



## Monitoring the behavior of freely moving lobsters with accelerometers

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**ABSTRACT.**—Accelerometers are useful devices for monitoring the activity of a variety of lobster species, both in the laboratory and the field. While the method has proven beneficial for determining when animals are active, it is more difficult to determine the actual distance animals travel or the intensity of their movements based on accelerometry. To achieve this goal, we monitored American lobsters, *Homarus americanus* H. Milne-Edwards, 1837, fitted with HOBO accelerometer dataloggers and Vemco V13AP accelerometer transmitters in the laboratory and simultaneously obtained time-lapse digital videos of their behavior. We used these data to convert accelerometer outputs to distances moved per unit time. The outputs of both types of accelerometers were well correlated with distance traveled. We then used this information to analyze data obtained in a previous study, using the same HOBO accelerometers. This made it possible to calculate to what extent activity and the distance traveled per hour changed on a seasonal basis over a year. This analysis also revealed that lobster activity in the field was significantly greater than activity in the lab at the same time of year, within similar enclosures. Overall, these results demonstrate that accelerometry is a suitable and accurate method for monitoring the relative activity of lobsters over long periods in the laboratory and field and the results compare favorably with other published studies of lobster movements.

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Lobster activity has been measured in multiple ways in the laboratory, including using shuttle boxes (Zeitlin-Hale and Sastry 1978, Reynolds and Casterlin 1979), infrared light and reed-switch gates (Jury et al. 2005), running wheels and treadmills (O'Grady et al. 2001, Jury et al. 2005), video systems (Lawton 1987, Cooke et al. 2004), and strain gauges (Koike et al. 1997). In the field, acoustic or electromagnetic tracking, telemetered tilt switches, and scuba observations have also been used to estimate the daily activity and movements of lobsters (Ennis 1984, Jernakoff 1987, Karnofsky et al. 1989, Smith et al. 1998, Golet et al. 2006, Jury and Childress 2006,

Scopel et al. 2009, Morse and Rochette 2016). More recently, the development of accelerometer dataloggers has made it possible to monitor daily patterns of activity in several lobster species including slipper [*Scyllarides latus* (Latreille, 1803): Goldstein et al. 2015], spiny [*Panulirus argus* (Latreille, 1804): Gutzler and Butler 2014, Gutzler et al. 2015], and clawed (*Homarus americanus* H. Milne-Edwards, 1837: Lyons et al. 2013) lobsters. Finally, acoustic transmitters employing accelerometers are now being used with freely moving animals to monitor habitat specific levels of activity (Gutzler et al. 2015), metabolism (Wilson et al. 2006, Lyons et al. 2013), and the expression of specific behaviors (e.g., daily or circadian rhythms, foraging behaviors, etc.) (Nathan et al. 2008, 2012, Watanabe and Takahashi 2013, Goldstein et al. 2015, Nakamura et al. 2015).

The American lobster, *H. americanus*, is a highly mobile crustacean whose movements have been investigated over a range of time scales, and distances (reviewed in Lawton and Lavalli 1995, Childress and Jury 2006, Golet et al. 2006, Scopel et al. 2009, Goldstein and Watson 2015, Morse and Rochette 2016). Seasonal movements by lobsters typically include annual inshore-to-offshore movements in the fall, and offshore-to-inshore excursions in the spring. While offshore lobsters have been shown to make long distance migrations (Cooper and Uzman 1980, Campbell and Stasko 1986, Childress and Jury 2006), lobsters inhabiting nearshore areas tend to limit their movements to much shorter distances (10s of kilometers per year, Lawton and Lavalli 1995, Goldstein and Watson 2015). Daily movements are generally shorter and primarily involve nocturnal excursions away from, and back to, their home shelters (Golet et al. 2006). These daily patterns of activity, driven in part by their circadian clocks (Jury et al. 2005), are also strongly influenced by external stimuli, such as tides and inter- and intra-specific interactions (reviewed in Lawton and Lavalli 1995, Pittman and McAlpine 2003, Childress and Jury 2006).

Multiple studies on the activity patterns and movements of *H. americanus* have been conducted in estuarine and near-coastal areas (Watson et al. 1999, Jury et al. 2005, Golet et al. 2006, Scopel et al. 2009, Jury and Watson 2013). The Great Bay estuary (New Hampshire, USA) is a well-described ecosystem where several studies of lobster movements have been carried out using methods other than accelerometry (see Table 1). Lobsters in this system are exposed to a broad range of environmental conditions, especially large seasonal fluctuations in temperature and salinity, that influence the magnitude, timing, and direction of their locomotory activity (Watson et al. 1999, Jury and Watson 2013; Fig. 1).

Lobster movements are influenced by many factors, but water temperature is one of the most prominent. American lobsters prefer water temperatures of approximately 16 °C and they behaviorally thermoregulate by avoiding water that is <5 and >20 °C (Crossin et al. 1998). As a result, during the spring and fall, when the most dramatic changes in nearshore and estuarine water temperatures occur, lobsters tend to move the greatest distances. In the spring, they generally move inshore because the water warms faster in those areas, and in the fall they move offshore because inshore waters cool faster (Watson et al. 1999, Jury and Watson 2013, Goldstein and Watson 2015). Lobsters might also move more during certain times of year because warmer water increases their metabolism (McLeese and Wilder 1958). These general patterns are likely evident in other estuarine and coastal areas, and lobsters have been shown to express a variety of different activity patterns that are based, in part, on where they are found and the prevailing environmental conditions. Recently, to further address

