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MICROECOLOGICAL IMPACTS OF GLOBAL WARMING ON CRUSTACEANS—TEMPERATURE INDUCED SHIFTS IN THE RELEASE OF LARVAE FROM AMERICAN LOBSTER, *HOMARUS AMERICANUS*, FEMALES

MICHAEL TLUSTY,[1]* ANITA METZLER,[1] ELON MALKIN,[1,2] JASON GOLDSTEIN[1,3] AND MAUREEN KONEVAL[1]

[1]*New England Aquarium, Central Wharf, Boston, Massachusetts, 02110;* [2]*Present address: College of Marine Science, University of South Florida, St. Petersburg, Florida 33701;* [3]*Present address: University of New Hampshire, Center for Marine Biology and Dept. Zoology, Durham, New Hampshire 03824*

ABSTRACT As ocean temperatures increase, crustaceans become subjected to more immediate, microecological impacts because of their exothermically-driven growth and development. In this laboratory-based study, ovigerous American lobster (*Homarus americanus*) were allowed to incubate their eggs for either a normal period of time (7–9 months including time at temperatures <10°C), or were held in water >10°C to speed up the rate of egg development (4–6 months). Females that had shorter incubation times had longer periods of larval release compared with females that incubated eggs for a normal period of time. Females incubating eggs for a shorter period of time also produced more larvae, and this was explained by the daily loss of a small number of eggs. Subsequent modeling of the relationship between dates of egg extrusion and hatching using data compiled from Massachusetts Bay demonstrated that there was a critical period in the fall at which larval development would switch from a resultant hatch in the spring to a hatch in the late fall or winter. The short-term implications of global warming on egg development and hatching in lobsters is discussed, including the production of larvae at suboptimal times of the year, as well as a temporal change in the abundance of larvae during the hatching season. Either of these events can lead to an increase in larval mortality and hence a decrease in population productivity.

KEY WORDS: American lobster, *Homarus americanus*, temperature, global warming, hatching, larval release

INTRODUCTION

Ocean temperatures have increased 0.6°C over the past 100 y (Millennium Ecosystem Assessment 2005), with winter temperatures in the North Atlantic as much as 3°C higher than average (Drinkwater et al. 2003). Whereas this is enough to promote macroecological (sensu Bhaud et al. 1995) changes (i.e., a shift in the distribution of animal ranges) (Oviatt 2004), in crustaceans, it will have a more immediate and severe impact (microecological), because temperature is one of the most significant environmental factors impacting crustacean growth and development (Phillips et al. 1980). Changes in the thermal environment (e.g., seasonal fluctuations, cumulative degree days) can physiologically influence total time for crustacean egg development (Templeman 1940, Perkins 1972) as well as the time necessary for postlarval animals to recruit to the fishery (Hofmann & Powell 1998, Whale 2003, Lawrence & Soame 2004).

The eggs of American lobsters, *Homarus americanus* Milne-Edwards, typically take 9–11 mo to develop from extrusion in the fall to hatch in the summer months (Aiken & Waddy 1980). Small increases in temperature can speed up egg development with hatching occurring in as short as 9 wk at 25°C, whereas lower temperatures can significantly increase the amount of time necessary for hatch (39 wk at 10°C, Perkins 1972).

However, there will likely be consequences of changing the thermal regimen of developing eggs. On a population-level scale, Aiken and Waddy (1985) briefly noted that in their hatcheries, hastening embryonic development might lead to unnaturally lengthy hatch-cycles. In nature, it appears that, whereas larval lobsters may be present in abundance for up to three months (Ennis 1995), there is often a short peak of maximum abundance lasting two to four weeks (Harding et al. 1982, Incze et al. 2000). A temperature change that affects the length of time over which eggs are released could alter the abundance of lobster larvae in the Gulf of Maine, thereby dramatically altering the planktonic food dynamics (Lawrence & Soame 2004). At an individual-level scale, the time for eggs to hatch will directly affect the offspring's lipid and energy content (Pandian 1970). One result is that hatchery larvae may differ in size and biochemical composition from those found in nature because of suboptimal feeds, photoperiod, or other related culturing conditions. These discrepancies then may account for the low spawning success of hatchery-produced lobsters (Aiken & Waddy 1985). Whereas understanding the exogenous factors controlling the release of larvae will assist in perfecting enhancement programs, ultimately, it will help to predict the peak of abundance of larval lobsters at certain times of the year.

