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Influence of Natural Inshore and Offshore Thermal Regimes on Egg Development and Time of Hatch in American lobsters, *Homarus americanus*

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Abstract. Some egg-bearing (ovigerous) American lobsters (*Homarus americanus*) make seasonal inshore-to-offshore movements, subjecting their eggs to different thermal regimes than those of eggs carried by lobsters that do not make these movements. Our goal was to determine if differences in thermal regimes influence the rate of egg development and the subsequent time of hatch. We subjected ovigerous lobsters to typical inshore or offshore water temperatures from September to August in the laboratory (n = 8 inshore and 8 offshore, each year) and in the field (n = 8 each, inshore and offshore), over 2 successive years. Although the rate of egg development did not differ significantly between treatments in the fall ($P \sim 0.570$), eggs exposed to inshore thermal regimes developed faster in the spring ($P < 0.001$). "Inshore" eggs hatched about 30 days earlier (mean = 26 June) than "offshore" eggs (mean = 27 July), and their time of development from the onset of eyespot to hatch was significantly shorter (inshore = 287 ± 11 days *vs.* offshore: 311.5 ± 7.5 days, $P = 0.034$). Associated growing degree-days (GDD) did not differ significantly between inshore and offshore thermal treatments ($P = 0.061$). However, eggs retained by lobsters exposed to offshore thermal regimes accumulated more GDD in the winter than did eggs carried by inshore lobsters, while eggs exposed to inshore temperatures acquired them more rapidly in the spring. Results suggest that seasonal movements of ovigerous lobsters influence the time and location of hatching, and thus the transport and recruitment of larvae to coastal and offshore locations.

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Abbreviations: CL, carapace length; GDD, growing degree-days; PEI, Perkins Eye Index.

Introduction

North American lobsters (*Homarus americanus*) are endemic to coastal and offshore waters ranging from Labrador, Canada, to North Carolina, United States, and have adapted to a wide range of thermal regimes (Fogarty, 1995; ASMFC, 2009). Like many large decapod crustaceans, American lobsters are highly mobile and thermoregulate behaviorally by moving into areas with water temperatures they find preferable and away from areas with temperatures they find aversive (Reynolds and Casterlin, 1979; Crossin *et al.*, 1998; Jury and Watson, 2000, 2013). These movements invariably lead to changes in the thermal regimes to which lobsters are exposed and this, in turn, influences their metabolism, growth, life cycle, and possibly even life span (reviews in Talbot and Helluy, 1995; Waddy *et al.*, 1995; Hawkins, 1996).

It has been proposed, for egg-bearing (ovigerous) lobsters in particular, that seasonal movements in the late fall from coastal to offshore waters expose lobsters and their eggs to thermal regimes "associated with maximizing degree-days needed for molting, growth, gonad development, egg extrusion, and egg development" (Campbell, 1986). Water temperature has a clear influence on egg development in *H. americanus,* with eggs developing much faster in warmer water (Templeman, 1940; Pandian, 1970; Perkins, 1972; Aiken and Waddy, 1980). Both Perkins (1972) and Helluy and Beltz (1991) quantified the effect of temperature on embryonic development and time to hatch in the laboratory by exposing eggs to a range of temperatures and measuring embryonic eye size as an index of development. Subsequent studies have served as a basis for temperature-mediated growth

models for egg development in other lobster species, such as the European lobster, *Homarus gammarus* (Charmantier and Mounet-Guillaume, 1992) and New Zealand rock lobster, *Jasus edwardsii* (Tong *et al.*, 2000). However, in these kinds of studies, eggs were exposed to the same temperature throughout their development. Therefore, while they are relevant to the management of captive broodstock and the operation of year-round hatcheries, they do not fully address how naturally fluctuating temperatures experienced by eggs carried by lobsters in their natural habitat influence the rate of egg development and, therefore, the time from egg extrusion to hatch.

Herrick (1895, 1909) and Bumpus (1891) provide the most comprehensive descriptions of *H. americanus* embryology, including developmental rates of eggs at various temperatures and corresponding staging tables. Likewise, Templeman (1940) reported the time between the 16-cell stage of development and eyespot formation at a variety of temperatures. Finally, Perkins (1972) described a series of developmental curves for lobster eggs exposed to different temperatures, giving rise to the Perkins Eye Index (PEI) function (scale 0–560 $\pm$ 20 μm). However, as mentioned above, these studies were not designed to deal fully with the rate of egg development when eggs are exposed to naturally fluctuating water temperatures.

Lobster movements at both seasonal (*e.g.,* inshore-to-offshore migrations) and local (*e.g.,* daily movements, home ranges) scales may influence the thermal regimes they experience (Cooper and Uzmann, 1980; Lawton and Lavalli, 1995; Watson *et al.*, 1999; Golet *et al.*, 2006; Bowlby *et al.*, 2007; ASMFC, 2009; Scopel *et al.*, 2009; Goldstein and Watson, 2015). In areas where large thermal gradients exist, even relatively short migrations or movements (<10 km) can significantly affect growth and molting (Waddy and Aiken, 1995), egg development (Campbell, 1990; Cowan *et al.*, 2007), and size-at-maturity (Landers *et al.*, 2001; Little and Watson, 2005). While numerous studies have documented the long-distance migrations and local movements of American lobsters (reviewed by Cooper and Uzmann, 1980; Haakonsen and Anoruo, 1994; Lawton and Lavalli, 1995; Childress and Jury, 2006), few have focused on ovigerous lobsters and how their movements may influence egg development and time to hatch. The generally accepted paradigm is that ovigerous lobsters seek deeper (offshore) waters in the fall and winter because these areas tend to be warmer and more thermally stable compared with inshore habitats over the same time period (Campbell, 1986; Robichaud and Campbell, 1995; Lawton and Lavalli, 1995; Cowan *et al.*, 2007). It has also been suggested that some of these lobsters move back inshore in the spring and summer to gain the advantage of warmer inshore waters, and thus accelerate egg development; however, there are few data to substantiate this hypothesis.

Cowan *et al.* (2007) demonstrated that small (<93-mm carapace length) ovigerous females, tracked using ultrasonic telemetry in mid-coast Maine, tended to remain closer to shore than larger ones and, as a result, their eggs were exposed to more extreme thermal fluctuations. However, in only a few cases could it be determined when these eggs hatched. In New Hampshire (NH) coastal waters (southern Gulf of Maine), we recently showed that the majority of ovigerous lobsters (60%) tracked using ultrasonic telemetry moved offshore in the winter and appeared to remain there until after their eggs hatched in the summer (Goldstein, 2012; Goldstein and Watson, 2015). However, in only a few cases were we able to determine the exact date of hatching, and we were not able to plot the rate of egg development in these lobsters while they were at-large. The goal of the present study was to accurately determine the rate of egg development and time of hatching of eggs exposed to natural seasonal fluctuations in water temperature. We exposed ovigerous lobsters, both in the laboratory and *in situ,* to thermal regimes mimicking those experienced by lobsters that remained inshore and those that moved offshore. Overall, we found that eggs developed faster and hatched earlier when they were exposed to inshore thermal regimes.

