PATTERNS OF DIEL ACTIVITY AND MOVEMENTS OF THE AMERICAN LOBSTER, *Homarus americanus*, AS DETERMINED BY ULTRASONIC TELEMETRY

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Patterns of Diel Activity and Movements of the American Lobster, *Homarus americanus*, as Determined by Ultrasonic Telemetry

by

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A Thesis Submitted to the School of Graduate Studies in Partial Fulfilment of the Requirements for the Degree of Master of Science

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ABSTRACT

The diel activity and nocturnal movements of the American lobster, *Homarus americanus*, were studied using a fixed hydrophone array tracking system at Broad Cove, Conception Bay, Newfoundland. Twenty lobsters tagged with ultrasonic transmitters were monitored at various times between September, 1987 and August, 1990, providing 291 nights of tracking data of which 246 were complete (i.e. an animal was monitored for the entire period of darkness). Positional information on active lobsters was recorded every two minutes, providing both temporal and spatial information on activity and movements. It was assumed that tagging did not have a pronounced or prolonged effect on the activity or movements of subjects.

Lobsters were active on 28.5 % of all tracking nights. Time of onset of activity in the initial shelters averaged 1.5 h after sunset while time of onset of movement from them averaged 2.4 h after sunset. Lobsters were active at or within the final shelter an average of 52 min while the average time of cessation of activity at the final shelter was 5.7 h after sunset. The duration of the activity period, which corresponded to the interim between onset of activity at the initial shelter and cessation of activity at the final shelter, ranged from 6 min to 12.8 h with a mean of 4.0 h. Total out-of-shelter time ranged from 4 min to 12 h with a mean of 2.3 h. The out-of-shelter period was characterized by movement or stationary behaviour. Behaviour was considered stationary if the transmitter position remained the same for a minimum of five minutes. Otherwise, the lobster was considered to be moving. Average movement times and out-of-shelter stationary times were 1.3 h and 1.2 h, respectively, while respective ranges were 4 min to 6 h, and 0 to 10.2 h.

There was also considerable variation within and between individual lobsters with

respect to distance moved. Two measures of distance were calculated; the maximum distance (MD) of a lobster from its initial shelter and the approximate total distance (ATD) moved by a lobster while out-of-shelter. The averages of maximum distance from the initial shelter and approximate total distance moved were 24 m and 64 m, respectively. The respective ranges of these two variables were 2 to 74 m and 5 to 361 m. On average, large lobsters (> 81 mm carapace length) moved a maximum distance of 27 m from the initial shelter compared to 21 m for small individuals (< or = 81 mm carapace length). Average approximate total distance moved was essentially the same for both size groups. Movements were either simple (mostly straightline movement with little or no path crossover) or complex (numerous abrupt direction changes with much path crossover). Both types were characterized by extensive, wide-ranging patterns and restricted, tight patterns.

Thirty percent of the lobsters returned to the same shelter on the same night while 25 % of the lobsters returned to a particular shelter after periods of absence exceeding one day. Certain shelters appeared to be preferred by either one individual or numerous individuals. Shelter fidelity was quite variable between individuals. Some lobsters used the same shelter numerous times while others changed shelters during each activity bout. The average entrance height : width ratio of shelters occupied (0.96) by monitored lobsters was only slightly lower than that of unoccupied shelters (0.97).

Over seventy percent of the total stationary time occurred in areas with boulder and outcrop substrate. The greatest percentage of total stationary time (49 %) occurred in areas with scattered horse mussel and green sea urchin distributions.

Large lobsters (> 81 mm carapace length) moved more frequently (32.5 % vs. 28.8 %) than smaller ones (< or = 81 mm carapace length) but the smaller individuals averaged

longer activity bouts (5.1 h vs. 2.8 h). Large males (35.3 %) and small females (38.7 %) were active more frequently than small males (21.4 %) and the large female (21.3 %). Tagged ovigerous and molted individuals displayed activity consistent with the behaviour described in literature for lobsters in these physiological conditions. Tagged individuals were less active at times of oviposition and molting.

In general, activity was greatest at times when water temperature exceeded 8° C (after July 1). Storm events sometimes resulted in the downslope movement of tagged individuals. Lobster activity was slightly higher at times of new moon and first quarter moon compared to times of full moon and last quarter moon.

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A special thanks belongs to 'Robbie' who lived nearby the tracking station. His youthful enthusiasm brought many a grin to my face.

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Another special thanks to Niki who put up with my constant complaining and the frequent cheques written to pay continuance fees.

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Finally, three cheers to the individual or individuals who were responsible for the 'seven year limit'.

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INTRODUCTION

The American lobster, *Homarus americanus* (Milne-Edwards), is a decapod crustacean distributed throughout the waters of the continental shelf of the western North Atlantic from the Strait of Belle Isle to South Carolina (Herrick 1909; Phillips et al. 1980). Known depths at which it is found range from 1 m below low tide to > 700 m in submarine canyons off the Continental Shelf, south of the southern Scotian Shelf (Herrick 1909; Cooper and Uzmann 1980; Phillips et al. 1980). This species is important for both commercial and scientific reasons. It has been a valuable target species for major fisheries in both Canada and the United States since about 1840 (Dow 1980) and has therefore been the subject of numerous scientific investigations. Besides its commercial importance, the American lobster represents an "excellent and fertile substrate for physiological, biochemical, and neurobiological research" because it is large, long lived, abundant and ecologically consequential (Phillips et al. 1980).

1.1 Lobster Movement

The broad aspects of American lobster life history and behavior are relatively well known. Studies under both natural and laboratory conditions have provided much information about this animal. An aspect of the American lobster's behavior which has received much attention is its pattern of movement, especially over distances measured in kilometers (i.e. migration). Migration can be defined as directed simultaneous movement by a large segment of a population over large distances, usually on a seasonal basis (Ennis, pers. comm.). Some lobsters migrate to deeper water during the winter months and back inshore to shallower, warmer water in the springtime (Uzmann et al. 1977; Fogarty et al. 1980; Campbell and Stasko 1986). Various populations display different scales of migration. American lobsters which display large scale migration include those on the Scotian Shelf (Campbell and Stasko 1985; Pezzack and Duggan 1986; Campbell 1989), in the Bay of Fundy (Campbell 1986; Campbell and Stasko 1986), off Prince Edward Island (Wilder 1963), and off the northeastern U.S. coast (Morrissey 1971; Fogarty et al. 1980; Krouse 1980). Lobsters tagged off Grand Manan, for example, showed seasonal shallow-deep movements exceeding 20 km, with recaptures in shallow water (< 20 m) during summer-fall and in deep water (> 200 m) during winter-spring (Campbell 1986). Some lobsters display homing behaviour as evidenced by their return to essentially the same region after more than 10 months and 200 km of movement (Pezzack and Duggan 1986). Others appear to be more nomadic, seeming to move inshore and offshore in a more random fashion without homing to previously visited locales (Harriman 1952; Spurr 1974).

Similar migratory behaviour is evident in other lobster species. The rock lobster, *Jasus edwardsii*, for example, which was monitored through tagging studies in New Zealand, reportedly migrates seasonally over distances exceeding 20 km (Street 1969; Annala 1981; McKoy 1983; Annala and Bycroft 1993).

Stasko (1980) discussed the hypothesis that lobsters in the Gulf of St. Lawrence and around Newfoundland do not undertake long distance movements. He concluded that lobsters in the southern Gulf of St. Lawrence appear to be restricted in their movements with the average distance between release and recapture being < 15 km, and that they may also undergo seasonal short-distance movement between shallow water in the summer and deep water in the winter. Lobster size appears to be an important factor in the extent of movement since larger, sexually mature individuals demonstrate the most migratory behaviour (Krouse 1980). Stasko (1980) reported that Newfoundland lobsters appear to be restricted to shallow waters, mostly in large bays, with no demonstrated movement between bays, and that they exhibit short-distance seasonal movements between shallow and deeper water (Stasko 1980). However, some individuals do disperse considerable distances (Templeman 1935, 1940). Ennis (1983) also reported that the depth distribution of Newfoundland lobsters changed seasonally, but usually the extent of the upslope-downslope movements is less than 100 to 200 m.

While some data has been obtained on the time of peak diel activity and the use of specific shelters (Ennis 1983, 1984a; Karnofsky et al. 1989a, 1989b; Haakonsen et al. 1993), a gap exists in our understanding of the fine-scale localized movement of lobster. For example, little is known about the frequency of movement of individuals, the temporal and spatial extent of their movements, or the functions of out-of-shelter activity. Need for the study of these aspects of activity and the potential value of ultrasonic telemetry in such studies was identified by Caddy and Campbell (1986).

Numerous studies in both the laboratory and field have shown that *Homarus americanus* is primarily nocturnally active (i.e. moving outside of the shelter during periods of darkness) (Zeitlin-Hale and Sastry 1978; Ennis 1983; Lawton 1987; Karnofsky et al. 1989a; Koike et al. 1993; Spanier et al. 1994). Such nocturnal activity appears to be characteristic of other species of lobster, including *Nephrops norvegicus* (Chapman and Johnstone 1975), *Panulirus cygnus* (Jernakoff 1987; Jernakoff et al. 1987; Cobb 1981), *Panulirus argus* (Kanciruk and Herrnkind 1973), and *Jasus spp.* (Fielder 1965; Williams and Dean 1989). Generally, out-of-shelter activity peaks shortly after dusk and continues at lower levels for a variable portion of the remainder of the dark period. Ennis (1983, 1984a) reported a peak in activity about 2 to 3 hours after the onset of darkness, and a subsequent lessening in activity before dawn based on a series of year-round diurnal and nocturnal SCUBA surveys of a lobster population in Bonavista Bay, Newfoundland. He reported that the duration of out-of-shelter activity was highly variable and he speculated that the length of nocturnal activity of individuals is related to availability of food.

The limited data available also indicate that the distance moved on a given night can be quite variable. Cooper and Uzmann (1977) found that individuals rarely moved > 300 m but they observed one American lobster that moved almost 2000 m in one night. MacDiarmid et al. (1991) reported maximum nightly movement distances by male and female spiny lobster *(Jasus edwardsii)* of 87 and 99 m, respectively. Ninety five percent of the western rock lobster *(Panulirus cygnus)* monitored by Jernakoff et al. (1987) moved between 72.5 and 585 m per night, the median distance being 310 m per night.

Environmental factors other than light intensity which appear to affect the activity of American lobster include water temperature (Herrick 1909; McLeese and Wilder 1958; Ennis 1984a, 1984b) and turbulence/turbidity induced by storms (Ennis 1983, pers.comm.). Nocturnal activity increases with increasing water temperature and remains relatively high until water temperatures begin to drop. Lobsters sometimes move downslope in apparent response to a substantial increase in water turbulence and turbidity and later return to upslope locations once the storm effects have subsided (Ennis 1983).

Out-of-shelter activity is presumably primarily related to foraging and activities relating to mating and territoriality (Phillips et al. 1980) but it has also been suggested that lobsters move simply to familiarize themselves with the surrounding benthic habitat (Karnofsky et al. 1989a).

Lobsters forage on a variety of prey including crabs, molluscs, sea stars, sea urchins, polychaetes and fish (Ennis 1973; Carter and Steele 1981a, 1981b; Elner 1980; Elner and Campbell 1987). Selection of prey appears to depend on different factors which include lobster size, prey size and availability, and the lobster molt stage. Although the American lobster has been described as an opportunistic feeder (Weiss 1970; Cooper and Uzmann 1980), numerous studies have shown this species' selectivity in foraging (Evans and Mann 1977; Hirtle and Mann 1978; Leavitt et al. 1979), especially at critical stages of the molting cycle. Seasonal shifts in prey preference or abundance may be responsible for seasonal changes in activity patterns.

Moody and Steneck (1993) reported that American lobsters frequently carried prey back to a shelter rather than eating it at the site of capture.

1.2 Habitat and Shelter Preference

During the first few years of benthic life, American lobsters of the approximately 5 to 40 mm carapace length range are strongly associated with habitats which provide cover for small animals (e.g. cobble and small boulder) (Wahle and Steneck 1991) but this association decreases as they grow, presumably due to reduced risk of predation (Wahle and Steneck 1992) and an increased ability to modify the substratum (Wahle 1992a). However, larger lobster (carapace length > 35 mm) are most frequently found on substrate with some boulder or other cover (Wahle 1992a). Cobb (1971) found that American lobsters generally occupied shelters in which height of the opening was less than the width, resulting in lower profile shelters. He described significant relationships between lobster size and shelter size, specifically the area of the opening. Spanier and Zimmer-Faust (1988) reported that spiny lobster *(P. interruptus)* preferred shelters with small entrances relative to the inner shelter diameter.

Stewart (1970, 1972) described two types of space use behaviour in American lobsters based on his observations of shelter occupancy - transient and resident. He defined transient behaviour as the occupation of different shelters for short periods and resident behaviour as the occupation of the same shelter for an extended period. Ennis (1983) and Karnofsky et al. (1989a) noted both types of behaviour in Newfoundland and Massachusetts lobsters. While past studies have indicated particular requirements for shelter by adult lobsters, they have provided little information on the long term use of shelters by individuals.

Homing behaviour, exhibited by both transient and resident lobsters, is characterized by periodic excursions from a shelter and the subsequent return to the original or to a nearby shelter (Chittleborough 1974; Ennis 1983; Jernakoff 1987). Homing can occur after an absence of a few hours or several days. Data on this topic has been limited to date.

Observations of American lobster homing on a localized scale under field conditions include those by Ennis (1983, 1984a) and Karnofsky et al. (1989a). Ennis reported individuals who returned to the shelters that they had left the same night as well as individuals who returned to shelters after lengthy absences. Karnofsky et al. conducted three homing experiments in which they removed individual lobsters from their shelters and then released them about 40 m away. In all three homing trials, the lobsters returned to their home shelters within 24 h.

Various techniques have been used to study the fine-scale activity and movement patterns of lobsters. The studies by Ennis (1983, 1984a) employed SCUBA and direct observation. Ultrasonic telemetry, on the other hand, can provide continuous monitoring. In another approach, Karnofsky et al. (1989) attached strobe lights to the carapaces of two lobster to monitor their movements. While these studies provided valuable data, they had shortcomings, especially with respect to the discontinuous nature of the monitoring or the small number of animals observed. Spanier et al. (1994) used a remotely operated vehicle (ROV) to observe the behaviour of American lobster but this is costly and provided limited results. Telemetry was also used by Chapman and Johnstone (1975) and Jernakoff et al. (1987) in their studies on the movements of *N. norvegicus* and *P. cygnus*, respectively. Chapman and Johnstone used ultrasonic telemetry while Jernakoff et al. used an electromagnetic telemetry system. This electromagnetic system involved the detection of pulses of electromagnetic energy by aerials installed on the seabed. Signals were relayed to a receiver and monitored on an oscilloscope. However, the small reception range of these signals requires many aerials to cover a rather limited study area and, therefore, more system maintenance (Phillips et al. 1984).

Ultrasonic transmitters have been used in the past to investigate movement by large decapod crustaceans but only on a limited basis (Lund and Lockwood 1970, Haakonsen et al. 1993).

The approach taken in the present study was to use a fixed hydrophone tracking system that enabled individual lobsters to be tracked for long periods from a shore based facility. This has some advantages over the previous systems used. The slow rate of movement by lobsters on the bottom is well suited to this type of tracking system which is most sensitive horizontally along the sea bed (Hawkins et al. 1980). These conditions are ideal for the collection of data on such parameters as distance moved, rate of movement and direction of movement. Preliminary tracking indicated that tagged lobsters tended to remain within the array area for extended periods but in the event that animals became more widely ranging, hydrophones could be moved relatively easily to enlarge the array area. The hydrophones could be sited in relation to the sea bed topography to minimize signal blockage and indirect signal reception (through the sea bed) and thereby maximize the accuracy of time delay measurement (Hawkins et al. 1974). Another significant advantage of this tracking technique is that signal data can be recorded on site and then subjected to more detailed analysis at a later time.

Although underwater biotelemetry requires the use of an extensive electronic system, the components (transmitters, receiving systems, data loggers, etc.) have become better designed and more user friendly. This method's capability to provide continuous data and, therefore, a more complete representation of an animal's activity far outweighs its added logistics and expense.

1.3 Objective of Present Study

During this study, ultrasonic tracking was used to monitor the movements of individual American lobster during their nocturnal activity periods for extended times. The general objective was to provide a more detailed description of the temporal and spatial components of the behaviour of individual lobsters in their natural environment. Specific questions which were addressed included the following:

1. How often do individuals display out-of-shelter activity?
2. When do individuals initiate movement from shelter and how long do they remain out of shelter?
3. How is out-of-shelter time apportioned between moving and stationary behaviour?
4. How far do individuals move while out-of-shelter?
5. Do lobsters spend varying amounts of time in areas with different substrata and macrobenthos distributions?

6. What, if any, are the differences between seldom occupied and often occupied shelters?
7. Do lobsters demonstrate shelter homing after short-term and long-term absences?
8. Are there different trends in activity between lobsters of different sex and size?
9. Are there different trends in lobster activity under varying environmental conditions?

Methods used in past investigations of this type of activity were unable to produce the real-time data and detailed activity patterns made possible by ultrasonic tracking. While this study is largely descriptive, results do suggest numerous directions of subsequent research. In a continuation of my work, more specific hypotheses concerning homing, shelter selection and resource use, and the possible effects of environmental and biological parameters on lobster activity, can be generated and tested.

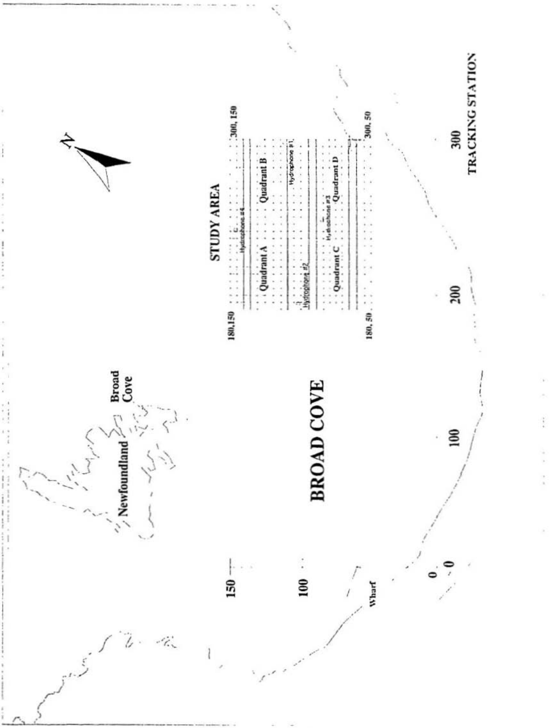
MATERIALS AND METHODS

2.1 Tracking System

Field studies on the activity and movements of mature American lobster were conducted in Broad Cove, Conception Bay, Newfoundland (Figure 1). A fixed hydrophone array tracking system, similar to that described by Hawkins et al. (1974; 1980), Clark and Green (1990), and Bradbury (1993), was used to track individual lobster. The hydrophone array consisted of four omnidirectional hydrophones mounted in aluminum frames on the sea floor at depths of 8 - 12 m. Hydrophones were raised above the seabed by about 1 m to limit the amount of signal blockage which often occurs when working with specimens which live on the substrate (Urquhart and Smith 1992). Lobsters were tagged with cylindrical ultrasonic transmitters (VEMCO Ltd.) measuring 48 mm in length and 15 mm in diameter with frequencies ranging from 54.6 to 76.8 kHz. Reception of a transmitter by at least three hydrophones was necessary to determine the lobster's position.

Hydrophones were connected by cable to a 4 - channel telemetric receiver located onshore in the field station at Broad Cove. The receiver filtered out extraneous background noise and passed the cleaned signals to a four - channel oscilloscope. The oscilloscope displayed time intervals (or time delays) between the reception of the signal by the first hydrophone and its reception at subsequent hydrophones. Each time delay could be translated into a hyperbola between the two hydrophones (using the speed of sound in water). The intersection point of the two hyperbolae translated from the two time delays indicated the position of the lobster. Delay times were recorded by hand to the nearest millisecond. FISHTRAK, computer software written by Prof. M. Bruce-Lockhart (Dept.

Figure 1. Location of study area (gridded region) in Broad Cove, Conception Bay, Newfoundland.


N
Broad Cove
Newfoundland
STUDY AREA
180,150
300, 150
Hydrophone #4
Quadrant A
Quadrant B
Hydrophone #1
Hydrophone #2
Hydrophone #3
Quadrant C
Quadrant D
180, 50
300, 50
BROAD COVE
150
100
Wharf
0
0
100
200
300
TRACKING STATION

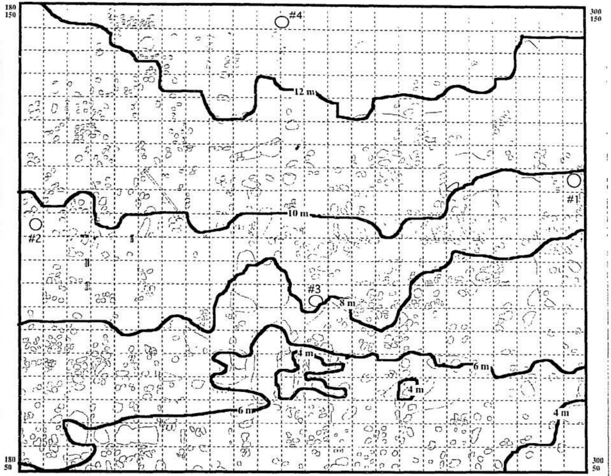
of Engineering, Memorial University of Newfoundland), used the delay time to calculate the position of the transmitter. FISHTRAK calculates the position of a transmitter to within a theoretical distance of 0.1 m. However, delay times were only measured to the nearest millisecond, limiting the accuracy of positioning to about 1 m. Therefore, position fixes calculated by FISHTRAK were rounded off to the nearest meter. The arrangement of the four hydrophones usually allowed the location of a tagged lobster with this accuracy within the study site described below. This accuracy was decreased when background noise was high due to heavy seas or when a tagged lobster was sheltered among rocks.

Suspect readings recorded from the oscilloscope were removed from the data through visual inspection. These readings would infrequently occur because of random noise or poor signal transmission or reception.

At least three times per year throughout the study, the tracking system's accuracy was ground-truthed. This was accomplished by placing transmitters at known locations relative to the array system. Commonly used fixed positions were the northeastern corner of the eastern-most wharf (position 0, 50) and the 'point' (position 290, 65) (Figure 1). Positions of the transmitter calculated from the time delays were then compared to the known positions of these sites.

The hydrophone array covered the study site - a 120 m x 100 m area ranging in depth from 3.4 to 13.4 m (mean low water, MLW) (Figure 2). Between May 1990 and August 1991, this area was mapped on a cell by cell basis (each cell measured 5 m x 5 m) in terms of bottom topography, faunal cover, water depth, and lobster shelters. Three quadrants (each 60 m x 50 m) were surveyed in 1990 while quadrant 'D' was surveyed in 1991. Two permanent transect lines were placed on the bottom; one (T1) extended from position 180, 100 to 300, 100, and the other (T2) extended from 240, 50 to 240, 150.

Figure 2. Depth contours and locations of large boulders and rock outcrop, hydrophones and debris of human origin at the study site in Broad Cove, Newfoundland. The bottom survey was performed in 1990 and 1991.


180
150
300
150
180
50
300
50
#4
12 m
#1
#2
10 m
#3
8 m
4 m
6 m
4 m
6 m
4 m

These lines partitioned the study area into four sectors, each one measuring 60 m x 50 m. Both permanent lines were marked off every 5 m. Beginning at the point of intersection of T1 and T2 (240, 100), a movable line, also marked off in 5 m increments, was run perpendicular to T1 at each of the 5 m marks. This was done on a sector by sector basis. A composite map was developed using the 480 cells.

2.2 Description of the Study Site

The bottom slopes gradually seaward to the outer edge of the array except at position 246, 75 to 275, 74 where there is an abrupt depth change (dropoff) from 4.0 to 6.5 m (Figure 2).

Bottom topography in the study area consisted mainly of bedrock outcrops and sand interspersed with regions of small to large boulders and cobble (Table 1; Figure 3). Depending upon the predominant substrate type, each cell was categorized as: 1) sand; 2) sand with boulder and/or cobble; 3) cobble with boulder and/or outcrop; 4) outcrop; and 5) boulder and outcrop.

The predominant animals in the study area considered to be prey for lobster were horse mussels (*Modiolus modiolus)* and green sea urchins (*Strongylocentrotus droebachiensis*). Occasional seastars *(Asterias spp.)* were encountered but their numbers were low compared with mussels or urchins. The number of horse mussels at any one site in the study area varied from 0 to dense beds (areas where individual mussels contacted adjacent ones). Sea urchins were also absent in some cells while covering as much as 25% of the bottom in others.

Based on a visual estimate of the density of horse mussels and sea urchins, each cell was categorized as one of the following: 1) mussel beds with urchins; 2) mussels only

Table 1. Percentage cover of various substrate types and horse mussels and sea urchins within the 120 m x 100 m study site at Broad Cove, Newfoundland. See text for description of how the survey was done.

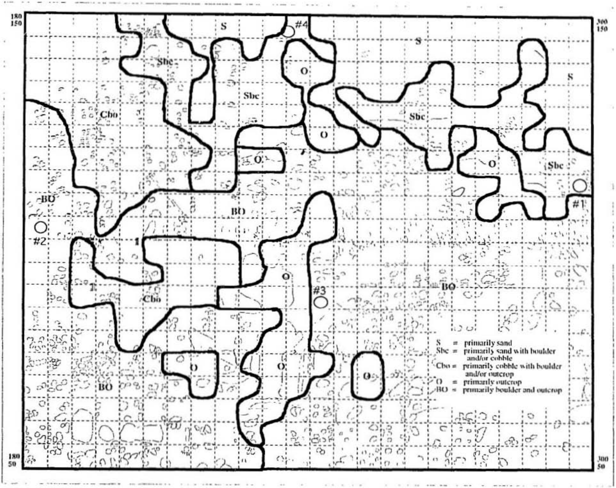
Substrate Type	Description	Area (m2)	Proportion of study site (%)
S	Sand	50	10.4
SBC	Sand with boulder and/or cobble	82	17.1
CBO	Cobble with boulder and/or outcrop	55	11.5
O	Outcrop	36	7.5
BO	Boulder and outcrop	257	53.5

Macrobenthos Type	Description	Area (m2)	Proportion of study site (%)
MB	Mussel bed with urchins	37	7.8
M	Scattered mussels	4	0.8
MU	Scattered mussels and urchins	262	54.6
U	Scattered sea urchins	144	30.0
NMU	Neither mussels nor urchins	33	6.8

Sand - Loose materials consisting of grains < 4.0 mm in diameter.
Cobble - Rock fragment between 64 and 256 mm in diameter.
Boulder - Rock fragment > 256 mm in diameter.
Outcrop - Naturally protruding rock bed.

(definitions from Owens, 1977)

Figure 3. Distribution of substrate types within the study site at Broad Cove, Newfoundland. See text for explanation of how survey was conducted.


180
150
300
150
180
50
300
50
S
Sbc
O
Cbo
BO
#1
#2
#3
#4
S = primarily sand
Sbc = primarily sand with boulder and/or cobble
Cbo = primarily cobble with boulder and/or outcrop
O = primarily outcrop
BO = primarily boulder and outcrop

(scattered distribution); 3) mussels (scattered distribution) with urchins; 4) urchins only (scattered distribution); or 5) neither mussels nor urchins (Table 1; Figure 4). Categories 2 and 3 had the same estimated density of mussels.

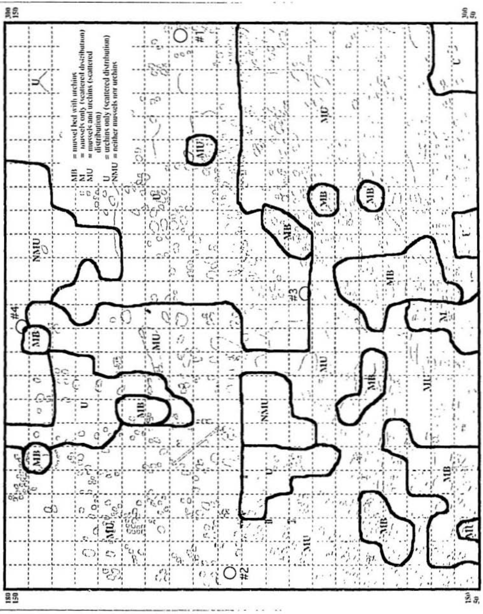
As each cell was mapped, all potential lobster shelters were marked with numbered painted rocks and measured for entrance height and width and shelter length. It was also noted whether a shelter had been excavated. Excavated shelters showed physical evidence in the form of removed substrate while non-excavated shelters either lacked such evidence or were on hard substrate. Excavated shelters were not necessarily prepared by lobsters since eel pout *(Macrozoarces americanus)* also excavate similar shelters. Regardless of the original excavator, these shelters could be used by either animal. Whether a shelter was occupied by a lobster at the time of the survey was also noted.