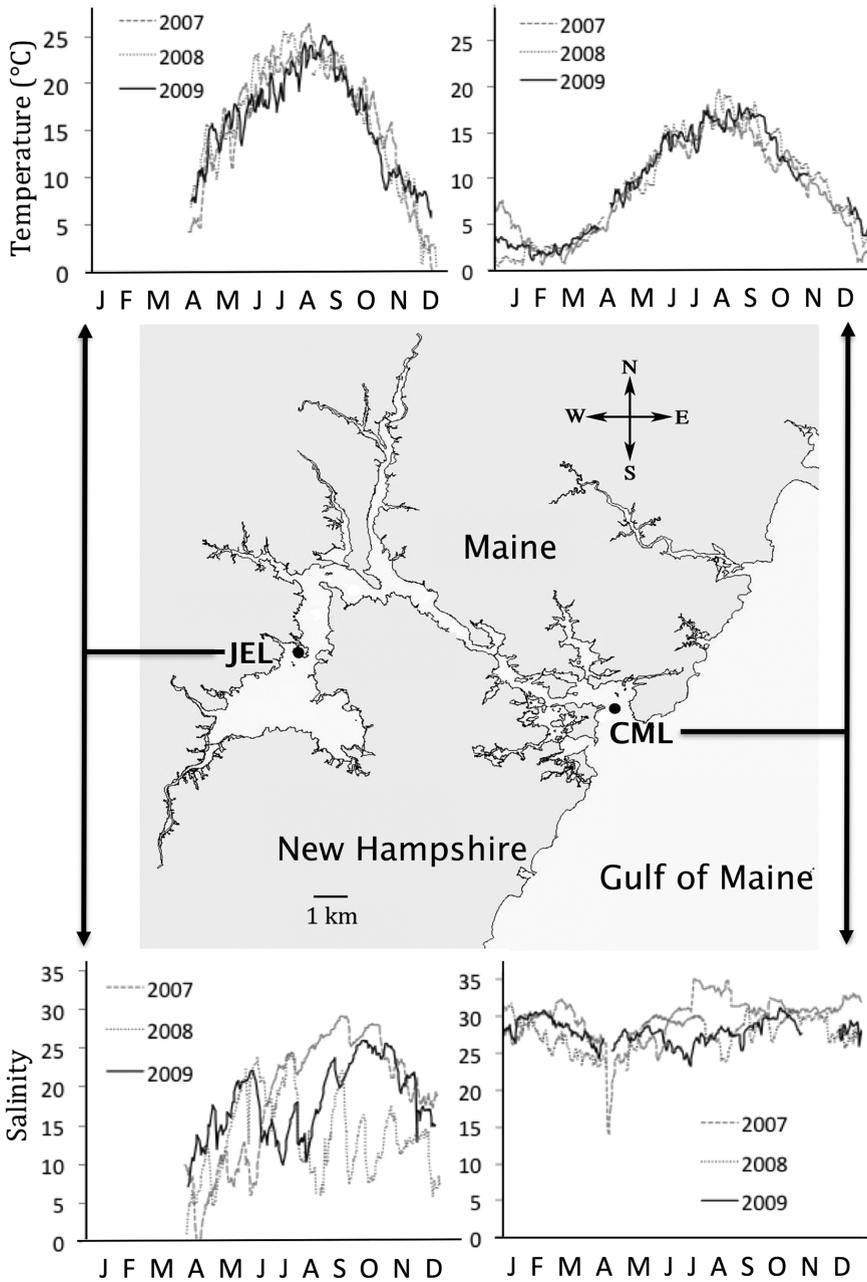


Figure 1. Annual estuarine (Jackson Estuarine Laboratory, or JEL) and coastal (Coastal Marine Laboratory, or CML) temperatures and salinities from 2007 to 2009. Temperatures were significantly higher in the summer in the estuary and above the upper limit of 20 °C that is considered stressful for *Homarus americanus*. At both the estuary and the coast, temperatures dropped below 5 °C in December–March. The salinity at the coast remained above 25 in all seasons, but in the estuary in 2008–2009, particularly wet years, the salinities were low and variable. Temperature and salinity data were obtained from Great Bay National Estuarine Research Reserve (<https://cdmo.baruch.sc.edu/get/landing.cfm>). Letters on x axis represent months, ranging from January to December (left to right).

the question of whether seasonal differences in activity were simply due to changing temperatures, or if other variables, such as day length, played important roles, we measured the activity of lobsters using accelerometers throughout the year (Langley 2017). However, while these data clearly indicated when animals were active (i.e., increased locomotion), it did not allow us to determine how active they were (i.e., distance travelled per unit time). A major goal of the present study was to determine if it is possible to convert these accelerometer data into distance traveled data, which would be useful both to interpret our previous studies and to make it possible for future studies to determine both when, and how far, lobsters moved.

While data-logging accelerometers, such as the HOBO Pendant G (Onset Computer Co., Bourne, MA), are useful for laboratory studies, most fieldwork involving accelerometers involves the use of acoustic telemetry, with acceleration data transmitted at user-defined intervals by devices such as the V13AP acoustic tag (Vemco-Amirix Co., Halifax, Canada). The transmitted data are then logged by arrays of VR2W receivers for subsequent analysis (*see* <https://vemco.com/>). The major advantage of this approach is that these animals can move freely in their natural habitat and the tags do not have to be retrieved to obtain the data. The major disadvantage is that, if animals move out of the range of a receiver, no data are logged during that time period and tags may be lost altogether. Moreover, as previously mentioned, it is challenging to translate acceleration data into distance traveled and to know if the acceleration data obtained represent actual locomotion or simply shuffling around in a shelter or on uneven substrates. Therefore, the second major objective of our study was to determine if we could calibrate acoustic accelerometer tags so that their output could be translated into distance traveled by a lobster.

Accelerometers transduce acceleration, or a change in movement, into a proportional electrical signal (e.g., mV/g). The tri-axial accelerometer dataloggers (HOBO Pendant G, Onset Computer Co.) and acoustic transmitting tags (V13AP, Vemco Co.) used in the present study measure both acceleration due to gravity (static acceleration) and acceleration from the motion of the animal in three axes (dynamic acceleration, Lyons et al. 2013). By filtering the data output from the three axes against the overall level of background output that does not equate to movement, various algorithms can be used to develop species- and behavior-specific data per unit time. For example Lyons et al. (2013) were able to correlate overall dynamic body acceleration (OBDA) with oxygen consumption in *H. americanus* to estimate metabolic rate in the lab. In previous studies with lobsters, accelerometers have been used only to determine when lobsters were active and not their relative level of activity or distance traveled (Goldstein et al. 2015). This made it possible to assess their daily patterns of activity, but it was not possible to determine if they were more active at certain times of the day, or month, than other times. In studies with *P. argus* (Gutzler and Butler 2014, Gutzler et al. 2015), a similar approach was used with acoustic accelerometer tags to demonstrate that lobsters in artificial shelters were significantly more active at night than individuals in natural shelters. The present study sought to determine both when and how far lobsters moved based on the output of accelerometers by obtaining time-lapse videos of adult lobsters fitted with accelerometer dataloggers or acoustic tags, and then using the video data to convert accelerometer outputs to distance traveled. This information was then used to calculate the distance they traveled per unit time based solely on the accelerometer data obtained from a separate study.

While several techniques, including accelerometry, have been used to study patterns of locomotory activity in large decapods, none of these have compared lab and field data concurrently and few long-term studies have been conducted over multiple seasons with the same individuals (e.g., Curtis and McGaw 2008). In the present study, we first calibrated two different accelerometers (HOBO Pendant G datalogger, Onset Computer and V13AP, Vemco, Inc.) vs actual distance traveled, as described above, and then these data were used to interpret several long-term datasets. By using this method in both the lab and the field to determine relative distances moved by *H. americanus*, we have expanded upon previous observations and experiments by showing: (1) lobsters differ in their timing and level of activity between the estuary and the coast, (2) there are significant differences in activity between lobsters monitored in the laboratory vs those in the field, and (3) distances moved by adult lobsters in this system are similar independent of the methods used.

## METHODS

**ANIMAL COLLECTION, STUDY TIMES AND LOCATIONS.**—All lobsters were obtained from commercial lobster fishers who fished in either the near coastal waters or the Great Bay estuary of New Hampshire. Only adult male and female intermolt animals were used for all studies. Laboratory video calibration trials were conducted in the summer and fall of 2016 and spring of 2017 in 1.8 m diameter recirculating seawater tanks either at Southern Maine Community College's (SMCC) marine lab in South Portland, Maine (containing temperature-controlled natural seawater from Casco Bay, Maine) or flow-through ambient seawater tanks at UNH's Coastal Marine Laboratory (CML) in Newcastle, NH. Lobsters for the HOBO calibration trials ( $n = 6$ ) had mean length of 84.0 (SD 1.8) mm CL (range: 81–87 mm CL) and lobsters for the VEMCO calibration trials ( $n = 5$ ) were larger at 95.4 (SD 9.6) mm CL (range: 90–105 mm CL), to allow for the simultaneous attachment of both a HOBO and a VEMCO tag (Fig. 2). We estimate these lobsters weighed approximately 1 kg and the combination of the V13AP tag and the HOBO tag, which was positively buoyant, added <12 g (weight of the V13AP tag in water). Therefore, these tags were approximately 1%–2% of the weight of the lobsters. This is consistent with the size recommended for fish telemetry (Baras and Lagardere 1995, Winter 1996, Jepsen et al. 2002). This is also similar to the weight of tags used in our previous telemetry studies on lobsters, where no impact of the tags on behavior was evident (Scopel et al. 2009, Watson et al. 2009, Goldstein and Watson 2015).

