

Movements and activity levels of juvenile American lobsters *Homarus americanus* in nature quantified using ultrasonic telemetry

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ABSTRACT: In this study we expand the size range of American lobsters *Homarus americanus* tracked in nature by quantifying for the first time the movements and activity levels of juveniles using ultrasonic telemetry. Ten individuals 20–47 mm carapace length (≈ 1 –4 yr old) were tracked for 21 d in August 2010 on a shallow nursery ground in southwest Bay of Fundy, Canada, using the Vemco VRAP tracking system. Many of our results are consistent with the literature on juvenile lobster ecology, which is largely based on laboratory experiments and short-term field observations. For example, the juvenile lobsters were significantly more active at night (71 % of all activity) than during the day (29 %), and they behaved as central place foragers, displaying movements that greatly limited their dispersal from the nursery habitat. However, the average amount of time individuals spent outside of shelter (≈ 2.2 –32.7 % of each day, or 0.5–7.8 h) and the average size of their daily home ranges (≈ 27.4 –111.6 m²) did not increase with increasing body size, as was predicted based upon the literature. We also report for the first time evidence of a tidal (12.4 h) cycle of activity in juvenile lobsters, which was displayed more consistently at night than during the day. This study advances our understanding of the behavioural ecology of juvenile lobster on nursery grounds, and it suggests that these young individuals spend more time outside of shelters than might currently be concluded from the literature.

KEY WORDS: American lobster · *Homarus americanus* · Juvenile · Ultrasonic telemetry · Movement · Behaviour · Activity

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INTRODUCTION

Animal movement is an important ecological process that affects the demography and genetic structure of populations (McCauley 1995, Hanski & Gilpin 1997, Wiens 2000). This is certainly true in the marine environment, where many species have a multi-phase ontogeny, with each phase usually displaying spatially and temporally distinct movements (reviewed by Pittman & McAlpine 2003). While animal movements have been described for over 100 yr in both terrestrial (e.g. bird banding; Bartsch 1904) and aquatic (e.g. lobster tagging; Bumpus 1901) environments, technological developments continue to advance what can be quantified and learned about

these movements (reviewed by Morales et al. 2010). An example of these technological advances in aquatic environments is ultrasonic telemetry systems, which are comprised of animal transmitters (tags), which emit a sonic pulse at a certain radio frequency and time interval, and hydrophones, which listen for and decode this information. When ultrasonic telemetry was first used to track adult American lobsters *Homarus americanus* in the field (e.g. Watson et al. 1999, Tremblay et al. 2003), the smallest animal tags available were ≈ 60 mm long and 16 mm in diameter (i.e. ultrasonic tags from Sonotronics and VEMCO). Animal tags are now commercially available that are less than 5 % the volume and mass of these early tags, measuring only 12–17 mm in length and

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5–6 mm in diameter (i.e. HTI 795-LM and VEMCO V5). Miniaturization advancements such as these allow for smaller-bodied species and life stages to be tagged, enabling in the latter case more detailed studies into the ontogeny of a species' movement ecology.

In what is arguably the most detailed and recent life history scheme for the American lobster, the species' life cycle is proposed to have 7 'phases' (Lawton & Lavalli 1995). The first phase is a pelagic larva ($\approx 2\text{--}4$ mm carapace length [CL]), which drifts in the surface waters for the first 11–54 d after hatch, dependent in part on water temperature, potentially over 100s of kilometers (reviewed by Cobb & Castro 2008). The second phase is the postlarva ($\approx 4\text{--}5$ mm CL), which makes the transition between pelagic and benthic life; the postlarva chooses an appropriate place on the bottom to settle and finds or builds its first shelter. Once successfully settled onto the bottom, the lobster begins its third phase and is referred to as a shelter-restricted juvenile ($\approx 4\text{--}14$ mm CL). Lobsters of this size are highly vulnerable to predators and are thought to spend almost 100% of their time under shelter (Roach 1983, Hudon 1987, Wahle & Steneck 1991), where they are hypothesized to be opportunistic scavengers and/or suspension feeders (Barshaw & Bryant-Rich 1988, Lavalli & Barshaw 1989, Sainte-Marie & Chabot 2002). When the lobster begins to venture outside of shelter, making limited movements to find food, it begins its fourth phase and is known as an emergent juvenile ($\approx 15\text{--}25$ mm CL). The fifth phase is the vagile juvenile (≈ 25 to ≈ 40 mm CL), during which more extensive movements outside of shelter are undertaken. During the 3 juvenile phases (shelter-restricted, emergent and vagile; ≈ 4 to ≈ 40 mm CL) foraging excursions outside of shelter are hypothesized to gradually increase due to increasing metabolic demands and decreasing susceptibility to predation (Wahle 1992, Wahle & Incze 1997, Selgrath et al. 2007, Émond et al. 2010, Wahle et al. 2013). The sixth and seventh phases are adolescents and adults, respectively, which behave similarly in many regards (Lawton & Lavalli 1995) and are differentiated based upon physiological and functional maturity. Adolescents begin ≈ 50 mm CL, and in the Bay of Fundy 50% of individuals have mature sexual organs at ≈ 104 mm CL (DFO 2001).

Scientists and fishermen have studied the movement of American lobster, particularly the adolescents and adults, for over 110 yr (Bumpus 1901). In certain parts of the species' range, some adults have been documented to undergo seasonal movements or long-range migrations, which are thought to help

meet physiological requirements of molting, mating, egg extrusion, and embryonic development (reviewed by Lawton & Lavalli 1995). These studies have also shown, however, that not all animals within the same location undertake these long-distance migrations. Indeed, and notwithstanding potential bias towards recapturing animals that move less, in the majority of tagging studies most lobsters are recaptured within 5 km of their original tagging location, even after a number of years at large.

While we have some knowledge of large-scale movements displayed by adolescent and adult American lobster, much less is known about the small-scale movements they undertake while occupying a particular habitat for more than a few days. Such small-scale daily movements are driven by important ecological factors and processes, such as habitat requirements, foraging needs, territoriality, predator–prey relationships and reproduction (Pittman & McAlpine 2003). It is widely accepted that adolescent and adult American lobsters are nocturnally active, and many studies have observed them retreating to shelters during the day, emerging from burrows in the evening, displaying peak activity in the first few hours following sunset and then gradually decreasing overall activity as sunrise approaches (reviewed by Lawton & Lavalli 1995). However, more recent observations in the laboratory (Jury et al. 1995) and telemetry work in the field (Golet et al. 2006) have shown that activity rates and patterns can vary widely between individuals on a particular day, and also between days, for the same individual. Fine-scale telemetry studies have also revealed that the location of adolescent and adult lobster home ranges changes often (every 1–2 d), but their size generally remains fairly consistent ($\approx 315\text{--}786$ m²) from day to day (Tremblay et al. 2003, Scopel et al. 2009, McMahan et al. 2013). The average size of daily home ranges was not found to be influenced by body size among adolescent and adult lobsters but was shown to be negatively affected by the presence of adult cod *Gadus morhua*, predators of the American lobster (McMahan et al. 2013).

Relatively little is known about the activity and movements of juvenile lobsters, probably in large part because of their cryptic nature and reduced propensity to enter baited traps. Accordingly, and importantly, what we do know about juvenile lobster activity and movements is based on laboratory experiments and short-term field observations and experiments. In the laboratory, juveniles have been observed to display nocturnal peaks in activity and feeding, similar to adolescents and adults (Lawton

1987). This hypothesis has not, however, been empirically tested in nature, nor has the possibility that juveniles display other activity cycles (e.g. tidal). In the field, juveniles have been observed to move more frequently within contiguous cobble habitat than in patchy habitat (Hovel & Wahle 2010) and to move into empty cobble plots in response to overcrowding (Wahle & Incze 1997). No data concerning these animals' 'home range', i.e. the area over which they normally travel and search for food (Burt 1943), exist, and the hypothesis that they behave as 'central place foragers', undergoing foraging excursions from a 'central' shelter (Lawton 1987, Wahle 1992), has also not been tested. Another important hypothesis that has not been empirically tested in nature is that the frequency and magnitude of movements increase during the juvenile's ontogeny (Wahle 1992, Lawton & Lavalli 1995, Selgrath et al. 2007, Émond et al. 2010, Wahle et al. 2013).