2.3 Tagging

Transmitters (VEMCO Ltd.) emitted pulsed signals at frequencies of 52 - 69 kHz with pulse rates between 50 and 60 pulses per minute. The length and weight of the transmitters were 60 mm and 8 g, respectively. Each transmitter was marked with an identifier number and a contact phone number in case of capture of the lobster in a fisherman's trap. Tranmitters used in 1987 and 1988 had non-replaceable batteries while those used in 1989 and 1990 had removable batteries. Battery life was approximately twenty-one days, depending on ambient water temperatures.

Lobsters were captured within the study area by SCUBA divers and then returned to shore for transmitter attachment. The main criterion for lobster selection was that they were large enough for transmitter attachment. The smallest animal tagged had a carapace length of 69 mm and the largest had a carapace length of 109 mm. Animals were measured

Figure 4. Distributions of horse mussels and sea urchins within the study site at Broad Cove, Newfoundland. See text for explanation of how survey was conducted.


300
150
300
50
180
150
180
50
MB = mussel bed with urchins
M = mussels only (scattered distribution)
MU = mussels and urchins (scattered distribution)
U = urchins only (scattered distribution)
NMU = neither mussels nor urchins
#1
#2
#3
#4
U
NMU
MB
MU
M

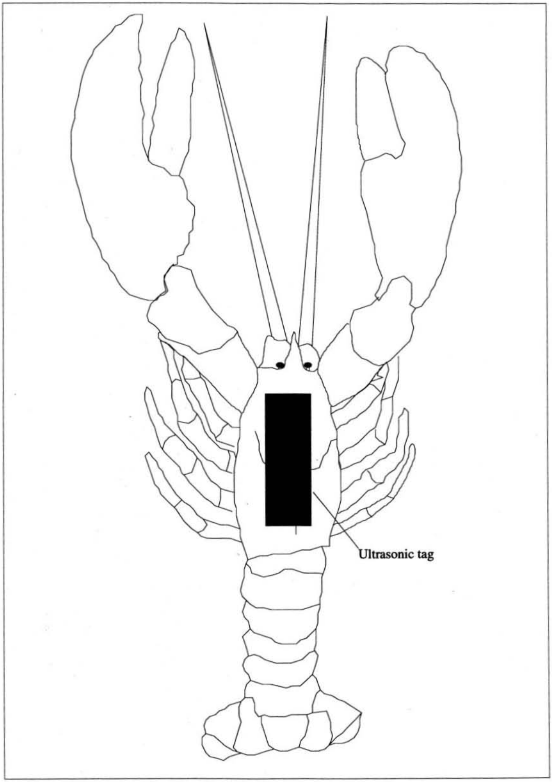
for carapace length and sexed prior to commencing the tagging procedure. The dorsal side of the carapace was dried and lightly sanded to provide a better surface for epoxy adhesion. The tag was attached to the lobster with a rapid set epoxy resin such that the transmitter end was oriented towards the rostrum of the animal (Figure 5). This orientation maximized the chances of signal detection when the animal was near the mouth of the shelter since lobsters orient themselves with their head toward the shelter opening. After tagging, the lobster was kept on shore under moist conditions (kelp or moist cloth cover) until the epoxy had set (approximately 15 min). It was then returned to the capture site, usually a shelter, and held for one or two minutes until a good set of time delays was recorded. The animal was then released into the shelter from which it was taken.

Twenty lobsters were tracked at various times during the periods of September 16 to November 25, 1987; June 7 to November 27, 1988; May 12 to September 27, 1989; and June 20 to August 29, 1990. This provided 291 nights of tracking data, 265 of which were complete (i.e. an animal was monitored for the entire period of darkness). Individual lobster tracking periods ranged from 4 to 86 days while the number of actual tracking nights for individuals ranged from 4 to 63. In 1987 and 1988, only one lobster was tracked at any one time. In 1989, there were periods between July and September when two animals were tracked simultaneously, and in 1990, three lobsters were tracked at the same time from June to July.

2.4 Activity

Several measures of lobster activity were calculated, based on positional data recorded every two minutes during the animal's activity period. Positions could only be calculated if a signal was received by three hydrophones. Monitoring on a continuous

Figure 5. Position of ultrasonic transmitter on lobsters tagged at Broad Cove, Newfoundland.


Ultrasonic tag

basis was not begun until one hour prior to sunset since lobsters become most active after the onset of darkness.

When a lobster was in its shelter, either no signal was received or a weak audio signal was received on one or more hydrophones. When it moved to the shelter mouth, the audio signal usually increased markedly. The time of signal strengthening was called 'onset of activity'. Sometimes the signal was strong enough to be received by three hydrophones, resulting in consistent time delays. Usually, consistent time delays were received shortly after the marked increase in the audio signal. The time from increase in audio signal to changing time delays (indicating position change or movement) was called 'initial shelter time'. It was not possible to distinguish between when a lobster was actually in or just outside the shelter.

The time when time delays started to change was called 'onset of out-of-shelter activity'. The distinction between out-of-shelter stationary time and movement time was set at 5 min without a position change. Although somewhat arbitrary, this was based primarily on observed rates of movement by tagged lobsters which, on average, were low. If time delays were changing at least every five minutes, a lobster was considered to be moving and these periods were called 'movement time'. Any out-of-shelter period exceeding five minutes during which time delays did not change was called 'stationary time'. Each stationary period, regardless of duration, was called a 'stop'. A lobster was considered to be out-of-shelter until such time that the signal weakened and remained so for a prolonged period (i.e. > 10 min). Usually the signal would disappear from the oscilloscope and then the audio signal would sharply drop. The period between when the last movement occurred and the loss of or sharp drop in audio signal was called 'final shelter time'. The time of final audio signal loss was called 'cessation of activity'. The oscilloscope signals were generally strong just prior to when a lobster entered a shelter so it was possible to calculate the shelter's position. In some instances, the occupancy of a particular shelter was verified the following day with a handheld hydrophone while SCUBA diving or snorkelling.

Onset of activity, onset of out-of-shelter activity (movement), and cessation of activity were expressed in relation to the official time of sunset.

'Total activity time' was defined as the period between onset of activity and cessation of activity; i.e. the sum of initial shelter time, movement time, stationary time and final shelter time.

An 'active night' was defined as any monitoring session during which a lobster moved outside of its shelter. Occasionally, a lobster moved towards its shelter mouth, as indicated by a strengthening of the signal, yet did not show any change in position. Monitoring sessions with only this type of behaviour were not considered active nights. 'Percent active nights' refers to the proportion of all monitoring sessions classified as active nights.

The majority of monitoring sessions lasted for the entire period of darkness. However, some sessions did not include the entire period of darkness and were called 'incomplete monitoring nights'. On some monitoring nights, loss of signal was misinterpreted as a lobster entering its final shelter for that night. This became obvious when they were found in a different shelter the next day. Although these sessions did not record all lobster activity on a given night, they did monitor a full 'bout' of activity. That is, a lobster left its shelter and eventually entered another (i.e. weak or no signal). Therefore, results were presented on the basis of fully monitored activity bouts. General results from fully monitored active nights were also presented but when addressing specific temporal and spatial activity, all results were from fully monitored activity bouts unless otherwise stated

Two measures of distance moved by lobster were recorded. They are the maximum distance of a lobster from its initial shelter and the approximate total distance moved by a lobster during an activity bout. These two measures will be referred to as 'maximum distance' (MD) and 'approximate total distance' (ATD), respectively. Maximum distance is the straightline distance between a lobster's initial shelter and its positional fix furthest from the initial shelter. Approximate total distance was calculated by summation of all distances between consecutive positional fixes recorded every two minutes during an activity bout. Any time that a lobster made a directional change which exceeded 90°, the event was called an 'abrupt turn'.

Individuals of vertebrates and the higher invertebrates commonly restrict their activities to a definite area, called the 'home range' (Odum, 1971). The movements of frequently active tagged lobsters were considered in relation to home ranges.

2.5 Biological Variables

Lobsters were divided into two groups based on carapace length. A smaller lobster was one with a carapace length of 69 to 81 mm while larger lobsters exceeded 81 mm. This discriminating size provided a relatively even division of the monitored nights of tagged animals. The 81 mm length represents the minimum commercial size for lobster in Newfoundland and coincidentally approximates the size at which female lobsters in Newfoundland waters become sexually mature (Ennis 1980).

Tracking was divided into three time periods; before July 1, July 1 to August 15, and after August 15. These periods were based on findings by Ennis (1973) on seasonal changes in serum protein concentration for American lobster in Bonavista Bay, Newfoundland. Serum protein concentrations can be directly linked to the molting stages of lobsters. The tracking time periods 'before July 1', 'July 1 to August 15', and 'after August 15' roughly correspond to the molting stages 'inter-molt', 'pre-molt', and 'post-molt/recovery', respectively.

2.6 Environmental Conditions

Water temperature was monitored on a daily basis during tracking in 1989 to 1990. During the field season in 1989, a Ryan thermograph situated on the sea floor immediately offshore of the dropoff (243, 76) at a depth of 6.5 m provided temperature data. Temperatures were monitored in 1990 by means of a thermistor probe at Hydrophone No. 3 (Figure 1). No water temperatures were recorded in 1987 while in 1988, readings were recorded at least every second day with a standard mercury thermometer located at a depth of 5 m.

Sea state was recorded at sunset of each monitoring night using the following criteria: 1 = no wave action, 2 = < 0.25 m, 3 = 0.25 - 0.50 m, 4 = > 0.50 m.

Moonphase data were obtained from the Observer's Handbook (Bishop ed. 1987 - 1990) resulting in the following criteria: NM = new moon ± 3 days, FQ = first quarter ± 3 days, FM = full moon ± 3 days, LQ = last quarter ± 3 days.

2.7 Analysis of Data

2.7.1 Mapping

All positional data were plotted using MINICAD, a computer aided design program which can mimic a GIS (geographical information system) at a most basic level. Data collected during the survey of the study area were mapped onto various layers using the above software (e.g. various types of substrate, standardized water depth, locations of physical obstructions, patches of prey, etc.). This made it possible to view the lobster tracks in relation to various features of the study area. For example, layering a lobster track over the macrobenthos data indicated what benthos was present at stop sites. Interchanging layers in this manner helped to provide information pertaining to the nocturnal movements of tracked lobsters.

2.7.2 Statistical analysis

Descriptive statistics were used to summarize the data. In addition to standard deviation, the coefficient of variation was calculated to present the amount of variability associated with activity variables.

Correlation analysis was used to investigate the relationship between maximum distance from initial shelter and approximate total distance, and between lobster carapace length and the square root of shelter mouth area. The Mann-Whitney Unpaired U Test was used to analyze characteristics of shelters used and unused by tagged lobsters.

RESULTS

3.1 General Observations of Lobster Activity

Frequency of out-of-shelter activity was highly variable between individual lobsters (Table 2). Ten of the twenty experimental animals moved from their shelters on at least 25 % of the nights during which they were monitored (Table 2).

Eleven of the seventeen lobster tagged between 1988 and 1990 exhibited activity on the day of tagging (Table 2; Appendix 1). Two of these (lobsters 4 and 5) exhibited unusual behaviour. Lobster 4 initiated activity on the day following tagging 79 minutes before sunset (Table 3; Appendix 1). Lobster 5 was active for almost four hours immediately following tagging in the early afternoon, and on the following day it initiated activity over three hours prior to sunset (Table 3; Appendix 1). The other ten lobsters did not become active on the tagging day until after sunset (range of onset of activity = 16 - 366 min after sunset) (Table 3; Appendix 1). No other tracked lobster were known to be active prior to sunset.

3.1.1 Completely monitored activity bouts

Times after sunset of onset of activity and onset of out-of-shelter activity for all monitored activity bouts ranged from -185 min (3.1 h) (negative value indicates time before sunset) to 390 min (6.5 h) and 2 to 415 min (6.9 h), respectively (Table 3). Fifty percent of observed onsets of activity occurred at least 72 min (1.2 h) after sunset while 50 % of movement commenced at least 118 min (~2 h) after sunset. Activity cessation times ranged from 51 to 898 min (~ 15 h) after sunset (Table 3), the median value being 344 min (5.7 h).

Table 2. Sex, size, tracking period and percentage of active nights of the twenty American lobsters monitored at Broad Cove, Newfoundland, 1987 - 1990.

Lobster No.	Sex	Carapace Length (mm)	Tracking Period	Tracking Nights	Active Nights	% Active Nights
1	?	81+	16/09/87 - 20/09/87	4 [3]	1	25.0
2	?	81+	24/09/87 - 05/10/87	11 [9]	6	54.5
3	?	81+	04/11/87 - 25/11/87	14 [9]	3	21.4
4	M	69	07/06/88 - 17/06/88	11	1	9.1
5	F	70	24/06/88 - 15/07/88	17	5	29.4
6	F	75	09/11/88 - 27/11/88	16 [4]	4	25.0
7	M	79	12/05/89 - 31/05/89	19	1	5.3
8	M	94	06/06/89 - 26/06/89	19 [3]	6	31.6
9	F	85	04/07/89 - 27/09/89	63 [4]	13	20.6
10	M	75	17/07/89 - 24/07/89	7 [1]	2	28.6
11	M	77	28/07/89 - 30/08/89	23	1	4.3
12	M	104	13/09/89 - 27/09/89	7 [1]	5	71.4
13	F	76	20/06/90 - 25/06/90	6	1	16.7
14	F	80	26/06/90 - 14/07/90	18 [3]	9	50.0
15	M	78	26/06/90 - 07/07/90	12 [4]	7	58.3
16	M	109	29/06/90 - 11/07/90	13 [1]	3	23.1
17	M	105	17/07/90 - 20/07/90	4	3	75.0
18	M	76	23/07/90 - 10/08/90	12 [2]	6	50.0
19	M	83	07/08/90 - 18/08/90	8	1	12.5
20	F	77	21/08/90 - 29/08/90	7 [1]	5	71.4
			Total	291	83	

Bracketed values refer to the number of nights with incomplete tracking
(45 in total with activity observed during 26 of them).

Table 3 Ranges of maximum distance, approximate total distance, number of stops and turns, distance between initial and final shelters, total activity time, shelter times, movement times, stationary times, times of onsets of activity and movement, and time of cessation of activity of twenty lobsters monitored at Broad Cove, Newfoundland, 1987-90 **Included are both complete and incomplete nights of monitoring (all activity bouts).**

Lobster no.	Sex	Carapace length (mm)	Nights with bouts of activity (n)	Maximum distance (m)	Approximate total distance (m)	Number of stops	Number of abrupt turns (> 90 ° change)	Distance between initial and final shelter (m)	Initial shelter time (min)
1	?	81+	1	28	82	1	3	30	10
2	?	81+	6	14 - 53	14 - 179	0 - 5	0 - 8	3 - 33	21 - 107
3	?	81+	3	25 - 38	50 - 114	0 - 2	1 - 6	0 - 27	25 - 35
4	M	69	1	7	23	1	3	11	197
5	F	70	5	4 - 65	5 - 214	0 - 9	0 - 13	7 - 34	2 - 245
6	F	75	4	14 - 35	42 - 76	2 - 7	2 - 6	2 - 33	0 - 97
7	M	79	1	8	13	0	0	8	20
8	M	94	6	6 - 74	6 - 107	0 - 3	0 - 3	6 - 74	0 - 50
9	F	85	13	9 - 63	9 - 128	0 - 7	0 - 7	0 - 52	0 - 135
10	M	75	2	10 - 23	10 - 27	0 - 2	0	11 - 24	7 - 20
11	M	77	1	18	18	0	0	20	25
12	M	104	5	35 - 63	64 - 361	2 - 5	3 - 15	0 - 39	10 - 100
13	F	76	1	8	8	0	0	8	17
14	F	80	9	5 - 43	7 - 121	0 - 5	0 - 7	0 - 43	0 - 120
15	M	78	7	7 - 23	8 - 171	0 - 5	0 - 12	0 - 18	0 - 210
16	M	109	3	7 - 47	12 - 54	0 - 1	0 - 1	0 - 46	15 - 25
17*	M	105	3	14	14	0	0	13	20
18	M	76	6	33 - 71	31 - 287	0 - 13	0 - 13	7 - 67	10 - 255
19	M	83	1	9	9	0	0	9	55
20	F	77	5	2 - 30	7 - 105	1 - 7	1 - 6	0 - 10	0 - 130
All lobsters			**83**	**2 - 74**	**5 - 361**	**0 - 13**	**0 - 15**	**0 - 74**	**0 - 255**

* only audio tracking on 2 of the 3 nights of activity; i.e. data not presented as ranges represents only one night of activity.

Table 3. Continued.

Lobster No.	Sex	Carapace length (mm)	Nights with bouts of activity (n)	Final shelter time (min)	Stationary time (min)	Movement time (min)	Time after sunset of onset of activity (min)	Time after sunset of onset of out-of-shelter activity (min)	Time after sunset of cessation of activity (min)
1	?	81+	1	24	10	26	70	62	122
2	?	81+	6	0 - 170	0 - 55	7 - 60	120 - 356	141 - 386	174 - 626
3	?	81+	3	5 - 25	0 - 162	45 - 143	208 - 284	233 - 344	419 - 543
4	M	69	1	0	27	30	79 (prior)	118	175
5	F	70	5	0 - 193	0 - 127	11 - 171	185 (prior) - 58	32 - 275	129 - 475
6	F	75	4	0 - 87	55 - 612	26 - 106	77 - 366	77 - 366	217 - 898
7	M	79	1	35	0	10	164	184	229
8	M	94	6	2 - 201	0 - 56	4 - 60	40 - 327	58 - 332	73 - 476
9	F	85	13	1 - 165	0 - 227	5 - 193	37 - 191	44 - 239	79 - 479
10	M	75	2	1 - 210	0 - 52	27 - 128	16 - 78	23 - 98	51 - 488
11	M	77	1	37	0	10	390	415	462
12	M	104	5	2 - 70	50 - 120	37 - 360	29 - 220	44 - 245	287 - 566
13	F	76	1	20	0	7	337	354	381
14	F	80	9	0 - 310	0 - 170	15 - 170	13 - 268	73 - 268	224 - 508
15	M	78	7	1 - 187	0 - 305	15 - 225	2 - 147	2 - 357	212 - 507
16	M	109	3	0 - 27	0 - 20	10 - 75	32 - 187	47 - 202	82 - 324
17*	M	105	3	55	0	5	14 - 249	269	298 - 474
18	M	76	6	0 - 115	0 - 259	12 - 260	20 (prior) - 29	20 - 282	58 - 533
19	M	83	1	0	0	15	22	77	92
20	F	77	5	0 - 180	55 - 195	30 - 215	11 - 119	11 - 148	186 - 598
All lobsters			**83**	**0 - 310**	**0 - 612**	**4 - 360**	**185 (prior) - 390**	**2 - 415**	**51 - 898**

* only audio tracking on 2 of the 3 nights of activity, i.e. data not presented as ranges represents only one night of activity

Total activity and movement times ranged from 6 to 769 min (12.8 h) and 4 to 360 min (6 h), respectively (Table 3). Fifty percent of all observed total activity times were 217 min (3.6 h) or more while 50 % of all movement times were 50 min or more (Figure 6).

Stationary times ranged from 0 to 612 min (10.2 h), with 50 % exceeding 28 min (Table 3; Figure 7). Initial shelter and final shelter times ranged from 0 to 255 min (4.2 h), and 0 to 310 min (5.2 h), respectively (Table 3). Median values of time in the initial and final shelters were 25 min and 22 min, respectively.

Proportions of total activity time accounted for by in-shelter and out-of-shelter behaviour were as follows. Initial shelter / total activity ranged from 0 to 0.92 while the range of final shelter / total activity was 0 to 0.73. Movement / total activity ranged from 0.03 to 0.77 while the range of stationary / total activity was 0 to 0.80 (Table 3). The medians of initial shelter / total activity and final shelter / total activity proportions were 0.17 and 0.12, respectively. Movement / total activity and stationary / total activity proportions had median values of 0.29 and 0.16, respectively.

Maximum distance and approximate total distance ranged from 2 to 74 m and 5 to 361 m, respectively (Table 3). The median maximum distance for fully monitored activity bouts was 18 m (Figure 8) while the median approximate total distance for fully monitored activity bouts was 46 m (Figure 8).

Abrupt turns and stops during the out-of-shelter activity periods ranged from 0 to 15 and 0 to 13, respectively (Table 3). The median values for abrupt turns and stops were 2 and 1, respectively.

3.1.2 Completely monitored active nights

Ranges of the lobster activity variables addressed in the previous section were much

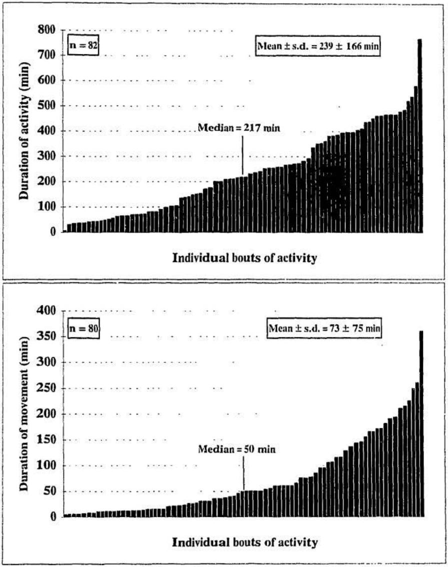


Figure 6. Duration of activity (upper histogram) and movement (lower histogram) for all monitored bouts of activity of tagged lobsters.

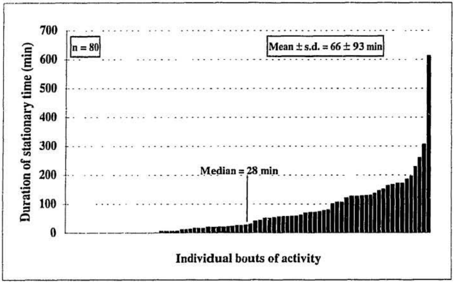


Figure 7. Duration of out-of-shelter stationary behaviour for all monitored bouts of activity of tagged lobsters.

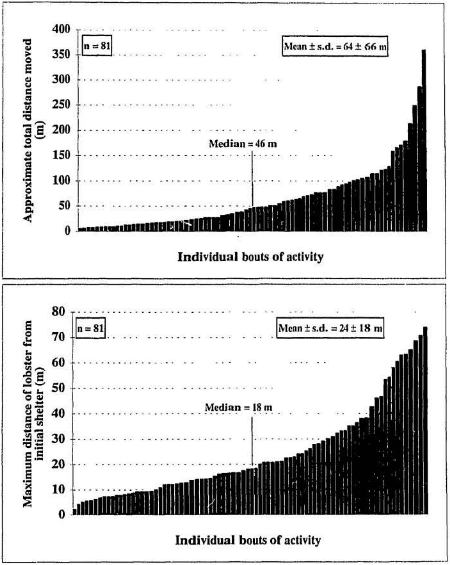


Figure 8. Approximate total distance moved (upper histogram) and maximum distance from initial shelters (lower histogram) of tagged lobsters during all monitored bouts of activity.

the same during completely monitored active nights as those for completely monitored activity bouts (Table 4). Figures 9 and 10 present range, mean ± s.d., and median of total activity time, movement time and stationary time of all completely monitored nights with activity. Figure 11 presents range, mean ± s.d., and median of approximate total distance and maximum distance of all completely monitored nights with activity.

3.1.3 Inactivity

There was no detected lobster movement on 189 (77 %) of the 246 fully monitored nights. Thirteen of the twenty tagged lobsters were inactive on more than 50 % of the monitored nights (Table 2). Inter-individual variation in frequency of activity was high. Of the seven individuals tracked for at least sixteen days, the least active lobster moved only once in twenty-three days (4 % activity) while the most active animal moved nine times in eighteen monitored days (50 % activity) (Table 2).

There were nineteen instances of unobserved activity bouts during periods thought to be fully monitored. Lobsters were found in shelters different than the ones they had entered at the end of activity bouts thought to be their most recent.

Tracking of lobsters 5, 7 and 9 provided reliable data pertaining to patterns of activity of individual lobsters. Lobster 5 was inactive on only the third night of the first four monitored nights. No movement was observed after Day 4 until Day 17, although three of the intervening nights were unmonitored. However, the shelter at which activity was initiated on Day 17 was the same one at which activity ceased on Day 4. Either the lobster remained in that shelter (#101) for thirteen days or it returned to it on one of the three unmonitored nights.

Lobster 7 did not appear to move from its capture shelter (#65) until sixteen days

Table 4. Ranges of maximum distance, approximate total distance, number of stops and turns, distance between initial and final shelters, total activity time, shelter times, movement times, stationary times, times of onsets of activity and movement, and time of cessation of activity of twenty lobsters monitored at Broad Cove, Newfoundland, 1987-90. **Included are only completely monitored nights with out-of-shelter movement.**

Lobster no.	Sex	Carapace length (mm)	Complete nights with activity (n)	Maximum distance (m)	Approximate total distance (m)	Number of stops	Number of abrupt turns (> 90 ° change)	Distance between initial and final shelter (m)	Initial shelter time (min)
1	?	81+	1	28	82	1	3	30	10
2	?	81+	1	18	70	2	4	3	30
3	?	81+	2	25 - 28	50 - 114	2	1 - 6	0 - 13	25 - 35
4	M	69	1	7	23	1	3	11	197
5	F	70	5	4 - 65	5 - 214	0 - 9	0 - 13	7 - 34	2 - 245
6	F	75	2	16- 21	60 - 76	4 - 7	5	12 - 15	51 - 97
7	M	79	1	8	13	0	0	8	20
8	M	94	3	14 - 74	25 - 107	1 - 3	2 - 3	9 - 74	0 - 50
9	F	85	11	9 - 63	9 - 128	0 - 7	0 - 7	0 - 52	0 - 135
10	M	75	1	23	27	2	0	24	20
11	M	77	1	18	18	0	0	20	25
12	M	104	4	35 - 63	102 - 361	2 - 5	3 - 15	0 - 38	10 - 25
13	F	76	1	8	8	0	0	8	17
14	F	80	6	5 - 21	7 - 121	0 - 5	0 - 7	0 - 22	0 - 110
15	M	78	3	7 - 19	8 - 88	0 - 3	0 - 2	8 - 18	20 - 55
16	M	109	2	7 - 47	15 - 54	0 - 1	0 - 1	0 - 46	15 - 25
17*	M	105	1	14	14	0	0	13	20
18	M	76	4	33 - 68	37 - 287	2 - 13	2 - 13	7 - 67	10 - 255
19	M	83	1	9	9	0	0	9	55
20	F	77	4	2 - 30	7 - 105	1 - 7	1 - 6	0 - 10	0 - 35
All lobsters			**55**	**2 - 74**	**5 - 361**	**0 - 13**	**0 - 15**	**0 - 74**	**0 - 255**

* only audio tracking on 2 of the 3 nights of activity, i.e. data not presented as ranges represents only one night of activity

Table 4. Continued.

Lobster No.	Sex	Carapace length (mm)	Complete nights with activity (n)	Final shelter time (min)	Stationary time (min)	Movement time (min)	Time after sunset of onset of activity (min)	Time after sunset of onset of out-of-shelter activity (min)	Time after sunset of cessation of activity (min)
1	?	81+	1	24	10	26	70	62	122
2	?	81+	1	170	20	50	356	386	626
3	?	81+	2	5 - 25	40 - 162	115 - 143	208 - 255	233 - 290	470 - 543
4	M	69	1	0	27	30	79 (prior)	118	175
5	F	70	5	0 - 193	0 - 127	11 - 171	185 (prior) - 58	32 - 275	129 - 475
6	F	75	2	0	128 - 612	26 - 106	129 - 207	180 - 344	458 - 898
7	M	79	1	35	0	10	164	184	229
8	M	94	3	33 - 201	15 - 56	13 - 60	70 - 194	70 - 206	141 - 476
9	F	85	11	1 - 165	0 - 136	5 - 193	42 - 191	44 - 239	142 - 479
10	M	75	1	210	52	128	78	98	488
11	M	77	1	37	0	10	390	415	462
12	M	104	4	2 - 70	50 - 120	50 - 360	29 - 220	44 - 245	372 - 566
13	F	76	1	20	0	7	337	354	381
14	F	80	6	45 - 180	0 - 170	15 - 170	13 - 123	73 - 203	224 - 483
15	M	78	3	5 - 187	0 - 305	15 - 105	13 - 78	43 - 98	278 - 430
16	M	109	2	0 - 27	0 - 20	15 - 75	53 - 187	78 - 202	93 - 324
17*	M	105	1	55	0	5	249	269	329
18	M	76	4	11 - 115	20 - 259	60 - 260	20 (prior) - 27	20 - 282	197 - 533
19	M	83	1	0	0	15	22	77	92
20	F	77	4	0	100 - 195	30 - 165	11 - 119	11 - 134	186 - 412
All lobsters			**55**	**0 - 210**	**0 - 612**	**4 - 360**	**185 (prior) - 390**	**20 - 415**	**92 - 898**

* only audio tracking on 2 of the 3 nights of activity; i.e. data not presented as ranges represents only one night of activity.

