ULTRASONIC TRACKING OF ACTIVITY AND MOVEMENT PATTERNS OF FEMALE CUNNER, TAUTOGOLABRUS ADSPERSUS, IN BROAD COVE, CONCEPTION BAY, NEWFOUNDLAND

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Ultrasonic Tracking of Activity and Movement Patterns of Female Cunner, *Tautogolabrus adspersus*, in Broad Cove, Conception Bay, Newfoundland

by

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ABSTRACT

Ultrasonic tracking using a fixed hydrophone array system was conducted in Conception Bay, Newfoundland, to study the activity and movement patterns of female cunner, Tautogolabrus adspersus, (Walbaum 1792). Eight female cunner were monitored at various times from June 17 to November 24, 1991, providing 107 days of tracking. The tracking system provided positional information on individual cunner at 15- second intervals. Ultrasonic transmitters had an average life of 17 days. Transmitters were attached externally through the dorsal musculature. Transmitters had no adverse effect on equilibrium or swimming ability and produced no detectable changes in female activity or movement.

Fish were active diurnally, commencing activity on average 55 minutes after sunrise and ceasing activity about 60 minutes after sunset. Fish were assumed active whenever positional information was obtained on movement. The active period, ranging from 11 to 16.5 hrs, corresponded to the interim between daily onset and cessation of activity and was interrupted by periods of inactivity lasting between 5 and 15 minutes. Several factors influenced the activity of female cunner. As daylength shortened, cunner had a corresponding decrease in the duration of their diurnal activity. Increases in water temperature resulted in a decrease in the length of inactivity bouts. At temperatures below 5°C cunner seek shelter and remain inactive. During increased surface waves cunner remained inactive for longer periods of time.

Activity was uninfluenced by cloud cover and tidal cycle. Activity did not differ between morning and afternoon observations, but over the observation period between June and November inactivity bouts became more numerous and lasted for longer periods.

Female cunner exhibited limited movements, remaining within 80 m of their original point of capture. The home range areas of 8 female cunner ranged in size from 300 to 2353 m^2. Females utilized space disproportionately within the boundaries of their home ranges, spending 60% of their time in 30% of their home range.

As water temperatures increased, both on a daily and seasonal basis, females occupied smaller home ranges. Home range areas were larger during the afternoon than the morning. Size of home range areas were not affected by sea state, but increased as cloud cover increased. Seasonally the largest home ranges occurred in June-July, followed by October-November, and lastly August-September.

While daily changes in environmental variables (i.e. water temperature, cloud cover, and sea state) affect activity and movement patterns of female cunner, changing energetic requirements associated with spawning and overwintering torpor appear to play a more important role.

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INTRODUCTION

The cunner, Tautogolabrus adspersus, (Walbaum 1792), is the only Labrid fish found in Newfoundland waters. Throughout its range, from Chesapeake Bay to the Strait of Belle Isle, this species is associated with shallow inshore reefs, sheltered rock substrates, wrecks, and wharves. These habitats provide protective shelter both during nocturnal quiescence and overwintering torpor as well as a suitable substrate for the benthic organisms on which cunner feed (Pottle and Green 1979a; Pottle and Green 1979b).

Rather than retreating to deeper, warmer waters similar to other Newfoundland coastal fishes, cunner enter the substrate in the late fall or early winter and remain inactive until the water temperature reaches 5°C late the following spring (Green and Farewell 1971). Olla et al. (1974) and Dew (1976) also observed cunner overwintering in their summer habitats off Long Island and Connecticut, respectively.

There are conflicting results in the literature concerning winter migration and activity of cunner. Several authors have shown that cunner undergo small-scale migrations, moving into deeper, warmer waters during winter, and returning to shallow subtidal areas in spring (Chao 1973; Ojeda and Dearborn 1990). These seasonal movements occur in response to changes in water temperature and probably to physical disturbances such as strong water surges and storms along some exposed coasts (Ojeda and Dearborn 1990). Most studies documenting the presence of cunner in inshore habitats during winter, however, have been conducted in bays or in other protected areas away from extensive water motion (e.g. Green and Farewell 1971; Olla et al. 1975; Dew 1976).

