Use of ultrasonic telemetry to determine the area of bait influence and trapping area of American lobster, *Homarus americanus*, traps

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Abstract Using ultrasonic telemetry, we measured the distance of attraction to a baited trap and then used this value to calculate the "area of bait influence". This value, along with the mean daily home range for the same animals, was used to calculate the "trapping area" of an individual trap. Lobsters (n = 25)were tracked inside a large underwater mesocosm containing a single baited lobster trap. During the study, 14 of the 25 lobsters approached the trap from a mean (\pm SEM) distance of 11.0 \pm 0.7 m. Using this distance as the radius of a circle, the resulting circular area of bait influence was 380 m². The movements of 18 lobsters were used to calculate a mean daily home range of 1002.4 ± 195.7 m². The radius of a circle with this area (17.8 m) was then combined with the mean distance of bait attraction to calculate the trapping area, defined as: the total area from which the catch is drawn (2604.0 m²; a circle with a radius of 28.8 m or 17.8 m + 11.0 m). A demonstration of the potential use of empirical data about lobster home ranges, trap dynamics and area of bait influence to improve our understanding of the relationship between the density of lobsters on the bottom and catch is included.

Keywords CPUE; trap; video; tracking; home range

INTRODUCTION

It is widely accepted that there is a complex relationship between abundance and catch-per-uniteffort (CPUE) in baited trap fisheries (Addison & Bell 1997). These issues have been reviewed elsewhere for baited trap fisheries as a whole (Stoner 2004) and for lobster trap fisheries specifically (Fogarty & Addison 1997; Addison & Bannister 1998; Bell et al. 2001; Cobb & Castro 2006). In general, the probability that a lobster will enter a trap and be captured is a function of its: (1) ability to detect the bait; (2) motivation to approach and enter the trap; (3) interaction with other lobsters in and around the trap; and (4) chances of escaping from the trap before it is hauled to the surface. Despite the inherent challenges, trying to quantify the relationship between catch and abundance remains an important goal for fisheries management.

Several empirical models have been developed to estimate abundance using behavioural information of the target species to better understand how lobster traps function (Addison & Bell 1997; Fogarty & Addison 1997; Addison & Bannister 1998; Bell et al. 2001). The majority of these models focus on either how the interactions taking place in and around the trap influence catch or how to accurately determine abundance from catch. To be able to translate catch into the actual density of animals on the bottom, two crucial model components must be understood: "area of bait influence" (ABI) and the "trappable area" (TA) of the trap. Bell et al. (2001) defined ABI (their term was "area of influence") as "the area within which the bait can be detected where it exerts a measurable influence on orientation and movement of the target species". Studies on the western rock lobster, Panulirus cygnus, and edible crab, Cancer pagurus, indicate that the ABI may

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be as far as 120 or 48 m, respectively (Jernakoff & Phillips 1988; Skajaa et al. 1998). However, it is difficult to determine in these studies if the animals approached the trap because of bait attraction, or if they were returning to the same place where they fed the previous day. McQuinn et al. (1988) used a slightly different approach to determine the distance travelled by whelks (Buccinum undatum) to reach a baited trap in 24 h. They found that the majority of whelks captured in the trap came from a distance of <18 m (McQuinn et al, 1988), which is similar to the maximum distance of bait attraction (20 m) estimated for the same species by Lapointe & Sainte-Marie (1992). To our knowledge, despite an abundance of data on the olfactory system of lobsters (Atema 1995), it is not known how far the smell of bait travels before it can no longer be detected by a lobster, or how spatial and temporal variability in the environment, and the physiological state of lobsters, influences their responses to odorants. Moreover, it is not clear if all lobsters will respond to particular odours if they can perceive them. Currently, one of the best estimates of the ABI was obtained from a study on American lobster, Homarus americanus, by Smith & Tremblay (2003), using traps fished a known distance apart. They concluded, based on measuring the relative catch and composition of catch in adjacent traps, and traps at the end of the string versus the middle, that the ABI is 9-17 m (Smith & Tremblay 2003). A main goal of the present study was to expand upon the work of Smith & Tremblay (2003) using a different approach. We tracked the movements of individual lobsters in the area around a single lobster trap and measured the ABI based upon the expression of a measurable change in orientation and movement (Bell et al. 2001) when they walked in the vicinity of a trap.