Hatchery studies can provide a powerful insight into how crustacean biology can change by careful manipulation of simulated ocean temperatures. In hatchery operations, managers can take advantage of this variation in hatching time to obtain year-round production, which has historically been the case for *H. americanus* (Aiken & Waddy 1985). In this study, we examined how ovigerous female lobsters responded to laboratory manipulations of thermal regimen reflected in their time at hatch, hatching duration, and the percent of the clutch that survived to hatch. In addition, water temperature data from Massachusetts Bay was used to model the relationship between egg extrusion and egg hatch to analyze how different thermal regimes can influence the development of larvae.

METHODS

The New England Aquarium has been producing larval and juvenile American lobsters for close to 20 y, *via*. This program

*Corresponding author. E-mail: mtlusty@neaq.org

relied on the collection of egg bearing females from New England waters under appropriate state permits and did not include a breeding program. Beginning in 1998, as part of the normal hatchery operations, the total number of larvae released per day per female was counted. Over this seven-year period, the distribution of larval releases was counted from a total of 95 female lobsters (73.6–119.4 mm carapace length).

Once females were collected, they were held at temperatures <10°C or at 16°C to 18°C depending more on hatchery programmatic needs as opposed to a strict experimental design. The goal of the program was to have one to two females hatching at all times. Holding eggs at <10°C has the effect of ceasing further egg development beyond 80% of full development, until the temperature crosses the threshold (Helluy & Beltz 1991). The end result of this thermal regimen manipulation was that females began to release larvae in all months except September, whereas August and October each had only one female initiate release (Fig. 1). These two thermal treatments were used to divide the females into two groups. Females that initiated release in October through March ($n = 40$) were held at warmer temperatures and were referred to as "winter" females. In contrast, females initiating release April through August ($n = 55$) were held at more typical temperatures and were referred to as "summer" females. The summer female treatment will also include females that were caught in the late winter or early spring and brought into the hatchery and subsequently released larvae. All females were held in compartmentalized (screened partitions) fiberglass tubs in a semirecirculating seawater system (32–35 psu) and a photoperiod of 12L:12D. Hatchery seawater was treated by both mechanical (5 μm) filtration and UV sterilization and water quality monitored at regular intervals.

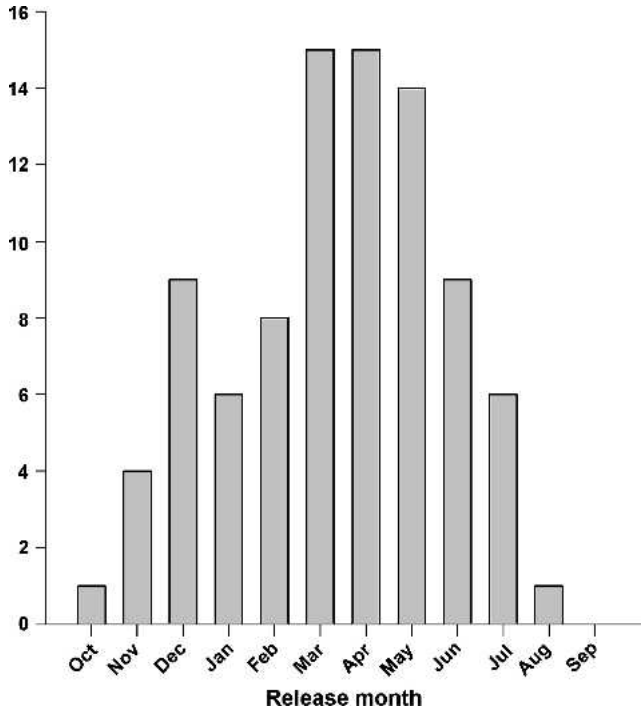

Figure 1. The number of females that initiated larval release each month 1998 to 2005. Winter females are those that initiate larvae release in October to March, whereas all other females are referred to as "Summer."

