Movements of egg-bearing American lobsters *Homarus americanus* during late stage brooding and hatching

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ABSTRACT: Although the large-scale movements of ovigerous (egg-bearing) American lobsters have been well-studied, their finer scale movements before, and during, the time when their eggs hatch are poorly understood. In this study, acoustic telemetry was used to track 12 ovigerous lobsters, carrying late-stage eggs, near the Isles of Shoals in the southern Gulf of Maine. In the spring of 2016 and 2017, lobsters were captured, fitted with acoustic tags that transmitted both depth and activity data, and released within an array of receivers. Eleven of the 12 lobsters moved from relatively shallow water (12 m) to deeper water (>29 m) approximately 2 wk prior to the time when their eggs were predicted to hatch. Four of these lobsters were within the array when their eggs most likely hatched, while 8 left the array towards even deeper water (>35 m). These data, taken together with previous data from research traps, suggest that egg-bearing lobsters tend to move to deep water prior to the time when their eggs are due to hatch, which may be beneficial for the dispersal and survival of their larvae.

KEY WORDS: Lobster · Telemetry · Reproduction · Daily rhythms · Migrations · Ovigerous · Larvae

1. INTRODUCTION

In the USA, the American lobster *Homarus americanus* (H. Milne-Edwards, 1837) fishery is managed by the Atlantic States Marine Fisheries Commission (ASMFC) in cooperation with both state and federal agencies. Protection of egg-bearing lobsters (EBLs) has long been an effective management strategy (ASMFC 2006, 2009, 2015, Lebris et al. 2018), and although there has been extensive research conducted on this segment of the population (Saila & Flowers 1968, Campbell 1986, 1990, Waddy & Aiken 1995, Estrella & Morrissey 1997, Watson et al. 1999, Cowan et al. 2007, Goldstein & Watson 2015a), little is known about their overall activity and movements around the time of egg hatch. The location of EBLs during this critical period determines the release point of stage I larvae, and thus directly impacts the oceanographic conditions they may encounter for dispersal as well as where they might settle. Moreover, as climate change continues to impact the Gulf of Maine ecosystem (Mills et. al 2013, Pershing et al. 2015, Lebris et al. 2018), gaining a better understanding of EBL movements, and the environmental cues that guide them, is critical for determining how larval dynamics, connectivity, and recruitment could change under different climate scenarios.

Some brooding animals have evolved to express specific migrations or movements in order to optimize the survival of their offspring. This behavior has
been observed in amphibians and terrestrial crustaceans that routinely return to water to release their eggs or larvae (see review in Dingle 1996). Some ovigerous marine crustaceans (spiny lobsters and crabs) that maintain external egg masses and hatch pelagic larvae have also been reported to undergo similar movements, and these species appear to selectively position their progeny for transport away from deleterious environments and into areas that favor larval advection and development. For instance, Caribbean spiny lobsters *Panulirus argus* migrate to deeper water just prior to the time when their eggs hatch and then move back to their home habitats after their eggs have hatched (Bertelsen & Hornbeck 2009, Bertelsen 2013). It has been proposed that this behavior enhances the survival of phyllosomal larvae because it positions them in areas with a prevalence of food at the shelf break (Phillips & McWilliam 2009). Atlantic blue crabs *Callinectes sapidus* mate in low-salinity areas of estuaries, then move to tidal creek mouths where their eggs hatch and are transported into higher salinity areas (Tankersley et al. 1998). Fiddler crabs (*Uca minax* and *U. pugnax*) release their larvae at spring high tides to aid in the transport of zoeae into estuaries, where salinities are more appropriate for their development (Epifanio et al. 1988). Thus, it would not be surprising if egg-bearing American lobsters *H. americanus* also moved to areas that were favorable for larval dispersal and survival prior to the time when their eggs are nearing hatch.