Effective fishing area (EFA) was initially described by Miller (1975), as the area around a baited trap in which all animals have a 100% probability of capture. Traditionally, EFA is measured as the catchability coefficient (q) (Miller et al. 1987, Miller 1995). To determine the EFA, divers first conduct a survey to determine the density of lobsters in the area being fished. They then divide the catch per trap by the density to yield the EFA (Miller 1995). So, if the CPUE and the density of lobsters are known, then it is conceptually possible to estimate the area (in units of $m^2/trap$) required for a trap to capture that many animals, based on the assumption that all lobsters in that area are actually captured. The concept of EFA has been a relatively inexpensive statistic to develop and it has proven useful for comparing the relative catchability of lobsters in different seasons (Tremblay 2000), or of different sizes or sexes (Tremblay et al. 2006). Using this approach, reported estimates of the EFA range from 7 to 860 m² (Miller 1989, 1995; Tremblay 2000; Tremblay et al. 2006).

Despite its usefulness, estimates of EFA determined using this approach are often difficult to interpret, because EFA "is a purely notional area of sea bed containing as many animals as were trapped" (Bell et al. 2001), not the actual area from which the lobsters captured in the trap were drawn (trapping area). There are several reasons why EFA and trapping area differ. First, lobster traps are inefficient and capture only a small fraction of the lobsters present in a certain area as has been demonstrated in the laboratory (Karnofsky & Price 1989), as well as in the field (Jury et al. 2001). This inefficiency is primarily the result of intra-specific antagonistic interactions outside of and within traps, so that they quickly saturate (Richards et al. 1983; Jury et al. 2001). Second, not all animals that enter the area of bait influence will approach the trap, for reasons that are not clearly understood. Finally, during the soak time of a trap, lobsters will wander into the area of bait influence from an unknown distance. Therefore, although previous studies using EFA acknowledge the limitations of the approach, given the dynamics of the trapping process, there remains a need to develop a method for estimating the density of lobsters on the bottom that is based on known values for trap efficiency, lobster home ranges, and the ABI.

MATERIALS AND METHODS

In this study we enclosed a large area of the ocean floor so that we could limit lobster movements to this region and ensure that only a single lobster trap was being fished in a given area. We then used a fixed array ultrasonic telemetry system (see below) to continuously track lobsters equipped with ultrasonic tags during days with and without a trap deployed within the mesocosm. Data from days without a trap present were used to calculate daily home ranges, whereas data from days with the trap present were used to calculate the ABI. We then used a combination of home range values, ABI measurements and data concerning trap dynamics from Jury et al. (2001), to calculate the daily trapping area of a standard lobster trap.

Study site

This study was conducted in a cove offshore of New Castle Island, New Hampshire, United States, from June to October 2002. All lobsters were tracked within a large (3125 m²) underwater mesocosm/ enclosure that has been previously described (Golet et al. 2006). The average depth within the mesocosm was 7-8 m and the bottom consisted of two distinct habitat types: sand and fine sediment (75%) and eelgrass beds (25%). Bottom temperatures were monitored with HOBO temperature data loggers (Onset, Inc, United States) and ranged from 8 to 19°C during the course of the study. Current speeds and directions were monitored with a current meter (Model 2ACM-CBP-S, Falmouth Scientific Inc, United States) located 1 m above the bottom in the centre of the enclosure and ranged from 0.03 to 28.9 cm s⁻¹. The current direction shifted throughout the tidal cycle, with no dominant direction.