For each female, the total number of days over which larvae were released (first egg to last egg) was typically quantified by the daily netting or siphoning individual larvae from specialized hatching tanks (one individual/tank) into large vessels for subsequent counting. Because often only one or two eggs would hatch on the first day of the release period (and prone to not being observed), the 10th, 25th, 75th, and 90th percentiles were calculated from which the inner 50th and inner 80th were calculated. Parametric statistical parameters were not calculated (e.g., average eggs per day, coefficient of variation in daily larvae production) because daily larval counts were sporadically missed because of staffing shortages. Thus occasionally a single day's count was the sum of the previous two days (<3% of all observations) in which case, the two day sum was divided equally so that every day had an observation. Because of this counting issue, it was deemed that this dataset was best addressed nonparametrically through the use of percentile of development. The total number of larvae released per female was analyzed as the percent of the total clutch that hatched, where the estimated number of eggs was determined by Herrick's (1894) equation (from Nicosia & Lavalli 1999):

$$\log_{10}(\text{egg\#}) = -2.4505 + 3.3545 \log_{10}(\text{CL}).$$

In addition to counting larvae, female holding tanks were also assessed daily for the number of eggs in the bottom of each individual female's compartment. These eggs were herein referred to as "routine dropped eggs," and were likely a result of several observed behaviors such as the female cleaning and removing diseased or dead eggs, or complications associated with egg attachment (Talbot & Harper 1984). Larger losses of eggs (>1,000) could also be associated *via* an extenuating circumstance ("catastrophic loss") such as a tail flip (Herrick 1909). This behavior almost always would jar loose large numbers of eggs. Therefore, great care was given in the handling and moving of all hatchery-resident animals in lieu of these potential effects. Females that demonstrated catastrophic egg loss ($n = 3$) were omitted from this analysis. Counts of routine dropped eggs were conducted for the period when eggs were <80% developed. Occasionally eggs dropped close to hatch would complete development. By truncating the observation period to <80%, the analysis includes eggs that would not have successfully developed into larvae. The count of egg drops therefore is likely a conservative estimate of the egg loss. Eggs were occasionally observed in the females' feces, but could not be quantified. Daily egg drops were recorded in 2003 and 2004 for 15 females with a minimum of 12 days of data per female.

Temperature Analysis

Bottom temperature data sets were obtained for 9.1 or 21.3 m in Buzzards Bay, MA (R. Glenn, MA Department of Marine Fisheries) or from 38.4 m in Massachusetts Bay (J. Manning, Environmental Monitors on Lobster Traps, National Oceanic and Atmospheric Administration) for the period of May 1, 2002, through December 31, 2003. Using these daily temperatures, the total period of time (days) for an egg to fully develop was calculated. Perkins (1971) equation for temperature specific development times was modified so that an egg's daily development at a specific temperature could be determined ($d_t = (0.066 * T_{°C}) - 0.212$). The amount of time for an egg to fully develop was then calculated as the number of days for

the sum of all consecutive daily development increments to sum to 100. Beginning on May 1, 2002, and every 10 days thereafter (extrusion dates), the number of days to develop was calculated using the daily temperature data. For each extrusion date, the total number of days for eggs to reach 100%, the date at which the egg would hatch, and the degree days (>10°C) were determined.

Statistics

For the variables time (days) spent in hatchery prior to larvae release, time to release all larvae (days) and number of larvae, the difference between winter and summer females was analyzed by a nonparametric Kruskal-Wallis one-way ANOVA on ranked data. In all cases, values are reported as means ±1 SE of unranked data.

RESULTS

Laboratory Observations:

Winter females took longer to release their larvae than did the summer females (Kruskal-Wallis one-way ANOVA, H = 40.43, $P < 0.001$), with the time to release larvae nearly doubling in the winter females (Table 1). The distribution (kurtosis) of the larval release did not change with temperature, because the trend for longer times in the winter females was maintained for both the inner 50% (Kruskal-Wallis one-way ANOVA on ranks, H = 21.68, $P < 0.001$) and inner 80% (Kruskal-Wallis one-way ANOVA on ranks, H = 19.79, $P < 0.001$) ranges of hatch time. In addition to taking longer to release their larvae, winter females also produced nearly 150% the larvae of summer females (Kruskal-Wallis one-way ANOVA on ranks, H = 5.32, $P < 0.03$, Table 1). Whereas larger females produced more larvae (#larvae = (253.82*CL) –18350.85, $P < 0.001$, $r^2 = 0.41$), female size did not differ with temperature manipulation (Kruskal-Wallis one-way ANOVA on ranks, H = 0.568, $P > 0.4$). Therefore, the analysis of the percent of eggs that hatched, a measure of larval production independent of female size indicated that winter females hatched a greater proportion of their complement of eggs than did summer females (Kruskal-Wallis one-way ANOVA on ranks, H = 4.02, $P < 0.05$, Table 1).

