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American Lobster, *Homarus americanus*, Reproduction and Recruitment in a New England Estuary

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Abstract

While egg-bearing (ovigerous) American lobsters are found in estuaries, it is not known if they are present when their eggs hatch. The major goal of this study was to test the hypothesis that a portion of the larvae that serve as new recruits to the Great Bay Estuary lobster population originate from females that are year-around residents. First, a total of nine ovigerous lobsters were fitted with acoustic transmitters and tracked from October through the following spring-to-early summer. We found that all lobsters overwintered in the estuary and were located again within 1 km of their fall positions the following May–June, when their eggs likely hatched. Second, sea sampling surveys carried out in the spring revealed that ovigerous lobsters in the estuary were carrying more developed eggs than their coastal counterparts. Third, through a series of laboratory-based studies, we calculated the putative hatch dates of egg clutches carried by estuarine and coastal lobsters and show that estuarine lobster eggs likely hatch 2–3 weeks earlier than eggs carried by coastal females. Finally, plankton tow surveys in the estuary revealed that stage I larval lobsters (zoeae) were present in the estuary from May to July, which encompasses the predicted hatching period for both estuarine and coastal eggs. Therefore, new recruits to the Great Bay Estuary lobster population likely come from both resident estuarine lobsters and coastal females.

Keywords *Homarus americanus* · Lobster · Larvae · Recruitment · Estuary · Acoustic telemetry

Introduction

The American lobster (*Homarus americanus*) ranges from North Carolina to Newfoundland and Labrador, and encompasses both wide-spread inshore and offshore subpopulations. While they are most abundant in offshore and coastal waters, lobsters of all life stages do have a limited ability to osmoregulate (Dall 1970; Jury et al. 1994a; Charmantier et al. 2001) and commonly inhabit estuaries, bays, and inlets ranging from Rhode Island to Atlantic Canada and Quebec (Thomas 1968; Thomas and White 1969; Munro and Therriault 1983; Wahle 1993; Howell et al. 1999; Rowe 2001; Short et al. 2001). From spring through early fall, these habitats tend to be warmer and it has been suggested that lobsters migrate into these comparatively warmer water systems to aid in somatic growth and limb regeneration (Aiken and Waddy 1986; Moriyasu et al. 1999), as well as to accelerate egg development (Templeman 1940; Aiken and Waddy 1986; Little and Watson 2003).

It is generally accepted that the abundance of lobsters in estuaries fluctuates because of their migrations in the spring and fall (Templeman 1935; Munro and Therriault 1983; Watson et al. 1999), driven by seasonal fluctuations in temperature and salinity. For example, lobsters of all life stages can sense, and will avoid, low salinity water (Jury et al. 1994a, b, 1995; Charmantier et al. 2001; Dufort et al. 2001). Furthermore, their movements further up into the estuary typically take place after the spring runoff, when salinities are the lowest (Watson et al. 1999). Lobsters are also very sensitive to water temperature (Jury and Watson 2000) and use this information to behaviorally thermoregulate (Crossin et al. 1998).

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Furthermore, it has also been proposed that the differential sensitivity of male and female lobsters to warmer water temperatures (Jury and Watson 2013) and lower salinities (Jury et al. 1994b) is the underlying cause of the skewed sex ratio and paucity of ovigerous (i.e., berried or egg-bearing) lobsters in locations such as the Great Bay Estuary (GBE), in New Hampshire (Howell et al. 1999; Jury et al. 2019). This has also led to the assumption that there is very limited lobster reproduction and recruitment within the GBE and that new recruits to this estuarine system originate from coastal lobster populations. This view is further supported by data from a survey of Narragansett Bay (Rhode Island), where Wahle (1993) found a gradient of newly settled lobsters, with the highest abundance close to the mouth of the bay and in deeper water (Wahle et al. 2015). However, while lobsters are capable of moving long distances and many undergo long seasonal migrations (reviewed in Lawton and Lavalli 1995), there is also considerable evidence that lobsters, including ovigerous females, remain in local areas and maintain subpopulations (Rowe 2001; Øresland and Ulmestrand 2013; Goldstein and Watson 2015a). In particular, while ovigerous lobsters are capable of large migrations before they extrude their eggs (Cooper and Uzmann 1971; Campbell 1986; Cowan et al. 2007), these animals typically show less movement during the later stages of egg development (Saila and Flowers 1968; Jarvis 1989; Watson et al. 1999; Goldstein and Watson 2015a). In fact, because the location of ovigerous lobsters carrying late-stage eggs tends to coincide with the site where their larvae hatch, the movements of egg-bearing females to specific areas might have evolved to enhance the survival of hatching larvae (Jarvis 1989; Goldstein and Watson 2015a; Carloni and Watson 2018).

In previous studies, ovigerous lobsters were captured in the GBE, but their eggs were not staged (Goldstein and Watson unpub data), so it is not known if they are present in the estuary when their eggs are close to hatching. Furthermore, larvae have been found in the GBE during plankton tows, but these past surveys were carried out from late June to early September. As a result, it has been assumed, because these surveys coincided with the time frame during which larvae were also captured in NH coastal waters (Grabe et al. 1983; Normandeau 2015), that these larvae originated from coastal females (New Hampshire Fish and Game unpub data). Therefore, when the present study was initiated, it was not clear if lobster eggs hatch, and the subsequent larvae are retained, within the estuary.

The overall objective of this study was to determine the source of new recruits to the GBE lobster population. To address this objective, we set out to answer the following four questions: (1) Do ovigerous lobsters overwinter in the GBE? (2) Are ovigerous lobsters present in the estuary in the spring when their eggs are ready to hatch? (3) Do these eggs hatch earlier than those carried by NH coastal lobsters because the estuary warms up faster in the spring than the coast? (4) Are larvae present in the water column while eggs are hatching in the estuary, and before they hatch along the coast, suggesting they are sourced from estuarine females?

Materials and Methods

Study Site

The Great Bay Estuary (GBE), located in southeast New Hampshire, is comprised of three distinct bodies of water: the Piscataqua River; Little Bay, and Great Bay proper (Fig. 1). The GBE extends ~25 km inland from the coast; the upper estuary is characterized by mudflats and soft sediment, while the habitat is more complex within Little Bay and the Piscataqua River, featuring hard-bottom and tidal rapids (Grizzle et al. 2008). GBE is also a well-mixed, fairly unstratified system due to its hydrodynamics and bottom hydrology (reviewed in Short 1992). A deep channel ranging from 8 to 20 m deep runs the length of the estuary, from the coast to the middle of Great Bay. Water temperatures and salinities fluctuate seasonally (15–30 psu, 2–24 °C; Fig. 1 in Jury et al. (1995); Fig. 2 in Howell et al. (1999); Fig. 1 in Watson et al. (1999); Fig. 3 in Fulton et al. (2013), and Fig. 2 and Fig. S1 in this paper) with a gradient of decreasing salinity and increasing temperatures the further one moves up into the estuary. It should also be noted that in a typical year, salinities average >