Tracking system

A commercially available ultrasonic tracking system (VRAP model, VEMCO Ltd, Canada), consisting of a three-buoy array and base station, was deployed at the site. The buoys were moored along the sides of the enclosure and communicated to a shore station that was located approximately 300 m from the study site. The system plotted real-time positions of tagged lobsters based on signal arrival times received by each buoy (for a complete description of the tracking system see Klimley et al. 2001). The buoys listened to each transmitter for 25 s and then used the best 70% of the signals received to plot an average X,Y position. A group of 2-4 lobsters were tracked at any given time, with positions calculated every 2 min for each animal. Under optimal conditions it has been estimated (VEMCO Ltd, www.vemco. com), and determined experimentally in the field (Tremblay et al. 2003; Golet et al. 2006), that the system has a resolution of <2 m when animals are within the array triangle. One of the main reasons for using the mesocosm was to restrict the movements of lobsters to the centre of the array triangle where the resolution of the VRAP system was optimal. Crystal controlled transmitters (V8SC-2L, 28 mm × 9 mm, 3 g in water) that produced an ultrasonic pulse every 2 s, were pre-set to transmit at a fixed, stable, frequency (63–84 kHz) so that multiple tags could be tracked at any given time. A single reference transmitter (Vemco, V16) was anchored in the centre of the enclosure and data from this transmitter were used to compensate for positional errors owing to buoy movements.

Tracking protocol

Thirty-six lobsters of both sexes, with carapace lengths (CL) ranging from 62 to 87 mm, were tracked during the study period. Typically, four lobsters at a time were tracked for at least 5 days. At the beginning of these trials, SCUBA divers captured two male and two female lobsters that were already in residence within the mesocosm and attached ultrasonic transmitters onto the dorsal carapace of each lobster by connecting a cable tie, to which the transmitter was connected inside a section of Tygon[®] tubing, between the second and third pair of walking legs. The tagging process took 2-3 min, lobsters were not brought to the surface, and they were immediately released at the point of capture to minimise handling artifacts. All lobsters removed from shelters for tagging were returned to the same shelter. No ovigerous lobsters were used in this study. Upon completion of a trial, divers recovered the lobsters, removed the transmitters and released the lobsters outside of the mesocosm. Of the original 36 animals tagged, 11 were not used for subsequent data analyses because they lost their tags or escaped the enclosure and moved outside the detection range of the system within 3 days. Therefore, the results presented are based on data obtained from the remaining 25 lobsters.

After 2 days of continuous tracking, a modified double-parlor lobster trap (Jury et al. 2001) was baited and deployed inside the enclosure. Because lobsterfishers refrained from fishing within the mesocosm, it was the only trap in the area. The kitchen (entrance compartment) held a bait bag containing approximately 1 kg of fresh or frozen herring. The parlor (holding compartment) contained two standard escape vents, $15.9 \text{ cm} \times 4.5 \text{ cm}$. A video camera was attached above the trap using a PVC frame. A lowlight, black-and-white, CCD video camera (0.05 lux, Model RHP-320WP, Rock House Products, United States) was mounted 1 m above the trap. The field of view included the entire trap and about 0.5 m around the trap. A custom-built buoy on the surface provided power to the camera via a waterproof electrical cable and also received video signals from the camera. It housed three 12-volt batteries (Yuasa Inc), one CCTV 900 Rx video transmitter (Eye Spy video systems, CD3 Security Systems, United States), and a timer. Signals from the camera were transmitted from the surface buoy to the University of New Hampshire Coastal Marine Laboratory and recorded with a Panasonic AGRT600 time-lapse video recorder.

The trap was fished for 24 h (most traps saturate within this time; Richards et al. 1983), hauled, baited

again, and deployed each day, for a total of 3 days. Although this approach is not typically used in the commercial fishery, it did minimise any potential loss in trap attractiveness owing to bait degradation. In general, the trap was deployed in an area of the enclosure that had not been visited by any of the animals that were being tracked during the previous 2 days of the experiment. The position of the trap was monitored at all times using a VEMCO transmitter (V16) attached to the trap.

Data analyses

There are a number of factors that influence the accuracy of the positional fixes obtained using the VRAP tracking system. To improve accuracy, all data were filtered to remove points that appeared to be erroneous (see Golet et al. 2006 for details). This filtering process removed approximately 46% of the points, yielding an average of 312 positional fixes for each animal during a 24 h period.