The main objective of this study was to quantify, for the first time, the activity levels and fine-scale movements of juvenile American lobster in nature. As a secondary objective we wanted to test the usefulness of a fixed ultrasonic telemetry system to track small cryptic marine invertebrates that live in complex habitats and remain sheltered for large portions of the day. We used the tracking data of juvenile lobsters to (1) quantify the amount of time they spend actively roaming outside of shelters every day, (2) determine if there is evidence of cyclicity (e.g. diel, tidal) in their activity patterns, (3) quantify the size of their home range and (4) determine if they behave as central place foragers. We then used the data to test the hypotheses that the frequency and magnitude of movements outside of shelter displayed by juvenile lobsters increase with their body size (Wahle 1992, Lawton & Lavalli 1995, Selgrath et al. 2007, Émond et al. 2010, Wahle et al. 2013).

MATERIALS AND METHODS

Experimental design

The study was conducted in August 2010 in Birch Cove, southwest Bay of Fundy, Canada (45° 8' 32.2" N, 67° 1' 59.7" W). The study site was previously found to be a nursery for American lobster *Homarus americanus*, with an average of 0.1–0.3 juveniles m⁻² in the shallow subtidal (Lynch & Rochette 2009). The study site was comprised primarily of 1 to 2 layers of cobble (≈6–25 cm) sitting on mud within most of the area where the ultrasonic

telemetry system was placed, a combination of cobble, gravel (≈2–5 cm) and mud in deeper portions of the tracking area, and mostly mud in deeper water outside the tracking area (Lynch & Rochette 2009).

We utilized the VEMCO radio-acoustic positioning telemetry system (VRAP), which consists of 3 hydrophones mounted on surface buoys and a base station with antenna and computer; we moored the buoys ≈100 m apart in an equilateral triangle and set up the base station in a building ≈300 m from the study site. The water depth within the tracking area generally ranged between 3 and 7 m at low tide. Due to the large tidal range at the site (daily average of 6 m during the study, with the exception of a 5 d period where it averaged 8 m due to a spring tide) each buoy was moored using an elastic bungee cord with a 100 percent stretch, which kept the buoys relatively straight over their mooring while water level fluctuated. Each buoy had a hydrophone, which listened for tags (both animal and reference), as well as a radio, which sent the data to the base station, where the position of each tag was triangulated based on the difference in signal arrival times to the 3 hydrophones. A complete description of the VRAP tracking system, including positioning accuracy testing (±3 m), can be found in Tremblay et al. (2003).

We tracked 10 juvenile American lobsters ranging in size from 20–47 mm CL. The largest individual tracked falls between the upper range of the juvenile phase (≈40 mm CL) and the lower range of the adolescent phase (≈50 mm CL), as defined by Lawton & Lavalli (1995), and whereas we refer to this individual as a juvenile, it should probably be considered in transition between the juvenile and the adolescent life phases. We estimate, based on recent work in the region (Tang et al. 2015) involving a novel age-determination technique for crustaceans (Kilada et al. 2012), that the lobsters in this study were between 1 and 4 yr of age. The lobsters weighed between ≈50 g (20 mm CL) and ≈150 g (47 mm CL) in air. We collected these lobsters under cobble within the VRAP buoy triangle by hand using SCUBA, tagged them (Fig. 1) and released them in immediate vicinity of abundant cobble shelter within an area of ≈100 m². The animal tags used in this study, which are the smallest ultrasonic tags currently available for the VRAP system, were the V7-1L coded tags (VEMCO, 18 × 7 mm, 1.4 g in air, 0.7 g in water). In preparation for tagging, the tags were first epoxied onto a cardboard harness (<1 g), which created a larger surface area for attachment to the animal. During tagging the lobsters carapace was dried, cleaned with ethanol to remove biofilm, and the tag harness was glued using



Fig. 1. Smallest juvenile lobster used in this study (20 mm carapace length; ≈ 50 g in air), tagged with a VEMCO V7-1L ultrasonic tag prior to deployment

HomeBond Superglue (Home Hardware). Lobsters were kept under moist paper towel (apart from where the tag harness was being attached) throughout the tagging procedure, which lasted a maximum of 10 min. Each animal tag emitted a single and unique acoustic pulse train at 69 kHz on average every 120 s. In order to reduce collisions between pulse trains emitted by the different tags in the study, each tag was programmed to transmit randomly once every 60–180 s. In addition to the 10 animal tags, we also moored 1 coded V16-1L tag (VEMCO Ltd, 58×16 mm) on the bottom near the centre of the triangle to act as an unmoving reference tag (Payne et al. 2010). The reference tag transmitted once every 240–360 s.

One concern associated with tagging studies is that the act of tagging, or the tag itself, may alter the behaviour and movements of the tagged animal. Our smallest lobsters (20 mm CL) weighed ≈ 50 g in air, meaning our telemetry tags (1.4 g) were 2.8% of their body mass, while our larger lobsters weighed ≈ 75 –150 g in air, meaning the tags weighed ≈ 1.9 –0.9% of their body mass. Many fish biologists adhere to the guideline that a tag's mass in air should be 2% or less of the fish mass in air (first proposed by Winter 1983), although more recent research has questioned the necessity for this very low 2% guideline (reviewed by Jepsen et al. 2005). No similar guidelines exist for decapods. To rigorously assess the possibility of a tag bias, we conducted a laboratory experiment in which we quantified the ability of tagged and non-tagged juvenile lobsters of the same size as used in our study to sustain rapid movement over a relatively long period of time. To do this we

placed individually 20 lobsters (10 tagged and 10 untagged) measuring 21–39 mm CL in a 2 m diameter circular flume (≈ 30 cm corridor) with ≈ 10 cm s^{-1} current, and we quantified their movements over a 45 min period. In order to encourage fast and continued movement, to provide a rigorous test of the tag-bias hypothesis, we ran the trials in full light and on a relatively smooth substrate of aquarium gravel with no shelter. Each trial was videotaped, and after the experiment was completed, we counted the number of laps each lobster did around the circular flume in 45 min. We compared the number of laps completed by tagged and non-tagged lobsters using an ANCOVA in which carapace length was the covariate.

We conducted the study between August 6 and 30, 2010. Nine lobsters were tagged on August 6 and a tenth was tagged on August 14. On August 22 the batteries were changed in the hydrophones of the VRAP buoys, and a technical problem reduced system activity until August 24. After data from all 25 d of the study were compiled, 4 d were removed (first day, last day, and the 2 d surrounding when the hydrophone batteries were changed), as the likelihood of tag detection and positional estimates on those days could have been affected by buoy movement, boat noise, scuba divers in the water and reduced system activity. Analyses are thus based on 21 d of tracking data.

Analysis of activity patterns

The amount of time each lobster spent actively roaming outside of shelter was determined based on the detection/non detection of their individualized tag by the 3 buoyed hydrophones of our telemetry system, because the 69 kHz sound pulse emitted by these tags is not detected by hydrophones when line of sight is blocked by rocks (Tremblay et al. 2003, Heupel et al. 2006, Welsh et al. 2012), which juvenile lobsters shelter under. In order to further validate within the context of our study the assumptions that animals were (1) sheltered when their tags were not heard and (2) outside shelters when they were heard, we used the speeds of the non-moving reference tag (i.e. reflecting positioning error) and animal tags for each pair of consecutive position estimates over the duration of the study (Table 1). Support for the assumption that animals were outside shelter when their tags were heard comes from the observation that speeds of their tags were markedly (Table 1) and highly significantly ($t = -32.96$, $df = 3924.99$, $p <$

Table 1. Estimates of the speed of the stationary reference tag (i.e. reflecting positioning error) and the 10 animal tags for successive positional estimates separated by different time intervals. Reference and animal tags emitted a sound pulse at 5 and 2 min intervals, respectively, which is why no values could be estimated for the former over the 2 min time interval. Also shown is the number and cumulative proportion (in parentheses) of these estimates that fell within each time-interval category