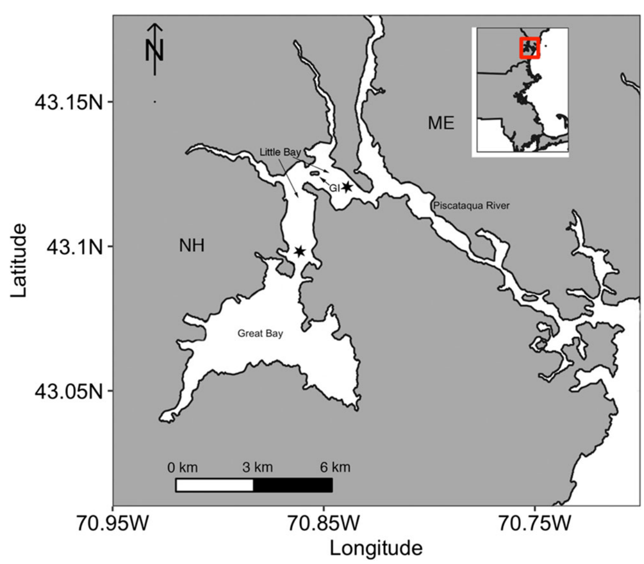

Fig. 1 Study area within the Great Bay Estuary in New Hampshire, Gulf of Maine. Little Bay is the location where much of the acoustic telemetry work was conducted, especially in the vicinity of Goat Island (GI). Star symbols (✱) depict the two locations where larval tows were conducted (15 and 18 km up-estuary). Bathymetric details about the Great Bay can be seen in Figure 3 in Schaller et al. (2010) and at the following website: http://ccom.unh.edu/project/great-bay/available-maps-data

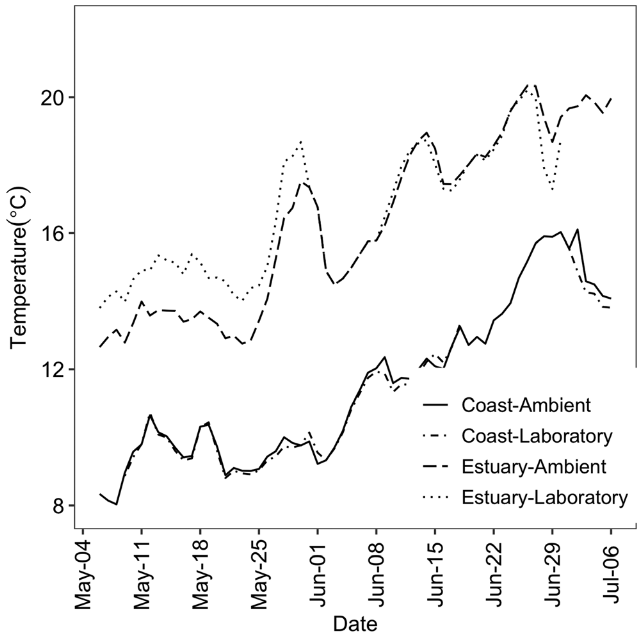

Fig. 2 A comparison of ambient and laboratory water temperatures at the coast and estuary from May to July in 2015. For additional temperature and salinity data, see Fig. 1 in Jury et al. (1995), Fig. 2 in Howell et al. (1999), and Fig. 1 in Watson et al. (1999). A full year of temperature and salinity data for 2018 can also be seen in Supplemental Figure S1

20 psu during most months except April, when levels may drop to between 15 and 19 psu (papers cited herein) due to the spring runoff of freshwater from melting snow and ice.

Movements and Distribution of Ovigerous Lobsters

To determine if ovigerous lobsters overwinter in the GBE, a total of 9 female lobsters (5 in October of 2007 and 4 in September of 2008) carrying early- to mid-stage eggs (average = 45 ± 15.5% developed; determined as described in Goldstein and Watson 2015b) were collected by commercial lobstermen in Little Bay, fitted with transmitters (Vemco V13-1L acoustic coded transmitters, 69 kHz, 6 g in water, estimated battery life ~ 3 20 days; Vemco-Amirix Systems Inc., Halifax, NS) and released in Little Bay (approximately 17 km from the coast in 2007 and 18 km away in 2008, Figs. 1 and 3). The tagging process took ~ 15 min and tagged lobsters were placed into a lobster trap with a large escape vent, from which they could easily vacate (Golet et al. 2006; Goldstein and Watson 2015a), and lowered back to the bottom of the estuary. The transmitters were programmed to transmit data every 1–2 min for a duration of 8–9 months.

A system of 13 fixed underwater hydrophones ("gates") were set up in Little Bay at depths ranging from 3 to 15 m. Each receiver (VR2W, Vemco-Amirix Systems Inc.) was attached to a dock or large mushroom mooring and all receivers were affixed vertically (facing down) to the mooring line or dock, 2 m from the surface. Using a series of range tests (Vemco 2015) prior to the study, to evaluate the strength of detecting tags under varying environmental conditions, we

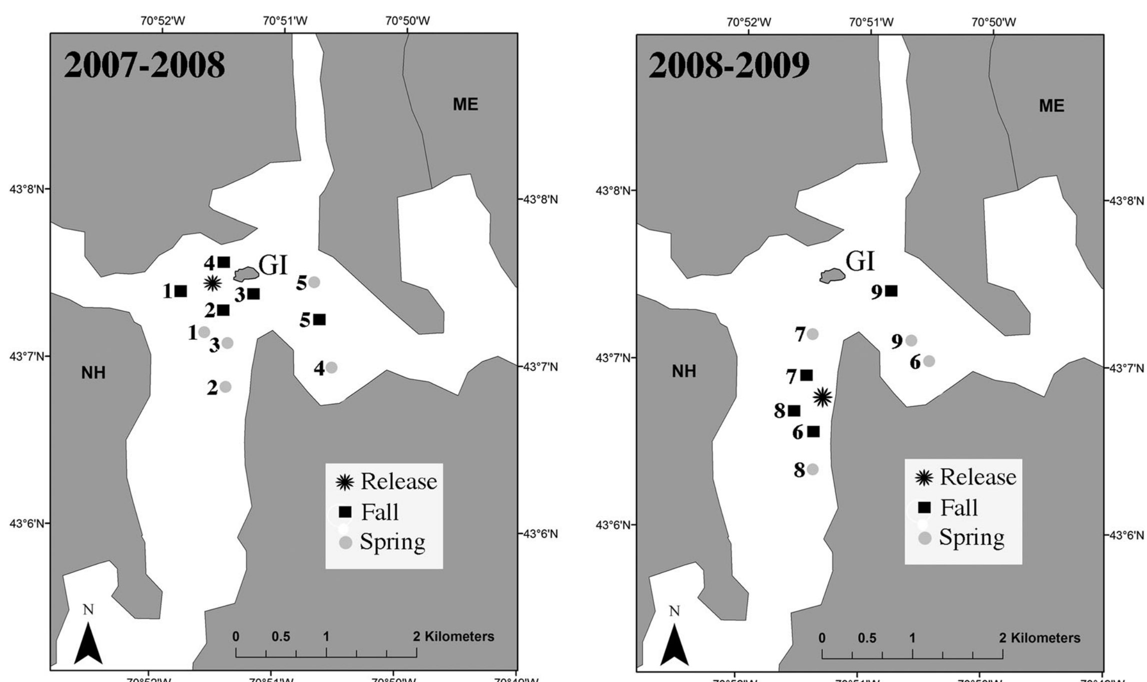

Fig. 3 The location of the nine ovigerous female lobsters that were tracked in 2007–2009 in Little Bay (see Fig. 1). The star indicates where they were captured, fitted with transmitters, and released in the early fall (October) of each year. Note this location was slightly different in 2007 vs 2008. The last location obtained from each lobster in the late fall/early winter (December), before tracking was suspended for the winter, is indicated by a small square. The circles represent the location of each of the lobsters the following spring (June). GI = Goat Island

