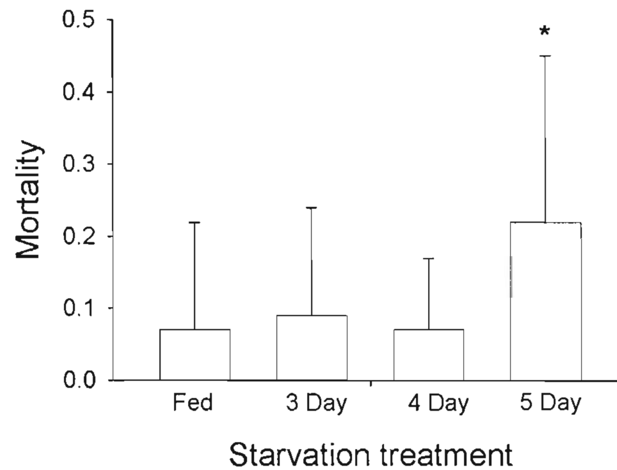


Figure 1.6. Mortality (mean ± 1 S.D.) in stage I larvae in *ad libitum* feeding and starvation treatments. Data from both maternal size categories has been pooled by treatment to test for treatment effects with ANOVA. Significant differences (P < 0.05) are denoted by an asterisk (*).

Year	2000		2001	
Variable	Pearson Index	Bartlett χ^2	Pearson Index	Bartlett χ^2
Larval Mass (stage I)	0.669	0.017 *	0.755	0.003 *
Carapace Length (stage I)	-0.343	0.275	0.450	0.093
Molt Increment (first molt)	0.624	0.030 *	-0.110	0.697
Stage I Duration (stage I)	0.243	0.447	0.114	0.685
Carapace Length (postlarvae)	-0.073	0.822	0.572	0.032 *
Mortality (cumulative)	0.234	0.464	0.150	0.593
Development Time (to postlarva)	-0.037	0.910	-0.025	0.933

Table 1.4. Pearson correlation coefficients and associated probabilities (Bartlett Chi-squared) for embryo weight versus developmental variables in larvae reared with *ad libitum* feeding. Significant correlations (P < 0.05) are denoted by an asterisk (*).

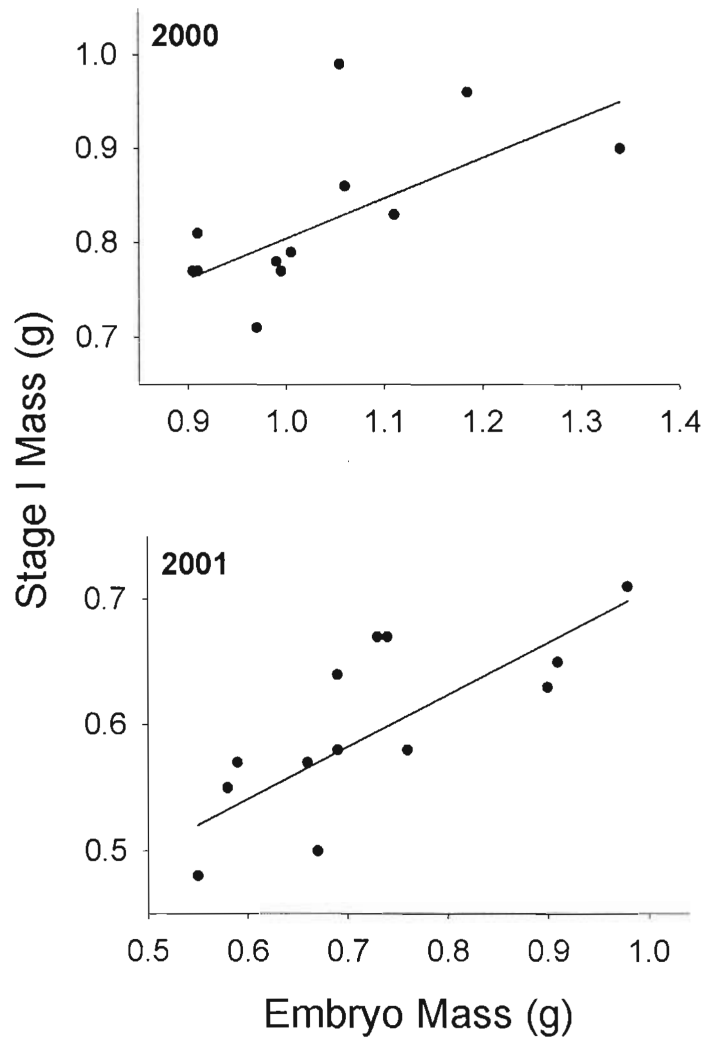


Figure 1.7. Average mass (dry weight) per newly hatched stage I larvae as a function of mass per embryo in 2000 (top) and 2001 (bottom). Regressions were significant in both 2000 ($Y = 0.428X + 0.377$, $r^2 = 0.44$, $n = 12$, $P = 0.020$) and 2001 ($Y = 0.414X + 0.293$, $r^2 = 0.58$, $n = 13$, $P = 0.003$).

these analyses. There was no statistically significant correlation between embryo mass and stage I larva CL in either year, but significant positive correlations were detected between embryo mass and molt increment in 2000, and postlarval CL in 2001. Stage I mortality was not included as a factor in the correlation matrix due to the high number of zeros (only 3 non-zero points). Cumulative mortality (first three instars), duration of stage I, and total development time (through postlarval instar) were not correlated with embryo mass.

Egg mass and stage I duration were negatively correlated in starvation treatments (Table 1.5). As embryo mass increased, the development time decreased linearly (Fig. 1.8). One case in the 5 d starvation treatment was identified as an outlier (Dixon test, Sokal and Rohlf 1995) and was not included in the correlation analysis. Stage I mortality declined with embryo mass only in the longest initial starvation treatment. Total development time (to postlarval instar) also decreased with increasing embryo mass in the 4 d starvation treatment. We found no significant correlations between embryo mass and any of the other developmental variables measured.

Discussion

Female size was a poor predictor of mass per embryo for lobsters in central Maine coastal waters in 2000 and 2001. Embryo mass increased slightly with maternal carapace length as reported for Gulf of Saint Lawrence populations (Attard and Hudon 1987, Ouellet et al. 2003), but the relationship was not statistically significant (Fig. 1.2) and explained less than 15% of the variation in embryo mass. We also found no consistent relationship between the sizes of reproductive females and stage I larvae (Fig. 1.3).

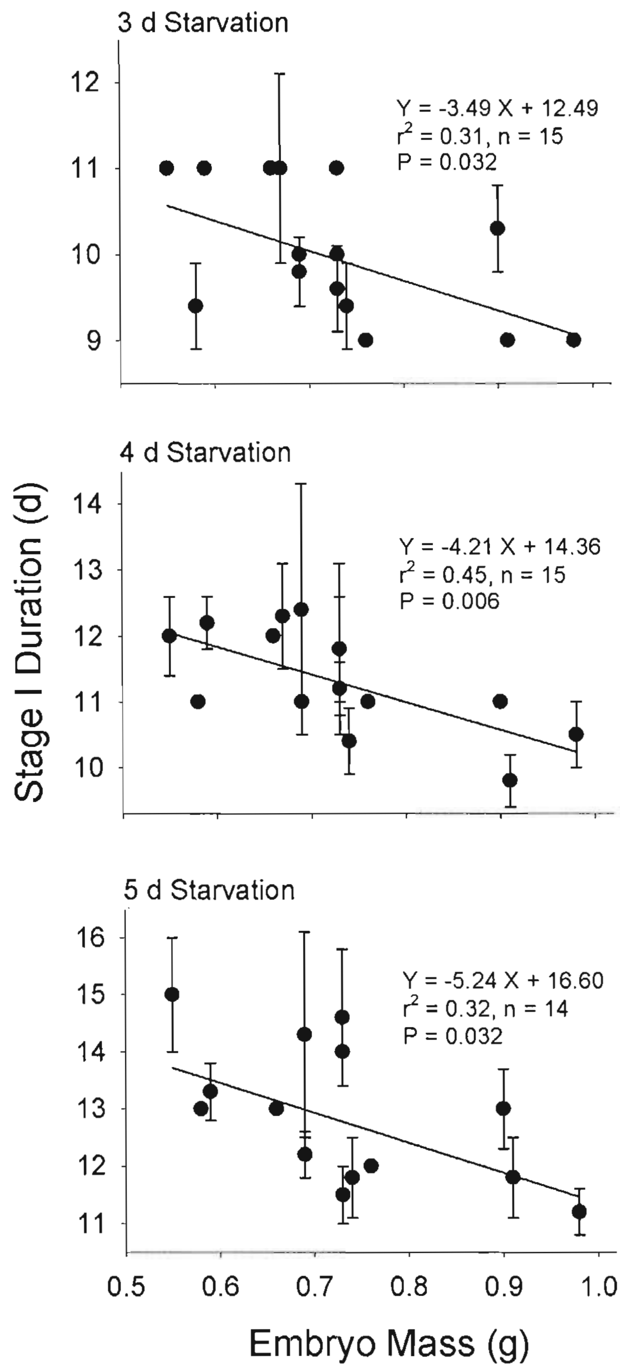


Figure 1.8. Duration of stage I (mean ± S.D.) as a function of mass per embryo (dry weight) in larvae subjected to initial starvation periods of 3 d (top), 4 d (middle), and 5 d (bottom). Regressions were significant in all three treatments.

Variable	Treatment	Pearson Index	P
Molt Increment (first molt)	3 Day	-0.080	0.777
	4 Day	0.194	0.489
	5 Day	0.419	0.120
Stage I Duration	3 Day	-0.556	0.031 *
	4 Day	-0.660	0.007 *
	5 Day	-0.565	0.035 *
Mortality (stage I)	3 Day	0.109	0.700
	4 Day	0.362	0.185
	5 Day	-0.643	0.010 *
Carapace Length (postlarvae)	3 Day	0.139	0.622
	4 Day	0.284	0.326
	5 Day	0.336	0.286
Mortality (cumulative)	3 Day	-0.031	0.912
	4 Day	-0.332	0.226
	5 Day	-0.240	0.389
Development Time (to postlarva)	3 Day	-0.288	0.298
	4 Day	-0.625	0.017 *
	5 Day	-0.510	0.090

Table 1.5. Pearson correlation coefficients and associated probabilities (Bartlett Chi-squared) for embryo mass (dry weight) versus developmental variables in larvae subjected to initial starvation periods of 3, 4, and 5 d. Significant correlations ($P < 0.05$) are denoted by an asterisk (*).

It is possible that the lack of statistical significance resulted from insufficient samples size as only 12 and 15 lobsters were used in the 2000 and 2001 experiments respectively. However, Plante (2001) found a statistically significant increase in stage I size with increasing maternal carapace length using only 8 females from Anticosti Island in the Gulf of Saint Lawrence. Similarly, Sibert *et al.* (2004) found that larger eggs were produced by the larger of 7 lobsters used in their experiments. This suggests that our sample sizes should not have prevented us from detecting a pattern. Variation in among individual females is high with respect to both embryo mass and stage I CL even when significant relationships exist. Plante (2001) sampled at the extremes of female size to capture the greatest possible effect of size, but still found that half of the small lobsters had an embryo mass and larval size that would be expected from a large lobster. Furthermore, female size typically accounts for less than 25% of the variation in embryo size making it difficult to use the size of reproductive females as a predictive tool (Attard and Hudon 1987, Ouellet et al. 2003).

The inter-annual difference in embryo mass was greater than variation within each year, and may have resulted from lower winter temperatures in 2001. Embryogenesis is highly temperature dependent with negligible development occurring below 4°C (Perkins 1972, Sibert et al. 2004). Preceding the 2001 hatch winter bottom temperature fell below 4°C one week earlier and returned to temperatures above 4°C one month later than in 2000 (Fig. 1.1). Sasaki *et al.*(1986) reported lower lipid reserves in embryos reared at colder temperatures and interpreted the difference as the combined effects of less efficient development at low temperatures and the metabolic cost of longer development time at colder temperature. The incubation period preceding the 2001 hatch

had lower cumulative degree days, and fewer days above 4°C providing a possible explanation for lower embryo mass. Alternatively, the difference in embryo mass could have been due to the use of different preservation methods each year. Preservation methods and sample handling including formaldehyde, freezing, and distilled water rinses reduce dry weight measurements in zooplankton (Omori 1987, Williams and Robins 1982), and embryo mass reported here is probably an underestimate. While the formaldehyde preservation and distilled water rinses were similar for both years, the freezing of 2001 samples prior to chemical preservation could have resulted in greater loss of biomass. Thus, we could not discount the possibility that preservation methods were responsible for lower embryo mass in 2001.

The importance of the relationship between maternal size and embryo size appears to vary regionally and possibly as a function of bottom temperature regime. In areas with warmer summer temperatures such as the Gulf of Saint Lawrence, southern Gulf of Maine and south of Cape Cod the developmental variables of the offspring (e.g. embryo mass, egg diameter, or stage I larva CL) increase significantly with maternal carapace length (Attard and Hudon 1987, Estrella and Cadrin 1995, Plante 2001, Sibert et al. 2004). Lobsters in these areas reach maturity at a smaller size (Fogarty 1995, Waddy and Aiken 1991). If small lobsters allocate proportionally more energy to growth and less to reproduction as suggested by Attard and Hudon (1987), first time spawners may produce significantly smaller embryos in areas such as the Gulf of Saint Lawrence and southern Gulf of Maine. Larger size at maturity in the central and northern Gulf of Maine and the Bay of Fundy (Waddy and Aiken 1991) may offset the difference in egg size among first time spawners resulting in a poor relationship between maternal size and

egg mass. Lobsters collected around Grand Manan Island (Bay of Fundy) had no relationship between maternal CL and egg diameter (Ouellet et al. 2003), and we found no significant relationship between maternal CL and either egg mass or stage I larva CL in lobsters from the central Maine coast. Patterns of seasonal migration and wintering temperature may also contribute to regional differences. The reproductive lobsters near Grand Manan Island typically migrate to deeper, warmer water in the Gulf of Maine during the winter to maximize degree-days for embryo development (Campbell 1986, Campbell 1990). A similar offshore movement occurs in the central Maine coast (R. S. Steneck, unpublished data) suggesting that these populations share a common winter temperature regime. Seasonal migration of lobsters in the Magdalen Islands appears to be more restricted with lobsters over-wintering near the mouth of lagoons (Munro and Therriault 1983), resulting in exposure to colder winter temperatures in the Gulf of Saint Lawrence (Campbell and Stasko 1986). If small lobsters start out with slightly smaller eggs, the additional metabolic demand of colder winter bottom temperatures (Sasaki et al. 1986), coupled with lower developmental efficiency in small eggs (Sibert et al. 2004), could serve to exacerbate differences in embryo mass as a function of maternal size.

None of the larval development variables corresponded with maternal size (Table 1.2), probably due to the lack of relationship between maternal size and either embryo mass or larval CL. Larval development times and sizes were consistent with previous studies (MacKenzie 1988, Sasaki et al. 1986, Templeman 1936), but we found no difference between maternal size classes with respect to larval size, molt increment, or development time. We found no difference in mortality between maternal size classes, but high variability among individual females and between years made trends in mortality

difficult to detect. The survival time of newly hatched larvae in response to complete starvation showed no significant difference between maternal size classes (Fig. 1.4). Lack of a relationship between maternal size and embryo mass indicates that there was no initial difference in energy reserves that might lead to differential survival. None of the development variables varied among maternal size classes in any of the sub-lethal starvation treatments (Table 1.3). With respect to the variables measured here, we found no survival or developmental advantage imparted to larvae as a function of maternal size for lobsters in the central Maine coastal waters.

The experiments examining development and starvation were conducted with the null hypothesis that there was no difference between larvae from large and small lobsters. The preponderance of negative results raises the possibility of type II error (accepting a null hypothesis that is false). With the exception of mortality, the variance was typically very low (S.E. $<$ 5% of the mean; Table I, II); if substantial differences existed we should have been able to detect them. Even if a type II error occurred the difference between means was so small that its biological relevance would be questionable. Furthermore, there were no consistent trends between years suggesting that there was no difference between maternal size groups rather than actual differences that were too small to be distinguished with the sample sizes used in this study.

We found significant treatment effects in the initial starvation period experiment in both stage duration and mortality, and the response of *H. americanus* to starvation periods was consistent with observations in other decapod crustaceans. Mortality in stage I larvae increased with starvation (Fig. 1.6), but only in the 5 d starvation treatment. The point of no return (PNR_{50} *sensu* Anger and Dawirs 1981) occurs when 50% of starved

larvae can no longer complete development even if feeding commences. PNR_{50} occurs in *Hyas araneus* zoeae at approximately half of the maximum survival time during starvation (Anger and Dawirs 1981), or approximately eight days for *H. americanus* based on our complete starvation experiment. Our starvation treatments did not extend to the PNR_{50}, but if Anger and Dawirs's sigmoidal mortality curve is correct and is applicable to *H. americanus*, we would have reached PNR_{50} after seven or eight days of starvation. The linear delay in stage I duration (Fig. 1.5) was similar to that described for several species of crab zoeae (Anger and Dawirs 1981, Anger et al. 1981b). Anger and Dawirs (1981) observed that the regression of larval instar duration versus initial starvation period in *Hyas araneus* (brachyurian crab) was higher than would be expected if the delay in development were equal to the duration of the starvation period. They suggested that this reflects compensation for energy losses during starvation. Our regression line falls very close to the expected delay in the shorter starvations treatments but is higher than expected in the longer starvation treatments. This suggests that the deleterious effects of starvation increase with the starvation period. Deviation from the expected delay in *H. araneus* was most evident in starvation periods exceeding five days (Anger and Dawirs 1981) and it is seems likely that longer starvation periods would have yielded similar results in our experiments.

Developmental variables varied as a function of embryo mass indicating that embryos with greater mass do produce larvae that are potentially more viable (Tables 1.4 and 1.5). Others have proposed that greater egg mass in lobsters (positively correlated with caloric content) confers energetic advantages to the larvae (Attard and Hudon 1987, Sasaki et al. 1986), but it is not known if this additional energy is actually transferred to

newly hatched larvae. If mass is considered a proxy for caloric content our results suggest that the advantage is indeed conferred upon the larvae as heavier embryos produced heavier stage I larvae (Fig. 1.7). Our findings are consistent with the relationship between embryo and zoea I mass reported for the crab *Chasmagnathus granulata* (Gimenez and Anger 2001).

Our results indicate that newly hatched larvae from heavier embryos are more resistant to starvation. Stage I duration did not vary with embryo mass in the fed treatments (Table 1.4), but in starvation treatments the larvae from heavier embryos experienced less delay in development (Fig. 1.8). Lipids and carbohydrate are metabolized first in response to starvation in decapod crustacean larvae (Anger 2001) and greater mass probably reflects higher lipid content in lobster embryos (Sasaki et al. 1986). Therefore, it is likely that increased resilience of larvae from heavier embryos was due to greater lipid stores in the newly hatched larvae. Another developmental advantage imparted to the larvae of heavier embryos appears to be lower rate of mortality in response to starvation. The 5 d initial starvation was the only treatment to exhibit elevated mortality in response to starvation (Fig. 1.6), and mortality within that treatment decreased with increasing embryo mass (Table 1.5). Patchy distribution of plankton (Omori and Hammer 1982, Verity and Smetacek 1996) can result in periods of limited food availability, and Thorson (1950) proposed that starvation in the plankton played an important role in the successful recruitment of benthic species with planktonic larvae. The effects of larval starvation are thought to be particularly important in crustaceans (Olson and Olson 1989), and the initial feeding period is critical to their successful development (Anger and Dawirs 1981, Anger et al. 1985). The larvae from heavier

embryos exhibited greater resilience to periods of starvation which is likely to provide a survival advantage in the field.

In fed larvae, molt increment at first molt and postlarval size both increased with embryo mass (Table 1.4). While there appears to be an advantage to the developing larvae, the results were inconsistent between years and should be interpreted cautiously. Increased carapace length in postlarvae that are competent to settle could provide a survival advantage as recapture rates of tagged newly settled postlarvae indicate that post-settlement mortality decreases with increasing size (James-Pirri and Cobb 2000). The advantage of greater molt increment is less clear but may confer a size dependent advantage in the second instar or simply reflect more robust development.

Our observations of development and response to starvation are consistent with previous studies of larval development in crabs and *H. americanus*. We conclude that heavier embryos do produce larvae with developmental and survival advantages including faster recovery and improved survivorship in response to starvation. Contrary to our expectations, we found no evidence of developmental advantage as a function of maternal size due to a lack of relationship between maternal CL and embryo mass. In regions where embryo mass is proportional to maternal size we would expect larval success to vary as a function of maternal size. Unfortunately, the relationship between maternal CL and egg weight is typically fraught with high variation among individuals indicating that further research needs to address the factors driving intra-specific variation in embryo size. Variables such as maternal diet (Castell and Budson 1974) and winter bottom temperature (Sasaki et al. 1986) may play a greater role in caloric content of embryos at the time of hatch and successful larval development than the maternal size.

Regional and inter-annual variation in these factors may provide a basis for incorporating variable egg quality into management of the fishery.

2. TEMPERATURE EFFECTS ON VERTICAL DISTRIBUTION OF LOBSTER POSTLARVAE (*HOMARUS AMERICANUS*)

Abstract

Planktonic larvae regulate depth based on the interaction between environmental variables, ontogenetic changes in behavior, and physiological tolerances of the organism. American lobster (*Homarus americanus*) postlarvae are predominately neustonic, yet we understand little about their behavioral response *in situ* to changing environmental conditions and ontogenetic changes. Understanding how these responses affect the vertical distribution will improve estimates of abundance which are typically based on neuston samples and rely on knowing what portion of the population is represented at the surface.

Direct observation of postlarvae *in situ* was used to quantify behavioral regulation of depth with respect to intrinsic and extrinsic factors. Postlarvae spent 65% of the time at the surface (0-0.5m depth), which is lower than expected from previous surveys using plankton nets. More importantly, the proportion of time spent at the surface decreased over the course of the season (from ~0.80 to ~0.57) and was correlated with increasing depth of the 12°C isotherm. Postlarvae remained above the 12°C isotherm suggesting that it may serve as a minimum temperature threshold. Daily variation around the seasonal trend was correlated with the depth of the thermocline. Seasonal and daily trends were removed and residual data were averaged over the entire season to examine vertical distribution as a function of the time of day. Postlarvae spent more time at the surface in the morning and late afternoon while the proportion of time spent at the surface

was lowest at noon. This shift in vertical distribution was not correlated with light intensity indicating that is may be part of an endogenous rhythm. When the data were parsed with respect to light intensity and developmental stage, an ontogenetic shift was observed from positive to negative phototaxis within the postlarval stage. The relationship of postlarval vertical distribution to the intrinsic and extrinsic factors considered was consistent with previous laboratory and field observations of behavior and improves our ability to predict the proportion of the population represented in neuston samples.

Introduction

Larval settlement often drives the abundance and distribution of marine benthic organisms (Gaines and Roughgarden 1985). However, the interplay between larval behavior and hydrography leading to settlement is poorly understood for many species. This is due in part to the inherent difficulty of sampling a planktonic phase which is often hyper-dispersed, patchily distributed, or of unpredictable vertical distribution. The planktonic larvae stage of many species includes a neustonic phase (e.g. fish (Doyle et al. 1995), spiny lobsters (Lyons 1980), crabs (Shanks 1985), and barnacles (Grosberg 1982)) which may facilitate quantitative sampling by concentrating larvae in surface waters, effectively limiting the distribution to two dimensions. However, this methodology relies on the tacit assumption that the larvae remain in the neuston for the duration of that stage. If significant intra-stage behavioral or environmental changes occur, estimates of distribution and abundance based on neuston samples could be in error.

The larvae of the American lobster (*Homarus americanus*) provide an excellent example of a life stage that has been quantified extensively using surface sampling techniques. While its first three larval stages are broadly distributed in the water column, the fourth planktonic stage (postlarva) is believed to be primarily neustonic and has been sampled at the surface in most studies quantifying distribution and abundance (Ennis 1995). Such abundance estimates have been used to estimate postlarval production, its relationship to settlement (Incze and Wahle 1991, Incze et al. 1997, Incze et al. 2000b), and ultimately landings in the lobster fishery (Fogarty and Idoine 1986, Miller 1997). The accuracy of abundance estimates derived from plankton samples relies on knowing what proportion of the population resides in the neuston. Most estimates from plankton net samples place 75-90% of the postlarval population in the top 0-0.8m of the water column (Harding et al. 1987, Harding et al. 1982, Hudon et al. 1986), but is the proportion constant or does it vary with changing environmental conditions?

