Vol. 661: 163–173, 2021
https://doi.org/10.3354/meps13629

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 4

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

Joshua T. Carloni[1,*], Jason S. Goldstein[2], Winsor H. Watson III[3]

[1]New Hampshire Fish and Game, Durham, NH 03824, USA
[2]Wells National Estuarine Research Reserve, Maine Coastal Ecology Center, Wells, ME 04090, USA
[3]Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, USA

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

---

*Corresponding author: joshua.carloni@wildlife.nh.gov

Publisher: Inter-Research · www.int-res.com

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

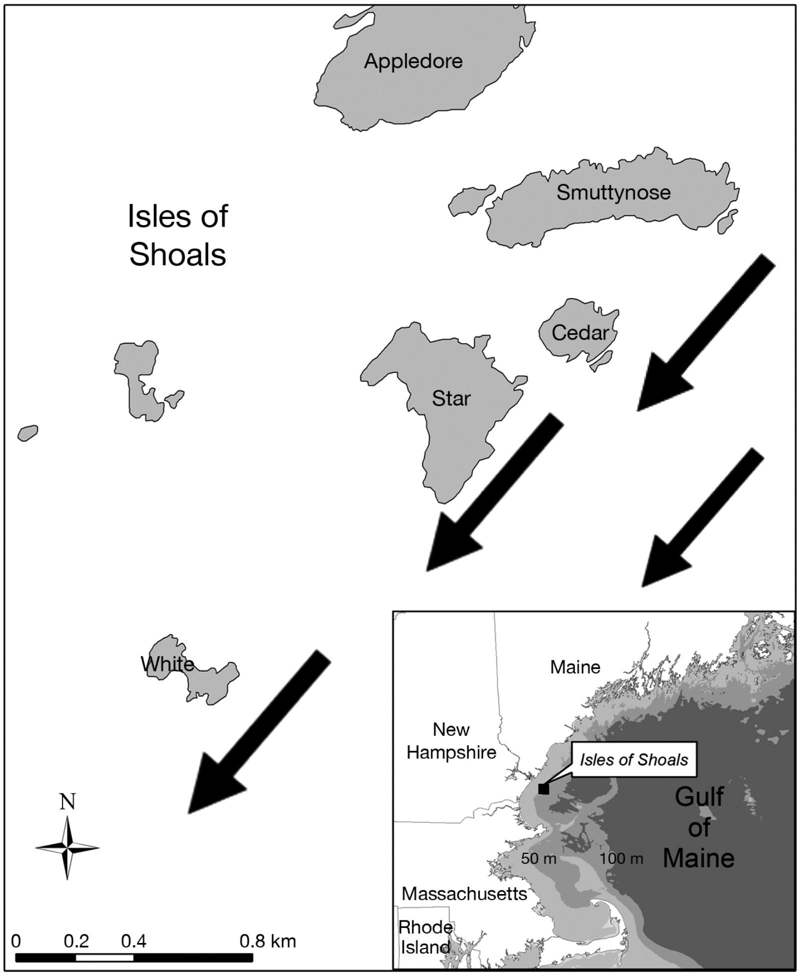


Fig. 1. Study area (Isles of Shoals), located approximately 10 km off the coast of NH (southern Gulf of Maine), USA. Arrows indicate the predominate direction of the Gulf of Maine Coastal Current in this general area

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 (httpp://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 ($\alpha = 0.05$) 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.

$$\frac{\textit{Lat.}\,(\textit{receiver } \boldsymbol{A}) \times (\textit{\# of detections of ID})}{\textit{Total detections for all receivers of ID}} + \frac{\textit{Lat.}\,(\textit{receiver } \boldsymbol{B}) \times (\textit{\# of detections of ID})}{\textit{Total Detections for all receivers of ID}} = \textit{Weighted average position}$$

$$\frac{\textit{Long.}\,(\textit{receiver } \boldsymbol{A}) \times (\textit{\# of detections of ID})}{\textit{Total detections for all receivers of ID}} + \frac{\textit{Long.}\,(\textit{receiver } \boldsymbol{B}) \times (\textit{\# of detections of ID})}{\textit{Total detections for All receivers of ID}} = \textit{Weighted average position}$$