determined that our acoustic tags could be heard from a distance of ~ 100–300 m depending on tides, boat noise, habitat structure, and the thermocline. Our array design enabled us to confidently hear all transmitters in the study area while making sure that lobsters could not move past these gates without being detected. Lobster positions were also tracked manually using a VR100 receiver and a handheld directional or omnidirectional hydrophone (VH110 and VH165, Vemco-Amirix Systems Inc.). The omnidirectional hydrophone was towed behind a research vessel and then when a tagged lobster was detected, the directional hydrophone was used to triangulate the approximate position (within 10–15 m) of the animal. Four times monthly, from October–December 2007, March–August 2008, October–December 2008, and March–August 2009, as many lobsters as possible were located using these manual surveys. When lobsters were detected multiple times during the same hydrophone survey, the location used for analyses was obtained by averaging the positions. The location of lobsters was also determined using a high-resolution VRAP system (Vemco-Amirix Systems Inc.) located around the release locations in each of the 2 years. This system uses three buoys to triangulate tag positions with an accuracy of up to 1 m (see details in Golet et al. (2006); Scopel et al. (2009)).

Because the goal of this portion of the present study was to determine if ovigerous lobsters overwintered in the estuary and remained there until their eggs hatched in the spring, the following data were calculated using the positional fixes that were obtained as described above: (1) the distance each lobster moved from the time they were originally tagged and released in October until the time when we obtained the last position for them that year (fall movement and their overwintering position), which was typically in November or December; (2) the distance tagged lobsters moved between their overwintering location and the time their eggs likely hatched in May or June (their spring movement), or the last time they were detected; (3) the total distance they traveled, which was obtained by adding their fall and spring movements together and; (4) their "net" distance traveled, which was calculated by adding together the distances they moved in the fall and spring, but assigning positive values to up-estuary movements and negative values to down-estuary movements.

Sea Sampling

Ovigerous female lobsters were collected during a series of sea sampling trips with commercial lobstermen in the spring and summer of 2015 to confirm the presence of lobsters carrying late-stage eggs in the GBE and in coastal NH state waters. Sampling primarily took place in Little Bay, and along the NH coastline (Fig. 1). For every ovigerous lobster captured during each trip, the carapace length (CL, in mm) was measured and 15–20 eggs were removed from the midpoint of the abdomen, between the second and third rows of pleopods (Helluy and Beltz 1991). Egg samples were not collected from lobsters that were already hatching their eggs, but it was noted that these lobsters were carrying eggs that were hatching. Egg samples were stored in small 2.0-mL labeled vials of chilled, sterilized seawater for subsequent determination of their developmental stage in the laboratory. Lobsters were then immediately released where they were captured. A subset of 10 intact eggs from each egg sample was selected haphazardly and used to determine developmental status, as described in Goldstein (2012) and Goldstein and Watson (2015b). Digital pictures were taken of each egg using an Olympus SZX7 dissecting scope and Nikon camera (SMZ 2T) at 32 × magnification. Images were uploaded to Image J software (v.1.50i, http://nihimage.gov) to measure the size of the eyespots for each egg. Eyespots have an oval shape and so mean diameter (μm) was calculated for each eyespot for each sample (Perkins 1972). These data were then used to determine the rate of egg development for both locations (estuary and coast).

Development of Eggs in the Laboratory

The Perkins Eye Index (PEI, Perkins 1972) is effective for predicting hatch dates of eggs at a given temperature and the function is defined as:

$$PEI = \frac{W_h - W_i}{-8.3151 + 2.6019 T_{i\,^\circ C}}$$

where W_i is the mean diameter of the eye, W_h is the size at which egg development is complete (adapted from Helluy and Beltz 1991) and $T_{i\,^\circ C}$ is the mean temperature regime. However, it is not optimal for predicting the hatch dates of lobster eggs exposed to a naturally changing thermal regime (see Goldstein and Watson 2015b; Fig. 2). As the objective of this present study was to predict hatch dates as accurately as possible, the PEI was modified to include an additional term, to allow us to predict when an egg of a given stage, exposed to a given thermal history, would hatch. The term derived to account for the effects of temperature on egg development and includes the term ΔT, which is the change in temperature.

$$\frac{\left(\Delta T * W_h / W_i\right) * (W_h - W_i)}{7}$$

This term was derived by comparing the rate of egg development of eggs carried by nine lobsters obtained during the Great Bay sea sampling trips in 2015, to the rate of temperature change they experienced while being held in ambient flow-through tanks at the UNH Jackson Estuary Laboratory in Durham, NH. A similar analysis was carried out with a second group of lobsters ($n = 7$) obtained during coastal sea sampling trips the same year, that were held at the UNH

Coastal Marine Lab in Newcastle, NH. All lobsters were measured, tagged with sphyrion tags (Floy Tag & Mfg., Inc., Seattle, WA), and held in 0.9 m round fiberglass tanks supplied with ambient seawater. Lobsters were partitioned into separate areas of the tank, provided with shelters and a natural cobble bottom, exposed to natural light:dark conditions, and fed live mussels, rock crabs, and Atlantic herring weekly. HOBO temperature loggers (model UA-002-64, Onset Computer, Bourne, MA) were used to record both tank and ambient water temperatures at both locations (Fig. 2).

Weekly sub-samples of five eggs were obtained from each female to monitor egg development using the methods described above. Egg clutches were checked visually each week for signs of hatching and once they were near hatching, they were checked more frequently. We designated the date when larvae were first observed in the water as the "hatch date" for the clutch of eggs carried by each lobster. Larvae were retained in tanks by placing fine mesh over the outflow in the center of the tank. Additionally, the range of hatch dates was compared between the estuary and coast using a nonparametric Kruskal-Wallis ANOVA ($\alpha = 0.05$), and also compared with in situ hatching dates. All statistical analyses were conducted in R Studio (v.3.4.2 R Core Team 2018) and all figures were created in the R package ggplot2 (Wickham 2016).