Materials and Methods

Lobster collection and environmental conditions

Ovigerous lobsters were collected in late August and early September in 2007 and 2008 along the New Hampshire (NH) seacoast, near Rye, NH, and Gunboat Shoals (inshore, 43°.0274N; 70°.6938W), as well as near the Isles of Shoals (offshore, 42°.5812N; 70°.3712W), by licensed commercial lobstermen using standard baited traps. Lobsters were transported to the University of New Hampshire (UNH) Coastal Marine Laboratory in Newcastle, NH, and initially held in large 1200-l fiberglass tanks containing PVC shelters. Tanks were exposed to ambient light and received sand-filtered ambient seawater (temp_{AVG} = 15.3 °C $\pm$ 0.5 SEM, $\text{salinity}_{\text{AVG}}$ = 30.7 $\pm$ 0.18 psu). Lobster carapace length (CL) was measured to the nearest 1 mm using digital calipers (Mitutoyo IP 65, Mitutoyo Corp., Japan), and a single circular, laminated disc tag (diameter = 2.0 cm, Floy Tag Inc., Seattle, WA) was fastened to the claw knuckle of each animal for identification during the study.

A series of four 1-m diameter (600 l) tanks were used to hold lobsters under simulated inshore or offshore temperature regimes. Inshore temperature regimes were designed to mimic locations <5 km from shore (8–10-m depth), while offshore thermal regimes were more typical of locations 12–20 km from shore (20–30-m depth). Trials were conducted over two consecutive years (fall 2007 to summer 2008 and fall 2008 to summer 2009), using two groups of 16 lobsters, with two tanks per treatment (n = 32 total). Lobster CLs averaged 91.2 $\pm$ 2.4 mm (CL range = 76–117,

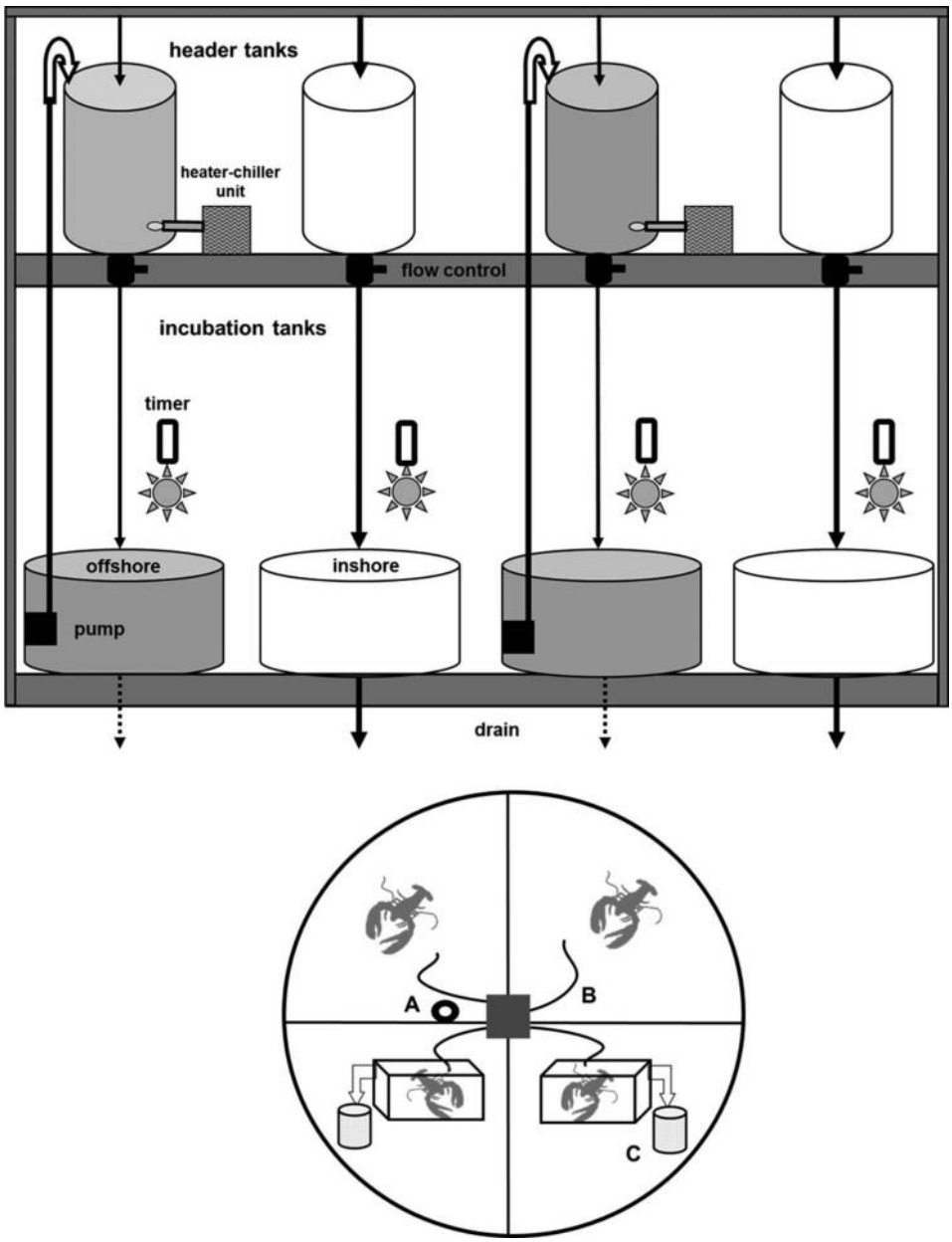

Figure 1. Tank arrangement for holding lobsters. (Top) Tank design for exposing lobsters to simulated inshore and offshore temperature regimes. Shaded containers had simulated offshore conditions, with incoming seawater pretreated (heated or cooled) in the header tanks before being gravity-fed into treatment tanks (0.91-m diameter, 600 l) holding lobsters; inshore tanks received ambient seawater. All tanks were maintained on a seasonal photoperiod. (Bottom**)** Incubation chambers housing individual lobsters. Prior to the time when the eggs were due to hatch, lobsters were maintained in separate areas of the tank using mesh dividers. This tank was outfitted with a temperature logger (A) and seawater inputs (B). Close to hatch time, lobsters were placed into tanks with individual seawater inputs (bottom two lobsters in figure), and larvae drained through a small one-way valve into a collection basket (C).

mode = 80). All tanks were insulated with Formular 5-cm-thick insulation (R-value = 10, Owens Corning Co., Toledo, OH) and were divided into four sections (one lobster/section) using coated lobster-trap wire mesh (Fig. 1).