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

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

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
2825	82	131	632	6/17/2016	6/30/2016	6/17/2016	**29**	Did not leave
2827	80	131	863	6/17/2016	7/31/2016	Stayed shallow	**12**	Did not leave
2829	88	131	827	6/17/2016	6/26/2016	6/23/2016	**29**	Did not leave
2831	79	16	592	6/17/2016	7/7/2016	6/30/2016	37	East
2833	98	16	123	6/17/2016	7/13/2016	6/28/2016	38	Northeast
2835	80	30	127	6/17/2016	8/10/2016	7/16/2016	38	Southwest
329	126	6	327	6/16/2017	7/4/2017	6/20/2017	31	South
831	117	14	840	6/16/2017	6/21/2017	6/17/2017	**31**	Southwest
833	116	46	643	6/16/2017	8/4/2017	7/30/2017	37	Southwest
835	109	45	180	6/16/2017	8/19/2017	7/29/2017	38	Northeast
837	101	14	656	6/16/2017	7/9/2017	6/24/2017	38	Northeast

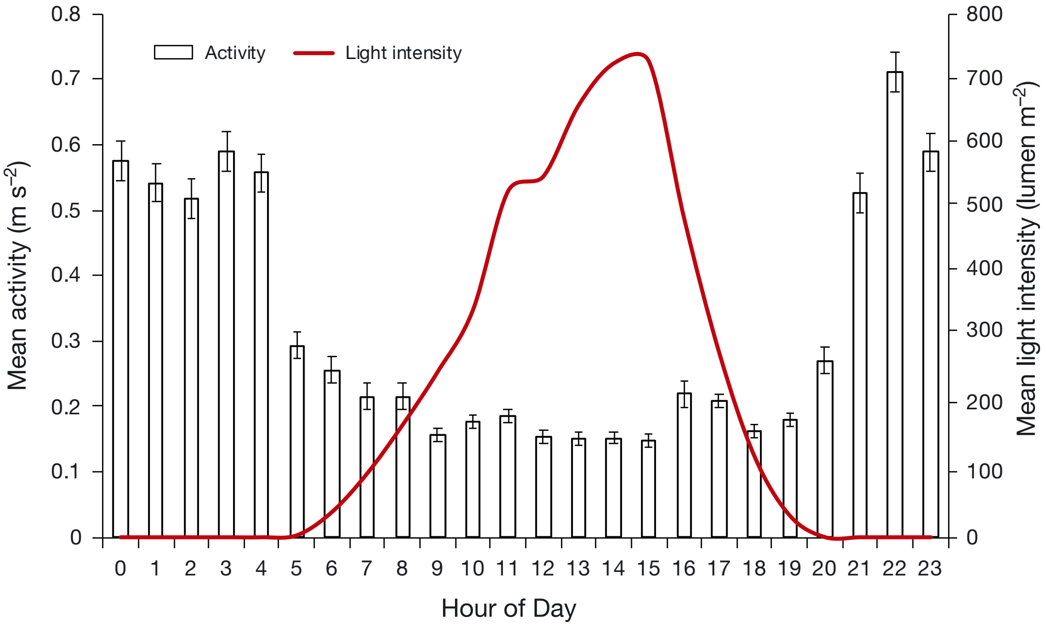


Fig. 2. Nocturnal pattern of activity expressed by one ovigerous female American lobster from 6/17/2016–7/4/2016. This same daily pattern of activity held true for all 12 tagged lobsters. Red line: light levels (lumen m^{-2}) at 14 m. Acceleration values below 0.2 m s^{-2} during the day are indicative of very low levels of activity, such as grooming or movement within a shelter, as established by Jury et al. (2018)