Egg Development and Hatch Predictions

One goal of the present study was to determine if the eggs carried by estuarine lobsters hatch earlier than those carried by coastal females. To estimate when the eggs obtained from females during sea sampling would have hatched, we used the following modification of the PEI:

$$Z_{i\rightarrow h} = PEI - \frac{\left(\Delta T * W_h / W_i\right) * (W_h - W_i)}{7}$$

where $Z_{i\rightarrow h}$ is the number of weeks until hatching, W_i is the mean diameter of the eye, W_h is the size at which egg development is complete (Helluy and Beltz 1991). The term W_h was standardized to 570 μm, because it represents the eyespot size when lobster eggs in New Hampshire coastal waters complete development (Goldstein and Watson 2015b). Weekly bottom temperatures were collected (T), as it reflected the thermal regime change that lobsters were exposed to during the spring and summer. In addition, the PEI equation was modified by adding a term to compensate for the effects of rate of temperature change (ΔT) on the rate of egg development. The rate of temperature change was calculated by taking the slope of temperature change from May to July, when temperatures plateaued. Once predicted hatch dates were obtained for all egg samples, the range of these dates was compared between the estuary and coast using a nonparametric Kruskal-Wallis ANOVA ($\alpha = 0.05$) in R v.3.4.2 (R Core Team 2018).

Larval Tows

Larval lobsters were collected using plankton nets in 2015 during the time of year that lobster eggs were likely to be hatching in the estuary (confirmed by our laboratory study). Collections were made using paired plankton nets (1 m diameter, 0.5 μm mesh size), and larvae were sampled from the top 1–2 m of water at two fixed stations during morning and evening (low light) hours, twice a week, over an 11-week period (May–July). Each tow was 30 min in duration, and nets were deployed 3–4 m astern from a 6-m Eastern Seaway with a 70 hp. outboard engine. Tow speed was held at ~ 3 kts to prevent a wake. Stations were chosen at geographic bottlenecks within the estuary (15 and 18 km up-estuary, Fig. 1), that were close to where ovigerous lobsters tended to overwinter, based on our telemetry and survey data. Water volume sampled was measured using a General Oceanics flowmeter (model 2030R) and the abundance of larvae was quantified as the number of larvae per 1000 m^3 of filtered water. A total of 38 tows were carried out in the GBE between May 27 and July 29, 2015. The mean volume of water sampled per tow was 2116 ± 148 m^3 and ranged from 875 to 3066 m^3. The mean volume of water sampled per tow during the upper Little Bay transects (2110 ± 205 m^3) did not differ from the volume of water sampled in lower Little Bay (2122 ± 229 m^3, $P = 0.97$, $df = 35.8$). The geometric mean of larval abundance per week was compared over time using a nonparametric Kruskal-Wallis ANOVA ($\alpha = 0.05$).

Hatch Prediction

Larvae captured during plankton tows were morphologically staged using the methods outlined by Aiken and Waddy (1986). Larval age (i.e., the number of days post hatch) was calculated by using the following stage-specific equation, derived from Harding et al. (2005) and adapted from Mackenzie (1988) (T is mean weekly temperature):

$$Days = 1305T^{-2.02}$$

The number of days from hatch was subtracted from the capture date of individual larvae to provide an estimated date of when each larva hatched. These data were then compared with the predicted hatch dates for eggs carried by the ovigerous females sampled at sea. These comparisons were used to determine if larvae obtained in plankton tows were more likely to have originated from the estuary, the coast, or both. All means are given with ± standard deviations (sd).

Results

Acoustic Telemetry

A total of nine ovigerous lobsters (mean CL = 82.3 ± 4.0 mm) were fitted with acoustic tags in October of 2007 ($n = 5$), or 2008 ($n = 4$), and tracked until the following spring-to-summer (see summary Table 1). These nine lobsters remained at large for 153–359 days (mean = 291 ± 21.8 (sem) days) and during this time period, they moved a mean of 1.77 ± 0.3 km (range = 0.30–2.77 km, Fig. 3). However, because these lobsters moved both up (positive values) and down (negative values) the estuary, their net movements averaged − 0.46 ± 0.5 km (range = − 2.77–1.62 km). Lobsters tagged and released in the fall of 2008 tended to move further down the estuary (net movement of − 1.03 km) than those released in 2007 (0.24 km). Even though these lobsters traveled a total of less than 2 km, all five of the acoustically tagged lobsters released in 2007 followed a pattern reported in previous studies; moving down towards the coast in the fall (− 0.11 km) and then back up in the spring (0.45 km). Most importantly, all 9 of the lobsters were still present in Little Bay the following spring and summer. Therefore, we conclude that the majority of ovigerous lobsters that are present in, and around, Goat Island in Little Bay in the fall probably remain there until the following spring, and it is likely that their eggs hatch while they are in the estuary at this time (confirmed by our surveys and predictive model). In fact, two of the lobsters we tracked were caught by lobstermen in late May in Little Bay and they had late-stage eggs, and one of these was recaptured again in Little Bay in early August and the eggs had hatched.

Hatch Predictions for Eggs

Lobsters Collected During Sea Sampling

In 2015, a total of 64 ovigerous lobsters were captured during four sea sampling trips in the GBE and 39 were caught during three trips along the NH coast. The sizes of the lobsters obtained from each area were similar (estuarine lobsters = 85.08 ± 4.50 mm CL, coastal lobsters = 86.13 ± 11.07 mm CL, unpaired t test $P = 0.58$). However, the eggs carried by estuarine lobsters were always more developed (Fig. 4). The modified Perkins Equation was used to predict when eggs collected from lobsters while sea sampling would hatch. Of the lobsters captured in the estuary, six were already hatching (visually assessed) in May, while none of the coastal females were in this condition until June (although observations were limited to one prior sea sampling trip in early May). Estuarine lobster eggs were predicted to hatch ~ 3 weeks earlier (May 21 to June 23; mean hatching date, June 9 ± 11.8 days) than those carried by coastal females (mean hatch date, July 1 ± 9.5 days, range = June 11 to July 23, Fig. 4). When comparing the mean predicted hatching dates, the eggs carried by estuarine lobsters hatched significantly earlier than those carried by lobsters from the coast (Kruskal-Wallis H-test, $P < 0.001$, $df = 1$, Figs. 5 and 6). In addition, the duration of time when hatching was likely to occur in the estuary was shorter than the predicted coastal hatching period (34 vs 42 days). The period during

Table 1 Biological data (size, egg stage) and summary tracking data (tag date, days-at-large, and distances) for all lobsters released and tracked in (a) 2007 and (b) 2008. Lobster ID denotes the acoustic tracking code for each lobster while the adjacent number in () can be used to identify the location of each lobster mapped in Fig. 3

Lobster ID	CL (mm)	% Egg Develop.	Tag Date	DAL	Total Dist. (km)	Net Dist. (km)
2007 lobsters ($n = 5$)						
6779 (1)	81	32	10/16/07	353	2.07	− 0.29
6780 (2)	82	45	10/17/07	244	3.50	1.62
6781 (3)	82	48	10/18/07	258	0.79	− 0.79
6805 (4)	82	38	10/24/07	307	0.30	− 0.30
6808 (5)	77	29	10/24/07	359	1.97	− 0.63
Average	80.8	38.4		304.5	1.73	0.10
Stdev	2.2	8.1		52.8	1.25	1.03
Sem	1.0	3.6		23.6	0.56	0.46
2008 lobsters ($n = 4$)						
52782 (6)	77	33	10/17/08	307	1.75	− 1.75
52783 (7)	84	78	10/17/08	344	0.76	− 0.60
52790 (8)	89	56	10/17/08	294	2.03	1.01
811 (9)	87	54	10/17/08	153	2.77	− 2.77
Average	84.3	55.3		274.5	1.83	− 1.03
Stdev	5.3	18.4		83.7	0.80	1.60
Sem	2.3	8.2		37.4	0.40	0.80