Observations in the field and laboratory suggest that the proportion of postlarvae at the surface is not constant, and that the swimming behavior of the postlarvae varies with intrinsic and extrinsic factors. Temperature sensitivity with respect to both behavior and development are potential mechanisms for changes in vertical distribution. Strong thermoclines may serve as a thermal barrier to vertical movements with postlarvae remaining above the thermocline. The most convincing evidence of this comes from laboratory studies by Boudreau et al. (1991, 1992), who demonstrated in an artificial water column that the proportion of postlarvae at the surface increased with decreasing thermocline depth and increasing thermocline strength (although their thermocline strength was much stronger than thermoclines typically encountered in the field). In

addition to the thermal structure of the water column the actual temperature may also play a role in vertical distribution as growth and development of postlarvae are highly temperature dependent with an optimal growth rate in the 15-17°C range and a sharp increase in mortality at temperatures below 12°C (MacKenzie 1988). Thus, there is a strong incentive for postlarvae to remain in warm surface waters. Light intensity has also been implicated as a controlling factor in the field where more postlarvae are captured at the surface on cloudy days than in bright sun (Hudon et al. 1986), and anecdotal reports indicate the abundance of postlarvae in surface waters is lowest at noon and highest near sunrise and sunset (Harding et al. 2000, R.J. Miller personal communication, personal observation). However, both laboratory and field studies have reported no difference in the vertical distribution between day and night (Boudreau et al. 1992, Ennis 1975, Harding et al. 1987). An ontogenetic shift in phototaxis from positive to negative observed in laboratory studies (Botero and Atema 1982, Hadley 1908) provides an intrinsic mechanism for deeper vertical distribution with age.

Environmental factors such as light and thermal structure likely interact with larval behavior and ontogeny to drive changes in the proportion of the population residing in surface waters, but we have yet to account for these factors in estimates of total abundance derived from plankton samples. This is because we have a poor understanding of the relationship between environmental conditions and the proportion of postlarvae represented in surface samples. Lobster postlarvae are naturally low in abundance (typically < 20 $1000m^{-3}$, Incze et al. 1997) making it difficult to quantify vertical distribution using plankton net samples (Fogarty 1983, Harding et al. 1987), and temporal changes in a surface abundance may be due to changes in environmental

variables or simply the advection of organisms to and from the sampling site (Incze et al. 2000a). Although laboratory studies have provided detailed accounts of larval swimming behavior and vertical distribution, these results have not been validated *in situ* using natural populations of postlarvae.

The objective of the present study was to quantify the behavioral response of postlarvae to changing environmental conditions *in situ*. How do the intrinsic characteristics of postlarval behavior interact with the extrinsic hydrographic and environmental conditions in the period leading to settlement? Specifically, I tested the hypotheses that thermocline depth and magnitude, temperature, light intensity, and the age of postlarvae exert control over postlarval vertical distribution. To circumvent problems associated with plankton net sampling, I observed individuals *in situ* to quantify the vertical distribution of postlarvae. Behavioral observations of larvae *in situ* have been used in studies of fish (Leis and Carson-Ewart 1997, 2001), ascidians (Bingham and Young 1991, Stoner 1992, Young 1986), and crabs (Shanks 1985). Previous observations of lobster postlarvae *in situ* have provided valuable information on behavior, settlement, and swimming direction and speed (Cobb et al. 1983, Cobb et al. 1989b, Ennis 1975), suggesting that the method might be useful for quantifying the vertical distribution of postlarvae.

Methods

Experiments were conducted in the coastal waters of the Gulf of Maine off Boothbay, Maine, USA (~ 43°45.5' N, 69°38.0 W), at least 1 km from the nearest shore with a minimum water depth of 30m. Lobster postlarvae were collected in the morning

(0700-1000 local time) using a neuston net that sampled to a depth of 0.5 m. Neuston tows were limited to ten minutes to minimize damage to postlarvae in the codend, and only individuals with both claws and no signs of damage were used in experiments. These individuals were presumed to be in good health as they survived for several weeks when held in aquaria after capture (personal observation). Postlarvae were held individually in 500 ml clear polycarbonate containers in a water bath at ambient light intensity and sea surface temperature until their release (< 5 hours). SCUBA divers released a postlarva at a depth of 0.5-1.0 m and followed it for ten minutes with ~0.5 m separation between diver and postlarva. A small CTD (Minisonde 4a, Hydrolab Corporation) was mounted on the diver's forearm so that sensors could be maintained at the same depth as the postlarva to record a depth profile and environmental parameters (5s sample interval). The postlarva was recaptured in the jar at the end of the trial and transported to lab for determination of molt stage (methods of Sasaki 1984). Observations were limited to a maximum depth of 15 m and trials were terminated when the postlarva descended below this depth. Observation of postlarvae *in situ* without prior capture as a control for handling effects was not feasible due to the low abundance of postlarvae in the plankton. In over 50 person-hours of underwater observation time during the trials we encountered only one free-swimming postlarva.

Environmental parameters were recorded for each trial including: CTD cast 0-20 m (SBE-19, Sea Bird Electronics, Seattle, WA), light intensity from 0-10 m (Li-Cor, LI-188b with a LI-193SB spherical quantum sensor), wind velocity (Kestral 2000 wind meter), wind direction (hand held compass), and wave height (estimated). CTD casts were used to determine thermocline, halocline, and pycnocline depths and gradients, and

the depth of isotherms from 11-18°C (in 1°C increments). Clines were identified by calculating the rate of change of the measurement with depth (data were averaged in 0.5 m bins). The depth bin with the greatest rate of change was considered the depth of the cline and the rate of change reported as the gradient of the cline. Light attenuation at 1 and 5 m depths was calculated relative to light intensity approximately 2 m above the sea surface. 168 trials were completed between July 19 and September 14, 2002 (4-15 trails per day) between 0930 and 1500 local time. Twenty-seven postlarvae were lost before the ten minute trial was completed but the data were included in the analyses.

The total amount of time each postlarva spent above 0.5 m depth was used to determine the proportion of time at the surface. Proportion at the surface values had lower variance during the first minute of the trials, but variance increased by about 15% between the first and second minute and remained at that level or slightly higher for the last nine minutes of the ten minute trial period. Low variance in the first minute was likely due to the postlarvae being released at the same depth. Accordingly, the first 60 seconds of data were omitted from all analyses. Minimal increases in variance during the last nine minutes of the trial suggest that the trial duration was sufficient to quantify the vertical swimming behavior of the postlarvae.

Seasonal variation in the proportion at the surface was examined with correlation and regression analyses to determine relationships between daily averages of proportion at surface and environmental variables. Daily variation in the proportion at the surface was examined by removing the seasonal trend and re-analyzing the residuals with respect to environmental variables. Time of day effects were also examined using the de-trended data, but the proportion at the surface was pooled from the entire season and averaged in

1 hour bins rather than using daily averages. Analysis of molt stage and light intensity effects was also conducted on proportion at surface values pooled over the whole season but the seasonal trend was not removed because there was no seasonal trend in molt stage and necessary temperature data were not available for many of the trials (the 12°C isotherm was below the depth of the CTD cast).

Results

Vertical swimming behavior was qualitatively categorized with respect to vertical position as surface, subsurface, or sounding (Fig. 2.1). "Surface" individuals spent the majority of time in the top 0.5 m of the water column. "Subsurface" postlarvae spent most of their time below 0.5 m but typically remained in the top 4.0 m. Individuals exhibiting "sounding" behavior descended below 4.0 m, usually followed by a return to shallower depth. In half of the observations of sounding behavior the dive was initiated near the end of the trial and the return to the surface was not observed. On two occasions individuals sounded to a depth in excess of our working depth resulting in the termination of the trial. The swimming behavior of postlarvae resulted in a continuum of dive profiles between the categories depicted in Figure 2.1, but most could be categorized as one of the three behavior types.

Postlarvae swam in a manner consistent with previous observations using pleopods with claws either together and extended forward or held apart at approximately 45° to the body axis (Botero and Atema 1982, Cobb et al. 1983, Ennis 1975). Swimming was nearly continuous in all trials, though postlarvae spent up to a minute orienting immediately following release. Ascent and descent were typically active, involving a

change in the angle of swimming, but descents were occasionally passive. In these cases the postlarva ceased swimming, spread its claws, arched its tail and allowed itself to sink. Postlarvae actively avoided floating weed, seagrass, and debris by swimming either around or below the obstacles but never taking refuge near them. The vertical position of postlarvae was unaffected by sea state, even when trials were conducted in seas exceeding 1 m. Breaking waves and occasional boat wakes tumbled postlarvae swimming very near the surface, but postlarvae quickly reoriented and usually continued swimming near the surface.

Observation of behavior *in situ* raises the question of whether observer presence influences the behavior of the organism. This possibility cannot be completely discounted, but the presence of divers appeared to have little effect on the behavior of the postlarvae. Lobster postlarvae use a tail-flick escape behavior but rarely exhibited this behavior during trials. Orientation with respect to the diver was not consistent and on several occasions postlarvae were lost when they turned and swam directly into the diver. Previous *in situ* observations of behavior have also reported that the postlarvae appeared uninfluenced by diver presence (Cobb et al. 1983, Ennis 1975).

Postlarvae spent more time in the top 0.5 m than at any other depth (Fig. 2.2). The time spent in the 0-0.5 m depth bin accounts for 65% (± 3, S.E.) of the observation time when averaged over all 168 trials. Observations in the top 4.0 m account for 94% (± 1, S.E.) of the total time. The average swimming depth was 0.92 m (± 0.11, S.E.) and the average maximum depth reached was 2.23 m (± 0.22, S.E.). The maximum depth reached by an individual was 16.48 m and this individual was recaptured while continuing to descend. During the 168 trials, 28 individuals exhibited sounding behavior

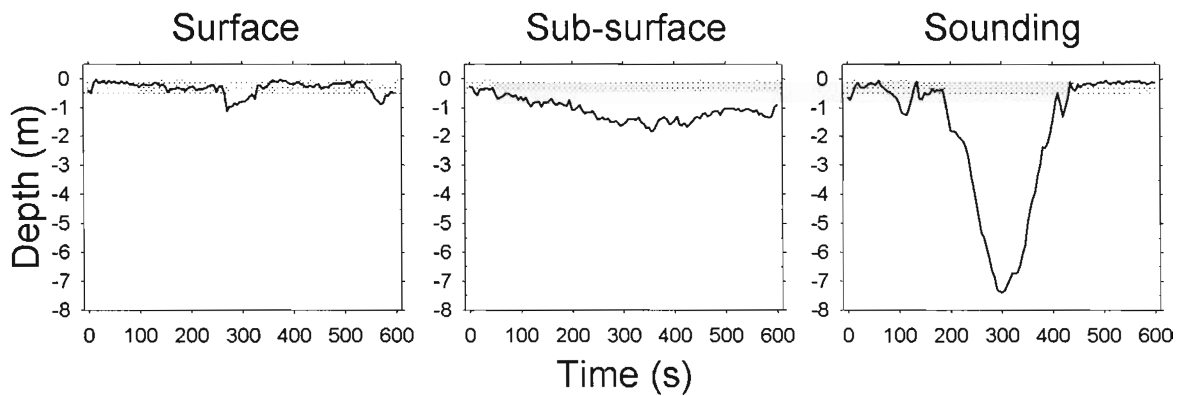


Figure 2.1. Representative dive profiles of three lobster postlarvae illustrating the three defined swimming behaviors: surface, subsurface, and sounding. Depth profiles were recorded with a CTD mounted on a divers forearm in five second intervals. The shaded area denotes the 0-0.5 m depth bin typically sampled by neuston nets.

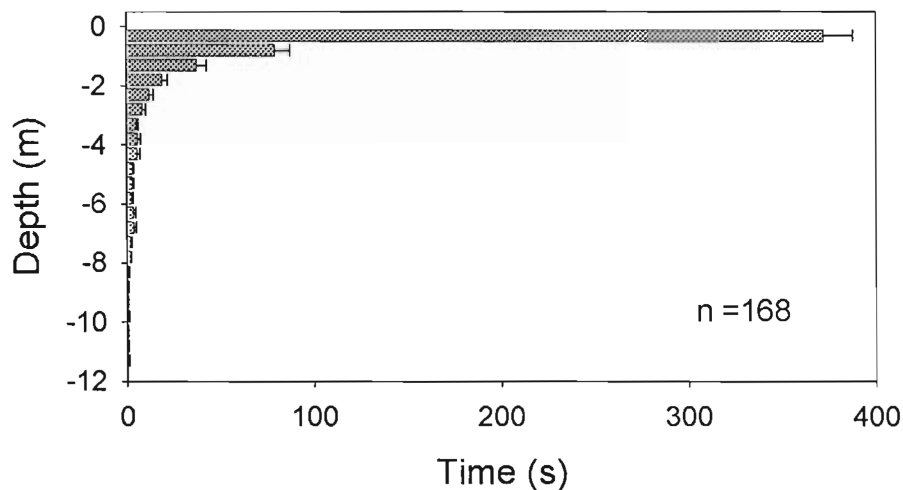


Figure 2.2. Vertical distribution of postlarvae as a function of the average amount of time spent at in each 0.5 m depth bin. Time spent in the surface 0-0.5 m bin accounts for 65% of the total observation time. Error bars denote +1 S.E.

and the frequency of sounding was 1.08 dives $indiv^{-1}hour^{-1}$ (*sensu* Incze and Wahle 1991). The sample size was insufficient to determine whether diving frequency increased with molt stage.

Postlarvae spent the greatest amount of time in water temperatures between 15.5 and 16.5°C, and rarely descended into water below 12°C (Fig. 2.3). Time spent at each temperature (0.5°C intervals) was summed across all 168 trials, and the amount of time spent at each temperature reflects the combined effects of larval swimming behavior and the distribution of available temperatures. The dotted line in Figure 2.3 illustrates the availability of temperatures as the proportion of trials in which each temperature was present (in the upper 20 m of the water column). It is noteworthy that the cumulative time spent at each temperature below 16°C decreased despite an increasing proportion of trails in which the temperature was available. This suggests that the decrease in time spent at lower temperatures was the result of larval swimming behavior rather than availability of the temperature. In contrast, time spent at temperatures above 17°C may have resulted from decreasing availability of the temperature in the trials.

Proportion of time at the surface decreased from ~ 80% to ~ 57% over the course of the season (based on regression values from Fig. 2.4). Each data point represents the daily average of the proportion at the surface including all trials from that day (n = 4-17). Data from one day (DOY 214) were discarded from this analysis as an outlier. Subsequent analyses addressed the environmental factors driving the seasonal trend in proportion at the surface using correlation analysis of the daily averages. Proportion at the surface increased significantly with decreasing isotherm depth for both the 11 and 12°C isotherms (Table 2.1, Fig. 2.5). A similar relationship existed with temperatures 13,

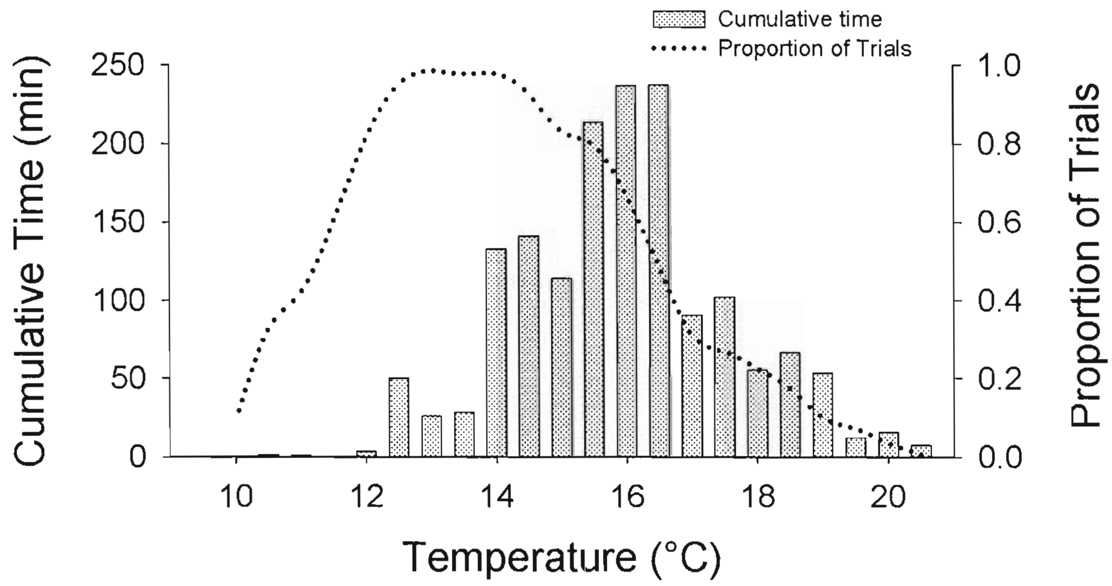


Figure 2.3. The cumulative amount of time spent at each temperature in 0.5°C increments (bars) and the proportion of trials for which that temperature was present (dotted line). The cumulative amount of time at each temperature reflects postlarval behavior and the proportion of trials represents the availability of each temperature.

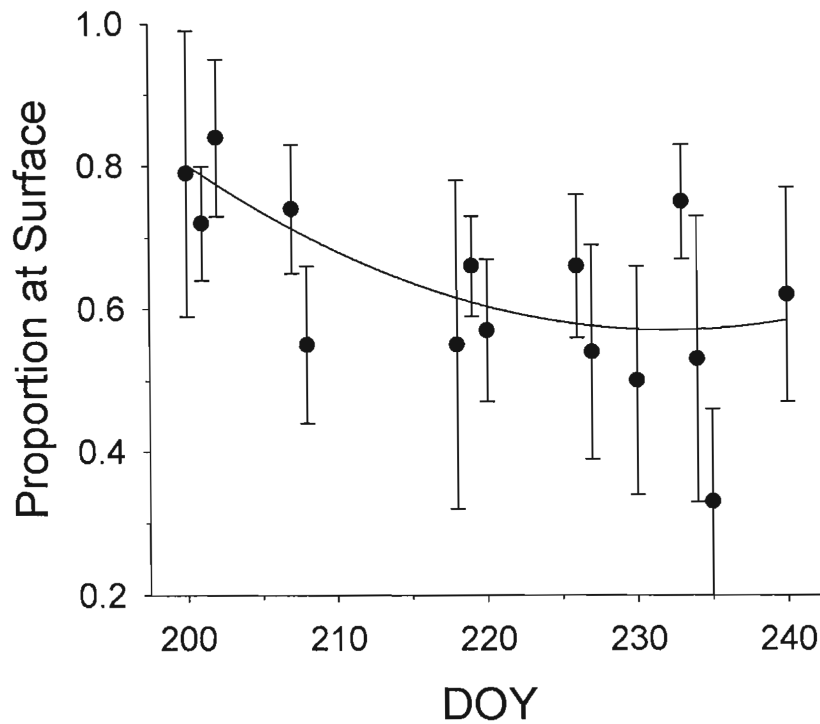


Figure 2.4. Seasonal progression of mean proportion at the surface from July 19-August 28, 2002. Proportion at the surface represents the proportion of time each postlarva spent in the 0-0.5 m depth bin during a 10 min trial. Daily means include data from 4-15 trials and error bars denote ± 1 S.E. Data were fitted to the regression equation: $Y = 0.0002X^2 - 0.104X + 12.642$ ($r^2 = 0.44$, $P = 0.032$).

14 and 15°C but the correlations were not significant ($0.05 < P < 0.10$). No other environmental variables were significantly correlated with the proportion at the surface. The 12°C isotherm was selected for regression analysis because the time spent at temperatures below 12°C was negligible (Fig. 2.3), suggesting that it may be a minimum temperature threshold for postlarvae. The 12°C isotherm descended linearly during our sampling period (Fig. 2.6), and late in the season the deeper isotherm depth corresponded to lower proportion at the surface values.

The seasonal progression of the 12°C isotherm only explained 49% of the variation in the proportion at the surface. To determine the nature of daily variation about this seasonal trend, I de-trended the daily averages of proportion at the surface data by subtracting the regression in Figure 2.5, and used correlation analysis to identify relationships between the residuals and environmental variables (Table 2.1). The depth of the thermocline and the pycnocline were the only two significant correlations and halocline depth was nearly significant ($P = 0.07$). In most trials the thermocline, halocline, and pycnocline all occurred at the same depth so the correlation of all of these variables with the residuals was expected. The residuals increased with decreasing thermocline depth (Fig 2.7), and these daily variations in thermocline account for 44% of the variance about the seasonal trend. Although the thermocline was deepest at the end of the season it was highly variable throughout and did not exhibit a significant linear trend (Fig. 2.8). There was no relationship between the proportion at the surface residuals and the magnitude of the temperature gradient. The minimum and maximum thermocline gradients were 0.16 and 2.73°Cm^{-1} respectively and the average was 1.20°Cm^{-1} (based on temperature change over 0.5 m increments).

	Proportion at the surface		Residuals	
Environmental Variable	**Coefficient**	**P**	**Coefficient**	**P**
Surface temperature (0.5 m depth)	-0.470	0.090	0.224	0.441
Themocline depth	0.189	0.518	0.595	*0.025
Themocline gradient	0.302	0.293	-0.148	0.613
Halocline depth	0.301	0.295	0.501	0.068
Halocline gradient	0.140	0.634	0.165	0.573
Pycnocline depth	0.265	0.359	0.568	*0.034
Pycnocline gradient	-0.072	0.808	0.240	0.408
11°C isotherm depth	0.815	**0.007	-0.231	0.508
12°C isotherm depth	0.700	**0.008	0.201	0.490
13°C isotherm depth	0.497	0.071	0.315	0.273
14°C isotherm depth	0.479	0.083	0.227	0.435
15°C isotherm depth	0.522	0.067	0.301	0.318
16°C isotherm depth	0.212	0.531	0.002	0.996
17°C isotherm depth	-0.080	0.865	-0.333	0.465
Age (molt stage)	-0.375	0.168	-0.161	0.581
Wind velocity	-0.284	0.305	-0.259	0.371
Wind direction	-0.167	0.552	0.083	0.777
Wave height	-0.279	0.314	-0.464	0.095
Light intensity (in air)	0.027	0.925	0.301	0.295
Light intensity (0.5 m depth)	-0.180	0.521	0.170	0.561
Light attenuation (1.0 m depth)	-0.342	0.213	0.064	0.827

Table 2.1. Correlation analysis of proportion at the surface values and residuals versus environmental variables. Analysis was performed using daily means of the proportion at the surface and environmental variables (left columns). Proportion at the surface values were de-trended by subtracting the regression of 12°C isotherm depth versus proportion at the surface. The residuals were and reanalyzed with respect to environmental variables (right columns. Significant relationships are denoted one ($P < 0.05$) or two ($P < 0.01$) asterisks (*).

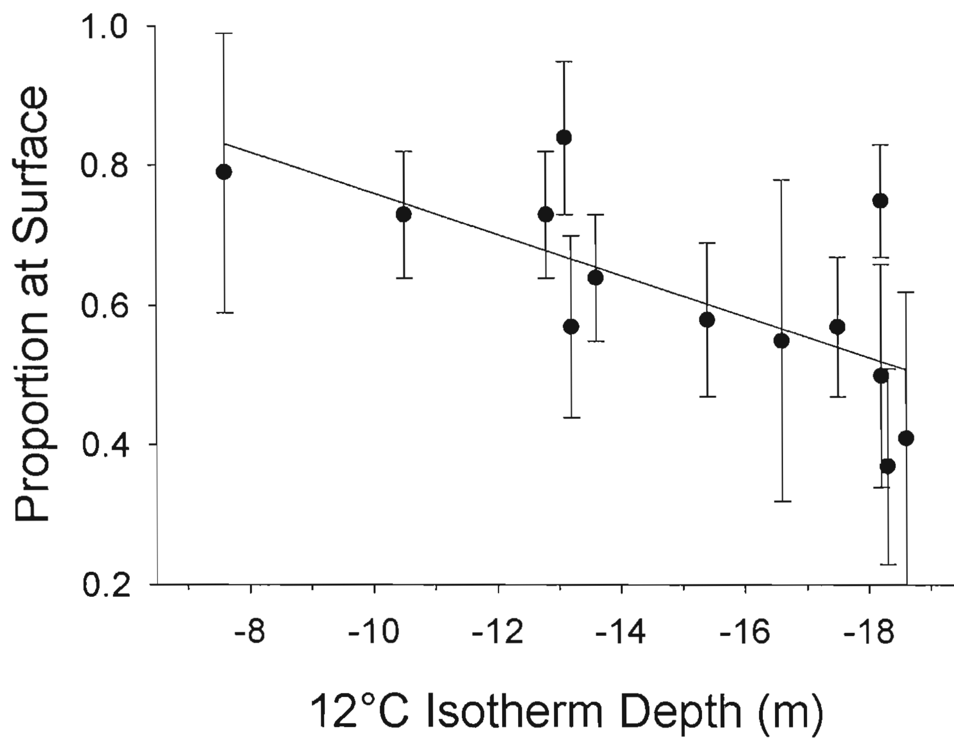


Figure 2.5. Effect of 12°C isotherm depth on proportion at the surface. Isotherm depth was determined using CTD data from casts conducted during each trial and daily mean proportion at the surface values (mean ± 1 S.E.) are as described in Figure 2.4. Data were fitted to the regression equation: $Y = 0.029X + 1.055$ ($r^2 = 0.49$, $P = 0.008$).