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,

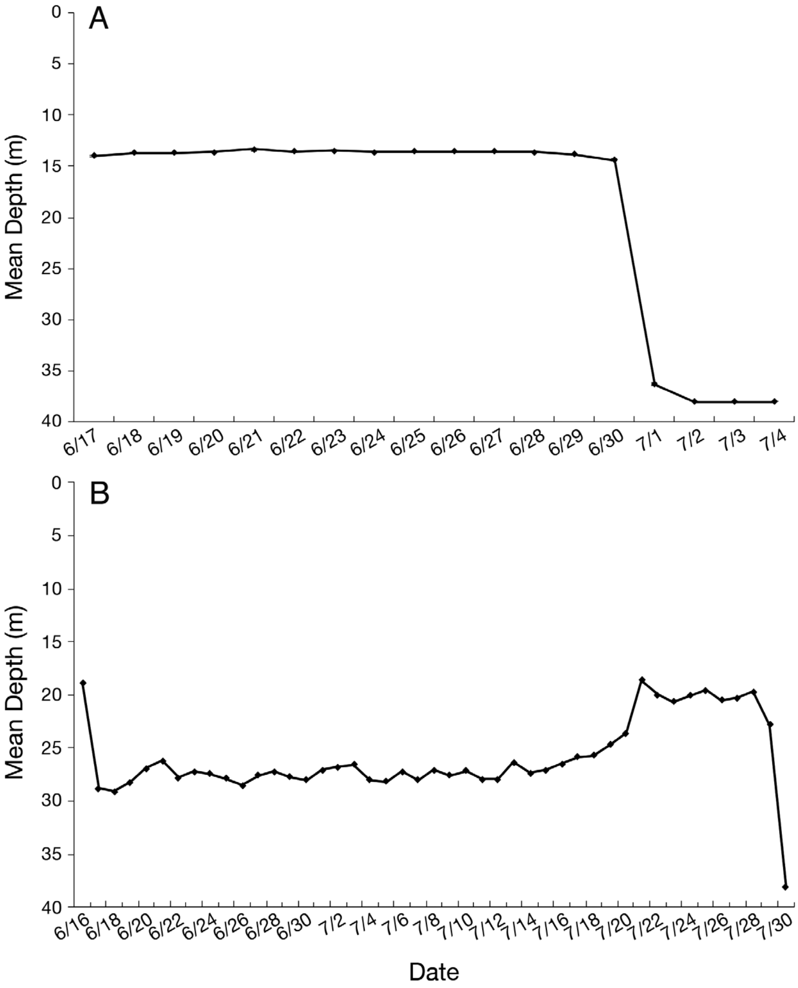


Fig. 3. Depth-related movements of 2 American lobsters prior to the time their eggs were due to hatch, exemplifying the 2 basic patterns that emerged. (A) One of the 8 lobsters that remained in shallow water for a period of time after tagging, and then moved to deeper water prior to the time of estimated egg hatch (7/14/2016). (B) One of the 3 lobsters that immediately moved to deep water after being tagged, then back to shallow water and then to deep water prior to the estimated time of egg hatch (8/19/2017). Standard error for all daily depth estimates is <0.1 m for (A) and <0.6 m for (B)