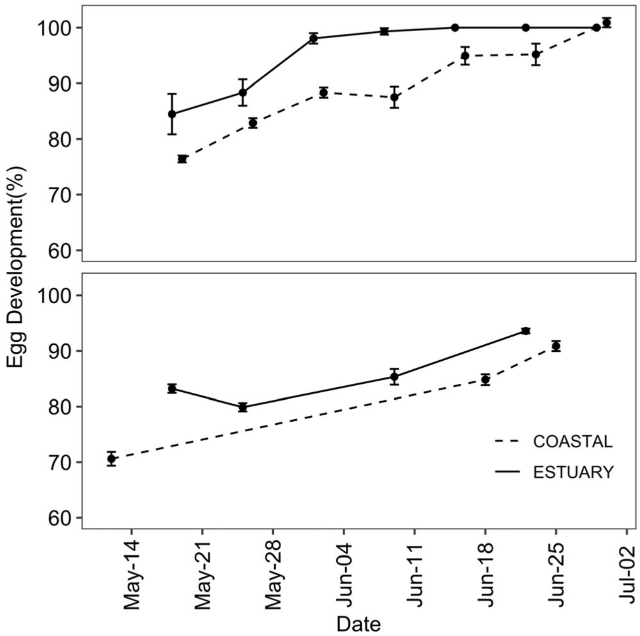

Fig. 4 Rate of development of estuarine and coastal eggs. **Top**: the development of eggs carried by lobsters that were held in either the Jackson Estuarine Laboratory ($n = 6$) or Coastal Marine Laboratory ($n = 4$) and exposed to ambient water temperatures in 2015. Only data from lobsters held for the same exact time frame are shown in this figure. **Bottom:** the rate of development of eggs obtained during sea sampling trips that were carried by estuarine lobsters ($n = 64$) and coastal lobsters ($n = 39$). Error bars indicate the standard errors

which hatching was occurring in both regions was predicted to cover only a few weeks (Fig. 6).

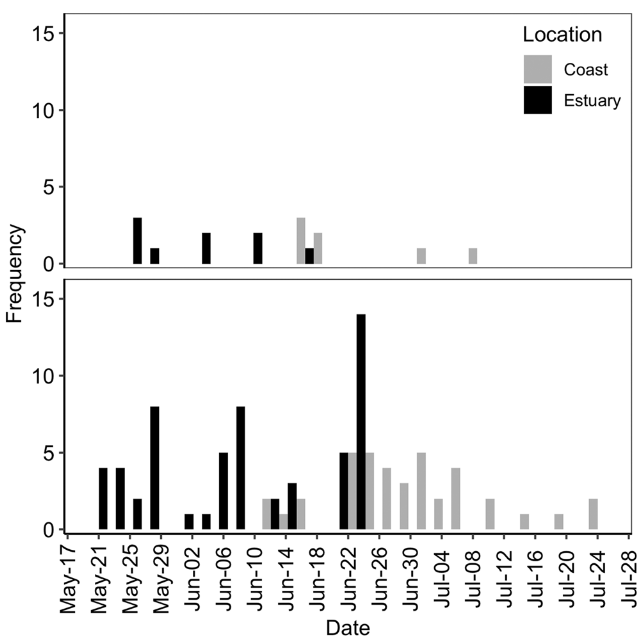

Fig. 5 A comparison of predicted and actual hatch dates for eggs carried by estuarine and coastal females. **Top:** empirical hatch dates for the eggs carried by the lobsters held in the lab-based incubation study in 2015. **Bottom:** predicted hatch dates, based upon eggs obtained from ovigerous lobsters during sea sampling

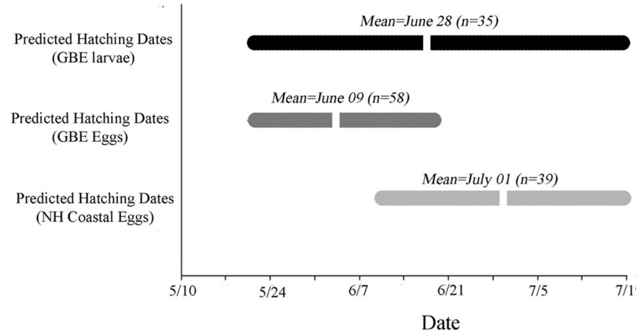

Fig. 6 The predicted hatch dates of eggs collected from ovigerous lobsters (black bars) captured during sea sampling trips in the estuary and the coast in 2015, compared with the predicted hatch dates of larvae captured in plankton tows in the estuary (light gray bar)

Lobsters Held in the Laboratory

When the PEI equation was modified to take changing water temperatures into account, it was possible to more accurately predict the hatch dates for early-stage eggs. Eggs from lobsters held in the estuary hatched a full 3 weeks earlier and hatching was completed 2 weeks earlier than coastal lobsters. Based on these calculations, the eggs carried by estuarine lobsters hatched much earlier than those at the coast (Kruskal-Wallis H-test, $P = 0.005$). The mean CL of the ovigerous lobsters captured and held at the coast (87.4 ± 12.47 mm CL, $n = 6$) was similar to the size of those captured and held in the estuary (83.2 ± 3.73 mm CL, $n = 4$; unpaired t test, $P = 0.44$) and both groups of lobsters experienced natural thermal regimes for the duration of the incubation study (Fig. 2).

Larval Studies

Plankton Tows in the Great Bay Estuary

Of the 35 larvae captured in the GBE, 66% were captured at the lower station (15 km mark, Fig. 1), and 34% were captured at the upper stations (18 km mark). Although more larvae were captured at the lower station, there was no significant difference in the density of larvae captured at either station (0.82 ± 0.36 larvae/1000m^3 and 0.29 ± 0.08 larvae/1000m^3, respectively; Kruskal-Wallis H-test, $P = 0.35$, $df = 1$) and therefore, sites were combined for further analysis. Weekly larval density ranged from 0 to 1.96 larvae /1000m^3.

Predicted Hatch Dates of Larvae Captured in the Field

All 35 larvae that were captured in the GBE were identified as stage I, ranging from recently hatched to late stage I. The predicted hatch dates for the 35 larvae captured during plankton tows ranged from May 21 through July 19, with a mean hatching date of June 28 ± 17.91 days (Fig. 6). This range encompasses nearly 2 months, which is longer than the hatch range predicted from eggs obtained either from estuarine or coastal ovigerous lobsters (1 month and 6 weeks, respectively). Importantly, larvae were captured in the estuary from the time when eggs commenced hatching in the estuary until the time hatching subsided along the coast and corroborated our egg development schedules at both locations. Therefore, it appears that the larvae captured in May most likely originated from estuarine ovigerous females, while the larvae sampled in July came from coastal ovigerous females, and those captured in June were derived from both sources (Fig. 6).