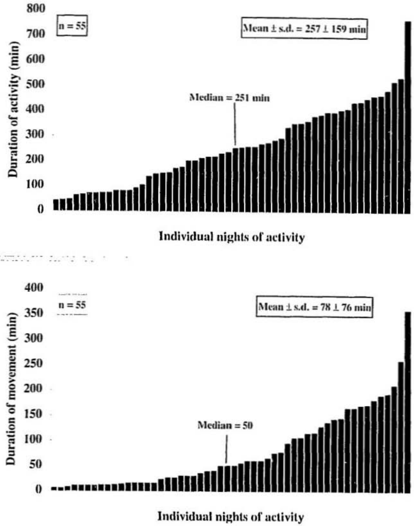


Figure 9. Duration of activity (upper histogram) and movement (lower histogram) for all completely monitored nights of activity of tagged lobsters.

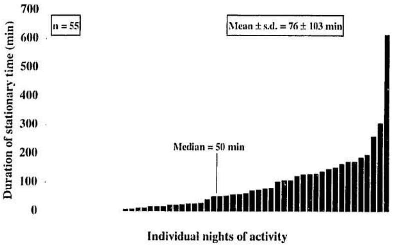


Figure 10. Duration of out-of-shelter stationary behaviour for all completely monitored nights of activity of tagged lobsters.

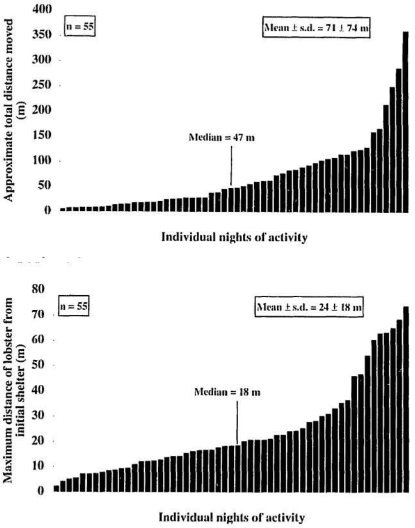


Figure 11. Approximate total distance moved (upper histogram) and maximum distance from initial shelters (lower histogram) of tagged lobsters during all completely monitored nights of activity.

after tagging. Day 14 was an unmonitored night during this period. No more activity by this animal was observed after Day 16.

Lobster 9 remained in its capture shelter until Day 4 of the monitoring period and then became inactive until Day 8. No more movement was observed until Day 15 but it was apparent that the animal had changed shelters at some time after Day 8. There was one unmonitored night between Days 8 and 15.

3.2 Total Activity

Fifty percent of the monitored lobsters had total activity times in excess of 410 min (6.8 h). The average duration of lobster activity on fully monitored activity bouts was 239 min (4.0 h) (s.d. = 166 min).

With respect to the eight lobsters which had at least five fully monitored activity bouts (lobsters 5, 8, 9, 12, 14, 15, 18 and 20 which will be referred to as '5+ lobsters'), lobsters 14 and 15 showed the least variability in total activity time (range = 3.3 - 7.8 h; c.v. = 0.28) while lobster 8 displayed the most (range = 6 min - 4.7 h; c.v. = 1.07).

Lobsters 14, 15 and 18 had the highest average activity times (> 5.5 h) while lobster 8 displayed the lowest average activity time (1.75 h).

Percentages of total activity time accounted for by initial shelter time, stationary time, movement time and final shelter time were similar for both fully monitored bouts and fully monitored nights (Figure 12). Based on these results, the proportions of various activities during an activity bout may closely reflect the activity type proportions during a full night which could include multiple activity bouts.

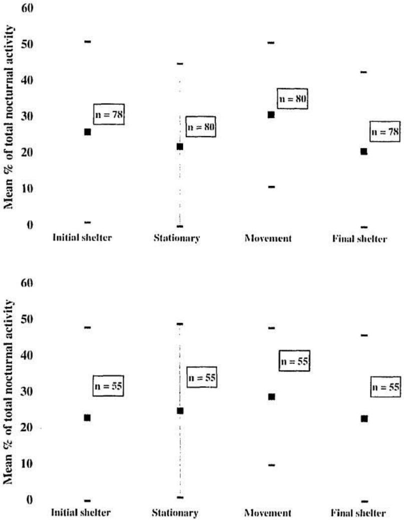


Figure 12. Mean percentage of total activity of in-shelter behaviour and out-of-shelter stationary and movement behaviour during all monitored bouts (upper graph) and all completely monitored nights (lower graph) of tagged lobsters. Standard deviations are indicated by the vertical bars.

3.2.1 Initiation of in-shelter activity and out-of-shelter movement

Average times after sunset of initial shelter activity and out-of-shelter activity onset during all monitored activity bouts were 100 min (1.7 h) (s.d. = 106 min) and 151 min (2.5 h) (s.d. = 103 min), respectively. During activity bouts, the average time difference between the initiations of initial shelter activity and out-of-shelter activity was 52 min (s.d. = 63 min) but on 50 % of the nights with movement, there was only a 25 min lag between onset of activity at the initial shelter and movement away from it. Over 50 % of all out-of-shelter activity bouts commenced within the 2 h period following sunset (Table 5). Less than 20 % of all out-of-shelter activity bouts began more than 4 h after sunset. Times of onset of movement were less variable than those of activity onset.

Occurrence of out-of shelter activity peaked 2 to 4 h after sunset although the levels during the 2 h blocks preceding and following the peak period were only slightly lower (Table 5).

There was considerable variation within and between individual lobsters with respect to initiation of activity and movement.

Of the '5+ lobsters', three had coefficients of variation (c.v.) associated with time of onset of activity which exceeded 1.0. Lobster 9 which moved at least thirteen times during its monitoring, exhibited a range of activity initiation time after sunset of 37 to 191 min (3.2 h) with an associated c.v. of 0.55. Conversely, lobster 18 which moved six times, commenced activity from 20 min before sunset to 29 min after sunset and had a c.v. of 1.46.

Length of time after sunset of movement initiation was also least variable with lobster 9 (range = 44 - 240 min / 4 h; c.v. = 0.48) and most variable with lobster 18 (range = 20 min - 4.7 h; c.v. = 1.04). Overall, this initiation time showed less variation than

Table 5. Post-sunset times of out-of-shelter activity commencement and occurrence. Nonparenthesized values refer to number of occurrences and parenthesized values refer to percentages of total number of occurrences.

	Post-Sunset Time Block (h)					
	0-2	2-4	4-6	6-8	8-10	>10
Onset of out-of-shelter activity	40 (51.2 %)	23 (29.5 %)	13 (16.7 %)	2 (2.6 %)		
Occurrence of at least a portion of out-of-shelter activity bout	40 (22.9 %)	51 (29.1 %)	45 (25.7 %)	28 (16.0 %)	8 (4.6 %)	3 (1.7 %)

activity initiation as six of the '5+ lobsters' displayed c.v.'s less than 1.0.

Times of activity initiation were quite different between the eight '5+ lobsters'. On average, lobsters 8 and 12 did not initiate activity until more than 2 h after sunset while lobsters 18 and 20 became active in their initial shelters an average of less than 40 min after sunset.

Of the '5+ lobsters', average movement initiation times after sunset were greatest for lobsters 8 and 12 (> 2.5 h) and least for lobsters 18 and 20 (< 1.8 h). Average elapsed times between activity initiation and movement initiation were greatest for lobster 18 (> 1.5 h) and least for lobster 8 (14 min). Average differences for the other six lobsters ranged from 35 min to 1.1 h.

3.2.2 Initial shelter activity

During fully monitored activity bouts, lobsters, on average, were active within their initial shelters for 50 min (s.d. = 61 min) before commencing movement. Fifty percent of the monitored lobsters had activity times at the initial shelter exceeding 97 min (1.6 h). The average percentage of total activity time which involved stationary time at the initial shelter was 26 % (s.d. = 25 %) with 50 % of the observations equalling or exceeding 17 %.

All '5+ lobsters' showed a high degree of variability with respect to activity time at the initial shelter. Lobster 8 had initial shelter time ranging from 0 to 50 min with a c.v. of 1.33. Lobster 5, which had the least variability, had initial shelter times ranging from 2 min to 4.1 h, and a c.v. of 0.99. Lobster 5 also had the highest average initial shelter time (1.9 h) while lobster 8 had the lowest, an average of 14 min. The average individual times of the remaining '5+ lobsters' ranged from 35 min to 1.6 h.

3.2.3 Out-of-shelter activity

Out-of-shelter times ranged from 4 to 718 min (~ 12 h) (Table 3) and averaged 139 min (2.3 h) (s.d. = 138 min). Fifty percent of all observations on fully monitored activity bouts equalled or exceeded 103 min (1.7 h).

Durations of out-of-shelter activity time were least variable for lobster 14 (range = 15 min - 5.2 h; c.v. = 0.59) and lobster 20 (range = 2.2 - 6 h; c.v. = 0.46). The most variability was shown by lobster 8 (range = 4 min - 1.8 h; c.v. = 0.98) and lobster 9 (range = 5 min - 4.7 h; c.v. = 1.05).

Five of the '5+ lobsters' had similar average out-of-shelter activity times (> 3.2 h) but lobsters 8 and 9 had substantially shorter average out-of-shelter activity periods (< 1.7 h).

The stationary time : movement time ratios of fully monitored activity bouts ranged from 0.1 to 7.2 with a median value of 0.4 (Figure 13). Therefore, the majority of the monitored out-of-shelter activity was characterized by more movement than stationary behaviour. Figure 13 also presents ratios from fully monitored nights of activity.

3.2.3.1 Movement

3.2.3.1.1 Temporal and spatial aspects

Lobsters averaged 73 min (1.2 h) (s.d. = 75 min) of movement per fully monitored activity bout. Fifty percent of the monitored lobsters displayed movement times exceeding 106 min (1.8 h). The average percentage of total activity time which involved movement was 31 % (s.d. = 20 %) with 50 % of the observations equalling or exceeding 29 %.

Lobster 14 showed the least variability in movement time of all '5+ lobsters'. Its

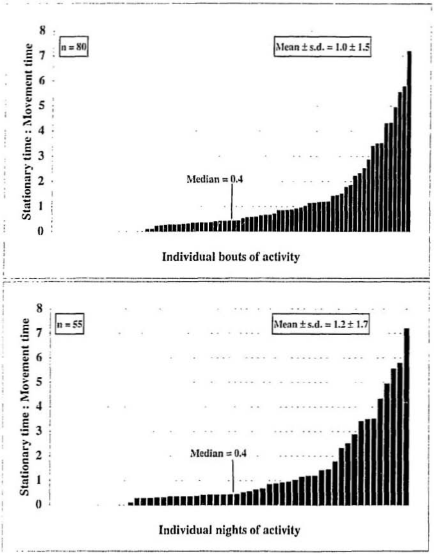


Figure 13. Out-of-shelter stationary time : movement time ratio of tagged lobsters during all monitored bouts of activity (upper histogram) and all complete nights of tracking (lower histogram).

range of movement times was 15 min - 2.8 h with a c.v. of 0.68. Lobsters 8 and 9 again displayed the highest variability. Their movement time ranges were 4 min - 1 h, and 5 min - 3.2 h, respectively, and the associated c.v.'s were 1.00 and 1.18, respectively.

The average movement times of lobsters 12 (2.8 h) and 18 (2.3 h) were clearly longer than those of the other '5+ lobsters', especially lobsters 8 and 9 whose movement times averaged 21 min and 45 min, respectively.

During fully monitored activity bouts, the distance between a lobster's initial shelter and its positional fix furthest from the initial shelter averaged 24 m (s.d. = 18 m). Eleven of the twenty monitored lobsters were over 25 m from their initial shelters during at least one of their movements.

The lobsters with most variability in maximum distance (MD) from initial shelter of the '5+ lobsters' were 5 and 8. For lobster 5, the distance ranged from 4 to 65 m with a c.v. of 1.01. For lobster 8, the range was 6 to 74 m, with a c.v. of 0.93. Least variability was associated with lobsters 12 and 18. The c.v.'s were 0.30 (range = 35 - 63 m) and 0.35 (range = 29 - 71 m), respectively.

Lobsters 12 and 18 also exhibited the highest average MDs. The average values were 47 m and 50 m, respectively. The lowest averages were shown by lobster 15 (13 m) and lobster 20 (14 m).

The approximate total distance (ATD) moved by lobsters on fully monitored activity bouts averaged 64 m (s.d. = 66 m). Nine of the twenty lobsters moved more than 100 m at least once during a nocturnal activity bout.

Lobsters 5, 8 and 15 showed the highest variability of this parameter of the '5+ lobsters'. For these lobster, the c.v.'s were 1.01 (range = 5 - 214 m), 0.96 (range = 6 - 107 m), and 1.00 (range = 8 - 171 m), respectively. As was the case with MD from initial shelter, lobsters 12 (range = 64 - 361 m; c.v. = 0.72) and 18 (range = 31 - 287 m; c.v. = 0.79) had the least inter-activity bout variability.

Lobsters 12 (162 m) and 18 (136 m) averaged the longest ATD's while lobsters 8, 9, 14, and 20 moved, on average, the shortest distances (range = 44 - 47 m).

There was a high correlation between ATD and MD during fully monitored activity bouts ($r = 0.67$, $p < 0.0001$).

3.2.3.1.2 Directional changes

Lobsters averaged 3.1 abrupt directional changes per night of movement (s.d. = 3.4). Fifty percent of fully monitored nights with movement were characterized by at least two changes in direction (Table 6). Twenty-four of observed lobster movements did not display any abrupt turns. Excluding these nights without direction change, fifty percent of movement nights had at least four abrupt turns (Table 6).

Of the '5+ lobsters', lobsters 5, 9, 14, 15, and 18 displayed high variability (c.v. > 1.0) with respect to the number of abrupt directional changes made during out-of-shelter movements on fully monitored nights. Lobster 20 showed the least variability (c.v. = 0.57).

Lobsters 5 and 12 each averaged over six abrupt turns per movement on fully monitored nights while lobsters 8, 9, and 14 each averaged < 3 turns per movement.

3.2.3.1.3 Net direction of movements and depth changes

Forty-three of the observed lobster movements (53 %) resulted in net offshore movement while twenty-six (32 %) resulted in inshore displacement (Table 6). The remaining 15 % were neither offshore nor inshore by the end of the movement.

Table 6. Number of directional changes, net directions of movement and net depth changes by lobsters at Broad Cove, Newfoundland, 1987 - 1990.

Lobster	Date of activity	Number of directional changes	Net direction of move	Net depth change (m)	Lobster	Date of activity	Number of directional changes	Net direction of move	Net depth change (m)	Lobster	Date of activity	Number of directional changes	Net direction of move	Net depth change (m)
1	16/09/87	3	i	-1.8	9	7/7/89	7	n/c	0.0	14	4/7/90	3	n/c	0.0
2	27/09/87	0	o	1.1	9	11/7/89	4	i	-2.3	14	5/7/90	7	o	-0.2
2	29/09/87	4	o	0.6	9	18/7/89	0	i	-2.1	14	6/7/90	6	o	-0.1
2	30/09/87	0	o	n/a	9	15/8/89	0	o	2.8	14	9/7/90	5	n/c	0.0
2	2/10/87	3	o	1.0	9	17/8/89	0	i	-1.7	15	26/6/90	0	o	0.0
2	3/10/87	8	o	0.9	9	23/8/89	0	i	-1.3	15	28/6/90	12	o	1.1
2	4/10/87	4	i	-0.3	9	26/8/89	5	o	-0.6	15	29/6/90	5	i	-0.6
3	7/11/87	6	i	-0.8	9	30/8/89	5	n/c	0.0	15	1/7/90	5	o	-0.1
3	11/11/87	1	n/c	0.0	9	1/9/89	1	n/c	0.0	15	2/7/90	1	n/c	0.0
3	23/11/87	3	o	n/a	9	8/9/89	0	i	-3.7	15	5/7/90	2	n/c	0.0
4	8/6/88	3	o	1.0	9	9/9/89	6	n/c	0.0	15	6/7/90	2	i	0.4
5	24/6/88	5	o	1.5	9	10/9/89	2	i	-3.3	16	29/6/90	0	o	2.3
5	25/6/88	11	o	1.4	9	19/9/89	2	o	4.0	16	30/6/90	0	i	-1.2
5	27/6/88	1	o	0.5	10	17/7/89	0	o	1.0	16	3/7/90	1	n/c	0.0
5	10/7/88	0	o	0.2	10	19/7/89	0	o	1.5	17	17/7/90	0	i	-2.4
5	11/7/88	13	o	0.3	11	29/7/89	0	o	1.8	18	23/7/90	2	o	1.9
6	9/11/88	2	i	-2.1	12	13/9/89	5	o	3.0	18	24/7/90	0	i	-3.0
6	10/11/88	6	o	0.0	12	14/9/89	15	o	-0.1	18	26/7/90	13	o	0.6
6	11/11/88	5	i	-0.5	12	17/9/89	8	n/c	0.0	18	29/7/90	3	i	-1.2
6	14/11/88	5	i	-1.9	12	18/9/89	3	o	1.0	18	30/7/90	2	o	1.8
7	27/5/89	0	i	-1.2	12	19/9/89	3	o	1.9	18	31/7/90	7	i	n/a
8	7/6/89	0	o	0.5	13	23/6/90	0	o	-0.1	19	7/8/90	0	o	0.3
8	8/6/89	1	o	0.6	14	26/6/90	1	o	0.5	20	21/8/90	6	o	0.6
8	14/6/89	3	i	n/a	14	27/6/90	0	o	0.0	20	22/8/90	4	n/c	0.0
8	16/6/89	2	i	n/a	14	29/6/90	2	o	0.7	20	23/8/90	2	i	-0.6
8	18/6/89	0	o	n/a	14	30/6/90	0	i	-1.2	20	24/8/90	4	i	-0.6
8	21/6/89	2	i	n/a	14	2/7/90	0	o	3.4	20	27/8/90	1	o	0.0

'o' denotes net offshore movement
'i' denotes net inshore movement
'n/c' denotes neither net inshore nor net offshore movement
'n/a' denotes unavailable data

Consequently, the average depth change resulting from movement was slightly positive (0.06 m ± 1.4); i.e. movement to deeper water. Depth change ranged from -3.7 m to 4.0 m (Table 6). Variability within and between lobsters was substantial with respect to net direction of movement and net depth change (Table 6).

3.2.3.2 Stationary (stop time)

3.2.3.2.1 Temporal and enumerative aspects

The average amount of time spent stationary by lobsters while out-of-shelter during fully monitored activity bouts was 66 min (1.1 h) (s.d. = 93 min). Fifty percent of the monitored lobsters displayed out-of shelter stationary times exceeding 55 min. The average percentage of total activity time which involved out-of-shelter stationary behaviour was 23 % (s.d. = 23 %) with 50 % of the observations equalling or exceeding 16 %.

Of the '5+ lobsters', out-of-shelter stationary behaviour times were most variable for lobster 9 (range = 0 - 3.8 h; c.v. = 1.47) and lobster 18 (range = 0 - 4.3 h; c.v. = 1.38). Lobsters 12 and 20 showed the least variability. Lobster 12's out-of-shelter stationary time ranged from 50 min to 2 h (c.v. = 0.36) and lobster 20's time ranged from 55 min to 3.2 h (c.v. = 0.44).

With respect to between lobster variability, lobsters 14, 15 and 20 had the highest average stationary times while out-of-shelter (> 1.7 h) compared to lobsters 8, 9, and 5 whose average times were 21 min, 46 min, and 52 min, respectively.

Lobsters 5, 18 and 20 each averaged over four stops per night of movement compared to the average of < 2 stops of lobsters 8, 12, 14, and 15.

3.2.3.2.2 Use of different substrate and macrobenthos types

A total of 183 stops were made by the lobsters during their nocturnal movements. The average number of stops per activity bout was 2.3 (s.d. = 2.6). The total stationary time related to these stops was approximately 88 h, 48.5 % of the total time spent outside of shelter.

One hundred and six of all stops (57.8 %) made by lobsters occurred in regions where the dominant substrate was boulder and outcrop (Table 7). The high percentage of stops on this substrate is to be expected considering 53.5 % of the study site bottom is characterized by boulder and outcrop (Table 1). Stationary time on this substrate type totalled over 62 h, 70.8 % of all stationary time. The average duration of a stop on boulder/outcrop substrate was 35.3 min.

The fewest number of stops occurred on sand with boulder and/or cobble and cobble with boulder and/or outcrop substrate. Each of these substrate types accounted for < 12 % of the entire study site (Table 1). Twelve stops (6.6 %) were made on the former and fifteen (8.2 %) were made on the latter (Table 7). Despite the low number of stops on these substrate types, the average duration of a stop exceeded 25 min. The lowest total stationary time (255 min / 4.2 h) and average stop duration (10.2 min) occurred on sand substrate (Table 7).

Seventy-three stops (39.9 %) (Table 8) were made in regions with a scattered mussel and urchin distribution (54.6 % of study site) (Tables 1). Regions with scattered urchins only and dense mussel beds had 51 and 41 stops, respectively. Interestingly, forty-one stops represent over 22 % of the total while mussel beds account for < 8 % of the study site macrobenthos (Table 1). The areas with scattered mussel and urchin distributions also had the most stationary time (43 h, 49.0 % of total) and the longest

Table 7. Frequency of lobster 'stops' and length of 'stop time' on different substrate types within the study area at Broad Cove, Newfoundland, 1987 - 1990.

Dominant substrate type	Percentage of study site (%)	Total no. of stops	Percentage no. of all stops (%)	Total time (min)	Percentage of total stop time (%)
1. Sand	10.4	25	13.7	255	4.8
2. Sand with boulder and/or cobble	17.1	12	6.6	317	6.0
3. Cobble with boulder and/or outcrop	11.5	15	8.2	474	9.0
4. Outcrop	7.5	25	13.7	497	9.4
5. Boulder and outcrop	53.5	106	57.8	3741	70.8
Total	100.0	183	100.0	5284	100.0

Table 8. Frequency of lobster 'stops' and length of 'stop time' on different macrobenthos types within the study area at Broad Cove, Newfoundland, 1987 - 1990.

Dominant macrobenthos type	Percentage of study site (%)	Total no. of stops	Percentage no. of all stops (%)	Total time (min)	Percentage of total stop time (%)
1. Mussel bed with urchins	7.8	41	22.4	970	18.4
2. Mussels only (scattered)	0.8	0	0.0	0	0.0
3. Mussels and urchins (scattered)	54.6	73	39.9	2587	49.0
4. Urchins only (scattered)	30	51	27.9	1371	25.9
5. Neither mussels nor urchins	6.8	18	9.8	356	6.7
Total	100.0	183	100.0	5284	100.0

average stop duration (35.4 min) (Table 8). Excluding the lone Type M area (scattered mussels only), stop number and time were least in areas lacking both mussels and urchins. These areas had only 18 stops, 356 min (5.9 h) of stationary time, and an average stop duration of 19.8 min (Table 8). However, these areas lacking both species accounted for < 7 % of the study site. The third most frequent number of stops occurred in areas with mussel beds although this macrobenthos type represents only 7.8 % of the study area (Table 1).

Average stop durations were less prior to July 1 in all macrobenthos cover types except scattered mussel and urchin. The average stop duration in dense mussel beds was slightly higher between July 1 and August 15 (31.5 min) than after August 15 (21.0 min). The opposite was true in areas with either scattered urchins or without mussels or sea urchins. Average stop durations in areas of scattered mussel and urchin distribution were essentially the same during the two post-July 1 periods (~32%).

3.2.3.3 Home range

The maps in Appendix 1 show the movement patterns of the lobsters monitored from 1987 to 1990. There was a high degree of variability between individuals with respect to the area covered by cumulative movements. Lobsters 6, 9, 14, 15, and 20 confined their movements to a relatively small area. Each moved over essentially the same region on successive nights of activity. Conversely, lobsters 2, 5, 8, 12, and 18 ranged widely over the study site.

3.2.4 Final shelter activity

Length of lobster activity at the final shelter averaged 51 min (s.d. = 68 min). Fifty percent of the lobsters had final shelter times exceeding 87 min (1.4 h). The average percentage of total activity time represented by time at the final shelter was 22 % (s.d. = 22 %) with 50 % of the observations equalling or exceeding 12 %.

Final shelter activity times of only two of the eight '5+ lobsters' had c.v.'s less than 1.0. Lobster 20 clearly had the most variability (range = 0 - 3 h; c.v. = 2.22) while lobsters 12 and 14, whose final shelter activity times ranged from 2 min - 1.2 h, and 0 - 5.2 h, respectively, had c.v.'s under 0.86. All '5+ lobsters had average final shelter activity times under 1 h except for lobster 14. This animal averaged just over 2 h of activity at its final shelters during its eight activity bouts.

3.2.5 Cessation of out-of-shelter movement and final shelter activity

The average times after sunset for the cessation of activity during activity bouts was 340 min (5.7 h) (s.d. = 164 min). Activity decreased significantly 6 to 8 h after sunset and was virtually over 8 to 10 after sunset (Table 5). Only 6.3 % of movements were observed 8 h after sunset.

There was considerable variation within and between individual lobsters with respect to cessation of activity and movement. Times after sunset of activity cessation for each of the '5+ lobsters' had a c.v. less than 0.66. Lobsters 12, 14 and 15 showed the least variation (range = 3.5 - 9.4 h; c.v. < 0.28) while the times of lobster 8 were most variable (range = 1.2 - 7.9 h; c.v. = 0.65). Lobsters 8 and 9 averaged the earliest cessation of activity after sunset (< 4.4 h) of '5+ lobsters'. On average, lobsters 12 and 14 remained active the longest after sunset (> 7.3 h).

3.3 Shelter use

Numerous prospective lobster shelters were identified and assessed during the survey of the study area conducted in 1990 and 1991 (Figure 14, Appendix 2). Maps in Appendix 1 show the positions of the shelters occupied by individual lobsters during their monitoring periods. Table 9 presents shelter information associated with each observed lobster movement including initial and final shelter identifications and the linear distances between them. Also included in Table 9 are data on the time between days with movement.

3.3.1 Distances between initial and final shelters

The average distance between initial and final shelters was 17 m (s.d. = 17 m), including the nights when lobsters returned to their initial shelters after their out-of-shelter movement. Fifty percent of the movements during fully monitored activity bouts resulted in relocation to a shelter at least 12 m from the initial one (Figure 15). Figure 15 also presents data on distance between initial and final shelters used during the fully monitored nights of activity.

3.3.2 Homing

Homing, which includes the consecutive and inconsecutive use of the same shelter following movement, was observed only 27 times in 81 occurrences of out-of-shelter activity (33 %) among 11 of the 20 lobsters (55 %).

There were twelve occurrences of an animal returning to the shelter from which it had initiated movement that same night (15 %). This consecutive use of the same shelter was observed among eight individuals (40 %). Lobsters 9, 14, and 20, animals tracked the longest, were the only ones to demonstrate this behaviour more than once. Lobsters that

Figure 14. Distribution of prospective lobster shelters in the study area at Broad Cove, Newfoundland, surveyed in 1990 and 1991. Numbered asterisks refer to shelters which were occupied by monitored lobsters while unnumbered ones are shelters which were not used by monitored lobsters during the tracking periods. Also shown are boulders and rock outcrop, hydrophones and debris of human origin.

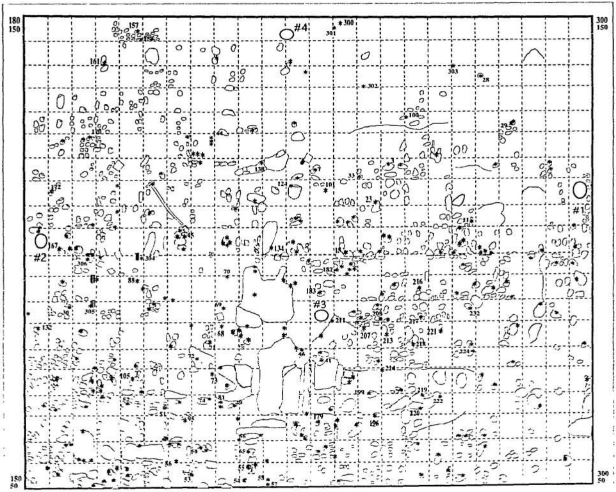

180
150
300
150
180
50
300
50
#1
#2
#3
#4

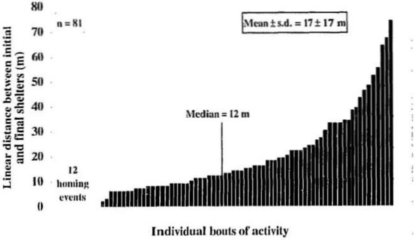
Table 9. Initial and final shelters of each observed lobster movement at Broad Cove, Newfoundland, 1987 - 1990. Included are distances between initial and final shelters, maximum distances of lobsters from their initial shelters, approximate total distances moved, absence or presence of homing, and description of time between observed movements ('Inc' = incomplete night of monitoring, 'UnM' = unmonitored night, 'Moved' = unobserved change of shelter followed by bracketed linear distance between observed final shelter and new shelter).