Time between positions (min)	Reference tag			Animal tag		
	Sample size (%)	Average speed (m min ⁻¹)	10th/90th percentile speed (m min ⁻¹)	Sample size (%)	Average speed (m min ⁻¹)	10th/90th percentile speed (m min ⁻¹)
0–2	–	–	–	1338	2.50	0.36/5.58
0–5	2639 (56)	0.47	0.08/0.90	3736 (50)	1.86	0.26/3.98
5–10	1274 (83)	0.25	0.06/0.52	1485 (70)	0.72	0.15/1.50
10–20	684 (98)	0.16	0.04/0.33	1010 (84)	0.43	0.10/0.92
20–30	82 (99)	0.12	0.03/0.24	364 (89)	0.26	0.06/0.53
30–40	19 (100)	0.08	0.01/0.14	179 (91)	0.20	0.04/0.34
40–50	5 (100)	0.08	0.04/0.14	108 (93)	0.17	0.04/0.23
50–60	0 (100)	–	–	62 (94)	0.15	0.04/0.30
60–120	2 (100)	0.44	0.11/0.77	181 (96)	0.09	0.02/0.18
120–180	1 (100)	0.14	–	72 (97)	0.05	0.01/0.08
180–300	1 (100)	0.005	–	85 (98)	0.03	0.008/0.08
300–600	0 (100)	–	–	100 (100)	0.02	0.007/0.05
600 +	0 (100)	–	–	36 (100)	0.02	0.003/0.07

0.00001) greater than those of the reference tag for the shortest comparable (i.e. 5 min) time interval between consecutive detections. In fact, 62% of the animal speeds based on 5 min ping intervals were greater than the 90th percentile value of speeds for the reference tag over the same ping interval, confirming that animals were generally moving outside of shelter and not sitting at the entrance of a shelter when we detected them; many of the animals with movements that were not distinguished from those of the reference tag in this manner (38%) were also likely roaming outside shelter, given the relatively high error on some of the reference tag positional estimates (maximum of 12.6 m; 10th percentile = 0.6 m, median = 1.3 m, 90th percentile = 4.1 m). Support for the assumption that animals were sheltered when their tags were not heard comes first from the observation that the speed estimated from their tags initially decreased with increasing inter-ping interval (Table 1), which would not be expected to occur if the animals were actually outside roaming during periods when they were not being detected. Secondly, speeds of the animal tags gradually became similar to those of the reference tag with increasing inter-ping interval, and they did not increase ($R^2 = 0.03$, $n = 28$, $p = 0.43$) with increasing inter-ping interval between 30 and 210 min, which again is consistent with the assumption of no movement over these longer periods of radio silence. Finally, whereas the reference tag almost never went unheard for more than 30 min, 11% of inter-ping intervals of the animal tags were greater than 30 min, with a small proportion of these being up to 5 h, despite the fact that the animal

tags emitted a sound pulse at greater frequency than the reference tag (2 vs. 5 min intervals). Whereas these findings do not confirm that our assumptions hold 100% of the time, they do indicate that they are generally true and (most importantly) suitable to address this study's hypothesis that activity levels increase with body size of juvenile lobsters.

It is important to stress that while using this approach to describe activity levels we only considered animals to be outside of shelter when their tag was simultaneously detected by all 3 hydrophones and their position could be estimated, to decrease the incidence of false positives; sheltered animals stationed near the mouth of their shelter may have been detected by 1, or perhaps even 2 receivers, but they would not have had 'line of sight' to all 3 receivers and would thus not have been included in this analysis. Whereas the approach likely led to some mistaken identifications, it revealed some interesting and unambiguous patterns (see 'Results') based on a critical aspect of the animal's behavioural repertoire (utilizing shelter). The 'daily activity level' of each lobster was assessed as the number of positional estimates obtained over a 24 h period divided by the number of pulses emitted over this period ($n = 720$). We did this for each of the 21 d of the study, for all 10 animal tags as well as for the reference tag. When these calculations were completed, it was found that the reference tag was only detected (by the 3 buoys) on average approximately 74% of each day, even though it was in the same location 100% of the time. This reduced detection rate of the reference tag was likely due to interference by background noise, such

as the 'ping' of a lobster tag, boat noise and/or waves. Importantly, this finding means that we also likely detected only approximately 74% of the animal pings on average every day. In order to estimate the true activity of the juvenile lobsters, we calculated an 'adjusted daily activity estimate' by assuming that each animal emitted pings at the same rate as the reference tag. As the 'inactivity' of the reference tag varied between days, the 'adjusted daily activity estimate' of each lobster was calculated on a daily basis, based upon the 'inactivity' value of the reference tag on that particular day. We then expressed both the observed and adjusted daily activity estimates as study length daily averages (with 95% confidence intervals), for each tag separately, and determined whether study length activity values were correlated to lobster carapace length to test the hypothesis that the activity of juvenile lobsters increases with their body size.

To determine if lobster activity levels changed with time of day, we created actograms and periodograms for each of the 10 animal tags separately, for all animal tags combined, and also for the reference tag. The freeware program Actogram J (Schmid et al. 2011) was used to construct actograms and chi-square periodograms (Sokolove & Bushell 1978). We investigated for activity cycles following a 480 min (8 h) period up to a 1920 min (32 h) period, in 10 min time steps, using activity data from the 21 d of the study. We used chi-squared goodness-of-fit tests to complement the periodogram analyses by contrasting the observed activity data to the actual timing of the cycles proposed by the periodogram analyses; diel cycles were tested by comparing the number of pings detected during the day and night to the numbers expected based on the sunrise and sunset times during the study period (i.e. 0.6/0.4; day/night); tidal cycles by comparing the number of pings detected during 'high tide' and 'low tide' to the numbers expected following division of the tidal cycles in 2 equal halves (i.e. 0.5/0.5; high/low), and the interaction between these 2 cycles by comparing the number of pings detected during 'Daytime High Tide', 'Daytime Low Tide', 'Nighttime High Tide' and 'Nighttime Low Tide' to the numbers expected based on the overlap of the 2 cycles (i.e. 0.3/0.3/0.2/0.2; DHT, DLT, NHT, NLT). To elucidate significant outcomes of the later tests, we conducted pairwise chi-squared goodness-of-fit tests involving the NHT and NLT periods (expected 0.51/0.49), DHT and DLT (0.50 / 0.50), NHT and DHT (0.42/0.58), and NLT and DLT (0.42 / 0.58) (we used a Bonferroni-adjusted α level of 0.0125 for these 4 post-hoc comparisons).

Analysis of movements and home range

We estimated the movement and home range of the tagged lobsters using the 21 d of telemetry data but removing periods where 'movement' of the reference tag indicated that the accuracy of the tracking system was compromised. The VRAP system has been shown to have a positioning accuracy of $\approx 1\text{--}3$ m when the tags are within the triangle of the 3 hydrophones (Tremblay et al. 2003). However, there were periods during our study when our bungee system failed to keep the hydrophones aligned with their moorings, most notably during spring low tides. Therefore, for these analyses of movements and home range we removed any period when the reference tag was estimated by the system to be more than 3 m away from its known location, which resulted in removal of 21.7% of the study duration.

In order to assess the extent to which the movement of juvenile lobster constrained their dispersal, which will occur if they are central place foragers, we compared the dispersal of each individual to that expected under a 'random walk model'. For each tagged lobster the number of observed 'movement steps' during the 21 d period was counted, and the length of each step was measured. We defined a 'movement step' as the linear distance between 2 successive positions estimated by the telemetry system. A random walk analysis was then run 100 times, for each lobster separately, using the Hawth's Tools plug in for ArcGIS. During each run a step length was drawn at random from the lobster's dataset of step lengths and used to move the theoretical lobster by the selected step value in a direction chosen at random between 0° and 360° ($\pm 1^\circ$), and this process was repeated until every observed movement step was used once for that lobster. In order to contrast the homing tendency of different-sized lobsters, we synthesized the relationship between the observed and expected movements of each lobster in 3 steps. First, we calculated the maximum observed displacement for each individual lobster (maximum distance observed relative to the starting location). Second, we calculated the maximum displacement expected under the random walk model (mean of the maximum distances observed in the 100 random walk runs of the 'movements expected' data set). Finally, we expressed the observed displacement of each individual as a percentage of the distance expected under the random-walk model (max. observed/max. expected $\times 100$). We then used correlation analysis to test the hypothesis that

the percentage of possible distance moved away from the starting location increases with lobster size.