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

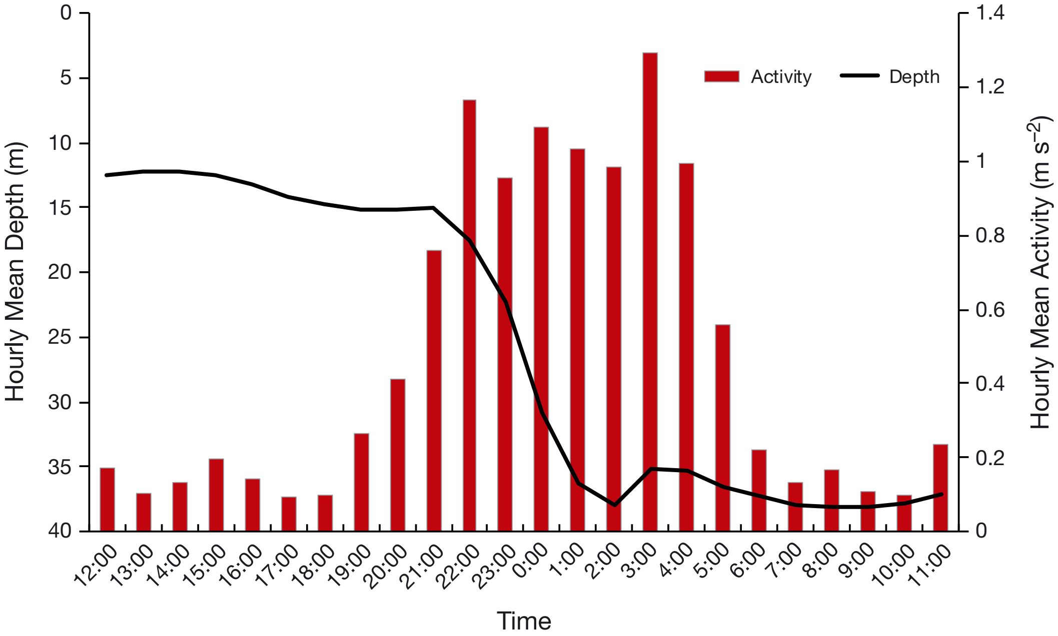


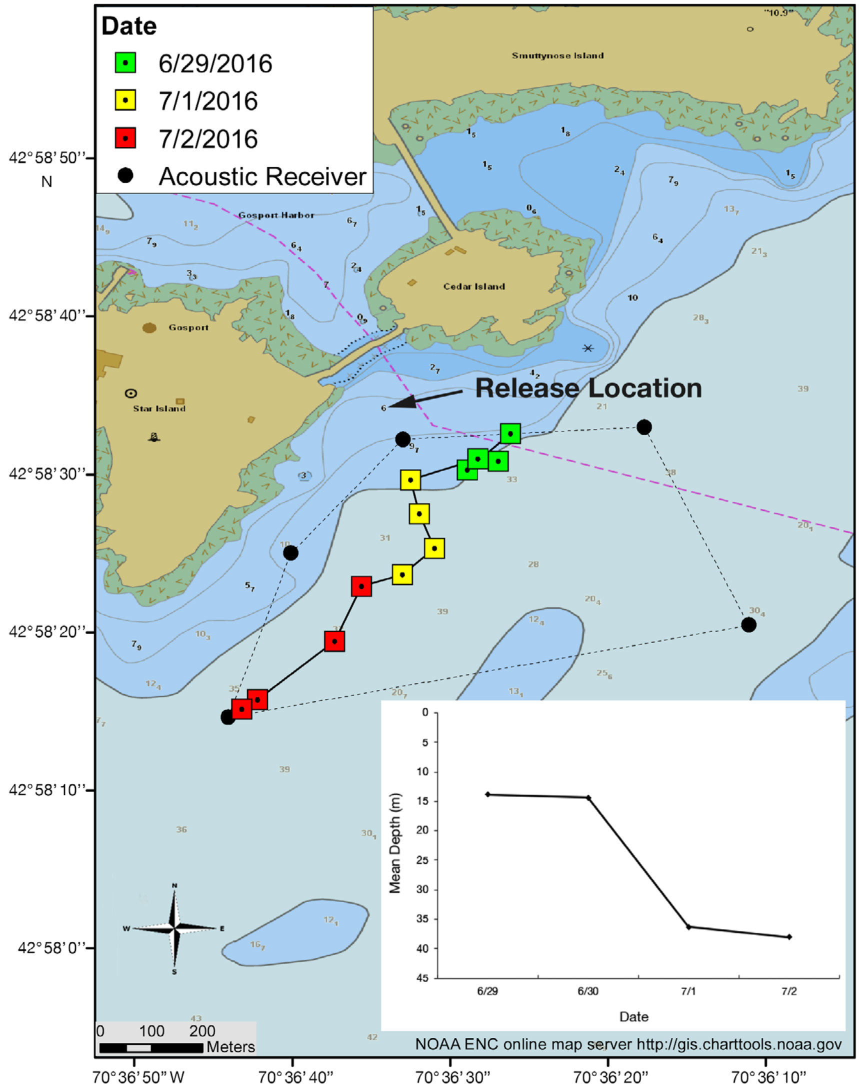
Fig. 4. Relationship between activity and movement to deep water by one egg-bearing American lobster between 6/30/2017 and 7/1/2017. Note how the individual started to become active around sunset and then initiated migration to deeper water about 3 h before midnight. It took several hours for the lobster to reach deep water; it continued to be active until sunrise

region of the NH coast. 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



NOAA ENC online map server http://gis.charttools.noaa.gov

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

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, Kanciruk & 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