Results from past tagging studies have demonstrated that many ovigerous lobsters exhibit seasonal depth-related migrations (Uzmann et al. 1977, Campbell 1986, Steneck 2000), and it has been hypothesized that shoalward movements in the spring serve to increase the number of degree-days for embryo development (Templeman 1940, Perkins 1972, Uzmann et al. 1977, Talbot & Helluy 1995, Goldstein & Watson 2015b). Moreover, Campbell (1990) documented aggregations of EBLs in shallow water around Grand Manan, Canada, and theorized that lobsters may aggregate in shallow water not only for the thermal properties, but also due to currents, which may aide in larval dispersal. Goldstein & Watson (2015a) reported that ovigerous American lobsters that moved offshore of the coast of New Hampshire (NH) in the fall stayed offshore through the time their eggs were presumed to hatch the following year. They suggested that survival and eventual settlement of larval lobsters may be enhanced in areas away from shore due to prevailing currents that would carry larvae parallel to the shoreline instead of towards it, thus avoiding the possibility of larval wastage (Marta-Almeida et al. 2008).

More recently, Carloni & Watson (2018) documented high densities of EBLs near the Isles of Shoals, a group of islands located off the NH coast. They found that late-stage, pre-hatch lobsters were more common in shallow water, and significantly more females in the process of hatching eggs were captured in adjacent deeper water, suggesting EBLs were moving to deeper water just before releasing larvae (i.e. eggs hatching). These findings advocate for the possibility that American lobsters undertake reproductive movements just prior to when their eggs would hatch, perhaps to position their larvae near prevailing currents that may aid in larval development and dispersal to favorable areas for settlement. The overall goal of this study was to test this hypothesis.

2. MATERIALS AND METHODS

2.1. Study site

In order to build upon a previous study by Carloni & Watson (2018), this work was conducted on the eastern side of the Isles of Shoals (IOS), NH, USA (Southern Gulf of Maine; Fig. 1). This island archipelago is located ~10 km from the NH coast, near the 50 m isobath. The bathymetry in this area changes abruptly, with depths ranging from 1 to 50 m, and the bottom is comprised of rocky reefs and a mixture of gravel, sand, and other fine sediments (Sowers et al. 2020). Currents in the area are dominated by the Gulf of Maine Coastal Current (GMCC), which flows in a southwesterly direction, is centered on the 100 m isobath, and extends to within ~10 km of shore (Churchill et al. 2005).

2.2. Acoustic tagging

Egg-bearing American lobsters *Homarus americanus* were caught using standard lobster traps fished at a depth of 12 m, fitted with acoustic transmitters, and released in the same location. The transmitters used in this study were Vemco V13AP coded tags (69 kHz, 147–153 dB, 13 mm diameter, 36 mm long, 6 g in water; VEMCO AMIRIX Systems), which recorded and transmitted both pressure (depth in m) and acceleration (activity, m s⁻²) data. Pressure data were transmitted every 60–180 s
on an irregular schedule, while accelerometer data were transmitted as a digital value that represented an average level of activity over a sampling period, in units of m s⁻² (calculated as \(\sqrt{X^2 + Y^2 + Z^2}\)). Immediately after the V13AP tag transmitted a depth value, it would start sampling raw acceleration data from each of the XYZ axes at 10 Hz for a period of 27 s, and then transmit an average level of activity approximately every 90 s. Ultrasonic tags were secured to the lobsters as described in Goldstein & Watson (2015a), using a dorsally mounted harness on each lobster; special care was given to the placement of each tag so that it was in a consistent location and orientation. Small disk tags were also attached to each lobster with instructions for fishermen if they captured one of the subjects. The entire tagging process took 3–5 min; lobsters were then placed in a cage that was designed so they could easily escape and lowered to the sea floor at the original location of capture (~14 m deep).

2.3. Receiver array design

A total of 5 omni-directional VR2W (VEMCO, AMIRIX System) acoustic receivers were deployed at depths ranging from 10 to 35 m, spaced approximately 400 m apart in a polygon shape (based on coordinates from Google Earth). Receivers were moored to the bottom via lobster traps weighted with lead bricks, and each receiver was connected to the mooring line 3 m above the trap. A small float was attached to the VR2W to keep it upright in the water column at all times to maximize logging efficiency. Receivers recorded tag number, depth (m), mean acceleration (m s⁻²), date, and time to the nearest 1 s.

