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# Estimates of in situ Larval Development Time for the Lobster, Homarus Americanus

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# ESTIMATES OF IN SITU LARVAL DEVELOPMENT TIME FOR THE LOBSTER, *HOMARUS AMERICANUS*

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A B S T R A C T

Larval development time is a critical factor in assessing the potential for larval transport, mortality, and subsequently, 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. For larvae of the American lobster (*Homarus americanus*), temperature-dependent development times have been established in previous laboratory studies. Here, 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 assess development time in the field. We were unable to reproduce the timing of the seasonal abundance curves using laboratory development rates in our model. Our results suggest that larval development in situ may be twice as fast as reported laboratory rates. This will result in reduced estimates of larval transport potential, and increased estimates of instantaneous mortality rate and production.

## INTRODUCTION

Planktonic larval duration is the most important intrinsic factor used to estimate the dispersal of larvae and the potential for self-recruitment in marine populations (Sponaugle et al., 2002). Coupled biological-physical models use development time and circulation to assess the potential connectivity of populations (Cowen et al., 2000; Harding et al., 2005; Incze and Naimie, 2000; Roberts, 1997). Development time also affects estimates of instantaneous mortality rate and larval production, which are inversely proportional to larval duration. Historically, larval development times have been determined in laboratory studies under what are often described as optimal conditions for growth. Laboratory studies provide carefully controlled conditions that are useful for developing growth curves and assessing relative responses to changing environmental and feeding conditions, but the application of these laboratory derived growth rates to natural populations remains tenuous (Anger, 2001).

There is a paucity of information on larval invertebrate development times in nature, but for many crustacean species development time in the field is shorter than that observed in the laboratory (Ebert et al., 1983; Gonzalez-Gordillo and Rodriguez, 2000; Harms et al., 1994; Welch and Epifanio, 1995). This suggests that laboratory conditions may be less than ideal, and a correction for laboratory development times may be needed to prevent overestimation of transport potential and underestimation of larval production and mortality rates. Development time is difficult to determine from field samples due to the variable nature of the oceans and the populations being studied. Yet, field data on the timing of first appearance and peak abundance of larval developmental stages can provide useful reference points for evaluating how well the laboratory rates predict field conditions. Even in an open system the timing of these events may provide valuable information if there is sufficient local retention of larvae or hatching times are similar over a broad area.

The American lobster, *Homarus americanus* (Milne Edwards, 1837), provides an excellent model for comparisons of field and laboratory development times. Lobster is the most economically important species in the northwestern Atlantic, and the benthic population is driven by the supply of planktonic larvae (Incze et al., 1997; Steneck and Wilson, 2001). As such, duration of the planktonic larval phase (including three larval stages and one postlarval stage) has a direct effect on the transport potential of larvae and the connectivity of benthic populations through larval exchange.

Established laboratory development times for lobster larvae reflect a consensus in the literature spanning a period of nearly 100 years with generally consistent results among studies (Annis, 2004; Hadley, 1906; Hughes and Matthiessen, 1962; MacKenzie, 1988; Templeman, 1936). However, there is evidence that development time in situ may occur faster than indicated by established laboratory rates. Sampling conducted in Penobscot Bay in 1999 (immediately northeast of the area considered in the present study) indicated that approximately 14 d elapsed between peak stage I and postlarval abundance (L. S. Incze, unpublished data), yet laboratory development rates suggest that development to the postlarval stage should require approximately 20-30 d at local water temperatures. Further analysis with respect to development time was not possible due to low sampling frequency, but these data prompted our present examination of in situ development times. Strong evidence for faster development in the field was reported by Juinio and Cobb (1994) who estimated the growth rate of laboratory reared and field caught postlarvae using RNA:DNA ratios and concluded that growth of postlarvae as a function of protein accumulation was approximately twice as fast in the field as in the laboratory. Incze and Naimie (2000) conducted inverse analyses of a physical-biological model to determine
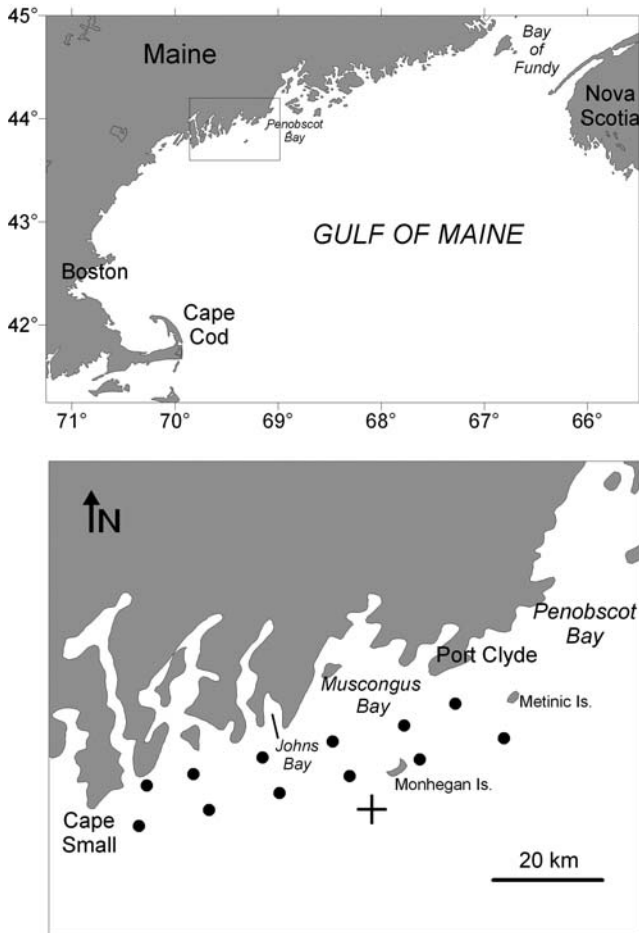
Fig. 1. The region of study was located in the northern Gulf of Maine (top) between Cape Small and Port Clyde, Maine (bottom). The sampling stations (●) encompassed an area approximately 15 × 50 km. The cross (+) denotes the location of GOMOOS Buoy E.