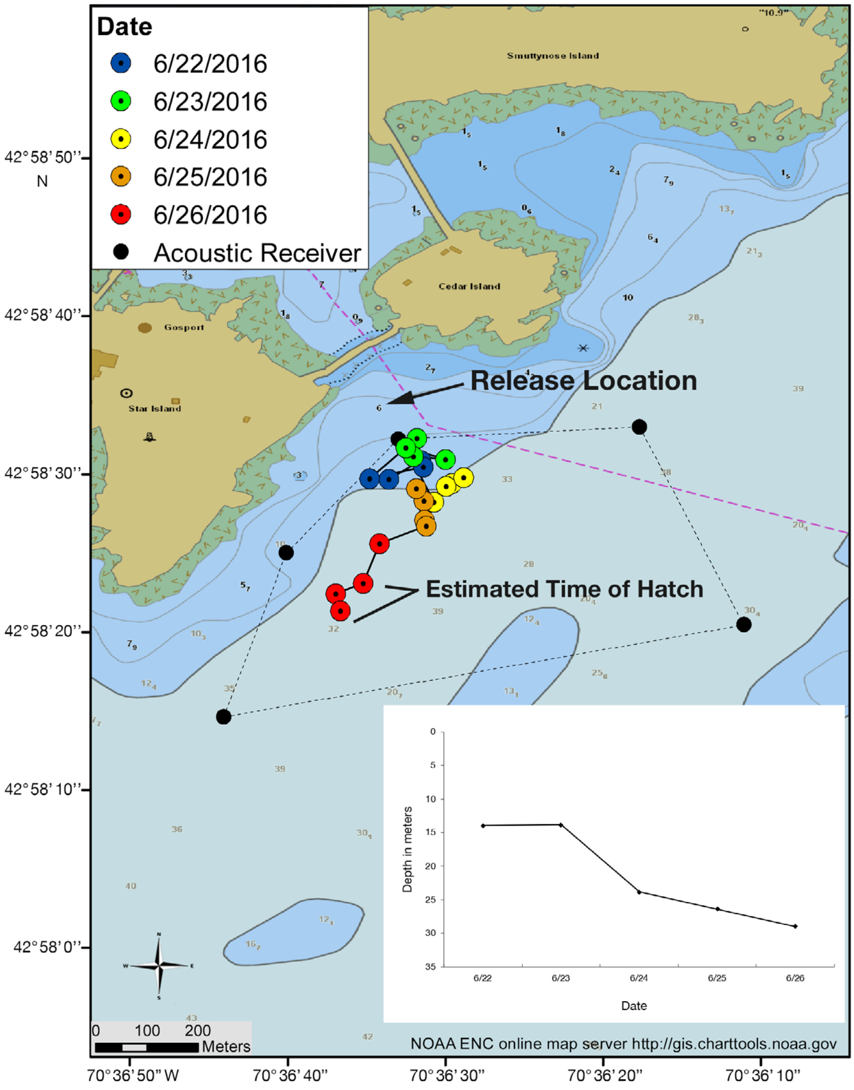


Fig. 6. Path and depth profile of a lobster (ID = 2829) that moved to deeper water and remained within the acoustic array during the time when the eggs were predicted to have hatched. All lobsters that displayed deep water movement and stayed within the array were at a depths ≥29 m when their eggs likely hatched

food sources, would greatly increase our understanding of why these directed deep-water movements might have evolved and their implications for recruitment processes.

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.

Acknowledgements. We thank Kara Villone, Megan Owings, and Joe Golter for help in the field with tagging lobsters. Additionally, Bill Hoffman provided advice for setting receivers. Special thanks to Dale Webber and Matthew Holland from Vemco for assistance with design and analysis and Catherine Callahan for her expertise with GIS plots. This research was funded by Wildlife Heritage Foundation of New Hampshire, and the University of New Hampshire's Marine Biology Graduate Program Grants.