Individual lobster tracks were plotted with the position of the trap to identify which lobsters approached the trap. Lobsters were identified as approaching the trap if they turned sharply (an angle of >30 degrees from their previous localisation) toward the trap, walked directly toward it, and then remained for more than 5 min at the trap. If a lobster was expressing an erratic pattern of walking before approaching the trap, it was not used for our calculations because it was not clear when it detected the bait and made the decision to move toward the trap. If lobsters only walked past the trap but did not change orientation, it was not considered to be an approach. When an approach was identified, the distance from the trap to the point where the lobster first turned toward the trap was measured-referred to as the distance of attraction (DA). The area of bait influence (ABI) was then determined using the mean DA as the radius to calculate the area of a circle around the trap. It is likely that the shape of the odor plume was not a circle (Lokkeborg 1990), but given the variable and dynamic direction of the current within the area tested, over a 24 h period, it was difficult to determine what shape was best to use. Time spent at the trap was determined by calculating the duration a lobster spent inside the ABI for that particular deployment. In many instances, time spent at the trap was confirmed through observations of the videos obtained during each trial. The DA and subsequent ABI were calculated from 14 lobsters that approached the trap, and the mean daily home range from 18 of the original 25 lobsters tracked (Scopel et al. unpubl. data). These data were then used to estimate the trapping area (TA).

Daily home ranges were calculated using the Animal Movement Analysis Extension (AMAE) for ArcView 3.3 (ESRI, United States). All "days" began at 0000 h and ended at 2400 h midnight. The home range for each day that an animal was tracked was calculated using the fixed kernel method, which generates a use distribution (UD) that describes the probability of finding an animal within a given area. The 95% UD was used to designate the daily home range. Only 18 animals were used to calculate the mean home range size because 3 full days of data were not available for all animals, and several animals were excluded from data analysis because they expressed patterns of movement that were not consistent with a lobster that was a resident inside the mesocosm. These animals spent considerable time near the mesocosm wall, and were consistently active, as if they were attempting to move to a new location (Golet et al. 2006).

RESULTS

Of the 25 lobsters tracked while a trap was deployed, 14 (56%) approached the trap at least once (Fig. 1A), but only one was captured in the trap. Six of these 14 lobsters approached the trap more than once during the 3 days it was deployed. Four of the lobsters approached the trap more than once within a given 24 h soak period. The average DA was 11.0 ± 0.7 m (mean \pm SEM), but varied considerably between and within runs (5-21 m). Using the DA as the radius of a circle, the average ABI was 380 m². On 27 occasions lobsters passed within the ABI but did not move toward the trap (Fig. 1B). The full range of size classes of lobsters studied approached the trap, ranging from a 62 mm CL female to an 87 mm CL male. Ten of the 14 lobsters that approached the trap were female. The one lobster that was captured was an 82 mm CL female.

The time spent near or in the trap was relatively variable ranging from 10 min to over 12 h, with longer times possibly owing to lobsters being transiently retained inside the trap before escaping. Lobsters approached the trap at all hours of the day and night; 77% of the approaches took place at night and 33% during the day. The only lobster captured entered the trap at 1720 h and remained inside the trap until it was hauled the following morning.

The mean daily home range (n = 18) was 1002.0 \pm 195.7 m² (mean \pm SEM), which is equivalent



Fig. 1 Representative tracks of lobsters walking in the vicinity of a lobster trap. A, Female lobster (closed circles, 78 mm carapace length (CL)) approaching a baited trap (open circles) at night. Arrows illustrate direction of movement and time of day is indicated on two occasions. At 2309 h, the lobster turned sharply and approached the trap from a distance of 8.3 m. B, Female lobster (80 mm CL) walking by a trap. Points were obtained every 2 min. The scatter of points that indicate the position of the trap in A are the result of small positioning errors by the VRAP system.

to a circle with a radius of 17.8 m. We used a combination of home range data and ABI data to calculate trapping area (Fig. 2). We assumed that for a lobster to be captured, it needed to wander within the ABI during the soak time, and thus its home range would have to overlap that area. Therefore, the radius of a circle encompassing the trapping area would have a radius equal to the DA (11.0 m) plus the radius of the mean home range (17.8 m), or 28.8 m. A circle with this radius yields a trapping area of 2604.0 m². Because home range size was not correlated with lobster size within the size range examined (Scopel et al. unpubl. data), the trapping area also did not correlate with lobster size.