Fig. 2. The proportion (P) of stage I larvae captured in neuston tows (0-0.5 m depth) relative to multiple oblique tows (0-21 m depth); $P = 0.3442 * e^{(-0.0012*X)}$ ($r^2 = 0.87$, $P < 0.001$, d.f. = 9). Data were binned by light intensity in 200 $\mu$mol m$^{-1}$ s$^{-2}$ increments. Data are means ± 1 SD.

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 reverse development placed them in temperatures too cold for early growth. They concluded that the modeled development times were probably too long. Finally, there is general consensus that laboratory reared postlarvae are deficient in several aspects of development relative to their wild counterparts in that they are typically smaller, have weaker exoskeletons, swim more slowly, lack the dark pigmentation, and exhibit poorly developed predator avoidance (Annis, 2004; Castro and Cobb, 2005; James-Pirri and Cobb, 1997; Juinio and Cobb, 1994; Rooney and Cobb, 1991). Given the deficiencies observed in laboratory reared larvae, we might also expect development to be slower in the laboratory.

The objective of the present study was to determine if development of lobster larvae occurs faster in nature than in the laboratory. We estimated a correction factor for in situ development time using semiweekly field sampling for larval abundance over an area of approximately 750 km$^2$, coupled with a model of temperature dependent development based on development times reported by MacKenzie (1988). Specifically, we assessed whether accepted laboratory development rates accurately predicted the time lag
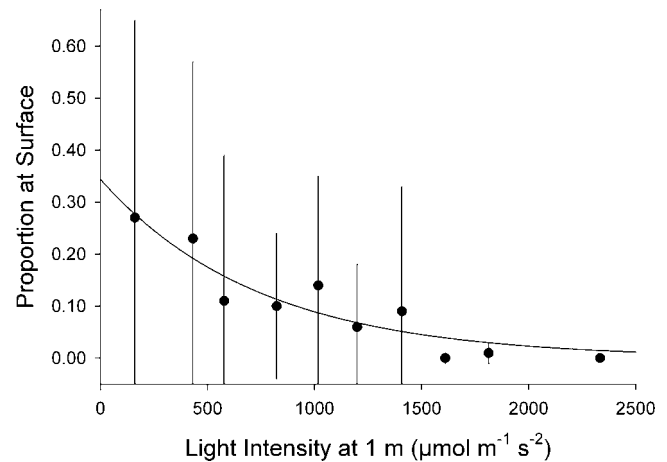
between first appearance and peak abundance of the first and last planktonic stages in the field.

## MATERIALS AND METHODS

### Field Collected Larvae

The study area was located in the Gulf of Maine between Cape Small and Port Clyde, Maine, U.S.A., encompassing approximately 15 × 50 km (Fig. 1) with water depths from 0-100m. This is an area of historically high postlarval delivery and settlement (Annis, 2004; Incze et al., 1997; Incze et al., 2006; Steneck and Wilson, 2001; Wahle and Incze, 1997; Wahle et al., 2004). Residual alongshore flow is 4-8 km d$^{-1}$ in the coastal current offshore of our study area based on current data from Gulf of Maine Ocean Observing System (GOMOOS) Buoy E located in 100m water depth at 43°42′47″N, 69°21′20″W. Circulation model results indicate that the residual flow is usually slower within the study area shoreward of the buoy (Xue et al., in press). A study of egg hatching times revealed similar timing of hatching over most of the Maine coast (C. Wilson, unpublished data), so advective losses and gains from the study area should affect the apparent timing of the larval stages only insomuch as the temperature and feeding histories of the larvae differed.

In 2001, we collected larvae at 12 stations over the course of the larval season from 5 June-2 October (YD 156-275) with a sampling interval of 3-4 d during peak larval abundance. Water depth at these stations ranged from 18 to 85 m. Surface tows were conducted with a 1 m wide neuston net with a sampling depth of 0.5 m and either 500 or 1000 $\mu$m mesh. Oblique tows were conducted from the surface to a mean depth of 21.7 ± 1.7 m (S.D.) using a 1 × 1 m square opening net with 1000 $\mu$m mesh. Both nets had calibrated mechanical flow meters mounted in the opening to calculate the volume of water filtered. Neuston tows lasted 10 min at a speed of ~1.6 m s$^{-1}$ and filtered ~450 m$^3$; oblique tows lasted 30 min at ~1.1 m s$^{-1}$ and filtered ~2000 m$^3$. We conducted neuston tows at every station throughout the season, while oblique tows were conducted on 18 of the sampling dates. We conducted a total of 245 neuston and 107 oblique tows. We conducted a CTD cast (Sea Bird Electronics, SBE-19) and light intensity profile (Li-Cor Instruments, LI188b with a LI193SB spherical quantum sensor) at each station. We determined molt-cycle stage in the laboratory immediately following field collections (methods of Sasaki, 1984).