Lobster	Date of activity	Description of time since last date of activity	Maximum distance of positional fix from initial shelter (m)	Approximate total distance moved (m)	Initial shelter	Final shelter	Distance between initial and final shelters (m)
1	16/09/87		28	82	232	196	30
2	27/09/87		33	34	138	158	33
2	29/09/87	Inc	53	179	144	158	26
2	30/09/87	Inc	14	14	Outside grid	Outside grid	14
2	2/10/87	UnM	26	47	7	100	24
2	3/10/87	Inc	32	63	100	300	23
2	4/10/87 *	Inc	18	70	Outside grid	301	3
3	7/11/87		28	114	124	134	13
3	11/11/87 **	Inc	25	50	170	170	0
3	23/11/87	Inc, UnM	38	76	Outside grid	Outside grid	27
4	8/6/88		7	23	41	207	11
5	24/6/88		24	72	41	183	15
5	25/6/88		24	166	183	124	22
5	27/6/88		5	10	124	101	7
5	10/7/88	UnM	4	5	101	33	8
5	11/7/88		65	214	33	29	34
6	9/11/88		35	42	68	54	33
6	10/11/88 *	Moved (19 m)	14	68	74	81	2
6	11/11/88	Moved (20 m)	21	76	69	72	12
7	14/11/88	UnM	16	60	71	74	15
7	27/5/89		8	13	65	57	8
7	7/6/89		6	6	41	46	6
8	8/6/89	Moved (57 m)	58	94	302	161	55
8	14/6/89	Moved (92 m)	74	107	Outside grid	Outside grid	74
8	16/6/89	UnM	14	25	Outside grid	157	9
8	18/6/89		9	9	157	Outside grid	9
8	21/6/89	Moved (5 m)	22	38	Outside grid	161	22
9	7/7/89 **		31	128	41	41	0
9	11/7/89		13	83	41	199	12
9	18/7/89	UnM	16	17	41	196	16
9	15/8/89	UnM	18	18	222	217	18
9	17/8/89	UnM	18	20	213	224	19
9	23/8/89	Inc, UnM	9	9	208	218	9
9	26/8/89	UnM	12	45	213	217	8
9	30/8/89 **	UnM	12	59	208	208	0
9	1/9/89 **		9	17	208	208	0
9	8/9/89	UnM	17	17	208	219	18
9	9/9/89 **	Moved (18 m)	21	76	208	208	0
9	10/9/89	Moved (8 m)	14	27	218	220	14
9	19/9/89	UnM	63	92	208	302	52

Table 9. Continued.

Lobster	Date of activity	Description of time since last date of activity	Maximum distance of positional fix from initial shelter (m)	Approximate total distance moved (m)	Initial shelter	Final shelter	Distance between initial and final shelters (m)
10	17/7/89		10	10	41	207	11
10	19/7/89	Moved (11 m)	23	27	41	15	24
11	29/7/89		18	18	41	187	20
12	13/9/89		38	64	41	45	39
12	14/9/89	Moved (12 m)	60	361	70	304	19
12	17/9/89 **	UnM	36	159	306	306	0
12	18/9/89		35	123	306	172	16
12	19/9/89		63	102	172	Outside grid	38
13	23/6/90		8	8	30	132	8
14	26/6/90		5	7	53	50	6
14	27/6/90		12	12	50	49	12
14	29/6/90	Inc	12	27	81	73	6
14	30/6/90		21	24	73	53	22
14	2/7/90		43	47	53	88	43
14	4/7/90 **	Moved (43 m)	6	19	53	53	0
14	5/7/90	Moved (4 m)	21	97	86	55	14
14	6/7/90		21	121	55	53	7
14	9/7/90 **		11	61	53	53	0
15	26/6/90		7	8	51	52	8
15	28/6/90		23	171	52	105	6
15	29/6/90	Moved (14 m)	9	50	95	66	12
15	1/7/90	Moved (12 m)	7	21	95	74	6
15	2/7/90 **	Moved (31 m)	8	16	305	305	0
15	5/7/90	Moved (42 m)	20	88	53	58	18
15	6/7/90		16	46	58	Outside grid	16
16	29/6/90		47	54	49	216	46
16	30/6/90		12	12	216	221	11
16	3/7/90 **	Moved (32 m)	7	15	179	179	0
17	17/7/90		14	14	41	214	13
18	23/7/90		33	37	23	303	33
18	24/7/90		29	31	303	11	34
18	26/7/90	Moved (22 m)	46	287	3	100	7
18	29/7/90	UnM	68	114	23	167	67
18	30/7/90		71	100	167	33	64
18	31/7/90	Moved (81 m)	54	250	Outside grid	28	48
19	7/8/90		9	9	41	211	9
20	21/8/90		30	105	23	33	6
20	22/8/90 **		8	32	33	33	0
20	23/8/90	Moved (17 m)	17	27	100	3	10
20	24/8/90		15	47	3	23	9
20	27/8/90 **	UnM	2	7	33	33	0

* denotes return to within 5 m of initial shelter; ** denotes return to the initial shelter



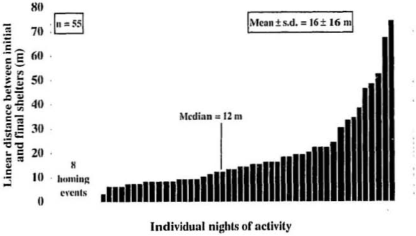


Figure 15. Distance between initial and final shelters of all tagged lobsters during monitored bouts of activity (upper histogram) and complete nights of monitoring (lower histogram).

homed once included 3, 12, 15 and 16.

Inconsecutive use of the same shelter was observed fifteen times (18 %) among eight lobsters (40 %). Lobster 9, which displayed consecutive use homing most frequently, also exhibited inconsecutive use most frequently (6 times). Lobster 14 returned to a previously used shelter three times after more than a one day absence.

Lobsters that homed were both male and female, with carapace lengths ranging from 77 to 109 mm. All homing events involving the consecutive use of the same shelter occurred after July 1.

Lobster 9's initial homing event ,which involved shelter 41, coincided with the first observed movement of this animal 4 days after tagging (July 7, 1989). The lobster's out-of-shelter activity time during the homing event was 4.5 h and it moved as far as 31 m from the shelter. Lobster 9's second homing event (August 30) involved a shelter (# 208) which it had occupied seven days before. It was outside the shelter for 1.7 h and moved at least 12 m from the shelter. After approximately 48 h, the animal again exhibited homing to this shelter (September 1). This time the lobster remained outside the shelter for only 20 min and moved a maximum of 9 m from the shelter. Eight days later, lobster 9 again homed (September 9) to shelter 208. Since the last homing event, the lobster had been observed moving out-of-shelter for only a short time (~15 min). On September 9, homing involved 4.7 h of activity outside of shelter during which the animal moved at least 21 m from the shelter. Ten days later (September 19), lobster 9 was again in shelter 208.

Lobsters 14 and 20 exhibited homing behaviour twice. Lobster 14 homed to shelter 53 and lobster 20 homed to shelter 33.

Lobster 14 was tagged at shelter 53 eight days before its first homing incident on July 4, 1990 and used other shelters during the intervening time. Shelter 53 was used four days before the initial homing behaviour was observed. Lobster 14's second homing event occurred five days later on July 9. On both nights of homing, lobster 14 was outside of the shelter for more than 3.5 h but was never more than 11 m from it.

Lobster 20's homing behaviour occurred on the second night after tagging (August 22, 1990). The animal was out of shelter for 4.5 h but moved less than 8 m from it. Five nights later, homing occurred again after 2.25 h of out-of-shelter activity. This night the animal moved less than 6 m from the shelter mouth. Lobster 20 used three different shelters between the homing events.

Each of lobsters 3 and 12 moved at least 25 m from its shelter and spent at least 4 h outside of shelter during its homing activity bout. Neither of lobsters 15 and 16 moved more than 8 m from its shelter during homing. Out-of-shelter activity times of the homing events of 15 and 16 were 50 min and 131 min (2.2 h), respectively.

Lobsters 2 and 6 returned to the vicinity of their initial shelters but did not use them. The maximum distances from initial shelter and out-of-shelter activity times of lobsters 2 and 6 were 18 m and 70 min (1.2 h), and 14 m and 140 min (2.3 h), respectively. Whether these shelters were occupied by other animals was not determined.

Lobsters 2, 6, 8, 9, 10, 14, 15, 18 and 20 homed to shelters they previously occupied after multiple day absences (Table 9). Homing occurred after 2 to 18 days (Table 9).

Lobster 8 used shelter 161 on June 8, 1989 and again on June 21. Between these dates, it used five other shelters. Two of these were more than 50 m from shelter 161.

Lobster 9 also returned to a shelter after several days absence. On August 23, 1989 and again on September 10, it used shelter 218. During the intervening period, it used four other shelters, all within 10 m of shelter 218.

3.3.3 Shelter characteristics

At least 74 different shelters were used by the twenty monitored lobsters (Tables A2-1 and A2-2, Appendix 2; Table 10). Of the six (23, 33, 41, 53, 100, 208) which were used more than twice (Table 10), all but shelter 100 were located in areas with primarily boulder cover.

The most frequently used shelter, # 41, was often checked first when searching for lobsters to tag. Therefore, its multiple use can be misleading when compared to the other shelters. Nine of the twenty lobsters tagged were from shelter 41. Shelter 23 was the only other shelter where lobsters were captured for tagging more than once (twice). Shelters 33, 53 and 208 were each used at least six times by lobsters on nontagging days. Shelters 53 and 208 were each used seven times but by only two and one lobster, respectively. Shelter 33 was occupied six times by three lobsters, shelter 23 four times by two lobsters, and shelter 100 three times by three lobsters.

Of the twenty shelters that were occupied twice, seven showed occupancy by two animals at different times. Forty shelters were used only once while one hundred and twenty-seven marked shelters were never observed in use by tagged lobsters during this study.

There apparently was no difference in substrate and macrobenthos type between locations of shelters used and unused by tagged lobsters (Tables A2-1 and A2-2, Appendix 2). Over 61 % of the shelters unused by tagged lobsters were excavated while almost 52 % of used shelters were of this type. The ranges of mouth height : width ratios (h : w) for used and unused shelters were 0.37 to 2.0[illegible] and 0.24 to 2.80, respectively. The mean h : w for used shelters was 0.96, compared to 0.97 for unused shelters (Figure 16). Mouth areas of used and unused shelters ranged from 40 to 360 cm^2 and 24 to 1215 cm^2,

Table 10 Shelters used by monitored lobsters, the number of times each was used, and the lobsters that occupied them at Broad Cove, Newfoundland, 1987 - 1990.

Shelter Number	No. of Uses	Occupying Lobsters *	Lobsters Initially Captured at Shelter
3	2	18 (1), 20 (1)	
7	1	2 (1)	
11	1	18 (1)	
15	1	10 (1)	
23	4	18 (2), 20 (2)	18, 20
28	1	18 (1)	
29	1	5 (1)	
30	1	13 (1)	13
33	6	5 (1), 18 (1), 20 (4)	
41	12	4, 5, 8, 9 (3), 10 (2), 11, 12, 17, 19	4, 5, 8, 9, 10, 11, 12, 17, 19
45	1	12 (1)	
46	1	8 (1)	
49	2	14 (1), 16 (1)	16
50	1	14 (1)	
51	1	15 (1)	15
52	1	15 (1)	
53	7	14 (6), 15 (1)	14
54	1	6 (1)	
55	1	14 (1)	
57	1	7 (1)	
58	1	15 (1)	
65	1	7 (1)	7
66	1	15 (1)	
68	1	6 (1)	6
69	1	6 (1)	
70	1	12 (1)	
71	1	6 (1)	
72	1	6 (1)	
73	1	14 (1)	
74	2	6 (2)	
81	2	6 (1), 14 (1)	
86	1	14 (1)	
88	1	14 (1)	
95	2	15 (2)	
100	3	2 (1), 18 (1), 20 (1)	
101	2	5 (2)	
105	1	15 (1)	
124	2	3 (1), 5 (1)	3
132	1	13 (1)	
134	1	3 (1)	

Table 10. Continued.

Shelter Number	No. of Uses	Occupying Lobsters *	Lobsters Initially Captured at Shelter
138	1	2 (1)	2
144	1	2 (1)	
157	1	8 (1)	
158	2	2 (2)	
161	2	8 (2)	
167	1	18 (1)	
170	2	3 (2)	
172	1	12 (1)	
179	2	16 (2)	
183	1	5 (1)	
187	1	11 (1)	
196	2	1 (1), 9 (1)	
199	1	9 (1)	
207	2	4 (1), 10 (1)	
208	7	9 (7)	
211	1	19 (1)	
213	2	9 (2)	
214	1	17 (1)	
216	1	16 (1)	
217	2	9 (2)	
218	2	9 (2)	
219	1	9 (1)	
220	1	9 (1)	
221	1	16 (1)	
222	1	9 (1)	
224	1	9 (1)	
232	1	1 (1)	1
300	1	2 (1)	
301	1	2 (1)	
302	2	8 (1), 9 (1)	
303	1	18 (1)	
304	1	12 (1)	
305	2	15 (2)	
306	2	12 (2)	
	126		

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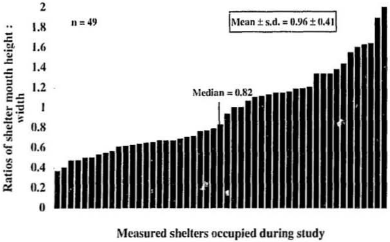
* Numbers in parentheses represent the number of times lobsters used specific shelters.



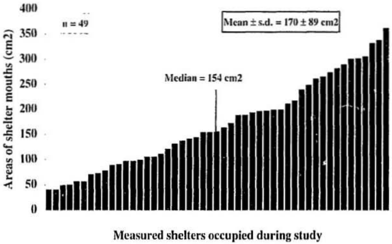


Figure 16. Mouth height : width ratios (upper histogram) and mouth areas (lower histogram) of measured shelters occupied by tagged lobsters.

respectively. The mean mouth area for used shelters was 170 cm^2 compared to 235 cm^2 for unused shelters (Figure 16). Neither shelter measurement was substantially different between used and unused shelters.

Shelters 41, 33 and 53, often used shelters, had mouth h : w ratios of 0.67, 1.33, and 0.70, respectively, and mouth areas of 216, 192, and 280 cm^2, respectively. These data were not available for shelter 208. All four shelters were located on boulder and outcrop substrate but their associated macrobenthos types differed. Shelter 33 was located in an area with a scattered sea urchin distribution and no mussels, whereas shelters 41 and 53 were located in regions with scattered distributions of both sea urchins and horse mussels. Shelter 208 was found within a mussel bed with scattered sea urchins. Shelters 41, 33 and 53 had all been excavated. Lobsters were present in only shelters 33 and 53 at the times they were surveyed.

The only apparent association between lobster size and shelter dimension was with respect to the mouth height : width ratio. Larger lobsters appeared to select shelters with the smallest ratios. For example, lobsters with carapace lengths under 79 mm used shelters with h : w ratios ranging from 0.37 to 2.0 (mean ± s.d. = 0.95 ± 0.40). Lobsters of carapace lengths exceeding 93 mm used shelters with h : w ratios ranging from 0.40 to 0.82 (mean ± s.d. = 0.65 ± 0.13). The h : w ratios of shelters used by large lobsters were not significantly different from those used by small individuals.

The minimum number of shelters used by individual lobsters was highly correlated with the duration of the monitoring period ($r = 0.61$). Based on frequency of use, lobsters 9, 14 and 20 seemed to prefer particular shelters over others ('home shelters') (Table 11). Lobster 9 used shelter 208 seven times, lobster 14 used shelter 53 six times, and lobster 20 used shelter 33 four times. Nine other lobsters used certain shelters twice.

Table 11. Minimum number of shelters used and most often used shelters of lobsters monitored at Broad Cove, Newfoundland, 1987 - 1990.

Lobster	Minimum number of different shelters used	Most often used shelter(s) (times used)	Duration of monitoring period (days)
1	2		5
2	7	#158 (2)	12
3	3	#170 (2)	22
4	2		11
5	6		22
6	7	#74 (2)	19
7	2		20
8	5	#161 (2)	21
9	12	#208 (7), #41 (3), #'s 213, 217, 218 (2)	86
10	3	#41 (2)	8
11	2		34
12	6	LORA block (2)	15
13	2		6
14	8	#53 (6)	19
15	8	#95, Angle iron pile #2 (2)	12
16	4	#179 (2)	13
17	2		4
18	8	#23 (2)	19
19	2		12
20	4	#33 (4), #23 (2)	9

Ranges of distances between the often used shelters and other used shelters during the monitoring period by lobsters 9, 14 and 20 were 3 to 50 m, 4 to 43 m, and 5 to 17 m, respectively (Figure 14).

Twelve activity bouts originating at shelter 41 (representing 9 lobsters) are presented in Figure 17. Ranges of maximum distance (MD) and approximate total distance (ATD) were 6 to 38 m, and 6 to 128 m, respectively. Most of the movements were directed downslope, probably due to the dropoff located immediately inshore of the shelter.

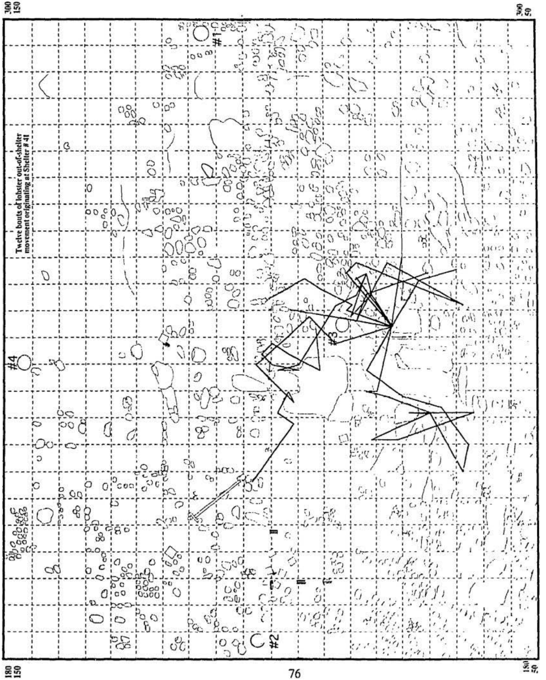
3.4 Trends of Lobster Activity Possibly Related to Biological and Environmental Factors

Although movements of male lobsters tagged in this study were, on average, longer in duration and distance, females averaged more time out-of-shelter due to their substantial stationary time (Table A3-1, Appendix 3). Females (30.1 %) had a slightly higher frequency of movement than the males (26.7 %). None of these activity differences due to sex were statistically significant ($p > 0.05$, Mann-Whitney Unpaired U Test).

Large lobsters (> 81 mm carapace length) were active more frequently (32.5 % compared to 28.8 % for smaller lobsters) and averaged greater distance from the initial shelter although these differences were not statistically significant ($p > 0.05$, M-W). On the other hand, smaller individuals (69 - 81 mm carapace length) averaged significantly longer activity bouts ($p < 0.01$, M-W) with movements over greater distances than larger lobsters.

Large males (35.3 %) and small females (38.7 %) were significantly active more frequently than small males (21.4 %) and the one large female (21.3 %) ($p < 0.05$, Kruskal-Wallis Test). Large and small males moved farthest ($p > 0.05$, K-W) while small

Figure 17. Movement paths of all out-of-shelter activities originating at shelter 41, Broad Cove, Newfoundland. Tagged lobsters involved included 4, 5, 8, 9, 10, 11, 12, 17 and 19.



Twelve bouts of lobster out-of-shelter movement originating at Shelter # 41 lobsters of both sexes displayed the highest average times of total activity ($p < 0.05$, K-W), in-shelter activity ($p > 0.05$, K-W) and out-of-shelter activity ($p > 0.05$, K-W).

Lobsters monitored after August 15 were active most frequently although the differences between the time periods were not statistically significant ($p > 0.05$, K-W). The percent active nights in this period was > 40 % compared to < 30 % prior to July 1 and between July 1 and August 15 (Table A3-2, Appendix 3).

Average distances moved and average times of out-of-shelter activity by individuals were greater after July 1 than before. Average total activity time was highest during the July 1 to August 15 period and essentially the same during the preceding and following periods. Differences in distance moved, duration of out-of-shelter activity, and duration of total activity were not statistically significant ($p > 0.05$, K-W). The average percentage of total activity time accounted for by stationary or stop time was significantly higher after August 15 than before ($p < 0.01$, K-W). The average numbers of stops and abrupt turns per activity bout of tagged lobsters were highest after July 1 but not significantly different than those prior to July 1.

Obviously, time of year and water temperature are interrelated. More often than not, the time periods exhibiting most activity also were characterized by highest water temperature. The frequency of activity at water temperatures exceeding 8 °C (30.5 %) was slightly higher than when temperatures equalled or were less than 8 °C (25.0 %). All average spatial and temporal aspects of activity shown by tagged lobsters were highest above 8 °C except for in-shelter activity (Table A3-2, Appendix 3). On average, activity and movement of lobsters monitored at times of lower water temperatures commenced later and ceased earlier after sunset than those of animals tracked when water temperatures > 8 °C. The average number of stops and abrupt turns per activity bout of tagged lobsters was highest at times of higher water temperature. Figure 18 presents the mean monthly water temperatures measured at Broad Cove between 1988 and 1990 as well as frequency of tagged lobster movement on nights with both monitoring and temperature data.

Frequency of lobster activity was slightly higher at times when wave height was greatest. Out-of-shelter activity occurred on 42 % of the monitored nights with wave height exceeding 0.5 m compared to slightly under 30 % activity occurrence on the monitored nights with wave heights less than 0.5 m.

All average spatial and temporal aspects of activity shown by tagged lobsters, except for in-shelter activity, were either highest or among the highest when wave heights exceeded 0.5 m (Table A3-3, Appendix 3). These include time after sunset of activity cessation and number of stops and turns.

Out-of-shelter activity at times of highest sea state was characterized by offshore or downslope movement more often than activity during other sea states. There are some interesting examples of considerable downslope movements at times of extremely rough seas. Lobster 2 (Day 4), lobster 9 (Day 78), and lobster 12 (Day 7) all moved considerable distances offshore. Ranges of horizontal downslope movement distance and depth change were 33 to 52 m, and 1.1 to 4.0 m, respectively.

Frequency of activity of tagged lobsters was highest at times of new moon and first quarter moon. No trends with respect to spatial and temporal specifics of lobster activity under different moon phases were obvious (Table A3-3, Appendix 3).

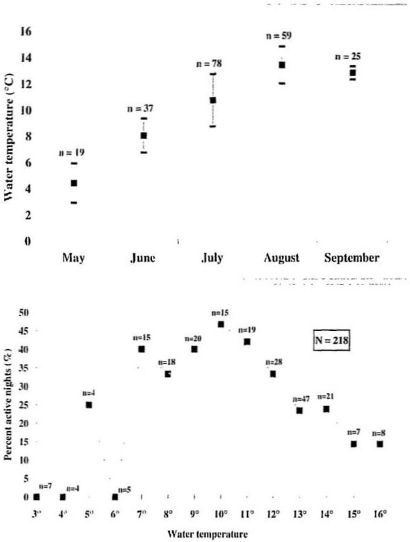


Figure 18. Mean monthly water temperatures ± standard deviations (upper graph) and percentage of monitored nights with lobster movement against water temperature (lower graph) at Broad Cove, Newfoundland, 1988 to 1990.

DISCUSSION

4.1 Response to Transmitter Attachment

The stationary tracking system used in this study permitted continuous nightly data collection on the activity of individual lobster. However, the quality of the data partly depends on the effect on the lobsters of transmitter attachment and its subsequent presence.

The attachment of a transmitter to the dorsal surface of a lobster carapace has not been a common procedure in the past. This method has been used for *Homarus americanus* (Lund and Lockwood 1970; Karnofsky et al. 1989a; Haakonsen et al. 1992), *Homarus gammarus* (Collins et al. 1991), and *Panulirus cygnus* (Jernakoff 1987; Jernakoff et al. 1987). Lund and Lockwood, Karnofsky and Jernakoff et al. reported that tagged animals appeared to behave normally during the monitoring period although capture and handling effects may have persisted for one or two days after tagging. Neither Haakonsen et al. nor Collins et al. discussed the possible effects of transmitter attachment, but presumably they thought it had little effect on their subjects.

Although attempts were made to minimize stress to the animals during tagging, some individuals appeared to be temporarily affected by the tagging procedure. This was inferred from the occurrence of out-of-shelter activity by two lobster during daylight hours on or shortly after the day of tagging. The majority of tagged individuals moved on the day of transmitter attachment but mostly after sunset.

The presence of the tag on the lobster carapace added 1 cm to the height of the animal which could have affected the size of a shelter opening which the lobster was capable of entering. However, all shelters in which individuals were initially found had openings large enough to accommodate the added lobster height.

That lobster 9 successfully spawned, lobster 10 successfully molted, and numerous lobsters showed homing behaviour following tagging collectively suggest that tagging did not have a substantial effect on their subsequent behaviour. Lobster 9 extruded eggs at some time between 14 and 38 days after transmitter attachment and lobster 10 molted within eight days of tagging. The spawning and molting conditions seemed to substantially reduce the activity levels of both animals. Seven of the twenty tagged lobsters exhibited same night homing, some more than once. Lobster 9 returned to the tagging shelter on its first night of observed activity after tagging (Day 4) while lobster 14 homed to its tagging shelter twice, on Days 9 and 14 of the monitoring period. Lobster 14 had left its tagging shelter on the first night of monitoring so its homing events to the tagging shelter occurred after it had occupied several other shelters.

4.2 Lobster Activity

Ennis (1983, 1984a) reported nocturnal activity indices (NAIs) for lobsters in the field, determined from May to November. NAI was calculated by dividing the number of lobsters seen out-of-shelter by the total number of lobsters seen on the dive and ranged from 0.10 to 0.60. Karnofsky et al. (1989b) who used the same index to investigate lobster activity levels under field conditions found a May to November range of 0.35 to 0.80. Although these NAI values are not directly comparable to data collected in the present study, they were essentially the only measures of lobster activity available until now. Karnofsky and Price (1989) conducted experiments under semi-natural conditions and found that , on average, 70 % of lobsters were in their shelters during after dark census times. The frequencies of individual out-of-shelter movement determined in the present study are the best data of this type to date. There was a great deal of variability with respect to how often individual lobster at Broad Cove moved from their shelters (4.3 to 71.4 % of monitored nights). The average frequency of lobster activity in the present study was 30.5 % which indicated that the tagged lobsters remained in or at their shelters on about twice as many nights as they left them.

Numerous field studies have indicated that American lobster nocturnal activity begins around dusk and peaks within 2 to 3 h after sunset (Cooper and Uzmann 1980; Ennis 1983, 1984a; Karnofsky et al. 1989a, 1984b;). Similar observations have been made under natural conditions on other lobster species including *Jasus lalandei* (Fielder 1965) and *Panulirus cygnus* (Jernakoff 1987; Jernakoff et al. 1987). These findings were corroborated by the present study. On average lobster initiated shelter activity 1.5 h after sunset and left shelter 50 min later, 2.3 h after sunset. Ennis (1983) found that lobster activity remained high for at least 2 to 3 h after peak activity but he could only speculate as to whether the level remained high until sunrise or tapered off gradually to a low pre-dawn level. The present study indicated that relatively little out-of-shelter activity is still occurring 6 h after sunset. Haakonsen et al. (1992), however, using ultrasonic telemetry, monitored the movement of two American lobsters and found that they remained out-of-shelter considerably longer than 6 h after sunset. They commenced out-of-shelter activity at dusk and remained outside of shelter until shortly after sunrise. Rare diurnal out-of-shelter sightings in this study were also the case in other studies (Ennis 1983, 1984a; Lawton 1987; Karnofsky and Price 1989; Karnofsky et al. 1989a, 1989b; Haakonsen et al 1992). Other than on the day of tagging, none of the tracked lobsters were observed out-of-shelter prior to sunset. During more than 50 h of daytime diving at the study site, fewer than 20 observations were made of lobsters out-of-shelter. Only the fact that the lobsters were out of shelter was noted and no observations regarding their activities were made.

However, according to Steneck (pers. comm.), snorkelling rather than SCUBA diving provides a much better opportunity to make observations on daytime out-of-shelter lobster activity. It is possible that some of the unobserved shelter changes on nights considered to be fully monitored occurred during daylight hours. Ennis (pers. comm.) reported that daytime sightings of postmolt lobsters foraging out-of-shelter was relatively common in a Placentia Bay population compared to a Bonavista Bay population. He considers lobster density to be a likely factor in diurnal lobster movement. Lobster density at Broad Cove is more similar to that of the study site at Bonavista Bay than at Placentia Bay (Ennis, pers. comm.). It is assumed that other than foraging, day time lobster movement was primarily for the purpose of shelter change.

Although Ennis (1983, 1984a), Karnofsky et al. (1989a, 1989b) and Haakonsen et al. (1992) provided information on the timing of lobster out-of-shelter activity, they did not address in-shelter activity or the spatial and more specific temporal aspects of out-of-shelter activity. My data includes active times in or at shelter, stationary time out-of-shelter, movement time, and measures of distance moved by lobsters while out-of-shelter.