Ambient seawater from an intake pipe at a depth of 8 m was run through sand-filtration, UV sterilization (model E120S, Emperor Aquatics, Pottstown, PA), and 100-μm cotton-wound filter canisters before being distributed into either inshore or offshore header-tanks (500 l, Fig. 1). Lobsters in the inshore tanks were simply exposed to ambient seawater. Seawater for the offshore tanks was pretreated (heated or cooled) in each header tank before being

fed into holding tanks, and then pumped (Maxijet 1200, 295 GPH, Aquatic Ecosystems, Apopka, FL) back into the header tanks. A steady trickle of fresh seawater was administered into the offshore system as well, creating a semi-closed system. Seawater was heated using two 1500-W titanium immersion heaters (model QDTYL5, Cleveland Process Corp., Homestead, FL) and cooled with portable bath cold-finger chiller units (Cyclone model CY-2 1/5 hp, Aqualogic Inc., San Diego, CA). Heating and cooling regimes were controlled with digital thermostat controllers (model Nema type 4X, Aqualogic Inc., San Diego, CA) and adjusted twice weekly. Offshore temperature regimes were based on temperature data obtained from (1) buoys (GoMOOS Buoy B01; 43°.1051N, 70°.2540W, 20-m depth) situated at the western edge of the Gulf of Maine (NERACOOS 2014); and (2) HOBO pendant temperature loggers (model UA-002-64, Onset Computer, Bourne, MA) mounted on commercial lobster traps (20–30-m depth) at the Isles of Shoals (43°.0050N, 70°.5905W), that logged temperature at 30-min. intervals. These data were obtained during the year prior to this study. Water temperatures in each treatment tank were monitored using submersible HOBO temperature loggers (accurate to ± 0.47 °C) as well as small digital thermometers (Coralife CD-18773, Aquatic Ecosystems, Apopka, FL). Temperature data were downloaded at regular intervals using HOBOware Pro. software (ver. 3.0). Weekly inshore salinity values were not different from those obtained from archival offshore data over the same time frame (Student's *t*-test, $P = 0.612$). Photoperiod was controlled using an astronomic timer (model SS8, Intermatic, Inc., Spring Grove, IL) adjusted for seasonal changes in photoperiod. Lighting was provided by 20-cm-diameter 40-W hooded lamp lights filtered with Roscolux colored lighting gels to simulate natural daylight (#61 for inshore, transmission = 62%; #388 for offshore, transmission = 76%, Rosco Labs, Inc., Stamford, CT).

All lobsters were provided with shelters (clay flower pots) and fed fresh squid, shrimp, or mussels twice weekly. Uneaten food was removed to maintain water quality. Tanks were cleaned once per month and were continuously aerated. When embryos were close to hatching, lobsters were placed into individual holding tanks (32 cm × 18 cm × 12 cm; L × W × D) with separate seawater supplies and drains for each tank. Tanks were designed so that hatching larvae would exit the drain line and collect in attached screened baskets (Fig. 1). This configuration also served to avert any conspecific chemical cues associated with hatching (*e.g.*, Ziegler and Forward, 2007). The first signs of hatch (observed in collection baskets) provided a benchmark date that was then used to estimate a median hatch date (based on the total number of hatching days), or the date at which about 50% of the eggs had hatched.

Lobster incubation cages (field component)

In parallel with the laboratory-based study, we also assessed the development of eggs exposed to natural thermal regimes in the field. A total of 16 ovigerous lobsters ($CL_{AVG} = 95.3 \pm 5.0$ mm, range = 77–131, mode = 79) were held in cages in two locations: (1) off Newcastle Common, NH (depth ~8–10 m, inshore); and (2) near Duck Island, Isles of Shoals, Maine (depth ~30 m, offshore). Two cages were placed at each location with four lobsters/cage ($n = 8$ per location). In addition, there was also a "mixed" treatment (conducted in year-2 only) containing two cages with three lobsters each (originally captured inshore, $n = 6$ total). This trial was designed to simulate a scenario in which lobsters migrate offshore in the fall and then move back inshore in the spring before their eggs hatch (Campbell, 1990). For this treatment, cages were located near Duck Island in the fall and winter and were moved, by a commercial lobster boat, to an area near Newcastle Common (inshore) the following spring (10 March), where they remained until their eggs hatched.

For all field treatments, lobsters were held in standard vinyl-coated lobster traps (1.2 m × 0.6 m × 0.4 m, 3.8-cm-square mesh) (Friendship Trap Company, Friendship, ME) constructed without vents or entrances and divided into four sections by the insertion of additional coated wire mesh. A single lobster was placed into each compartment. Offshore traps were weighted with concrete blocks to minimize excessive movement from offshore winter storms, and temperature loggers were fastened with cable ties to each trap. All cages were pulled fortnightly, and lobsters were checked and provided with fresh bait in a bait bag. When lobster eggs reached late stages of development (typically ~1 month prior to hatch), individual females were isolated in screened baskets within traps so that hatched larvae could be retained and observed.

Egg staging and eye indices

For each lobster, a set of 10–15 eggs was removed at monthly intervals, placed in plastic 2.0-ml storage tubes, preserved in a solution of 4% formalin and sterile seawater, and stored at 4 °C. Bi-weekly samples were taken during the first and last months for more accurate assessment of the rapid changes that occur during early development and close to hatch (see Sibert *et al.*, 2004). Eggs from each sample were staged according to Helluy and Beltz (1991). Digital pictures were taken of each egg under a dissecting microscope (Nikon SMZ-2T, Nikon USA Inc., Melville, NY) at a magnification of 25× using a scope-mounted Nikon Coolpix 995 digital camera. All egg image files were imported into image processing software (ImageJ ver. 1.35, see http://rsb.info.nih.gov/ij/), and the maximum length and width of each egg's eyespot was measured digitally to generate an eye index (0–570 μm, PEI, Fig. 2). All eyespot