Eggs were routinely observed in the female's container, which were "dropped" prior to fully developing. An average of 12.3 ± 20.4 (average ± 1 SD) eggs were lost per day with individual females ranging from 4.4–35.6 per day. In context, this means that a female incubating a clutch for 9 mo would lose over 3,000, or upwards of 30% of her eggs. This chronic egg loss is also significant enough to explain the difference in the number of larvae observed between winter and summer females; the shorter incubation time of winter females would result in fewer lost eggs. Egg loss did not appear to be solely a function of spending time in the hatchery, as there was no difference in the amount of time that the winter and summer females spent in the hatchery prior to the initiation of hatching (Kruskal-Wallis one-way ANOVA on ranks, H = 0.26, $P > 0.60$, Table 1 and Fig. 2).

TABLE 1.

Values for American lobster females that release their larvae in the winter (October to March) or summer (April to September). Similar superscripts denote statistical similarity. Vales are means ± 1 S.E..

	Summer	Winter
Time to release larvae (d)	15.1 ± 1.34[a]	31.1 ± 1.42[b]
# of larvae released	3425.9 ± 347.0[a]	5108.3 ± 727.4[b]
% of clutch to hatch	31.80 ± 2.91[a]	41.05 ± 3.92[b]
Time in hatchery prior to release	124.4 ± 14.0[a]	110.0 ± 6.9[a]

Environmental Modeling

Using the Perkins (1971) model of egg development overlaid on bottom temperature data for three sites in Massachusetts yielded divergent results. The deep site (Massachusetts Bay) had the longest development times, a result of the spring temperature never surpassing 10°C until October. This temperature reinitiates development of eggs beyond 80%, and as a result, the hatch date for all extrusion dates was December 23, 2003 (Fig. 3). For the Buzzards Bay sites, a temporal shift in development time was observed (Fig. 3), with the inflection point

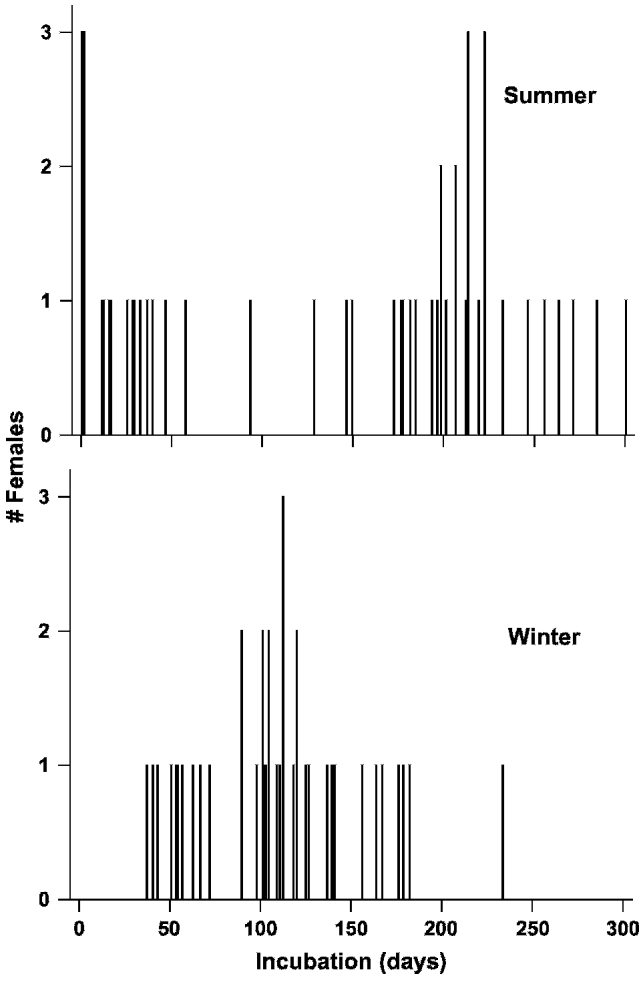

Figure 2. The number of days between the accession of the female, and the initiation of larval release. Data for summer females are on the top, whereas winter females are on the bottom.