Pair spawning has been described for a number of labrid species (Randall and Randall 1963; Youngbluth 1968; Roede 1972; Reinboth 1973; Nakazono and Tsukahara 1974; Potts 1974; Robertson and Chaot 1974; Moyer and Shepard 1975; Olla and Samet 1977; Pottle and Green 1979a). Although pair spawning by territorial males with territorial and nonterritorial females was the primary mode of reproductive behaviour used by T. adspersus in Conception Bay, smaller nonterritorial males have been observed engaging in sneak spawning (Pottle and Green 1979a). Pottle et al. (1981) and Wicklund (1970) also observed smaller nonterritorial males engaging in group spawning in Bonne Bay, Newfoundland and New Jersey, respectively. During pair spawning, reproductive behaviour is initiated by a territorial male's 'courtship approach' to a female within his territory (Pottle and Green 1979a). The duration of a full bout of reproductive behaviour from courtship to spawn, usually ranges from 3 to 10 minutes (Pottle and Green 1979a). At this time male and female gametes are released into the water column where pelagic eggs are distributed by water currents.

The spawning season in Conception Bay spans a 4- to 5- week period from early July to early August, with most spawns occurring during the first 2-3 weeks (Pottle and Green 1979a). During this time both males and females are capable of multiple spawns per day on more than one day of the season (Pottle and Green 1979a). Only territorial females, however, have been observed spawning with the same male on more than one day (Pottle and Green 1979a). For a further discussion on female territoriality see Pottle and Green (1979b).

Males establish territories within a few days of emerging from overwintering torpor (around mid-June) and remain within them until just prior to entering torpor in late November (Pottle and Green 1979a). Evidence has shown that at least some males defend the same territories from year to year (Pottle and Green 1979b). Pottle and Green (1979a) found 10 male cunner occupied territories ranging in size from 16.1 to 74.3 m^2 ($\bar{X}$=44.7 m^2). Similar findings were obtained by Martel and Green (1987) who found the territories of 16 males to range from 19 to 103 m^2, having a mean surface area of 49.6 m^2. These relatively large territories have been shown to serve both as mating and feeding space for their owners (Pottle and Green 1979b).

Past studies have indicated that females are restricted in their movements (Pottle and Green 1979a; Pottle and Green 1979b), but no specific data has been collected on the size of home ranges or on seasonal variation in the range of female movements. Pottle (1979) found most females remained within 25 m of their initial tagging sites. Based on relatively limited data collected during the spawning season, some females were found to restrict their movements to a few square meters of a male's territory (Pottle and Green 1979a; Pottle and Green 1979b). Other, non-territorial females, were found to swim over areas where male territories were located during mid-afternoon (Martel 1983; Martel and Green 1987).

Thus females may follow more than one reproductive mode; some remain within and defend part of a male's territory against other females during part or all of the spawning season, and may spawn only with that male, while others appear to move from one territory to another, spawning with a number of males.

Tautogolabrus adspersus feeds primarily upon molluscs and benthic crustaceans, including mussels, limpets, chitons, mysids, and amphipods, although a variety of other invertebrates, both benthic and planktonic, are consumed (Chao 1973; Olla et al. 1975; Shumway and Stickney 1975; Dew 1976; Green et al. 1984). Essentially opportunistic feeders, cunner also consume carrion and fish offal.

A common problem for animals is how to allocate time to foraging and reproductive activities in a way which maximizes lifetime reproductive success. Territorial male cunner change their activity patterns in response to the reproductive period (Martin 1979; Green et al. 1985), but it is not known for certain whether females show similar types of responses. During the spawning season, when territorial and reproductive activities peak, territorial male cunner shift most of their foraging activities to the morning (Martin 1979; Green et al. 1985). Females, however, were observed foraging during most of the time they were active (Martin 1979) and this even distribution of foraging throughout the day was not shown to change during the spawning season (Green et al. 1984). Even though no significant difference was found between morning and afternoon observations in the number of feeding responses, there was a trend however towards increased foraging during the afternoon which peaked between 1300-1700 h.

Numerous techniques have been used to study the activity and movement patterns of fish, ranging from direct underwater observations to the use of complex electronic tracking equipment. While direct observational information has been collected on the activity and movement patterns of territorial male cunner, similar studies on females have not been possible due in part to their more extensive range of movement. During this study, ultrasonic tracking was used to monitor the movements of individual female cunner throughout their entire active period.

Ultrasonic tracking is important to researchers since it has the potential of precisely locating individual animals as often as desired. By frequently locating an animal throughout the day this provides excellent insight into an animal's daily movement patterns which can give a good approximation to an individual's home range if sufficient locational fixes are obtained over time. When locations are taken at regular intervals one can also determine the intensity with which an animal is using various parts of its home range. If good habitat information is available, habitat selection by a species can also be studied (Kohn and Mooty 1971; Nelson 1979).