More than half of the stations had samples only from the neuston sampler. For those stations we corrected for the unsampled portion of the population. For stage I larvae, we used relationships derived from paired (neuston-oblique tow) samples where both samplers had positive catches. We compared the proportion of stage I larvae in the neuston sampler, i.e., neuston:oblique tow, with light intensity ($\mu$mol m$^{-1}$ s$^{-2}$) at 0, 0.5, 1, 5, and 10 m depth; light attenuation at 1 and 5 m; thermocline and halocline depth; and depth of the 9, 10, 11, and 12°C isotherms. The relationship between proportion of stage I at the surface and light intensity at 1 m depth provided the best fit (Fig. 2) and was used to estimate abundance of stage I larvae in
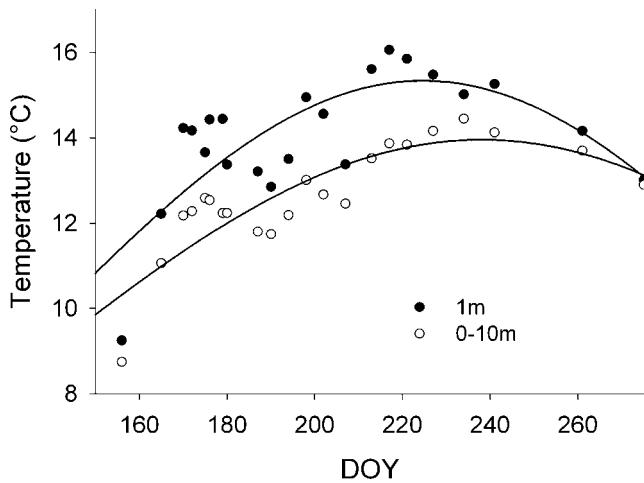
Fig. 3. Seasonal water temperature at 1 m (●) and averaged from 0-10 m (○) depths averaged over all stations. For 1 m: $T = 15.34 * e^{(0.5*((DOY-224.64)/89.43)^2)}$ ($r^2 = 0.59$, $P < 0.001$, d.f. = 21). For 0-10 m: $T = 13.96 * e^{(-0.5*((DOY-238.07)/105.61)^2)}$ ($r^2 = 0.74$, $P < 0.001$, d.f. = 21).
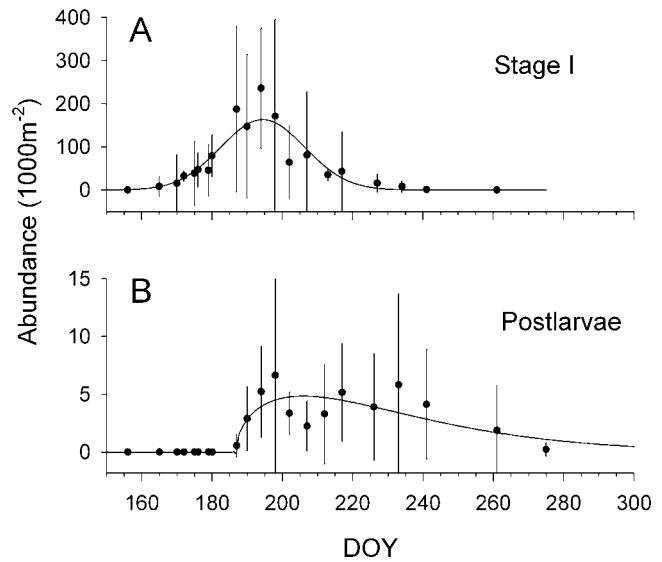


Fig. 4. Seasonal abundance curves for stage I (A) and postlarvae (B) during 2001. Stage I larvae were first observed on DOY 165 and postlarvae were first observed on DOY 187. Peaks in abundance were reached on DOY 194 (stage I) and DOY 206 (postlarvae). Larvae were collected in neuston and multiple oblique tows. The number of stage II and III larvae captured was insufficient to generate a seasonal curve. Data are means ($\pm$ 1 SD) from all 12 stations in the study area.

the upper 20 m of the water column for stations where we did not make oblique tows. At these stations, the abundance in the neuston sample was divided by the proportion at the surface to provide an estimate of abundance. Discrete depth sampling to 60 m in this region indicated that more than 50% of stage I larvae reside in top 20 m of the water column during daylight hours and they were not detectable below 30 m (L. S. Incze, unpublished data). Consequently, our estimates of abundance in the upper 20 m indicate trends in abundance but underestimate the total abundance of stage I larvae in the water column.