Karnofsky et al. (1989b) reported that some lobsters appeared at their shelters' openings at sunset but usually did not leave until approximately one hour later. This was the general pattern for the lobsters tracked in the present study as well. Active time spent by tagged lobsters at the initial shelter during each activity bout averaged just under one hour. Lobsters may be monitoring the environment in the vicinity of the shelter prior to emerging from it. Chemical cues play an important role in the foraging and social behaviours of lobsters (Moore et al. 1991) so it is reasonable for an animal to conduct an initial assessment of its surroundings before leaving the protective cover of shelter. Another possible reason for activity at the initial shelter prior to movement away from it is the lobster might be finishing off food previously brought to the shelter. However, this would not be likely if the lobster had not left the shelter for days.

More often than not during nights when tagged lobsters did not leave their shelters, the audio strength of the transmitter signal increased around sunset or shortly after. Usually the signal strengthening lasted under 30 min but sometimes persisted for up to 2 h. Moody and Steneck (1993) reported from their field observations that American lobsters commonly carried prey to shelter where they then proceeded to manipulate it. Ennis (1983) observed lobsters feeding at their shelters during the first couple of hours after sunset. However, he could not determine whether the prey had been collected that same night or had been stored from previous foraging movements. Persistent initial shelter activity on those nights without out-of-shelter movement may have been individuals feeding at or near the shelter mouth. Final shelter time in the present study might also represent such feeding behaviour by the tagged lobsters. In some cases, these shelters probably were not the final ones used during the night's activity but instead locations where substantial activity of some sort occurred before the movement recommenced that night.

Some out-of-shelter stationary time might also represent events where individuals were feeding in relatively sheltered locations. Results from the present study indicated that, on average, out-of-shelter activity of the tagged lobsters was almost equally partitioned into movement and stationary behaviour. Karnofsky et al. (1989a) reported that relatively few foraging behaviours (117) were observed during 333 h of observation. Many of these events involved lobsters carrying prey although their subsequent destinations were not reported.

Frequently, a lobster's activities on consecutive days varied markedly both temporally and spatially. Difference in the relative durations of movement and stationary behaviour suggest that in some cases, the function of out-of-shelter movement on adjacent nights was different. In addition to movement for foraging and resource assessment, social behaviour associated with territoriality and reproduction would have been exhibited by lobsters during out-of-shelter activity. The degree of territoriality in lobsters is still unclear but large dominant males are known to keep shelters adjacent to their preferred mating shelter. Possession is maintained by periodic visitations (Karnofsky and Price, 1989). Lobster 12 (104 mm carapace length) might be representative of a dominant male. This animal was very active between September 13 and 19, a period perhaps after peak mating time. However, it is likely that some female lobsters were still available for mating at this time of year (Atema and Cobb, 1980). On four of the five nights with observed movement, lobster 12 displayed extraordinary activity events (large compared to all other observations). Interestingly, none of these events involved much stationary behaviour but rather spatially and temporally long movements resulting in numerous shelter changes. The low proportion of stationary time might suggest behaviour other than foraging. Five of the seven occupied shelters were clustered in a common region while the other two were relatively distant, one inshore and the other offshore from the cluster. The area with the five closely situated shelters could possibly have represented the core of the lobster's territory.

Female lobster 6 (75 mm carapace length) also exhibited extraordinary activity. Its movement on November 11 had the highest total activity time and stationary time recorded during the study. Females do tend to feed at a high rate longer into the late fall than male lobsters (Ennis 1973). Based on the incidence of stop time, the complex and multidirectional nature of its path and its high frequency of activity during the monitored period, this female lobster may have been feeding to recover from a late molt.

Encounters between conspecifics also occur, usually resulting in dominance displays. These displays of dominance are related to mating, most of which occurs between June and September. A sexually mature female seeks out a dominant male, resulting in cohabitation at the mating shelter of the male. Mating usually occurs within hours of the female molting. Cohabitation continues after mating during which the male provides protection to the vulnerable softshelled female. Therefore, during the few days preceding their molt, females often show an increase in activity associated with mate selection (Atema and Cobb, 1980).

Late pre-molt male lobsters also display an increase in activity, presumably to obtain and defend appropriate shelter in which to molt (Tamm and Cobb 1978; Karnofsky et al. 1989a). Lobster 10, a 75 mm male, molted shortly after being tagged. The earliest the molt occurred was the fourth day of monitoring since substantial activity was observed on the third night. The molted shell with tag was discovered in an open area during a dive five days after the last observed movement. The shelters in the vicinity of where the tag was found, including the lobster's last known shelter, were searched but no soft individuals were located. The out-of-shelter activity shown by this premolt lobster on the third night of monitoring lasted for 4 h. During its slow movement to slightly deeper water, lobster 10 stopped near mussel beds twice, for approximately 30 min at each location. It may have been inspecting shelters along its way considering the high density of shelters on its path.

Lobster 19, captured on August 7, was a new-shelled postmolt individual. It moved on the first night of monitoring, possibly a reaction to tagging. Movement lasted for only 15 min and resulted in a downslope relocation of 8 m. No activity was observed during the remaining eleven nights of monitoring. Lobster are extremely vulnerable immediately following molting because of their softshell condition and normally seek shelter until the new shell hardens to some degree. Tamm and Cobb (1978), based on experiments under artificial conditions, indicated that immediately post-molt lobsters (4 - 5 days after molt) generally displayed evasive actions to avoid conspecifics. These actions included remaining in-shelter for prolonged periods.

Based on observations made while SCUBA diving, lobster 9 extruded eggs between July 18 and August 11, 1989. Between July 4 (day of tagging) and July 18, this large female had three activity bouts (~21 % of monitored nights). No movement was observed again until August 15 although there were some nights during which monitoring did not occur. Between August 15 and September 27, the frequency of active nights increased to 33 %. Karnofsky and Price (1989) found that under semi-natural conditions, large berried females had lower activity levels than large males, small males and females, and large unberried females. However, they had no data on activity during pre- and post-egg extrusion. Lobster 9 demonstrated an increase in activity following a period of inactivity. Although durations and distances of most out-of-shelter movements after August 11 were short, frequency of movement was higher compared to before the period of inactivity. Some of the post-oviposition activity bouts were characterized by numerous stops close to shelter and prolonged final shelter times which might indicate feeding. This individual also had three post-oviposition movements with some of the highest out-of-shelter stationary time : movement time proportions observed during the study. These high ratios might have indicated increased feeding behaviour, characteristic of recovering female lobsters shortly after egg extrusion (Squires et al. 1973).

Some animals remained inactive for several days between movement events (lobsters 5 and 9) while others were inactive only one night over a period of several days (lobsters 2 and 12). Other animals remained inactive for essentially the entire tracking period (lobsters 4 and 7). Ennis (1983) reported that lobster occupied the same shelter in Bonavista Bay for as long as forty days. While it may be unlikely that a lobster remained in its shelter for this entire period, based on the low incidence of homing in the current study it is justified to presume that there was little activity during the forty days. This is not to say that the animals were not feeding during these periods without out-of-shelter activity considering the evidence from other studies for in-shelter food storage and feeding (Cooper and Uzmann 1980; Richards et al. 1986).

Lobsters at Broad Cove demonstrated two types of movement path patterns; simple with few path crossovers and abrupt direction changes; and complex with numerous path crossovers and abrupt direction changes. Each of these patterns was characterized by both spatially extensive and limited movement. Generally, the simple direct patterns appeared to function as relocation movements whereas the complex patterns which included more stops and were characteristically longer in duration, probably involved foraging and social behaviour. Straightline movements usually resulted in a marked depth change whereas many of the more circuitous complex movements ended at a depth similar to that of the initial shelter. Karnofsky et al (1989a), during their lobster homing experiments, observed both simple and complex movement paths but could not relate them to specific functions.

Although previous studies have provided some information on timing of lobster activity, they have provided little data on the extent of movement of individuals. Horizontal displacements, maximum distances (MDs) and approximate total distances (ATDs), were quite variable within and between individuals. Some lobsters displayed wide ranges of each variable while others showed only extensive or limited movement during all activity bouts. The individual tracks with high ATDs were generally characterized by high MDs.

This might be expected since high ATDs probably result from searching movements which take the animal further from its shelter than if it were making directed, non-searching movements. Fifty percent of all lobster activity bouts at Broad Cove were characterized by MD's which exceeded 18 m. Haakonsen et al. (1992) reported an American lobster moving a maximum of 60 m from its burrow on a single night. Their observation of distance moved was well within the range seen at Broad Cove but considerably higher than the average of 24.1 m. Animals monitored at Broad Cove moved > 60 m from their shelters only seven times (9.4 % of all monitored activity bouts). Cooper and Uzmann (1980) reported that lobsters rarely moved more than 300 m during a nocturnal activity event. Of the seventy-four lobster movements observed at Broad Cove on fully monitored nights, only one had an approximate total distance greater than 300 m. The average total distance moved by lobsters at Broad Cove was four times the average distance of 16 m moved by lobsters studied under semi-natural conditions by Karnofsky and Price (1989). However, the indoor pool tank used by Karnofsky and Price was only 15 m in diameter and most probably had a limiting effect on movement, unlike the tracking conditions of the present study.

Three monitored lobster movements had ATDs equalling or exceeding 250 m, which compared to all observed ATDs, were considered extraordinary events. Two of these movements were exhibited by male lobster 18 (76 mm carapace length) and the other by male lobster 12 (104 mm carapace length). Lobster 18 showed above average activity throughout tracking. Being a smaller male at near peak time for mating and molting (late July), this individual may have been searching for an appropriate shelter in which to molt and/or have been experiencing eviction by more dominant males. The combination of its extensive movement, its use of widely separated shelters and its small size may imply that this individual was not perceived as dominant by other lobsters. Lobster 12, as discussed earlier, also displayed higher than average activity. However, considering its larger size and use of clustered shelters, along with its extensive movement, its activity might be representative of a dominant individual.

The home range of individual lobsters has never been demonstrated until the present study. Obviously, the higher the number of activity bouts recorded, the better the definition of the home range. Again, variability between individuals was large. Some lobsters seemed to demonstrate more fidelity to a region than others who appeared to wander in a more nomadic fashion. One might expect that an individual tracked over a long period of time would use a larger area on its cumulative movements. Lobster 9, for example, who was active thirteen of the eighty-six days monitored, maintained a relatively small home range. Conversely, lobsters 12 and 18 moved extensively over periods of less than ten days. Movement paths were not necessarily repeated but there were cases where an individual lobster moved over the same general area on different nights, lobsters 6, 9, 14 and 20, for example.

The nineteen cases of a lobster being found in a shelter different from the one where it had last been positioned were either due to displacement from the shelters during unmonitored daytime periods or to a second unmonitored bout of activity the same night. Large males do evict conspecifics from shelters as a demonstration of dominance. The evicted lobsters will often leave the immediate vicinity for areas where interaction with more dominant individuals are possibly not as likely (Karnofsky and Price, 1989). The unobserved shelter changes by small male lobsters 6 and 15 could possibly have been results of evictions. In some cases, the new location was quite close to the old one while in others, it was a considerable distance away.

Karnofsky et al. (1989b) did not observe any difference between male and female lobsters with respect to activity. The present study also indicates that males and females have similar patterns. Ennis (1973) found that female lobsters fed at a high rate longer into the winter than did males but this difference in behaviour occurred in late November to early December. Differences were more evident between large and small lobsters in the present study. However, the activity data of the large berried female may well have lowered the average values associated with large animals.

The results regarding activity differences between sex by size categories do not fully agree with the limited data from other studies on American lobsters. Karnofsky and Price (1989) found that large males were most active, used the fewest number of shelters, and had the longest tracks while small females were least active and moved the shortest distances. Large females used the most different shelters in their study. Ennis (1983) reported that small males seemed to show most preference for one shelter. At Broad Cove, large males and small females were most active while males of both size categories moved farthest. Small females used the most different shelters while small males used the least (not including the large female category). The large female category was represented solely by the female who was berried for most of her monitoring time.

Generally, activity of lobsters at Broad Cove was greater after July 1 than before. Most probably, the coupling of increased water temperature with this time of year was responsible for the increased activity. It is reasonable to assume that the molting stage of each individual influenced the observed differences in activity variables between subjects. Ennis (1983) observed that lobster activity was lowest in early July (later stages of intermolt) even when compared to earlier in the year. However, lobster activity in Bonavista Bay increased during July and dropped in early September, just as it did in

Broad Cove.

Ennis (1983) reported that the nocturnal activity index varied with temperature throughout the period of July to November. He observed low activity in early July, then an increase which was maintained until early September, and finally a decrease which corresponded to decreasing water temperature. McLeese and Wilder (1958) reported increases in lobster activity levels as water temperatures rose during the spring and early summer months.

The present study indicated an increase in activity frequency at water temperature 7 - 8 °C, approximately the same water temperature at which Ennis (1983) noted an increase in the nocturnal activity index. Lobster in Ennis' study maintained a high activity index until water temperatures began to fall. However, in the present study, the percent active nights began to decrease at 11 °C although activity levels remained higher than those at temperatures below 7 °C. There are various possible explanations for the irregular trend which commenced at 11 °C. These include low number of observations and that the lobsters which displayed egg extrusion and molting were monitored during times of high water temperature. Their inactivity contributed substantially to the falling activity levels seen above 10 °C. Karnofsky et al. (1989b) found that lobster activity did not follow temperature as closely as Ennis indicated especially above water temperatures of 10 °C. In fact, they found that lobster activity decreased at times of water temperature increase and vice versa.

Data from the present study could not identify any trends associated with possible effects of daily water temperature fluctuation on lobster activity, mainly because water temperatures never changed that much within a 24 h period.

Ennis (1983, 1984a) and Cooper et al. (1975) observed lobsters moving to slightly deeper water at times of stormy weather and subsequently, rougher seas. The animals then returned to shallower water after storm effects had subsided. Broad Cove lobsters showed similar movements which coincided with higher seas and, thus, support the observations of Ennis and Cooper et al. The most graphic examples of directed downslope movement by lobsters were at times of extremely rough seas. Interestingly, stationary times in both initial and final shelters were much lower at times of greater wave height. If the storm effect was great enough to increase turbulence at the seafloor, it is reasonable to speculate that the chemical stimuli normally monitored by lobsters would be rather erratic. Perhaps this is sometimes the cue for lobster to move to a less affected location. If the chemical stimuli are erratic and provide less information to the lobster, there is perhaps little need to remain at the shelter mouth unless the animal is feeding on stored food.

There appeared to be a substantial difference in percent activity between nights of new moon / first quarter (37 %) and nights of full moon / last quarter (24 %). However, this remains speculative. No other studies on American lobster have investigated the effects of moonphase on activity and further study is required to determine if the trend seen in the present study is real.

4.3 Shelter Use

Little previous data exist on shelter use by individual lobsters. What does exist was either collected under artificial conditions or by field sampling on a short and discontinuous basis.

Past studies have indicated that large, more dominant lobsters tend to occupy fewer shelters than smaller individuals (Cobb and Tamm 1975; O'Neill and Cobb 1979). Dominant animals are less likely to be evicted and since they probably occupy the better quality shelters, they are less likely to voluntarily move. The Broad Cove study does not provide a clear trend of larger lobsters occupying fewer shelters than smaller ones. However, since the study site was rated as excellent lobster habitat (Ennis, pers. comm.) and prospective shelters seemed to far outnumber the lobsters (based on the number of empty shelters seen during SCUBA surveys), competition for shelter may not be as important in determining shelter use patterns as in other areas. If numerous shelters are available, lobsters of the size range tagged in this study might demonstrate more movement between shelters than in locations where shelters are at more of a premium. On the other hand, empty shelters are often an indication of eviction due to competition (Steneck pers. comm.). Most of the shelters used by an individual were often located in the same vicinity. For example, lobster 9, during its eighty-six days of monitoring, used twelve different shelters but all were within 30 m of one another. Exceptions to this were the shelters used by lobsters 5 (small female), 8 (large male) and 18 (small male). These lobsters were relatively wide ranging during the approximate three weeks of monitoring, shelters sometimes being as far as 90 m apart. Lobsters 8 and 18 accounted for five of the six largest distances between initial and final shelter observed during the entire study. Of the fourteen instances observed between 1988 and 1990 when the initial to final shelter distance exceeded 30 m, ten involved male lobsters.

Ennis (1983, 1984a) made thirteen observations of individual lobsters who had changed shelters on consecutive days. In all but three cases, the new shelter was less than 15 m from the original one. The study area surveyed by Ennis was approximately 250 m x 50 m. In the present study, 50 % of all movements resulted in the final shelter being located less than 12 m from the initial one.

Cobb (1971) found significant correlations between lobster size and shelter size but his lobster sample size was far larger than twenty animals. Like Cobb, I observed that the shelters used most often were usually low profile in that the shelter mouth height was substantially less than the mouth width. This pattern of shelter use was less clear in the present study than in Cobb's work, probably due to the relatively small sample size. Cobb conducted field studies which showed that American lobsters generally occupied shelters in which the height was less than the width. Eighty-seven percent of the shelters occupied in Cobb's study had h : w less than 1 and 44 % of them had h : 1/2w less than 1. Lobster size appeared most closely correlated with the square root of the mouth area ($r = 0.71$). In the present study, although the mean mouth height : width ratios of used and unused shelters were almost identical, the shelters with the largest ratios remained unused by tagged lobsters. The lower mean mouth areas of used shelters might indicate the importance of smaller openings to shelter selection but no substantial correlation was found between lobster size and mouth areas of shelters used at Broad Cove. The fact that large and small lobsters used the same shelters at different times might be further evidence that shelter competition was not an issue at Broad Cove. Conversely, Steneck (pers. comm.) notes that the competitive environment in lobster habitat changes nightly which might account for different occupants of the same shelter. Over 40 % of the shelters used by tagged individuals were occupied by lobsters at the time of the shelter survey while only 28 % of the shelters not used by tagged lobsters were occupied. It is not possible to conclude, however, that this percentage difference is a reflection of shelter quality.

Particular shelters were used by more than one individual during the study. Most of these shelters were found on boulder and outcrop substrate and near mussel patches but did not show a strong association between their dimensions and lobster carapace length. There was some indication that larger lobster used more shelters with mouth height : width ratios less than 1.0. These animals were perhaps dominant individuals and had choice of shelter over the smaller lobsters (Atema and Cobb 1980). Ennis (1983, 1984a) also found that certain shelters at his Bonavista Bay study area were being used by different animals at different times but he did not provide data on shelter characteristics other than depth and only limited data on the association between particular lobsters and shelters.

Differences in individual lobsters' shelter fidelities were also observed by Ennis (1983, 1984a), Karnofsky et al. (1984a), and Karnofsky and Price (1989). Ennis found that the number of shelters used per individual was a function of time. Those animals he observed for 1 to 2 months averaged two shelters each while those observed for 11 to 12 months averaged five shelters each. In the present study, lobsters tracked for under two weeks averaged 3.6 different shelters while those tracked for over two weeks, used an average of 5.3 different shelters.

The fact that three individuals accounted for 67 % of all incidents of same night homing reflects the variability associated with shelter fidelity. These individuals remained in more limited areas and, therefore, the probability of their returning to the initial shelter on the same night were high compared to those lobsters who were wider ranging. Same night homing by American lobster was also reported by Ennis (1983, 1984a) and Karnofsky and Price (1989). Ennis observed six same night events during which the lobsters were never observed more than 10 m from the initial shelters. The observed maximum distances from the initial shelter on same night homing events in the present study ranged from 2 to 36 m. Six of the twelve same night homing events were characterized by lobster position fixes greater than 10 m. Karnofsky and Price (1989) reported same night homing 34.5 % of the time during their experiments under semi-natural conditions. Same night homing occurred only 15 % of the time in the present study.

Possible reasons for a lobster not to return to its initial shelter include 1) it found another of equal or superior quality, 2) the initial shelter was taken by another lobster, 3) it was forced into another shelter as a result of an encounter with a predator or a more dominant conspecific, and 4) it moved into a shelter close to where it obtained prey in order to protect the food. If the second reason was the explanation, then the lobster would have to return to its initial shelter at some point during movement in order to determine occupancy by another. Tracks in the present study did not indicate this. Reasons one and three appear most applicable in this study but differentiation between the two scenarios remains difficult.

Most of the movement paths associated with the same night homing behavior were extremely circuitous. There was little indication of lobsters suddenly returning to the initial shelter after prolonged movement characterized by multiple path crossovers and numerous abrupt direction changes. Rather, the animals seemed to slowly wend their way back to the shelter, occasionally stopping on the way for whatever reason. In a couple of instances, lobsters took substantially less time to return to shelter from a location than move from the initial shelter to that location but even these were not directed movements.

Karnofsky et al. (1989a) reported on homing experiments conducted with two lobsters. These long-term resident lobsters, one male and one female, were captured near their shelters, tagged with light-emitting diodes and released approximately 35 m from their shelters. The animals were then followed by snorkellers. The male, released at 23:24, returned to his shelter within 2.25 h on a relatively simple path without crossovers. The female, released at 20:28, still had not returned to her shelter after 3.25 h but observations the next day found her there. The path she followed during the 3+ h after tagging was more complex than the male's and was characterized by numerous crossovers. The male was tagged a second time, sixteen days after the initial experiment. This time he demonstrated completely different behaviour. Immediately upon release, he entered a nearby shelter for 20 min and then was lost by the observers. Two nights later, a molted carapace with a flashing diode was located in front of the male's home shelter (site of capture).

Data collected on homing behaviour in the present study are a vast improvement over Karnofsky et al. (1989a). Less subject manipulation was used at Broad Cove so presumably all homing behaviour at the study site was less biased.

Nightly homing has also been observed in other lobster species such as spiny lobster, *Jasus edwardsii* (MacDiarmid et al. 1991), *Panulirus cygnus* (Cobb 1981; Jernakoff 1987; Jernakoff et al. 1987), and Norwegian lobster, *Nephrops norvegicus* (Chapman and Rice 1971).

4.4 Use of Different Substrata and Macrobenthos

Most of the stops (58 %) and shelter choices (66 %) were likely made on boulder and outcrop because this substrate was present in over half of the study site area. Such substratum is a common shelter-providing habitat for the American lobster throughout most of its range (Hudon 1987; Wahle 1990; Wahle and Steneck 1991). It has also been shown that kelp beds in association with this substratum provide suitable habitat for the animal (Bologna and Steneck 1993). Areas of the outcrop near the dropoff at Broad Cove had dense growths of *Desmarestia* and provided some shelter for lobsters. Lobsters, which appear to display central-place foraging behaviour, should prefer shelter locations which promote the least energy expenditure for maximum return (Lawton, 1987). There were instances in the present study where lobsters did return to a shelter with prey, perhaps enough to allow the lobster to remain in-shelter for a period of days and still be able to feed. Predator avoidance becomes less important to a lobster as it grows (Wahle, 1992b) so one might expect smaller individuals to spend a greater proportion of their time in shelters than larger lobsters. However, since all lobsters tagged in the present study were at least 69 mm carapace length, predator avoidance was probably a non-issue with most of them.

Average durations of stops gave better indications of preferred substrate for stationary behavior. The longest average stop durations, in descending order, occurred on 'boulder with outcrop', 'cobble with boulder and/or outcrop', and 'sand with boulder and/or cobble'. As expected, 'sand' and 'outcrop' substrates had the shortest average stop durations, perhaps because they provide little shelter or food.

Average stop durations were longest in areas dominated by scattered mussel and urchin distributions. This type of macrobenthos, which also had the highest percentage of all lobster stops, accounted for most of the macrobenthos cover in the study site area. Of all shelters used in this study, most were located in regions with scattered mussel and urchin distributions. Besides these species being prey for the American lobster (Squires 1970; Weiss 1970; Scarratt 1980; Elner and Campbell 1987; Hagen and Mann 1992), this distribution type also was present in over 50 % of the study area. Therefore, the probability of stops and shelters occurring in these regions was high. Conversely, dense mussel beds which comprised less than 8 % of the entire study area were sites of stops over 22 % of the time and accounted for over 18 % of all stationary time. The average stop duration in mussel beds was 23.7 min. A distinct preference for these beds appeared to be shown by some of the tagged lobsters.

Examination of the stop data in the various dominant macrobenthos types at different times of the year suggested that areas with scattered mussel and urchin distributions were selected most prior to July 1, mussels were preferred between July 1 and August 15, and finally urchins and mussels after August 15. The proportion of stops and stationary time in areas without mussels and urchins increased dramatically after August 15. It is difficult to speculate whether these seasonal differences are due to actual changes in prey preference or to coincidental proximity of the various macrobenthos distribution types. Other studies have indicated that the diet of American lobster does change with respect to physiological needs associated with the molting cycle (Ennis 1973; Leavitt et al. 1979). During June and July months, Ennis (1973) found that mussel shell fragments accounted for the highest proportion of stomach contents in lobsters from Bonavista Bay, Newfoundland while sea urchins made up the highest proportion in August and September. Data regarding lobster stops at Broad Cove may reflect this shift in diet. Polychaete remains were most evident in the Bonavista Bay lobster in August and September. Stops made by Broad Cove lobster on sandy substrate were most prevalent during monitoring times after August 15, but these relationships remain speculative until further research is conducted.

Leavitt et al. (1979) found that the stomach contents of hard-shell lobsters contained more protein constituents compared to mineral constituents while the opposite was true for soft-shell lobsters. Stop location and duration data from the present study may reflect these findings as more stationary behaviour between July 1 and August 15 occurred in areas with mussel patches compared to the other time periods. The July 1 to August 15 period probably best represents the time of peak change in shell condition, but again this requires further study.

Apparently some of the movements with stops had foraging purposes but they also appeared to serve other functions. It has been suggested that lobsters might remain in shelters between foraging activity events (Ennis 1983) however this study demonstrated lobster movement uncoupled with feeding behaviour. There were numerous examples of lobster out-of-shelter activity characterized by stationary time in prey poor areas and also movement uninterrupted by stationary time. Karnofsky et al. (1989a) were also surprised by the paucity of food obtaining behaviours demonstrated by lobsters during their nineteen month study.

4.5 Conclusion

This study has provided detailed information on aspects of American lobster behaviour under natural field conditions. It has examined activity / inactivity of lobsters, temporal and spatial aspects of out-of-shelter activity and its breakdown into movement and stationary behaviour, and duration of activity in shelters. Spatial aspects of out-of-shelter activity for which new knowledge was provided by this study included physical limits of movement by individual lobsters over multiple day periods, path patterns of movement, shelter homing by individuals on the same night of movement and after extended absences, shelter use on consecutive days, use of different substrate and dominant macrobenthos types, and short term vertical displacement (i.e., depth changes).

A weakness of the present study was that effects of biological and environmental factors could not be separated. To better understand the impact of these factors, one would have to collect much more data under more controlled conditions. For example, the investigator should be more selective with respect to the size and sex of the monitored lobsters and perhaps collect molting condition or serum protein data to replace the 'time of year' variable.

With the further development of computer software, time delay data can now be collected automatically as often as every 15 seconds and for indefinite durations. Events such as the unobserved shelter changes by lobsters would be recorded with continuous computer monitoring. More hydrophones placed within the study area would help to reduce the number of locations where the transmitter signal is either partially blocked or affected in such a way as to result in erratic and erroneous time delays at the receiver.

Ideally, a monitored lobster's suspected presence in a particular shelter should be verified by direct inspection on a daily basis. That is, SCUBA or remotely operated operations should be in effect each day.

Coupling the data collected to date with the above suggestions for study improvement, ultrasonic telemetry should be used to further investigate the various biological, physiological and environmental factors which account for the considerable variability associated with the diel activity of the American lobster.

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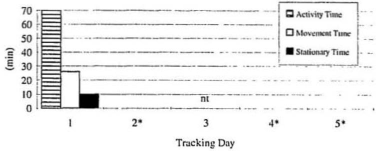
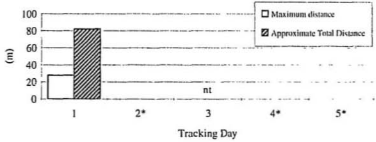
APPENDICES

Appendix 1. Activity and environmental data pertaining to the tracking periods of all lobsters monitored at Broad Cove, Newfoundland during the period of 1987 to 1990. Each lobster is represented by bar graphs displaying activity time, movement time, stationary time, maximum distance and approximate total distance moved and a table displaying mean water temperatures, sea states, moonphases and tracking day. All nights with movement partially or entirely within the study area are plotted on the study area map, one map per lobster. Information provided by the plots include lobster I.D., range of dates including movement, movement paths, used shelters, boulder and outcrop distribution, hydrophone locations, and bottom debris of human origin. Symbols encountered in tables displaying environmental factors include C (no waves), L (< 0.25 m), M (0.25 - 0.50 m), H (> 0.50 m), FQ (first quarter moon), FM (full moon), LQ (last quarter moon), and NM (new moon).