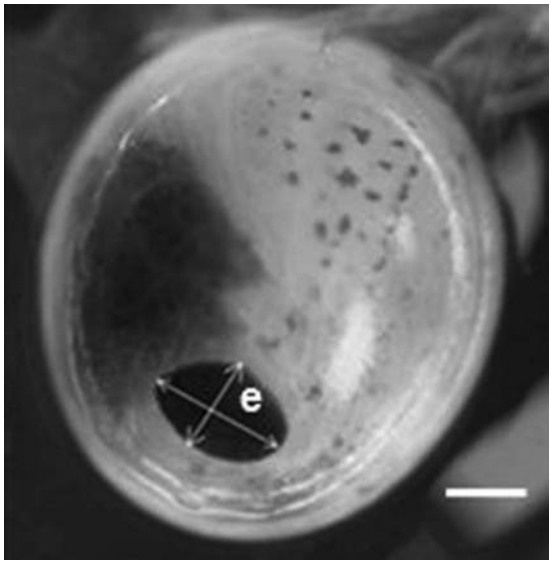

Figure 2. Example of a lobster egg and the digital measurements used to assess growth and stage. Arrows indicate the longest length and width measurements (eye size) obtained using ImageJ software. Measurements from all eggs in each sample were averaged (longest length and width/570 = the eye index prior to hatch) to obtain a mean Perkins Eye Index (PEI). Eyespot is indicated by 'e', scale bar = 300 μm.

measurements were made to the nearest 0.01 mm (then converted to micrometers), and values for all eggs in each sample were averaged (mean ± SEM).

Egg development calculations

Although we planned to evaluate the effects of temperature across the entire period of egg development from extrusion (*i.e.,* when eggs are fertilized and deposited along the underside of the female) through to hatching, this was not entirely possible using wild-caught ovigerous females. Even though we acquired all of our animals at the same time, there was no definitive way to determine when eggs had been extruded. Therefore, we selected only animals with egg clutches that were about the same age, based on the presence of small, early-stage eyespots. This resulted in the selection of eggs whose overall starting Perkins Eye Index (PEI) was about 12% (68 μm, range = 63–72 μm, or the time at which eye pigment is first visible, Helluy and Beltz, 1991). There were no significant differences between the mean initial stages of the eggs in the inshore group (PEI = 70.1 ± 5.8, or 13% developed) compared to the offshore group (PEI = 68.6 ± 6.1, or 12% developed) (unpaired *t*-test, $t_{1,\ 46} = 0.068$, $P = 0.946$).

All egg stages were calculated using the PEI equation: $Z_{i\rightarrow h} = (W_h - W_i)/(-8.3151 + 2.6019T_{i°C})$, where the number of weeks necessary for a lobster egg to hatch ($Z_{i\rightarrow h}$) is determined based on W_i, an average measurement of eye diameter; W_h, the size at complete development; and $T_{i°C}$, temperature (Perkins, 1972). The size of a lobster's eyespot at hatching (W_h) typically ranges from 560 to 580 μm (Helluy and Beltz, 1991). We chose a median PEI value of 570 μm (based on our observations of previous egg measurements) for a fully developed egg. Using the above equation, it can be shown that an egg that is 50% developed (285 μm) requires 15.8 more weeks to complete development at 10 °C, but only 9.1 weeks at a temperature of 15 °C. The median hatch date (when 50% of the eggs had hatched) for each clutch of eggs was also determined and converted to a Julian day (1–365), to facilitate the averaging of hatch dates for each clutch of eggs in each treatment. An ANOVA was used to determine if mean hatch dates differed between the three treatments. Cumulative growing degree-days (GDD) were calculated for the duration of egg development (from the onset of eyespot formation to 50% hatch) using the following method: (daily temperature – a thermal threshold value) × the total number of days of development. We used a value of 4 °C as our thermal threshold, based on a compilation of lobster reproduction reference values summarized in Waddy and Aiken (1992, 1995).

Egg development was analyzed using ANOVA in the statistical package JMP ver. 9.0.3 (SAS Institute, Cary, NC). Where the parametric assumptions of normality and homogeneity of variance were not met, data were transformed and re-evaluated. All *post hoc* tests were conducted using Tukey's HSD tests. A split-plot repeated measures ANOVA was used to investigate the effects of thermal treatment (inshore and offshore, factor 1) by month (12 levels, factor 2) with the potential effects of tank (whole-plot factor) and individual lobster (sub-plot factor). Associated temperature data (including GDD) were analyzed using a series of Student's *t*-tests and in all cases met parametric assumptions.

Larval measurements and survivorship

A secondary goal for this study was to assess if there were differences in the quality of larvae that hatched from eggs incubated under inshore *versus* offshore thermal regimes. Two assays were used to provide an index of larval quality. First, standard carapace lengths (CL_{STD}, from the posterior margin of the eye socket to the posterior edge of the median dorsal line of the carapace; Harding *et al.*, 1993) were measured for Stage I larval lobsters ($n = 15$/female) from a randomized sample of 6 lobsters from both inshore (laboratory and field) and offshore (laboratory and field) treatments ($n = 12$ lobsters or 180 larvae). Larvae were removed from collection vessels by washing them with seawater into individual sample jars at the time of about 50% hatch. Larval CL_{STD} values were averaged (±SEM) and compared between inshore and offshore (laboratory and field combined) treatments using a Mann-Whitney *U* test for nonparametric data. A subsequent assay measured the survivorship of first-stage larvae by determining how long they

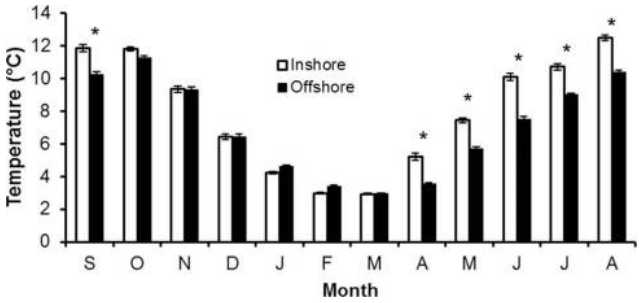

Figure 3. *In situ* mean (±SEM) water temperatures (from HOBO loggers) for inshore and offshore locations during the months when eggs were developing (2007–2009). Inshore and offshore water temperatures were similar from October through March, but from April–July inshore temperatures were as much as 2 degrees warmer than offshore temperature. Asterisks (*) above treatment month comparisons indicate significant differences ($P < 0.05$, $\alpha = 0.05$).

could survive without food (*e.g.,* Abrunhosa and Kittaka, 1997). For each cohort ($n = 15$ larvae $\times$ 12 females, total = 180), larvae were added in triplicate to clusters of six 15-ml individual wells (Costar 3516 culture clusters, Corning Inc., Corning, NY) (experimental unit = well, replicate = cluster). Clusters were labeled on one side and screened on the other to provide ample water exchange and circulation. All clusters were floated in a well-aerated temperature-controlled (18 °C) aquarium (40 l) at 32–35 psu and exposed to a 14:10 LD lighting regime. Water was changed every few days, and temperature was monitored *via* a digital data logger (HOBO, Onset Computer Corp.). Mortalities were checked daily, for 2 weeks, by observing larval activity and movement. Non-responsive larvae (mortalities) were removed immediately. Larval survival was analyzed by a Kaplan-Meier survival algorithm (Sokal and Rohlf, 1995) using the PROC LifeTest with SAS ver. 9.3 (SAS Institute Inc., Cary, NC).