We also used the filtered data set (78.3% of the 480 h) to calculate for each individual (1) an average daily home range (in m²) and (2) a study length home range. In both cases, we used the Adaptive LoCoH (Local Convex Hull) method to calculate each animal's 'home range', which was measured as the 90% activity isopleth (see Börger et al. 2006), either for a particular day or for the entire study period. The Adaptive LoCoH method used is a non-parametric kernel method, which has been demonstrated to be more appropriate than parametric kernel methods for constructing home ranges because of its ability to identify hard boundaries (e.g. rivers, cliff edges) and better identify areas that are not used by the animal (Getz et al. 2007). We counted the number of spatially segregated areas of high density of activity (darkest areas on the home range diagrams, which indicated the 30% activity isopleth) as potential indication of the number of separate 'sheltering areas' used by each lobster. We then used correlation analysis to test the hypotheses that (1) average daily home range, (2) study length home range and (3) number of sheltering areas used increase with lobster size.

RESULTS

Laboratory experiment to assess tag bias

During the laboratory experiment, the juvenile lobsters moved continuously for the entire 45 min experimental period, completing an average of 39 laps (min. = 21, max. = 52) of the 2 m diameter circular flume. Therefore, under relatively stressful conditions conducive to movements, the juvenile lobsters moved ≈230 m on average in 45 min. The number of laps completed increased significantly with lobster body size ($F_{1,16} = 32.273$, $p < 0.0001$), but it clearly did not differ ($F_{1,16} = 0.012$, $p = 0.915$) between similar-sized tagged (least square means [LSM] = 39.05, SD = 1.91) and non-tagged (LSM = 38.76, SD = 1.90) lobsters, and the interaction between body size and tagging was also non-significant ($F_{1,16} = 0.635$, $p = 0.437$).

Field experiment: tracking success

Of the 9 juvenile lobsters tagged at the beginning of the study, 7 were detected and successfully positioned throughout the 21 d study period, whereas 2

were only detected the first 4 and 10 d, respectively; the tenth lobster, which was added on the seventh day, was detected for the remaining 14 d of the study (Table 2). It is extremely unlikely that the 2 lobsters that were not tracked for the entire study duration moved outside the detection range of the hydrophones, given the frequency of sonic pulses (every 120 s on average) emitted by the tags; it is unlikely these individuals would have been able to travel the 30 m from the center to the outside of the tracking area without being positioned again, and even less so the ≈200 m away from the study triangle within which they should have been detectable (Tremblay et al. 2003). Instead, the loss of contact with these 2 lobsters was likely caused by transmitter malfunction, transmitter loss inside a shelter, or predation upon the animal inside a shelter.

Field experiment: activity patterns

The 10 juvenile lobsters were observed to have spent, over the 21 d study period, between 0 and 57.1% of any particular day outside of rock shelter, with an overall average of 11.8%, or 2.8 h. It must be noted, however, that these values almost certainly underestimate the amount of time juveniles truly spent outside of shelters, because on average only 73.6% of the signals emitted by the reference tag were detected (Fig. 2), even though the latter was

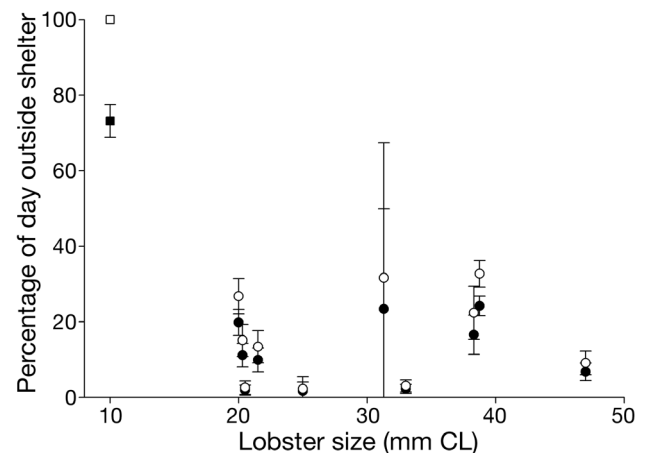


Fig. 2. Average ($\pm 95\%$ CI) percentage of each day that each of the 10 lobster tags (circles) and the reference tag (square) were positioned (i.e. detected by the 3 receivers) outside of a shelter. Black symbols: observed values; white symbols: 'adjusted values' based on the fact that the reference tag was not detected during some portions of the study, even though it was always in the center of the study area (see 'Materials and methods'). CL: carapace length

known to be in the open and in the middle of the receiver array during the entire study period. When these values were adjusted for the proportion of time each day the reference tag was not detected (see 'Materials and methods'), the 10 juvenile lobsters were estimated to have spent between 0 to 77.1% of each day outside of rock shelter, with an average of 15.9%, or 3.8 h. The 10 lobsters showed high inter-individual variability in activity, ranging from an average of 0.4 h (0.5 h after adjustment) to 5.8 h (7.8 h after adjustment) spent outside of shelter every day (Fig. 2). We found no significant correlation between lobster CL and average time spent outside of rock shelter in either the observed ($r = 0.000235$, $df = 8$, $p > 0.50$) or adjusted ($r = 0.000157$, $df = 8$, $p > 0.50$) data sets. Although one individual (31.3 mm CL) may appear to have displayed greater inter-day variability in activity (Fig. 2), this high variance is at least partly due to the low number of days this individual was tracked (4 d, relative to 21 d for most other individuals).

The actograms showed considerable variability in the activity of a same lobster on different days, as well as marked variability in the activity of different lobsters, but the latter was not related to lobster body size (Fig. 3). They also reveal the diurnal cycles documented by the periodogram analyses (e.g. lobsters 33 and 47 mm CL), where lobsters are more active at night than during the day. However, for some lobster these cycles are not as easily discernable (e.g. lobsters 20.3 and 38.8 mm CL), and for all lobsters they involve varying amounts of activity during the day. The tidal cycles are not as immediately obvious from the actograms because they are not strong, but some can nevertheless be gleaned (e.g. lobster 38.8 CL) from the gradual shift in activity towards the right of the actograms (more obvious during the day) in association with the advance of tidal highs and lows by ≈ 50 min every day.

The periodogram analysis revealed no significant cycles of activity for the reference tag data (Fig. 4), which indicates that any significant cycle in the animal tags was likely the result of animal activity and not temporal biases in the system's ability to detect the tags (e.g. better detection at high tide). There were 2 significant cycles of activity shown by the juvenile lobsters over the 4–21 d they were tracked during this study: diel and tidal (Table 2). When the activity data of the 10 juveniles lobsters were pooled in a same periodogram analysis, we found that as a group these lobsters showed highly significant cycles of activity on both diel (24 h) and tidal (12.4 h) periods (Fig. 4), and the chi-squared goodness-of-fit tests indicated that

they were significantly more active at night than during the day ($\chi^2 = 40.05$, $df = 1$, $p < 0.001$) and at high tide than at low tide ($\chi^2 = 16.63$, $df = 1$, $p < 0.001$). The diel cycle of this pooled data was relatively pronounced, with 71 and 29% of all 'animal pings' being detected during the night and the day, respectively, in comparison to the null expectation of 40 and 60%, respectively, considering the number of daylight hours. The tidal cycle was less pronounced, with 55 and 45% of all 'animal pings' being detected during high tide and low tide, respectively, in comparison to the null expectation of 50% for each.

When the juvenile lobsters were analyzed separately, the periodogram analyses revealed that 6 of the 10 lobsters displayed a significant diel cycle of activity (with a peak at 24 h), and the chi-squared goodness-of-fit tests confirmed that all 6 of these lobsters were significantly more active at night (N) than during the day (D) (all $\chi^2 > 12.06$, $df = 1$, all $p < 0.05$; average observed: 0.65 N/0.35 D; expected: 0.4 N/0.6 D). These analyses also revealed that 3 lobsters showed a tidal activity cycle (with a peak at 12.4 h), being significantly more active at high tide (HT) than at low tide (LT) (all $\chi^2 > 5.65$, $df = 1$, all $p < 0.05$; average observed: 0.63 HT/0.37 LT; expected: 0.5 HT/0.5 LT). The likelihood of lobsters displaying a significant diel or tidal rhythm was not significantly correlated with their size (diel–logistic regression: $R^2 = 0.20$, log likelihood $\chi^2 = 2.658$, $df = 1$, $p = 0.103$; tidal–logistic regression: $R^2 = 0.05$, log likelihood $\chi^2 = 0.558$, $df = 1$, $p = 0.455$) (Table 2).