Activity, movement and stationary times of lobster 1 tracked between September 16, 1987 and September 20, 1987 ('nt' is non-tracking day)

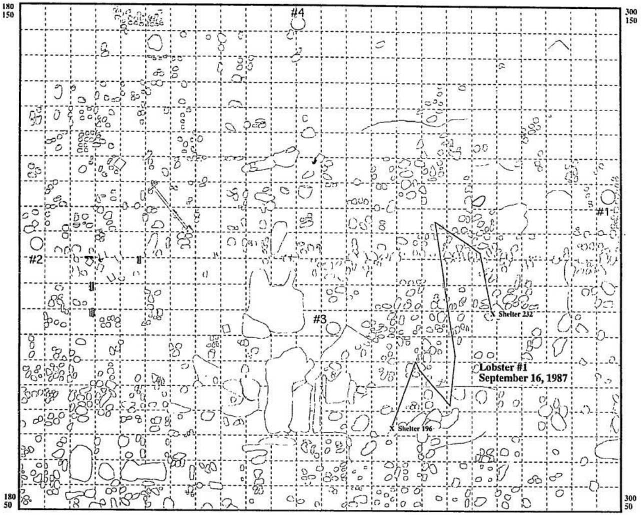


Maximum distance from initial shelter and approximate total distance moved by lobster 1 between September 16 and September 20, 1987 ('nt' is non-tracking day)

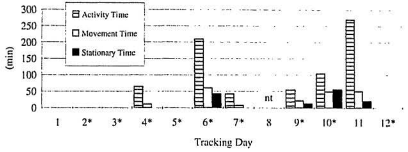


Water temperature (°C)	>8	>8	>8	>8	>8
Sea state	L	C		H	L
Moonphase	LQ+2				NM-3
Tracking day	1	2	3	4	5

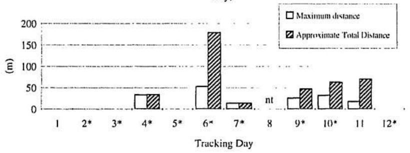
* denotes incomplete track


180
150
300
150
180
50
300
50
#4
#1
#2
#3
X Shelter 232
Lobster #1
September 16, 1987
X Shelter 196

Activity, movement and stationary times of lobster 2 tracked between September 24 and October 5, 1987 ('nt' is non-tracking day)



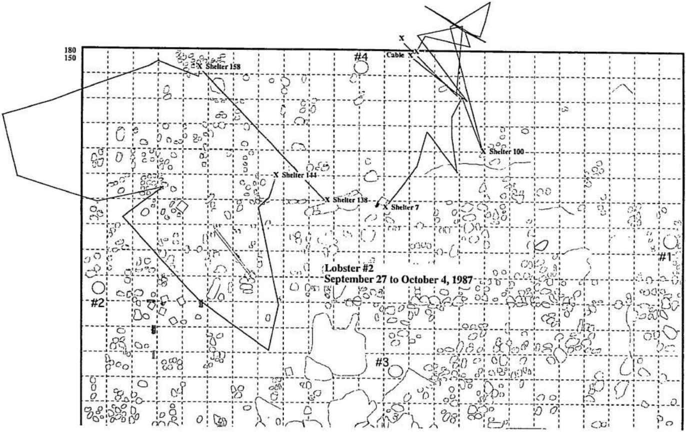
Maximum distance from initial shelter and approximate total distance moved by lobster 2 between September 24 and October 5, 1987 ('nt' is non-tracking day)

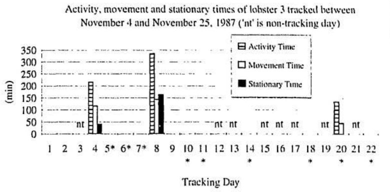


Water temperature (°C)	>8	>8	>8	>8	>8	>8	>8	>8	>8	>8	>8	>8
Sea state	C	C	H	M	M	L	L		H	L	L	H
Moonphase	NM+1						FQ					FM-2
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12

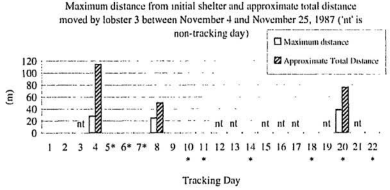
* denotes incomplete track

Movement path on Day 7 outside of study area; therefore not mapped.


180
150
300
150
X Shelter 158
#4
x
Cable X
X
X Shelter 100
X Shelter 144
X Shelter 138
X Shelter 7
Lobster #2
September 27 to October 4, 1987
#1
#2
#3



Activity, movement and stationary times of lobster 3 tracked between November 4 and November 25, 1987 ('nt' is non-tracking day)

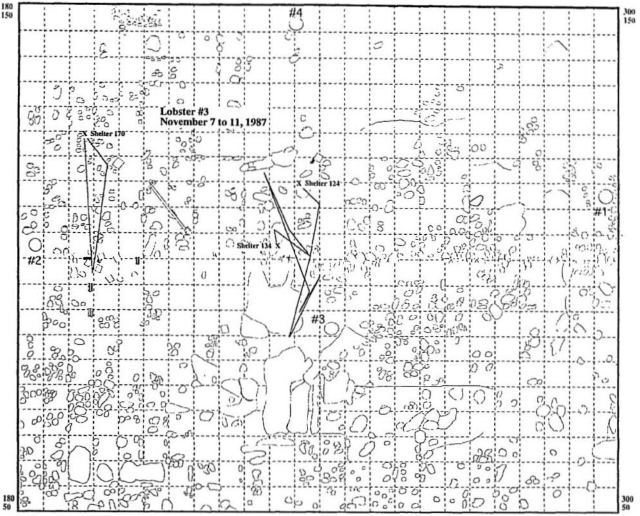


Maximum distance from initial shelter and approximate total distance moved by lobster 3 between November 4 and November 25, 1987 ('nt' is non-tracking day)

Water temperature (°C)	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8
Sea state	L	L		M	M	M	L	L	L	M	L	H	H	M				L		L		C
Moonphase		FM								LQ							NM					
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22

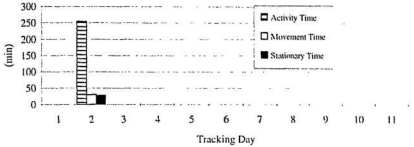
* denotes incomplete track

Movement path on Day 20 outside of study area; therefore not mapped.

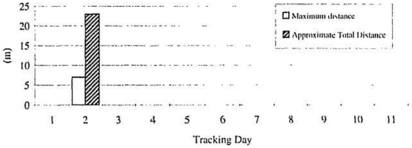


Lobster #3
November 7 to 11, 1987

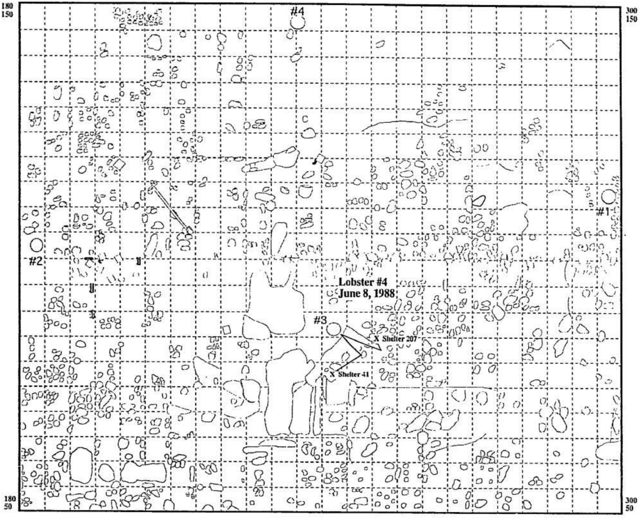
Activity, movement and stationary times of lobster 4 tracked between June 7 and June 17, 1988 ('nt' is non-tracking day)



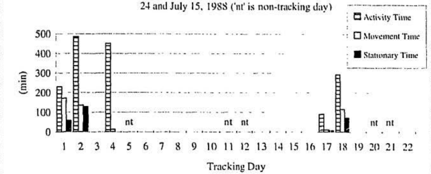
Maximum distance from initial shelter and approximate total distance moved by lobster 4 between June 7 and June 17, 1988 ('nt' is non-tracking day)



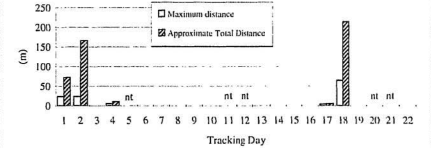
Water temperature (°C)	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8
Sea state	C	C	L	C	L	C	C	C	C	L	L
Moonphase	LQ							NM			
Tracking day	1	2	3	4	5	6	7	8	9	10	11


180
150
300
150
#4
#1
#2
Lobster #4
June 8, 1988
#3
X Shelter 207
X Shelter 41
180
50
300
50

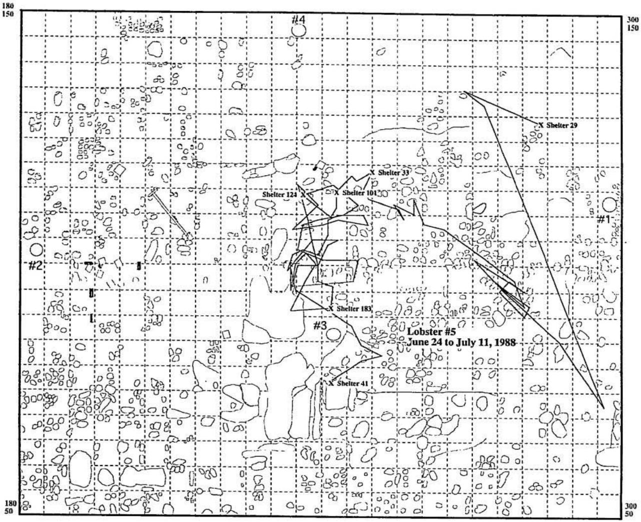
Activity, movement and stationary times of lobster 5 tracked between June 24 and July 15, 1988 ('nt' is non-tracking day)

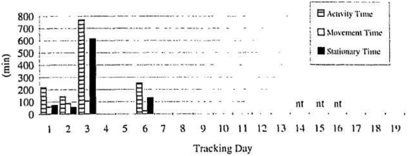


Maximum distance from initial shelter and approximate total distance moved by lobster 5 between June 24 and July 15, 1988 ('nt' is non-tracking day)

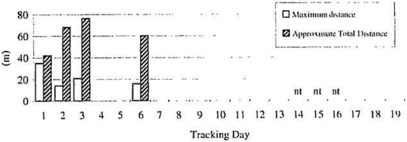


Water temperature (°C)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	>8	>8	>8	>8	>8	>8
Sea state	L	L	L	L	L	L	L	L	L	L	M	M	M	L	L	L	L	M	M	M	L	M
Moonphase						FM							LQ							NM		
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22


180
150
300
150
180
50
300
50
#1
#2
#3
#4
X Shelter 29
X Shelter 33
Shelter 124 X
X Shelter 101
X Shelter 183
X Shelter 41
Lobster #5
June 24 to July 11, 1988

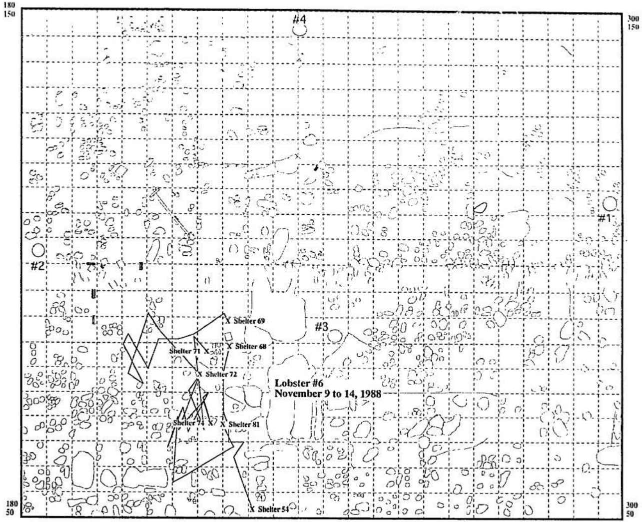


Activity, movement and stationary times of lobster 6 tracked between November 9 and November 27, 1988 ('nt' is non-tracking day)

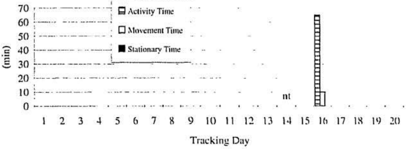


Maximum distance from initial shelter and approximate total distance moved by lobster 6 between November 9 and November 27, 1988 ('nt' is non-tracking day)

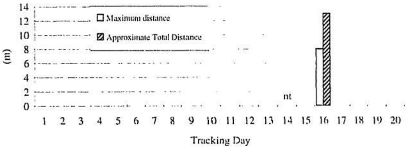
Water temperature (°C)	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8	<8
Sea state	L	M	H	H	M	H	C	M	L	M	M	M	L	M			M	H	H
Moonphase	NM							FQ							FM				
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19


180
150
#4
300
150
#1
#2
X Shelter 69
#3
Shelter 71 X
X Shelter 68
X Shelter 72
Lobster #6
November 9 to 14, 1988
Shelter 74 X
X Shelter 81
X Shelter 54
180
50
300
50

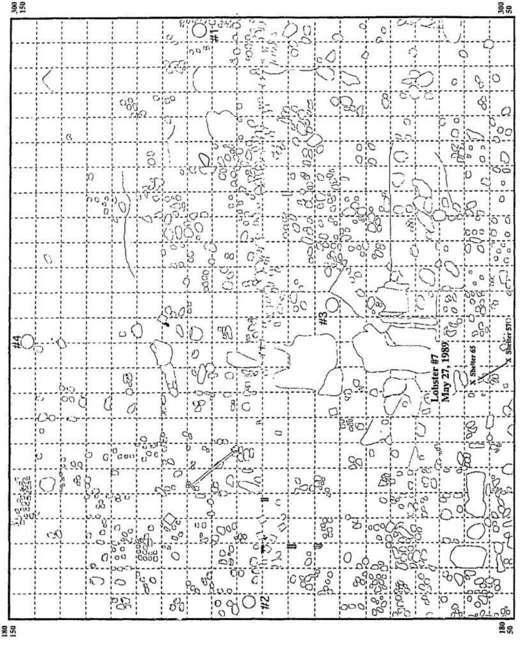
Activity, movement and stationary times of lobster 7 tracked between May 12 and May 31, 1989 ('nt' is non-tracking day)



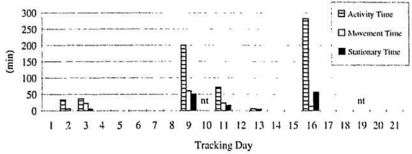
Maximum distance from initial shelter and approximate total distance moved by lobster 7 between May 12 and May 31, 1989 ('nt' is non-tracking day)



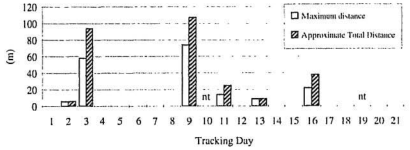
Water temperature (°C)	5	3	3	3	3	3	3	3	4	4	4	4	5	6	7	7	7	6	6	6
Sea state	C	H	H	C	C	C	C	C	L	C	C	C	C	C	L	C	L	M	L	L
Moonphase	FQ								FM							LQ				
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20


300
150
300
50
180
150
180
50
#1
#2
#3
#4
Lobster #7
May 27, 1989
X Shelter 65
X Shelter 570

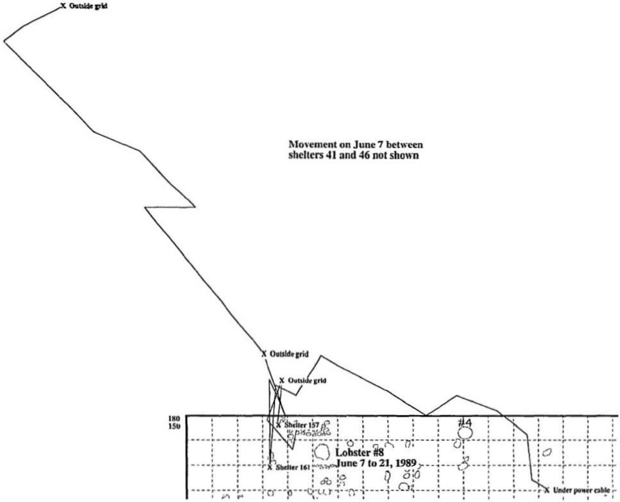
Activity, movement and stationary times of lobster 8 tracked between June 6 and June 26, 1989 ('nt' is non-tracking day)



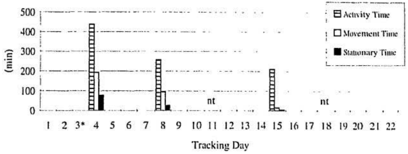
Maximum distance from initial shelter and approximate total distance moved by lobster 8 between June 6 and June 26, 1989 ('nt' is non-tracking day)



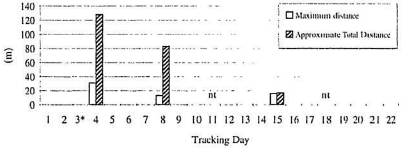
Water temperature (°C)	8	8	9	9	5	7	8	7	7	8	8	8	9	9	9	9	8	8	9	9	9
Sea state	C	C	M	M	M	L	L	L	L	L	M	L	L	C	C	C	C	C	C	C	C
Moonphase						FQ								FM							LQ
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21


X Outside grid
Movement on June 7 between
shelters 41 and 46 not shown
X Outside grid
X Outside grid
180
150
X Shelter 157
X Shelter 161
Lobster #8
June 7 to 21, 1989
#4
X Under power cable

Activity, movement and stationary times of lobster 9 tracked between July 4 and July 25, 1989 ('nt' is non-tracking day)

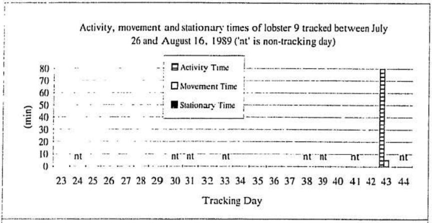


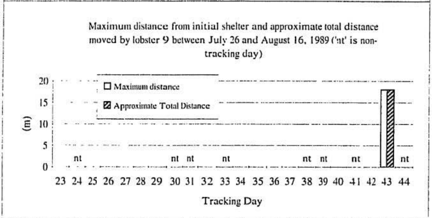
Maximum distance from initial shelter and approximate total distance moved by lobster 9 between July 4 and July 25, 1989 ('nt' is non-tracking day)



Water temperature (°C)	12	12	12	11	11	11	10	11	11	11	10	7	9	11	11	12	13	13	13	13	13	13
Sea state	M	L	M	M	C	C	C	L	L	L	L	L	L	M	C	C	M	M	M	L	L	M
Moonphase							FQ								FM							LQ
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22

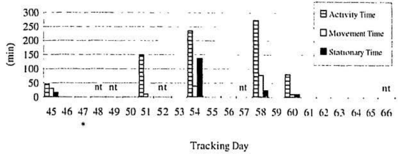
* denotes incomplete track


Activity, movement and stationary times of lobster 9 tracked between July 26 and August 16, 1989 ('nt' is non-tracking day)

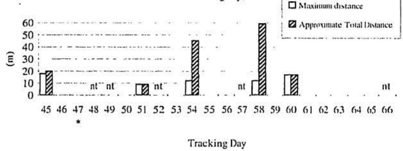

Maximum distance from initial shelter and approximate total distance moved by lobster 9 between July 26 and August 16, 1989 ('nt' is non-tracking day)

Water temperature (°C)	13	13	14	14	14	14	15	16	16	16	15	15	15	14	11	12	12	13	13	12	13	14
Sea state	M		L	L	C	L	C			L		M	M	L	L			M		M	L	
Moonphase							NM							FQ								FM
Tracking day	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44

Activity, movement and stationary times of lobster 9 tracked between August 17 and September 7, 1989 ('nt' is non-tracking day)



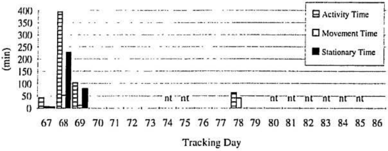
Maximum distance from initial shelter and approximate total distance moved by lobster 9 between August 17 and September 7, 1989 ('nt' is non-tracking day)



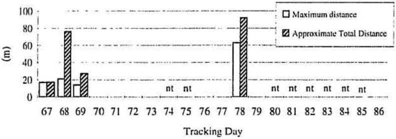
Water temperature (°C)	16	16	16	15	13	13	13	13	13	13	13	13	12	12	12	12	11	11	11	11	11	11
Sea state	M	H	H			C	L		L	M	M	L		L	M	M	M	L	L	L	C	C
Moonphase							LQ							NM								
Tracking day	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66

* denotes incomplete track

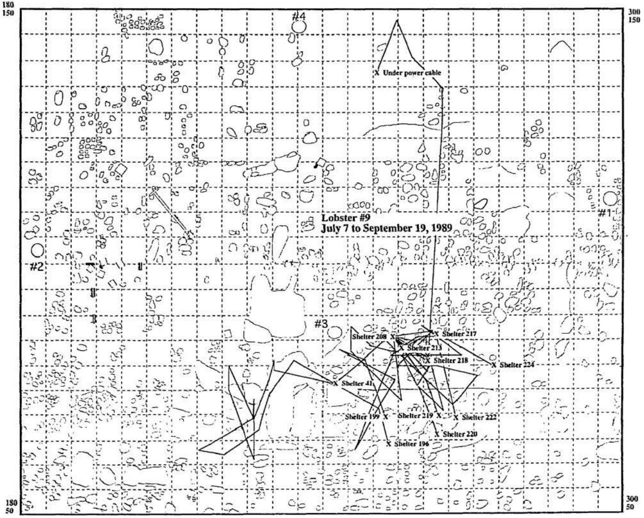
Activity, movement and stationary times of lobster 9 tracked between September 8 and September 27, 1989 ('nt' is non-tracking day)



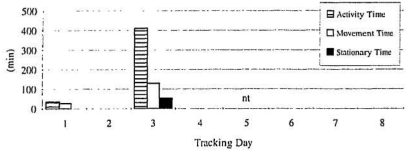
Maximum distance from initial shelter and approximate total distance moved by lobster 9 between September 8 and September 27, 1989 ('nt' is non-tracking day)



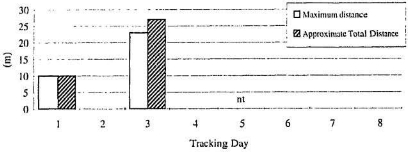
Water temperature (°C)	13	13	13	14	14	13	13	13	13	13	13	12	12	12	13	12	13	13	12	13
Sea state	C	C	C	C	L	L	C			M	H	H	M							H
Moonphase	FQ							FM							LQ					
Tracking day	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86


180
150
300
150
180
50
300
50
Lobster #9
July 7 to September 19, 1989
#1
#2
#3
#4
X Under power cable
Shelter 208 X
X Shelter 217
X Shelter 213
X Shelter 218
X Shelter 224
X Shelter 41
Shelter 199 X
Shelter 219 X
X Shelter 222
X Shelter 220
X Shelter 196

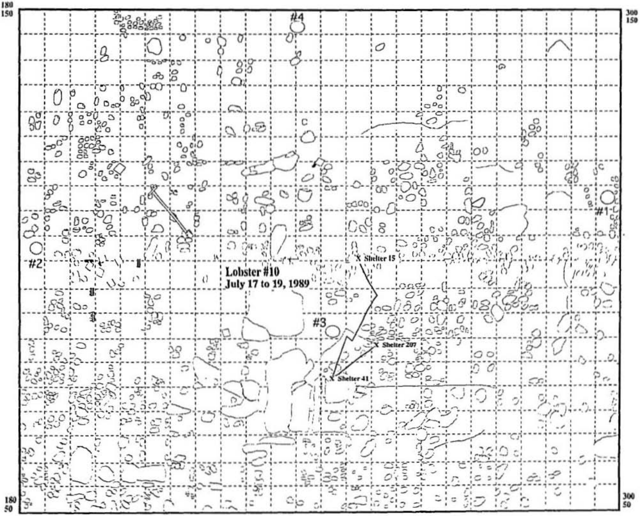
Activity, movement and stationary times of lobster 10 tracked between July 17 and July 24, 1989 ('nt' is non-tracking day)

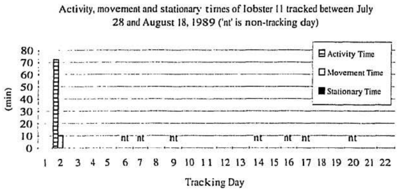


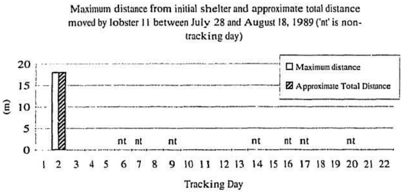
Maximum distance from initial shelter and approximate total distance moved by lobster 10 between July 17 and July 24, 1989 ('nt' is non-tracking day)



Water temperature (°C)	11	11	12	13	13	13	13	13
Sea state	M	C	C	M	M	M	L	L
Moonphase		FM						LQ-1
Tracking day	1	2	3	4	5	6	7	8

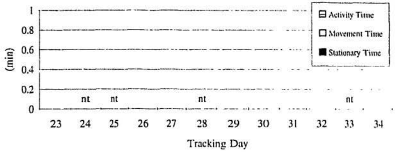

180
150
#4
300
150
#1
#2
Lobster #10
July 17 to 19, 1989
X Shelter 15
#3
X Shelter 207
X Shelter 41
180
50
300
50


Activity, movement and stationary times of lobster 11 tracked between July 28 and August 18, 1989 ('nt' is non-tracking day)

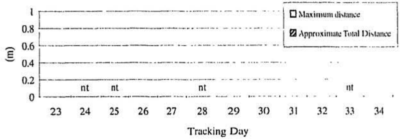

Maximum distance from initial shelter and approximate total distance moved by lobster 11 between July 28 and August 18, 1989 ('nt' is non-tracking day)

Water temperature (°C)	14	14	14	14	15	16	16	16	15	15	15	14	11	12	12	13	13	12	13	14	16	16
Sea state	L	L	C	L	C			L		M	M	L	L			M		M	L		M	M
Moonphase					NM							FQ								FM		
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22

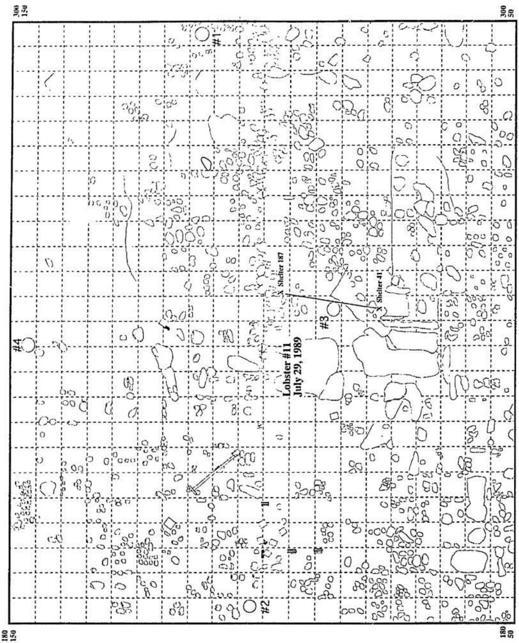
Activity, movement and stationary times of lobster 11 tracked between August 19 and August 30, 1989 ('nt' is non-tracking day)



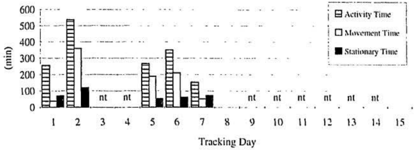
Maximum distance from initial shelter and approximate total distance moved by lobster 11 between August 19 and August 30, 1989 ('nt' is non-tracking day)



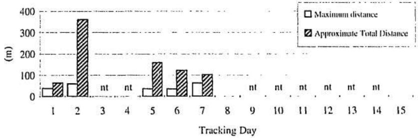
Water temperature (°C)	16	15	13	13	13	13	13	13	13	13	12	12
Sea state	H			C	L	L	L	M	M	L	L	L
Moonphase					LQ							NM
Tracking day	23	24	25	26	27	28	29	30	31	32	33	34


300
150
300
50
180
150
180
50
#1
#2
#3
#4
X Shelter 187
X Shelter 41
Lobster #11
July 29, 1989

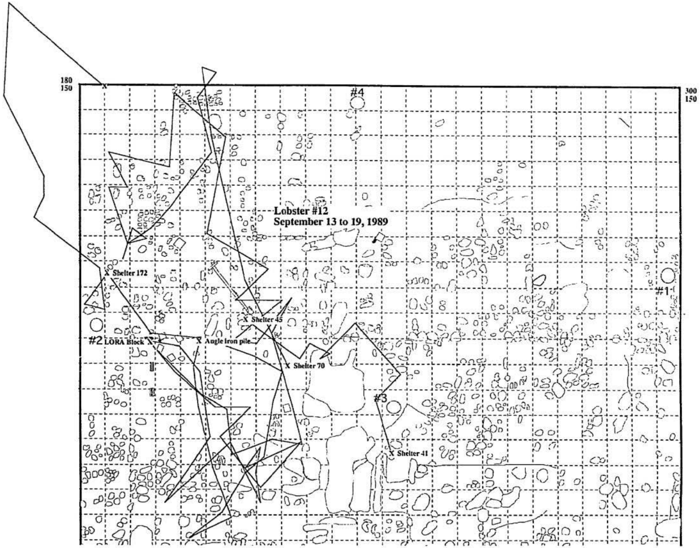
Activity, movement and stationary times of lobster 12 tracked between September 13 and September 27, 1989 ('nt' is non-tracking day)