Results

Inshore versus *offshore water temperatures* (in situ)

From October to March, inshore and offshore water temperatures were similar, but from April to September, there were significant differences (ANOVA, $F_{1, 24} = 2.20$, MS = 2.85, $P = 0.045$, Tukey HSD, $P < 0.05$, $\alpha = 0.05$, Fig. 3). Average monthly seawater temperatures for the months of September, April, May, June, and July were significantly warmer inshore; in January and February it was slightly warmer offshore. As a result of being exposed to inshore water temperatures that were much warmer in April through July, inshore lobsters accumulated 336.3 growing degree-days (GDD) during this time period compared to only 163.8 GDD for offshore lobsters. In addition, inshore lobster eggs grew at a faster rate than offshore eggs during this interval.

Laboratory and field (cage) temperature comparisons

In the laboratory, 14 ovigerous females (two mortalities from 16 original; $n = 6$ in 2007; $n = 8$ in 2008) were held in the laboratory September–July of 2007–2008 and 2008–2009, under thermal regimes comparable to those that they would experience if they resided in inshore waters. Inshore water temperatures averaged 6.7 ± 0.18 °C (min = 2.8 °C, max = 13.5 °C) in 2007–2008, and 7.3 ± 0.22 °C (min = 1.5 °C, max 15.0 °C) in 2008–2009. Because there were no significant differences in mean water temperatures between the two years (paired *t*-test, $t_{1,11} = 2.015$, $P = 0.072$), data were pooled for subsequent analyses. Similarly, 16 ovigerous females ($n = 8$/year) were held at simulated offshore water temperatures that averaged 6.9 ± 0.10 °C (min = 2.6 °C, max = 13.7 °C) in 2007–2008 and 7.2 ± 0.10 °C in 2008–2009 (min = 2.6 °C, max 13.1 °C). There were no significant differences between the mean offshore temperature regimes for the two trials (paired *t*-test, $t_{1,11} = 1.902$, $P = 0.065$), so these data were also pooled. In the field, 8 ovigerous females were kept in holding cages submerged at an inshore location ($n = 4$ in 2007–2008 and $n = 4$ in 2008–2009), and an additional 8 were held at an offshore site ($n = 3$ in 2007–2008, $n = 5$ in 2008–2009). Inshore temperatures were the same as in the laboratory trials (*i.e.,* same source of water); however, offshore temperatures were slightly cooler than those simulated in the laboratory, but these differences were not significant (paired *t*-test, $P = 0.22$; 6.8 ± 0.40 °C, min = 2.8, max = 11.2 °C, in 2007–2008 and 6.4 ± 0.32 °C, min = 3.1 °C, max = 10.6 °C, in 2008–2009).

In an attempt to simulate the natural movements of lobsters to offshore waters in the fall (move September–October and remain offshore until March) and then back to inshore waters in the spring (move April–May and remain until hatching in May–June), the cages of the mixed treatment group of animals ($n = 6$) were moved back to inshore waters on 10 March, resulting in a large spike in water temperature and cumulative GDD of 840.1 (Fig. 4).

Egg development

Developmental rates of eggs exposed to inshore and offshore thermal regimes were significantly different (ANOVA, $F_{1, 604} = 37.37$, MS = 23458, $P < 0.0001$, $\alpha = 0.05$). However, there were no significant differences between the rates of development of eggs incubated by lobsters in the laboratory *versus* those held in the field, under the same thermal regimes (ANOVA block effect in analysis, $F_{2, 604} = 1.37$, MS = 858.1, $P = 0.256$, $1\text{-}\beta = 0.58$). The development of all eggs (inshore and offshore) followed the same general trend each year, with rapid development in the fall, followed by a plateau at about 50% development (Perkins Eye Index [PEI] $\sim$ 250–300 μm) during the colder months, and then a rapid increase in developmental rate just

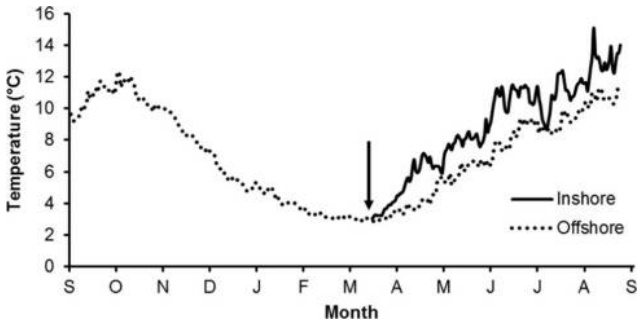

Figure 4. *In situ* temperature profiles for lobsters subjected to offshore conditions in the fall and winter and to inshore thermal conditions in the spring and summer ("mixed" treatment, field study, $n = 6$). Arrow indicates when cages were moved from offshore to inshore in the spring (10 March), leading to a sudden change in the thermal profile (solid line). The offshore profile (dotted line) is continued for comparison. This scenario was designed to simulate the temperature regime that lobsters experience when they undertake seasonal movements.

prior to hatching in the warmer months (Fig. 5). Differences in the rate of egg development between inshore and offshore treatments were associated with the temperature differences in those same months. When water temperatures were similar between locations, as in the late fall and winter, developmental rates were also similar. However, growth rates diverged while inshore waters warmed more rapidly than offshore waters in the spring and summer. Cumulative GDD, from the appearance of the eyespot to hatch, did not differ significantly between inshore and offshore thermal treatments ($\text{mean}_{\text{inshore}} = 938.0 \pm 10.3$ GDD, $\text{mean}_{\text{offshore}} = 904.7 \pm 13.0$ GDD; $t_{1,38} = 2.01$, $P = 0.061$). Although eggs carried by animals exposed to offshore thermal regimes accumulated more GDD in the winter, eggs carried by inshore lobsters acquired them much more rapidly in the spring and early