To estimate the abundance of postlarvae in the water column we adjusted the neuston samples based on relationships reported by (Annis, 2005), who found that the proportion of postlarvae in surface samples decreases linearly with increasing depth of the 12°C isotherm ($Z_{12°C}$, $r^2 = 0.49$, $P = 0.008$, d.f. = 12):

$$\text{Proportion at surface} = (0.0293 * Z_{12°C}) + 1.0547. \qquad (1)$$

This value [1] was subtracted from the proportion at the surface to remove the apparent effect of the 12°C isotherm, and the residuals were reanalyzed with respect to environmental variables. The first residuals decreased linearly with increasing depth of the thermocline ($Z_{dT}$, $r^2 = 0.44$, $P = 0.008$, d.f. = 13):

$$\text{First Residual} = (0.0300 * Z_{dT}) + 0.2518. \qquad (2)$$

Annis (2005) used the first residual to examine diel effects, but in the present study we subtracted the regression (Equation 2) from the first residuals and generated a second residual which we used to analyze diel effects. The second residuals were fit to the regression ($r^2 = 0.55$, $P = 0.13$, d.f. = 5):

$$\text{Second Residual} = (5.416 * t^2) - (5.909 * t) + 1.535, \qquad (3)$$

where $t$ is the proportion of daylight hours elapsed. Though Equation 3 is not statistically significant at the 0.05 level, the regression has the same form as the significant ($P < 0.05$) relationship reported by Annis (2005). The residuals are additive, and the use of the second residual permits the summation of equations 1, 2, and 3 to provide an estimate of the proportion of postlarvae at the surface for each neuston tow. 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 constrained 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 0.3-0.8. The proportion at the surface values were not permitted to exceed 1.0.

Larval abundance data were tested for normal distribution and homogeneity of variance. Stage I and postlarval data had non-homogeneous variance and were square root transformed (Sokal and Rohlf, 1995). The regression output and data were back transformed to illustrate seasonal abundance curves (Fig. 4).

### Development Model

We developed a model of larval production to generate hypothetical abundance curves for each larval stage based on the laboratory rates reported by MacKenzie (1988), then adjusted development times to reproduce the timing observed in the field. The construct of the model is as follows:

$$A_t = P_t + R_t, \qquad (4)$$

where A is the total abundance (individuals 1000 m²) of a larval stage at time, $t$. The model has a one-day time step, and $P_t$ is the daily production of larvae due to hatching (stage I) or molting from the previous stage (in the case of stage II, III, and postlarva). $R_t$ is the sum of larvae remaining from daily production on previous days:

$$R_t = \sum_{n=1}^{D} N_t, \qquad (5)$$

where D is the stage duration in days calculated from the temperature dependent development time equations in Table I and temperatures in Fig. 2. Temperature regimes used in the model were derived from average temperatures from CTD casts at each station over the course of the season to approximate the temperatures encountered by larvae captured during the temporal and spatial extent of our study. Durations of stages I-III were calculated using the mean temperature between 0 and 10 m. The vertical distribution of larvae extends below this depth range (Harding et al., 1987) and larvae most likely develop at temperatures lower than used in our model. The use of warmer temperatures in the model results in faster development and biases downward the correction factor needed to achieve the timing of field observations. The temperature at 1 m was used for postlarvae to reflect their near-surface vertical distribution (Annis, 2005). Both temperature regimes were based on polynomial equations fit to temperatures averaged over our study area throughout the course of the larval season (Fig. 3). $N_t$ is the number of larvae remaining in each day's production of larvae after mortality (Table I). Each day's production 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 constituted the daily production for the next stage. We used an instantaneous mortality rate of 0.07 d⁻¹ for all developmental stages

Table I. Equations used in the larval development model. Temperature-dependent duration for stages I-III from MacKenzie (1988), postlarval duration from Incze and Naimie (2000) based on MacKenzie's study, and instantaneous mortality from Rumrill (1990). Temperatures used in these equations were determined using the seasonal temperature curves in Fig. 2.

| Variable | Equation | Terms |
|---|---|---|
| Stage I duration | $D = 851 * (T - 0.84)^{-1.91}$ | $D$ = duration (d), $T$ = average temperature (°C) from 0-10 m |
| Stage II duration | $D = 200 * (T - 4.88)^{-1.47}$ | $D$ = duration (d), $T$ = average temperature (°C) from 0-10 m |
| Stage III duration | $D = 252 * (T - 5.30)^{-1.45}$ | $D$ = duration (d), $T$ = average temperature (°C) from 0-10 m |
| Postlarval duration | $D = 703.5 * (T)^{-1.26}$ | $D$ = duration, $T$ = average temperature at 1 m |
| 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) |

(Incze et al., 2003). Sensitivity analysis determined that changes in mortality did not affect the timing of the postlarval peak.

Values from the abundance curve for stage I larvae in the field (Fig. 4) were used as initial values for the model, and an inverse calculation was used to estimate daily production of stage I larvae. The first non-zero abundance on the regression line provided the first day of larval production in the model. This permitted the calculation of $R_t$ (Equations 4 and 5) for subsequent days and the daily production was then calculated by subtracting $R_t$ from the field abundance. The daily production of larvae for subsequent stages (stage II, III, and postlarva) was the sum of all larvae completing the previous developmental stage. We removed postlarvae from the model at molt-cycle stage $D_{2-3}$ because few late-stage postlarvae were collected in our field samples. Development to $D_{2-3}$ accounts for approximately 89% of the total stage duration (Sasaki, 1984). Accordingly, we multiplied postlarval stage duration by 0.89. The potential for indeterminate development time was not included in the model calculations. Stage duration (D; Table I) for all stages was multiplied by a correction factor (between 0 and 1) to allow adjustment of development times. Thus, as the correction factor decreased, the time between stage I and postlarval appearance and peak abundance in the model output also decreased.