Here I describe the long- and short-term effects of environmental variables (daylength, water temperature, cloud cover, sea state, and tidal cycle) on the activity and movement patterns of female cunner to assess the role such variables might have in mediating cunner activity and movements. I also looked at whether females change their activity and movemnets in response to the reproductive season and in anticipation of entering torpor in the fall. Thus in describing seasonal changes in activity and movement patterns an attempt was made to provide insights into the ecological significance of the use of time and space by individual female cunner.

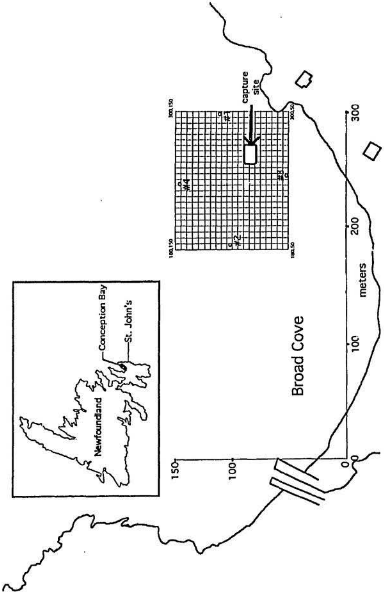
MATERIALS AND METHODS

2.1 TRACKING SYSTEM

Field studies on the activity and movements of female cunner 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) and Clark and Green (1990), was used to locate individual females. The hydrophone array consisted of 4 omnidirectional hydrophones mounted in small frames on the sea floor at depths of 5-13 m. Raising the hydrophones above the seabed was necessary to limit the amount of signal reflection which often occurs when working with fish on rocky ground (Urquhart and Smith 1992). Fish were tagged with cylindrical ultrasonic transmitters measuring 35 mm in length and 7 mm in diameter. Reception of the signal by at least three hydrophones was necessary to determine the fish's position.

Hydrophones were connected by cable to a 4-channel telemetric receiver located in the field station at Broad Cove. The receiver deleted extraneous background noise and passed the transmitter signals to either Fishtrak or Graftrak; computer software programs written by M. Bruce-Lockhart, Department of Engineering, Memorial University of Newfoundland. These programs calculate a fish's position based on the delay times of the transmitter signal at the first hydrophone and its reception at subsequent hydrophones (using the speed of sound in water). A bi-coordinate position was

Figure 1 Location of stationary hydrophone array in Broad Cove, Conception Bay. Capture area of all tagged cunner is shown.


Newfoundland
Conception Bay
St. John's
capture site
#1
#2
#3
#4
Broad Cove
150
100
0
0
100
200
300
meters

calculated every time an acoustic pulse was emitted by a transmitter, a rate of approximately one per second. To provide a more accurate estimate of a fish's location, Urquhart and Smith (1992) used the mean of a group of fixes over a predetermined length of time, while the median of a set of fixes obtained every 15 seconds was used in this study. For a description of some of the errors associated with position fixing using ultrasonic tracking and possible sources of improvement see Urquhart and Smith (1992).

To determine the potential accuracy of the tracking system, the standard deviations of both x and y measurements were calculated for a series of positional fixes obtained while tracking a stationary transmitter. The standard deviations for x coordinate fixes ranged from 0.07 to 0.71 m (N=30). The standard deviations for y coordinate fixes ranged from 0.14 to 0.78 m (N=30).

'Spurious' readings which may have been due to random noise or resulted from poor signal transmission or reception were eliminated from the data through visual inspection. To lessen data handling problems, actual position fixes were rounded by hand to the nearest meter. Positional information was summarized into minute-by-minute data sets by choosing the first 15-second positional fix during each one minute interval. Fish positions calculated at 1 min intervals provided a detailed description of the movements of the fish while at the same time generating a volume of data which could be easily handled by a computer.

At various times throughout the study 'ground-truthing' of the tracking system's accuracy was carried out through direct underwater observations and by placing stationary transmitters at known locations.

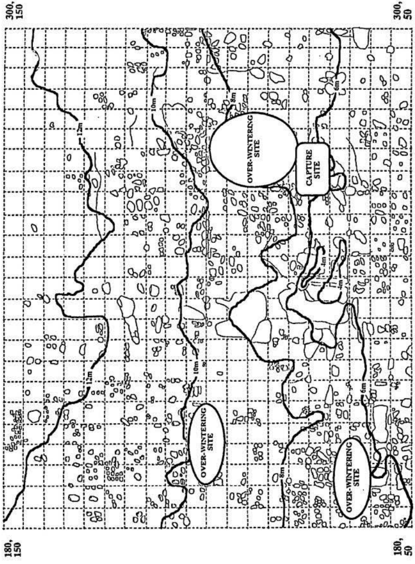
Based on the arrangement of the four hydrophones, the range over which a tagged fish could be accurately located was within an area about 150 m in diameter. This range decreased when background noise was high due to heavy seas or when the tagged individual was sheltered among rocks.