2.4. Egg staging

Prior to releasing each EBL, its egg clutches were inspected, and eggs were staged based upon a modified version of the system used by Helluy & Beltz (1991; https://www.youtube.com/watch?v=cJogiaAoFcg). In addition, approximately 20–25 eggs were gently removed from each female’s clutch and placed in 2 ml labeled sampling tubes containing a 4% formalin-seawater fixative for later determination of a more precise egg stage based on the Perkins Egg Index (Perkins 1972). Staging eggs made it possible to estimate, given their stage and water temperature, when the eggs carried by each female would hatch (Goldstein & Watson 2015b).

2.5. Environmental data

Bottom temperature and light were monitored with HOBO data loggers (Model #UA-002-64; Onset Computer Corp) during both years of the study; the loggers were secured in both shallow (14 m) and deep areas (37 m). Additionally, daily mean wave height was downloaded from NERA-
COOS buoy BO1 (http://www.neracoos.org/datatools/realtime/all_data) on the Western Maine Shelf to identify potential storm events that could possibly promote movement of lobsters to deep water. A series of Student’s t-tests were used to compare distributions of both temperature (°C) and light intensity (lumen m−2) between shallow water (14 m) and deep water (37 m).

2.6. Data processing

2.6.1. Activity and depth

Accelerometers were used to determine daily lobster movements by calculating mean daily activity (m s−2) for each lobster; we then used the equation from the regression in Jury et al. (2018) to estimate mean daily distance moved (km). To compare activity levels between day and night, accelerometer readings were averaged for each hour (0:00–23:00 h); we then ran a non-parametric Wilcoxon’s test for significance (α = 0.05) between mean hourly accelerometer activity levels during hours of light and hours of darkness. The number of hours of light and dark were based on sunrise and sunset times (https://www.weather.gov/mrx/sr_ss). We used Wilcoxon’s test as data did not satisfy the normality assumption based upon a Shapiro-Wilk test. Additionally, we used the HOBO light logger (lumen m−2) to provide an index of light intensity, expressed as an hourly mean during the time lobsters were being monitored.

2.6.2. Lobster positions

Average hourly positions were calculated for each lobster based upon an algorithm that was similar to the one developed by Simpfendorfer et al. (2002). These estimated positions were determined based on the probability that a single omni-directional receiver will log a transmitter given the distance between the transmitter and the receiver, using the equation below. Note that this estimation was conducted for each receiver with detections for a specific lobster. The example below only illustrates a computation for 2 different receivers.

\[
\text{Weighted average position} = \frac{\text{Long. (receiver } A \text{) } \times \# \text{ of detections of } ID}{\text{Total detections for all receivers of } ID} + \frac{\text{Lat. (receiver } B \text{) } \times \# \text{ of detections of } ID}{\text{Total detections for all receivers of } ID}
\]

2.6.3. Assumptions

This method assumes that (1) all receivers detect transmitters equally well, even though receivers might experience different conditions which can impact receiver performance; (2) transmitter collisions can bias data, and this is a concern if there are a large number of tags present around one receiver for a given period of time; and (3) all transmitters have a clear line of sight to receivers, so any transmitter being shadowed will result in a bias.

We used this method to estimate the general direction that lobsters were moving as they left the array and to estimate the approximate area where lobsters were located when their eggs probably hatched. The locations were confirmed using the depth data obtained at the same time. The average depth for each lobster during each day was also calculated and plotted to determine if lobsters changed depth before, during, or after their eggs hatched. All error estimates are described as standard error of the mean (SE).

3. RESULTS

3.1. Daily patterns of activity

Acoustic tags were affixed to EBLs in June 2016 (n = 7) and June 2017 (n = 5). The lobsters ranged in size from 78 to 126 mm in carapace length (CL), with a mean of 96.2 ± 5.0 mm (Table 1). Lobsters were detected within the array for an average of 49.9 ± 14.5 d, with a mean of 547.3 ± 81.5 detections d−1 (Table 1). Tagged lobsters moved an average of 0.39 ± 0.04 km (range: 0.17–0.66 km) each day. Lobsters were significantly (p < 0.05) less active during daylight hours compared to night (Fig. 2), and all were most active just after sunset, between 21:00 and 23:00 h (Fig. 2).