When the 2 activity cycles were analyzed together, all 10 juvenile lobsters showed significant differences in activity between the 4 periods (all $\chi^2 > 18.4$, $df = 3$, all $p < 0.001$), with highest activity being observed during high tides at night (observed: 0.39; expected: 0.20) and lowest activity during day low tides (observed: 0.13; expected: 0.30). Post-hoc comparisons used to assess the interaction between the 2 cycles for individual lobsters showed that the diel pattern was significant for 6 of the 10 lobsters during low tides (all $\chi^2 > 18.1$, $df = 1$, all $p < 0.001$; average observed: 0.32 DLT/0.68 NLT; expected: 0.58 DLT/0.42 NLT) and also 6 lobsters during high tides (only 2 being the same individuals as for low tide) (all $\chi^2 > 34.3$, $df = 1$, all $p < 0.001$; average observed: 0.39 DHT/0.61 NHT; expected: 0.58 DHT/0.42 NHT), and that the tidal pattern was significant for only 1 of the 10 lobsters during the day ($\chi^2 = 34.7$, $df = 1$, $p < 0.001$; observed: 0.43 DLT/0.57 DHT; expected: 0.5 DLT/0.5 DHT) and 9 at night (all $\chi^2 > 17.6$, $df = 1$, all $p < 0.001$; observed: 0.32 NLT/0.68 NHT; expected: 0.49 NLT/0.51 NHT).

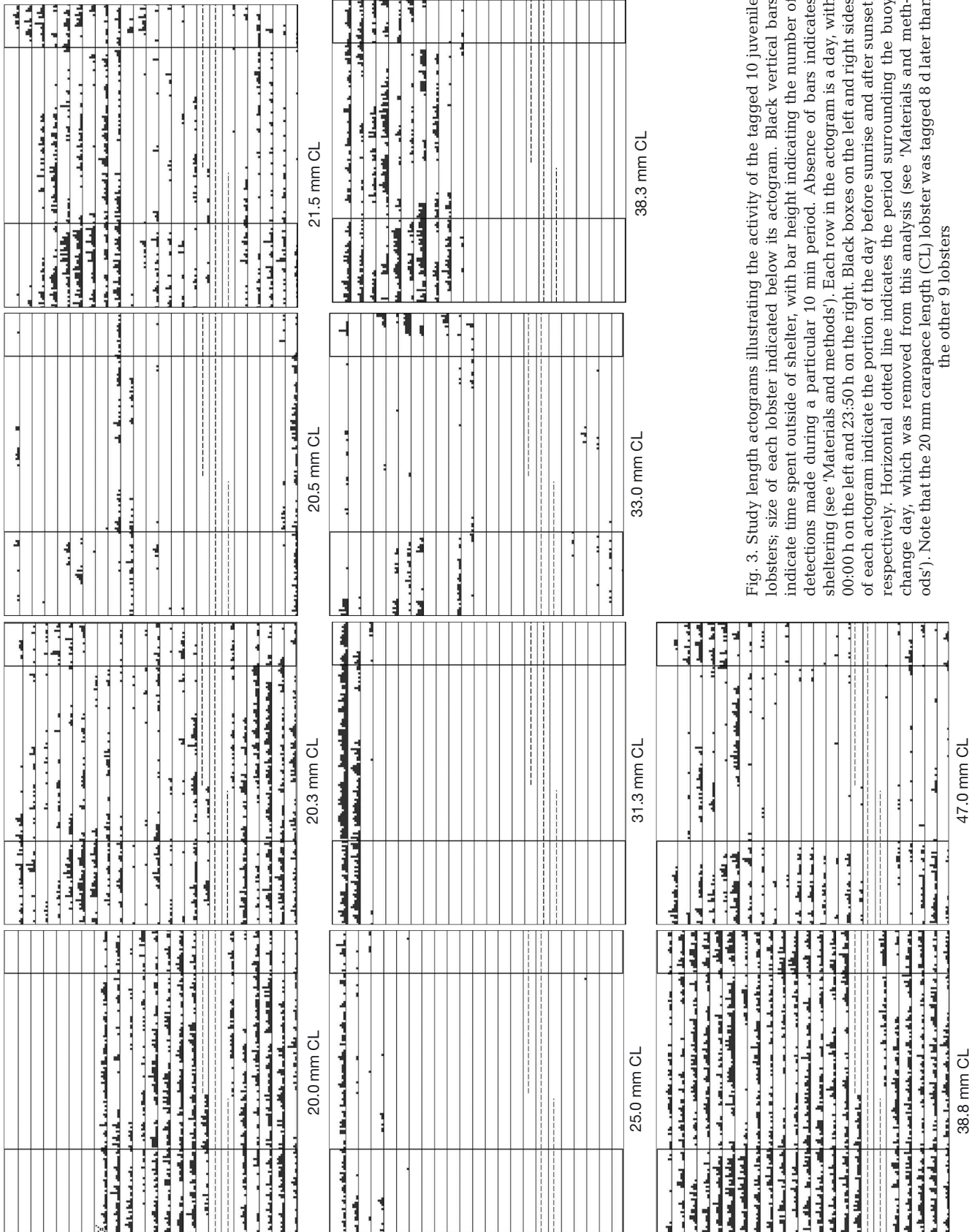


Fig. 3. Study length actograms illustrating the activity of the tagged 10 juvenile lobsters; size of each lobster indicated below its actogram. Black vertical bars indicate time spent outside of shelter, with bar height indicating the number of detections made during a particular 10 min period. Absence of bars indicates sheltering (see 'Materials and methods'). Each row in the actogram is a day, with 00:00 h on the left and 23:50 h on the right. Black boxes on the left and right sides of each actogram indicate the portion of the day before sunrise and after sunset, respectively. Horizontal dotted line indicates the period surrounding the buoy change day, which was removed from this analysis (see 'Materials and methods'). Note that the 20 mm carapace length (CL) lobster was tagged 8 d later than the other 9 lobsters

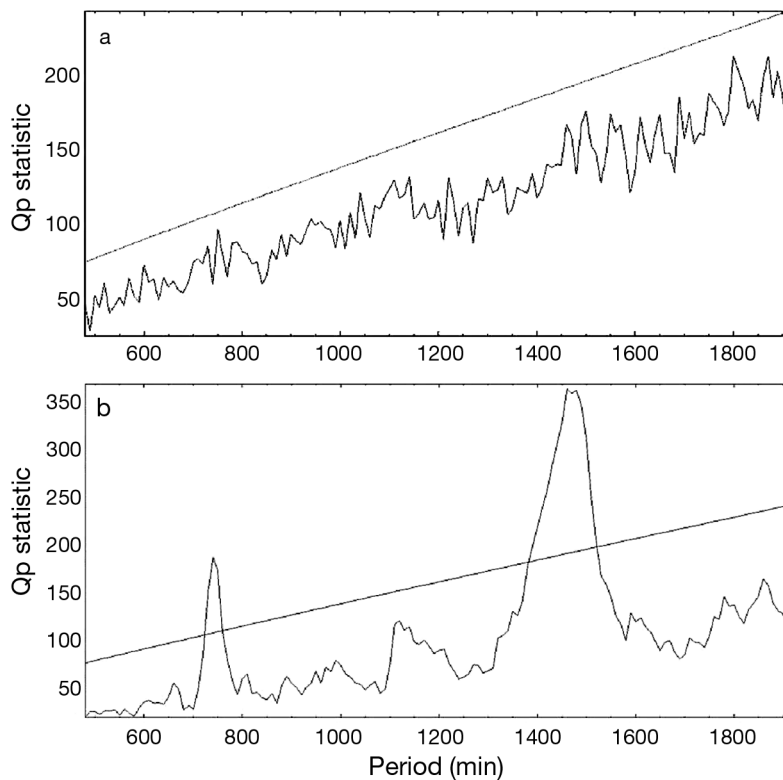


Fig. 4. Periodograms calculated for (a) the reference tag and (b) the pooled juvenile lobster tags, based on the detection (pings) of these tags by the 3 receivers. Observed values that are greater than the straight line indicate significant ($\alpha = 0.05$) rhythmicity in activity at the corresponding period (Schmid et al. 2011)