Discussion

The overall objective of the present study was to examine the reproductive dynamics of lobsters in the GBE and test the hypothesis that this estuary contains a resident and self-recruiting lobster population. Collectively, the data from our telemetry, sea sampling, egg development, and plankton tow studies all support this hypothesis. However, this work also revealed that the GBE lobster population is likely also subsidized by some coastal lobsters whose larvae are transported into the GBE during regular flood tides (see Xue et al. 2008).

Distribution of Ovigerous Females

Previous studies in the GBE indicated that lobsters undergo seasonal migrations, moving into, or further up the estuary, in the spring and towards the coast in the fall (Watson et al. 1999). Furthermore, it has been demonstrated that the GBE has a skewed sex ratio, with fewer females present in areas furthest from the coast (Howell et al. 1999; Jury and Watson 2013). Based on these data, and other studies, it has been proposed that the differential movements of male and female lobsters, due to the differences in how they respond to temperature and salinity gradients, is what gives rise to this skewed sex ratio (Jury et al. 2019). Moreover, partly due to this perspective, it has often been assumed that reproductive females are not present in the estuary when their eggs hatch because they have migrated to the coast. However, in this study, we demonstrated that the majority of the ovigerous females we captured in the GBE and tracked with acoustic telemetry overwintered in the GBE and remained there until the following spring when their eggs were confirmed to hatch. Lobsters in 2008 were released further up the estuary in Little Bay (Fig. 3), and therefore had to move further down-estuary to be in the vicinity of Goat Island, which is where the majority of ovigerous females appeared to prefer to overwinter. It should be noted that dive and video surveys of the areas where these tagged ovigerous females tended to aggregate revealed a habitat that was much more complex than found further up-estuary. In many respects, these habitats resemble coastal benthic habitats similar to those along the NH coastline that include hard-bottom areas and large macroalgal beds (Grizzle et al. 2008; Goldstein 2012) conducive for sheltering.

Egg Development and Hatching

In general, the eggs carried by lobsters in the GBE developed and hatched earlier than those carried by coastal lobsters, presumably due to their exposure to a generally warmer thermal regime. In the spring, ovigerous lobsters were also carrying late-stage eggs at a time of the year when it is unlikely that coastal lobsters had started to migrate inshore, or up into the estuary (Goldstein and Watson 2015a, b). Eggs carried by estuarine lobsters were further along in their development for the entire duration of the hatching season and, as a result, their mean hatching date was approximately 3 weeks earlier than the mean hatching date of the eggs carried by coastal lobsters. The time period during which hatching occurred was shorter for eggs carried by estuarine females compared with those exposed to coastal conditions (33 days and 42 days, respectively). In fact, two estuarine lobsters completed hatching all of their eggs on May 25 (Moore pers. obs.), well before hatching at the coast was predicted, or observed, to have started.

One of the most important environmental factors that influences egg development is temperature (Templeman 1936; Hughes and Matthiessen 1962; Perkins 1972; Sastry and Vargo 1977; Goldstein and Watson 2015b). As such, time of hatch differs regionally and eggs carried by lobsters in colder waters experience a delayed hatch (Templeman 1940; Aiken and Waddy 1986; Quinn et al. 2013). The GBE was consistently 5 °C warmer than coastal waters during most of the study (except during the winter), and water in the estuary warmed at a rate of 0.135 °C/day during the spring-to-summer, while water at the coast only warmed at a rate of 0.117 °C/day (Fig. 2). As a result, lobster eggs in the estuary hatched about 3 weeks earlier than those carried by coastal lobsters. In some lobster populations, peak hatching has been linked to peak summer temperatures, and has been predicted to reach a maximum a month after hatching starts (Harding and Trites 1988). Hatching in the GBE started when water temperatures exceeded 12 °C, but no clear peak was observed because there appears to be multiple larval inputs. This also suggests that initial hatching is dependent on the rate of temperature change, which was also the conclusion reached by Goldstein and Watson (2015a, b) when they compared the rate of development for eggs carried by coastal lobsters with those that overwintered offshore. This study found that, even though mean temperatures during egg incubation were similar, eggs carried by inshore lobsters hatched several weeks earlier than offshore eggs, most likely because the rate of warming of inshore waters in the spring was much greater. This pattern is also very evident when comparing coastal vs estuarine water temperatures in the spring (Fig. 2). Templeman (1940) also observed a difference in egg development and hatching at two adjacent areas (Grand Manan and West Northumberland Strait in Canada) that experienced disparate thermal regimes, with hatching occurring earlier and over a shorter time period in the warmer area. While the rate of change of water temperature appears to have the greatest impact, other variables may also have an influence on rate of egg development, such as lobster size. For example, larger lobsters tend to hatch their eggs earlier than smaller lobsters (Attard and Hudon 1987). However, in this study, estuarine lobsters were roughly the same size as the coastal lobsters, so maternal size effects are unlikely the cause of the differences in egg development and hatching we observed.

Lobster Larvae Distribution and Abundance

Larvae were captured in the GBE over a period of time that spanned the hatching periods of eggs carried by lobsters in the estuary and the coast. Lobster larvae were first captured in the estuary at the end of May, then consistently captured there until the end of July, and the relative abundance of larvae remained constant in June and July (data were insufficient for comparison with May). Based on data from ovigerous lobsters held in the laboratory, and the predicted time of hatching eggs carried by lobsters obtained while sea sampling, stage I larvae from estuarine lobsters would have first appeared in the water column at the end of May (see Fig. S1), and then would have been present until the middle of June. In contrast, coastal larvae should have first appeared around the middle of June through the middle of July. Previous studies reported that larvae were captured along the NH coast starting in early June and were found at densities similar to our results (Grabe et al. 1983; Normandeau 2015), while we demonstrated the presence of larvae in the estuary in May. Taken together, our egg development, hatching, and plankton tow data strongly suggest that larvae captured in the GBE at the beginning of the season originate from estuarine lobsters, and those obtained later in the season are likely coastal in origin. Moreover, because the period of hatching of coastal and estuarine eggs overlapped, the highest abundance of larvae in the GBE was during the time when there was a confluence of both sources of recruits.

Evidence of a Resident Population

Several of our findings support the hypothesis that there exists a resident, self-recruiting, lobster population in the GBE. First, the nine lobsters that we tracked with acoustic telemetry remained in the GBE throughout the winter and all lobsters were present in the spring when their eggs likely hatched. Second, each type of egg development data obtained indicated that the eggs carried by estuarine lobsters developed faster and hatched earlier than those carried by coastal lobsters. Third, early-stage lobster larvae were captured at a time of year when hatching was occurring exclusively in the estuary. Finally, at the temperatures the stage I larvae experience in the GBE, they should rapidly molt to stage II larvae in 4–6 days (Mackenzie 1988; Annis et al. 2007). Thus, the young larvae captured in the GBE most likely originated there.

It should also be noted that during the time period when this study took place, there were only moderate low salinity events resulting from spring runoffs in April, during which the salinity can drop to ~ 15 psu (see Fig. S1 as well as Fig. 1 in Jury et al. 1995; Fig. 2 in Howell et al. 1999; Fig. 1 in Watson et al. 1999; and Fig. 3 in Fulton et al. 2013), which is close to lethal levels for larvae (Charmantier et al. 2001). However, it should also be pointed out that larvae are not hatched until the middle of May through June, which is well after salinity levels typically increase to > 20 psu. Furthermore, during the time period of this study, there were no significant episodic events (e.g., hurricanes in the fall), which can also lead to dramatic drops in salinity and cause adult lobsters to move down the estuary towards the coast (Jury et al. 1995). Therefore, while the data presented provides good evidence for a resident population of lobsters in the GBE, it is likely that there is a considerable amount of variability in the number of resident lobsters in the GBE depending on the magnitude of low salinity events that are associated with the spring runoff and fall storms.