Lobsters used for independent analyses were taken from a data set collected from 2008 to 2009. These lobsters were fitted with HOBO accelerometers (Fig. 2A), logging at 1-min intervals, and they were held for approximately 1 yr in small mesh enclosures (45 cm diameter) either at the UNH Jackson Estuarine Laboratory (JEL) or CML (see Fig. 1). These enclosures were constructed of 1-cm<sup>2</sup> vinyl-coated hardware mesh, with a PVC shelter in the middle. In addition, black plastic sheeting was affixed to some sides of the enclosure to prevent lobsters in adjacent activity chambers from seeing each other. The HOBO Pendant G accuracy is  $\pm 0.105$  g ( $1.03$  m s<sup>-2</sup>) and resolution is 0.025g ( $0.245$  m s<sup>-2</sup>) within the temperature range tested, and the tag is 58 × 33 × 23 mm (Onset Computer, Inc.). The lobsters ( $n = 6$ ) held at JEL had a mean length of 85.5 (SD 2.8) mm CL, and those at CML ( $n = 7$ ) were 86.0 (SD 6.2) mm CL. Finally, to be able to compare the activity of animals held in the laboratory with lobsters in the

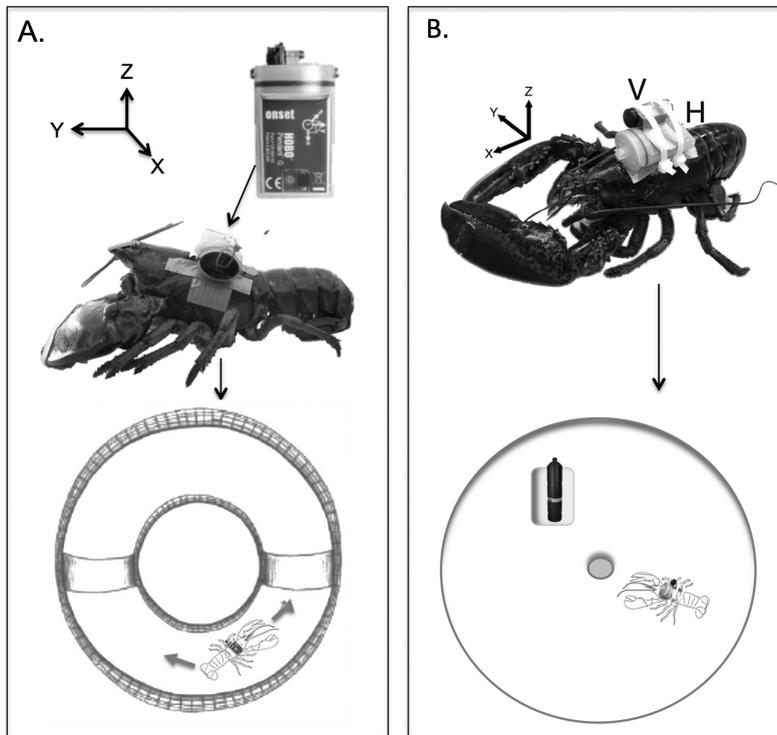


Figure 2. Accelerometer tag attachments and configurations. (A) HOBOTag Pendant G accelerometer tag attached to a lobster such that the  $y$  axis output indicates the primary direction of forward-to-backward movement. Lobsters were placed into circular racetracks (0.7 m diameter) to monitor distances moved per unit time with time-lapse video. (B) Lobster with both a HOBOTag (H) and a Vemco V13AP transmitter (V) attached such that the  $x$  axis output indicates the primary direction of forward-to-backward movement. Transmitter output was recorded by a Vemco VR2W receiver mounted on a shelter in a 2 m diameter tank and distance moved was determined using a time-lapse video system.

field, seven lobsters were held for one month in the fall of 2009 in tanks on the pier at CML, and another five lobsters were held in enclosures on the bottom at a depth of 5–6 m, within 100 m of the pier. These lobsters were 84.0 (SD 3.6) and 79.8 (SD 3.0) mm CL, respectively. All these lobsters were placed in the same 45 cm diameter enclosures described above, and the ones on the pier were placed inside a 3 m diameter flow-through holding tank that received water pumped from under the pier. Therefore, most of the conditions were similar for the two sets of animals, except those on the bottom were exposed to some additional stimuli due to currents, tides, substrate, and the presence of other organisms around them.

**RECORDING LOBSTER ACTIVITY WITH ACCELEROMETER DATALOGGERS AND TAGS.**—HOBOTag Pendant G acceleration dataloggers (Onset Computer Corp., Bourne, Massachusetts) were affixed to the dorsal carapace of each lobster using a “backpack” comprised of a cable tie loop and duct tape in an H-shaped harness (Fig. 2, see details in Goldstein et al. 2015). This arrangement allowed for periodic removal of the HOBOTag to download it and then place it back on the animal. The accelerometers detected when a lobster moved in any one of the three planes of motion ( $x$ ,  $y$ , and  $z$

axes). For all trials with only a HOBO datalogger attached (Fig. 2A), the  $y$  axis corresponded to forward and backward movements. For trials with both the HOBO datalogger and V13AP transmitter attached, the orientation of the backpack was rotated to allow for better attachment and thus the  $x$  axis corresponded to forward and backward movements, and the  $x$ ,  $y$  and  $z$  axes were the same for each tag type. Acceleration, in terms of G-forces, were recorded at 1-min intervals in tandem with the date and time. At this sampling rate, accelerometers stored up to 15 d of data and were downloaded every 2 wks using HOBOWare Pro software.

Vemco V13AP accelerometer acoustic transmitters were attached to the dorsal carapace of lobsters in a manner similar to that described above for the HOBO dataloggers (Fig. 2B). However, V13AP transmitters first process and combine the three axes of acceleration before transmitting the data using the formula: acceleration in  $\text{m s}^{-2} = \sqrt{(x^2 + y^2 + z^2)}$ . For the purpose of our study, pingers were programmed to transmit data at 1-min intervals, although often during actual experiments in the field, data were transmitted at longer intervals. Lobsters used for our study were placed individually in a 2 m diameter tank at the UNH CML, which received a constant input of ambient seawater. The tank also contained a PVC shelter and a Vemco VR2W receiver to log the outputs of the transmitter (Fig. 2B).