Table 2. Characteristics of the 10 juveniles lobsters used in this study, including carapace length (CL), approximate age based on CL (see Tang et al. 2015), number of days positioned during the study, evidence of cyclicity in activity (based on periodogram analysis), and the estimated number of shelter areas used during the study (based on home range analysis). Significant diel (24 h) or tidal (12.4 h) cycle was (Yes) or was not (No) observed during the tracking period for a particular lobster. Relevant information also provided for the stationary reference tag

Lobster size (mm CL)	Approximate age (yr)	Total study days	Periodogram results		No. of shelter areas
			Diel	Tidal	
20.0	1–3	14	No	No	2
20.3	1–3	21	Yes	No	4
20.5	1–3	21	No	No	1
21.5	1–3	21	Yes	Yes	4
25.0	1–3	21	No	No	1
31.3	2–4	4	No	No	2
33.0	2–4	21	Yes	No	1
38.3	2–4	10	Yes	Yes	1
38.8	2–4	21	Yes	Yes	1
47.0	2–4	21	Yes	No	1
Reference tag		21	No	No	

Field experiment: home range

The 10 juvenile lobsters displayed movements that greatly limited their dispersal during the study period (Fig. 5), only travelling between 3.1 to 8.6% of the distance away from their starting point that was expected under the random walk model, which is consistent with the hypothesis that they are central place foragers. There was no significant correlation between the size of individuals lobsters and the distance they moved away from their starting point relative to the displacement expected under the random walk model ($r = 0.000317$, $df = 8$, $p > 0.50$).

The average daily home range of the 10 tagged juvenile lobsters over the 21 d study period ranged from 27.4 up to 111.6 m², and it varied markedly between days for the same individual (Fig. 6). It must be noted that these values overestimate to some extent the true home range of individual lobsters, as the stationary tag was estimated to have an average daily home range of 8.3 m², due to precision limits of the system. We found no evidence of a gradual increase in average daily home range with increasing lobster size ($r = 0.000325$, $df = 8$, $p > 0.50$), although the largest individual, which should probably be considered in transition between the juvenile and adolescent phases (see 'Materials and methods'), did have the largest home range.

We also found no correlation between the size of juvenile lobsters and their study length home range, using the 7 individuals that were positioned for the full 21 d of the study ($r = 0.000012$, $df = 6$, $p > 0.50$). The study length home range did vary greatly between individual lobsters, but not in relation to their size; both the smallest and largest study length home ranges were recorded for 20 mm CL lobsters, and the 2 largest study length home ranges were recorded for the largest and the smallest lobsters in the study (Fig. 7).

The study length home range diagrams appeared to reveal inter-individual variability in patterns of residency and site fidelity (Fig. 8) and suggested that different individuals occupied between 1 and 4 'central place areas' over the 21 d study period (Fig. 8, Table 2). As the positioning system is only precise to ± 3 m, we cannot quantify the number of shelters

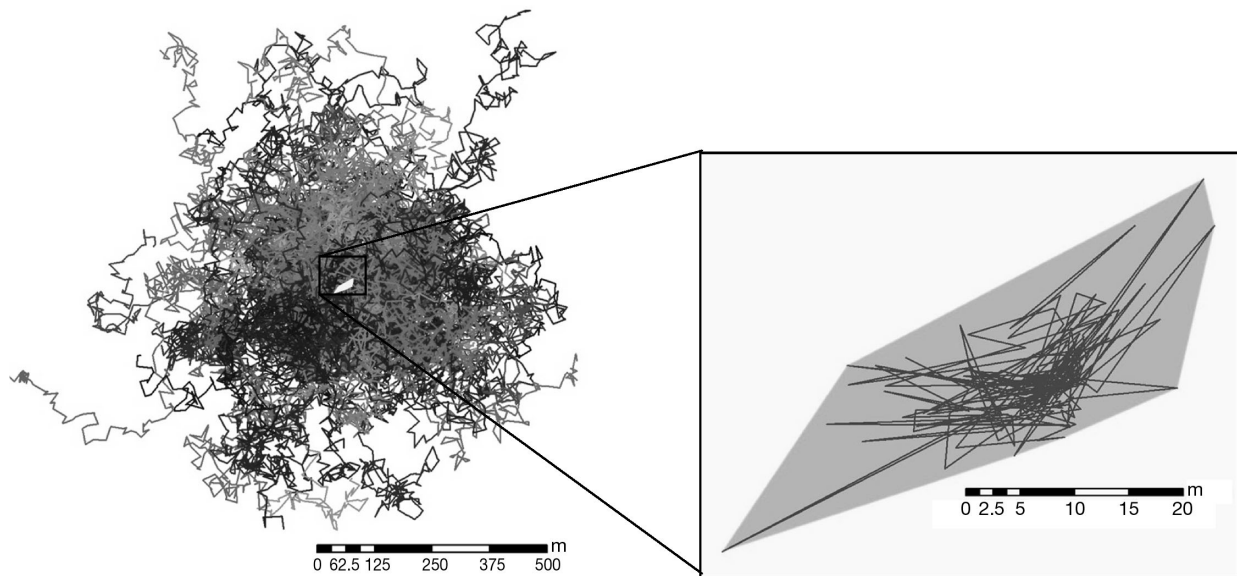


Fig. 5. Comparison of the movements recorded by the telemetry system for a 20.5 mm carapace length lobster over the 21 d study period (192 steps) (on right, and inset polygon on left) to the movements expected based on 100 runs (on left; each line is 1 run) of the random walk model for the same lobster and number of movement steps. See 'Materials and methods' for details of the random walk model

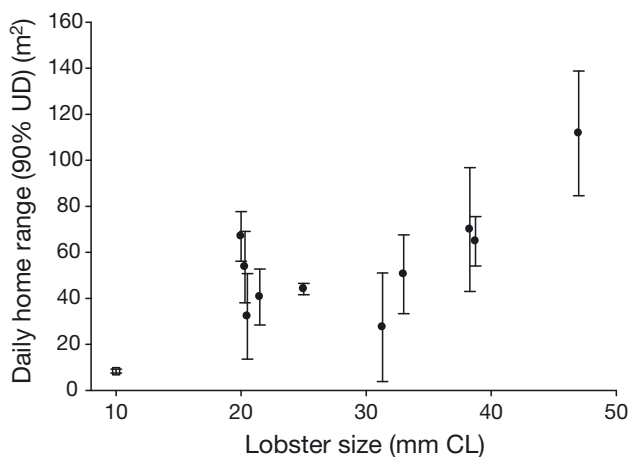


Fig. 6. Average ($\pm 95\%$ CI) daily home range (m^2) of the reference tag (open square) and the 10 tagged juvenile lobsters (black circles) over the 21 d study period, measured as the 90% activity isopleth (see 'Materials and methods') calculated by the LoCoH home range method. CL: carapace length; UD: utilization distribution

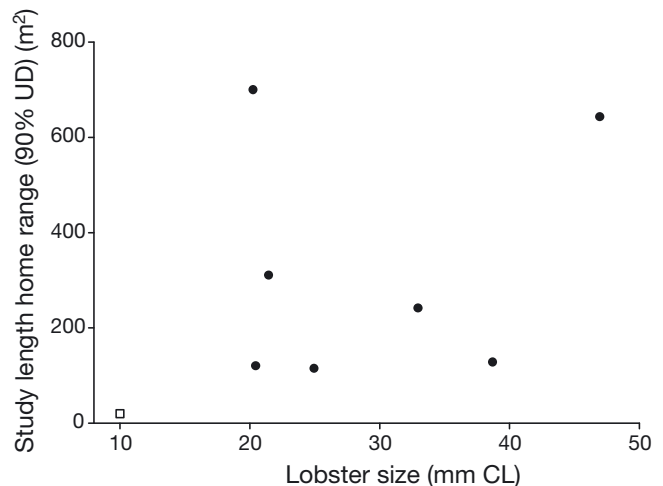


Fig. 7. Study length home range (m^2) of the reference tag (open square) and the 7 tagged juvenile lobsters (black circles) that were tracked for all 21 d of the study. The home range was measured as the 90% activity isopleth (see 'Materials and methods') calculated using the LoCoH home range method. CL: carapace length; UD: utilization distribution

each lobster used within those areas, but it is clear that some lobsters moved between areas of greater residency during the study (Fig. 8). Overall, 6 of the 10 lobsters stayed in the same shelter area over the study period, whereas 3 of the 5 smallest lobsters and 1 of the 5 largest lobsters appear to have utilized more than one shelter area (Table 2). There was no

significant correlation between lobster size and number of shelter areas used during the study ($r = -0.00533$, $df = 8$, $p > 0.50$), although there was some evidence that the likelihood of lobsters utilizing more than one shelter decreased with body size (logistic regression based on all 10 lobsters: $R^2 = 0.23$, log likelihood $\chi^2 = 2.80$, $df = 1$, $p = 0.094$; logistic regression