While our data clearly support the hypothesis that the GBE supports a resident, self-recruiting subpopulation of lobsters, it is also apparent that there is a considerable amount of mixing of estuarine and coastal populations. For example, larvae were captured during the time of year when estuarine lobsters were hatching as well as later in the summer when the eggs of coastal lobsters were hatching. It is possible that new recruits to the estuary come from both estuarine and coastal females and there is considerable connectivity between the two populations (Scheltema 1986; Sponaugle et al. 2002; Cowen and Sponaugle 2009). This study did not include the collection of data on the retention time or advection rate of larvae within the estuary. Additionally, no late-stage larvae were captured, although this may have had to do with the sampling depth of the plankton tows. Several stage IV (postlarvae) have been captured in previous years in GBE (Goldstein unpub data). Lastly, the relatively short and early hatching season in the GBE may provide a robust and suitable source of larvae that are able to settle faster and survive better due to early and favorable thermal conditions (Scarratt 1964; Pandian 1970; Caddy 1979; Harding et al. 1983; Quinn and Rochette 2015). Collectively, our data suggest that the GBE is a semi-closed system with several recruitment sources, including both estuarine and coastal lobsters. It should be noted that on rare years, like 2006, the combination of strong storms and melting snow and ice can cause very large drops in salinity and lobster mortalities are common. Fortunately, larval inputs that help to rebuild the estuarine lobster population come from both coastal and estuarine females, which makes this population resilient enough to recover from these rare disturbances.

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References

Aiken, D.E., and S.L. Waddy. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: A perspective. *Canadian Journal of Fisheries and Aquatic Sciences* 43 (11): 2258–2270.

Annis, E.R., L.S. Incze, N. Wolff, and R.S. Steneck. 2007. Estimates of in situ larval development time for the lobster, *Homarus americanus*. *Journal of Crustacean Biology* 27 (3): 454–462.

Attard, J., and C. Hudon. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Sciences* 44 (6): 1157–1164.

Caddy, J. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapports et Proces-verbaux des Reunions. *Conseil International pour l'Exploration de la Mer* 175: 204–216.

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 43 (11): 2197–2205.

Carloni, J.T., and W.H. Watson III. 2018. Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. *Bulletin of Marine Science* 94 (3): 555–570.

Charmantier, G., C. Haond, J. Lignot, and M. Charmantier-Daures. 2001. Ecophysiological adaptation to salinity throughout a life cycle: A review in homarid lobsters. *Journal of Experimental Biology* 204 (Pt 5): 967–977.

Cooper, R.A., and J.R. Uzmann. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. *Science* 3968: 288–290.

Cowan, D.F., W.H. Watson, A.R. Solow, and A.M. Mountcastle. 2007. Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. *Marine Biology* 150 (3): 463–470.

Cowen, R.K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1 (1): 443–466.

Crossin, G., S. Al-Ayoub, S. Jury, and W. Howell. 1998. Behavioral thermoregulation in the American lobster *Homarus americanus*. *Journal of Experimental Biology* 201: 365–374.

Dall, W. 1970. Osmoregulation in the lobster *Homarus americanus*. *Journal of the Fisheries Research Board of Canada* 27 (6): 1123–1130.

Dufort, C.G., S.H. Jury, J.M. Newcomb, D.F. O'Grady, and W.H. Watson III. 2001. Detection of salinity by the lobster, *Homarus americanus*. *Biological Bulletin* 201 (3): 424–434.

Fulton, B.A., E.A. Fairchild, and R. Warner. 2013. The green crab *Carcinus maenas* in two New Hampshire estuaries. Part 1: Spatial and temporal distribution, sex ratio, mean size and mass. *Journal of Crustacean Biology* 33 (1): 25–35.

Goldstein, J.S. 2012. The impact of seasonal movements by ovigerous American lobsters (*Homarus americanus*) on egg development and larval release. PhD Dissertation. University of New Hampshire, Durham New Hampshire.

Goldstein, J.S., and W.H. Watson. 2015a. Seasonal movements of American lobsters in southern Gulf of Maine coastal waters: Patterns, environmental triggers, and implications for larval release. *Marine Ecology Progress Series* 524: 197–211.

Goldstein, J.S., and W.H. Watson. 2015b. Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus*. *Biological Bulletin* 228 (1): 1–12.

Golet, W.J., D.A. Scopel, A.B. Cooper, and W.H. Watson III. 2006. Daily patterns of locomotion expressed by American lobsters (*Homarus americanus*) in their natural habitat. *Journal of Crustacean Biology* 26 (4): 610–620.

Grabe, S.A., J.W. Shipman and W.S. Bosworth. 1983. New Hampshire lobster larvae studies. In: Distribution and relative abundance of American lobster, *Homarus americanus*, larvae: New England investigations during 1974-70. *NOAA Technical Report NMFS SSRF-775*. Pp. 53–57.

Grizzle, R.E., M.A. Brodeur, H.A. Abeels, and J.K. Greene. 2008. Bottom habitat mapping using towed underwater videography: Subtidal oyster reefs as an example application. *Journal of Coastal Research* 241: 103–109.

Harding, G.C., and R. Trites. 1988. Dispersal of *Homarus americanus* larvae in the Gulf of Maine from Browns Bank. *Canadian Journal of Fisheries and Aquatic Sciences* 45 (3): 416–425.

Harding, G.C., K.F. Drinkwater, and P.W. Vass. 1983. Factors influencing the size of the American lobster stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: A new synthesis. *Canadian Journal of Fisheries and Aquatic Sciences* 40 (2): 168–184.

Harding, G.C., K.F. Drinkwater, C.G. Hannah, J.D. Pringle, J. Prena, J.W. Loder, S. Pearre, and W.P. Vass. 2005. Larval lobster (*Homarus americanus*) distribution and drift in the vicinity of the Gulf of Maine offshore banks and their probable origins. *Fisheries Oceanography* 14 (2): 112–137.

Helluy, S.M., and B.S. Beltz. 1991. Embryonic development of the American lobster (*Homarus americanus*): Quantitative staging and characterization of an embryonic molt cycle. *Biological Bulletin* 180 (3): 355–371.

Howell, W.H., W.H. Watson, and S.H. Jury. 1999. Skewed sex ratio in an estuarine lobster (*Homarus americanus*) population. *Journal of Shellfish Research* 18: 193–201.

Hughes, J.T., and G.C. Matthiessen. 1962. Observations on the biology of the American lobster, *Homarus americanus*. *Limnology and Oceanography* 7 (3): 414–421.

Jarvis, C. 1989. Movement patterns of late-stage ovigerous female lobsters (*Homarus americanus* Milne-Edwards) at Jeddore, Nova Scotia. M.S. Thesis. Dalhousie University, Halifax, Nova Scotia, Canada.