**CALIBRATION OF THE ACCELEROMETERS IN TERMS OF DISTANCE MOVED BY LOBSTERS.**—The goals of this portion of the study were to determine the relationship between lobster movements and accelerometer outputs, as well as to compare the data provided by both types of accelerometers. To accomplish these goals, we simultaneously recorded accelerometer outputs and time-lapse videos of lobster movements (Fig. 3). Lobsters ( $n = 6$ ) fitted with HOBO accelerometers were placed individually in a recirculating seawater tank containing a 0.7 m diameter  $\times$  25 cm wide “racetrack” (see Fig. 2) made of lobster trap wire mesh, similar to the arrangement used in Jury et al. (2005). A Brinno time-lapse video camera (<http://www.brinnousa.com>) was used to capture digital video frames at 5-s intervals for 24 hrs. Lobsters could move freely in the racetrack and distances moved were determined by multiplying the number of times they made a complete revolution of 1 m ( $1/2$  of the circumference of the racetrack). Various iterations of output from the  $x$ ,  $y$ , and  $z$  axes were then compared to the video data, and we found that the  $y$  axis of the loggers in studies with only the HOBO attached was the most representative of lobsters walking (which coincides with the forward/back direction when the device was attached in the orientation shown in Fig. 2A). This was also the case for the studies with both the HOBO and V13AP attached where the  $x$  axis of the loggers was the most representative of lobsters walking in the forward-to-backward direction (Fig. 2B). To eliminate periods when the animal was tilted to one side or the other, but not moving, we used two methods. The first method involved taking the absolute value of the difference between consecutive minutes of forward-to-backward axis data. The second method involved examining the baseline value of the forward-to-backward axis and subtracting that value, if it was more than zero, from all the data points. The modified accelerometer output was then further calibrated by using an activity threshold ( $g \geq 0.2$ ) to eliminate values that did not represent actual walking. This threshold was determined by examining the time-lapse video recordings and determining the accelerometer values obtained when lobsters moved at least one body length. These relative activity data were then summed for each hour and correlated

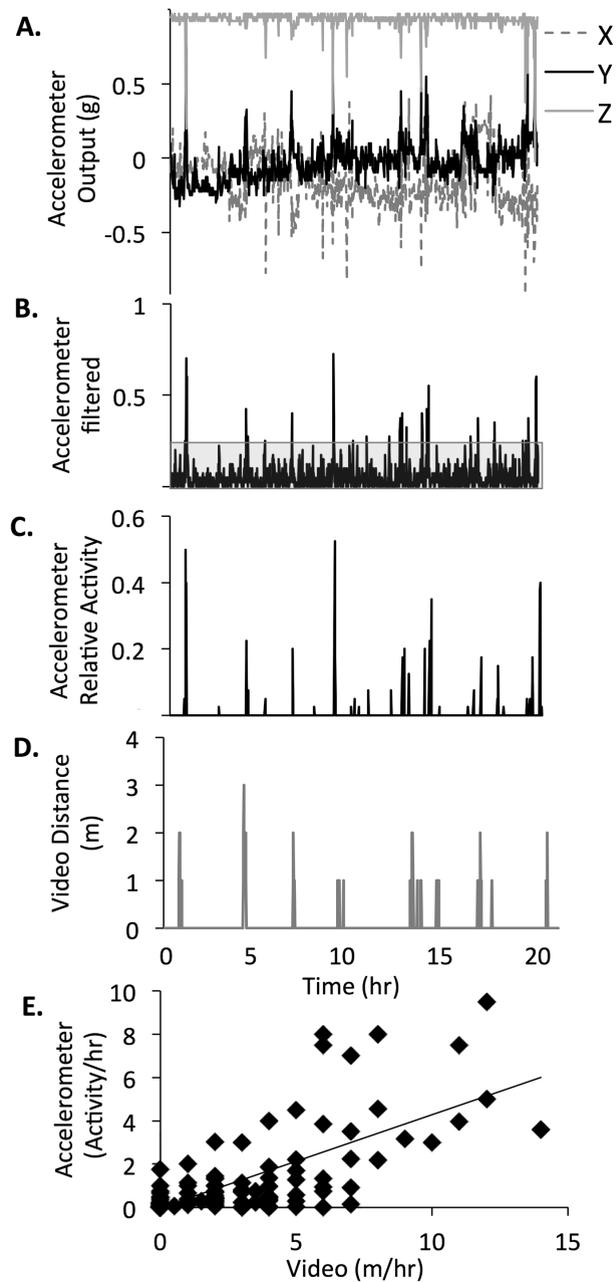


Figure 3. Calibration of HOBO accelerometer dataloggers. (A) The  $x$ ,  $y$ , and  $z$  axes output of an accelerometer for a 20-hr period, logged at 1-min intervals, for one representative lobster tagged as in Figure 2A ( $y$  axis is solid dark line). (B) The  $y$  axis data filtered, (C) the filtered  $y$  axis data in units of relative accelerometer activity output that were ultimately compared to video observations of distances moved. (D) The distances moved based on video observation for this same lobster. (E) The correlation, using this approach, for all lobsters ( $n = 6$ ) that were observed for hourly distances moved by time-lapse video and correlated to accelerometer relative activity per hour.

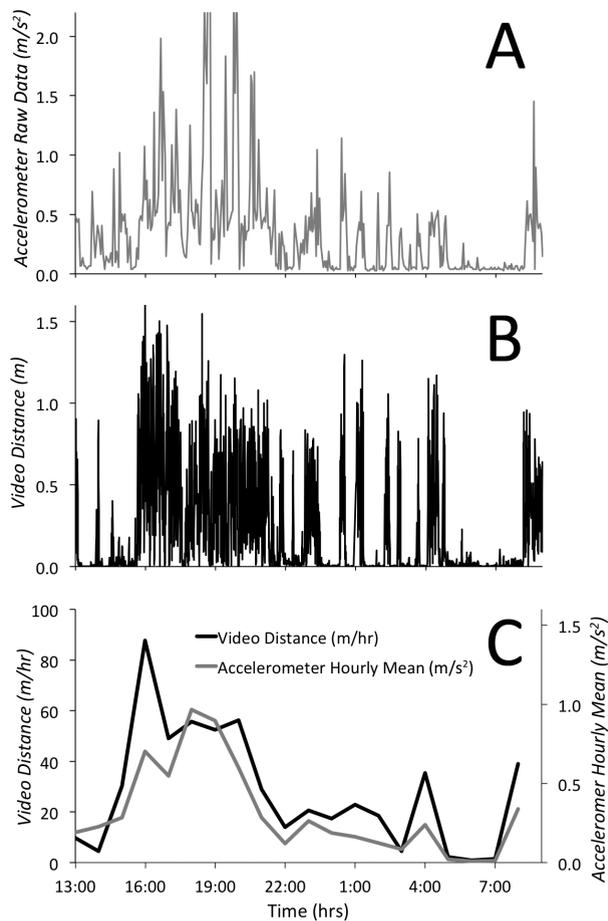


Figure 4. Representative example of VEMCO V13AP accelerometer transmitter in terms of distance moved per hour. (A) The  $x$  axis raw output of an accelerometer for a 20-hr period for one representative lobster tagged as shown in Figure 2B. (B) The distance moved by the lobster, as measured by tracking the lobster's movements with time lapse video analyzed by Ethovision. (C) Compares hourly total distance traveled (left  $y$  axis) with mean hourly accelerometer output (right  $y$  axis).

to the observed movement in the racetracks in  $\text{m hr}^{-1}$  (Fig. 3). The regression equation from this relationship was then used to convert the accelerometer output from relative activity to distance moved in  $\text{m hr}^{-1}$  in two independent data sets (*see below*). This approach is similar to the methods used with accelerometer data obtained from freely moving horseshoe crabs and outlined in Watson et al. (2016).