3.2. Depth related movements

Of the 12 lobsters, 11 moved to deeper water (>29 m) prior to the time we estimated their eggs
would hatch (Fig. 3, Table 1). The single individual that did not follow this pattern stayed in shallow water at a depth of ~15 m. Two basic patterns emerged for lobsters that moved to deeper water prior to their eggs hatching: (1) Eight (73%) lobsters stayed in shallow water for a period of time after they were released, and then moved to deep water prior to the time of estimated egg hatch (Fig. 3A); (2) Three lobsters (27%) moved to deeper water less than 24 h after they were tagged, then moved back to shallow water before eventually moving deep again prior to the estimated time of hatch (Fig. 3B).

All lobsters initiated deep water movements at night, between 21:00 and 01:00 h, and a majority of them (82%) started their migrations just after sunset.

| Lobster ID | Carapace length (mm) | No. of days in the array | Mean detections d⁻¹ | Date tagged | Date of estimated hatch | Date initiated deep water movement | Depth at estimated hatch (bold) or left array | Direction of movement out of array |
|------------|----------------------|--------------------------|----------------------|-------------|------------------------|----------------------------------|-----------------------------------------------|----------------------------------|
| 2823       | 78                   | 18                       | 757                  | 6/17/2016   | 7/14/2016              | 6/30/2016                       | 38 Southwest                         | Did not leave                      |
| 2825       | 82                   | 131                      | 632                  | 6/17/2016   | 6/30/2016              | 6/17/2016                       | 29 Did not leave                     | Southwest                         |
| 2827       | 80                   | 131                      | 863                  | 6/17/2016   | 7/31/2016              | 6/23/2016                       | 12 Did not leave                     | Did not leave                      |
| 2829       | 88                   | 131                      | 827                  | 6/17/2016   | 6/26/2016              | 6/23/2016                       | 29 Did not leave                     | Northeast                         |
| 2831       | 79                   | 16                       | 592                  | 6/17/2016   | 7/7/2016               | 6/30/2016                       | 37 East                              | Did not leave                      |
| 2833       | 98                   | 16                       | 123                  | 6/17/2016   | 7/13/2016              | 6/28/2016                       | 38 Northeast                         | Did not leave                      |
| 2835       | 80                   | 30                       | 127                  | 6/17/2016   | 8/10/2016              | 7/16/2016                       | 38 Southwest                         | South                            |
| 329        | 126                  | 6                        | 327                  | 6/16/2017   | 7/4/2017               | 6/20/2017                       | 31 South                              | Did not leave                      |
| 831        | 117                  | 14                       | 840                  | 6/16/2017   | 6/21/2017              | 6/17/2017                       | 31 Southwest                         | Did not leave                      |
| 833        | 116                  | 46                       | 643                  | 6/16/2017   | 8/4/2017               | 7/30/2017                       | 37 Southwest                         | Southwest                         |
| 835        | 109                  | 45                       | 180                  | 6/16/2017   | 8/19/2017              | 7/29/2017                       | 38 Northeast                         | Did not leave                      |
| 837        | 101                  | 14                       | 656                  | 6/16/2017   | 7/9/2017               | 6/24/2017                       | 38 Northeast                         | Did not leave                      |

Table 1. Information for individual lobsters, providing summary of detections as well as specific information for movement to deep water and direction of travel out of the array. Dates are given as mm/dd/yyyy

Fig. 2. Nocturnal pattern of activity expressed by one ovigerous female American lobster from 6/17/2016–7/4/2016. This same daily pattern of activity held true for all 12 tagged lobsters. Red line: light levels (lumen m⁻²) at 14 m. Acceleration values below 0.2 m s⁻² during the day are indicative of very low levels of activity, such as grooming or movement within a shelter, as established by Jury et al. (2018)
between 21:00 and 22:00 h (Fig. 4). Lobsters displayed a mean descent of 17 ± 1.7 m during deep water movements, which took between 1 and 11 d. Lobsters with eggs estimated to hatch within 3 wk of tagging (n = 5) moved to deep water earlier than those with eggs estimated to hatch later in the season (>3 wk; n = 6).