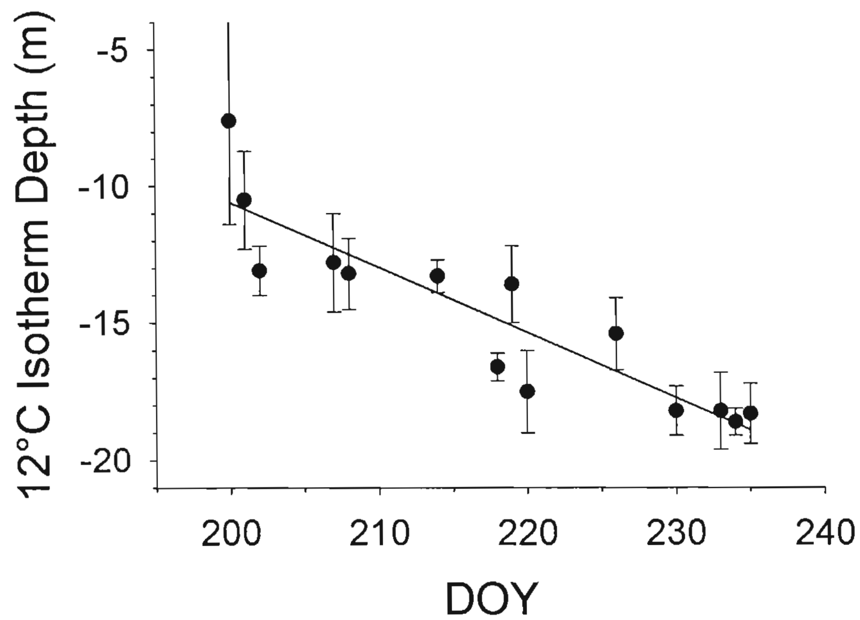


Figure 2.6. Seasonal progression of the 12°C isotherm depth from July 19-August 23, 2002. Daily averages of isotherm depth (mean ± 1 S.D.) calculated from CTD casts conducted during each trial. The 12°C isotherm descended below the depth of the CTD casts (20 m) after August 23. Data were fitted to the regression equation: $Y = -0.240X + 36.83$ ($r^2 = 0.81$, $P < 0.001$).

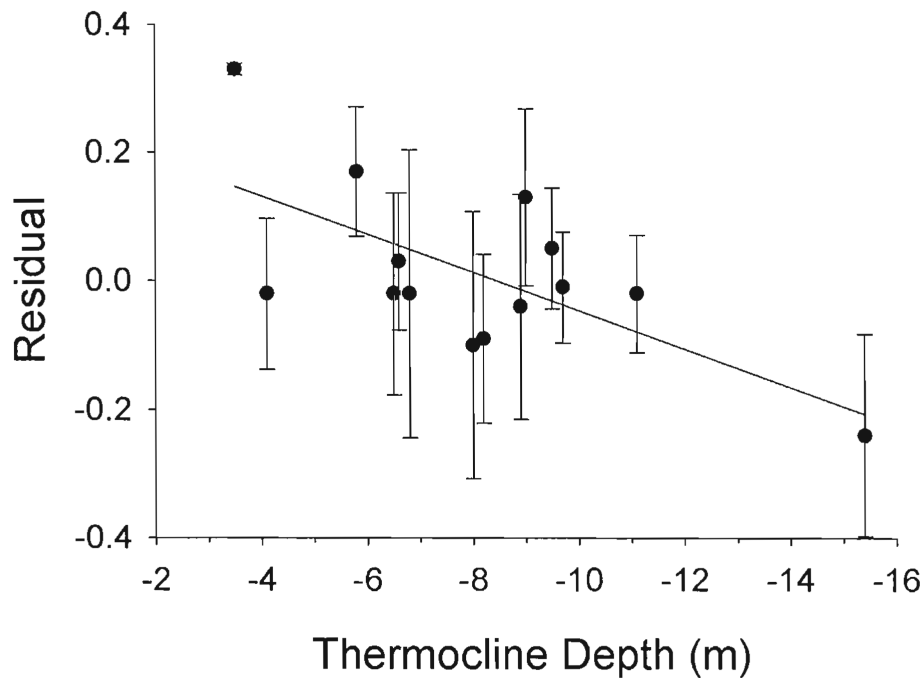


Figure 2.7. Effect of thermocline depth on proportion at the surface residuals. Daily average proportion at the surface values were de-trended by subtracting the regression of 12°C isotherm depth and proportion at the surface. The residual reflects daily variation about the seasonal trend (Fig. 2.5). Thermocline depth was determined from CTD casts conducted with trials. Data are daily means ± 1 S.E. and were fit to the regression: $Y = 0.0300X + 0.2518$ ($r^2 = 0.44$, $P = 0.008$).

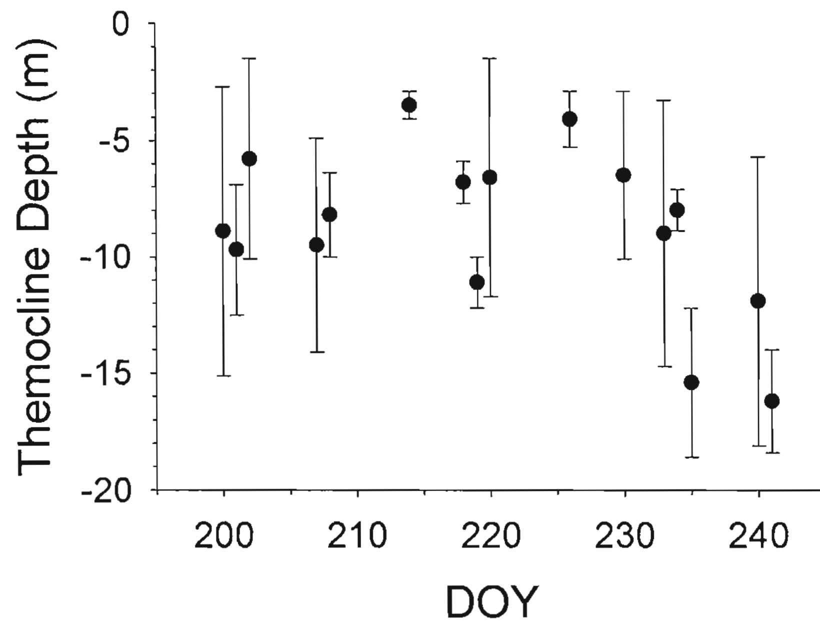


Figure 2.8. Seasonal progression of thermocline depth. Thermocline depths were determined from CTD casts taken during each trial. The thermocline deepened late in the season, but no significant relationship was found. Data are daily means ± 1 S.D.

Time of day also played a role in proportion at the surface with the lowest proportion occurring midday and the highest in the morning and late afternoon (Fig. 2.9). Logistically, we were unable to maintain a strict regime of sampling times, but analysis of time of day effects was possible by pooling the proportion at the surface data for all trials and de-trending them with respect to 12°C isotherm depth (to remove seasonal trend). The residuals were averaged by one hour bins between 0900 and 1600 local time. Due to variation in cloud cover, light levels (at 0.5m depth) did not exhibit a characteristic peak at midday in our samples. Hourly average light intensity was 1150-1300 μmol $s^{-1}m^{-2}$ from 0900 to 1300, dropped to 950-1050 μmol $s^{-1}m^{-2}$ between 1300 and 1500, and returned to 1250 μmol $s^{-1}m^{-2}$ for the 1500 to1600 period. There was no significant relationship between hourly averages of light intensity and the proportion at the surface residuals. The average proportion of stage development completed was 81-86% except for the 1500 to 1600 period which was only 75% complete. There was no correlation between hourly averages of molt stage and the proportion at the surface residuals, and it is unlikely that molt stage had a significant influence on the time of day analysis.

In contrast to hourly averages of the data, the proportion at the surface values did vary with light intensity when averaged by the molt stage of the larvae. The ontogenetic shift in phototaxis was confirmed *in situ* with early molt stage exhibiting positive phototaxis and late molt stage exhibiting negative phototaxis (Fig. 2.10). The proportion at the surface in low light (< 800 μmol $s^{-1}m^{-2}$) conditions increased with molt stage progression, and the proportion at the surface in bright conditions (> 800 μmol $s^{-1}m^{-2}$) decreased as the molt stage progressed. Pairwise comparisons (t-test) for each molt stage

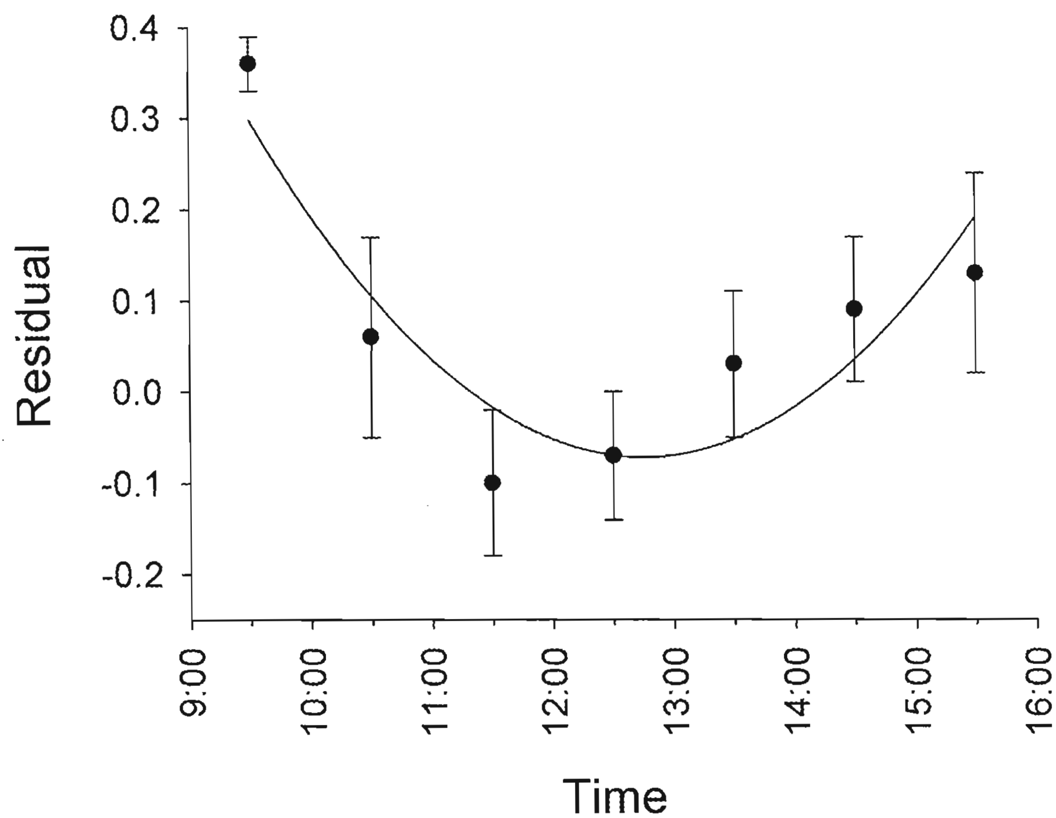


Figure 2.9. Effect of time of day on proportion at the surface residuals. Residuals (de-trended with respect to isotherm effects, Figure 2.5) for all 168 trials were pooled and averaged by time of day in one hour bins (mean ± 1 S.E.). Trials were conducted between 0900 and 1600 local time. Data were fitted to the regression equation: $Y = 20.15X^2 - 21.41X + 5.62$ ($r^2 = 0.81$, P= 0.036).

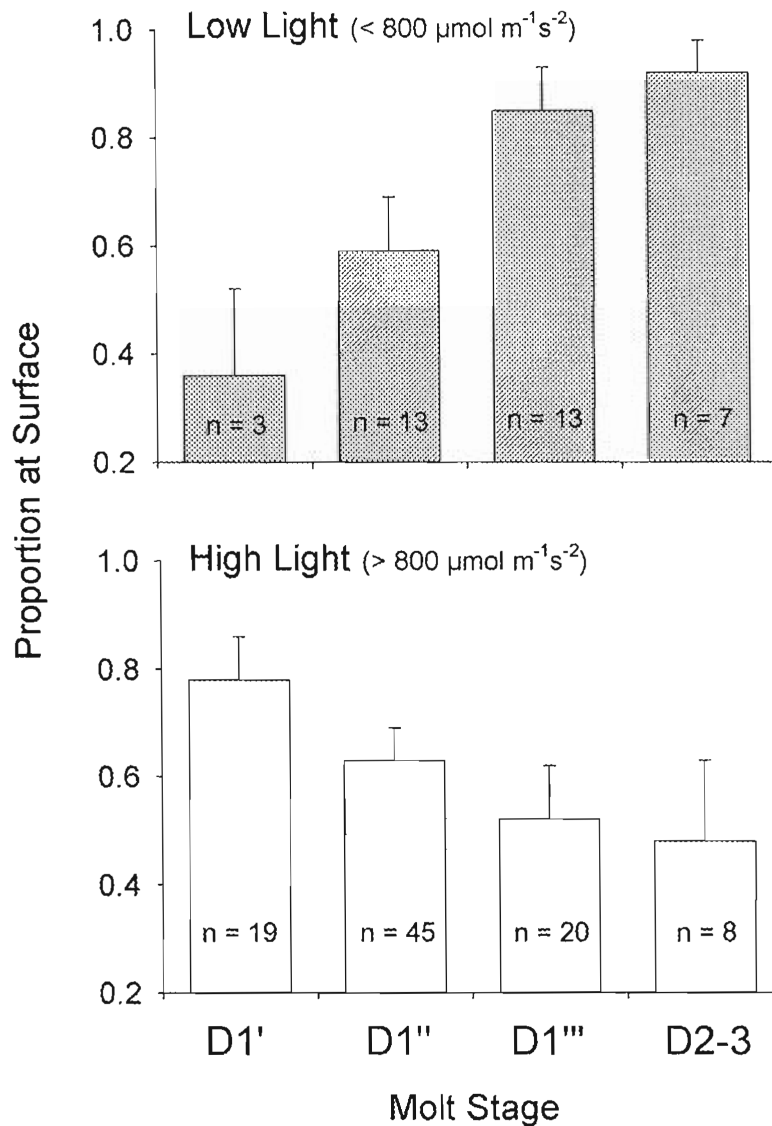


Figure 2.10. Effect of light intensity on proportion at the surface (means ± 1 S.E.) as a function of postlarval development (molt stage). Molt stage of postlarvae increases from left to right. Light intensity was measured at 0.5 m depth for each trial and 800 µmol $s^{-1}m^{-2}$ represented a natural break in the data due to the presence or absence of cloud cover.

indicated that D1' postlarvae (early molt stage) spent significantly greater proportion of time at the surface in bright light than in low light (P = 0.017), while the proportion at the surface was significantly lower in bright conditions for both D1''' (P = 0.004) and D2-3 (P = 0.006) molt stages (late molt stages). There was no significant difference in the D1'' molt stage (P = 0.275), indicating that it is may be a transitional molt stage between positive and negative phototaxis. Light intensity of 800 μmol $s^{-1}m^{-2}$ (at 0.5 m depth) represented a natural break in the light data that primarily reflected cloud cover. Molt stages A and B were absent from my samples, and only one C and three D0 molt stages were collected which was insufficient for analysis. The molt stage composition of postlarvae in my collections did not vary predictably over the course of the season, therefore it was not necessary to de-trend the proportion at the surface data with respect to the seasonal effects of the 12°C isotherm before conducting this analysis. This also made the shift in phototaxis with molt stage negligible with respect to elucidating the seasonal trends in proportion at the surface.

Discussion

Vertical Distribution

Postlarvae spent less time at the surface than was expected based on previous studies of vertical distribution (Fig. 2.2). The average proportion of time at the surface of 0.65 observed here suggests that on average 65% of the population resides in the top 0.5 m. Previous estimates of abundance report 75-90% of the population represented in surface samples (Harding et al. 1987, Harding et al. 1982, Hudon et al. 1986), indicating that total abundance has been chronically underestimated. More importantly, the

proportion of postlarvae at the surface is not constant and decreases from 0.80 to 0.57 as the postlarval season progresses. The results presented here support the efficacy of surface sampling for postlarvae as they spent more time at the surface than any other depth, but suggest that assumptions of the proportion of the population represented in surface samples needs to be re-evaluated.

Temperature

Temperature was the primary determinant of the vertical distribution of postlarvae. The proportion at the surface decreased with increasing depth of the 12°C which appeared to be driving the seasonal progression of the proportion at the surface. This evokes the question: how is the 12°C isotherm influencing the vertical distribution when it is ten meters below the typical vertical range of the postlarvae? Similar relationships between isotherm depth and the proportion at the surface were evident for the 13, 14, and 15°C isotherms. Though these relationships were not statistically significant, they suggest that postlarvae may be responding behaviorally to any temperatures below 16°C. The response to temperatures below 16°C was is also evident in the cumulative amount of time spent at each depth which decreases below 16°C. Early in the postlarval season, the colder temperatures were close to the surface, effectively compressing the vertical range and resulting in a higher proportion at the surface. As the season progressed colder temperatures were found deeper in the water column, thereby increasing the available vertical range and resulting in a lower proportion at the surface. While the 12°C isotherm provides a significant correlation with the seasonal trend of decreasing proportion at the surface, it seems likely that the behavioral response to

temperature is occurring at temperatures between 12 and 16°C. Interestingly, only 2% of the postlarvae descended to temperatures of 12°C and below suggesting that it may serve as a thermal threshold for larval behavior.

Daily fluctuation in thermocline depth was a secondary factor controlling vertical distribution. Trials were conducted in coastal waters where thermocline depth and temperature gradient fluctuate daily with factors such as cloud cover, wind stress, air temperature, internal waves, and tidal mixing. The depth of the thermocline was responsible for daily variation about the seasonal trend of proportion at the surface with a shallow thermocline resulting in higher proportion at the surface. Thus, the vertical distribution of postlarvae varied as a function of thermal structure through the coupled influence of the 12°C isotherm and the thermocline, and in both instances the postlarvae remained above the thermal structure.

Behavioral regulation of depth often changes ontogenetically in decapod crustacean larvae with the final planktonic instar exhibiting precise depth regulation (Anger 2001, Sulkin 1984). *Homarus americanus* exhibits a similar change in vertical distribution with early larval stages distributed over the upper 40 m of the water column (Harding et al. 1987, E.R. Annis unpublished data) and the postlarval stage restricted to the top 5 m (presented here). The change in vertical distribution is accompanied by an ontogenetic shift in thermal tolerance which may provide an intrinsic mechanism for regulating vertical distribution. MacKenzie (1988) reported increasing stage specific mortality with developmental stage in larvae reared at 10°C with mortality of 10, 39, 74, and 81% for stages I, II, III and postlarva respectively. Postlarval mortality increased from 18% to 81% as temperature dropped from 12 to 10°C, and postlarvae in 10°C water

rarely succeeded in molting to the next instar. Thus, 12°C appears to be the minimum temperature at which postlarvae remain viable, indicating a strong selective pressure to remain above the 12°C isotherm. In contrast, stage I larvae showed no significant increase in mortality below 12°C and are distributed throughout the upper 40m of the water column (Harding et al. 1987, E. R. Annis unpublished data). The vertical distributions of stage II and III larvae are not as well defined but they also exhibit a greater vertical range than postlarvae (Harding et al. 1987). MacKenzie (1988) also found that postlarvae have a maximum growth rate (based on dry weight) between 15 and 17°C. The histogram of time spent at each temperature had a mode at 16°C, and postlarvae spent ~56% of their time between 15 and 17°C, indicating that postlarvae spent the majority of time at the optimal temperature for growth (Fig 2.3). Whether this is serendipitous or the postlarvae are actively optimizing their growth by maintaining the appropriate temperature could not be determined from these results.

Boudreau et al. (1991, 1992) proposed that thermocline strength and depth were the primary factors influencing vertical distribution of postlarvae. In laboratory studies, they found that postlarvae stayed above the thermocline and settlement was greatly reduced in the presence of a strong thermocline. Their results illustrate the potential importance of the thermocline in vertical distribution of postlarvae but are confounded by the magnitude of the thermal gradient. They found significant effects only when the temperature gradient of the thermocline was ~10°Cm^{-1} or greater (interpreted graphically based on temperature change over 0.5 m). A slope of ~4.5°Cm^{-1} had no significant effect the vertical distribution of postlarvae. Therefore, it is not surprising that there was no effect of the strength of the thermal gradient in the present study as all of the trials had a

gradient less than 2.73°Cm^{-1}. Despite weaker thermoclines *in situ*, the depth of the thermocline was correlated to daily variations in proportion at surface. However, the relationship was not evident until the data were de-trended with respect to the seasonal progression of the 12°C isotherm and only explained 44% of the daily variation about the seasonal trend (Fig. 2.7). The importance of thermocline in maintaining vertical distribution was probably diminished by the substantially weaker thermoclines found *in situ*. In contrast to studies by Boudreau et al. (1991, 1992), I found that a specific temperature (12°C) had a greater effect on vertical distribution *in situ* than the thermocline structure.

Time of Day

Proportion at the surface also varied during the course of the day with the most time spent at the surface in the morning and late afternoon (Fig 2.9). This is consistent with observations that postlarvae are least abundant in surface samples mid-day (Harding et al. 2000, R. J. Miller personal communication, E. R. Annis unpublished data). The shift in vertical distribution over the course of the day was independent of light intensity which suggests that the vertical migration may be part of an endogenous rhythm over which reactions to light intensity may be superimposed. The lack of correlation between light intensity and proportion at the surface in this analysis was probably due to a similar distribution of molt stages in each of the hourly averages. The phototactic response of the postlarvae varies with molt stage but hourly averages were comprised of a mix of positively and negatively phototactic postlarvae resulting in no correlation with light.

It would be inappropriate to extrapolate these results beyond the limits of the data, but they do suggest that the most effective time to sample postlarvae at the surface is either before 1000 h or after 1400 h. Harding et al. (1987) found no difference in vertical distribution between day and night, but it is possible that higher proportion at surface in the morning and late afternoon is part of a crepuscular migration that would not be detected in a simple comparison of day and night samples. This is consistent with observations that postlarval abundance in neuston tows is often higher at sunrise and sunset (Harding et al. 2000, E. R. Annis unpublished data).

Light

Postlarvae exhibited a shift in phototaxis from positive to negative with increasing age (molt stage, Fig. 2.10), consistent with the shift in phototaxis reported by Hadley (1908) and Botero and Atema (1982). The shift in phototaxis may be an intrinsic mechanism driving settlement: as the postlarvae get older and more negatively phototactic (and photopathic) they are more likely to leave the surface waters for the dark crevices of the benthos (Botero and Atema 1982, Boudreau et al. 1990). This is supported by observations that when released at depth, early postlarval stages swim toward the surface while late stage postlarvae tend to stay near the bottom (Cobb et al. 1983, Ennis 1975). Here, postlarvae in molt stage D1 appeared to be in transition between positive and negative phototaxis with no significant difference in proportion at surface between high and low light conditions. The final molt stages (D1''' and D2-3) spent significantly more time below the surface in bright conditions, suggesting that postlarvae become behaviorally competent to settle during the D1'' molt stage or ~75% of

the postlarval period (*sensu* Sasaki 1984). Previous laboratory studies predict that this transition occurs closer to molt stage C (Botero and Atema 1982, Cobb et al. 1989a) or approximately midway through the postlarval period (Herrick 1909). However, in plankton surveys of Buzzards Bay (Massachusetts) and Block Island Sound (Rhode Island) Cobb et al. (1989a) found abundant D0 or D1 molt stages indicating that settlement does not occur until the later half of the postlarval stage. In the present study area the molt stage D2-3 is often abundant (Incze et al. 2000a, Incze et al. 1997) suggesting that settlement occurs late in the postlarval stage. Differences between studies may reflect problems extrapolating laboratory results to the field or simply regional variations in behavior (Cobb et al. 1989a, Incze et al. 1997). It is important to note that behavior is highly variable among individuals and while the predominate shift in phototaxis occurred during the D1" molt stage, individuals exhibited sounding behavior prior to achieving that developmental stage. The stages of the lobster life cycle are morphologically defined and the shift in phototaxis during the postlarval stage illustrates that significant ontogenetic changes in behavior do not necessarily coincide with clearly defined morphological stages.

Implications for Settlement

The thermally mediated behavior observed here suggests that settlement may also be influenced by the depth of the 12°C isotherm. If 12°C serves as a minimum temperature threshold for postlarvae as suggested by the swimming behavior, successful settlement should be greatly influenced by the amount of time bottom temperature exceeds 12°C. Thus, settlement may vary not only as a function of postlarval production

(Incze et al. 1997, Incze et al. 2000b) and available substrate (Botero and Atema 1982, Boudreau et al. 1990, Wahle and Steneck 1991), but as a function of whether the bottom temperature reaches 12°C or the number of days that bottom temperature exceeds 12°C. This may help to resolve the biogeography of settlement in both horizontal and vertical scales.

Spatial patterns of settlement show a distinct shift from low settlement in eastern Maine to high settlement in western Maine coastal waters (Steneck and Wilson 2001). The bottom temperature at eastern sites (~10 m depth) is strongly influenced by the cold waters of the Eastern Maine Coastal Current which is well mixed vertically and rarely exceeds 12°C (Brooks 1985, Townsend 1991). In contrast, western sites (Penobscot Bay and west) are characterized by warmer stratified waters in the summer, and bottom temperatures exceeding 12°C (~10 m depth; N. Pettigrew, L. S. Incze, E. R. Annis unpublished data). My observations of postlarval behavior suggest that these regional settlement patterns may be driven in part by the bottom temperature or the depth of the 12°C isotherm.