A similar approach was used for calibrating the V13AP transmitters (Fig. 4). However, those lobsters ( $n = 5$ ) were free to move in any direction in a large 1.8 m diameter tank and the distance they moved was determined using Ethovision software (<http://www.noldus.com>) to analyze video from the Brinno time-lapse camera. While efforts were to standardize the orientation of the transmitter on each lobster, the transmitters were not identical when mounted on each individual. Thus the value reported by the transmitter when each lobster was stationary was estimated by inspection of the data and used as a threshold. This threshold value was subtracted from each of the raw data points (rather than the differences between each point,

as with the HOBO dataloggers) to create a consistent baseline between lobsters. An hourly mean was then calculated from these data and compared with the total distance moved within each hour, as well as the hourly mean of the HOBO datalogger affixed alongside the V13AP tag. Thus, as with the lobsters with only HOBO dataloggers, we were ultimately able to compare the distance moved by freely-moving lobsters with the output of the V13AP transmitters.

**MOVEMENTS IN ESTUARINE VS COASTAL CONDITIONS.**—In the summer of 2008, lobsters with HOBO accelerometers were placed individually into circular “activity enclosures” in outdoor flow-through seawater tanks at both the UNH Jackson Estuarine Lab (JEL) ( $n = 6$ ) and the UNH Coastal Marine Lab (CML) ( $n = 6$ ), where they experienced natural light/dark conditions, as well as natural water temperatures and salinities over an entire year (Fig. 1). The activity enclosures were the same ones used to compare the activity of lobsters in the laboratory vs the field, as described above. During the winter and early spring, the lobsters at JEL were moved into an adjacent greenhouse because the flowing seawater was shut off to the outdoor tanks for those seasons. At CML, the lobsters remained in the outdoor tanks year round. Lobsters were fed salted herring to satiation once every 2 wks when the accelerometers were temporarily removed, downloaded, and reattached.

**LAB VS FIELD MOVEMENT.**—In a second study (fall 2008), to compare the activity of lobsters in the laboratory vs the field, lobsters ( $n = 7$ ) fitted with HOBO accelerometers in similar activity enclosures (*see above*) were placed either in recirculating tanks at the UNH CML research pier, or on the bottom of the ocean near the CML at a depth of 4–5 m ( $n = 5$ ). Both sets of lobsters received the water from the same source, but those in field likely experienced different environmental cues of lower light levels, tidal currents, olfactory stimuli, access to sediment, etc.

## RESULTS

**CORRELATION BETWEEN ACCELEROMETER OUTPUTS AND MOVEMENTS.**—Once the data were filtered to use only the  $y$  axis output and remove points below the activity threshold, we found that there was a good correlation between the movements of lobsters and the output of the HOBO accelerometers ( $r^2 = 0.53$ ,  $P < 0.05$ ; Fig. 3). Moreover, these analyses made it possible to convert accelerometer data into distance traveled, in terms of  $\text{m hr}^{-1}$ . Likewise, there was a similarly good relationship between the distance traveled by lobsters and the output of the Vemco V13AP accelerometers ( $r^2 = 0.63$ ,  $P < 0.001$ ; Figs. 4, 5).

**ESTUARY VS COAST MOVEMENTS.**—Adult lobsters caught at the coast and monitored in activity enclosures at the CML, where they were exposed to seawater directly from the mouth of the Piscataqua River/Great Bay estuary, showed similar daily patterns of activity when compared to lobsters that were caught in the estuary and monitored at the JEL in estuarine water from Great Bay (Fig. 6). At both sites, and in all seasons, lobsters were nocturnal, with peaks in activity coinciding with sunset, which is consistent with findings from prior studies (Jury et al. 2005, Golet et al. 2006). However, because of the change in the times of dusk and dawn throughout the year, the timing and duration of nocturnal activity differed between the seasons. Overall, the level of activity was higher in summer and fall in both the estuary

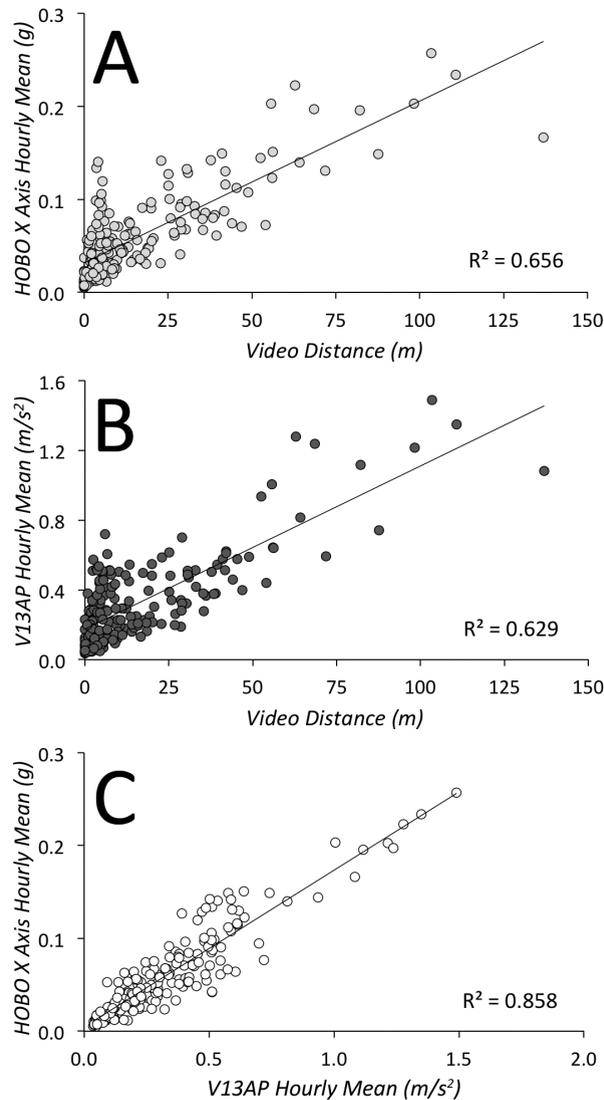


Figure 5. Calibration of V13AP accelerometer transmitters. Lobsters ( $n = 5$ ) were tagged with both V13AP transmitters and HOBO dataloggers (Fig. 2B) and distances moved were determined via time lapse video analyzed by Ethovision. (A) Comparison of the hourly mean  $x$  axis HOBO accelerometer data to the distances moved. (B) Filtered hourly mean V13AP accelerometer data compared to the distances moved. (C) The correlation of the HOBO vs V13AP accelerometer outputs.

and at the coast, with uniformly low levels throughout the winter. However, because this low level of activity occurred throughout the extended nocturnal period of the winter, there was a significant amount of activity even at cold temperatures (Fig. 1). Unexpectedly, there were high levels of activity in the spring in the estuary when compared to the coast, and higher levels of activity at the coast vs the estuary in the fall (Fig. 6). There were also occasional periods of high daytime activity, particularly in the summer, at both sites.