### 3.3. Hatching locations

Eight lobsters (67%) moved to deep water and then continued towards even deeper water before eventually leaving the array before the time when their eggs were estimated to hatch, as confirmed by our egg-staging data (Fig. 5). These lobsters initiated the transition to deep water 15.5 ± 2.5 d before the estimated time of hatching, and left the array in a variety of directions 12.0 ± 2.3 d before hatch (Table 1). Three lobsters (25%) stayed within the array at depths of 30–40 m for an average of 4.3 ± 2.3 d, which encompassed the time we estimated their eggs would hatch. Lobsters whose eggs likely hatched within the array continued to exhibit nocturnal activity patterns. These animals initiated their movements to deeper water 7 ± 4.0 d before the estimated time of hatch (Fig. 6, Table 1).

### 3.4. Environmental data

Both temperature and light levels varied by depth during the egg-brooding and hatching period. There was a significant difference in both water temperature and light intensity between 14 and 37 m (unpaired t-test, p < 0.05). The mean temperature at 14 m was 11.4 ± 0.16°C, while at 37 m it was 7.7 ± 0.12°C. The light intensity in shallow water was 175.5 ± 17.2 lumen m⁻², while in deep water it was only 1.40 ± 0.22 lumen m⁻². Finally, wave height varied between 0.28 and 1.17 m during the 2016 season and between 0.31 and 1.95 during the 2017 season.

### 4. DISCUSSION

The ability to monitor the depth, activity, and movement patterns of EBLs during their late-stage brooding and hatching period has provided new insight into the behavior of this important life stage of the American lobster *Homarus americanus*. In a previous trap-based study (Carloni & Watson 2018), we found that lobsters with late-stage, pre-hatch eggs were more abundant in the shallow waters, but those with eggs in the process of hatching were more abundant in deeper water (>30 m). This held true for areas around the IOS as well as the broader coastal
This observation led us to hypothesize that ovigerous lobsters move to deeper water just prior to the time when their eggs would hatch. The acoustic telemetry data obtained in this study further supports this hypothesis, with 92% of the tagged lobsters moving to deep water prior to the time their eggs were estimated to hatch.

Our results, in concert with previous work (Goldstein & Watson 2015a, Carloni & Watson 2018), provide strong evidence that American lobsters tend to hatch their eggs in deep water throughout this region. These deep offshore areas are significantly colder and darker, and the predominant coastal current is stronger (Churchill et al. 2005). While they can sense all 3 variables (Factor 1995, Jury & Watson 2000), at the present time it is not clear what specific cues lobsters might use to guide their movements. Moreover, it is not obvious why these locations are ideal for larval release. Lab-based studies provide evidence that low light levels and temperatures similar to those observed in deep water around the IOS would not hinder survival rates of newly hatched larvae (Templeman 1936, MacKenzie 1988), but they also would not aid in development. Thus, it seems most likely that these offshore areas provide a favorable location for larval dispersal and development due to the predominant coastal current in this region.

The GMCC is centered along the 100 m isobath and extends to within 10 km of the coast (Churchill et al. 2005). It has been reported that this current may influence the transport of larvae. Larvae from eggs that hatched inside the shoreward edge displayed different trajectories than those hatched within the GMCC (Incze & Naimie 2000, Incze et al. 2010, Goldstein 2012). It may be beneficial for larvae to develop within this current for 2 reasons. First, there is a very consistent flow that would transport larvae parallel to, rather than towards, the coast (Incze & Naimie 2000, Goldstein & Watson 2015a). Secondly, there is a higher abundance of *Calanus finmarchicus* (Runge et al. 2012), a potentially important, nutrient-rich food source for larval lobster development (Carloni et al. 2018). Interestingly, a majority of postlarvae settle near the coast in warmer shallow waters (Wahle et al. 2013), which begs the question as to the possible mechanisms at play for onshore transport of postlarvae to inshore shallow water nursery habitat, from areas farther offshore where hatching is predominantly occurring.