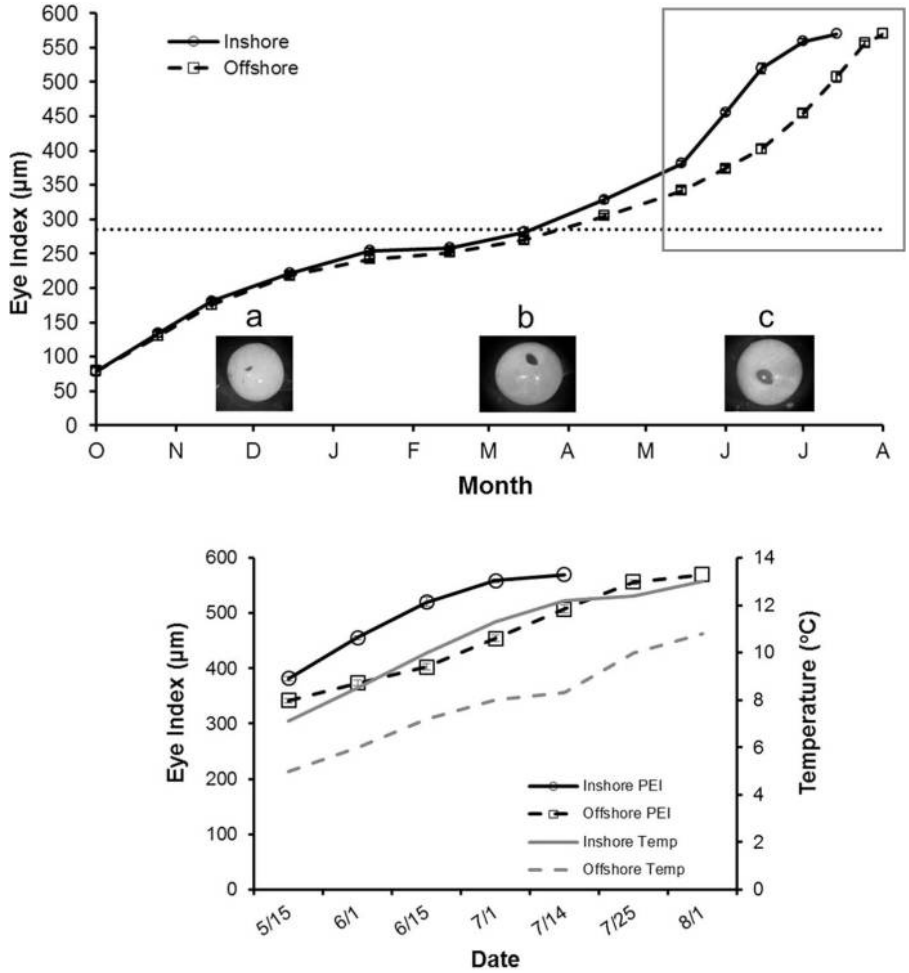

Figure 5. Rates of egg development for eggs exposed to different thermal regimes. (Top) Comparison of development rates for eggs exposed to inshore and offshore temperatures (all lobsters and both years combined). In general there was very limited growth in the winter and increased growth in the spring and summer. The dotted line at 50% development is the Perkins Eye Index (PEI) value equal to 285 μm. Egg images (a–c) correspond to three representative time points in egg development: early (PEI = 185), middle (PEI = 285), and late (PEI = 425). (Bottom) Rate of egg development (left) and water temperatures (right) for both inshore and offshore treatments over the final 4-month period.

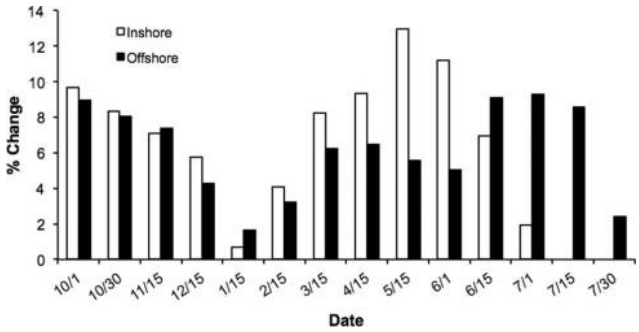

Figure 6. A comparison of the growth rates of eggs exposed to inshore *versus* offshore thermal regimes. Percent change in eye size over the course of development for both inshore and offshore treatments (laboratory and field data, combined). Although growth was similar in the fall and winter months, differences in egg development rates were most noticeable starting in March and were significantly different by May. Offshore growth extended through July as a result of longer egg development and delayed hatch.

summer (Figs. 5, 6). For example, between 1 April and 1 July, inshore sites accumulated a total of 336.3 GDD, compared to 163.8 for offshore sites. It appears that this difference, during April–July, is what caused eggs exposed to inshore temperatures to hatch sooner.

Time to hatch

Eggs incubated inshore hatched earlier and over a shorter period of time compared to eggs from offshore lobsters (Fig. 7). Eggs in both the laboratory and field trials showed clear differences in hatch as a function of temperature ($F_{2,67}$ = 64.73, MS = 183.55, $P < 0.0001$, $\alpha = 0.05$), and subsequent pairwise comparisons showed differences between all three thermal treatments (Tukey HSD, $q = 8.4$, $P < 0.0001$, inshore, offshore, and mixed, Fig. 7). Eggs that were incubated under inshore temperature regimes hatched earlier (time at 50% hatch = 177 ± 2.2 Julian days, median = 175, range = 161–196, or 10 June–15 July, 35 days total) than those in the offshore treatment (mean = 208 ± 3.3 Julian days, median = 211, range = 184–230, or 3 July–18 August, 46 days total, Fig. 7). Lobsters that underwent simulated seasonal movements (mixed treatment) hatched the earliest (mean = 165 ± 2.8 Julian days, median = 165, range = 141–200 Julian days, or 21 May–19 July, Fig. 7) and over the longest interval (59 days; Levene's $W = 2.83$; $P = 0.011$), suggesting that the variation in the mixed group is significantly different than that of the other two.

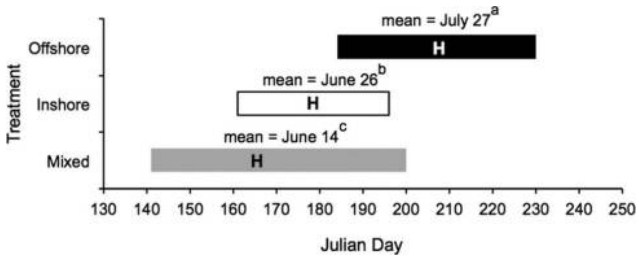

Figure 7. The impact of water temperature on mean hatch dates. The total number of lobsters with eggs hatching each week between June and August, for 2008 and 2009, represented as Julian day. Data are combined for animals exposed to laboratory and field conditions and subjected to one of three thermal treatments: inshore ($n = 22$), offshore ($n = 24$), or mixed ($n = 6$). Mean hatching dates for each group of animals (H) are inclusive of their associated range of hatching times. The mixed treatment group (simulating offshore-to-inshore migration) hatched first and exhibited the longest overall hatching time ($W = 2.83$, $P = 0.011$). Superscript letters (a, b, c) above mean dates indicate significant differences between treatments ($P < 0.0001$, $\alpha = 0.05$).