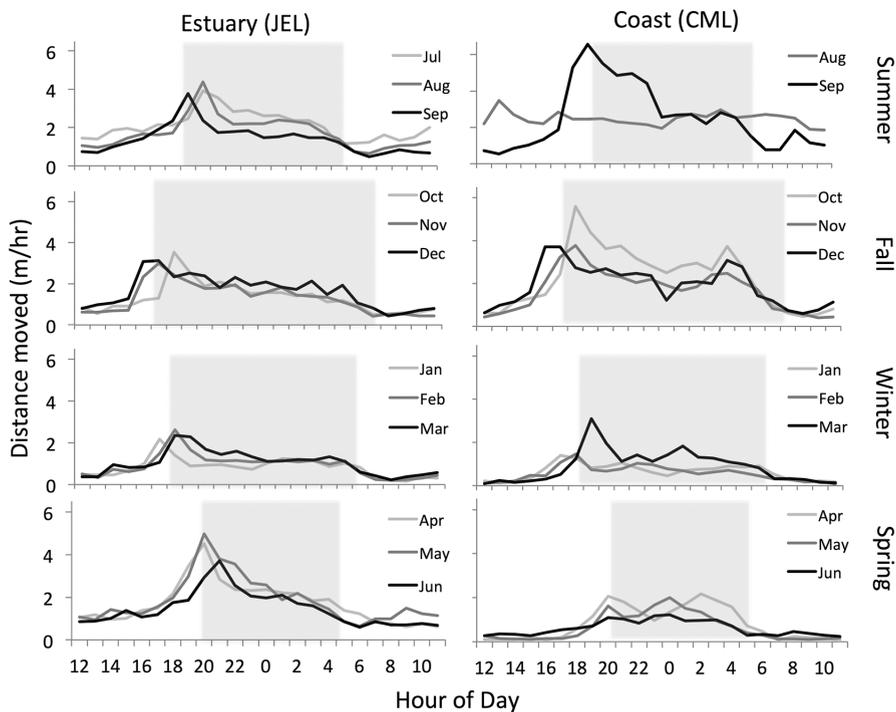


Figure 6. Daily activity patterns of all lobsters throughout the year at the estuary (Jackson Estuarine Laboratory, or JEL;  $n = 6$ ) vs the coast (Coastal Marine Laboratory, or CML;  $n = 6$ ). Both groups of animals were exposed to ambient seawater in flow-through tanks. Activity patterns were different between locations in the spring (April, May, June) and fall (October, November, December). Daily activity was consistently highest at dusk, followed by a period of elevated activity, and then a decrease in activity shortly before sunrise. During winter, when the water was  $<5^{\circ}\text{C}$  (January–March), hourly activity was much lower than during warm water months. Initiation of activity was also earlier in winter months with shorter days and later in the summer with longer days. Seasons were winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Gray background indicates the relative nocturnal period for each season.

Lobsters at the coast moved significantly farther, in terms of meters per day ( $\text{m d}^{-1}$ ), than estuarine lobsters in the late summer (August and September) and significantly less in the spring (April, May, and June) (Mann-Whitney U test:  $P < 0.05$ ; Fig. 7). Daily activity was lowest in both sites in the winter months, but still evident (i.e.,  $>0 \text{ m d}^{-1}$ ) even though water temperatures were regularly  $<5^{\circ}\text{C}$  (Fig. 1).

**LAB VS FIELD MOVEMENTS.**—In the fall of 2008, lobsters were placed in activity enclosures located either 5–6 m underwater in the field or in tanks on the pier at the CML. Those located in the field ( $n = 5$ ) had significantly higher levels of activity than those located in identical enclosures in recirculating tanks ( $n = 7$ ) on the pier  $<0.5 \text{ km}$  away, even though they were receiving water from approximately the same location and thus exposed to similar environmental cues (Mann-Whitney U test:  $P < 0.001$ ; Fig. 8). Lobsters exhibited crepuscular, nocturnal activity patterns similar to those from our other trials and reported in several previous studies (Jury et al. 2005, Golet et al. 2006), but overall levels of activity were significantly higher in the field, including more bouts of daytime activity than lobsters in the tanks on the pier. Lobsters

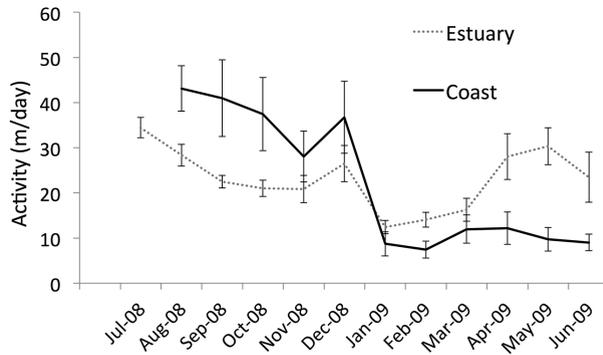


Figure 7. A comparison of the daily activity ( $m\ d^{-1}$ ) of lobsters in tanks experiencing coastal conditions (Coastal Marine Laboratory, or CML;  $n = 6$ ) vs. lobsters in tanks experiencing estuarine conditions (Jackson Estuarine Laboratory, or JEL;  $n = 6$ ). All points are mean (SE) meters moved per day shown for each month. There was significantly higher activity at the coast than in the estuary in the late summer (August and September), but significantly less activity at the coast as compared to the estuary in the spring (April, May, and June) (Mann-Whitney U test:  $P < 0.05$ ). Activity was not significantly different between sites in all other months. A decrease in temperature below  $5\ ^\circ C$  in January coincided with a sharp drop in activity, but activity levels never dropped to zero.

in the tanks moved an average of  $35.4$  (SE  $1.0$ )  $m\ d^{-1}$ , while those in rings underwater moved  $277$  (SE  $3.7$ )  $m\ d^{-1}$ . The distance traveled by the animals in their natural habitat were similar to estimates reported for free ranging animals in the Great Bay estuary, or coastal NH waters, based upon tag-recapture ( $210\ m\ d^{-1}$ ) or ultrasonic telemetry ( $290\text{--}664\ m\ d^{-1}$ ) data (Table 1).

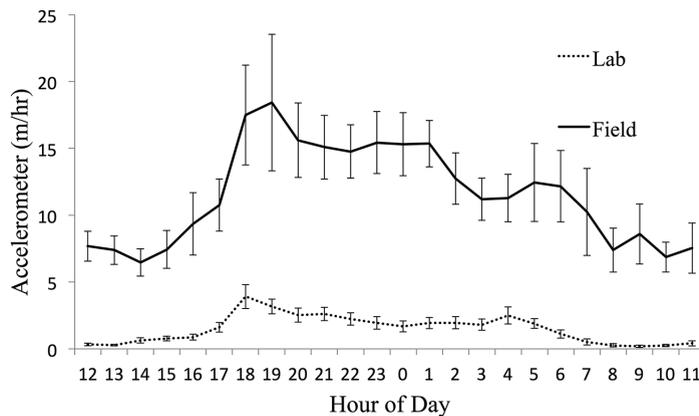


Figure 8. A comparison of the activity of lobsters in tanks on a pier ( $n = 7$ ) vs lobsters in the field ( $n = 5$ ) at the coast. While patterns of daily activity were the similar, lobsters in the field were significantly more active than lobsters in the tanks  $<0.5\ km$  away at all hours of the day. (Mann-Whitney U test:  $P < 0.005$ ). Lobsters in the field also showed surprisingly high levels of diurnal activity. This may be due to differences in the stimuli influencing activity (e.g., light, temperature, currents, etc.) that are present in the natural habitat vs lab tanks.