In the vertical scale settlement decreases with depth and is reduced to the limit of detection at 20 m (Wilson 1999), and the magnitude of settlement occurring below 20 m remains unknown. In the present study the 12°C isotherm only descended below 20 m late in the summer season, and it follows that the number of days that bottom temperature exceeds 12°C decreases with depth. If postlarvae tend to stay above the 12°C isotherm, the likelihood of successful settlement would decrease with increasing depth. This is consistent with a positive relationship between average bottom temperature and abundance of settlers in sites between 5 and 20 m depth reported by Wilson (1999).

Only two of the 168 (1.2%) postlarvae descended below the sampling depth of 15 m. If this is representative of the proportion of individuals sounding for bottom below 20 m, the equivalent dive frequency is 0.08 dives $indiv^{-1}hour^{-1}$. This is an order of magnitude lower than the shallow sounding frequency of 1.08 $indiv^{-1}hour^{-1}$ reported here and the range of 0.75 to 2.9 $indiv^{-1}hour^{-1}$ estimated by Incze et al. (1991). Forays to the bottom appear uncommon in deep water and settlement on an areal basis should be much lower. While there is more surface area available for settlement below 20 m, such that even low settlement rates could make a significant contribution to total settlement, much of the available area never exceeds 12°C indicating that successful settlement in deep water may be limited.

Correction Factor for Neuston Samples

The validity of abundance estimates derived from neuston samples relies on knowing the proportion of the population represented in the sample. That proportion varies with environmental conditions, and the relationships described here may be used to provide a proportion at the surface value specific to the environmental conditions at the time of collection. The effect of temperature drives seasonal trends in the proportion at the surface and the regression equation provides the basis for calculating a correction factor (Fig. 2.5). A proportion at the surface can be estimated for a neuston sample using depth of the 12°C isotherm from the water column where samples are collected, and that proportion can be used to estimate total abundance. The residual effect of daily variations in thermocline (Fig. 2.7) and the time of day (Fig. 2.9) can be estimated using their respective regressions and added to the estimated proportion at the surface. This

method will result in lower proportion at the surface and higher estimates of total postlarval abundance than previously reported. Because proportion at surface decreases with increasing depth of the 12°C isotherm over the course of the season, it will have the greatest impact on late season samples. However, the limitations of the correction factors must be acknowledged. Caution should be exercised in extrapolating beyond the bounds of the regressions as the minimum and maximum proportion of the surface has not been determined. Correction factors are most appropriately applied to water masses with hydrography similar to central Maine coastal waters as the vertical distribution may vary in areas with extreme temperatures or vertically mixed water columns. Potentially the correction factor could be confounded by large variations in molt stage composition, and the effect of proximity to shore on vertical distribution is unknown. A final consideration is that the postlarvae used in this study were collected from surface waters and therefore may have been predisposed to swimming near the surface. Accordingly, the proportion at surface reported here should be regarded as conservative and could actually be lower.

Conclusions

The vertical distribution of lobster postlarvae results from the interplay between intrinsic behavioral characteristics and extrinsic environmental conditions. Behavior was complex and highly variable among individuals, but variations in the proportion at the surface as a function of temperature, thermocline depth and time of day were consistent with thermal tolerances, ontogenetic changes in behavior, and previous observations in the lab and field. The neustonic phase of the life cycle presents a convenient opportunity to quantify larval abundance in the period leading to settlement, but we must recognize

that the population represented in neuston samples is not constant. Rather, it changes with hydrographic conditions and the ontogeny of the organism. The behavioral response to temperature, thermocline depth, and time of day were predictable and provide a basis for refining estimates of total abundance from neuston samples. Future work should attempt to expand the spatial extent in which these relationships may be applied: does behavioral regulation of depth change with proximity to shore? in vertically mixed water columns? in different regions? Furthermore, the relationship between bottom temperature and settlement should be examined with respect to the thermal threshold reported here.

3. ESTIMATES OF *IN SITU* LARVAL DEVELOPMENT TIME FOR THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*.

Abstract

Larval development time is a critical factor for assessing the potential for larval transport and the connectivity of marine populations through larval exchange. Most estimates of larval duration are based on laboratory studies and may not reflect development times in nature. Estimating larval duration *in situ* relies upon the accuracy of abundance estimates, the temperature regime used in calculations, and the frequency of sample collection. Larvae of the American lobster (*Homarus americanus*) provide an opportunity to compare *in situ* development time because temperature dependant development times have been established in previous laboratory studies. Evidence in the field studies suggests that *in situ* development times may be considerably faster.

Here we present an estimate of development time that indicates development *in situ* may be 1.4-3.0 times faster than previously reported in laboratory studies. We used the timing of seasonal abundance curves for newly hatched larvae (stage I) and the final plankonic instar (postlarva), coupled with a model of temperature dependent development to compare our field data with previous laboratory studies. We used this model to estimate a correction factor for the duration of the larval phase *in situ*. Improvements in our understanding of vertical distribution of the first and last planktonic stages and frequent sampling (3-4 d interval) of larvae provided the best possible estimate of the timing and magnitude of peak abundance. The development times proposed here are speculative but represent the best available estimate of larval duration *in situ*. If they

are correct, the 1.4-3.0 fold reduction in development time has important implications for larval transport potential, and estimates of mortality and production.

Introduction

Planktonic larval duration is the most important intrinsic factor used to determine the dispersal of larvae and the potential for self-recruitment in marine populations (Sponaugle et al. 2002). Coupled biological-physical models combine development time with local flow rates to assess the potential connectivity of populations (Cowen et al. 2000, Incze and Naimie 2000, Roberts 1997). Furthermore, development times have a cascading effect on estimates of instantaneous mortality rates and larval production which are inversely proportional to larval duration. Historically, larval development times have been determined in laboratory studies under what are usually described as optimal conditions for growth. Such studies are particularly useful for assessing relative responses to changing environmental and feeding conditions, but their application *in situ* remains tenuous (Anger 2001). Unfortunately, there is a paucity of information on development times in nature. In many cases, development time in the field is shorter than that observed in the laboratory suggesting that laboratory conditions may be less than ideal (Ebert et al. 1983, Gonzalez-Gordillo and Rodriguez 2000, Harms et al. 1994, Welch and Epifanio 1995). Thus, a correction is needed for laboratory development times to avoid overestimating potential transport, larval production and mortality rates.

The American lobster, *Homarus americanus*, is an excellent study organism for comparisons of field and laboratory development times. Laboratory rates of larval development are well established and are comparable over time and broad geographic

range (Annis et al. in press, MacKenzie 1988, Templeman 1936), yet there is evidence for higher growth rates *in situ* (James-Pirri and Cobb 1997, but see Hudon & Fradette 1988, Juinio and Cobb 1994, Wilder 1953). Lobsters are the most economically important species in the northwestern Atlantic, so there is a pressing need to understand how the population dynamics are affected by larval production, mortality, and transport. Estimates of these rates cannot be accomplished without correcting for development time under field conditions.

Making a quantitative estimate of the correction factor for larval development time in lobster larvae has been hindered by a lack of appropriate data. Field sampling is usually limited to the fourth and final planktonic instar (= postlarva) because postlarval delivery drives settlement (Incze et al. 1997, Incze et al. 2000b), and postlarvae are concentrated in surface waters which facilitates sampling (Annis in prep, Harding et al. 1987, Harding et al. 1982, Hudon et al. 1986, Scarratt 1973). Unfortunately, the first three planktonic stages have a broader vertical distribution (Harding et al. 1987), and are underrepresented in samples because sampling often begins too late in the season and is limited to surface waters. Finally, sampling is typically conduced at weekly intervals or longer which is insufficient to resolve the timing of abundance peaks. Thus, few data are available to assess the timing of developmental stages in the field.

The objective of our study was to determine if development time of lobster larvae is faster in nature than in the laboratory. We estimated a correction factor for *in situ* development time using the most current estimates of vertical distribution, semiweekly field sampling, and a model of temperature dependent development. Specifically, we assessed whether accepted laboratory development times established in previous studies

(MacKenzie 1988, Templeman 1936) are capable of reproducing the observed timing of peak abundance of the first and last planktonic stages in the field.

Methods

Field Collected Larvae

The study area was located in the Gulf of Maine between Cape Small and Port Clyde, Maine, USA, and encompassed an area approximately 15 x 50 km. (Fig. 3.1). This area was selected because it is an area of historically high postlarval delivery (Annis et al. in prep-a) and settlement (Incze et al. 1997, Steneck and Wilson 2001). Residual westward flow is 4-8 km d^{-1} offshore from our study area. We expect that flow is considerably slower within the study area due to increasing complexity of flow around headlands and boundary effects on the alongshore current with increasing proximity to shore (L.S Incze unpublished data). Therefore, it is likely that some portion of the larvae hatched within the area will complete development before being advected away.

In 2001 we collected larvae at 12 stations over the course of the larval season from June 5-Oct 2 (DOY 156-275) at an interval of 3-4 d during peak larval abundance. Surface tows were conducted with a neuston net measuring 1 m wide with a sampling depth of 0.5 m and either 500 or 1000 μm mesh. Multiple oblique tows were conducted between 0 and 21.7 ± 1.7 m (S.D.) with a 1 x 1 m square opening net and 1000 μm mesh. The amount of line required to reach the target depth for oblique tows was calculated using the angle of the tow line, and depth profiles of the oblique tows were recorded using a Cochran Instruments dive computer attached to the top of the net. Discrete depth sampling to 60 m in this region indicated that the larval lobsters reside in predominately

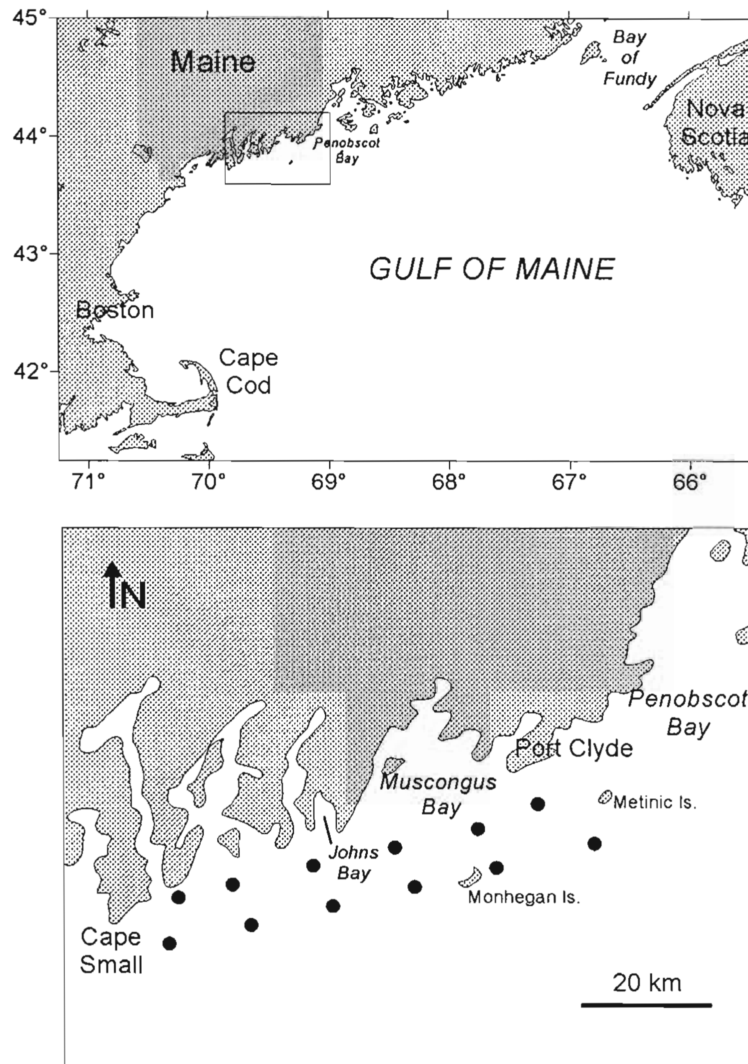


Figure 3.1. The region of study was located in the northern Gulf of Maine (top) between Cape Small and Port Clyde, Maine (bottom). The sampling stations (•) covered an area approximately 15 x 50 km.

the top 20 m of the water column (L. S. Incze unpublished data). Both nets had calibrated mechanical flow meters mounted in the opening to calculate the volume of water filtered. Neuston tows were 10 min at a speed of ~1.6 m s^{-1} and filtered ~450 m^3, and oblique tows were 30 min at ~1.1 m s^{-1} and filtered ~2000 m^3. Neuston tows were conducted at every station, but multiple oblique tows were only conducted on 18 d during the season. A total of 245 neuston tows were conducted and 107 multiple oblique tows. A CTD cast (Sea Bird Electronics, SBE-19) and light intensity profile (Li-Cor Instruments, LI-188b with a LI-193SB spherical quantum sensor) were conducted at each station. All postlarvae were taken to the laboratory where their molt stage was determined (methods of Sasaki 1984).

The proportion of stage I larvae represented in surface samples was determined using paired neuston and multiple oblique tows (proportion = $[\text{oblique}][\text{neuston}]^{-1}$). CTD casts made at the time of the tow were used to determine thermocline, halocline, and pycnocline depths and gradients, and the depth of isotherms from 9-12°C (in 1°C increments). Thermo-, halo-, and pycnoclines were identified by calculating the rate of change of the measurement with depth (data were averaged in 0.5 m bins). The depth bin with the greatest rate of change was considered the depth of the cline and the rate of change reported as the gradient of the cline. Light attenuation at 1 and 5 m depths was calculated relative to light intensity approximately 2 m above the sea surface. The proportion was examined with respect to environmental variables including light intensity from 0-10 m, light attenuation at 1 and 5 m, thermocline and halocline depth, and isotherm depth (9, 10, 11, and 12°C). Subsequently, the relationship between light

intensity (1 m depth) and proportion of stage I larvae at the surface was used to estimate total abundance at stations where only surface tows were conducted.

The proportion of postlarvae represented in surface samples was estimated using the combined effects of 12°C isotherm depth, thermocline depth, and time of day as described in Annis (in prep). The proportion of postlarvae at the surface decreases linearly with increasing depth of the 12°C isotherm over the course of the season and explained 49% of the variance in proportion at the surface (P = 0.008):

$$[3.1] \quad \text{Proportion at surface} = (0.0293*Z_{12°C})+1.0547,$$

where Z12C is the depth of the 12 degree isotherm. The regression was subtracted from the proportion at the surface data to remove the effect of the 12°C isotherm and the residuals were reanalyzed with respect to environmental variables. Proportion at the surface decreased linearly with increasing depth of the thermocline and explained 44% of the daily variation about the seasonal trend (P =0.008):

$$[3.2] \quad \text{First Residual} = (0.0300*Z_{dT})+0.2518,$$

where Z_{dT} was the depth of the thermocline. Annis (in prep) used the first residual to determine the effects of time of day on the residual values. For the present purposes we subtracted the regression from the first residuals and generated a second residual which we used to analyze the effects of time of day. The second residuals were fit to the following regression (P = 0.104):

$$[3.3] \quad \text{Second Residual} = (0.0350*t^2)-(0.8923*t)+5.6172,$$

where t is the time of day (minutes decimalized). Though it is not statistically significant at the 0.05 level, this equation has the same form and intercept as the first residual equations reported by Annis (in prep), and it accounts for 68% of the variance in the

second residual. The residuals are additive and the use of the second residual permits the summation of equations 3.1, 3.2, and 3.3 to provide an estimate of proportion at the surface for each neuston tow conducted. This proportion reflects the environmental variables at the time of sampling and may be used to estimate the total abundance of postlarvae based on surface samples. In some cases the variables measured during this study exceeded the bounds of the regressions and were conservatively constrained at the minimum and maximum values of the regression. Values for $Z_{12°C}$ were limited to a range of 6-20 m and values below or above the range were entered as 6 or 20 respectively. Similarly, Z_{dT} was limited to 2-20 m, and t was limited to 0900-1600. Proportion at the surface values were not permitted to exceed 1.0.

Estimates of larval production account for variable stage duration and the increase in probability of capture with increasing larval duration (Scarratt 1964). Production estimates represent the number of the larvae hatching or molting into a specific stage rather than abundance which is a measure of the standing stock. Weekly larval production for stages I and II were calculated as $[C_i]/D_i$, where C is the total abundance ($1000m^{-2}$) of the stage i for the week, and D is the stage durations based on the average temperature for the week (methods of Scarratt 1964). Stage duration was calculated from the temperature dependent development equations in Table 1 and temperatures from Figure 3.2. Production estimates incorporated our revised estimates of development time. Polynomial functions from field data (Figure 3.4) were used as postlarval abundance. Postlarval production was calculated after the method of Incze et al. (1997) and used the weekly production of each molt stage to determine production and $[PL_x]/D_x$, where PL is the sum of the week's catch of postlarvae in molt stage x, and D is the duration of the

molt stage. Duration of the molt stage was determined by multiplying the postlarval stage duration (as computed above) by the proportion of time spent in each molt stage (Sasaki 1984). All molt stages are then summed to provide true postlarval production for all stages (Incze et al. 1997). The instantaneous rate of mortality was calculated using estimated production as initial (N_0) and final numbers (N_t) of larvae in the mortality equation in Table 3.1. Time (*t*) was the development time from the midpoint of the first stage to the midpoint of the final stage.

Development Model

We developed a model of larval production to generate hypothetical abundance curves for each larval stage and adjusted development times to reproduce the timing of abundance curves observed in the field. The construct of the model was as follows:

$$[3.4] \quad A_t = P_t + R_t,$$

where A was the total abundance of a larval stage at time, *t*. The model had a one-day time step, and P_t was the daily production of larvae due to hatching or molting from the previous stage. Each day of larval production was considered a cohort. R_t was the sum of larvae remaining from production on previous days:

$$[3.5] \quad R_t = \sum_{n=1}^{D} N_t,$$

where D was the stage duration in days calculated from the temperature dependent development time equations in Table 3.1 and temperatures in Figure 3.2. Duration of stages I-III were calculated using averaged temperature between 0 and 10 m while the temperature at 1 m was used for postlarvae (to reflect differences in the vertical distribution of the stages). Both temperature regimes were based on polynomial

equations fit to the temperature data for the season (Table 3.1, Fig. 3.2). N_t was the number of larva remaining in each daily cohort of production after mortality (Table 3.1). Each cohort was included in the summation until the stage development was complete, at which point the remaining number of larvae "molted" into the next stage and were used as the daily production for the next stage.

Values from the abundance curve for stage I larvae in the field (Figure 3.4) were used as initial values for the model and an inverse calculation was used to estimate daily production (= cohort) of stage I larvae. The first non-zero abundance on the regression line provided the first daily cohort of larval production in the model. This permitted the calculation of R_t (equation 3.4) for subsequent days and the daily production was then calculated by subtracting the field abundance from R_t. The daily production of larvae for subsequent stages was the sum of all cohorts completing the previous developmental stage. We assumed the postlarvae settled by D2-3 molt stages (based on the low abundance of these late molt stage in our samples: see figure 3.5) which is equivalent to 89% of the total stage duration (Sasaki 1984). Accordingly, postlarval stage duration was multiplied by 0.89. Stage duration (D; Table 3.1) was multiplied by a correction factor (between 0 and 1) to allow adjustment of development times. As development times decreased, the time between stage I and postlarval peak abundance in the model output also decreased.

Variable	**Equation**	**Terms**
Stage I duration	$D = 851 * (T - 0.84)^{-1.91}$	D = duration, T = average temperature from 0-10m
Stage II duration	$D = 200 * (T - 4.88)^{-1.47}$	D = duration, T = average temperature from 0-10m
Stage III duration	$D = 252 * (T - 5.30)^{-1.45}$	D = duration, T = average temperature from 0-10m
Postlarval duration	$D = 703.5 * (T)^{-1.26}$	D = duration, T = average temperature at 1m
Temperature 0-10m	$T = 13.96 * e^{(-0.5 * ((DOY-238.07)/105.61)^2)}$	T = temperature, *e* = Naperian constant
Temperature 1m	$T = 15.34 * e^{(-0.5 * ((DOY-224.64)/89.43)^2)}$	T = temperature, *e* = Naperian constant
Mortality	$N_t = N_0 * e^{(-Mt)}$	N_t = number at time *t*, N_0 = initial number, *e* = Naperian constant, M = mortality rate (d^{-1}), *t* = time (d)

Table 3.1. Equations used in larval development model. The stage duration equations were reported by Incze and Naimie (2000) based on the work of MacKenzie (1988). Temperature equations are regressions fit to the mean temperature measured in our sampling area (Fig. 3.2). The equation for mortality was taken from Rumrill (1990).

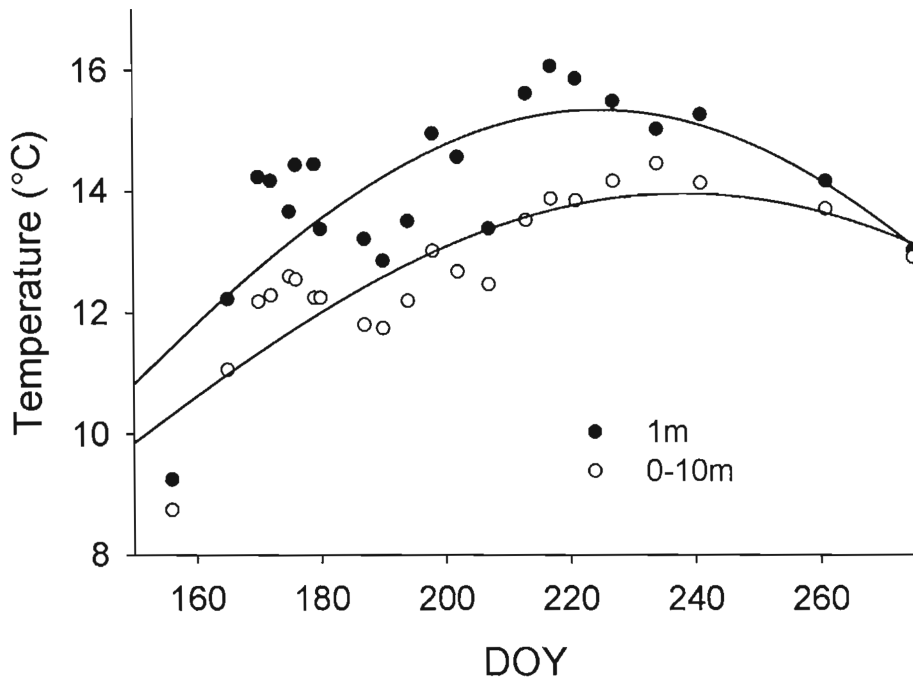


Figure 3.2. Seasonal water temperature at 1 m (•) and 0-10 m (○) depths averaged from CTD data from all stations in the study area. The 0-10 m temperatures were fit with the regression: $T = 13.96 * e^{(-0.5 * ((DOY-238.07)/105.61)^2)}$ ($r^2 = 0.74$, $P < 0.001$), and 1m temperatures we fit with the regression: $T = 15.34 * e^{(-0.5*((DOY-224.64)/89.43)^2)}$ ($r^2 = 0.59$, $P < 0.001$). These polynomial regressions were used as temperature input for the model of development time (Table 3.1).