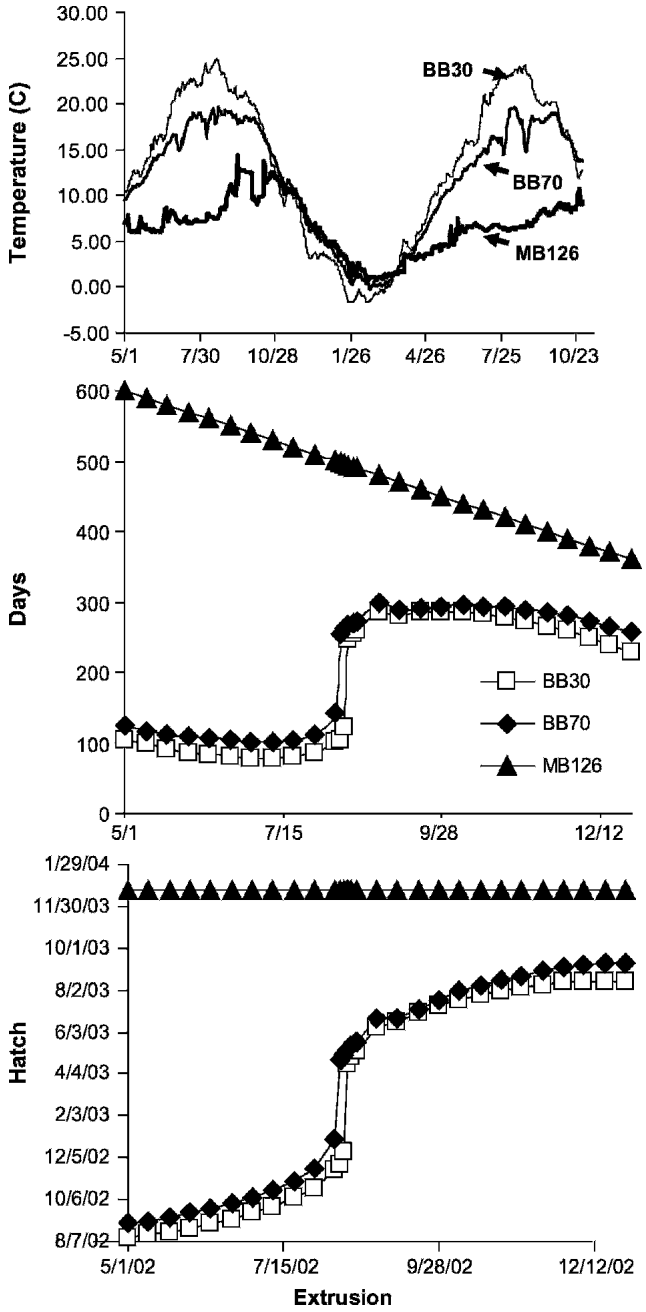

Figure 3. (Top) Bottom temperature (30, 70, or 126 feet) data from Buzzard's Bay MA, or Massachusetts's Bay from May 1–31, 2002 to October 2003. The relationship between the date of egg extrusion within a laying season (May 1 to Dec 27), and the (middle) number of days for development to occur, and the day that larvae are released (bottom, assuming 560 μm at 100% development, Helluy & Beltz 1991).

in the middle of August. Egg extrusion up until the middle of August resulted in the eggs hatching the following January, an average of 92.1 ± 7.3 days postextrusion. If the eggs were extruded after the middle of August, they would not hatch until the spring, an average of 266.6 ± 8.9 days (Fig. 3). The degree days followed a similar trend with regard to the inflection point. Eggs extruded on Aug 12 would hatch Nov 28 for a total of 807 degree days. However, if eggs were extruded four days later, they would not hatch until April 25 for a total of 1,490 degree days.