Table 1. Comparison of the distance traveled per day by lobsters tested over a variety of years using multiple methods. The distances moved per day (mean, SD in parentheses) were generally similar for studies done in the lab. However, the level of activity was consistently higher for lobsters in the field (indicated as “Field” in Site column). Note that most studies, other than the present one, did not include winter data when the activity levels were relatively low (see Fig. 7) which influenced the average. (\* value estimated from fig. 3 in Golet et al. 2006, † value is only for “mobile” lobsters at the coast in Watson et al. 1999). (JEL = UNH Jackson Estuarine Laboratory, CML = UNH Coastal Marine Laboratory, SMCC = Southern Maine Community College). Lab = Laboratory.

Location and year(s)	Site	Movement (m d <sup>-1</sup> )	Method	Reference
JEL 2008–2009	Lab	24.2 (10.8)	Accelerometry HOBO ( <i>n</i> = 6)	Present study
CML 2008–2009	Lab	22.5 (18.7)	Accelerometry HOBO ( <i>n</i> = 6)	Present study
CML 2008	Pier	35.4 (1.0)	Accelerometry HOBO ( <i>n</i> = 7)	Present study
Portsmouth Harbor 2008	Field	277.0 (3.7)	Accelerometry HOBO ( <i>n</i> = 5)	Present study
CML 2016	Lab	263.1 (113.3)	Accelerometry VEMCO ( <i>n</i> = 5)	Present study
SMCC 2016	Lab	71.8 (30.3)	Accelerometry HOBO ( <i>n</i> = 6)	Present study
CML 1998	Lab	88.0 (12.0)	Racetrack-reed switch ( <i>n</i> = 18)	Jury 1999
Portsmouth Harbor 1998	Field	249.0 (55.1)	Racetrack-reed switch ( <i>n</i> = 8)	Jury 1999
Great Bay Estuary 1999	Field	210.0 (370)	Tag-recapture ( <i>n</i> = 263)	Watson et al. 1999†
Great Bay Estuary 1999	Field	290.0 (20)	Acoustic telemetry array ( <i>n</i> = 26)	Watson et al. 1999
JEL 1998–2000	Lab	60.1 (6.5)	Racetrack-reed switch ( <i>n</i> = 43)	Jury et al. 2005
Plymouth State University 2000	Lab	36.6 (11.7)	Running wheel ( <i>n</i> = 10)	Jury et al. 2005
Portsmouth Harbor 2002–2003	Field	664.3	Acoustic telemetry array ( <i>n</i> = 44)	Golet et al. 2006*
Portsmouth Harbor 2002–2003	Field	532.2 (78.1)	Acoustic telemetry array ( <i>n</i> = 32)	Scopel et al. 2009

## DISCUSSION

While the use of accelerometers to monitor large marine invertebrates has been successful in the past [*H. americanus*, Lyons et al. 2013; *P. argus*, Gutzler et al. 2015; *S. latus*, Goldstein et al. 2015, *Limulus polyphemus* (Linnaeus, 1758), Watson et al. 2016; scallops, Robson et al. 2012], ours is the first study to use accelerometry as a method to directly evaluate the activity of lobsters over a long-term (approximately annual) basis, and to compare their activity in both field and laboratory settings. Moreover, this is one of the first attempts to convert accelerometer data into a form that is more directly related to distance traveled per unit time. Accelerometry appears to be a valid approach to estimate distances moved per unit time once appropriately calibrated for the attachment location, orientation, and type of accelerometer tag used. The application of accelerometers as tools to study the behavior of animals in the field is becoming increasingly common (Cooke et al. 2004, 2013, Watanabe and Takahashi 2013, Bom et al. 2014), in part because it is possible to use these in a variety of environments, over extended periods of time, and in the absence of potentially confounding variables associated with cameras or direct observations (Reynolds and Casterlin 1979, Ennis 1984, Karnofsky et al. 1989, Nathan et al. 2008). The technique used in the present study has several advantages over other options: (1) high turbidity and varying light levels do not affect recording; (2) additional light, which may affect behavior, is not necessary as in some techniques (i.e., video, diver observation); (3) the system is readily adaptable to field use, and is relatively inexpensive and non-invasive; and; (4) distance traveled and rate of movement can be estimated by calibrating accelerometer output vs actual movements. Therefore, once appropriately calibrated, accelerometry appears to be a suitable method for assessment of movement patterns and distance traveled by any animal that is large enough so that the

tags will not interfere with their normal behavior (Baras and Lagardere 1995, Lennox et al. 2017).

Historically, these types of data have been obtained using a combination of acoustic transmitters and a set of receivers arranged to monitor the location of the animals by triangulation, which requires the acoustic tag signal to be detected by at least three different receivers. The VRAP tracking array (VEMCO Ltd., Halifax, Canada) was one of the first telemetry systems to use this technology and we have used it successfully on several occasions to determine daily patterns of lobster activity in their natural habitats (Golet et al. 2006), their home ranges (Scopel et al. 2009), and their behavior with respect to traps (Watson et al. 2009). More recently, a number of studies have used large arrays of receivers (e.g., VR2 or VR2Ws by VEMCO Ltd., Halifax, Canada) and postprocessing software to track the movements of lobsters, as well as other species (Lennox et al. 2017). While the VRAP system allows users to accurately monitor the activity of animals in near real-time, a major drawback is that the subjects often wander outside the array and if all three buoys cannot detect the signal, no data are obtained. In contrast, acoustic arrays can be quite large, and despite the fact that the user must wait until each receiver is downloaded and the data processed to obtain results, less data are lost due to animals moving out of range. Clearly, both approaches have significant advantages for studying the behavior of marine species. However, as stated above, there are several advantages to using accelerometers vs acoustic receiver arrays including: (1) reduced cost; (2) less data are lost due to animals moving out of range; (3) small movements can be detected while the resolution of fixed arrays are on the order of 1–3 m; (4) specific behaviors can be identified and; (5) they can be used both in the laboratory and in the field.

One challenge to using accelerometers to measure distances moved per unit time is that non-target behaviors, such as slight movements that are not walking (i.e., shifting sides, twitching, leaning forward or backward, standing on uneven terrain, etc.), may change the value of at least one axis of the accelerometer, which can lead to a false positive indication of locomotion. In addition, excessive changes in acceleration, deceleration, or walking long periods at a constant velocity may also give anomalously high or low values when trying to determine distances moved per unit time (BC Gutzler, University of New Hampshire, unpubl data). However, by using video calibration to create a basal threshold of activity for particular life history stages, most of the anomalous movements can be minimized to obtain reasonable estimates of distances moved over hourly or daily intervals. Our data show a good correlation between the output of V13AP telemetry tags and HOBO dataloggers co-mounted on the same lobsters ( $r^2 = 0.86$ ,  $P < 0.001$ ; Fig. 5), indicating that both styles of accelerometer provide comparable results in terms of monitoring the activity of animals. Furthermore, both systems produced data that were significantly correlated with distance traveled by the subjects. Therefore, at least for certain applications, either type of accelerometer tag can be a suitable choice for monitoring the movements of freely moving animals. For freely ranging animals, transmitting telemetry tags (such as the V13AP) could provide real-time accelerometry data, but risk missing data points if the animal moves out of range of all the receivers in an array. Datalogging tags capture all the data points, but require recovery of the animal to download the data. Ideally, a hybrid tag that stored all the movement data, and then downloaded it when within the range of a receiver could be developed.