Results

Estimates of Larval Abundance

Surface tows captured a total of 1069 stage I, 27 stage II, 11 stage III larvae, and 422 postlarvae, while multiple oblique tows captured 1122 stage I, 29 stage II, 3 stage III larvae, and 28 postlarvae. The average proportion of stage I larvae in the surface tows was 0.15 ± 0.26 and increased with decreasing light intensity (Fig 3.3). Paired neuston and oblique tows were used to estimate the proportion at the surface for stage I larvae, and tows where no larvae were captured in either net were excluded from the analysis. The relationship with light intensity had the best fit using light intensity at 1m depth, but similar relationships occurred with light intensity 2 m above the surface and at depths of 0.5 m, 5 m, 10 m. High attenuation of light due to turbidity or low sun angle resulted in a higher proportion of stage I larvae at the surface which is consistent with the negatively phototactic response to light intensity. A greater proportion of stage I larvae were found at the surface in tows conducted before 0900 (t-test; $P < 0.01$, $df = 22$, $t = 1.72$). The average proportion (± 1 S.D.) at the surface for tows conducted before 0900 was 0.36 ± 0.37 while tows after 0900 averaged 0.09 ± 0.18. No relationships were found between proportion at the surface and the depth of thermocline, halocline, or temperature (9, 10, 11, 12°C). These results are consistent with previous reports indicating that the vertical distribution of stage I larvae varies diurnally (Harding et al. 1987) and with light intensity (Hudon et al. 1986). The relationship with light intensity was used to estimate a proportion at the surface and then to estimate total abundance of stage I larvae in the water column for stations where multiple oblique tows were not conducted. At these stations, the abundance in the neuston sample was divided by the proportion at the

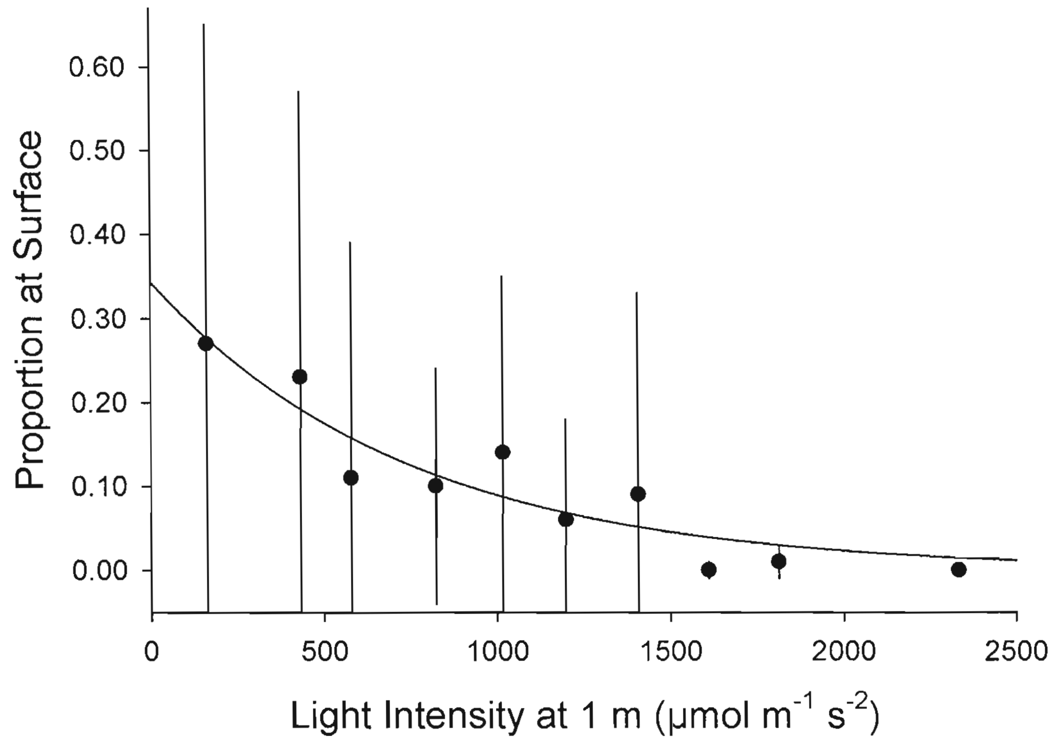


Figure 3.3. The proportion of stage I larvae captured in neuston tows (0-0.5 m depth) relative to multiple oblique tows (0-21 m depth). The relationship s described by the power function; $Y = 0.3442 * e^{(-0.0012 * X)}$, $r^2 = 0.87$, $P < 0.001$. Data were binned by light intensity in 200 µmol m^{-1} s^{-2} increments. Data are means ± 1 S.D.

surface to provide an estimate of total abundance. The abundance estimates of postlarvae were corrected for 12°C isotherm depth, thermocline depth, and time of day. The resulting values were 1.3 times higher on average than uncorrected neuston data suggesting that uncorrected neuston samples underestimate abundance by ~25%. The difference between corrected and uncorrected data increased as the season progressed and the greatest differences occurred in the second half of the season.

Seasonal Abundance

In 2001 stage I larvae were present from 14 June – 29 August (DOY 165-241) with peak abundance on 13 July (DOY 194, Fig 3.4). These data include the abundance estimates from multiple oblique tows and surface tows that have been corrected for light intensity at 1 m depth. Stage II larvae were present from 12 July (DOY 193) until the end of our sampling with a peak at 17 July (DOY 198). The seasonal curve for stage II larvae includes only data from multiple oblique tows because there were insufficient data to develop a correction for total abundance in neuston samples. The timing and magnitude of peak stage II larval abundance should be viewed cautiously as the sampling frequency for the multiple oblique tows was only 5-7 d. The stage I and II larval abundance data were fit to Gaussian form regression equations (SigmaPlot 8.02). The regression for stage I larval abundance was $Y = 12.781e^{(-0.5((X-194.457)/16.980)^2)}$ ($r^2 = 0.90$, $P < 0.001$), and the regression for stage II larvae was $Y = 9.660e^{(-0.5((X-200.579)/6.719)^2)}$ ($r^2 = 0.89$, $P < 0.001$). Stage I larval data were square root transformed for homogeneous variance and the regression output and data were back transformed for Figure 3.4 (Sokal and Rohlf 1995). Only three stage III larvae were captured in the multiple oblique tows

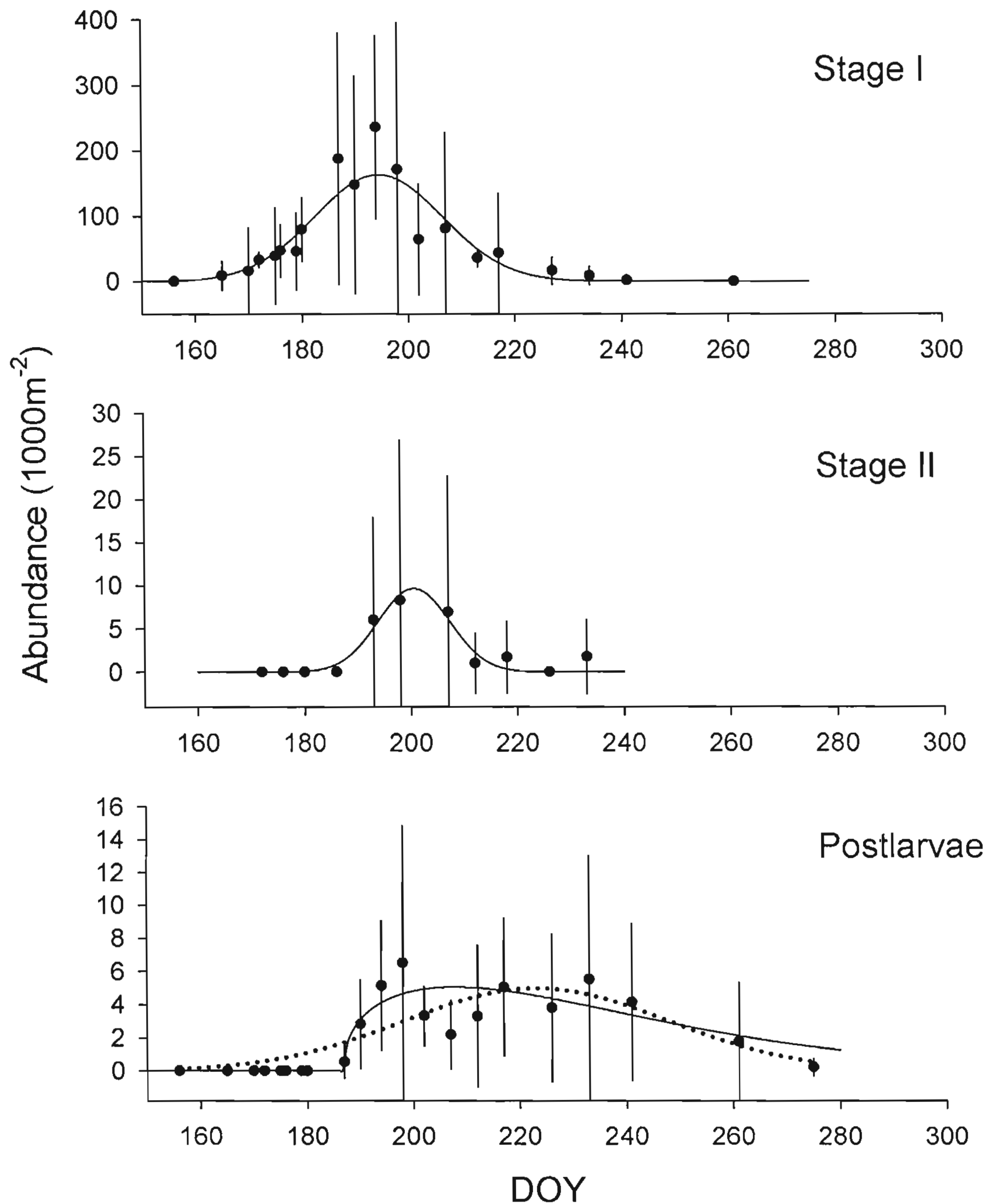


Figure 3.4. 2001 Seasonal abundance curves for stage I, II larvae and postlarvae. Larvae were collected in neuston and multiple oblique tows. Data are means (± 1 S.D.) from all 12 stations in the sampling area. Stage I and II larval abundance data were fit with Gaussian regression while the postlarval data were fit with a Weibull regression. The dotted line indicates the result of fitting a Gaussian regression to the postlarval data.

so we were unable to present a seasonal abundance curve. Postlarvae were caught in surface samples from 6 July (DOY 187) until the final day of sampling on 2 October (DOY 275), but their abundance had decreased nearly to zero at that date. Postlarval abundance was fitted to a Weibull form regression (SigmaPlot 8.02), because it more closely fit the rapid onset of postlarval abundance and the long tail extending late in the season, and it accounted for a greater proportion of the variance. The equation for postlarval abundance was: $Y = (\text{if } X \leq 207.299 - 56.041*((1.344-1)/1.344)^{(1/1.344)}$, then 0, if not then $4.608 * ((1.344-1)/1.344)^{((1-1.344)/1.344)} * (\text{abs}((X-207.299)/56.041+((1.344-1)/1.344)^{(1/1.344)})^{(1.344c-1)}) * e^{(-\text{abs}((X-207.299)/56.041+((1.344-1)/1.344)\wedge(1/1.344))\wedge 1.344+(1.344-1)/1.344)})$, $r^2 = 0.79$, $P < 0.001$. The Weibull regression for postlarval abundance peaks at 23 July (DOY 208), or 14 d after the peak in stage I larval abundance. Actual postlarval abundance declined during this period with peaks in abundance before and after. The trough in the abundance curve was coincident with a shift in wind direction from SW to NW (onshore to offshore), reversal of surface flow, and lower surface temperature consistent with offshore movement of surface waters (GOMOOS buoy data; www.gomoos.org)(Fig. 3.5). This suggests that postlarvae may have been advected offshore during this period. Thus, with respect to the development time, it is probably more appropriate to view the postlarval season as one curve rather than as two separate peaks. A conservative estimate of the timing of postlarval abundance was obtained using a Gaussian regression ($Y = 5.415e^{(-0.5((X-221.251)/23.476)^2)}$, $r^2 = 0.67$, $P < 0.001$), in which case the peak abundance in postlarvae occurred on August 10 (DOY 222), or 28 d after the peak in stage I larval abundance. The frequency distribution of the postlarval molt stage was skewed towards later stages with 94% of the postlarvae captured in the "D"

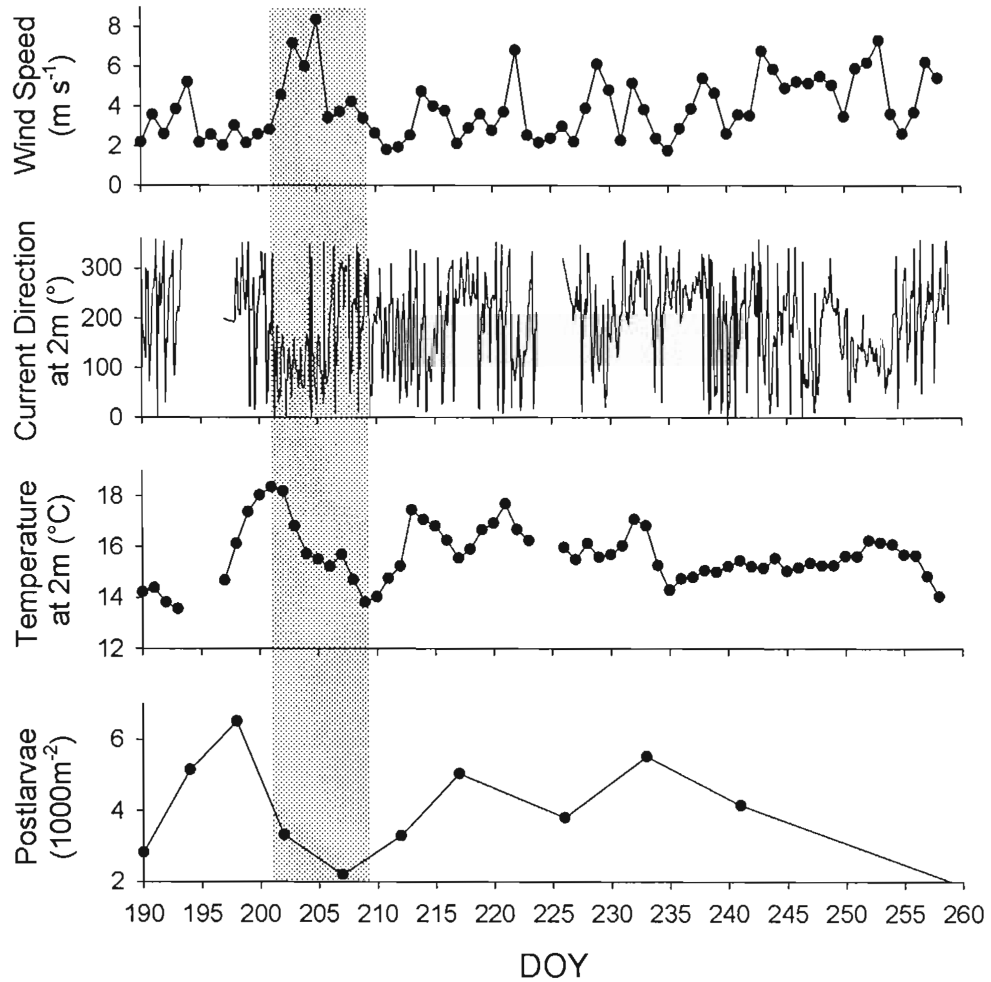


Figure 3.5. Wind speed, current direction and temperature at 2 m depth with respect to postlarval abundance. Data are daily means except for current directions which are hourly measurements. Current direction is reported in oceanographic convention (direction the current is moving towards in angular degrees). Environmental variables were measured at GOMOOS Buoy E located approximately 5 km offshore from our study area. Postlarval abundance data is from Fig. 3.4. The shaded area illustrates a northwesterly (offshore) wind event and corresponding offshore surface currents and reduction of surface temperature. Postlarval abundance was reduced in our sampling area during this period.

or pre-molt stage (Fig. 3.6). The low number of the inter-molt and post-molt stages (molt stage A-C) was consistent with previous reports of molt stage from this region (Incze et al. 2000a, Incze et al. 1997). In contrast to previous reports, we found large numbers of D0 and D1 stages and few D2-3 stages. In this area there is a gradient of molt stage with the earlier stages found offshore and the later stages found inshore. (E. R. Annis, unpublished data). Incze et al.'s collected data within John's Bay which is inshore of all the collection sites in our study and may explain the abundance of later molt stages in their study.

Development Time

We used our development model to simulate the timing of stage I and postlarval peaks by adjusting a correction factor for stage duration until the model output matched the timing of the field observations (Fig. 3.7). The peaks in stage I and postlarval abundance were separated by 14 d in the field data (Fig. 3.4). A correction factor of 0.32 was required to reproduce this separation in the model, suggesting that the development times may be as much as three times faster in the field than in previous laboratory studies (MacKenzie 1988). The average stage durations suggest that larvae may reach postlarval stage in 10-11 d at ambient temperatures (Table 3.2). Our estimate of the timing of peak abundance in the field was subject to potential errors due to the fit of the polynomial curve. Sensitivity analysis was conducted to determine the effect of these errors on the correction factor (Fig. 3.8). When the results of the Gaussian fit for the postlarval field data were used with a 28 d separation in peaks, the correction factor is 0.72, or approximately 1.4 times faster development in the field than in the laboratory.

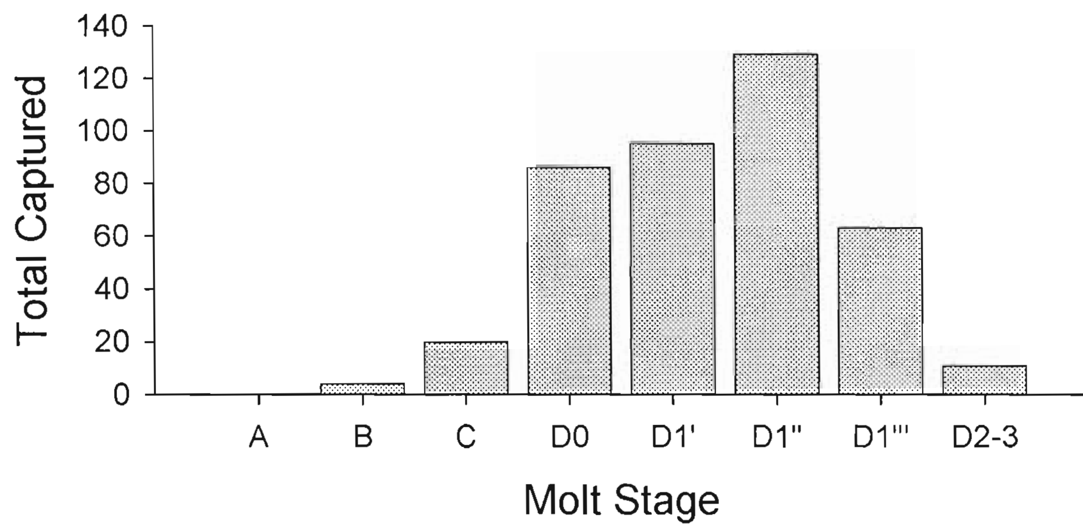


Figure 3.6. Cumulative molt stage composition of postlarvae using the stages defined by Sasaki (1984). Bars denote the total number of each molt stage caught over the course of the entire postlarval season.

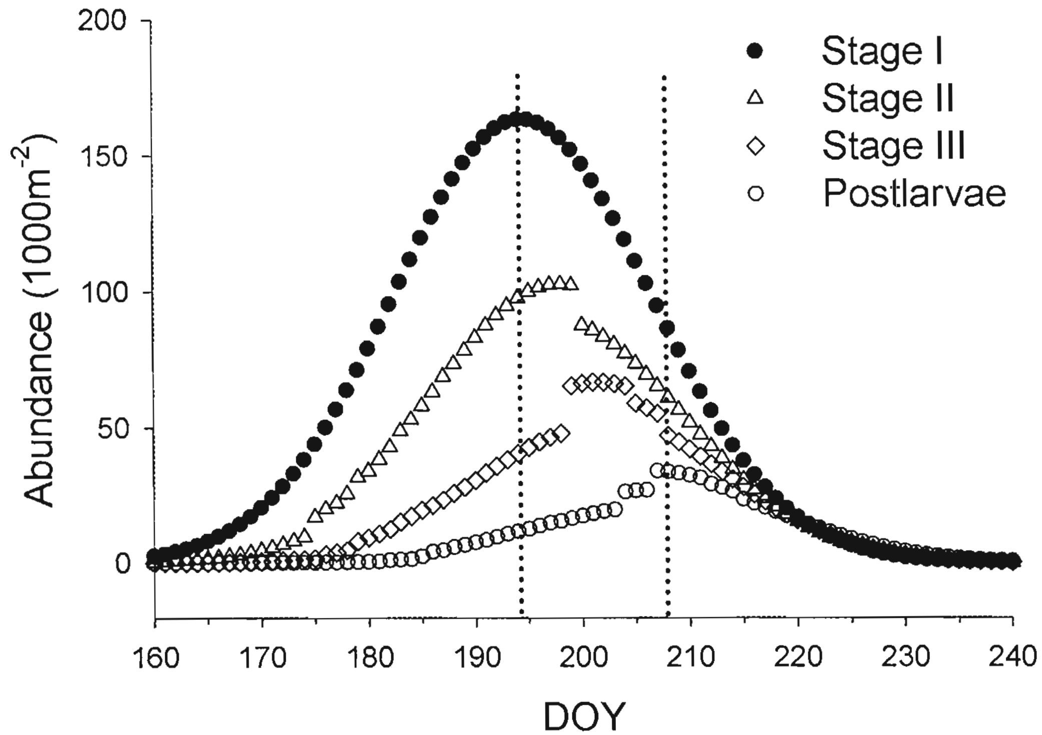


Figure 3.7. Development model output illustrating 14 day separation in estimated stage I and postlarval abundance peaks (dotted vertical reference lines). This run of the model used a stage duration correction factor of 0.32, mortality was set at 0.20 d^{-1} for illustrative purposes, and observed ambient temperatures were used to calculate development time.

Stage Duration (d)

SI	SII	SIII	PL
2.76 ± 0.82	3.11 ± 0.47	4.68 ± 1.35	8.45 ± 1.07

Table 3.2. Average development time (± 1 S.D.) from hatch to postlarva predicted by development model. Observed ambient temperatures were used to calculate development time.

The time step of the model was one day and any portion of a development day was rounded up to the nearest whole day, resulting in a slight overestimate of stage duration and a correspondingly lower correction factor to achieve the 14 d separation of peaks. When the model was run with rounding down to the nearest whole day it resulted in a one day shift in the peak postlarval abundance. Thus, the appropriate correction factor required to reproduce a 14 d separation in peaks falls somewhere between 0.320 and 0.349 or approximately one-third of the laboratory development time. The one day time step interacts with the curve used for temperature input to create the abrupt abundance shifts in model output. The changing temperatures in the model generate differences in stage duration between daily cohorts resulting in multiple cohorts entering or exiting the developmental stage on the same day. This effect does not occur when the model is run with a fixed temperature (and therefore fixed stage duration). The shifts in abundance had little effect on the timing of the peaks in the model runs. Mortality was set at 0.2 d^{-1} simply to illustrate an intuitive decrease in abundance from one developmental stage to the next, and is not meant to suggest that larval mortality occurred at that rate. Sensitivity analysis determined that changes in mortality did not affect the timing of the postlarval peak.

Production and Mortality Estimates

Estimates of stage I, II and postlarval production were probably higher than previous estimates due to higher estimates of abundance and shorter development time (Table 3.3). When postlarval abundance is not corrected for environmental variables, it yields a production estimate that is only 70% of the corrected neuston data (Table 3.4).

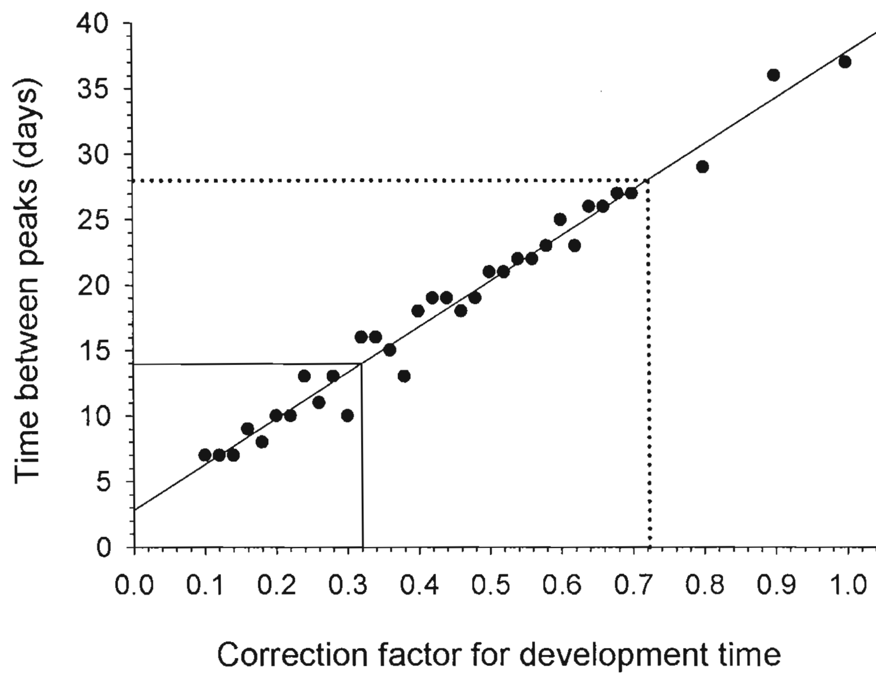


Figure 3.8. Separation time of peak stage I and postlarval curves generated by the model as a function of the correction factor used for development time. Multiple runs of the model were conducted while varying the correction factor between 0.1 and 1.0. The regression equation is $Y = 34.94X + 2.81$, $r^2 = 0.98$, $P < 0.0001$. Solid reference lines indicate the 0.32 correction factor required to generate a 14 d separation of peaks as observed in field data. Dotted reference lines indicate correction factor of 0.72 when the conservative estimate of a 28 d peak separation is used.

To facilitate comparison with other data from this study area, a production estimate was calculated using uncorrected postlarval abundance and full development time of MacKenzie (1988). The change in the stage duration correction factor results in a three-fold decrease in production, and the estimated postlarval production is little more than half of the average production for Johns Bay from 1989 to 1995 (Incze et al. 1997). The production in 2001 is very close to their lowest reported production of 9 per $1000m^2$ in 1993 and 1995. Stage III larvae were not abundant enough in our samples to make a meaningful estimate of production for the season.

Instantaneous rate of mortality ("M" in Table 3.1) was greatly increased by the shortened development time. The highest rate of mortality (1.226 d^{-1}) occurred in larvae between stage I and II. Mortality was exceptionally low between stage II and postlarvae. When mortality is incorporated in the development model it produces similar results but requires slightly higher mortality rates than those estimated from production values. Abundance curves of similar magnitude to the field observations can be achieved using a rate of 1.4 d^{-1} for stage I larvae and 0.08 d^{-1} for subsequent stages (Fig. 3.9). The model reproduced the general shape of the stage II larval curve, but the shape of the postlarval curve could not be simulated with any combination of mortality and development rate.