## 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 oblique tows captured 1122 stage I, 29 stage II, 3 stage III larvae, and 28 postlarvae. The proportion of stage I larvae in the neuston layer was negatively correlated with light intensity and averaged $0.15 \pm 0.26$, SD (Fig. 2). The relationship between proportion at the surface and light intensity had the best fit using light intensity at 1 m depth, and was used to estimate the proportion of the population represented in neuston samples. Similar relationships were evident with light intensity 2 m above the surface and depths of 0.5 m, 5 m, and 10 m. High attenuation of light due to turbidity or low sun angle also resulted in a higher proportion of stage I larvae at the surface. A greater proportion of stage I larvae were found at the surface in tows conducted before 09:00 (t-test; $P < 0.01$, d.f. = 22, t = 1.72). The average proportion ($\pm$ SD) at the surface for tows conducted before 09:00 was $0.36 \pm 0.37$ while tows after 09:00 averaged $0.09 \pm 0.18$. No relationships were found between proportion at the surface and the depth of thermocline, halocline, or isotherm (9, 10, 11, 12°C).

The abundance estimates of postlarvae were corrected for 12°C isotherm depth, thermocline depth, and diel effects. The resulting values were 1.3 times higher on average than uncorrected neuston data suggesting that uncorrected neuston samples underestimate abundance by ~23%. The difference between corrected and uncorrected data increased as the season progressed. The number of postlarvae in each molt stage was: 0 (A), 4 (B), 20 (C), 86 (D0), 95 (D1′), 129 (D1″), 63 (D1‴), 11 (D2-3); 42 were not identified to molt stage.

### Seasonal Abundance

In 2001, stage I larvae were present in our samples from 14 June-29 August (DOY 165-241) with peak abundance on 13 July (DOY 194, Fig. 4). These data include abundance estimates from oblique tows and surface tows that were corrected for light intensity at 1 m depth. The stage I larval abundance data were fit to Gaussian form regression equation (SigmaPlot 8.02): $Y = 12.78e^{(0.5((X-194.46)/16.98)^2)}$ ($r^2 = 0.90$, $P < 0.001$, d.f. = 19). The low number of stage II and III larvae in our samples was insufficient for the purpose of generating a reliable seasonal curve of abundance. 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) with the following equation:

$$Y = \text{if } X \leq X_O - b * ((c-1)/c)^{(1/c)}, \text{ then } 0, \text{ if not then,}$$
$$a*((c1)/c)^{((1c)/c)} * (abs((X - X_O)/b + ((c-1)/c)^{(1/c)})^{(c-1)})$$
$$* e^{(-abs((X-Xo)/b+((c-1)/c)^(1/c))^c+(c-1)/c))},$$

where a = 2.20, b = 71.10, c = 1.24 and $X_O$ = 205.95 ($r^2 = 0.91$, $P < 0.0001$, d.f. = 20). The regression for postlarval abundance peaked on 21 July (DOY 206), or 12 d after the peak in stage I larval abundance. Observed 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, a corresponding shift in surface flow from alongshore to offshore, and lower surface temperature consistent with offshore movement of surface waters (Fig. 5; GOMOOS buoy data, www.gomoos.org).

### Development Time

Multiple runs of the development model were conducted with correction factors ranging from 0.1 to 1.0 to establish the relationship between the correction factor and the timing of postlarval appearance and peak abundance (Fig. 6). A correction factor of 0.53 was required to match the model predictions with the timing of first appearance of postlarvae in field observations (Fig. 6A). In our field observations, the peak abundance of stage I and postlarvae were separated by 12 d, and a correction factor of 0.26 was required to reproduce this separation in the model (Fig. 6B). The average development times generated by the model corresponding to these correction factors suggest that larvae hatching during the period of peak stage I abundance (DOY 180-210) may reach the postlarval stage in 8-16 d at ambient temperatures. In contrast, the model run without a correction factor, resulted in a predicted first appearance of postlarvae
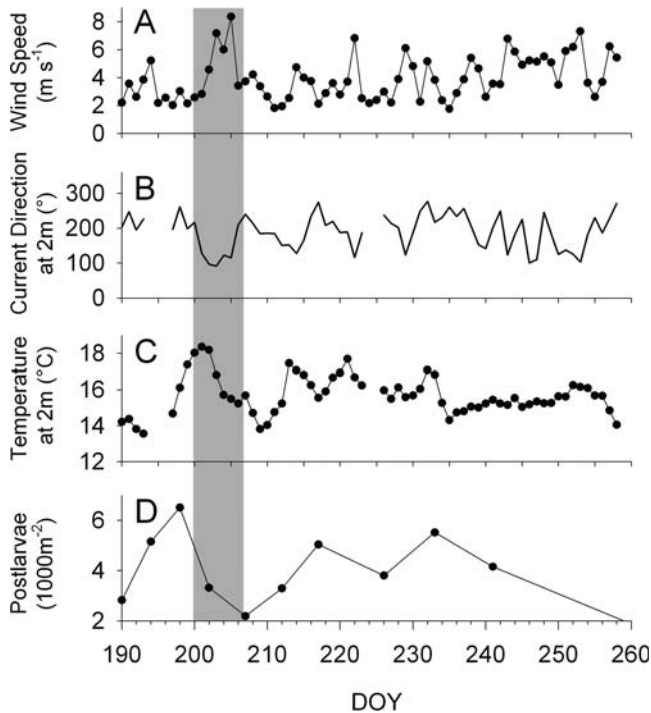
Fig. 5. Wind speed (A), current direction (B), temperature (C) at 2 m depth and postlarval abundance (D). All data are reported as daily means. Current direction is reported in oceanographic convention (direction the current is moving towards). Environmental variables were measured at GOMOOS Buoy E (see Fig. 1 for location). Postlarval abundance data are from Fig. 4. The shaded area denotes a northwesterly (offshore) wind event and corresponding offshore surface currents, reduction of surface temperature and decline in postlarval abundance.