DISCUSSION

Attraction to, and entry into, stationary gear depends on a variety of factors including, but not limited to, the motivational state of the animal (Zimmer-Faust



Fig. 2 Method used to calculate trapping area. Mean (\pm SEM) home range for lobsters investigated in this study was 1002.0 \pm 195.7 m², represented by a circle with a radius of 17.8 m. The mean distance of bait attraction was 11.0 \pm 0.7 m. Therefore, the furthest an animal could be from a trap and still wander within the area of bait influence during a 24 h soak time would be 28.8 m, yielding a circular trapping area of 2604 m².

et al. 1996), the quality, concentration, spread, and shape of the bait delivery system and subsequent odour plume (McQuinn et al. 1988; Lokkeborg 1990), and behavioural interactions around the trap (Richards et al. 1983; Jury et al. 2001; Stoner 2004; Archdale et al. 2006). In this study, we used ultrasonic telemetry to determine that, on average, American lobster are capable of detecting bait and making directed movements toward a trap from a distance of 11 m or less. The only comparable values obtained for American lobster were derived from trap studies by Smith & Tremblay (2003) and, at 9–17 m, they are similar to our measurements. Jernakoff & Phillips (1988) used electromagnetic telemetry to track juvenile western rock lobster P. cygnus and they observed animals approaching a trap from distances of up to 120 m. However, in their study it was difficult to determine if the lobsters detected the bait from this distance, or if they were returning to a known foraging area. Skajaa et al. (1998) reported bait attraction distances of up to 48 m for crabs (C. pagurus), which is also much greater than we observed. Skajaa et al. (1998) used speed of locomotion to determine when crabs were locating baited pots, whereas we used orientation towards the trap, in part because we did not observe lobsters altering their speed of locomotion when approaching traps. In addition, there may be differences in the olfactory-mediated behaviours of crabs and lobsters that influence the ABI for each group of animals. Many factors could lead to the range of results obtained in our study and others, including the type and amount of bait, currents (Zimmer-Faust et al. 1995), the motivational state of the animals (Zimmer-Faust et al. 1996), environmental conditions, the methods used to determine the ABI, and the presence and quality of competing odours and cues.

The amount of time lobsters spent near traps varied. The average time spent in the area of attraction was 81 min, and ranged from 10 min to over 12 h. These values are comparable to those recorded by Jernakoff & Phillips (1988) for western rock lobster. In their study, the average time spent at a trap was 3 h and 50 min, and ranged from 35 min to over 9 h (Jernakoff & Phillips 1988). In both studies, it was not possible to determine why lobsters spent so much time near the traps unless a trap was concurrently observed by video. We have observed and quantified the movements of lobsters in and around traps (Jury et al. 2001) and there are many reasons why they might remain in the vicinity of traps for so long. First, lobsters approach many times before actually entering the trap and, while outside of the trap, there are many agonistic encounters with other lobsters (Jury et al. 2001). Second, once they enter a trap they have a 90% chance of escaping from it, and once outside they might enter again (Jury et al. 2001). Low entry and retention rates of individual lobsters likely accounts for the finding that we only captured one of the 14 lobsters that approached the trap in this study. On average, lobsters of the size tracked in this study remain in a trap for less than 30 min (Jury et al. 2001), so feeding and retention in a trap is likely not the main factor that determined the amount of time they remained near the trap. Additional studies of lobster behaviour in the vicinity of traps under field conditions will be necessary to better understand the types of behaviours that occur at some distance from the trap and what factors influence their approach and entry rate. Studies of in situ animal behavior in response to traps, using multiple cameras, have recently been carried out by Mills et al. (2005), and the use of long-term continuous monitoring in situ is becoming more common in fisheries research (Stoner 2004).

In the present study, several lobsters returned to the trap multiple times. Four lobsters visited the trap more than once during a 24 h soak period, and 6 of the 14 lobsters that visited the trap did so on consecutive nights. Jernakoff & Phillips (1988) also reported that on five occasions rock lobster visited the trap on consecutive nights, and Skajaa et al. (1998) noted that 3 crabs returned to the trap several times. Multiple excursions to the trap may not necessarily indicate that animals fed the first time and then became hungry, because many lobsters that approach a trap do not enter, most often owing to interactions with conspecifics inside the trap (Richards et al. 1983; Jury et al. 2001). These data further substantiate the view that only a small proportion of lobsters that visit a trap are captured.