Larval size and survivorship

There were no significant differences in mean larval size (CL_{STD}) between inshore (mean CL_{STD} = 1.90 ± 0.018) and offshore (mean CL_{STD} = 1.98 ± 0.015) thermal treatments (Mann-Whitney, $U = 15002$, $P = 0.060$). Starvation trials also revealed no apparent differences between inshore and offshore larvae with respect to survivorship (SAS PROC LifeTest; $\chi 2 = 1.765$, df = 1, $P = 0.216$). Out of a starting sample of 90 larvae/treatment, the mean survival of inshore larvae was 45.3 ± 4.1% and for offshore larvae was 47.5 ± 3.6%, over the 14-day trial period.

Discussion

Most lobster species undertake seasonal movements, and numerous explanations for these excursions have been put forth. For example, it is generally accepted that the inshore-to-offshore movements of ovigerous American lobsters enhance egg development in the late fall and winter (Lawton and Lavalli, 1995). As a result of inhabiting deeper, warmer water during the coldest months of the year, eggs should gain more growing degree-days (GDD) and hatch sooner in the spring and summer. However, we found the opposite to be true: eggs exposed to offshore water temperatures developed over a longer period and hatched later compared to eggs exposed to inshore water temperatures (Figs. 5, 7). Therefore, at least in the coastal waters of New Hampshire, southern Maine, and northern Massachusetts, it appears as if the offshore movements of ovigerous lobsters might have evolved for some other purpose, such as positioning larvae in areas that are more conducive to survival and settlement.

Patterns of egg development and growth

Our findings corroborate previous work demonstrating the strong connection between water temperature and the development of lobster eggs (Templeman, 1940; Perkins, 1972; Helluy and Beltz, 1991; Gendron and Ouellet, 2009). The pattern of egg development we observed generally followed those described in previous studies (Bumpus, 1891; Herrick, 1895; Templeman, 1940; Helluy and Beltz,

1991; Sibert *et al.,* 2004; Gendron and Ouellet, 2009): (1) rapid development in the fall, when water temperatures were slowly decreasing; (2) a protracted period of developmental latency over the winter months at water temperatures <4 °C; (3) rapid growth in the spring as water temperatures increased; and (4) a brief pause in development about one month before hatch. In all treatment groups we observed a well-defined ~3.5-month plateau in growth at 50% development (PEI = 285 μm) over the winter months and a shorter and less well-defined one at 80% development (PEI = 455 μm) in the late spring and early summer. Interestingly, despite the differences in thermal profiles, inshore and offshore egg development trajectories were very similar until the spring (Fig. 5). The rate of temperature increase from May through August was significantly different between inshore and offshore treatments (Fig. 3), and it was during this interval that egg development diverged.

Developmental plateaus, during which neither the growth of the eye nor the cephalothoracic segment is evident, have been documented both in crabs (Stevens and Swiney, 2007; Stevens *et al.,* 2008) and lobsters (Helluy and Beltz, 1991). The earlier, more prolonged, developmental plateau we observed at 50% could be the result of the culmination of most of the morphological development and organogenesis that occurs before water temperatures decrease to suboptimal growth levels in the late fall and winter. However, Sibert *et al.* (2004) determined that almost 65% of the live biomass (total proteins) of hatching larvae accumulated during the last few weeks of development. Therefore, it is more likely that the lobsters in this study exhibited a plateau at 50% because of exposure to colder winter temperatures (Gendron and Ouellett, 2009). The later plateau at 80% seems to be related to the transition of the embryonic premolt stage in the metanaupliar molt cycle as the larva prepares for hatch; this is comparable to the pre-molt pause in growth documented in juvenile lobsters (Aiken, 1973; Helluy and Beltz, 1991). Helluy and Beltz (1991) observed developmental plateaus at a variety of stages (PEI = 350–450 μm, ~60%–80%), even at constant temperatures. However the cause of the 80% plateau remains largely unknown, and subsequent studies may help to elucidate the possible role of temperature.

Degree-days and growth

Historically, GDD have been used as an index of the thermal history experienced by ovigerous lobsters, and they are calculated based, in part, on a minimum threshold value below which no growth is assumed to occur (in this study that threshold was 4 °C). We calculated the number of GDD that accumulated from the onset of eyespot formation to hatch (905 for inshore and 938 for those residing offshore) and found that our values are lower than some previously reported values, but within the range of others. Because GDD are a function of both water temperature and the time it takes eggs to hatch, we observed that eggs that hatched first accumulated the fewest GDD, even though they were also exposed to the warmest water. However, we are aware that direct comparisons of GDD can be problematic for three main reasons. First, not all studies choose the same minimum temperature threshold (*e.g.,* 3.4–10.0 °C; Campbell, 1986; Cowan *et al.*, 2007; Tlusty *et al.,* 2008), which makes standardizing difficult. Second, in some field studies, the day of extrusion and hatch was estimated, while in other laboratory experiments these critical time points were known. Finally, in some cases, GDD have been calculated for both early- and late-spawners, meaning that the thermal regimes for each of these groups were different (*e.g.,* Gendron and Ouellett, 2009). Yet despite these differences, it may still be possible to use GDD, in a given region, as a technique for predicting when eggs will hatch. For example, as previously stated, eggs from all three groups hatched after they had accumulated approximately the same number of GDD.

We found no significant differences in GDD values for lobsters incubated at inshore and offshore temperatures, even though mean monthly water temperatures were different at certain times of the year. Moreover, even the GDD value for our mixed group (840.1) was not significantly different from that of either inshore or offshore treatments. Yet the mixed group eggs hatched first, followed by those of the inshore and then the offshore group. Therefore, we suggest that the key factor influencing the time of hatch in *H. americanus* eggs is the *rate of increase in water temperature during the spring and early summer*, rather than the total number of GDD accumulated throughout development. However, the relative number of GDD can be a good predictor of hatch since all lobsters hatched after about the same GDD, even though they hatched at different times. Both mean water temperature and GDD were very similar between our treatments during the first two-thirds of egg development, but then differed significantly during the last third, leading to earlier hatch for the eggs exposed to the most rapid increases in water temperature. Eggs carried by lobsters in the mixed treatment group gained both the extra warmth of offshore waters in the winter and the rapidly increasing temperature of inshore waters in the spring, and as a result, they hatched earlier than both other groups (Fig. 7).