Discussion

Larval Development Time

The development time of lobster larvae in the field was as little a one third that reported in previous laboratory studies (MacKenzie 1988, Templeman 1936). This has direct effect on estimates of larval production, mortality, and dispersal. Production and

Source	Production ($1000 m^{-2}$ $season^{-1}$)			Mortality Rate (d^{-1})			Percent Surviving	
	SI	SII	PL	SI to SII	SII to PL	SI to PL	SI to SII	SI to PL
This paper	1988.9	54.3	34.9	1.226	0.044	0.312	2.73	1.76
Scarratt (1964, 1973)	258 ± 106	36 ± 24	2.7 ± 3.4	-	-	-	13.29 ± 4.97	0.86 ± 0.82

Table 3.3. Estimates of stage duration, larval production and mortality calculated using the method of Scarratt (1964, 1973). Regressions from the abundance data in Figure 3.4 were used for these calculations. SI = stage I, SII = stage II, PL = postlarvae.

Source	Year	Stage duration correction factor	Estimate for postlarval abundance	Postlarval production ($1000 m^{-2}$)
This paper	2001	0.33	Corrected	34.9
This paper	2001	0.33	Uncorrected	24.4
This paper	2001	1	Uncorrected	8.1
Incze and Wahle (1997)	1989-1995	1	Uncorrected	14.9 (average)

Table 3.4. Postlarval production estimates for comparison of the effects of reduced development time, postlarval abundance correction, and previous values for our study area.

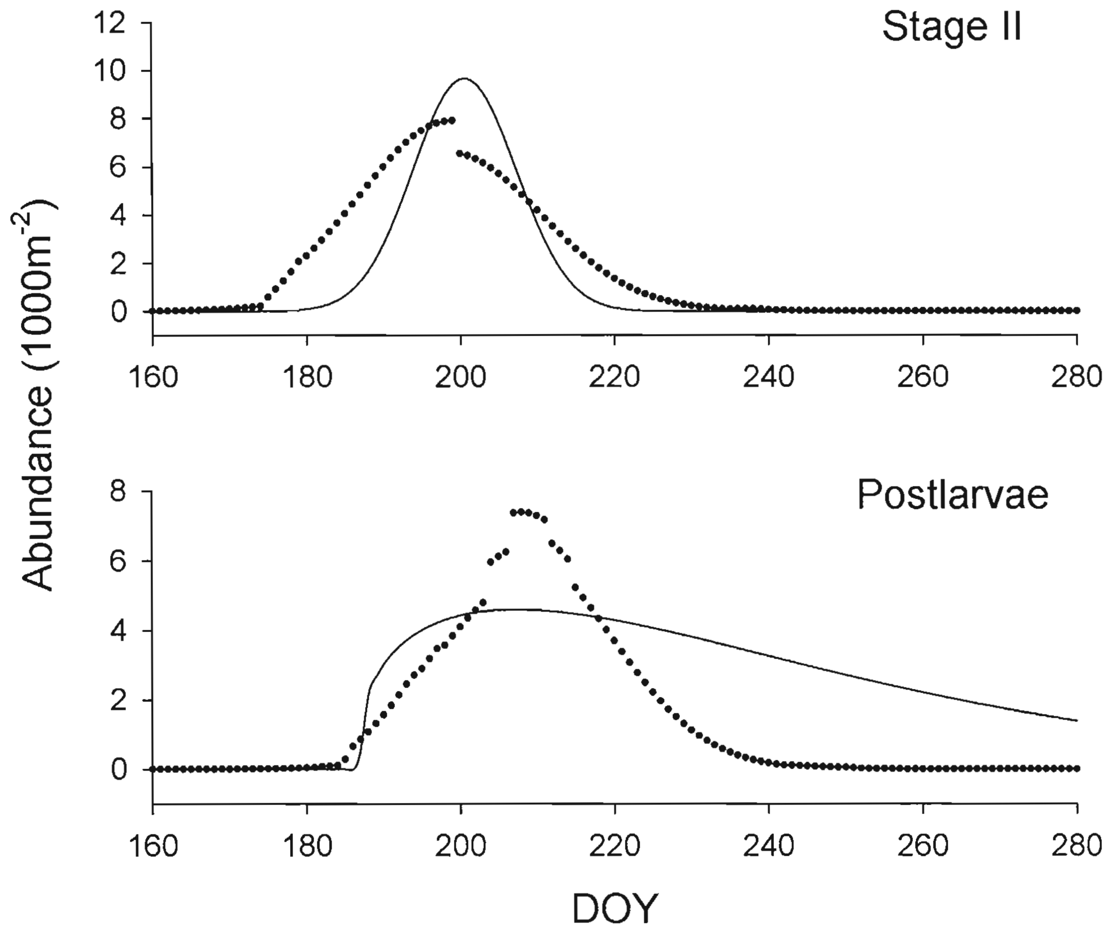


Figure 3.9. Comparison of stage II and postlarval abundance curves observed in the field (—) and those produced by the development model (●). The model used a stage duration correction factor of 0.32 and stage specific mortality rates of 1.4 d^{-1} (stage I) and 0.08 d^{-1} (stage II, III, and postlarva).

mortality estimates are inversely proportional to development time (Rumrill 1990, Scarratt 1964), and a three fold reduction in development time results in a three fold increase in production and mortality rates. Potential for larval transport is directly proportional to the amount of time spent in the water column, and reduced development time will result in shorter dispersal distance in coupled physical-biological models. Higher mortality rates will reduce the probability of long distance dispersal. This is particularly relevant to continuing efforts to assess connectivity through larval exchange of lobster populations in the Gulf of Maine.

Several lines of evidence support the thesis that development rate may be shorter *in situ* than in the laboratory. Laboratory reared postlarvae are deficient in several aspects of development such that they are typically smaller, have weaker exoskeletons, swim slower, and lack the dark pigmentation of field captured postlarvae (Annis et al. in press, James-Pirri and Cobb 1997, Juinio and Cobb 1994, Rooney and Cobb 1991). Perhaps the most convincing evidence comes from a study using RNA:DNA ratios to estimate the growth rate of postlarvae as a function of protein accumulation (in contrast to the present study which examines the development rate through multiple instars)(Juinio and Cobb 1994). Juinio and Cobb (1994) estimated the growth rate of field caught postlarvae and found that they were twice a fast as growth rates in laboratory reared postlarvae. Shorter development time has also been reported in laboratory studies at the St. Andrew's Biological Station (Bay of Fundy, N.B., Canada) where larvae developed to the postlarval stage in 36 d in 12°C water: a development time nearly twice that observed by MacKenzie. Incze and Naimie (2000) conducted inverse runs of a physical-biological model to determine potential origins of postlarvae arriving at the

perimeter of our study area. They were unable to return many of the larvae to a point of origin because the larvae could not complete the reverse development at the model temperatures using MacKenzie's (1988) equations for temperature-dependent development. They concluded that the modeled development rates were too slow to return the larvae all the way back to the time and point of hatching.

The timing of peak postlarval abundance and the underlying assumption that the peak reflects local larval production are fundamental to our estimates of development time and present the greatest potential source of error. The most important part of the postlarval abundance curve with respect to the timing of local larval development is the initial rise to peak values (Fig. 3.4). It is unlikely that larvae from sources outside our sampling area would have been present as postlarvae before locally hatched larvae. On the Maine coast, the residual current moves from northeast to southwest suggesting that potential larval sources will be found predominately in the upstream direction (consistent with modeled larval transport, Incze and Naimie 2000). Larval sources outside our study area are located from 0-250 km upstream from our study area (Annis et al. in prep-a), and water temperature decreases with increasing distance upstream. The timing of hatching is thought to be uniform along the coast of Maine (C. Wilson unpublished data). Larvae hatched locally and retained in the slower moving, warmer waters of our study area should develop faster and reach the postlarval stage before those hatched in colder upstream waters and advected to the study area. Therefore, the initial rise in postlarval abundance most likely to represents local larval production. We do not suggest that the postlarval abundance in our study area reflects only local larval production, only that the timing of the onset of postlarval abundance is probably a product of local hatching. More

importantly, if larvae hatch at the same time along the entire coast, the initial rise in postlarval abundance reflects the fastest development regardless of the source of larvae.

With respect to the timing and the fit of the postlarval abundance curve we expect that even the Weibull form regression provides a conservative estimate of larval development time due to the protracted tail of the season. This tail probably reflects late season local hatching and the arrival of larvae advected from outside the study area. Alternatively, the extended tail of the postlarval season may reflect indeterminate development of postlarvae that can delay settlement until they find favorable habitat (Botero and Atema 1982). In either case the tail of the season serves to shift the fitted peak in postlarval abundance later in the season, creating greater separation between stage I and postlarval curves and making our estimate of development time more conservative (slower).

Interpreting postlarval abundance as one curve rather than two overlapping peaks seems appropriate given the evidence that the trough between peaks was coincident with an offshore wind event. If two overlapping peaks were present it would suggest either multiple distinct hatches occurring in our sampling area, the presence of two larval sources with larvae appearing at our sampling area at different times, or differential development rates within locally hatched larvae. The abundance of stage I larvae had only one peak indicating that multiple distinct hatching periods did not occur. The possibility that larvae were imported from outside sources is likely given the location of larval sources (Annis et al. in prep-a) and the potential for larval transport along the Maine coast (Incze and Naimie 2000). We expect that these larvae would arrive later in the season making them a major component of the second peak, but we have no basis for

ascribing the peaks observed to distinct sources. It is also possible that local production would have variations in development time, given that differences in egg quality and larval viability are found among individuals (Annis et al. in press, Attard and Hudon 1987, Ouellet et al. 2003, Pandian 1970, Sibert et al. 2004). However, in the event of larval delivery or differential development, the first peak in abundance would still represent the fastest development time and would indicate even shorter development times than we propose here.

We have used a Weibull form for the regression of postlarval abundance in the field. While this is a different from than the Gaussian regression used on stage I and II larvae, we feel that it better reflects the rapid onset and protracted tail of the postlarval abundance. The Weibull form also explains a greater proportion of the variance in postlarval abundance. The Weibull regression shifts the peak abundance to earlier in the season which makes our estimates of development time faster than when we used a Gaussian regression. However, it is worth noting that the highest observed mean postlarval abundance during the season occurred ten days prior to the peak estimated by the Weibull regression. The 14 d separation between stage I and postlarval peak abundance using the Weibull regression is supported by seasonal abundance data collected in Penobscot Bay in 1999 (adjacent to the eastern end of our sampling area), suggesting a 14 d separation between peaks in stage I and postlarval abundance (L.S. Incze, unpublished data). This indicates that our observations were not an isolated event and that development times are indeed shorter than previous findings.

We acknowledge the potential shortcomings of defining the peak in postlarval abundance. In an effort to provide a range for the correction factor for development time

we have used the Gaussian regression fit to the postlarval abundance data to provide a conservative estimate of development time. We feel that this is a conservative estimate because it centers the peak abundance while the data is evidently skewed towards the early portion of the season, and it produces a separation of stage I and postlarval peaks twice as long as the Weibull regression. A correction factor of 0.72 was required to reproduce the 28 d separation in peaks in the development model. Thus, even a conservative estimate of the postlarval peak results in a 1.4 fold decrease in development time relative to laboratory rates.

In contrast to our results, Hudon and Fradette (1988) reported *in situ* development rates off the Magdalen Islands (Gulf of St. Lawrence) that were consistent with the laboratory rates of Templeman (1936). They estimated the development time based on the time at which 50% of the cumulative catch is attained. This method was not appropriate for our data as the protracted tail of the season (not present in their data) effectively shifts the 50% catch later in the season and biases the estimated development time. Irrespective of the method used to determine development time, there was a substantial difference in the timing of stage I and postlarval peaks between sites with about 35 d separation in the Magdalen Islands (Hudon and Fradette 1988, Hudon et al. 1986) and 14 d in mid-coast Maine. Development times may vary as a function of the over-wintering temperatures of the embryos. Adult lobsters in the Gulf of Maine undertake a seasonal migration to deeper warmer waters for the winter months thereby maximizing degree-days for the developing embryos (Campbell 1986, Campbell 1990). In contrast, adult lobsters of the Magdalen Islands undergo limited seasonal migration and over-winter near the mouths of lagoons where the winter temperatures are colder

(Campbell and Stasko 1986, Munro and Therriault 1983). Embryogenesis is temperature dependent (Perkins 1972) and embryos developing in cold water have fewer metabolic reserves at the time of hatch (Sasaki et al. 1986), thus providing an advantage to embryos developing at warm temperatures. Temperatures in our study area reached their peak earlier than the Magdalen Islands which could provide an advantage to larval development. The final weeks before hatch are the most critical time for the accumulation of proteins (Sibert et al. 2004) and earlier warming could provide a developmental advantage to larvae by imparting greater yolk reserves at the time of hatch. A final possibility is that longer development time in the Magdalen Islands may result from food limitation as it serves to slow larval development in lobster larvae (Anger and Dawirs 1981, Anger et al. 1981a, Anger et al. 1985, Annis et al. in press). Studies assessing the nutritional status of lobster larvae with triacylglycerol/sterol ratios suggest that a higher percentage of larvae are in poor nutritive condition in the Gulf of St. Lawrence than in the Gulf of Maine (Harding and Fraser 1999, Ouellet and Allard 2002). While the cause of slower development in the Magdalen Islands remains unresolved, it suggests that there may be regional variation in development times and the correction factor presented here may not be universal.

Larval Production

Our larval production estimates illustrate the effect of reducing the estimated development time of the larvae. Postlarval production was more than twice that reported for Johns Bay (Incze et al. 1997, Table 4). However, when we calculated the production using neuston data uncorrected for vertical distribution postlarvae (methods of Annis in

prep), we found that 30% of the production was missed due to the underestimation of postlarval abundance. Using the uncorrected postlarval abundance in conjunction with the full development time from MacKenzie (1988) provides a number for direct comparison with the Johns Bay data. These data indicate that larval production in 2001 was probably well below the average production value for this area. In fact, it is comparable to the lowest production years reported (Incze et al. 1997).

Our production estimates were also substantially higher than those of Scarratt (1964, 1973, Table 3.3), but probably due to a combination of reduced development time and higher larval production. If the production values from both studies are calculated using the same development time production values are about twice as high. This represents the top of the range that Scarratt encountered in 15 years of sampling and suggests that larval production in our study was probably higher than what was observed in Northumberland Strait between 1949 and 1963. Similar conclusions were reached by Incze et al. (1997) for the Johns Bay area.

Larval Mortality

Instantaneous rate of mortality is inversely proportional to development time and mortality rate was greatly increased by the reduction in development time. However, the high instantaneous mortality rate is due solely to the decrease in development time rather than a change in total mortality, and the proportion surviving to postlarval stage was actually higher in our study than reported by Scarratt (1964, 1973). Approximately the same proportion of the stage I larval production survived to the postlarval stage, but a

higher rate of mortality was required to accomplish it within the reduced development time.

The most striking aspect of the mortality estimates was the rate of mortality between stage I and II larvae. It appears that only 2.73% of the population survived to stage II. The average duration of stage I was only 2.76 days which means that an exceptionally high rate of mortality was required to reproduce the observed stage II larval abundance using the development model. Recent studies employing discrete depth sampling in the vicinity of our study area suggest that the total abundance of stage I larvae integrated over the top 50m of the water column are more than twice as abundant at night than during the day (L. S. Incze, unpublished data). Lobsters typically release their larvae shortly after sunset (Waddy et al. 1995) which would contribute to high abundance at night. Interestingly, the mortality rates presented here are sufficient to reduce the standing stock to less than half by the following day and are consistent with the two-fold decrease in stage I larvae during the day.

Development Model

The instantaneous rate of mortality calculated from production estimates provided a good approximation for the developmental model but the model required slightly higher rates to reproduce stage II and postlarval abundance curves similar to those observed in the field. This may result from an interaction between mortality rate and production in the estimation of stage I larval production from the seasonal abundance curve and warrants further exploration. The shape of the stage II larval abundance curve was easily replicated but appears slightly earlier than the observed stage II larval abundance (Fig.

3.9). However, the observed stage II larval curve is comprised of relatively few individuals and sampling was limited to multiple oblique tows which were less frequent than neuston tows so that the timing and magnitude of this peak has high risk of error. It was not possible to reproduce the observed postlarval curve using the model due to the extended presence of postlarvae in the area. Two likely explanations as addressed earlier in the discussion are that the postlarvae have indeterminate development and were delaying settlement, or postlarvae were advected from other areas and continued to be delivered after the local production of postlarvae had subsided. While a delay of settlement is possible, it seems unlikely given the low abundance of the last two molt stages (D2-3) in our samples which infers that they were either advected out of our sampling area, died, or settled. Our study area is thought to be a net sink for lobster larvae arriving from multiple sources both local and distant (Annis et al. in press, Incze and Naimie 2000, Steneck and Wilson 2001), and this seems to be a likely explanation for the extended tail of the postlarval season.

Conclusion

We have provided a new estimate of development time which has a cascading effect on production and mortality rate estimates. We advance these findings with the understanding that they are not a final solution to issues involving development time, but that they represent the best estimate given the available data and our knowledge of the larval biology of *Homarus americanus*. These estimates will support current efforts to create a biological-physical coupled model which accurately portray the potential for transport and connectivity of populations within the Gulf of Maine. Further work is

necessary to better understand the apparent regional differences in larval development time and the biological and physical factors contributing to these differences.

4. PATTERNS OF LARVAL DISTRIBUTION AND TWO POTENTIAL LARVAL SOURCE-SINK MODELS FOR LOBSTERS (*HOMARUS AMERICANUS*) IN THE NORTHERN GULF OF MAINE

Abstract

Patterns of larval distribution provide the basis for process oriented studies examining larval exchange between populations. We report results from the first broad-scale synoptic sampling for lobster larvae in the northern Gulf of Maine. On research cruises conducted in 1999 and 2001 we sampled lobster larvae over a 300 km length of coast from mid-Maine to the Bay of Fundy. We collected newly hatched larvae (stage I) and the final planktonic instar (postlarvae) in surface tows, and surveyed benthic lobsters with a ROV. We also pooled data from numerous studies between 1989 and 2003 to elucidate persistent patterns of postlarval abundance.

Postlarvae were most abundant at the downstream (western) end of the study area with average densities of 1.4-5.1 $1000m^{-2}$, corresponding to established areas of high settlement. We propose that this area represents a net sink for locally produced larvae and those advected from upstream sources. By contrast, upstream (eastern) sites had low postlarval density averaging 0.3-2.2 $1000m^{-2}$. This pattern was evident in both the synoptic sampling and the pooled long term data set. The density of adolescent phase lobsters on the bottom increased with postlarval abundance suggesting that the east-west pattern of postlarval abundance is persistent in time. Stage I larvae were located upstream from the proposed larval sink, and their abundance was positively correlated with reproductive phase lobster density indicating potential sources of larvae. Most

stage I larvae were captured immediately upstream of the proposed sink (extending 100 km upstream), but a second source of stage I larvae was located 250 km upstream in the mouth of the Bay of Fundy. The residual current in this area moves from northeast to southwest, providing a mechanism for larval transport between the identified sources and the proposed sink.

Our results reveal persistent spatial patterns of larval distribution that are consistent with two potential source-sink models: one which is largely self-recruiting and a second in which larvae are delivered from a distant source. The relative contribution of these models is unknown and warrants further investigation. The patterns described here will benefit future efforts to model larval transport and connectivity in the Gulf of Maine.

Introduction

In benthic marine invertebrates with complex life histories, larval delivery often shapes the demographics of the adult populations (Roughgarden et al. 1988), and the prevalence of planktonic larval forms in benthic invertebrates (Thorson 1950) has contributed to the traditional view that marine populations are fundamentally open. In open populations, larvae settling and recruiting to the local population are delivered from distant sources with relatively little if any recruitment of locally produced larvae (Caley et al. 1996). However, mounting evidence suggests that despite the potential for dispersal during the planktonic larval phase, many populations exhibit a large degree of self-recruitment (Jones et al. 1999, Swearer et al. 1999, Thorrold et al. 2001). The degree to which populations are open or closed has important implications for the ecology and management of species, and determining the level of connectivity presents a formidable

challenge (Sponaugle et al. 2002, Swearer et al. 2002, Warner and Cowen 2002). Patterns of larval abundance and distribution provide an important tool in assessing connectivity by identifying potential larval sources and sinks that support the adult populations. As such, they are a necessary first step in understanding the life history and population dynamics of organisms with complex life histories.

The American lobster, *Homarus americanus,* provides an excellent example of settlement driven demographics where settlement ultimately drives the abundance of adults. Settlement of planktonic larvae to the benthos is a function of larval delivery (Incze et al. 1997, Incze et al. 2000b), and there are direct linkages that extend through consecutive life phases from the newly settled "young-of-year" to adults of harvestable size (Steneck and Wilson 2001, Steneck et al. in prep). There are persistent patterns of settlement characterized by low settlement in areas east of Penobscot Bay (Figure 1) and high settlement west of the bay (Palma et al. 1999, Steneck and Wilson 2001, Wahle and Steneck 1991). Our understanding of the patterns of benthic phase lobsters on a scale of 100s of kilometers is relatively recent, and but we do not yet know if these patterns result from differences in larval supply.

The American lobster is the most valuable commercially harvested species in the northeastern United States, and yet the unprecedented growth of lobster populations in spite of fishing pressures remains an enigma. In some areas fishing mortality exceeds 90% of the harvestable population (Fogarty 1995), but despite intense harvest and forecasts of imminent collapse, fisheries landings and fisheries independent surveys indicate that the population has increased in size (ASMFC 2000, Steneck and Wilson 2001). The paradoxical resilience of the fishery is driving a movement towards more

ecologically based management of the species (e.g. Chen and Wilson 2002, Steneck and Wilson 2001). An important part of this strategy must be to determine whether the populations are functionally open or closed and the degree of connectivity between segments of the populations.

Here we provide the first comprehensive report of larval distribution patterns on the scale of 100s of kilometers in the northern Gulf of Maine. We use data pooled from numerous studies over the past 14 years and intensive sampling efforts in 1999 and 2001 to establish persistent patterns of larval distribution and abundance with respect to benthic populations and to identify potential larval source and sink relationships. While we cannot provide conclusive evidence for connectivity, our results provide a foundation for continuing efforts to model larval transport and determine the level of connectivity of lobster populations in the Gulf of Maine.

Methods

Larval Life Stages

Planktonic larvae of *Homarus americanus* are competent to settle after approximately 10-30 d depending on water temperature (Annis et al. in prep-b, Hudon and Fradette 1988, MacKenzie 1988). The first three planktonic instars are zoeal, while the fourth is a postlarval instar with morphology similar to the adult form (reviewed in Ennis 1995). In the northern Gulf of Maine, hatching of stage I larvae begins in early June and is completed by mid to late August (Annis et al. in prep-b, C. Wilson and L. S. Incze unpublished data). The timing of peak hatching appears to be uniform for the length of the coast (C. Wilson and L. S. Incze unpublished data). Postlarvae are present

in coastal waters in early July and their abundance tapers off by mid-September (Annis et al. in prep-b, Incze et al. 2000a, Incze et al. 1997). Stage I larvae and postlarvae are frequently taken in surface plankton samples with 1-30% of stage I and 55-80% of postlarvae residing at the surface (Annis in prep, Annis et al. in prep-b, Harding et al. 1987). Stage II and III larvae occur infrequently in surface samples and were not considered in the present study.

Circulation

The general circulation of the Gulf of Maine consists of a cyclonic gyre which produces a residual current moving from northeast to southwest along the Maine coastline (Figure 4.1). The predominant hydrographic feature of Maine coastal waters is the Eastern Maine Coastal Current (EMCC) originating at the Bay of Fundy and reaching a terminus just to the west of Penobscot Bay. Current speed in the EMCC averages 15-20 cm s^{-1} (Pettigrew et al. 1998). As it moves past the mouth of Penobscot Bay, portion of the current is deflected offshore to form a sub-gyre around Jordan Basin; another portion enters Penobscot Bay; and the remainder continues southwest to form the slower moving Western Maine Coastal Current. The behavior of the currents at this intersection is not well understood, but the intersection demarcates a shift in hydrographic regime from cold vertically mixed waters in the east to warmer seasonally stratified waters in the west.

Data Collection

To elucidate persistent spatial and temporal patterns of postlarval abundance in the northern Gulf of Maine, we pooled all available postlarval abundance data from previous studies between Seabrook, New Hampshire and the US-Canada border for the period 1989-2003 (Table 4.1). Data presented here are the culmination of numerous independent research projects providing the advantage of illustrating spatial and seasonal patterns without the logistical effort and expense of multiple, full-season, coast-wide surveys. The sampling efforts represent a combination of synoptic research cruises covering broad portions of the coast, and localized sampling efforts throughout the course of the season. Portions of this data set have been previously reported (Annis et al. in prep-b, Incze et al. 2000a, Incze et al. 1997, Incze et al. 2000b) but have not been placed in the context of coast-wide patterns. The dates of sampling efforts and general regions are provided in table 4.1. In addition to data from previous studies, we conducted sampling specific to this project in an area extending from Cape Small to Grand Manan Island in 1999 and 2001 between July 25 and August 18 (Table 4.1, Fig. 4.2). This sampling effort provided a synoptic view of the distribution of lobster larvae over a 300 km stretch of coast during the peak postlarval season.