American lobsters exhibit increased nocturnal activity throughout the year that is generally highest within 1 hr of sunset (Fig. 6; Reynolds and Casterlin 1979, Cooper and Uzmann 1980, Ennis 1984, Karnofsky et al. 1989, Jury et al. 2005). Some studies have also reported a secondary, smaller spike, in activity before sunrise (Reynolds and Casterlin 1979, Golet et al. 2006). This secondary peak in activity was observed only in the present study in the spring and the fall at the coastal site (Fig. 6). During the daytime, primarily in the summer and fall, activity was present, but occurred at a much lower intensity than activity during the night. This is consistent with other studies in this system where many lobsters show diurnal activity and are often as active during the day as during the night (Jury et al. 2001, 2005, Golet et al. 2006). Light seems to be the most important exogenous factor influencing the daily activity of lobsters (Zeitlin-Hale and Sastry 1978, Jernakoff 1987, Lawton 1987, Lawton and Lavalli 1995). Light levels not only change with the movement of the sun, but may also be affected by season, water depth, or water clarity (Cooper and Uzmann 1980, Smith et al. 1998). In our study, lobsters were active for larger portions of a 24-hr day in the winter than in the summer because the nights are longer in the winter (Fig. 6). In deeper, or turbid, water where light levels are lower, lobsters are often seen out of their shelters during the day (Briggs and Mushacke 1979, Howard and Nunny 1983, Karnofsky et al. 1989, Lawton and Lavalli 1995, Aguzzi and Company 2010). Light levels decrease as one moves up the Great Bay estuary and are generally lower in the spring than the summer, and fall due to runoff-induced changes in turbidity (Daly et al. 1979). This may in turn alter the day activity of lobsters in the estuary in comparison to coastal waters (Fig 7). Thus, even though lobsters are primarily active at night, some lobsters, particularly those in the field, show bursts of diurnal activity that may be related to tidally-variable light intensity or other factors.

Evidence for low, but consistent, diurnal activity is widely available for other lobster species (Lawton 1987, Smith et al. 1998, Aguzzi and Company 2010). Electromagnetic telemetry showed low, but consistent, movements of *Homarus gammarus* (Linnaeus, 1758) between reef units during diurnal periods even though nocturnal activity was much greater (Smith et al. 1998). The catch of *Nephrops norvegicus* (Linnaeus, 1758) was directly related to light level and light level was directly related to depth, such that *N. norvegicus* is active in day and night periods in deep water, but only at night in shallow water (Aguzzi et al. 2003, 2004, Aguzzi and Sarda 2008, Aguzzi and Company 2010). Another example of the strong inhibitory effect of light on activity is that the full moon has been shown to decrease catch of spiny lobsters (Nagata and Koike 1997). Thus, light appears to have a direct effect upon activity, but it may also have an indirect effect by controlling availability of food, activity of predators and prey, and susceptibility to predators.

When comparing activity patterns throughout the year between coastal and estuarine study sites, lobsters were more active at the coastal site in the summer and fall and more active in the estuarine site in the spring. This is likely due to the strong influence of water temperature on lobster activity, their tendency to carry out seasonal migrations in the spring and fall, and the fact that the estuary warms up faster in the spring and cools down faster in the fall (Jury 1999). Storm events leading to changes in barometric pressure and runoff events are also more prevalent in spring and fall (Daly et al. 1979), and they are known to trigger seasonal migrations or movements to avoid low salinity events that may influence movements as well (Jury et al. 1995, Goldstein and Watson 2015). Interestingly, a recent study by Goldstein and Watson

(2015) found that temperature reductions in the fall combined with turbulence due to fall storms likely trigger inshore-to-offshore migrations of coastal lobsters (Lawton and Lavalli 1995, Jury and Childress 2006). Moreover, animals in the Great Bay estuary that were being tracked at the same time did not migrate down toward the coast, even though they experienced the same drops in temperature (Langley 2017).

Karnofsky et al. (1989) conducted a seasonal study of lobster movements in southern Massachusetts and observed increased activity during May, late July and August, and October and November, with activity in the former months attributed to increasing temperatures and in the latter months to decreasing temperatures. Over the course of the present study, temperatures in the Great Bay estuary were very similar to those observed in Karnofsky et al. (1989); however, while we observed high levels of activity in the summer, the fall or spring increase was location dependent even within the same estuarine system. These changes in behavior in spring and fall documented by Karnofsky et al. (1989) and others in New Hampshire waters (Howell et al. 1999, Watson et al. 1999) may correlate with migratory movements into and/or out of the estuary.

It is generally accepted that lobsters in the field and the laboratory express similar patterns of activity (Cooper and Uzmann 1980, Ennis 1984, Karnofsky et al. 1989, Lawton and Lavalli 1995, Jury et al. 2005). However, we found that the overall amount of activity in lobsters was significantly higher in the field vs the lab, despite the fact that both treatments were exposed to the same water source. These findings are consistent with those of Jury (1999), where it was found that paired estuarine lobsters tested in racetracks in the laboratory and the field were significantly more active in the field. Lobsters in the field make daily foraging and meandering movements that are typically  $300 \text{ m d}^{-1}$  (Cooper and Uzmann 1980, Lawton and Lavalli 1995; Table 1). With the exception of some of the V13AP tagged large lobsters studied here moving freely in a large tank at the CML, lobsters in laboratory settings generally move  $<100 \text{ m d}^{-1}$ . Thus, it is important to consider the method of confinement when extrapolating lab activity and movement data to the field. The higher field activity is likely due to other factors in the natural habitat that might have an impact on their overall activity, including differences in light level, the presence of predator and prey cues, turbulence and tidal currents, substrate, and olfactory cues, as has been reported in other studies (Florey and Kriebel 1974, Jernakoff 1987, Lawton and Lavalli 1995, Smith et al. 1998).

In summary, accelerometry is a suitable method to determine the distance and rate of movement of American lobsters when appropriately calibrated in the laboratory. Accelerometer output can be calibrated by quantifying the actual distance traveled by lobsters while simultaneously monitoring accelerometer output. Then, once sufficient replications have been completed on a given species and ontogenetic stage, it may be possible to use a generic approach without further calibration. We are working to improve the ability to monitor different types of movements and behaviors on a range of sizes of lobsters and it is likely that species-specific and life history-stage specific (e.g., molting, ovigerous females, etc.) calibration of accelerometer output may be necessary. Nonetheless, accelerometry clearly can provide useful information on freely moving lobsters, as demonstrated by application of this technique to an independent data set. When we did this, we found that the activity levels and distances moved by *H. americanus* were both spatially and temporally variable due, at least in part, to seasonal changes in water temperature. Multiple factors (e.g., light,

predator, prey, food availability, etc.) present in their natural habitat also appeared to have a significant impact on their activity because even lobsters confined to activity chambers moved more in the field than in the lab. As has been found in other studies, the differences and similarities between the data obtained in the laboratory and the field further argue for complementing the control inherent in laboratory studies with the “reality” of field studies to best elucidate behavioral, physiological, and ecological relationships (Goldstein and Pinshow 2006, Simonik and Henry 2014, Auer et al. 2016, Lennox et al. 2017).

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