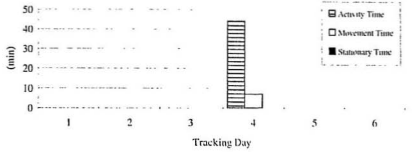
Maximum distance from initial shelter and approximate total distance moved by lobster 12 between September 13 and September 27, 1989 ('nt' is non-tracking day)



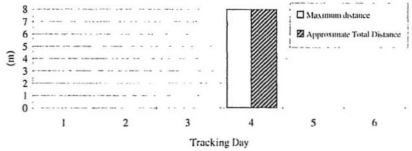
Water temperature (°C)	13	13	13	13	13	13	12	12	12	13	12	13	13	12	13
Sea state	L	C			M	H	H	M							H
Moonphase			FM							LQ					
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15


180
150
300
150
#4
Lobster #12
September 13 to 19, 1989
#1
X Shelter 172
X Shelter 45
#2 LORA Block X
X Angle iron pile
X Shelter 70
#3
X Shelter 41

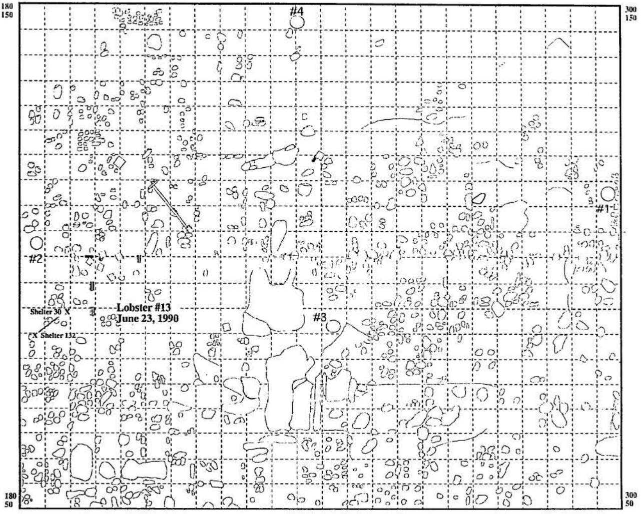
Activity, movement and stationary times of lobster 13 tracked between June 20 and June 25, 1990 ('nt' is non-tracking day)



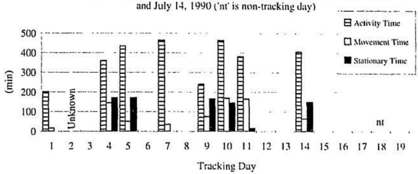
Maximum distance from initial shelter and approximate total distance moved by lobster 13 between June 20 and June 25, 1990 ('nt' is non-tracking day)



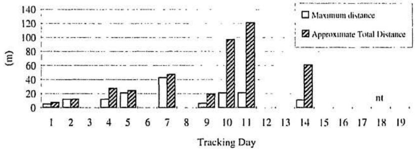
Water temperature (°C)	8	7	7	5	6	6
Sea state	L	L	L	L	L	L
Moonphase			NM			
Tracking day	1	2	3	4	5	6


180
150
300
150
#4
#1
#2
#3
Shelter 30 X
X Shelter 132
Lobster #13
June 23, 1990
180
50
300
50

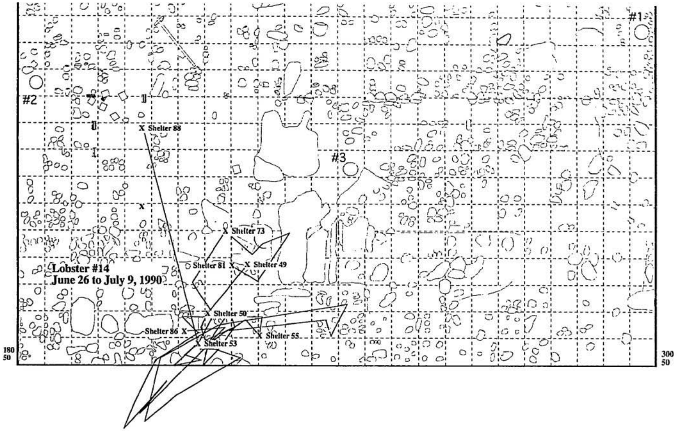
Activity, movement and stationary times of lobster 14 tracked between June 26 and July 14, 1990 ('nt' is non-tracking day)



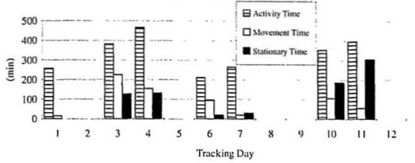
Maximum distance from initial shelter and approximate total distance moved by lobster 14 between June 26 and July 14, 1990 ('nt' is non-tracking day)



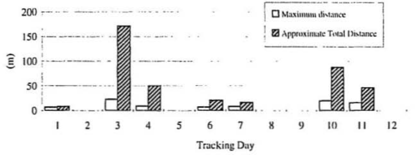
Water temperature (°C)	7	8	9	9	10	8	8	8	7	10	11	9	8	9	9	10	10	11	11
Sea state	L	M	M	M	L	L	L	M	M	H	M	M	M	L	M	M	M	M	M
Moonphase				FQ									FM						
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19


#1
#2
#3
X Shelter 88
X
X Shelter 73
Shelter 81 X
X Shelter 49
Lobster #14
June 26 to July 9, 1990
X Shelter 50
Shelter 86 X
X Shelter 55
X Shelter 53
180
50
300
50

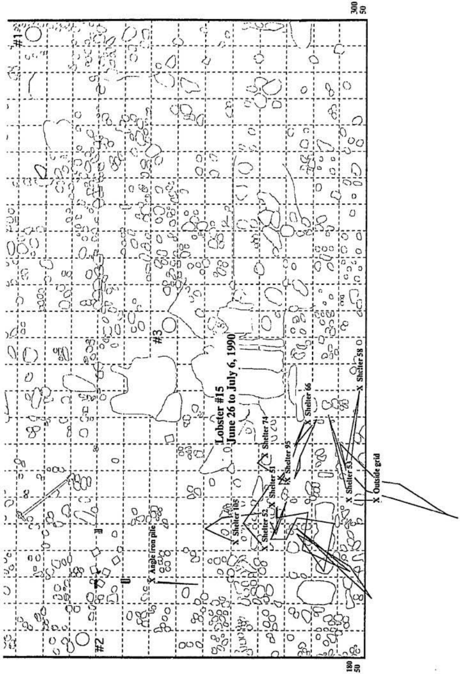
Activity, movement and stationary times of lobster 15 tracked between June 26 and July 7, 1990 ('nt' is non-tracking day)



Maximum distance from initial shelter and approximate total distance moved by lobster 15 between June 26 and July 7, 1990 ('nt' is non-tracking day)

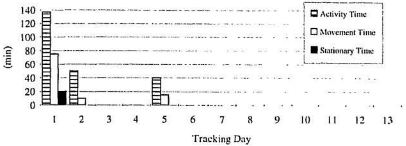


Water temperature (°C)	7	8	9	9	10	8	8	7	10	10	11	9
Sea state	L	M	M	M	L	L	L	M	M	H	M	M
Moonphase				FQ								FM-1
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12

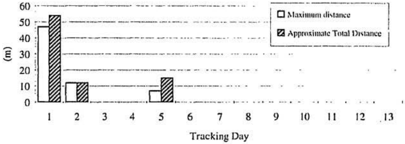


Lobster #15
June 26 to July 6, 1990
#1
#2
#3
X Angle iron pile
X Shelter 105
X Shelter 52
X Shelter 51
X Shelter 74
X Shelter 95
X Shelter 66
X Shelter 53
X Shelter 58
X Outside grid
300 50
180 50

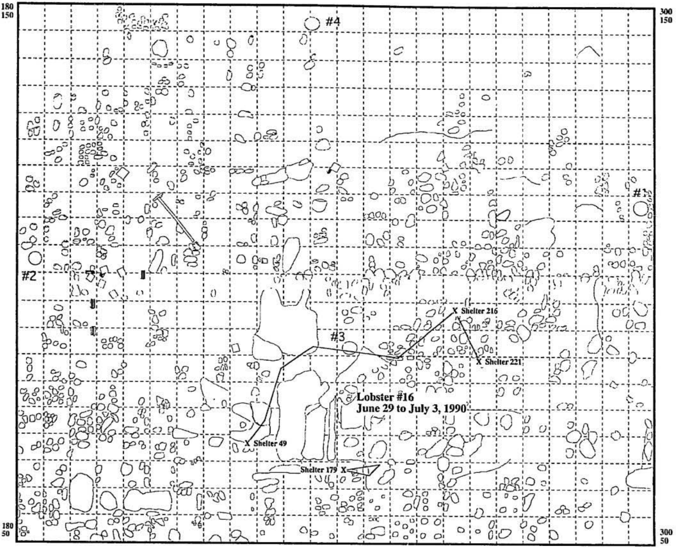
Activity, movement and stationary times of lobster 16 tracked between June 29 and July 11, 1990 ('nt' is non-tracking day)



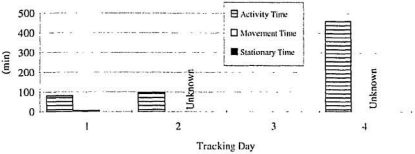
Maximum distance from initial shelter and approximate total distance moved by lobster 16 between June 29 and July 11, 1990 ('nt' is non-tracking day)



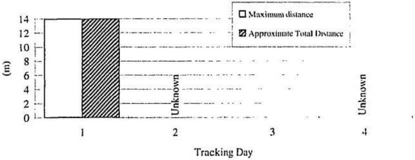
Water temperature (°C)	9	10	8	8	7	10	10	11	9	8	9	9	10
Sea state	M	L	L	L	M	M	H	M	M	M	L	M	M
Moonphase	FQ									FM			
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13


180
150
300
150
#4
#1
#2
X Shelter 216
#3
X Shelter 221
Lobster #16
June 29 to July 3, 1990
X Shelter 49
Shelter 179 X
180
50
300
50

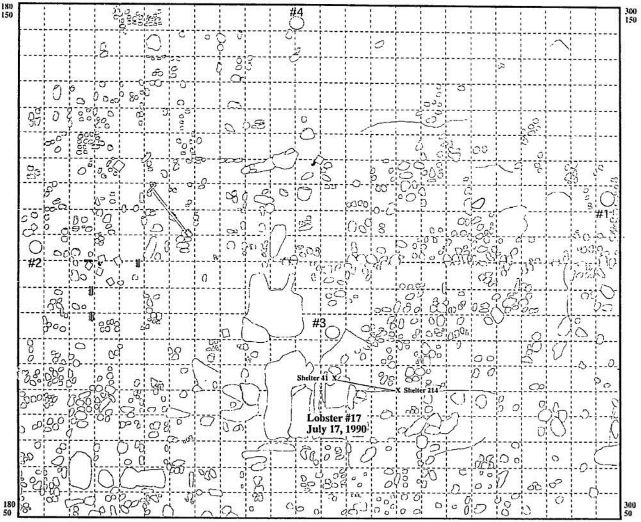
Activity, movement and stationary times of lobster 17 tracked between July 17 and July 20, 1990 ('nt' is non-tracking day)



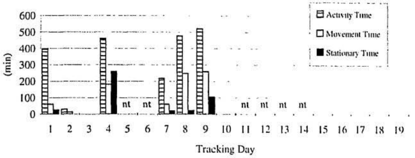
Maximum distance from initial shelter and approximate total distance moved by lobster 17 between July 17 and July 20, 1990 ('nt' is non-tracking day)



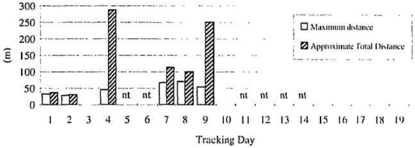
Water temperature (°C)	11	11	12	12
Sea state	L	C	L	M
Moonphase	LQ+2			NM-2
Tracking day	1	2	3	4


180
150
#4
300
150
#1
#2
#3
Shelter 41 X
X Shelter 214
Lobster #17
July 17, 1990
180
50
300
50

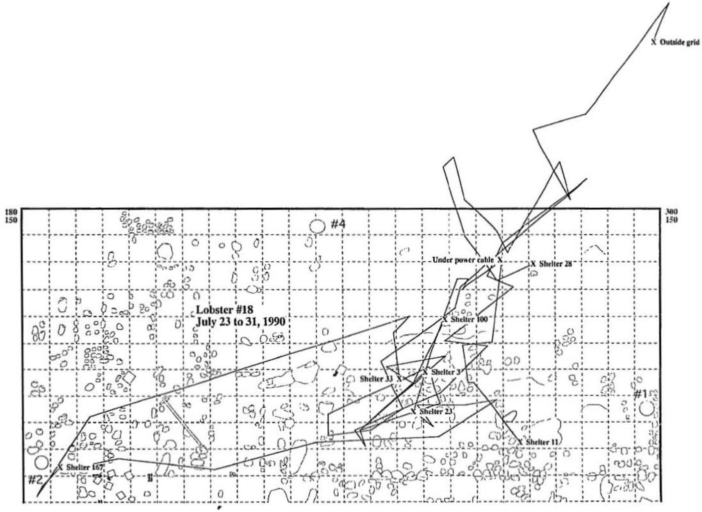
Activity, movement and stationary times of lobster 18 tracked between July 23 and August 10, 1990 ('nt' is non-tracking day)



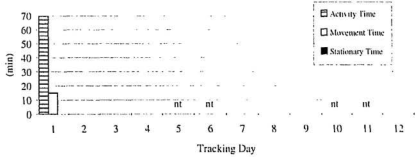
Maximum distance from initial shelter and approximate total distance moved by lobster 18 between July 23 and August 10, 1990 ('nt' is non-tracking day)



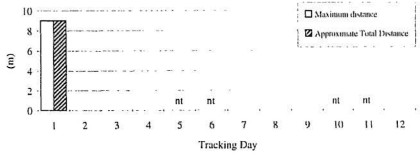
Water temperature (°C)	12	12	13	13	12	10	10	10	10	14	14	13	12	12	12	12	12	12	12
Sea state	C	C	M	M			L	L	L	L					C	C	C	L	L
Moonphase	NM+1						FQ								FM				
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19


X Outside grid
180
150
300
150
#4
Under power cable X
X Shelter 28
Lobster #18
July 23 to 31, 1990
X Shelter 100
X Shelter 3
Shelter 33 X
X Shelter 23
X Shelter 11
#1
X Shelter 167
#2

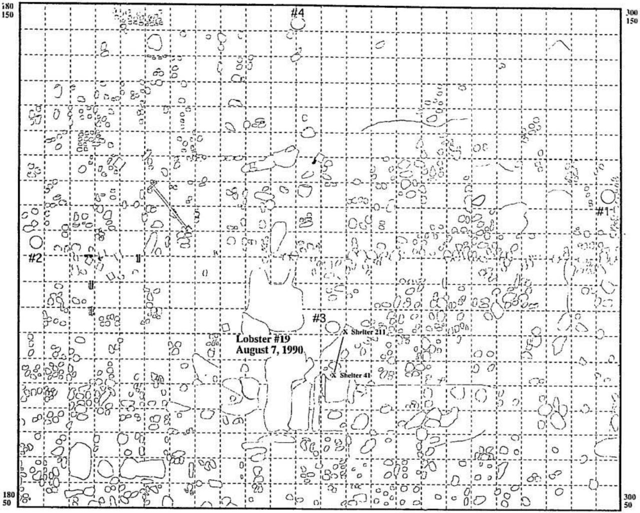
Activity, movement and stationary times of lobster 19 tracked between August 7 and August 18, 1990 ('nt' is non-tracking day)

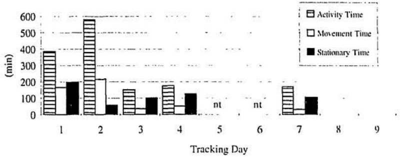


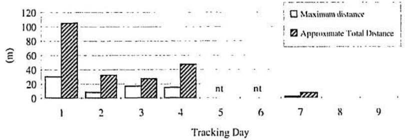
Maximum distance from initial shelter and approximate total distance moved by lobster 19 between August 7 and August 18, 1990 ('nt' is non-tracking day)



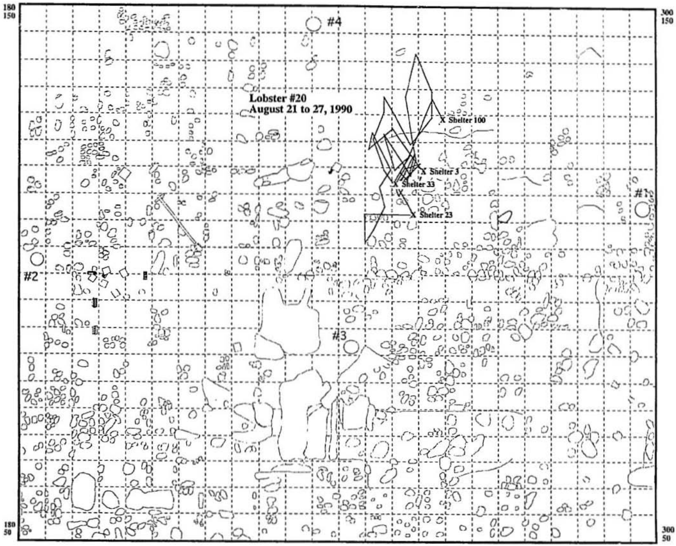
Water temperature (°C)	12	12	12	12	12	13	13	14	14	13	13	13
Sea state	C	C	L	L			L	L	M			M
Moonphase	FM+1						LQ					NM-2
Tracking day	1	2	3	4	5	6	7	8	9	10	11	12


180
150
#4
300
150
#1
#2
#3
X Shelter 211
Lobster #19
August 7, 1990
X Shelter 41
180
50
300
50


Activity, movement and stationary times of lobster 20 tracked between August 21 and August 29, 1990 ('nt' is non-tracking day)


Maximum distance from initial shelter and approximate total distance moved by lobster 20 between August 21 and August 29, 1990 ('nt' is non-tracking day)

Water temperature (°C)	15	14	14	14	14	14	14	14	14
Sea state	M	M	L	C			L	C	L
Moonphase	NM+1							FQ	
Tracking day	1	2	3	4	5	6	7	8	9


180
150
#4
300
150
Lobster #20
August 21 to 27, 1990
X Shelter 100
X Shelter 3
X Shelter 33
X Shelter 23
#1
#2
#3
180
50
300
50

Appendix 2. Data on shelters occupied and not occupied by tagged lobsters within the study site at Broad Cove, Newfoundland, 1987 - 1990. Shelter specifics include substrate type (S = sand, SBC = sand with boulder and/or cobble, CBO = cobble with boulder and/or outcrop, O = outcrop, BO = boulder and outcrop), macrobenthos type (MB = mussel bed with urchins, M = scattered mussels, MU = scattered mussels and urchins, U = scattered urchins, NMU = neither mussels nor urchins), entrance height, entrance width, shelter length, entrance height : width ratio, entrance area, construction type (excavated (E) or not (NE)), and absence (A) or presence (P) of lobster at survey time.

Table A2-1. Shelters occupied by monitored lobsters during tracking study.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height:width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
232	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
196	O	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
138	O	MU	15	13	53	1.15	195	E	A
158	SBC	MU	11	8	25	1.38	88	NE	P
144	SBC	MB	15	24	47	0.62	360	E	P
7	BO	U	17	9	50	1.89	153	NE	A
100	SBC	MB	9	8	25	1.12	72		P
124	BO	MU	11	30	46	0.37	330	NE	P
134	BO	MU	8	12	34	0.67	96	NE	P
170	CBO	MU	11	10	32	1.10	110	NE	A
41	BO	MU	12	18	35	0.67	216	E	A
207	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
183	BO	U	12	10	30	1.20	120	NE	A
101	BO	MB	10	7	30	1.43	70	n/a	P
33	BO	U	16	12	38	1.33	192	E	P
29	SBC	U	14	15	33	0.93	210	NE	A
68	BO	MU	13	19	40	0.68	247	E	A
54	BO	MU	8	5	21	1.60	40	E	A
74	O	MU	8	17	28	0.47	136	E	A
81	BO	MU	11	18	60	0.61	198	E	P
69	O	MU	11	17	38	0.65	187	E	A
157	SBC	MU	10	13	21	0.77	130	NE	P
72	BO	MB	8	7	30	1.14	56	E	A
71	BO	MU	18	11	50	1.64	198	NE	A
65	O	MU	19	16	42	1.19	304	E	A
57	BO	M	9	18	33	0.50	162	E	P
46	O	MU	13	20	32	0.65	260	NE	A
161	CBO	MU	14	17	32	0.82	238	E	P
199	O	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
222	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
217	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
213	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
224	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
208	BO	MB	n/a	n/a	n/a	n/a	n/a	n/a	n/a
218	BO	MB	n/a	n/a	n/a	n/a	n/a	n/a	n/a
219	BO	MB	n/a	n/a	n/a	n/a	n/a	n/a	n/a
220	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
15	BO	U	24	12	60	2.00	288	E	A

Table A2-1. Continued.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height : width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
187	BO	U	n/a	n/a	n/a	n/a	n/a	n/a	n/a
45	BO	U	9	19	37	0.47	171	NE	P
70	CBO	NMU	13	23	32	0.56	299	E	A
304	BO	U	n/a	n/a	n/a	n/a	n/a	n/a	n/a
306	CBO	U	n/a	n/a	n/a	n/a	n/a	n/a	n/a
172	BO	MU	10	14	19	0.71	140	E	A
30	BO	MU	9	17	28	0.53	153	E	n/a
132	BO	MU	8	13	30	0.62	104	E	A
53	BO	MU	14	20	30	0.70	280	E	P
50	BO	MU	7	11	31	0.64	77	E	A
49	BO	MU	11	14	49	0.79	154	E	A
73	O	MB	7	7	20	1.00	49	E	A
88	BO	U	7	14	32	0.50	98	E	P
55	BO	MU	17	16	58	1.06	272	E	A
51	BO	MB	14	14	46	1.00	196	E	P
52	BO	MU	8	7	31	1.14	56	NE	A
105	BO	MU	20	15	40	1.33	300	NE	A
95	BO	MU	8	6	30	1.33	48	E	P
66	O	MU	10	9	35	1.11	90	NE	A
305	CBO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
58	BO	M	8	12	43	0.67	96	NE	P
216	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
221	BO	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
179	BO	MB	4	10	20	0.40	40	NE	P
214	O	MU	n/a	n/a	n/a	n/a	n/a	n/a	n/a
23	BO	U	16	21	49	0.76	336	E	A
11	BO	MU	12	22	31	0.54	264	NE	P
3	BO	U	17	11	44	1.54	187	NE	A
167	BO	MU	13	11	60	1.18	143	NE	A
28	S	U	13	8	41	1.62	104	E	A
211	BO	MU	n/a	n/a	n/a	n/a	n/a	NE	n/a
300	S	NMU	n/a	n/a	n/a	n/a	n/a	NE	n/a
301	S	NMU	n/a	n/a	n/a	n/a	n/a	NE	n/a
302	S	NMU	n/a	n/a	n/a	n/a	n/a	NE	n/a
303	S	U	n/a	n/a	n/a	n/a	n/a	NE	n/a

n/a indicates that data was unavailable

Table A2-2. Shelters not occupied by monitored lobsters during tracking study.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height : width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
1	BO	U	9	16	28	0.56	144	NE	A
2	BO	U	28	10	57	2.80	280	E	P
4	BO	U	23	18	50	1.28	414	NE	A
5	SBC	U	15	10	61	1.50	150	E	A
6	BO	MU	13	15	46	0.87	195	NE	A
8	BO	U	15	10	30	1.50	150	NE	A
9	BO	U	19	18	33	1.06	342	NE	A
10	BO	U	27	19	45	1.42	513	NE	P
12	BO	U	6	16	33	0.38	96	E	P
13	BO	U	19	30	59	0.63	570	NE	A
14	BO	U	18	24	55	0.75	432	NE	A
16	BO	U	11	16	16	0.69	176	E	A
17	BO	U	22	13	55	1.69	286	E	A
18	O	U	18	20	50	0.90	360	E	A
19	O	MU	8	17	33	0.47	136	NE	A
20	BO	MU	13	17	25	0.76	221	NE	A
21	BO	U	20	34	50	0.59	680	E	A
22	BO	U	12	8	20	1.50	96	NE	A
24	BO	U	9	37	42	0.24	333	E	A
25	BO	U	17	18	38	0.94	306	E	A
26	BO	U	8	15	15	0.53	120	NE	A
27	O	U	13	18	26	0.72	234	E	A
31	SBC	U	15	10	44	1.50	150	E	A
32	BO	U	18	15	32	1.20	270	E	P
34	SBC	U	19	13	31	1.46	247	E	P
35	SBC	U	22	13	27	1.69	286	E	A
36	BO	U	14	14	31	1.00	196	E	A
37	BO	M	7	13	40	0.54	91	E	A
38	BO	M	8	33	80	0.24	264	NE	A
39	BO	U	19	17	45	1.12	323	E	A
40	BO	M	16	28	95	0.57	448	E	A
42	O	MU	10	13	45	0.77	130	NE	P
43	O	U	12	13	43	0.92	156	NE	A
44	O	U	7	11	26	0.64	77	NE	A
47	BO	MU	10	16	30	0.63	160	E	A
48	BO	MU	6	8	30	0.75	48	E	P
56	BO	MU	30	11	68	2.73	330	NE	P

Table A2-2. Continued.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height : width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
60	O	MU	15	30	70	0.50	450	E	A
61	BO	MU	20	35	70	0.57	700	E	P
62	BO	MU	4	6	20	0.67	24	E	P
63	BO	MU	9	12	45	0.75	108	E	P
64	BO	MU	30	13	38	2.31	390	NE	A
67	BO	MU	10	10	14	1.00	100	E	A
75	BO	MU	19	18	60	1.06	342	NE	A
76	BO	MU	12	15	32	0.80	180	NE	A
77	BO	MU	7	7	20	1.00	49	E	A
78	BO	MB	8	15	46	0.53	120	E	A
79	BO	MU	5	10	17	0.50	50	E	A
83	BO	MU	8	13	30	0.62	104	NE	A
84	BO	MU	9	20	30	0.45	180	NE	P
85	BO	MB	9	27	52	0.33	243	NE	P
87	BO	MB	11	23	25	0.48	253	NE	A
89	BO	MU	7	19	38	0.37	133	E	P
90	BO	MB	18	7	45	2.57	126	NE	P
91	CBO	U	13	6	50	2.17	78	NE	P
92	BO	MU	10	22	33	0.45	220	E	A
93	BO	MB	26	46	72	0.57	1196	E	P
94	BO	U	13	12	22	1.08	156	E	A
96	BO	U	9	30	26	0.30	270	E	A
97	CBO	NMU	12	9	20	1.33	108	E	A
99	CBO	U	8	12	38	0.67	96	E	A
102	BO	MB	30	18	49	1.67	540	NE	P
103	BO	MB	6	9	57	0.67	54	NE	A
104	BO	MU	9	17	20	0.53	153	NE	A
106	BO	MB	22	16	40	1.38	352	NE	A
107	BO	MB	27	45	62	0.60	1215	E	A
108	BO	MB	8	8	37	1.00	64	E	P
109	BO	MB	15	7	31	2.14	105	E	A
110	CBO	MU	6	11	33	0.55	66	E	A
111	BO	MB	20	18	50	1.11	360	NE	A
112	BO	MU	8	6	40	1.33	48	E	A
113	BO	MB	19	17	41	1.12	323	NE	A
114	BO	MB	12	14	51	0.86	168	E	A
115	BO	MB	8	9	43	0.89	72	E	P

Table A2-2. Continued.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height : width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
116	BO	MU	16	10	30	1.60	160	E	A
117	BO	MU	6	7	30	0.86	42	NE	A
118	BO	MB	17	15	70	1.13	255	NE	P
119	BO	MB	9	7	42	1.29	63	E	A
120	BO	MU	8	12	20	0.67	96	E	A
121	BO	MB	15	15	60	1.00	225	NE	A
122	BO	MU	14	19	40	0.74	266	E	A
123	BO	MU	14	12	41	1.17	168	NE	A
125	BO	MU	8	7	45	1.14	56	NE	P
126	BO	MU	13	5	30	2.60	65	E	A
127	BO	MU	9	11	20	0.82	99	E	A
128	BO	MU	10	16	42	0.63	160	E	A
129	SBC	MU	9	13	39	0.69	117	NE	A
130	O	MU	8	10	21	0.80	80	E	A
131	O	MU	11	16	24	0.69	176	E	A
133	BO	MU	7	9	27	0.78	63	NE	A
135	BO	MU	13	18	39	0.72	234	E	A
136	BO	MU	12	21	30	0.57	252	E	A
137	BO	MU	17	25	85	0.68	425	E	A
139	SBC	MU	7	15	38	0.47	105	NE	P
140	BO	MU	20	29	60	0.69	580	E	A
141	BO	MU	14	35	50	0.40	490	NE	A
142	BO	MU	12	16	40	0.75	192	E	P
143	SBC	NMU	17	14	38	1.21	238	E	P
145	SBC	MB	11	10	47	1.10	110	E	P
146	CBO	MB	20	24	60	0.83	480	NE	P
147	SBC	MB	8	7	35	1.14	56	E	P
148	CBO	MB	14	19	39	0.74	266	E	P
149	SBC	MB	6	5	46	1.20	30	NE	P
150	SBC	MB	20	15	55	1.33	300	E	A
151	BO	MU	18	8	52	2.25	144	NE	P
152	BO	MU	19	14	60	1.36	266	E	A
153	SBC	MU	14	15	34	0.93	210	E	A
154	CBO	MU	12	14	40	0.86	168	E	A
155	CBO	MU	13	14	38	0.93	182	NE	P
159	BO	MU	9	8	56	1.13	72	E	A
160	CBO	MU	8	6	21	1.33	48	E	A

Table A2-2. Continued.