In all studies (past and present) postlarvae were collected using either a 1 or 2 m wide neuston net with 500 or 1000 μm mesh that sampled the top 0.5 m of the water column. The net was towed at 3.5-7.0 km h^{-1} from the side of the vessel to minimize interference from propeller wash and bow wake. Flow was measured using a calibrated flow meter to estimate the volume of water filtered, and larval abundance is reported as individuals per 1000 m^2. In our sampling in 1999 and 2001, postlarvae were enumerated

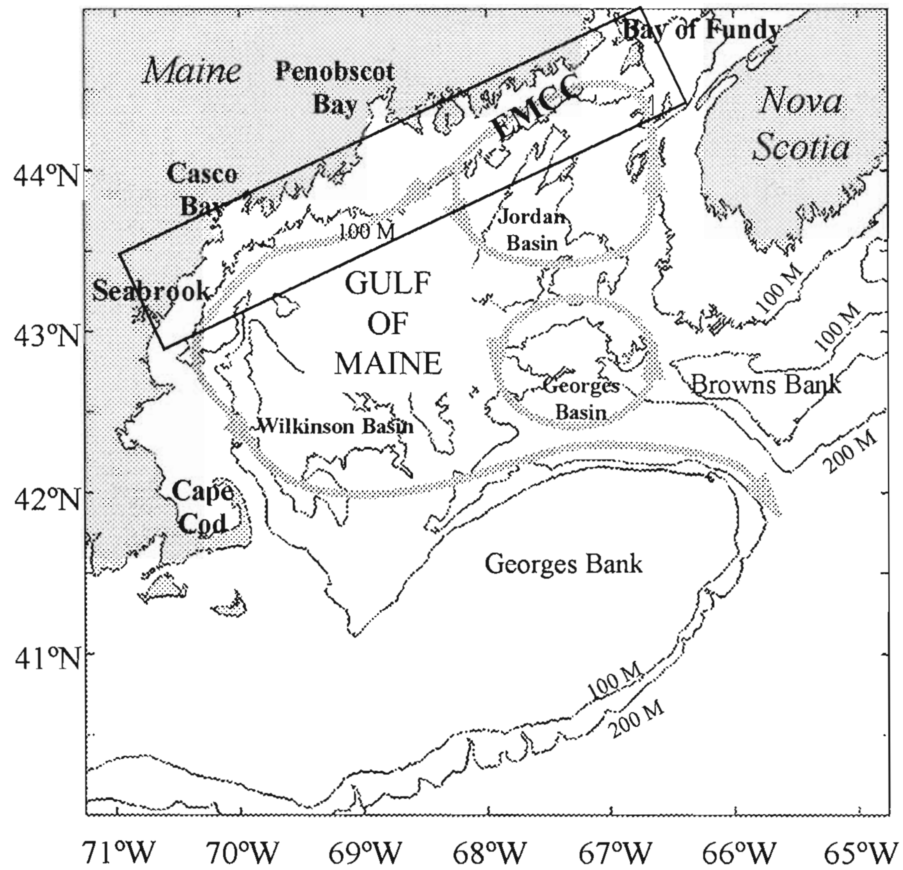


Figure 4.1. General circulation pattern in the Gulf of Maine. Our sampling region is indicated by the boxed area. The predominant hydrographic feature in the sampling area is the southwest flowing Eastern Maine Coastal Current (EMCC) extending from the mouth of the Bay of Fundy to Penobscot Bay (Brooks 1985).

Year	Dates	General Location	Vessel	Samples Type
1989	8/5-8/12	Seabrook, NH – Jonesport, ME	N/A	Neuston
1991	7/29-7/31	Seabrook, NH – Mount Desert Is., ME	M/V Argo Maine	Neuston
1989-2001	May – Oct.	Seabrook, NH	N/A	Neuston
1989-1995	June – Sept.	John's Bay, ME	N/A	Neuston
1999	June – Sept.	Narraguagus Bay, ME	F/V Southwind R/V Homarus	Neuston
1999-2003	June – Sept.	Penobscot Bay, ME	F/V Alice Siegmund	Neuston
*1999	7/30 – 8/8	Pemaquid Point, ME – Grand Manan Is., NB	R/V Connecticut	Neuston ROV
2000	July – Aug.	Boothbay, ME – Penobscot Bay, ME	R/V Nucella	Neuston
*2001	June – Sept.	Cape Small, ME – Penobscot Bay, ME	F/V Striker R/V Homarus	Neuston
*2001	7/5 – 8/4	Pemaquid Point, ME – Grand Manan Is., NB	R/V Connecticut	Neuston ROV
*2001-2002	7/30 – 8/22	Casco Bay, ME – US/Canada border	F/V Tenacious	Neuston
2002	July – Sept.	Boothbay, ME – Penobscot Bay, ME	R/V Nucella	Neuston
2002	7/29 – 8/6	Boothbay, ME – Penobscot Bay, ME	R/V Weatherbird	Neuston MOCNESS

Table 4.1. Sampling for postlarvae in the northern Gulf of Maine 1989-2002. Date ranges spanning multiple months indicate areas where localized sampling was conducted throughout the course of the postlarval season, and specific dates indicate synoptic research cruises. Sampling included neuston tows for larvae and remotely operated vehicle (ROV) transects for benthic phase lobsters. All data from these sampling efforts were included in the analyses of abundance by zone (Fig 4.3) and by temperature (Fig. 4.4). Years preceded by an asterisk (*) indicate data collections which were conducted specifically for this project and are presented in detail (Figures 4.5 – 4.8).

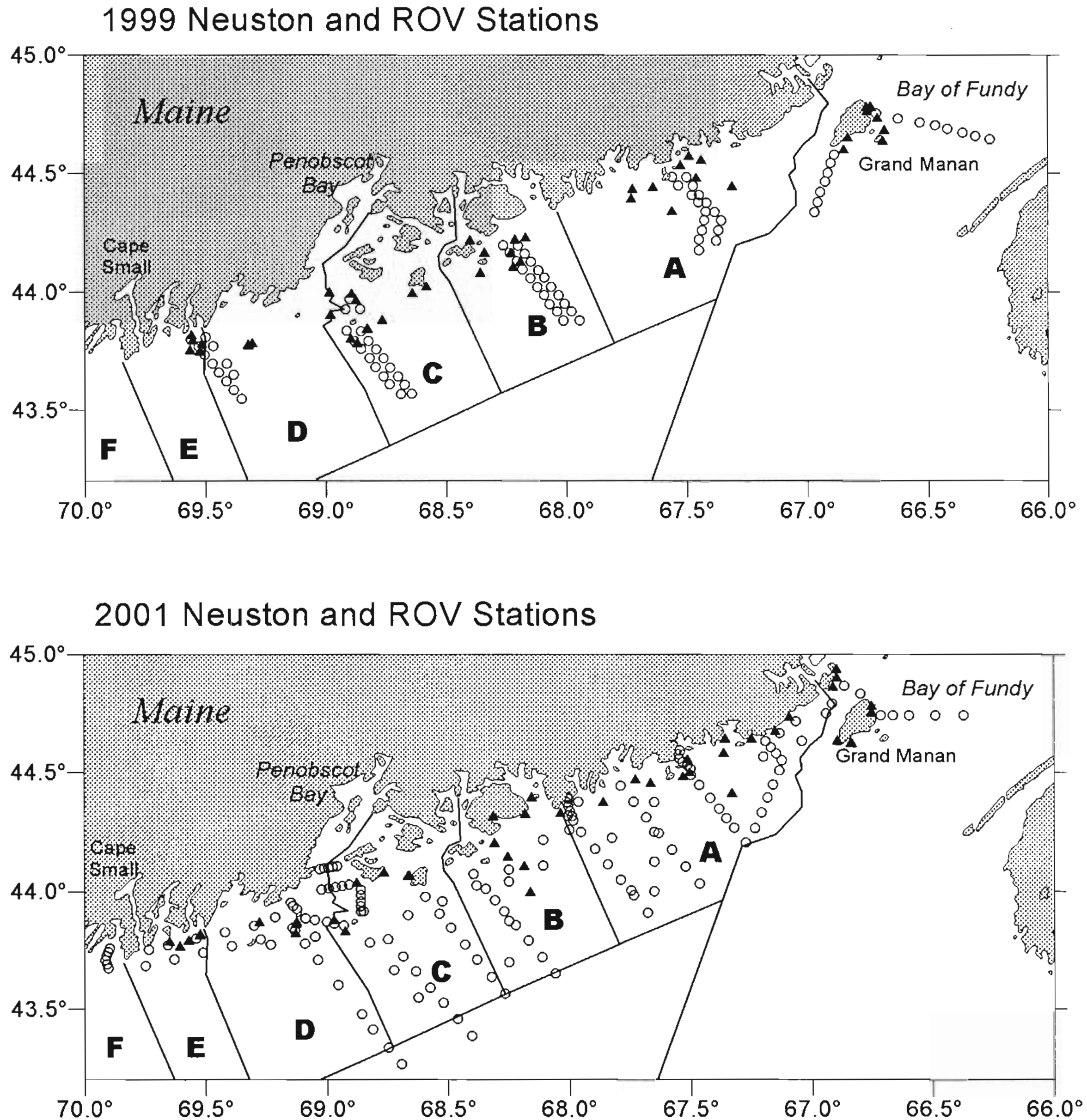


Figure 4.2. Northern Gulf of Maine sampling sites in 1999 (A) and 2001 (B). Site locations indicate postlarval sampling (○) and benthic ROV transects (▲). Collections were conducted between July 30 and August 8, 1999, and between July 5 and August 22, 2001. The region was divided using the bounds of existing Maine Lobster Management Zones A-F and the waters of Seabrook, NH (Seabrook appears in Fig 4.1).

in all neuston samples, while stage I larvae were enumerated in all 1999 samples and approximately 35% of the samples taken in 2001. Most collections were conducted during daylight hours, but on the 1999 and 2001 R/V Connecticut cruises we utilized a vessel of opportunity which required that we sample at night. Recent studies suggest that postlarvae may exhibit some form of diel vertical migration that could affect the abundance in surface samples (Annis in prep, Harding et al. 2000). We have included samples collected at night in our data analyses as our interest in distribution patterns requires only a relative difference in abundance rather than accurate estimates of abundance. As these cruises covered a large portion of the study area the larval abundance observed likely reflects coast-wide patterns. Water temperature (surface) was measured at collection sites using either a CTD, bucket thermometer, or hull mounted thermistor.

The distribution and abundance of benthic phase lobsters was recorded using remotely operated vehicle (ROV) surveys in both 1999 and 2001. Benthic transects with the ROV targeted sites from the Pemaquid region (Zone E) to the mouth of the Bay of Fundy (Fig. 4.2). Video analysis was used to enumerate and measure carapace length (CL) for lobsters on each dive. When the carapace of an individual was obscured, a regression of CL to claw length was used to estimate CL (Steneck et al. in prep). Lobsters with carapace length of 40-90 mm were identified as "adolescent phase" and lobsters > 90 mm were considered "reproductive phase" (Wahle and Steneck 1991). The width and length of each ROV transect was used to calculate the area sampled and lobster density was reported as individuals m^{-2}.

Abundance data for larvae and benthic phase lobsters were averaged by regions consistent with the Maine Lobster Management Zones established by the Maine Department of Marine Resources. We present data compiled for Zones A-E, Grand Manan Island (GM), and postlarval data from the Seabrook power plant in New Hampshire (Fig. 4.1 & 4.2). Postlarval abundance data from zones F and G was included with the Seabrook data because very few data were available.

Results

Postlarval Abundance by Region 1989-2003

A total of 3687 postlarval collections were pooled from past and present studies for the period between 1989 and 2003 (Fig. 4.3). Postlarvae were present in approximately 38% of the samples and their abundance was greater that 5 $1000m^{-2}$ in only 10% of the samples collected. Sampling effort was greatest in the western half of our sampling area (zones D, E, and Seabrook) due to proximity to research facilities. Despite the difference in effort, trends in the magnitude and timing of larval abundance were evident. Postlarvae were generally more abundant in the western zones (D, E and Seabrook), and less abundant in the eastern zones (A, B, and C). This was evident in both the mean and the maximum values for each zone, though both the mean and maximum were elevated in Zone B due to the presence of a high outlier and small number of samples. In zones A and B where abundance was generally low, all but one of the values above 5 postlarvae $1000m^{-2}$ were attributed to offshore sites and were typically on the offshore edge of the EMCC.

The timing of the postlarval season varied between eastern and western zones with an earlier season in the west. In zones D, E, and Seabrook the postlarvae were present in the first week of July (DOY 185), and the season extended though mid-September (DOY 260). In zones A, B and C, the postlarval season began about three weeks later in late July (DOY 205). The duration of the larval season in eastern zones appeared truncated relative to western zones and dissipated by late august (DOY 240). However, caution should be exercised in this interpretation as we have very few data which encompass an entire larval season in zones A and B.

When postlarval abundance was examined with respect to surface water temperature, we found that postlarvae were twice as abundant at temperatures ≥ 12°C than they were for temperatures < 12°C (Fig. 4.4). The samples for which surface temperature was available were averaged in one degree temperature bins, but the high variance associated with patchily distributed, hyper-dispersed postlarvae prevented the resolution of this difference statistically.

Stage I Larvae and Postlarval Abundance in 1999 and 2001

In 1999, stage I larvae were found in the eastern end of the EMCC and at the northern end of Grand Manan Island in the mouth of the Bay of Fundy (Fig. 4.5A). Stage I larvae were found infrequently and in low abundance in samples collected to the west of Schoodic Point. In 2001, stage I larvae were most abundant in a broad region extending from the middle of the mouth of Penobscot Bay eastward to Schoodic Point (Fig. 4.5B). A second center of abundance was located at the northern end of Grand Manan Island. Stage I larval abundance diminished at stations furthest from shore. However, in both

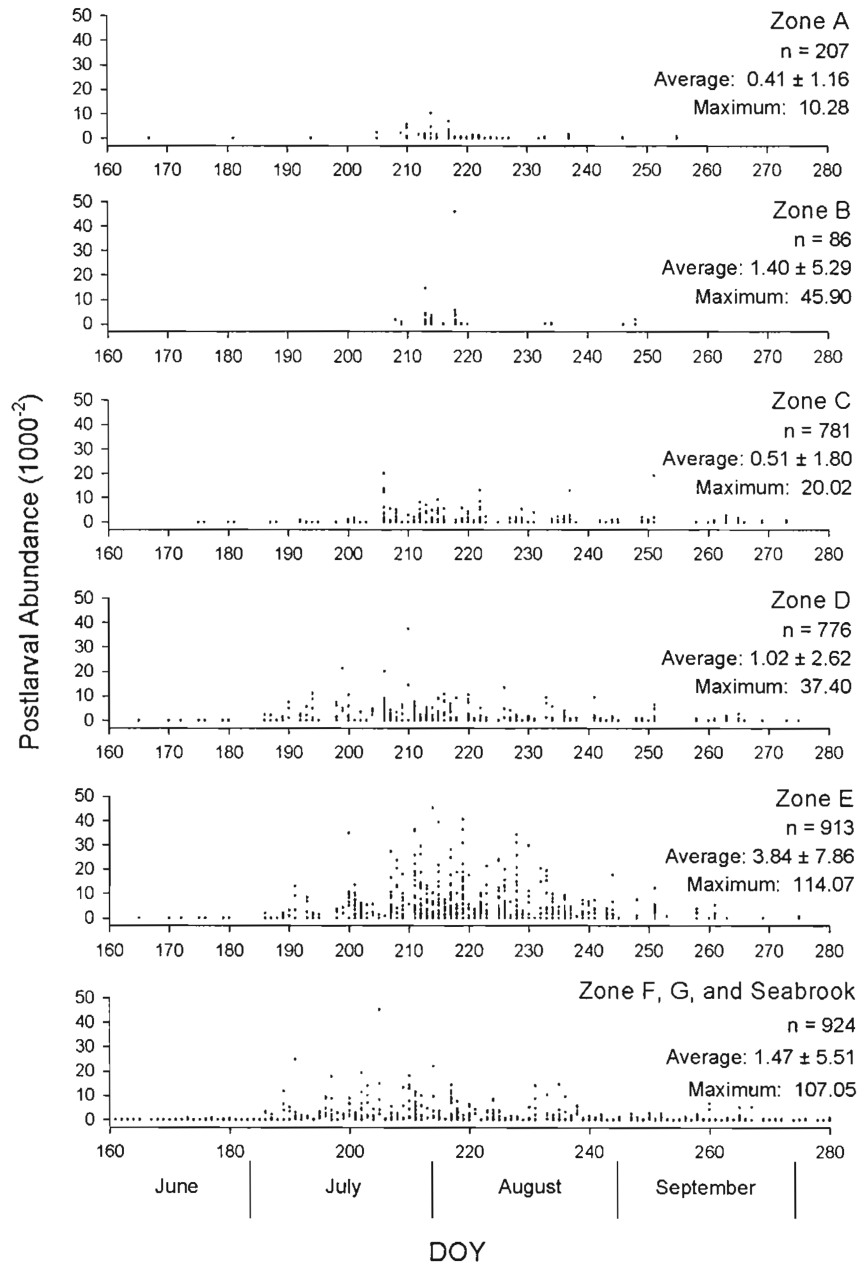


Figure 4.3. Postlarval abundance in each management zone between 1989 and 2003. Data (n = 3687) from past and present studies were parsed by zone and plotted by day of year (DOY). Each point represents a single neuston tow. Three points in Seabrook (DOY 225) and four data points in Zone E (DOY 211, 217, 219, 232) were greater than 50 $1000m^{-2}$ and do not appear in the figure.

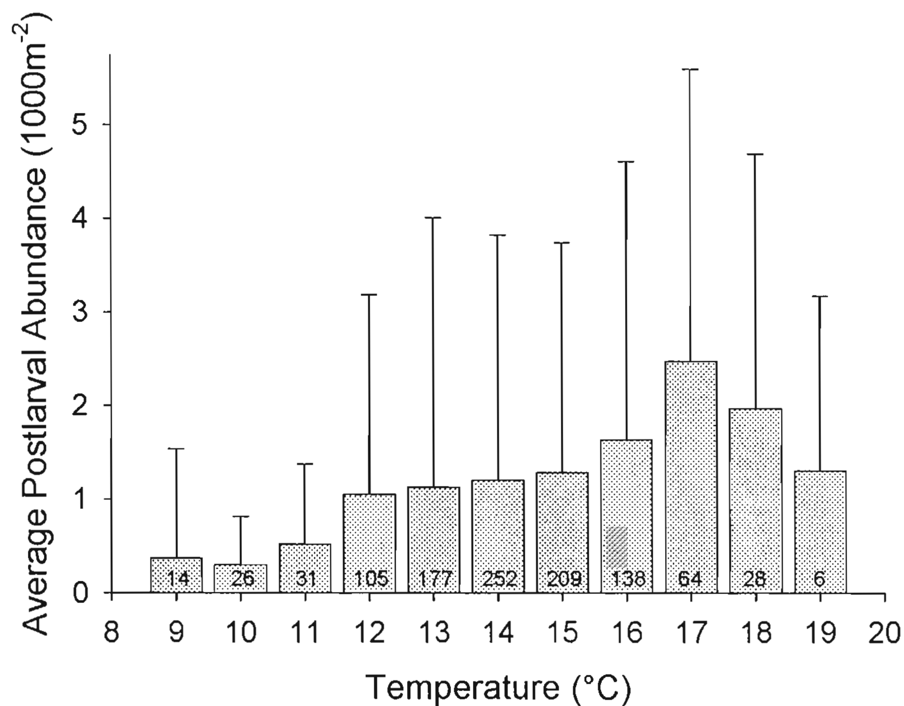
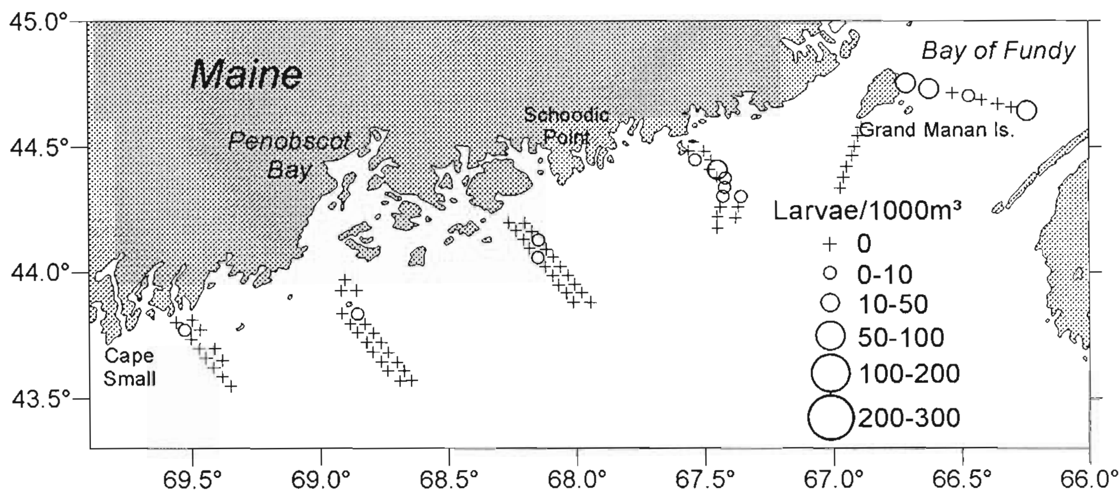


Figure 4.4. Postlarval abundance with respect to sea surface temperature. All postlarval data from Figure 4.3 for which temperature data was available were included (n =1050), and averaged by one degree temperature bins. Error bars denote + 1 S.D., and the number of samples for each bin is indicate within the bar. Sea surface temperature was measured with CTD, bucket thermometer, or thermistor on the hull of the vessel.

A) 1999 stage I larvae



B) 2001 stage I larvae

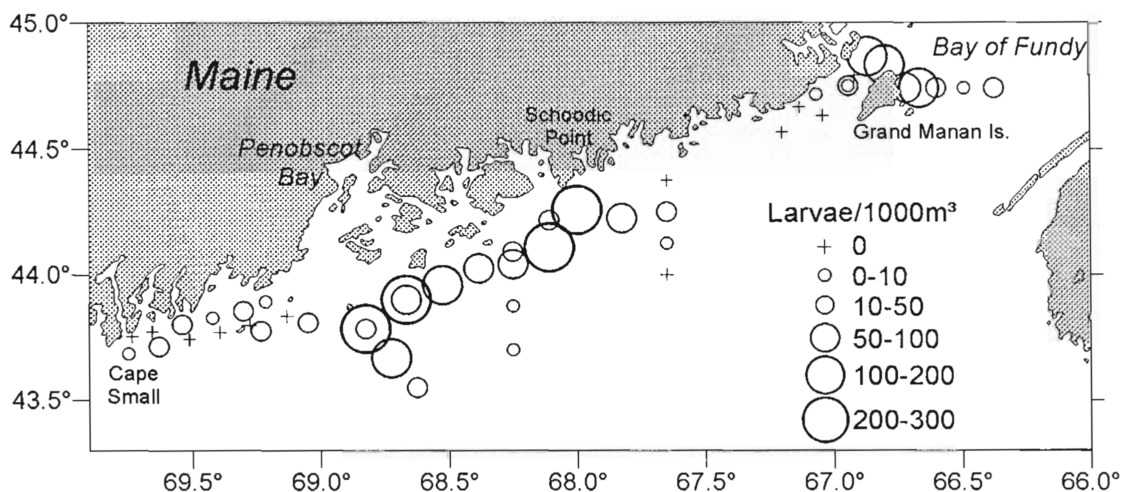


Figure 4.5. The distribution of stage I larvae in 1999 (A) and 2001 (B) in the northern Gulf of Maine. Each circle represents one neuston tow, and the size of the circle proportional to the density of larvae in the sample. Stations where no larvae were captured are denoted with a crosshatch. In 1999 most stations were sampled twice during the cruise and they have been offset in the figure.

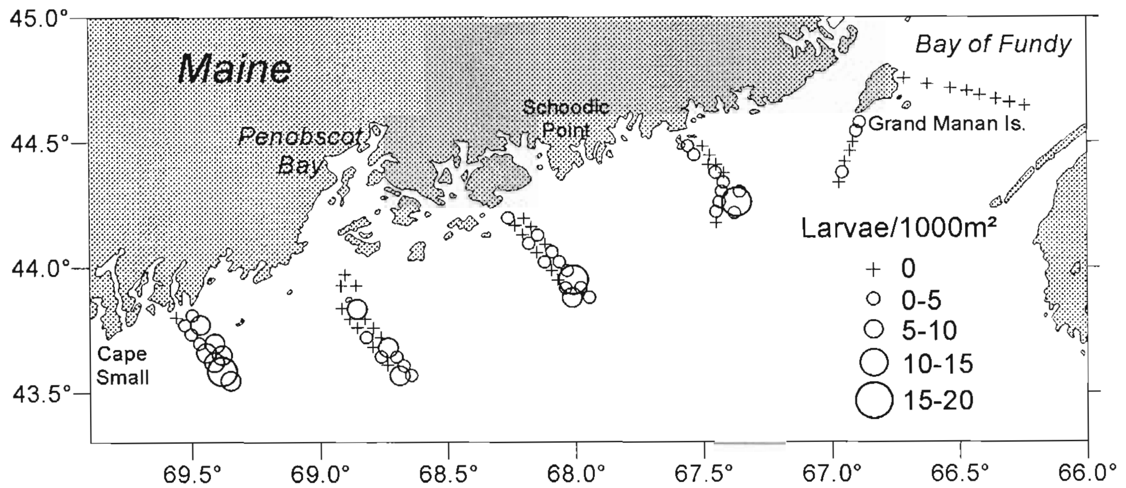
years stage I larvae were collected at stations far enough from shore to be entrained in the flow of the EMCC. Stage I larvae were enumerated in 91 and 48 samples in 1999 and 2001 respectively. The abundance for stage I larvae ranged from 0 to 317 $1000m^{-3}$. In 1999 stage I larvae were only present in 15% of the samples while they were present in 75% of samples in 2001.