In Southern New England, Katz et al. (1994) found a higher abundance of earlier stage larvae in offshore areas (up to 150 km offshore), but more mature larvae closer to shore, suggesting that the larvae originating from eggs that hatched offshore recruit to inshore, shallow waters. An empirical trajectory
model showed that passive drift of these larvae alone was not sufficient for these offshore populations to recruit inshore. However, when incorporating the swimming speed of postlarvae, transport and recruitment to inshore coastal waters was plausible. Thus, it is possible that in the Gulf of Maine, eggs hatched farther offshore could recruit to inshore coastal nursery habitats.

Reproductive movements of marine decapods (primarily crabs and lobsters) to and from varying depths prior to hatch is a well-documented pattern (reviewed in Bauer 2018), but this behavior has not been well documented in clawed lobsters. Perhaps the closest parallel to the behaviors documented in our study are those of the Caribbean spiny lobster *Panulirus argus*, where acoustic telemetry has been instrumental in gaining a better understanding of the movements of reproductive females (Bertelsen & Hornbeck 2009, Bertelsen 2013). Prior to these acoustic tagging efforts, it was widely reported that egg-bearing spiny lobsters migrated to offshore areas at the beginning of the reproductive season and then back in the fall (Allsopp 1968, Peacock 1974, Olsen et al. 1975, Canciruk & Herrnkind 1976, Davis 1977). However, Bertelsen & Hornbeck (2009) and Bertelsen (2013) provided evidence that reproductive lobsters migrate to deep water when their eggs are about to hatch and then back to home habitats after hatching, a trip that takes 3–7 d. They also found that animals began migrations between 23:00 and 01:00 h and moved in a southerly direction toward deeper water. We found similar behaviors in our study; animals initiated movement at night between 21:00 and 01:00 h and moved towards deep water, and in many cases left the array towards even deeper water just prior to egg hatch.

It is hypothesized that metamorphosis to the puerulus (postlarva) stage in *Panulirus cygnus* and other species of spiny lobster will not occur until some critical level of stored energy reserve is reached. The richest waters for zooplankton are usually farther offshore near the shelf-break, which is likely a critical area for successful metamorphosis for many species of spiny lobster (Phillips & McWilliam 2009). Therefore, the reproductive offshore migrations of female spiny lobsters likely aid in making sure the phyllosomes originating from their eggs are near favorable currents for dispersal and areas of higher food production. Though the life history of the American lobster is distinct from these species, the similar behaviors expressed by ovigerous females suggest that they might have evolved to serve a similar purpose. Additional research on the cues that guide and modulate the movements of American lobsters, and a more detailed understanding of the spatial distribution of larvae and their potential

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**Fig. 5.** General path and depth profile for a lobster (ID = 2823) that moved to deep water and the left the acoustic array towards even deeper water before the estimated time of egg hatch.
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Fitting lobsters with accelerometers made it possible to determine both the location of the ovigerous lobsters in this study and when they were most active. While it has been demonstrated that American lobsters *H. americanus* are generally nocturnal (Cobb 1969, Ennis 1984, Jury et al. 2005), the only rigorous study of the daily rhythms of lobsters in their natural habitat was carried out by Golet et al. (2006). To our knowledge the daily activity patterns of egg-bearing American lobsters *in situ* have not been documented, until the present. All lobsters in our study displayed clear nocturnal behavioral patterns, even when they were in deeper, darker waters, including during the time when their eggs were predicted to hatch. Furthermore, when we used the algorithm developed by Jury et al. (2018) to convert accelerometer data to distance traveled, the results obtained were consistent with previous studies in the laboratory and in the field, with lobsters moving between 200 and 400 m in a day, and being most active just after sunset.

In summary, a large majority (92%) of late-stage EBLs tagged in our study moved to deeper water prior to the time their eggs were predicted to hatch. Taken together with the results of Carloni & Watson (2018), the IOS appears to provide a favorable area for egg-bearing females to aggregate, due to the combination of warm shallow water for egg development and proximity to deep offshore water, which likely aid in dispersal and survival of larvae due to favorable currents and an abundance of food for development. The cues that lobsters are using to guide their movements to these areas are unknown; however, light, temperature, and currents likely play strong roles. Research is currently underway to better understand these cues, as well as the implications of eggs hatching offshore in deep water.

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