Shelter number	Substrate type	Benthos type	Entrance height (cm)	Entrance width (cm)	Shelter length (cm)	Mouth height : width	Mouth area (cm2)	Excavated (E) / Nonexcavated (NE)	Absence (A) / Presence (P) of lobster at time of survey
162	CBO	MU	12	16	24	0.75	192	E	A
163	CBO	MU	8	13	18	0.62	104	E	A
164	CBO	MU	21	39	100	0.54	819	NE	P
165	CBO	MU	13	12	33	1.08	156	E	A
166	BO	MU	23	33	32	0.70	759	NE	A
168	BO	MU	11	7	29	1.57	77	E	A
169	BO	MU	12	10	35	1.20	120	NE	A
171	BO	MU	10	12	39	0.83	120	E	P
175	BO	MU	12	13	29	0.92	156	E	A
177	BO	MB	14	28	35	0.50	392	E	A
178	BO	MB	15	18	12	0.83	270	E	P
180	BO	MB	16	20	60	0.80	320	NE	A
181	BO	MB	12	10	20	1.20	120	E	A
182	BO	MB	15	25	90	0.60	375	E	A
185	BO	MB	11	18	90	0.61	198	E	A
190	BO	MB	9	9	11	1.00	81	E	A

Appendix 3. Activity data presented through categorization by lobster sex (male or female), lobster size (small or large) , lobster sex x size (small male, large male, small female, or large female), time of year (prior to July 1, July 1 - August 15, after August 15), water temperature (</= 8°C or > 8° C), sea state (calm, < 0.25 m, 0.25 - 0.50 m, or > 0.50 m), and moonphase (first quarter, full moon, last quarter, new moon). Values presented are mean ± s.d., range, and sample size. Only fully monitored bouts are included except for 'percent active nights' for which remaining fully monitored nights are also included.

Table A3-1. Activity parameters categorized by lobster sex, size and sex-size interaction. Values presented are mean ± s.d., range, and sample size, respectively. Only fully monitored activity bouts are included except for 'percent active nights' for which remaining fully monitored nights are also included.

Behavioral Parameter	Sex		Size (Carapace length)		Sex x Size			
	Male	Female	Small (</=81mm)	Large (>81mm)	Small male	Large male	Small female	Large female
Percent active nights	26.7 (n=135)	30.1 (n=123)	28.8 (n=146)	32.5 (n=126)	21.4 (n=54)	35.3 (n=51)	38.7 (n=62)	21.3 (n=61)
Maximum distance of position fix from initial shelter (m)	28.3 ± 21.9 6.1 - 73.9 (n=34)	18.7± 14.1 2.2 - 65.1 (n=37)	21.3 ± 17.6 2.2 - 70.6 (n=42)	27.1 ± 18.2 6.1 - 73.9 (n=39)	25.4 ± 21.0 6.7 - 70.6 (n=18)	31.6 ± 23.0 6.1 - 73.9 (n=16)	18.3 ± 14.2 2.2 - 65.1 (n=24)	19.4 ± 14.3 8.6 - 63.0 (n=13)
Approximate total distance moved (m)	73.6 ± 85.6 6.0 - 361.0 (n=34)	53.0 ± 47.9 5.0 - 214.0 (n=37)	63.4 ± 67.5 5.0 - 287.0 (n=42)	64.8 ± 65.9 6.0 - 361.0 (n=39)	72.8 ± 83.7 8.0 - 287.0 (n=18)	74.5 ± 90.4 6.0 - 361.0 (n=16)	56.4 ± 53.2 5.0 - 214.0 (n=24)	46.8 ± 37.6 9.0 - 128.0 (n=13)
Duration of activity time (min)	232.8 ± 167.4 6.0 - 537.0 (n=36)	270.6 ± 171.8 42.0 - 769.0 (n=36)	308.3 ± 167.0 29.0 - 769.0 (n=41)	170.2 ± 134.0 6.0 - 537.0 (n=41)	292.3 ± 161.4 29.0 - 520.0 (n=18)	173.4 ± 155.4 6.0 - 537.0 (n=18)	320.8 ± 173.8 44.0 - 769.0 (n=23)	181.8 ± 131.6 42.0 - 437.0 (n=13)
Duration of movement time (min)	82.1 ± 92.4 4.0 - 360.0 (n=34)	70.2 ± 62.2 5.0 - 215.0 (n=36)	88.8 ± 73.4 7.0 - 260.0 (n=41)	56.3 ± 73.5 4.0 - 360.0 (n=39)	94.2 ± 86.1 10.0 - 260.0 (n=18)	68.4 ± 100.0 4.0 - 360.0 (n=16)	84.6 ± 63.5 7.0 - 215.0 (n=23)	44.9 ± 52.8 5.0 - 193.0 (n=13)
Duration of stationary time (min)	53.5 ± 74.5 0.0 - 305.0 (n=34)	86.8 ± 112.4 0.0 - 612.0 (n=36)	93.3 ± 113.7 0.0 - 612.0 (n=41)	37.4 ± 51.0 0.0 - 227.0 (n=39)	72.5 ± 93.8 0.0 - 305.0 (n=18)	32.1 ± 36.3 0.0 - 120.0 (n=16)	109.7 ± 126.7 0.0 - 612.0 (n=23)	46.3 ± 68.2 0.0 - 227.0 (n=13)
Duration of active time in initial shelter (min)	50.0 ± 67.9 0.0 - 255.0 (n=34)	52.0 ± 60.5 0.0 - 245.0 (n=36)	65.3 ± 75.1 0.0 - 255.0 (n=41)	32.6 ± 33.7 0.0 - 135.0 (n=37)	72.9 ± 85.0 0.0 - 255.0 (n=18)	24.3 ± 25.0 0.0 - 99.0 (n=16)	59.4 ± 67.8 0.0 - 245.0 (n=23)	38.8 ± 44.1 0.0 - 135.0 (n=13)
Duration of active time in final shelter (min)	44.6 ± 57.7 0.0 - 210.0 (n=34)	61.6 ± 77.4 0.0 - 310.0 (n=36)	60.8 ± 77.2 0.0 - 310.0 (n=41)	39.6 ± 54.2 0.0 - 201.0 (n=37)	52.7 ± 64.6 0.0 - 210.0 (n=18)	35.5 ± 49.4 0.0 - 201.0 (n=16)	67.1 ± 86.7 0.0 - 310.0 (n=23)	51.8 ± 59.4 1.0 - 165.0 (n=13)
Movement / Activity	0.34 ± 0.21 0.05 - 0.77 (n=34)	0.27 ± 0.19 0.03 - 0.74 (n=36)	0.29 ± 0.19 0.03 - 0.77 (n=41)	0.32 ± 0.20 0.05 - 0.71 (n=39)	0.32 ± 0.20 0.06 - 0.77 (n=18)	0.37 ± 0.23 0.05 - 0.71 (n=16)	0.27 ± 0.18 0.03 - 0.74 (n=23)	0.25 ± 0.21 0.06 - 0.65 (n=13)

Table A3-1. Continued.

Behavioral Parameter	Sex		Size (Carapace length)		Sex x Size			
	Male	Female	Small (</=81mm)	Large (>81mm)	Small male	Large male	Small female	Large female
Stationary / Activity	0.16 ± 0.19 0.00 - 0.77 (n=34)	0.29 ± 0.26 0.00 - 0.80 (n=36)	0.27 ± 0.25 0.00 - 0.80 (n=41)	0.18 ± 0.20 0.00 - 0.77 (n=39)	0.18 ± 0.23 0.00 - 0.77 (n=18)	0.14 ± 0.13 0.00 - 0.46 (n=16)	0.34 ± 0.26 0.00 - 0.80 (n=23)	0.22 ± 0.26 0.00 - 0.77 (n=13)
Shelter1 / Activity	0.26 ± 0.25 0.00 - 0.79 (n=34)	0.23 ± 0.25 0.00 - 0.92 (n=36)	0.24 ± 0.23 0.00 - 0.79 (n=41)	0.28 ± 0.28 0.00 - 0.92 (n=37)	0.28 ± 0.26 0.00 - 0.79 (n=18)	0.23 ± 0.24 0.00 - 0.79 (n=16)	0.20 ± 0.22 0.00 - 0.77 (n=23)	0.27 ± 0.31 0.00 - 0.92 (n=13)
Shelter2 / Activity	0.24 ± 0.23 0.00 - 0.73 (n=34)	0.21 ± 0.22 0.00 - 0.67 (n=36)	0.20 ± 0.22 0.00 - 0.73 (n=41)	0.22 ± 0.23 0.00 - 0.71 (n=37)	0.22 - 0.24 0.00 - 0.73 (n=18)	0.26 ± 0.23 0.00 - 0.71 (n=16)	0.19 ± 0.21 0.00 - 0.67 (n=23)	0.26 ± 0.23 0.01 - 0.62 (n=13)
Activity initiation relative to sunset (min)	90.1 ± 102.0 79.0* - 390.0 (n=36)	82.1 ± 99.4 185.0* - 366.0 (n=35)	71.4 ± 112.2 185.0* - 390.0 (n=40)	128.1 ± 91.6 14.0 - 356.0 (n=40)	57.1 ± 100.6 79.0* - 390.0 (n=18)	123.2 ± 94.9 14.0 - 327.0 (n=18)	83.0 ± 122.0 185.0* - 366.0 (n=22)	80.8 ± 44.3 37.0 - 191.0 (n=13)
Movement initiation relative to sunset (min)	139.1 ± 104.8 2.0 - 415.0 (n=34)	138.1 ± 92.0 11.0 - 366.0 (n=35)	141.0 ± 111.9 2.0 - 415.0 (n=40)	161.7 ± 93.8 44.0 - 386.0 (n=38)	130.0 ± 119.7 2.0 - 415.0 (n=18)	149.4 ± 87.8 44.0 - 332.0 (n=16)	150.0 ± 107.0 11.0 - 366.0 (n=22)	118.0 ± 56.9 44.0 - 239.0 (n=13)
End of activity relative to sunset (min)	323.0 ± 161.2 51.0 - 566.0 (n=36)	353.9 ± 169.2 79.0 - 898.0 (n=35)	381.6 ± 167.0 51.0 - 898.0 (n=40)	298.1 ± 151.2 73.0 - 626.0 (n=41)	349.4 ± 157.9 51.0 - 533.0 (n=18)	296.6 ± 164.5 73.0 - 566.0 (n=18)	407.9 ± 173.3 129.0 - 898.0 (n=22)	262.5 ± 119.2 79.0 - 479.0 (n=13)
Number of stops during movement	2.1 ± 2.8 0 - 13 (n=34)	2.6 ± 2.5 0 - 9 (n=37)	2.7 ± 3.0 0 - 13 (n=42)	1.7 ± 1.8 0 - 7 (n=39)	2.4 ± 3.4 0 - 13 (n=18)	1.7 ± 1.8 0 - 5 (n=16)	3.0 ± 2.7 0 - 9 (n=24)	1.8 ± 2.0 0 - 7 (n=13)
Number of > 90° turns	3.0 ± 3.9 0 - 15 (n=34)	3.3 ± 3.2 0 - 13 (n=37)	3.5 ± 3.6 0 - 13 (n=42)	2.7 ± 3.2 0 - 15 (n=39)	3.3 ± 3.9 0 - 13 (n=18)	2.7 ± 3.9 0 - 15 (n=16)	3.7 ± 3.4 0 - 13 (n=24)	2.5 ± 2.6 0 - 7 (n=13)

'*' denotes time prior to sunset

Table A3-2. Activity parameters categorized by 'time of year' and 'water temperature'. Values presented are mean ± s.d., range, and sample size, respectively. Only fully monitored activity bouts are included except for 'percent active nights' for which remaining fully monitored nights are also included.

Behavioral Parameter	Time of Year			Water Temperature	
	Prior to July 1	July1-Aug. 15	After Aug. 15	< or = 8 °C	> 8 °C
Percent active nights	28.8 (n=73)	24.6 (n=118)	40.7 (n=81)	25.0 (n=52)	30.5 (n=164)
Maximum distance of position fix from initial shelter (m)	19.4 ± 18.4 5.0 - 73.9 (n=21)	25.1 ± 19.9 4.1 - 70.6 (n=27)	26.2 ± 16.0 2.2 - 63.3 (n=33)	15.8 ± 20.1 5.4 - 73.9 (n=13)	25.7 ± 18.3 2.2 - 70.6 (n=48)
Approximate total distance moved (m)	44.6 ± 50.4 6.0 - 171.0 (n=21)	70.1 ± 75.9 5.0 - 287.0 (n=27)	71.6 ± 66.3 7.0 - 361.0 (n=33)	23.4 ± 27.4 6.0 - 107.0 (n=13)	71.3 ± 74.0 7.0 - 361.0 (n=48)
Duration of activity time (min)	222.0 ± 163.8 6.0 - 485.0 (n=20)	272.6 ± 165.0 29.0 - 520.0 (n=29)	220.4 ± 167.9 42.0 - 769.0 (n=33)	174.2 ± 129.4 33.0 - 465.0 (n=12)	257.1 ± 167.7 6.0 - 580.0 (n=50)
Duration of movement time (min)	59.2 ± 68.1 4.0 - 225.0 (n=20)	83.0 ± 76.4 5.0 - 260.0 (n=27)	73.4 ± 78.1 6.0 - 360.0 (n=33)	31.2 ± 29.4 5.0 - 95.0 (n=12)	87.3 ± 86.4 4.0 - 360.0 (n=48)
Duration of stationary time (min)	47.6 ± 61.3 0.0 - 170.0 (n=20)	62.3 ± 85.2 0.0 - 305.0 (n=27)	80.3 ± 112.4 0.0 - 658.0 (n=33)	23.3 ± 47.4 0.0 - 165.0 (n=12)	73.1 ± 77.5 0.0 - 305.0 (n=48)
Duration of active time in initial shelter (min)	58.6 ± 77.9 0.0 - 245.0 (n=20)	56.0 ± 67.1 0.0 - 255.0 (n=27)	38.7 ± 40.3 0.0 - 135.0 (n=31)	52.1 ± 64.1 0.0 - 210.0 (n=12)	42.5 ± 53.5 0.0 - 255.0 (n=48)
Duration of active time in final shelter (min)	56.6 ± 71.4 0.0 - 201.0 (n=20)	70.9 ± 78.5 0.0 - 310.0 (n=27)	29.4 ± 48.2 0.0 - 180.0 (n=31)	67.5 ± 93.2 0.0 - 310.0 (n=12)	53.3 ± 63.0 0.0 - 210.0 (n=48)
Movement / Activity	0.30 ± 0.23 0.03 - 0.74 (n=20)	0.29 ± 0.18 0.06 - 0.77 (n=27)	0.33 ± 0.19 0.07 - 0.71 (n=33)	0.21 ± 0.14 0.06 - 0.45 (n=12)	0.33 ± 0.21 0.05 - 0.77 (n=48)

Table A3-2. Continued.

Behavioral Parameter	Time of Year			Water Temperature	
	Prior to July 1	July1-Aug. 15	After Aug. 15	< or = 8 °C	> 8 °C
Stationary / Activity	0.15 ± 0.15 0.00 - 0.47 (n=20)	0.17 ± 0.22 0.00 - 0.77 (n=27)	0.31 ± 0.25 0.00 - 0.80 (n=33)	0.11 ± 0.20 0.00 - 0.69 (n=12)	0.25 ± 0.24 0.00 - 0.77 (n=48)
Shelter 1 / Activity	0.25 ± 0.23 0.00 - 0.78 (n=20)	0.29 ± 0.28 0.00 - 0.88 (n=27)	0.23 ± 0.25 0.00 - 0.92 (n=31)	0.33 ± 0.26 0.00 - 0.79 (n=12)	0.21 ± 0.22 0.00 - 0.92 (n=48)
Shelter 2 / Activity	0.30 ± 0.23 0.00 - 0.73 (n=20)	0.25 ± 0.23 0.00 - 0.69 (n=27)	0.13 ± 0.19 0.00 - 0.62 (n=31)	0.35 ± 0.25 0.00 - 0.73 (n=12)	0.21 ± 0.22 0.00 - 0.71 (n=48)
Activity initiation relative to sunset (min)	86.1 ± 123.2 185.0* - 337.0 (n=19)	73.4 ± 94.1 20.0* - 390.0 (n=29)	131.7 ± 99.2 11.0 - 366.0 (n=32)	101.0 ± 107.6 2.0 - 337.0 (n=12)	85.4 ± 86.8 20.0(prior) - 390.0 (n=50)
Movement initiation relative to sunset (min)	152.2 ± 92.9 32.0 - 354.0 (n=19)	126.3 ± 106.9 2.0 - 415.0 (n=27)	171.3 ± 104.7 11.0 - 386.0 (n=32)	153.1 ± 116.0 2.0 - 357.0 (n=12)	127.9 ± 87.6 11.0 - 415.0 (n=48)
End of activity relative to sunset (min)	307.8 ± 146.9 73.0 - 507.0 (n=19)	346.0 ± 154.0 51.0 - 533.0 (n=29)	351.7 ± 182.5 79.0 - 898.0 (n=33)	275.2 ± 143.4 73.0 - 508.0 (n=12)	342.5 ± 152.0 51.0 - 598.0 (n=50)
Number of stops during movement	1.5 ± 2.2 0 - 9 (n=21)	3.2 ± 3.2 0 - 13 (n=27)	2.7 ± 2.1 0 - 7 (n=33)	0.5 ± 0.9 0 - 3 (n=12)	2.5 ± 2.7 0 - 13 (n=48)
Number of > 90° turns	2.3 ± 3.4 0 - 12 (n=21)	3.1 ± 3.7 0 - 13 (n=27)	3.7 ± 3.1 0 - 15 (n=33)	1.2 ± 1.6 0 - 5 (n=12)	3.2 ± 3.5 0 - 15 (n=48)

'*' denotes time prior to sunset

Table A3-3. Activity parameters categorized by 'sea state' and 'moonphase'. Values presented are mean ± s.d., range, and sample size, respectively.
Only fully monitored activity bouts are included except for 'percent active nights' for which remaining fully monitored nights are also included.

Behavioral Parameter	Sea State				Moonphase			
	1 (calm)	2 (<.25 m)	3 (.25 - .50 m)	4 (> .5 m)	First quarter	Full moon	Last quarter	New moon
Percent active nights	25.4 (n=59)	30.9 (n=110)	31.0 (n=84)	42.1 (n=19)	42.1 (n=76)	26.2 (n=84)	19.2 (n=52)	31.7 (n=60)
Maximum distance of position fix from initial shelter (m)	20.2 ± 14.1 6.1 - 60.4 (n=14)	23.9 ± 20.2 2.2 - 73.9 (n=34)	23.7 ± 16.4 5.7 - 65.1 (n=25)	33.1 ± 19.4 16.5 - 63.3 (n=8)	27.2 ± 21.0 2.2 - 73.9 (n=32)	20.6 ± 12.8 5.0 - 60.4 (n=22)	25.6 ± 22.5 7.3 - 63.3 (n=9)	22.0 ± 15.4 4.1 - 65.1 (n=18)
Approximate total distance moved (m)	52.1 ± 90.7 6.0 - 361.0 (n=14)	53.8 ± 56.7 5.0 - 250.0 (n=29)	78.0 ± 70.9 10.0 - 287.0 (n=24)	85.6 ± 24.1 60.0 - 123.0 (n=7)	73.6 ± 71.7 7.0 - 287.0 (n=32)	68.5 ± 79.2 9.0 - 361.0 (n=22)	47.8 ± 36.3 9.0 - 102.0 (n=9)	50.1 ± 49.2 5.0 - 214.0 (n=18)
Duration of activity time (min)	206.2 ± 164.8 29.0 - 537.0 (n=15)	229.4 ± 144.7 6.0 - 520.0 (n=34)	250.9 ± 170.6 35.0 - 580.0 (n=25)	306.9 ± 237.1 62.0 - 769.0 (n=8)	256.5 ± 159.4 36.0 - 520.0 (n=31)	263.2 ± 157.1 6.0 - 537.0 (n=22)	149.6 ± 95.1 62.0 - 335.0 (n=10)	230.6 ± 205.2 29.0 - 769.0 (n=19)
Duration of movement time (min)	54.9 ± 93.9 5.0 - 360.0 (n=14)	58.6 ± 64.9 4.0 - 260.0 (n=34)	98.2 ± 73.5 10.0 - 225.0 (n=24)	91.0 ± 69.9 26.0 - 210.0 (n=8)	82.1 ± 77.7 6.0 - 260.0 (n=31)	85.0 ± 89.3 4.0 - 360.0 (n=22)	39.2 ± 41.9 5.0 - 143.0 (n=9)	60.0 ± 59.5 5.0 - 215.0 (n=18)
Duration of stationary time (min)	51.5 ± 66.7 0.0 - 227.0 (n=14)	42.0 ± 52.2 0.0 - 170.0 (n=34)	80.2 ± 86.9 0.0 - 305.0 (n=24)	151.5 ± 196.8 0.0 - 612.0 (n=8)	66.6 ± 71.2 0.0 - 259.0 (n=31)	66.6 ± 71.9 0.0 - 305.0 (n=22)	45.0 ± 63.8 0.0 - 162.0 (n=9)	74.9 ± 144.4 0.0 - 612.0 (n=18)
Duration of active time in initial shelter (min)	56.6 ± 77.8 0.0 - 255.0 (n=14)	66.8 ± 69.2 0.0 - 245.0 (n=32)	26.6 ± 36.1 0.0 - 130.0 (n=24)	39.9 ± 31.4 10.0 - 97.0 (n=8)	58.4 ± 65.1 0.0 - 217.0 (n=30)	41.0 ± 53.5 0.0 - 245.0 (n=22)	50.8 ± 67.5 5.0 - 197.0 (n=9)	45.6 ± 63.3 0.0 - 255.0 (n=17)
Duration of active time in final shelter (min)	51.1 ± 67.5 0.0 - 210.0 (n=14)	67.4 ± 78.6 0.0 - 310.0 (n=32)	37.1 ± 52.6 0.0 - 180.0 (n=24)	24.5 ± 32.8 0.0 - 75.0 (n=8)	53.1 ± 75.9 0.0 - 310.0 (n=30)	70.5 ± 75.7 0.0 - 210.0 (n=22)	20.6 ± 22.7 0.0 - 55.0 (n=9)	37.0 ± 52.3 0.0 - 180.0 (n=17)
Movement / Activity	0.21 ± 0.17 0.05 - 0.67 (n=14)	0.25 ± 0.18 0.03 - 0.74 (n=34)	0.43 ± 0.18 0.12 - 0.77 (n=24)	0.36 ± 0.19 0.10 - 0.65 (n=8)	0.31 ± 0.19 0.06 - 0.74 (n=31)	0.35 ± 0.24 0.03 - 0.77 (n=22)	0.26 ± 0.20 0.06 - 0.65 (n=9)	0.27 ± 0.14 0.12 - 0.61 (n=18)
Stationary / Activity	0.21 ± 0.27 0.00 - 0.77 (n=14)	0.16 ± 0.19 0.00 - 0.67 (n=34)	0.28 ± 0.22 0.00 - 0.77 (n=24)	0.37 ± 0.25 0.00 - 0.80 (n=8)	0.24 ± 0.22 0.00 - 0.77 (n=31)	0.21 ± 0.22 0.00 - 0.77 (n=22)	0.20 ± 0.24 0.00 - 0.58 (n=9)	0.23 ± 0.27 0.00 - 0.80 (n=18)

Table A3-3. Continued.

Behavioral Parameter	Sea State				Moonphase			
	1 (calm)	2 (<.25 m)	3 (.25 - .50 m)	4 (> .5 m)	First quarter	Full moon	Last quarter	New moon
Shelter 1 / Activity	0.33 ± 0.28 0.00 - 0.79 (n=14)	0.32 ± 0.28 0.00 - 0.92 (n=32)	0.14 ± 0.19 0.00 - 0.62 (n=24)	0.20 ± 0.15 0.03 - 0.39 (n=8)	0.26 ± 0.23 0.0 - 0.79 (n=30)	0.19 ± 0.25 0.0 - 0.88 (n=22)	0.33 ± 0.31 0.02 - 0.92 (n=9)	0.29 ± 0.27 0.0 - 0.77 (n=17)
Shelter 2 / Activity	0.25 ± 0.26 0.00 - 0.71 (n=14)	0.27 ± 0.24 0.00 - 0.73 (n=32)	0.15 ± 0.18 0.00 - 0.62 (n= 24)	0.07 ± 0.08 0.00 - 0.20 (n=8)	0.19 ± 0.22 0.00 - 0.73 (n=30)	0.25 ± 0.23 0.00 - 0.71 (n=22)	0.21 ± 0.26 0.00 - 0.69 (n=9)	0.21 ± 0.21 0.00 - 0.62 (n=17)
Activity initiation relative to sunset (min)	60.1 ± 74.1 79.0* - 202.0 (n=15)	110.9 ± 132.5 185.0* - 390.0 (n=32)	99.6 ± 88.9 13.0 - 327.0 (n=25)	130.0 ± 72.7 13.0 - 220.0 (n=8)	69.3 ± 91.4 185.0* - 327.0 (n=29)	107.7 ± 97.7 13.0 - 356.0 (n=22)	134.3 ± 97.1 79.0* - 249.0 (n=10)	118.7 ± 128.3 11.0 - 390.0 (n=19)
Movement initiation relative to sunset (min)	106.6 ± 75.2 11.0 - 282.0 (n=14)	179.1 ± 120.4 2.0 - 415.0 (n=32)	131.7 ± 87.9 23.0 - 332.0 (n=24)	174.9 ± 94.2 88.0 - 344.0 (n=8)	133.9 ± 102.0 2.0 - 357.0 (n=29)	148.3 ± 93.9 23.0 - 386.0 (n=22)	173.3 ± 76.7 62.0 - 269.0 (n=9)	170.9 ± 127.9 11.0 - 415.0 (n=18)
End of activity relative to sunset (min)	266.3 ± 171.0 58.0 - 566.0 (n=15)	340.9 ± 144.1 82.0 - 626.0 (n=33)	350.2 ± 151.8 51.0 - 598.0 (n=25)	437.0 ± 235.0 142.0 - 898.0 (n=8)	329.4 ± 140.9 79.0 - 533.0 (n=30)	371.4 ± 167.7 51.0 - 626.0 (n=22)	282.1 ± 125.4 122.0 - 543.0 (n=10)	349.3 ± 207.1 58.0 - 898.0 (n=19)
Number of stops during movement	1.8 ± 1.9 0 - 6 (n=14)	1.9 ± 2.4 0 - 9 (n=34)	2.8 ± 3.1 0 - 13 (n=25)	3.2 ± 2.2 0 - 7 (n=8)	2.6 ± 3.1 0 - 13 (n=32)	1.9 ± 1.6 0 - 5 (n=22)	1.4 ± 1.9 0 - 5 (n=9)	2.5 ± 2.6 0 - 7 (n=18)
Number of > 90° turns	2.4 ± 4.1 0 - 15 (n=14)	2.4 ± 2.7 0 - 11 (n=34)	4.2 ± 4.0 0 - 13 (n=25)	3.8 ± 1.8 2 - 7 (n=8)	3.5 ± 3.7 0 - 13 (n=32)	3.2 ± 3.7 0 - 15 (n=22)	1.9 ± 1.8 0 - 5 (n=9)	2.9 ± 3.3 0 - 13 (n=18)
Percent net offshore movement	42.9 (n=14)	52.9 (n=34)	52.0 (n=25)	62.5 (n=8)	53.1 (n=32)	50.0 (n=22)	44.4 (n=9)	55.6 (n=18)
Percent net inshore/ no change movement	57.1 (n=14)	47.1 (n=34)	48.0 (n=25)	37.5 (n=8)	46.9 (n=32)	50.0 (n=22)	55.6 (n=9)	44.4 (n=18)
Net depth change (m)	0.7(i) ± 1.8 3.7(i) - 1.9(o) (n=13)	0.2(o) ± 1.5 2.4(i) - 3.4(o) (n=29)	0.1 (o) ± 0.3 1.7(i) - 2.3 (o) (n=24)	0.7(o) ± 1.8 1.9(i) - 4.0(o) (n=8)	0.1(i) ± 1.6 3.7(i) - 3.4(o) (n=29)	0.3(o) ± 1.2 2.1(i) - 3.0(o) (n=19)	0.0 ± 2.0 2.4(i) - 4.0(o) (n=9)	0.1(i) ± 1.2 3.0(i) - 1.9(o) (n=17)

'*' denotes time prior to sunset
'i' denotes negative depth change; i.e. inshore movement
'o' denotes positive depth change; i.e. offshore movement