on DOY 214 and postlarval abundance peak on DOY 232 (38 d after peak stage I abundance peaked).

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 12 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 actual correction factor required to produce a 12 d separation in peaks falls between 0.26 and 0.29, and the correction factor for estimated first appearance of postlarvae falls between 0.53 and 0.55. Changing temperatures coupled with a one day time step generated differences in stage duration between larvae produced on consecutive days. Consequently, multiple days of larval production entering or exiting the developmental stage on the same day yielded abrupt shifts in abundance in the model output. This effect did not occur when the model was run with a fixed temperature and had no appreciable effect on the timing of the peaks in the model run. The model output was smoothed using a three-day running average when assessing the timing of peak abundance.

### DISCUSSION

#### Vertical Distribution and Abundance

The variable proportion of stage I larvae in surface samples compared with the oblique tows was consistent with pre-
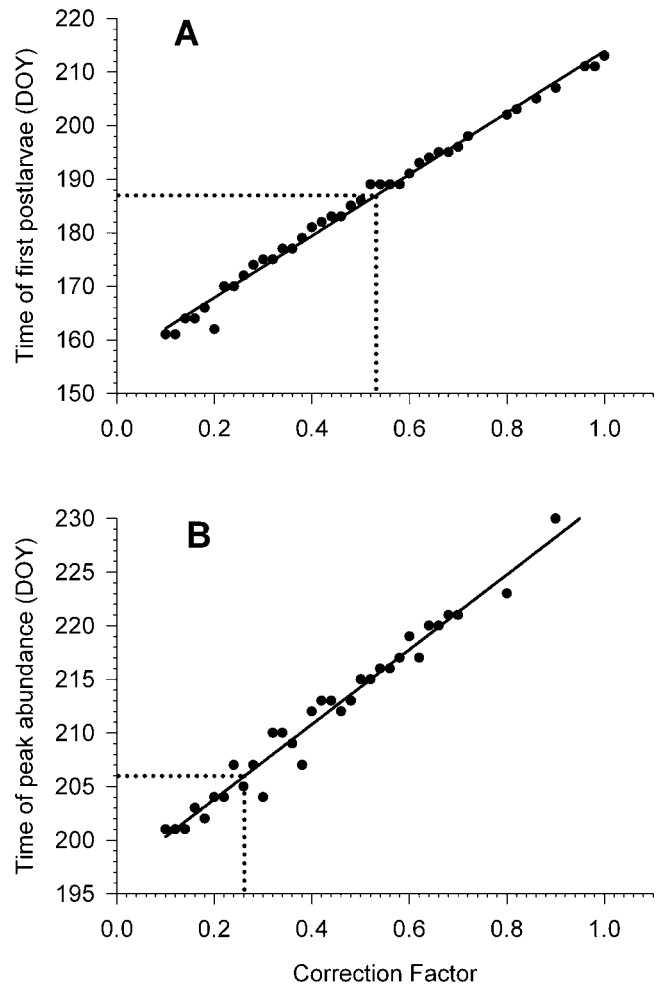


Fig. 6. Development model estimates of timing of first appearance (A) and peak abundance (B) of postlarvae as a function of development time. Development time is expressed as a multiple of laboratory development times and is equivalent to the correction factor applied to development times in the model. Multiple runs of the model were conducted while varying the correction factor between 0.1 and 1.0. To reproduce the timing observed in field data (Fig. 4), A correction factor of 0.53 (reference lines, A) was required to reproduce the first appearance on DOY 187 as observed in field data (Fig. 4). A correction of 0.26 (reference lines, B) was needed to reproduce the peak abundance on DOY 206 observed in field data (Fig. 4). Regression equations were $Y = 57.51X + 156.38$ ($r^2 = 0.99$, $P < 0.0001$, d.f. = 38) for first appearance, and $Y = 34.94X + 196.81$ ($r^2 = 0.98$, $P < 0.0001$, d.f. = 33) for peak abundance.