Approaches occurred at different hours of the day, but were most prevalent at night. This finding is consistent with our previous demonstration, in the same area, that although lobsters had an overall tendency to be nocturnal, daytime activity was also common (Jury et al. 2001, 2005; Golet et al. 2006). Karnofsky et al. (1989) recorded no differences in the number of lobsters caught in the day versus the night during a 2-month trapping study in a mesocosm in the laboratory. Wolcott & Hines (1989) noted that blue crab, Callinectes sapidus, foraged and fed with the same frequency during day and nighttime periods. In contrast, spiny lobsters appear to be considerably more nocturnal in their behaviour patterns, which is reflected in their behaviour around traps and subsequent catch (Jernakoff & Phillips 1988; Herrnkind & McLean 1971). These differences in the daily patterns of behaviour between groups of lobsters may result from variable risks of predation that are species- or location-specific.

The finding that 11 of the tagged lobsters did not enter the area of attraction during the entire period that the trap was deployed, even though they were always within 50 m of the trap within the mesocosm, highlights the variability in behaviour of individuals. In addition, many lobsters passed within the ABI and did not approach the trap regardless of the direction of the current. It seems likely that they were aware of the trap, but were not motivated to approach it. Similar observations were made by Jernakoff & Phillips (1988) and Skajaa et al. (1998). Studying the interactions of lobsters and traps in a large indoor mesocosm, Karnofsky et al. (1989) found that up to 40% of large lobsters were not caught despite being offered a baited trap on 20 different occasions over 2 months. These authors propose that certain portions of the lobster population may not be trappable, at least at certain times (Karnofsky et al. 1989). What motivates lobsters to approach traps remains an important area of investigation.

Historically, catchability coefficients have been used, in part, to estimate abundance based on catch in commercial traps. This method is susceptible to bias introduced by diver estimates that often misrepresent certain portions of the population, as well as from behavioural interactions that affect catch in the trap (Jury et al. 2001). For this reason, estimates of the trapping area in this study are considerably larger than the EFAs previously calculated using catchability coefficients (Miller 1989, 1995; Tremblay et al. 1998, 2006; Tremblay 2000). EFAs from these studies ranged from 7 to 860 m², whereas our estimate for the trapping area was 2604 m².

One of the overall goals of this study was to demonstrate if it is possible to estimate the density of lobsters on the bottom based on catch in traps. In a previous study (Jury et al. 2001), we determined the percentage of lobsters that approach a trap that enter, and the percentage of those entering that are ultimately captured. Using these values, we estimated the density of lobsters on the bottom, based on catch, using the following approach. In this study, the average CPUE was 2.75. We estimated, based on Jury et al. (2001), that only 6% of the lobsters that entered the trap were captured, so 45 lobsters must have entered the trap in 24 h to yield a CPUE of 2.75. Based on previously published research (Jury et al. 2001) and our own observations (W. H. Watson and S. Jury unpubl. data), we estimated that one of every three lobsters that approached the trap entered it. Thus, if 45 lobsters entered, then 135 must have approached the trap. We also know from this study that only 60% of the lobsters that moved into the ABI approached, so 225 lobsters most likely passed within the area of attraction and those 225 lobsters represent all the lobsters with home ranges that overlapped the ABI, or all those lobsters within the trapping area. Thus, if the trapping area was 2604 m², then the density of lobsters on the bottom would have been 0.086 lobsters/m². During the course of this study, on 4 diver surveys of the mesocosm, we counted a total of 577 lobsters and determined that the mean lobster density within the mesocosm was 0.090 lobsters/m² (W. H. Watson and S. Jury unpubl. data). In an earlier study, conducted 5 km away on a similar substrate, we conducted simultaneous trap and diver surveys on 32 occasions and found that the density of lobsters varied widely on a seasonal basis, from 0.001/m²-0.077/m² (Watson & Jury unpubl. data). The mean EFA was 87.5 m², which is substantially lower than the trapping area determined in the current study (2604 m²). This discrepancy between EFA calculated in the traditional manner and our estimate of trapping

area suggests that further research is necessary to determine the optimal method for estimating lobster density based on catch.

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