LITERATURE CITED

Allsopp WHL (1968) Investigations into marine fishery management, research and development policy for spiny lobster fisheries. Report prepared for the government of British Honduras. FAO, Rome

ASMFC (Atlantic States Marine Fisheries Commission) (2006) American lobster stock assessment for peer review. Stock Assessment Report No. 06-03 (Supplement) of the Atlantic States Marine Fisheries Commission. ASMFC, Boston, MA

ASMFC (2009) American lobster stock assessment for peer review. Stock Assessment Report No. 09-01 (Supplement) of the Atlantic States Marine Fisheries Commission. ASMFC, Boston, MA

ASMFC (2015) American lobster stock assessment for peer review. Stock Assessment Report No. 15-01 (Supplement) of the Atlantic States Marine Fisheries Commission. ASMFC, Boston, MA

Bauer R (2018) Life cycle and seasonal migrations. In: Welbon GA, Thiel M (eds) The natural history of the Crustacea, Vol. 5: life histories. Oxford University Press, New York, NY, p 203–229

Bertelsen R (2013) Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. Fish Res 144: 91–102

Bertelsen RD, Hornbeck J (2009) Using acoustic tagging to determine adult spiny lobster (*Panulirus argus*) movement patterns in Western Sambo Ecological Reserve (Florida, United States). NZ J Mar Freshw Res 43:35–46

Campbell A (1986) Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. Mar Biol 92:393–404

Campbell A (1990) Aggregations of berried lobsters (*Homarus americanus*) in shallow waters off Grand Manan, Eastern Canada. Can J Fish Aquat Sci 47:520–523

Carloni JT, Watson WH III (2018) Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. Bull Mar Sci 94:555–570

Carloni JT, Wahle R, Geoghegan P, Bjorkstedt E (2018) Bridging the spawner–recruit disconnect: trends in American lobster recruitment linked to the pelagic food web. Bull Mar Sci 94:719–735

Churchill JH, Pettigrew NR, Signell RP (2005) Structure and variability of the Western Maine Coastal Current. Deep-Sea Res II 52:2392–2410

Cobb JS (1969) Activity, growth and shelter selection of American lobster. PhD dissertation, University of Rhode Island, Kingston, RI

Cowan DF, Watson WH III, Solow AR, Mountcastle AM (2007) Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. Mar Biol 150:463–470

Davis GE (1977) Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. Bull Mar Sci 27: 223–236

Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, New York, NY

Ennis GP (1984) Comparison of physiological and functional size–maturity relationships in two Newfoundland populations of lobsters *Homarus americanus.* Fish Bull 82: 244–249

Epifanio CE, Little KT, Rowe PM (1988) Dispersal and recruitment of fiddler crab larvae in the Delaware River estuary. Mar Ecol Prog Ser 43:181–188

Estrella BT, Morrissey TD (1997) Seasonal movement of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts. Fish Bull 95:466–476

Factor JR (1995) Biology of the lobster *Homarus americanus*. Academic Press, San Diego, CA

Goldstein JS (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, NH

Goldstein JS, Watson WH III (2015a) Seasonal movements of American lobsters in southern Gulf of Maine coastal waters: patterns, environmental triggers, and implications for larval release. Mar Ecol Prog Ser 524: 197–211

Goldstein JS, Watson WH III (2015b) Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus.* Biol Bull (Woods Hole) 228:1–12

Golet WJ, Scopel DA, Cooper AB, Watson WH III (2006) Daily patterns of locomotion expressed by American lobsters (*Homarus americanus*) in their natural habitat. J Crustac Biol 26:610–620

Helluy SM, Beltz BS (1991) Embryonic development of the American lobster (*Homarus americanus*): quantitative staging and characterization of an embryonic molt cycle. Biol Bull (Woods Hole) 180:355–371

Incze LS, Naimie CE (2000) Modeling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. Fish Oceanogr 9:99–113

Incze L, Xue H, Wolff N, Xu D and others (2010) Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. Fish Oceanogr 19:1–20

Jury SH, Watson WH III (2000) Thermosensitivity of the lobster (*Homarus americanus*), as determined by cardiac assay. Biol Bull (Woods Hole) 199:257–264

Jury SH, Chabot CC, Watson WH III (2005) Daily and circadian rhythms of locomotor activity in the American lobster, *Homarus americanus.* J Exp Mar Biol Ecol 318: 61–70

Jury SH, Langley T, Gutzler BC, Goldstein JS, Watson WH III (2018) Monitoring the behavior of freely moving lobsters with accelerometers. Bull Mar Sci 94:533–553