Jury, S.H., and W.H. Watson III. 2000. Thermosensitivity of the American lobster, *Homarus americanus*. *The Biological Bulletin* 199 (3): 257–264.

Jury, S.H., and W.H. Watson III. 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Canadian Journal of Fisheries and Aquatic Sciences* 70 (11): 1650–1665.

Jury, S.H., M. Kinnison, H. Howell, and W.H. Watson. 1994a. The effects of reduced salinity on lobster (*Homarus americanus*) metabolism: Implications for estuarine populations. *Journal of Experimental Marine Biology and Ecology* 176 (2): 167–185.

Jury, S.H., M. Kinnison, H. Howell, and W.H. Watson. 1994b. The behavior of lobsters in response to reduced salinity. *Journal of Experimental Marine Biology and Ecology* 180 (1): 23–37.

Jury, S.H., W.H. Howell, and W.H. Watson. 1995. Lobster movement in response to a hurricane. *Marine Ecology Progress Series* 119: 305–310.

Jury, S.H., T.L. Pugh, H. Henninger, J.T. Carloni, and W.H. Waston. 2019. Patterns and possible causes of skewed sex ratios in American lobster (*Homarus americanus*) populations. *Invertebrate Reproduction & Development* 63 (3): 189–199.

Lawton, P., and K.L. Lavalli. 1995. Postlarval, juvenile, adolescent, and adult ecology. In *Biology of the lobster Homarus americanus*, ed. J.R. Factor, 47–81. San Diego: Academic Press.

Little, S.A., and W.H. Watson III. 2003. Size at maturity of female American lobsters from an estuarine and coastal population. *Journal of Shellfish Research* 22: 857–863.

Mackenzie, B.R. 1988. Assessment of temperature effects on interrelationships between stage durations , mortality, and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. *Journal of Experimental Marine Biology and Ecology* 116 (1): 87–98.

Moriyasu, M., W. Landsburg, E. Wade, and D.R. Maynard. 1999. The role of an estuary environment for regeneration of claws in the American lobster, *Homarus americanus* Milne Edwards. *Crustaceana* 72: 415–433.

Munro, J., and J.C. Therriault. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles- de-la-Madeleine. *Canadian Journal of Fisheries and Aquatic Sciences* 40 (7): 905–918.

Normandeau (Normandeau Associates, Inc.) 2015. Seabrook station 2014 environmental monitoring in the Hampton-Seabrook area. *A characterization of environmental conditions*. Prepared for NextEra Seabrook, LLC.

Øresland, V., and M. Ulmestrand. 2013. European lobster subpopulations from limited adult movements and larval retention. *ICES Journal of Marine Science* 70: 734–742.

Pandian, T.J. 1970. Yolk utilization and hatching time in the Canadian lobster *Homarus americanus*. *Marine Biology* 7 (3): 249–254.

Perkins, H.C. 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). *Fishery Bulletin* 70: 95–99.

Quinn, B.K., and R. Rochette. 2015. Potential effect of variation in water temperature on development time of American lobster larvae. *ICES Journal of Marine Science* 10: 79–90.

Quinn, B.K., R. Rochette, P. Ouellet, and B. Sainte-Marie. 2013. Effect of temperature on development rate of larvae from cold- water American lobster (*Homarus americanus*). *Journal of Crustacean Biology* 33 (4): 527–536.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 28 Sep 2017.

Rowe, S. 2001. Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 58 (7): 1336–1346.

Saila, S.B., and J.M. Flowers. 1968. Movements and behaviour of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. *ICES Journal of Marine Science* 31 (3): 342–351.

Sastry, A., and S. Vargo. 1977. Variations in the physiological responses of crustacean larvae to temperatures. In *Physiological responses of marine biota to pollutants*, ed. J. Vernberg, A. Calebrese, F.P. Thurberg, and W.B. Vernberg, 401–423. New York: Academic Press.

Scarratt, D.J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. *Journal of the Fisheries Research Board of Canada* 21 (4): 661–680.

Schaller, S.Y., W.H. Watson, and C.C. Chabot. 2010. Seasonal movements of American horseshoe crabs, *Limulus polyphemus*, in the Great Bay Estuary, New Hampshire (USA). *Current Zoology* 56 (5): 587–598.

Scheltema, R. 1986. On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. *Bulletin of Marine Science* 39: 290–322.

Scopel, D.A., W. Golet, and W.H. Watson III. 2009. Home range dynamics of the American lobster, *Homarus americanus*. *Marine and Freshwater Behaviour and Physiology* 42 (1): 63–80.

Short, F.T. 1992. *The ecology of the Great Bay estuary, New Hampshire and Maine: An estuarine profile and bibliography*, 222. Silver Spring: National Oceanic and Atmospheric Administration.

Short, F.T., K. Matso, H.M. Hoven, J. Whitten, D.M. Burdick, and C.A. Short. 2001. Lobster use of eelgrass habitat in the Piscataqua River on the New Hampshire/Maine Border, USA. *Estuaries* 24 (2): 277–284.

Sponaugle, S., R.K. Cowen, A. Shanks, S.G. Morgan, J.M. Leis, J. Pineda, G.W. Boehlert, M.J. Kingsford, K.C. Lindeman, C. Grimes, and J.L. Munro. 2002. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bulletin of Marine Science* 70: 341–375.

Templeman, W. 1935. Lobster tagging in the Gulf of St. Lawrence. *Journal of the Biological Board of Canada* 1 (4): 269–278.

Templeman, W. 1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster. *Journal of the Biological Board of Canada* 2 (5): 485–497.

Templeman, W. 1940. Embryonic developmental rates and egg laying of Canadian lobsters. *Journal of the Fisheries Research Board of Canada* 5: 71–83.

Thomas, M.L. 1968. Overwintering of American lobsters, *Homarus americanus*, in burrows in Bideford River, Prince Edward Island. *Journal of the Fisheries Research Board of Canada* 25 (12): 2725–2727.

Thomas, M.L., and G. White. 1969. Mass mortality of estuarine fauna at Bideford, P.E.I., associated with abnormally low salinities. *Journal of the Fisheries Research Board of Canada* 26 (3): 701–704.

Vemco. 2015. *Vemco range test software manual*. DOC-5583-02, accessed online at: https://www.vemco.com/vemco-range-test-software/. Accessed 29 Sep 2019.

Wahle, R.A. 1993. Recruitment to American lobster populations along an estuarine gradient. *Estuaries* 16 (4): 731–738.

Wahle, R.A., L. Dellinger, S. Olszewski, and P. Jekielek. 2015. American lobster nurseries of southern New England receding in the face of climate change. *ICES Journal of Marine Science* 72 (suppl_1): i69–i78.

Watson, W.H., A. Vetrovs, and W.H. Howell. 1999. Lobster movement in an estuary. *Marine Biology* 134 (1): 65–75.

Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag.

Xue, H., L. Incze, D. Xu, N. Wolff, and N. Pettigrew. 2008. Connectivity of lobster populations in the coastal Gulf of Maine. *Ecological Modelling* 210 (1-2): 193–211.