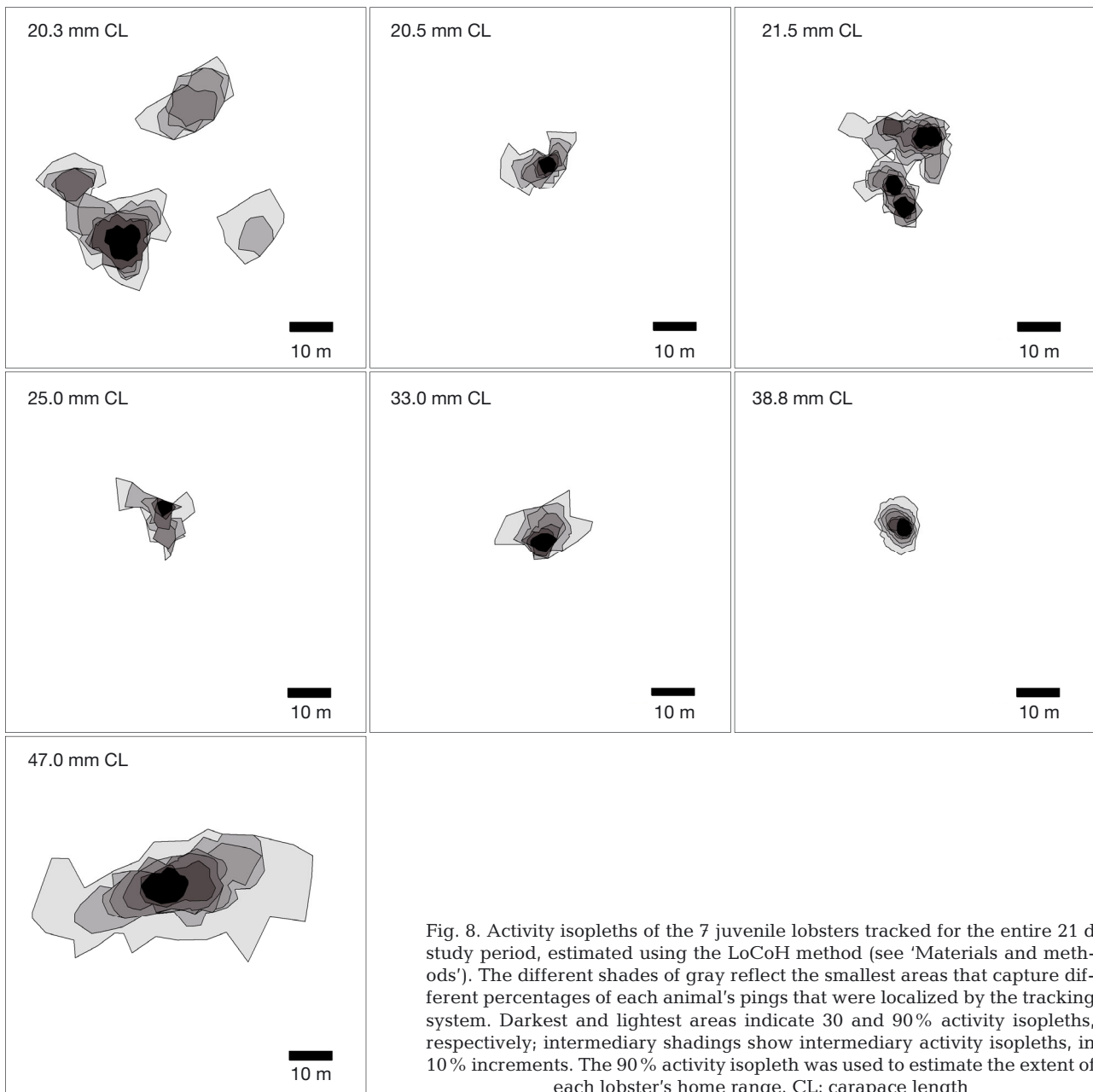


Fig. 8. Activity isopleths of the 7 juvenile lobsters tracked for the entire 21 d study period, estimated using the LoCoH method (see 'Materials and methods'). The different shades of gray reflect the smallest areas that capture different percentages of each animal's pings that were localized by the tracking system. Darkest and lightest areas indicate 30 and 90% activity isopleths, respectively; intermediary shadings show intermediary activity isopleths, in 10% increments. The 90% activity isopleth was used to estimate the extent of each lobster's home range. CL: carapace length

based on 7 lobsters tracked for the entire 21 d study period: $R^2 = 0.47$, log likelihood $\chi^2 = 3.9$, $df = 1$, $p = 0.048$).

DISCUSSION AND CONCLUSIONS

To the best of our knowledge this study provides the first empirical data concerning the activity levels and home ranges of juvenile (20–47 mm CL) American lobster *Homarus americanus* in nature. The data

confirm that juvenile lobsters are mostly nocturnal (Lawton 1987) and that they behave as central place foragers (Lawton 1987, Wahle 1992). They also reveal, however, that juveniles display frequent movements outside of shelters, and they provide no evidence of ontogenic shifts in juvenile behaviours or activity levels over the size range investigated. Finally, our results provide the first evidence that activity levels of juvenile lobsters can be influenced by the periodicity of the tides, at least in shallow waters where tidal amplitude is high.

Activity and movement of juvenile lobsters in nature: confirming current knowledge and assumptions

Our first analyses of the data ignored actual positional estimates and focused only on how frequently and when the 3 buoys of the tracking system detected the animal tags. Although these analyses use only a portion of the information available in the data, they are of considerable interest because they speak of an important dichotomy in the animals' behavior, that is, whether they are sheltered under cobble (not detected by the 3 buoys) or are outside of shelter (detected by the 3 buoys). This distinction is important, and in many regards more informative than step lengths or travel speeds, because it speaks of the animals' potential exposure to predation risk. When the activity data of the 10 juvenile lobsters used in this study (20–47 mm CL) were analyzed, the periodogram analysis and the chi-squared test showed that these juvenile lobsters were, as a whole, mostly nocturnal, which is consistent with results of Lawton's (1987) laboratory study with juvenile lobsters (20–46 mm CL) and results of other telemetry studies with adolescent and adult lobsters (61–93 mm CL) (Golet et al. 2006, Scopel et al. 2009, McMahan et al. 2013). As has been found in these other studies, though, this nocturnal bias in activity was far from complete, and 4 of the 10 lobsters did not show a significant diurnal rhythm over the course of the study, and all 10 lobsters spent some time out of shelter during the day.

Juvenile lobsters also showed evidence of a second activity cycle, one related to tides. More specifically, 3 of our 10 focal lobsters showed a significant 12.4 h cycle of activity, being significantly more active at high tide than at low tide. Similarly, when the 10 lobsters were analyzed together, they displayed a significant 12.4 h activity cycle, being overall more active at high tide than at low tide. These cycles were not very pronounced, but they were clearly present from a statistical standpoint. It is also noteworthy that when the diel and tidal cycles were analyzed together, 9 of the 10 lobsters showed more activity at high tide than low tide at night compared to only 1 during the day (and 3 when the cycles were analyzed separately in the periodograms), suggesting that tidal rhythmicity may become more apparent after more pronounced cycles of activity (e.g. diel) are somehow accounted for. These data represent the first evidence of tidal periodicity in juvenile lobsters, although our lab has observed similar circatidal rhythmicity in shallow-subtidal green crabs *Carcinus maenas* with the same telemetry system (Lynch & Rochette 2007). Experimental work would be needed

to elucidate the function of this activity pattern. Given the pronounced tidal amplitude and shallow nature of our study site (3–7 m at low tide over the study period and as low as 1.5 m during spring tide), the lobsters' reduced activity at low tide may have offered protection against waves, swell and potentially avian predators. It is unclear how consistently juvenile lobsters display such tidal rhythms in activity across the species' range, but it is possible that these are mainly limited to areas of shallow depth and high tidal amplitude, such as found at our study site.