If there is an advantage to eggs hatching in the spring rather than later in the summer, then it might be important for lobsters to undertake seasonal movements to help accelerate egg development in colder waters where it is difficult to accumulate GDD. These patterns of inshore-to-offshore movement in the fall, combined with offshore-to-inshore movement in the spring, have been documented for several different lobster populations (Cooper and Uzmann, 1980; Lawton and Lavalli, 1995). However, in coastal waters of southern Maine and New Hampshire, few of the ovigerous lobsters that move offshore in the fall migrate back inshore

in the spring while they are still carrying eggs (Goldstein, 2012; Goldstein and Watson, 2015). Rather, most remain offshore until their eggs hatch. This suggests that seasonal inshore-to-offshore movements might not have evolved simply to accelerate egg development, and thus it is worth considering what other purposes this behavior might serve.

Time to hatch

Our data do not support the hypothesis that offshore movements of ovigerous females result in a faster accumulation of GDD and therefore earlier hatching of larvae. Rather, eggs exposed to inshore water temperatures accumulated GDD at a faster rate in the spring and hatched an average of 4 weeks earlier than eggs incubated under offshore thermal regimes (*i.e.*, lobsters moving offshore hatched later than lobsters that remained inshore). Therefore, it is possible that offshore movements serve to delay rather than accelerate hatching, at least in this region of the American lobster range. Hatching later in the spring and summer may be significant for a combination of reasons that are framed by two long-standing hypotheses: (1) Hjort's (1914) critical period hypothesis contends that the presence and strength of larval year classes are determined by the availability of food during a "critical period"; while (2) Cushing's (1990) match-mismatch hypothesis states that variations in the timing of larval hatch may be a function of larval food supply (spring phytoplankton bloom). Although embryonic development rate in lobsters is most strongly influenced by temperature, the timing of the spring plankton bloom in coastal waters depends on a combination of factors, including seasonal changes in photoperiod, temperature, and circulation patterns (Starr *et al.*, 1990). Alterations in the timing of these events may influence the onset of hatching in marine crustacean larvae (including lobsters). These changes may also prevent hatching synchronized with the presence of plankton assemblages, thus affecting larval survival. Therefore, if the movements of ovigerous females have evolved to ensure that hatching occurs at the right time of year, when both sea surface temperatures (>12 °C, Mackenzie, 1988) and associated plankton blooms are optimal for larval survival, then these events should correlate with the occurrence of offshore, rather than inshore, larval hatch. In New Hampshire waters, there is a good correlation between water temperatures and larval hatch; however, it is not known if a relationship to optimal plankton assemblages exists.

In a series of laboratory rearing studies, MacKenzie (1988) demonstrated that larvae hatching at 10 °C can develop successfully through Stages I and II; however, warmer water is needed to complete development to Stage IV and the early benthic juvenile phase, Stage V (4% larval survivorship at 10 °C *versus* 56% at 12 °C; MacKenzie, 1988). Similarly, Harding *et al.* (1983) found that hatching usually occurred when water temperatures rose above 12 °C. We found that the average surface water temperature when inshore larvae hatched was 11.5–13.7 °C, compared to 10.5 °C for offshore waters over the same time (NERACOOS, 2014). Although offshore eggs hatched a month later, sea surface temperatures increased to 14.4–16.5 °C (NERACOOS, 2014). So, to some extent, the differences in hatch date allowed lobsters in both areas to hatch when water temperatures were favorable for larval growth and survival.

While Perkins's (1972) equation for predicting hatch in eggs incubated at constant temperatures has been very useful for laboratory- and hatchery-based research, it is not as biologically relevant for animals in natural habitats characterized by seasonal fluctuations in water temperature (Jarvis, 1989). We sought to test the usefulness of the Perkins equation for eggs exposed to naturally fluctuating water temperatures by using the mean temperature for the duration of the incubation period as the "constant" temperature. For a subset of ovigerous lobsters ($n = 4$, size range = 84–95 mm CL), we used the PEI equation to calculate predicted egg development times using the average temperatures (6.2 °C offshore, 6.7 °C inshore) during the time when egg development occurred in our study area (October–July). For animals subjected to offshore waters, PEI predicted that eggs would hatch about 93 days later than they actually did; for inshore eggs, the difference was even greater—100 days) ($G_{offshore} = 14.27$, $P < 0.001$; $G_{inshore} = 17.31$, $P < 0.001$). The discrepancy between predicted hatch dates and those derived empirically (this study) suggests that it is difficult to rely solely on Perkin's (1972) equation to predict the hatch dates of eggs *in situ*, and that improved, more realistic models should therefore be developed that take into account the effects of naturally changing temperatures on overall egg development.

Larval dispersal and survivorship

We found no apparent differences between inshore and offshore larval sizes or survivorship. Various indicators of larval variability in other crustacean and fish larvae have included size at hatch and lipid profiles (reviewed in Jaeckle, 1995). For example, after raising spiny lobster larvae (phyllosomas) at various thermal profiles, Smith *et al.* (2002) reported that Stage I phyllosomas cultured at warmer temperatures were smaller. Changes in incubation temperatures have also been shown to affect larval size in other lobsters (*e.g.*, *Jasus edwardsii;* Tong *et al.*, 2000) and also in crabs (Shirley *et al.*, 1987, 1990). One advantage of *H. americanus* eggs developing more slowly at colder temperatures could be related to the conservation of metabolic reserves (*e.g.*, lipids) during development, leaving more energetically rich reserves available for the first few days as larvae. However, this may not be a critical issue, because even lobster eggs cultured at elevated temperatures contain residual yolk at the time of hatching (Sasaki *et al.*, 1986).

Therefore, the differences in thermal regimes between inshore and offshore waters do not appear to have a major influence on the viability of lobster larvae, and thus the offshore movements of ovigerous females probably did not evolve for this purpose.

Another possible explanation for the migration of ovigerous lobsters offshore in the late fall and winter is that these movements serve to position larvae in areas optimal for survival and transport to favorable settlement locations, as has been conjectured for spiny lobsters (see Booth, 1997, for review). According to our ultrasonic tracking data, most ovigerous lobsters that migrate offshore remain there until after their eggs hatch the following spring and summer (Goldstein, 2012). Furthermore, preliminary data from surface ocean drifters released offshore at the time and location of hatching indicate that larvae from New Hampshire waters are most likely transported to coastal locales in the south (Massachusetts), where they settle about 3–4 weeks later (Goldstein and Watson, 2015). In contrast, drifters released inshore were frequently and rapidly transported farther inshore, presumably too soon for developing larvae to reach a stage at which they are competent to settle. Thus, hatching offshore appears to be more beneficial for larval survival and settlement and may explain why ovigerous females in this region of the Gulf of Maine remain offshore in the spring until their eggs hatch. The dynamics of lobster movements have a great impact on their distribution and abundance, and a continued knowledge of these patterns is integral to further elucidating the degree to which larval dispersal occurs and the scale of marine connectivity in the future management of this important fishery.

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