DISCUSSION

Ocean temperatures fluctuate seasonally, and overall appear to be increasing with negative impacts on all biota (Millennium Ecosystem Assessment 2005). The general perception is that the negative impacts occur when the temperature during the upper portion of the seasonal cycle reaches some threshold. Thus, high temperatures lead to drastic events such as coral bleaching (Graham et al. 2006) declines of commercially important species (Friedland et al. 2003). There is a growing body of evidence that for lobsters, high summer temperature anomalies are also implicated in population declines (LIS) and the incidence of disease (Glenn & Pugh 2006).

However, many crustaceans, including American lobsters (Waddy & Aiken 1995), rely on both photoperiod and a low winter temperature to assist in the setting of a reproductive schedule (Lawrence & Soame 2004). The absence of a low temperature will uncouple temperature and photoperiod greatly affecting a number of reproductive parameters (Lawrence & Soame 2004). American lobster eggs will cease development if the temperature drops below 5°C (Perkins 1972), and eggs will be brought out of a developmental stasis only when temperatures peak over 10°C (Helluy & Beltz 1991). Thus, the full thermal spectrum and not just maximal summertime temperature needs to be considered when assessing the impact of global warming in oceans on crustaceans.

The result that speeding the development of American lobster eggs increases the amount of time over which the full clutch hatches is a more rigorous analysis that supports previous observations (Hughes & Matthiessen 1962, Ennis 1975). Under appropriate conditions, which likely include a sudden warming of eggs late in the development cycle, the number of days for eggs to hatch can be reduced to as few as two to three (Hughes & Matthiessen 1962). Whereas this was occasionally observed within these data (females brought in from the wild near or at 100% egg development), there was no overwhelming evidence that this constantly occurred. The short temporal presence of larvae in nature suggests that the larvae are being released over a short time period (Incze et al. 2003). If thermal shock is the trigger to create a rapid synchronous release of larvae, then females may be moving to optimize their release of larvae (see Cowan et al. 2006).

In assessing how temperature impacts the time between extrusion and hatching, there is a very small window of time during the fall over which the eggs will switch from rapid development (ca. 125 d.) to a longer period of time (ca. >275 d.). However, the temperature model here is for a static location. Egg-bearing females move (Cowan et al. 2006) with the presumption that they are selecting a thermal regimen that controls egg development so that the eggs hatch to optimize survival of the larvae (Olive 1992, Reitzel et al. 2004). Survival of larval American lobster is low. Scarratt (1973) estimated planktonic survival rates of approximately 0.12%, whereas Incze et al. (2003) calculated an instantaneous mortality rate of 0.07 d^{-1} with 1% surviving the first year. Larval survival is increased by factors that will decrease predation rates (Reitzel et al. 2004), and in American lobsters, decreasing the amount of time in the planktonic stages, including hatching early in the season when

surface temperature is rapidly increasing, appears to be the best way to ensure survival to postlarval stages (Ennis 1995). Lobsters released at this time would also have more time to increase size before their first winter. Newly settled postlarvae have been observed in January (D. Cowan pers. comm.), indicating that for some reason, American lobsters will "miscalculate" their thermal regimen, and the eggs will be produced in a short amount of time prior to the optimal time for larval growth and survival. These miscalculations are likely by the smaller first time spawners (Cowan et al. 2006).

Small increases in oceanic temperatures will initially benefit American lobsters, in that their growth will be faster, larger number of larvae will survive to the postlarval stages, and ultimately more will recruit to the fishery (Oviatt 2004). If eggs are lost at a constant rate per day, then fewer days of incubation will result in more eggs reaching the hatch point. At the same time, these temperature increases will begin to increase the period over which lobsters release their larvae. This may serve to increase predation rates, because fewer animals will be present per day, but they will be present for a longer period of time (because of increased distribution in release from the females). It may also lead to more females releasing larvae early, particularly if they cannot access cold water in which to delay the rate of egg development. These microecological changes will all occur prior to there being any macroecological change in the distribution of this species. There is a significant correlation between the number of larvae, and abundance of young of the year (Incze et al. 2003). The microecological changes also provide a potential link to macrecological changes in other species. At a current estimate of 50 million females in the Gulf of Maine (ASMFC 2006), the production of lobster larvae is likely to be a significant contributor to the overall productivity of this ecosystem. Thus any changes in the distribution of abundance of this resource will quickly transfer to other species.

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