Kanciruk P, Herrnkind WF (1976) An indexed bibliography of spiny lobster, Family Palinuridae. Florida Sea Grant Program Report No. 8. State University System of Florida, Gainesville, FL

Katz CH, Cobb JS, Spaulding M (1994) Larval behavior, hydrodynamic transport, and potential offshore to inshore recruitment in the American lobster *Homarus americanus.* Mar Ecol Prog Ser 103:265–273

Le Bris A, Mills KE, Wahle RA, Chen Y and others (2018) Climate vulnerability and resilience in the most valuable North American fishery. Proc Natl Acad Sci USA 115: 1831–1836

MacKenzie BR (1988) Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. J Exp Mar Biol Ecol 116:87–98

Marta-Almeida M, Dubert J, Peliz A, dos Santos A, Queiroga H (2008) A modelling study of Norway lobster (*Nephrops norvegicus*) larval dispersal in southern Portugal: predictions of larval wastage and self-recruitment in the Algarve stock. Can J Fish Aquat Sci 65:2253–2268

Mills KE, Pershing AJ, Brown CJ, Chen Y and others (2013)

Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. Oceanogr Mag 26:191–195

Olsen DA, Herrinkind WF, Cooper RA (1975) Population dynamics, ecology and behavior of spiny lobster, *Panulirus argus*, of St. John, USVI: (I) introduction and general population characteristics. Sci Bull Nat Hist Mus Los Angeles County 20:11–16

Peacock NA (1974) A study of the spiny lobster fishery of Antigua and Barbuda. Proc Gulf Caribb Fish Inst 26: 117–130

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

Pershing AJ, Alexander MA, Hernandez CM, Kerr LA and others (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350:809–812

Phillips BF, McWilliam PS (2009) Spiny lobster development: Where does successful metamorphosis to puerulus occur? A review. Rev Fish Biol Fish 19:193–215

Runge JA, Jones RJ, Record NR, Pershing AJ (2012) Summer distribution of the planktonic copepod, *Calanus finmarchicus*, along the coast of Gulf of Maine. Report for the State of Maine's Department of Marine Resources, Augusta, ME

Saila SB, Flowers JM (1968) Movements and behaviour of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. ICES J Mar Sci 31: 342–351

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci 59:23–32

Sowers D, Dijkstra JA, Masetti G, Mayer LA, Mello K, Malik MA (2020) Application of the coastal and marine ecological classification standard to Gosnold Seamount, North Atlantic Ocean. In: Harris PT, Baker E (eds) Seafloor geomorphology as benthic habitat: GeoHab atlas of seafloor geomorphic features and benthic habitat, 2nd edn. Elsevier, Amsterdam, p 903–916

Steneck R (2000) Lobster tagging: How far, how deep and how fast? Report prepared for the Maine Department of Marine Resources, Augusta, ME

Talbot P, Helluy S (1995) Reproduction and embryonic development. In: Factor JR (ed) Biology of the lobster *Homarus americanus.* Academic Press, San Diego, CA, p 177–216

Tankersley RA, Wieber M, Sigala M, Kachurak K (1998) Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: evidence for selective tidal-stream transport. Biol Bull (Woods Hole) 195:168–173

Templeman W (1936) The influence of temperature, salinity, light, and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J Biol Board Can 2:485–497

Templeman W (1940) Embryonic development rates and egg laying of Canadian lobsters. J Fish Res Board Can 5a:71–83

Uzmann JR, Cooper RA, Pecci KJ (1977) Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the Southern New England continental shelf. NOAA Tech Rep NMFS-SSRF-705

Waddy SL, Aiken DE (1995) Temperature regulation of reproduction in female American lobsters (*Homarus americanus*). ICES Mar Sci Symp 199:54–60

Wahle RA, Bergeron C, Tremblay J, Wilson C and others (2013) The geography and bathymetry of American lobster benthic recruitment as measured by diver-based suction sampling and passive collectors. Mar Biol Res 9:42–58

Watson WH III, Vetrovs A, Howell WH (1999) Lobster movements in an estuary. Mar Biol 134:65–75

Editorial responsibility: Myron Peck,
Den Burg, The Netherlands
Reviewed by: E. Moland and 1 anonymous referee

Submitted: September 9, 2019
Accepted: January 5, 2021
Proofs received from author(s): March 1, 2021