vious reports that the vertical distribution of stage I larvae varies diurnally (Harding et al., 1987) and with light intensity (Hudon et al., 1986). The relationship reported here allowed us to estimate the total stage I larval abundance in the upper 20 m based on neuston samples and environmental conditions at the time of capture. While our sampling likely missed some stage I occurring below 20 m, we expect that our estimates reflect seasonal trends in abundance of this stage. Our estimates of postlarval abundance incorporated the relationships between vertical distribution and environmental variables proposed by Annis (2005), resulting in higher estimates of abundance than uncorrected neuston data. The effect of the correction was greater late in the season because the depth of the 12°C

isotherm was the primary correlate with vertical distribution. As the season progressed and the isotherm deepened, the proportion of postlarvae at the surface decreased, resulting in a greater correction. Our estimates of total postlarval abundance represent an improvement upon previous estimates that appear to have missed, on average, about 23% of the population. The values we used for proportion at the surface were specific to this study, and the geographic range over which this correction might be accurately applied is unknown.

## Larval Development Time

We were unable to replicate the timing of initial appearance and peak abundance of postlarvae observed in field data using a model of development with published laboratory development times. The model output using laboratory development times predicted the appearance of postlarvae and peak abundance nearly four weeks later than observed in the field (27 and 26 d later, respectively). The development model required development times at least twice as fast to reproduce the timing of field observations. Both laboratory and field data played an important role in our estimation of development times. Laboratory studies by MacKenzie (1988) provided an excellent functional response to temperature that was the basis for our temperature-dependent development model. These relationships would have been virtually impossible to determine using field data. The timing of developmental stages in the field provided a means of calibrating the absolute values predicted by temperature-dependent development relationships and allowed us to retain the relationships reported by MacKenzie (1988) while adjusting the estimated development time. The biological mechanism behind the discrepancy between the laboratory and field durations is unknown, but a plausible explanation is that higher quality food sources are available to larvae in the field (Juinio and Cobb, 1994). Another contributing factor could be selective survival of the fastest developing individuals as proposed for larval fishes (Rice et al., 1993) which would result in faster observed development time in the field.

We used two biological reference points, the timing of first appearance and peak abundance of postlarvae, to delimit a range of correction values. The timing of the first appearance of postlarvae resulted in an estimate of development time in the field of approximately half the laboratory development time. This is consistent with estimates by Juinio and Cobb (1994) that protein accumulation in postlarvae occurs twice as fast in the field. The onset of postlarval abundance in the field was distinct, and provided a clear temporal reference for estimating development time. This estimate may be slightly conservative, because postlarvae are hyper-dispersed and were likely molting to the postlarval stage prior to their abundance reaching the threshold of detection of field samples. As such, the actual development time may have been faster than estimated using this method. The timing of peak postlarval abundance suggests that development in the field may proceed at four times the laboratory rates, but this estimate is sensitive to errors in the fit of the seasonal abundance curve (discussed below) and represents the greatest modification

of laboratory development times that might be necessary to reproduce the timing of field observations.

Our estimates of development time rely on the assumption that the initial appearance and peak abundance of postlarvae are not strongly biased by advection of postlarvae in or out of our study area. While the coastal current indeed moves larvae to the southwest, the timing of the seasonal hatching curve is similar along the Maine coast (C. Wilson, unpublished data), permitting us to make the important assumption that the initial rise in postlarval abundance reflects the fastest development regardless of the source of larvae. Furthermore, it is unlikely that larvae from sources outside our sampling area would have been present as postlarvae before locally hatched larvae due to prevailing currents and spatial patterns of sea surface temperature. The residual current moves along the Maine coast from northeast to southwest with potential larval sources located to the northeast (consistent with modeled larval transport, Incze and Naimie, 2000) and sea surface temperature decreases with increasing distance upstream. 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 into our sampling area. Additionally, the abundance of postlarvae early in the season was highest in the western (downstream) half of our sampling stations, thereby increasing the likelihood that they resulted from larval production within our sampling area. We do not suggest that postlarval abundance in our study area resulted only from local larval production, only that the timing of the onset of postlarval abundance and initial rise to peak values was not strongly affected by advection.

The spatial and temporal resolution of our sampling provides a potential source of error in our estimates of the timing of seasonal abundance, but we expect that this did not strongly bias our field observations. Our sampling interval of 2-3 days at peak abundance was more frequent than the intervals typically employed for quantifying the abundance of lobster postlarvae (reviewed in Field et al., 2000). The spatial extent of our sampling incorporated a broad enough section of coast to insure that some portion of the larvae would likely be retained from hatch to postlarval stage. We did not sample further from shore because our previous attempts to sample offshore in this region have yielded few larvae, and our stations were evenly distributed and positioned away from headlands and islands to avoid accumulation effects (Wahle and Incze, 1997). Our intensive sampling efforts coupled with corrections for vertical distribution provided higher resolution seasonal abundance curves for stage I larvae and postlarvae than have been previously reported for the Gulf of Maine, and we expect that these data are representative of the larval population in our study area.