In addition to quantifying the amount of time juvenile lobsters spent outside of shelter, we quantified the magnitude of their movements when outside of shelter, and these analyses indicated that the movements of juvenile lobsters dramatically limited their dispersal from their starting positions. In fact, the 10 lobsters only travelled 3.1 to 8.6% of the distance predicted by the random walk model, which unequivocally demonstrates that they did not randomly nor broadly roam around the landscape, but rather behaved as 'central place foragers'. Juvenile lobsters have previously been shown to be central place foragers in the laboratory (Lawton 1987, Wahle 1992), undergoing foraging excursions from a 'central' shelter, but our telemetry data are the first to provide empirical evidence of this effect in nature (Table 2, Fig. 8). Such homing to and from a central place foraging location has also been observed in adult lobsters (reviewed by Lawton & Lavalli 1995). In juveniles, homing might be particularly important in keeping individuals in productive and shelter-rich nursery habitats while they mature, and it could potentially reduce competitive interaction for shelters while on these grounds, which in turn could reduce the risk of predation associated with spending time outside of shelter. Future studies should expand on this short-term experiment to determine if the movements of juvenile lobsters change seasonally, as they are predicted not to begin undertaking seasonal migrations until they reach adolescence (Lawton & Lavalli 1995).

Activity and movement of juvenile lobsters in nature: challenging current knowledge and assumptions

The 10 juvenile lobsters tracked in this study were observed to spend on average 11.8% percent of each day (i.e. 2.8 h) outside of shelter, with average daily values ranging between 1.7% (0.4 h) and 24.2% (5.8 h) for different individuals. For most individuals,

the estimated amount of time spent outside of shelter varied markedly from day to day, generally by $\geq 22.9\%$ (5.5 h) between the least and most active days; one individual spent as little as 0% (0 h) and as much as 57.1% (13.7 h) outside of shelter on different days. It is important to note that these activity values undoubtedly underestimate to some extent the actual amount of time these lobsters spent outside of shelter, given that (1) a ping had to be detected by all 3 buoys of the telemetry system for an animal to be considered outside of shelter, and (2) the reference tag was only positioned 73.6% of each day, on average, despite the fact that it was known to be in the open for the entire 21 d study period. The fact that the reference tag was not positioned 100% of the time was presumably due to background noise or collision between tag signals. If we assume that the lobsters were as active during the time when the reference tag was not detected as they were when the reference tag was detected, then the overall average adjusted daily activity level of the 10 juvenile lobsters increases from 11.8% (2.8 h) to 15.9% (i.e. 3.8 h). The higher daily activity estimates are obviously most influenced by this adjustment, and the greatest activity level estimated for a single day and lobster increased from 57.1% (13.7 h) to 77.1% (18.5 h). It is important to stress, however, that this uncertainty concerning the exact activity level of each lobster does not affect the main conclusions of our study, and in particular, there is clearly no relation between lobster size and activity levels whether we use adjusted or non-adjusted activity level values.

This is the first study to quantify the amount of time juvenile lobsters spend inside and outside of shelter in nature, and there are thus no values to which ours may be meaningfully compared. Nevertheless, we believe that the activity levels displayed by juvenile lobsters during our study may surprise some lobster biologists, given the emphasis that has been placed in the literature on their susceptibility to predation and the expectation that this causes them to display cryptic behaviours and low activity levels (reviewed by Lawton & Lavalli 1995). Field tethering experiments have shown that juvenile lobsters are more susceptible to fish predation when tethered in the open than in the presence of shelter (Wahle & Steneck 1992, Selgrath et al. 2007) and that smaller juveniles are more susceptible to predation than larger juveniles (Wahle et al. 2013). However, there exists no empirical data on mortality rates of free-roaming juvenile American lobsters in nature, and it is likely that predation pressure on these small lobsters is not as high as it may have been in the past,

given the reduced abundance of predatory ground-fish (e.g. Boudreau & Worm 2010, Wahle et al. 2013).

The literature predicts that juvenile lobsters will display greater movements and time outside shelter as they increase in size. This increase in activity is thought to occur between the time lobsters begin to emerge from shelter (≈ 14 – 20 mm CL) to forage for food, up to the time they reach adolescence (≈ 50 mm CL) because during this period their energetic requirements increase (Lawton 1987) and their susceptibility to predation decreases (Wahle 1992, Selgrath et al. 2007, Émond et al. 2010, Wahle et al. 2013). We found no evidence of such an ontogenic shift in behaviour and activity during our 21 d study, which involved juvenile lobsters measuring 20–47 mm CL (≈ 1 – 4 yr old), but see below for lobsters 14–19 mm CL. The absence of such a relationship was observed for all metrics of activity that we quantified. For example, there was clearly no increase in time spent outside of shelter with increasing lobster carapace length; out of the 10 juvenile lobsters studied, the largest individual actually had the fourth lowest average percentage of time spent outside of shelter, and the smallest individual had the third highest average percentage of time spent outside of shelter. Similarly, the carapace length of individual lobsters was not positively related to their mean daily home range, their study length home range or the number of shelter areas they exploited during the study. In fact, we found some evidence that the likelihood of juveniles utilizing more than one shelter area during the study decreased with their size, which we believe may have resulted from smaller individuals being chased out of shelter by larger and competitively superior individuals, as has been observed previously with adolescent and adult lobsters in the field (Golet et al. 2006, Scopel et al. 2009). Our results are, therefore, inconsistent with the suggestion that the movements and activity levels of lobsters increase with body size through the entire size range used to define juveniles. This suggests that these behaviours are unrelated to predation pressure and metabolic demands over this size range of juvenile lobsters (20–47 mm CL) or that predation pressure does not vary with juvenile lobster body size as is currently assumed. In a recent telemetry study it was observed that adolescent and adult lobsters (61–83 mm CL) had smaller home ranges in the presence than in the absence of adult cod *Gadus morhua*, predators of the American lobster, but the size of these home ranges was not related to lobster body size (McMahan et al. 2013). It should be noted that the largest lobster used in our study (47 mm CL) did have a larger daily home range

than all other lobsters tracked, which may reflect the existence of a shift in activity levels between juvenile and adolescent lobsters, rather than a gradual increase throughout the ontogeny of juveniles. Overall the average daily home ranges observed for juvenile lobsters in our study ($\approx 27\text{--}112\text{ m}^2$) were much smaller than those previously observed for adolescent and adult lobsters ($\approx 760\text{ m}^2$; Scopel et al. 2009, $\approx 315\text{--}786\text{ m}^2$; McMahan et al. 2013), further suggesting the presence of a shift in behaviour between juvenile and adolescent lobsters.

One important limitation to our ability to comprehensively test the hypothesis that the activity and movements of juvenile lobsters increases during their ontogeny is that the smallest lobster we were able to tag measured 20 mm CL, which means that our study does not include individuals belonging to the 'shelter restricted' phase (Lawton & Lavalli 1995), which are thought to remain under shelter 100% of the time. We are, therefore, unable to test this assumption and to determine at what size juveniles start moving outside of shelter to forage. However, our study suggests this event occurs relatively early in life, likely during the animal's first year of existence, as the 4 lobsters we tagged that measured 20–22 mm CL (likely 1–3 yr old) were as active and held similarly sized home ranges as the larger animals tagged (likely 2–4 yr old), with the exception of the largest lobster (47 mm CL), which should perhaps be considered to be in transition between the juvenile phase (≈ 4 to ≈ 40 mm CL) and the adolescent phase (begins at ≈ 50 mm CL) (Lawton & Lavalli 1995). Further field studies will need to be completed to elucidate this important ontogenetic behavioural transition by juvenile lobsters, but telemetry will not be an option to address this question until much smaller tags are available.

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