Postlarvae were most abundant at the western half of our surveys in both years in an area extending from the western mouth of Penobscot Bay westward to Cape Small (Fig 4.6). In 1999 postlarvae were found in high abundance at stations located offshore of the EMCC but were uncommon in inshore samples east of Penobscot Bay (Fig. 4.6A). The presence of postlarvae on the offshore side of the EMCC was also observed in 2001 but was less pronounced (Fig. 4.6B). While the stations surrounding the mouth of Penobscot Bay had high postlarval abundance, the stations located within the bay had lower abundance. The trend of increasing postlarval abundance to the west is also evident when the synoptic data is averaged by management zone (Fig. 4.7). A total of 91 and 167 postlarval samples were collected in 1999 and 2001 respectively, in both years postlarvae were present in 54% of the samples, and abundance ranged from 0 to 22 $1000m^{-3}$.

Reproductive and Adolescent Phase Lobster Abundance in 1999 and 2001

The highest densities of reproductive phase lobsters were found in an area extending from the eastern mouth of Penobscot Bay to Schoodic Point, and in a second area at the north end of Grand Manan Island. The distribution and abundance of these reproductive lobsters is reported in Steneck et al. (in prep). Adolescent phase lobsters

A) 1999 postlarvae



B) 2001 postlarvae

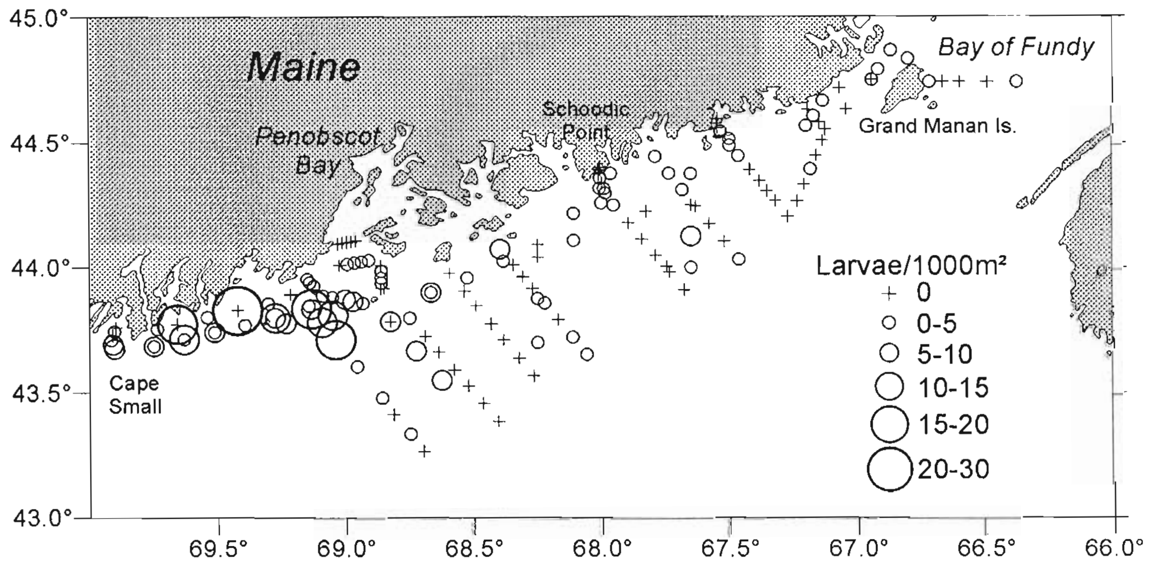


Figure 4.6. The distribution of postlarvae in 1999 (A) and 2001 (B) in the northern Gulf of Maine. Each circle represents one neuston tow, and the size of the circle proportional to the density of larvae in the sample. Stations where no larvae were captured are denoted with a crosshatch. In 1999 most stations were sampled twice during the cruise and they have been offset in the figure.

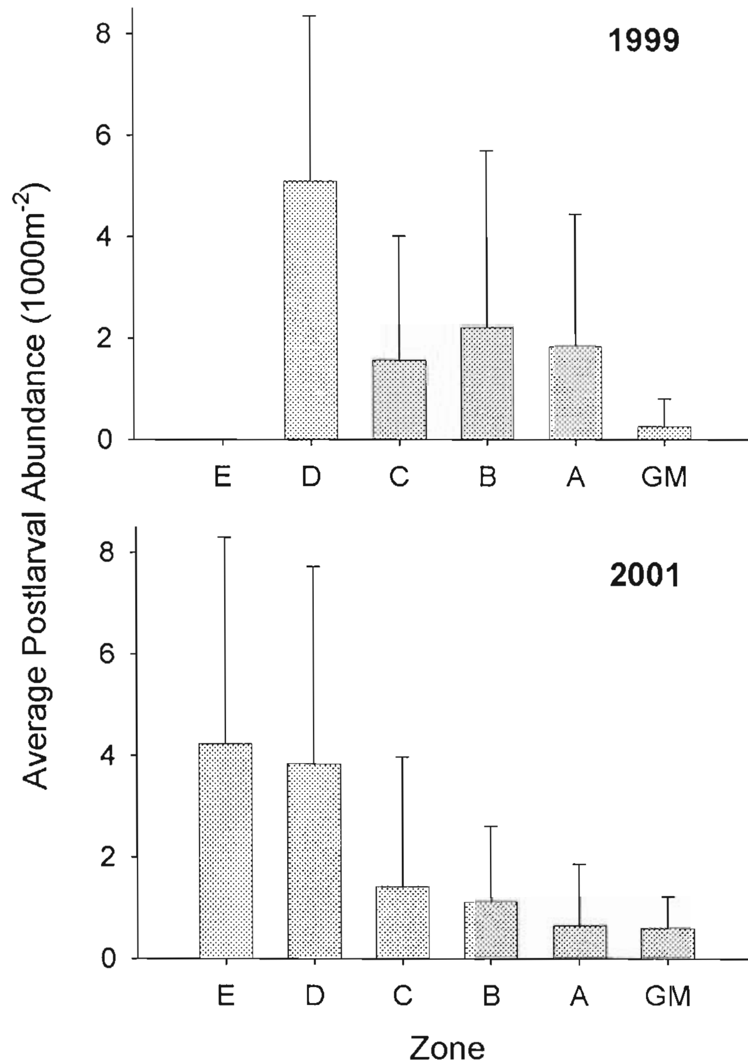
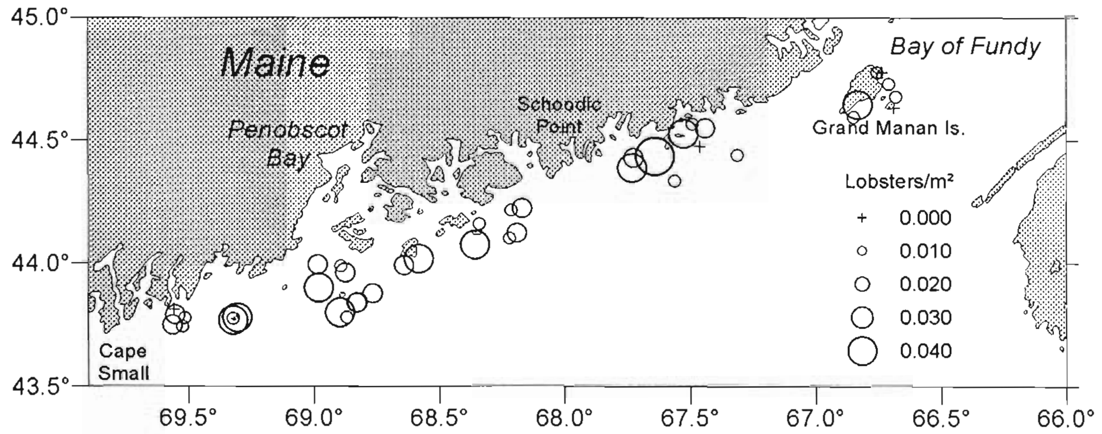


Figure 4.7. Postlarval abundance averaged by management zone for synoptic sampling in 1999 (top) and 2001 (bottom). The "GM" zone refers to samples taken around Grand Manan Island. No data was available for Zone E in 1999. Error bars denote + 1 S.D..

A) 1999 Adolescent Phase Lobsters



B) 2001 Adolescent Phase Lobsters

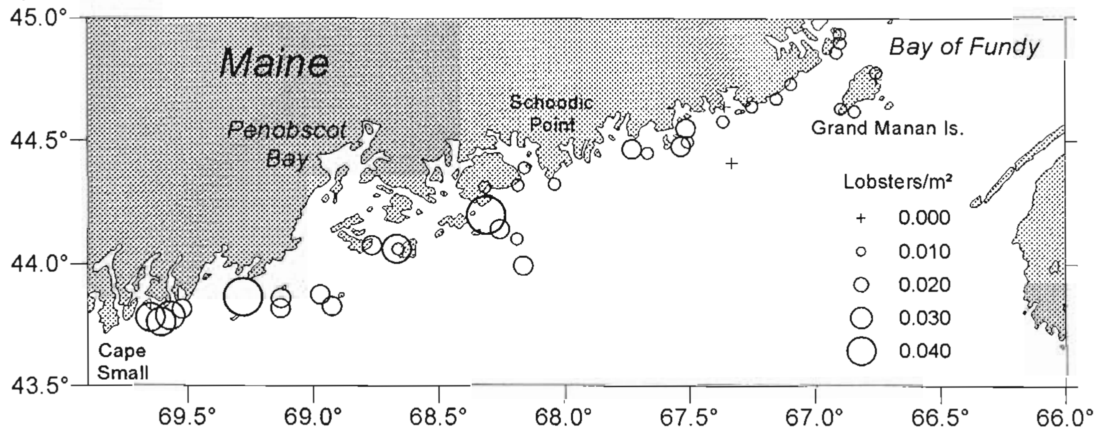


Figure 4.8. The distribution of adolescent phase lobsters in 1999 (A) and 2001 (B) in the northern Gulf of Maine. Each circle represents one benthic transect conducted with an ROV, and the size of the circle proportional to the density of lobsters in the transect. Stations where no adolescent lobsters were observed are denoted with a crosshatch.

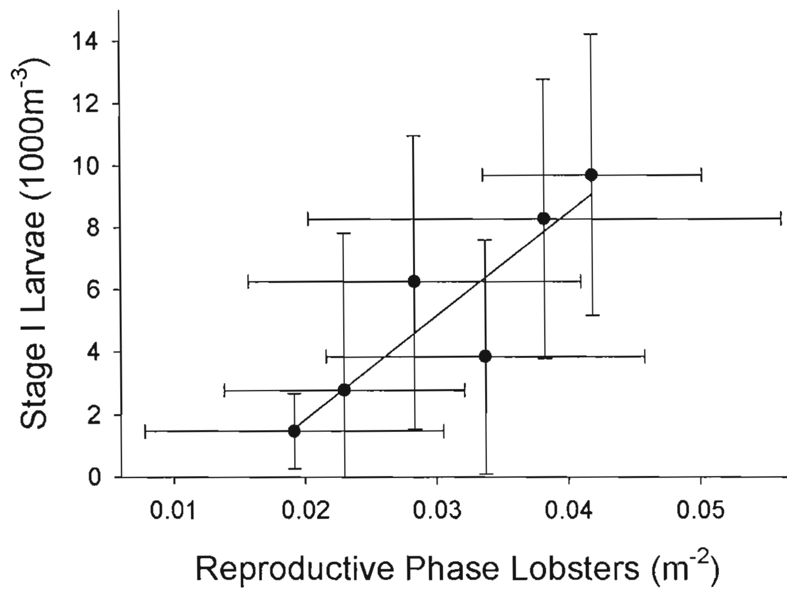


Figure 4.9. Stage I larval density as a function of reproductive phase lobster density (reproductive lobster data from R. S. Steneck unpublished data) averaged by zone. Data were square root transformed. There was a significant positive relationship between variables ($P = 0.014$, $r^2 = 0.81$, $df = 5$). Error bars denote ± 1 S.D. for larvae and ± 1 S.E. for lobsters.

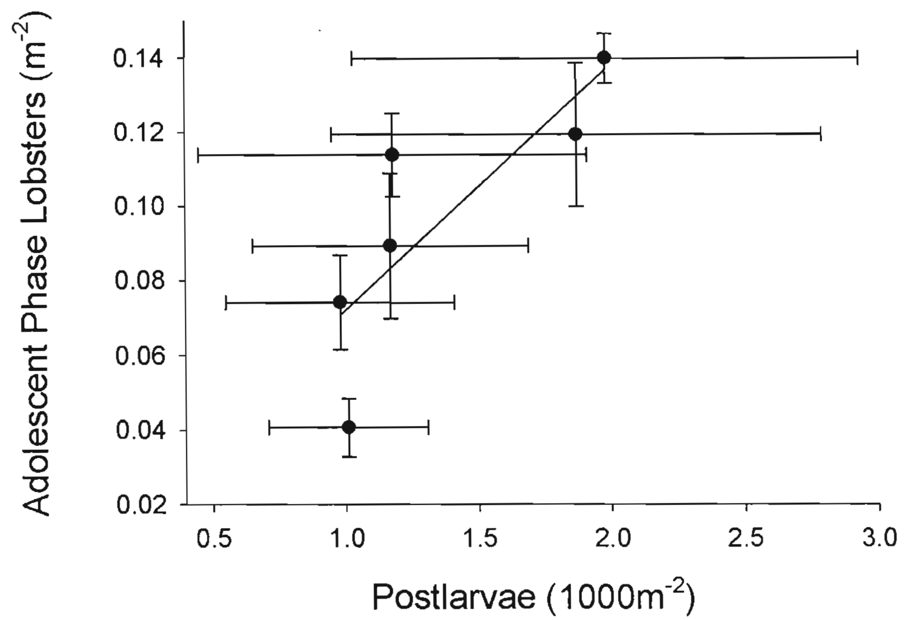


Figure 4.10. Adolescent phase lobster density as a function of postlarval density averaged by zone. Data were square root transformed. There was a significant positive relationship between variables ($P = 0.045$, $r^2 = 0.67$, $df = 5$). Error bars denote ± 1 S.D. for postlarvae and ± 1 S.E. for lobsters.

were most abundant to the west of Schoodic Point with higher densities in the mouth of Penobscot Bay and Pemaquid Point areas (Fig. 4.8). In 1999 high abundance of adolescent lobsters was also observed near Jonesport. Adolescent lobsters were more abundant in water < 50 m deep, but they were present in low numbers in surveys between 0-100 m. Forty-five dives were conducted in 1999, and 49 in 2001 with a total of 1207 lobsters observed during these surveys.

The abundance of stage I larvae increased with increasing density of reproductive lobsters when densities were averaged by management zone (Fig. 4.9; $P = 0.014$, $r^2 = 0.81$, $df = 5$). Data included in this analysis were limited to the 2001 sampling effort (Figures 4.5B, 4.6B, 4.8B). The density of reproductive lobsters was estimated using 2001 ROV data presented in Steneck et al. (in prep) averaged by management zone. Adolescent phase lobsters density increased with postlarval abundance when averaged by management zone (Fig. 4.10; $P = 0.045$, $r^2 = 0.67$, $df = 5$). There were no significant relationships between reproductive phase and postlarvae ($P = 0.23$, $r^2 = 0.34$, $df = 5$), or between adolescent phase and stage I larvae ($P = 0.33$, $r^2 = 0.23$, $df = 5$). All data had non-normal distribution and were square root transformed for statistics. The square root transformation is commonly used when data consist of counts and are not normally distributed (Sokal and Rohlf 1995).

Discussion

Our data from the northern Gulf of Maine reveal a persistent pattern of high postlarval abundance in the west and low postlarval abundance in the east. This pattern was evident in synoptic sampling of 300 km of the coast in 1999 and 2001 and was

supported by the cumulative effort of 14 years of sampling along the Maine and New Hampshire coasts. Moreover, these patterns are consistent with established patterns of settlement in which settlement is elevated west of Penobscot Bay and very low east of the bay (Palma et al. 1999, Steneck and Wilson 2001, Wahle and Steneck 1991). That postlarvae are most abundant at the downstream end of the area studied and coincide with areas of high settlement suggests that the area west of Penobscot Bay may serve as a sink for larvae released upstream. The sink occurs in a deceleration area for the coastal current which may serve to accumulate larvae at the terminus of the cold EMCC and accelerate their development to the postlarval stage as they enter the warm slower moving waters of the WMCC. The correlation between postlarval abundance and adolescent phase lobsters (Fig. 4.10) is remarkable because adolescent phase lobsters in this area are 4-7 years of age and therefore represent multiple year classes of settlement which occurred several years prior to our sampling in 2001. This is consistent with the hypothesized larval sink in the west and suggests that the sink is temporally persistent.

Stage I larvae were most abundant in locations upstream from the area of highest postlarval abundance (Fig 4.5), and stage I larval abundance was directly correlated with reproductive lobster density over the 300 km sampling area (Fig. 4.9). The correlation of broodstock with newly hatched larvae is greatly facilitated by the short development time of the first instar (Annis et al. in prep-b, MacKenzie 1988) which limits spatial separation. This relationship links reproductive broodstock to larval abundance and suggests potential sources of larvae that are both proximate to (eastern Penobscot Bay to Schoodic Point), and distant from (Grand Manan Island) the larval sink west of Penobscot Bay. These data provide only a synoptic view, but the 2001 stage I larval data

are consistent with the distribution of reproductive phase lobsters along the Maine coast (Steneck et al. in prep). In contrast, the distribution of stage I larvae in 1999 revealed a near absence of stage I larvae in the Penobscot Bay area (Fig. 4.5) despite the presence of reproductive lobsters (Steneck et al. in prep). The timing of hatch varies inter-annually and geographically and temperature probably plays an important role with colder temperatures resulting in later hatching (reviewed in Ennis 1995). Sea surface temperatures were slightly colder in 2001 than in 1999 during the spring months preceding the hatch (University of Maine Satellite Oceanography Data Laboratory, www.seasurface.umaine.edu). This a critical time for development of the embryo (Pandian 1970, Sibert et al. 2004) and colder temperatures may have delayed the hatch in 2001. It seems likely that our synoptic sampling in 1999 missed the stage I larval season while the 2001 sampling captured the tail end of the stage I larval season. Accordingly, the relationship between broodstock and newly hatched larvae should not be used in a quantitative predictive fashion as the stage I larval abundance reported here does not integrate the full season of hatching.

The distribution patterns of larval and benthic phase lobsters are consistent with two potential source-sink models. The first is a largely self-recruiting model in which larvae are hatched around the mouth of Penobscot Bay and settle in the larval sink immediately to the west. This might be accomplished either through retention within Penobscot Bay or advection to warmer waters to the west which would consequently slow transport and reduce development time. The second model involves a distant source of larvae in which larvae are hatched in the vicinity of Grand Manan Island and advected westward on the Eastern Maine Coastal Current to the larval sink west of Penobscot Bay.

In either case, the spatial disconnect between reproductive phase lobsters and postlarvae in our study suggests that larvae are advected away from the broodstock, and the location of broodstock and stage I larvae in position upstream from the postlarval sink is consistent with this hypothesis. The westward residual flow along the Maine coast provides a physical mechanism for transport between the larval sources in the east and the proposed sink in the west, and a model coupling physical flow with temperature dependent development suggests that transport on the spatial scale of our study area may be accomplished in a biologically relevant time frame (Incze and Naimie 2000). It seems likely that the hypothesized source-sink models function concurrently, and it is the relative contribution of these models to larval delivery that will help define the degree of connectivity among lobster populations in the northern Gulf of Maine.

There is little evidence at present to suggest that a reverse migration of adults occurs to compensate for the southwest transport of larvae along the coast. Tag and recapture studies have recorded seasonal offshore migrations along the Maine coast (R. S. Steneck, unpublished data) and at Grand Manan Island (Campbell 1986) in which lobsters move to deeper water for the winter and return to the same shallow water locations the following summer. Tagging of ovigerous females along the Maine coast suggests that there is a slight net movement of lobsters to the southwest (R. S. Steneck unpublished data). The means by which upstream broodstock are replenished remain unknown but may depend upon the limited larval settlement that occurs in eastern regions.

The striking difference east and west of Penobscot Bay with respect to lobster population densities and postlarval supply corresponds to a shift in thermal structure from

cold vertically mixed water in the east to warmer stratified conditions in the west. The abundance of postlarvae with respect to surface temperature (Fig. 4.4) suggests that postlarval abundance is reduced at temperatures below 12°C, and most samples below this temperature were collected in the eastern portion our sampling area. Several factors may contribute to the low postlarval abundance associated with low surface temperatures including seasonality, low broodstock abundance, faster advection, increased development time, and higher mortality. The seasonality of larval release may be timed so that postlarvae encounter the warmest water of the season (Hudon and Fradette 1988) or coincide with a specific temperature such as the 12.5°C threshold suggested by Harding et al. (1983). Reproductive phase lobsters were less abundant in the cold eastern region (with the exception of the north end of Grand Manan Island), and it is possible that local broodstock is not sufficient to produce an abundant supply of locally retained postlarvae. Colder summer water temperature in the Gulf of Maine is typically associated with areas of high advection with the primary hydrographic feature being the cold core of the EMCC. These areas would be less likely to retain larvae through the postlarval stage due to the coupled effects of increased development time (Templeman 1936) and rapid advection (Pettigrew et al. 1998). There is also an ontogenetic shift in thermal tolerance in lobster larvae with increasing sensitivity to cold temperatures. In laboratory studies, postlarvae exhibit higher mortality and greatly reduced development rate at temperatures below 12°C (MacKenzie 1988). Field studies have also demonstrated that postlarvae maintain a vertical position above the 12°C isotherm, suggesting that it may serve as a thermal threshold (Annis in prep). If 12°C does

represent a thermal threshold, it is likely that higher mortality contributes to the low abundance of postlarvae in cold water samples.

The east-west difference in thermal structure may also be responsible for later onset of the postlarval season in the east. Larval development accelerates with increasing water temperature (MacKenzie 1988, Templeman 1936), and the colder waters in the east may delay development and contribute to the three week lag in the onset of the postlarval season. The factors affecting the duration of the postlarval season in different zones is less clear but could reflect a difference in the magnitude of larval delivery from distant sources. In a closed system where the postlarval abundance is the product of local larval production we expect the duration of the postlarval season to be proportional to that of the stage I larval season as larvae are neither imported nor exported from the system. In contrast, the duration of the postlarval season in an open system could be shortened by the export of larvae from the area or lengthened by the late arrival of larvae advected from distant sources. In the vicinity of our proposed larval sink, the early postlarval season would likely reflect local larval production with rapid development in warm water and low rates of advection. Slower developing larvae hatched at cold water upstream sources would reach postlarval stage later in the season, thereby extending the postlarval season in the area of the sink.

In the Magdalen Islands in the Gulf of Saint Lawrence the lobster population is thought to be largely closed (Dubé and Grondin 1985, Ouellet et al. 2001), and the stage I larval season ranges from 9-12 weeks in duration (Hudon et al. 1986). The resulting postlarval season is 4-6 weeks in duration (Hudon et al. 1986, Ouellet and Sainte-Marie 1998). The western regions of our study area have a similar stage I larval season

(approximately 11 weeks Annis et al. in prep-b) but a postlarval season that is 5-13 weeks (Annis et al. in prep-b, Incze et al. 1997). The protracted duration of the postlarval season in the western region of our study area is consistent with the hypothesis that larvae are advected into the western zones from larval sources upstream.

By comparison, the truncated postlarval season in eastern Zones A and B may reflect both advection of larvae to the west and a lack of significant upstream sources of larvae. Alternatively, the shorter season may be a sampling artifact due to low abundance in the east and the threshold for detection when sampling hyper-dispersed postlarvae. If the shoulders of the season remained below detectable levels the season would appear shorter than it actually was. Temperature differences are probably not sufficient to explain the season duration as colder temperatures in the east would slow development and lengthen, rather than shorten the postlarval season (Scarratt 1964). While we cannot conclude with certainty why the postlarval season is longer in the west, the pattern appears to persist over time and probably contributes to the higher settlement observed west of Penobscot Bay.

The distribution patterns presented here suggest the presence of two larval sources and a larval sink that may be readily connected using predicted pathways for larval transport. Despite the potential for transport, the relative contribution of larval from local versus distant sources remains unknown and should be the focus of further investigation. The results also illustrate the importance of large scale synoptic sampling of multiple life phases in identifying population level patterns. It is our hope that the patterns established here will provide a basis for continuing efforts to model and understand the dynamics and larval connectivity of lobster populations in the Gulf of Maine.

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