Another potential source of error in our estimates arises from imprecise knowledge of the date of hatch and molt to the postlarval stage. If stage I larvae were about to molt to stage II or postlarvae had just molted it could result in an underestimate of the time between stages. Of the postlarvae captured in our study, 91% were between the D0 and D1‴ molt stages, indicating they were 55-89% through the

postlarval stage (Sasaki, 1984). This suggests that postlarvae in our samples had not recently molted, likely resulting in an overestimate of development time in the field (and smaller correction factor to laboratory rates). We did not identify the molt stage of stage I larvae in our samples. However, laboratory development times (MacKenzie 1988) indicate that the postlarval stage is more than three times longer than the duration of stage I. Therefore, it is likely that the overestimate of development time due to sampling the postlarvae in the latter half of the stage outweighs the potential underestimate resulting from not capturing stage I larva at the time of hatch. A further consideration is that stage I larvae are more positively phototaxic closer to hatch (Hadley, 1908). The majority of our collections were surface samples, potentially creating a bias for collecting more recently hatched stage I larvae.

We fit the postlarval abundance curve with a Weibull form regression because it represented the rapid onset, early peak, and protracted tail of postlarval abundance better than the Gaussian regression form. The Weibull form explained a greater proportion of the variance in postlarval abundance, and estimated peak abundance earlier in the season thereby capturing the portion of the seasonal curve most likely to reflect the development time of locally hatched larvae. By contrast the latter half of the season is more likely to be influenced by advection of larvae from distant sources, or through indeterminate development of postlarvae that delay settlement until they find favorable habitat (Botero and Atema, 1982). The primary weakness of the regression fit is that the peak is rather broad and sensitive to small changes in the data, leaving the precise timing of peak poorly defined. This presents a large potential source of error in the estimate of development time based on the timing of peak abundance, and requires that we interpret these data with caution. The use of initial appearance of postlarvae to estimate development time resulted in a correction factor of 0.53 that corresponds to a peak in postlarval abundance at DOY 215. Given the variable abundance observed in the field and the uncertainty associated with the regression peak, it is reasonable to expect the peak abundance could have occurred on DOY 215. Beyond this point, however, the peak would be in the later half of the postlarval season, and abundance would be increasingly subject to the contributions of larval advection from upstream sources and indeterminate development of postlarvae. While there is room for interpretation of the curve, the peak most certainly occurred before DOY 232 as predicted using laboratory development rates, indicating that development is faster in the field.

Postlarval abundance was interpreted as one curve rather than two overlapping peaks because the trough between peaks was coincident with an offshore wind event that may have advected postlarvae offshore of our sampling area. If two overlapping peaks were present it would suggest it was the product of two distinct hatching peaks 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 in locally hatched larvae. The abundance of stage I larvae had only one peak in our study area indicating that multiple distinct hatching periods

did not occur. Our study area is thought to receive lobster larvae from multiple sources both local and distant (Annis, 2004; Incze and Naimie, 2000; Incze et al., 2006; Steneck and Wilson, 2001), and we expect that larvae from upstream sources would arrive later in the season contributing to the second peak and the protracted tail of the season. However, we have no direct evidence to suggest that the observed peaks may be ascribed 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, 2004; Attard and Hudon, 1987; Ouellet et al., 2003; Sibert et al., 2004). However, in the event of differential development or larval delivery from outside sources, the first peak in abundance would still represent the fastest development time and would indicate even shorter development times than we propose here.

Hudon and Fradette (1988) observed a ~35 d separation between stage I and postlarval abundance peaks off the Magdalen Islands (Gulf of St. Lawrence) and concluded that in situ development rates were consistent with the laboratory rates of Templeman (1936). However, the approximately two week separation in peaks reported here suggests that there is a difference in the timing of larval development between the Magdalen Islands and coastal Maine. This apparent difference may reflect differences in thermal regime or food availability. Some adult lobsters in the Gulf of Maine undertake a seasonal migration to deeper warmer water for the winter months thereby maximizing degree-days for developing embryos (Campbell, 1986; Campbell, 1990). In contrast, adult lobsters of the Magdalen Islands are thought to undergo only a 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 warmer water have greater metabolic reserves at the time of hatch (Sasaki et al., 1986). Timing of the spring warming may also play a role as temperatures in our study reached their peak earlier than reported for the Magdalen Islands (Hudon and Fradette, 1988), potentially providing a metabolic advantage to developing embryos during a critical period for protein accumulation (Sibert et al., 2004). Food limitation also slows development in lobster larvae (Anger et al., 1985; Annis, 2004) and might contribute to longer development time in the Magdalen Islands, as triacylglycerol/sterol ratios suggest that a higher percentage of larvae are nutritionally deficient 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 is regional variation in development times and the correction factor presented here is not universal.

Our analysis indicates that laboratory development times cannot sufficiently account for the timing of postlarval arrival and peak abundance observed in the field, but the actual rate of development in the field remains unknown. We suggest, based on our modeling efforts, development in the region of our study occurs about two times faster than laboratory rates, perhaps more. There are potential sources of error in our estimates, but they represent the best data and

the most rigorous attempt to quantify the difference between laboratory and field development times presently available. These estimates will support efforts to develop biological-physical coupled models that more accurately portray the potential for transport and connectivity of populations within the Gulf of Maine. Further work is necessary to refine estimates of in situ development time, identify regional differences, and to improve our understanding of the biological and physical factors contributing to differences in larval development time.

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