2.2 STUDY SITE

The hydrophone array enclosed a 120 m x 100 m area ranging in depth from 3.4 to 13.0 m (mean low water, MLW). This area had previously been mapped in terms of bottom topography, vegetation, and water depth as part of a study of lobsters, Homarus americanus (J. Christian, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland in preparation - see Figure 2). The bottom slopes gradually seaward to the outer edge of the array except at the drop-off (extending from 246,75 to 275,74) where there is a sharp drop from a depth of 4 to 6.5 m (Figure 2). A 5 m x 5 m grid was superimposed over a map of the area for ease of scaling.

Bottom topography in the array consisted of bedrock outcrops and sand interspersed with expanses of large and small boulders. Based on the predominant bottom substrate, the array area was subdivided into 5 sections. In order of increasing structural complexity, these were Sand (Appendix A, Section A), Rock Outcrop (Appendix A, Section D), Mixed-combinations of boulder, outcrop,

Figure 2 Hydrophone array showing water depth contours, bottom topographical features (i.e. rocks), and locations of overwintering sites.


300, 150
300, 50
180, 150
180, 50
12m
10m
8m
6m
4m
OVER-WINTERING SITE
CAPTURE SITE
OVER-WINTERING SITE
OVER-WINTERING SITE

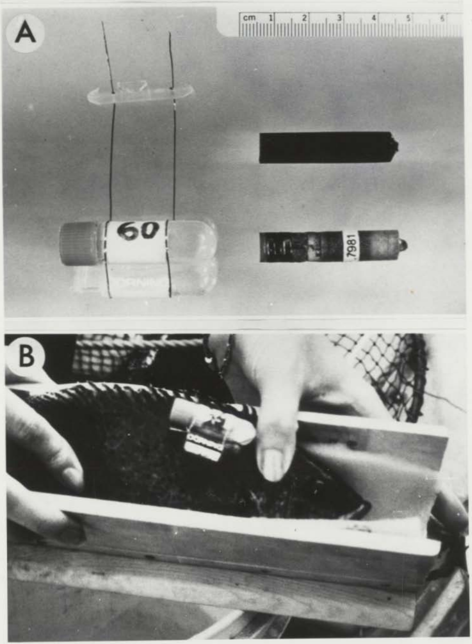
cobble, and sand in varying proportions (Appendix A, Section B), Boulder\Outcrop I (Appendix A, Section C), and Boulder\Outcrop II (Appendix, Section E). For details on descriptions and relative proportions of various substrate types refer to Appendix B.

2.3 TRANSMITTERS AND ATTACHMENT

The transmitter holder consisted of two plastic tubes fitted together with silicone and secured using stainless steel wires (Figure 3A). Transmitters (V2B-1L-R, VEMCO Ltd.) emitted pulsed signals at frequencies of 54-71 kHz with pulse rates between 50-60 pulses per min. Either a real or dummy transmitter was placed in the lower of the two tubes. The upper tube was partially filled with water to make the whole package neutrally buoyant. A printed label with the date and a request for the return of the tag was also placed in the upper tube. The stream-lined shape of the holder reduced drag resistance, prevented the accumulation of weeds, and improved the overall stability of the package during locomotion. Each transmitter holder was distinctively numbered, permitting identification of subjects at distances up to 5 m (Figure 3A). The life expectancy of batteries was between 20-30 days. When possible transmitters were recovered for battery replacement.

The transmitter package was attached through the dorsal musculature with stainless steel wires inserted just below the midpoint of the dorsal fin. This resulted in the transmitter lying close to the body of the fish immediately below and parallel to the

Figure 3 A) Photograph of transmitter and transmitter holder; B) Photograph of female cunner with transmitter attached through the dorsal musculature.


A
cm 1 2 3 4 5 6
60
7981
B

dorsal fin (Figure 3B). To prevent the flesh from tearing and for improved retention, a piece of plastic was placed on the opposite side of the fish's body, adjacent to the transmitter holder. At the start of the field season, cunner of both sexes were equipped with transmitter holders but only females were later provided with transmitters.

Fish for transmitter attachment were caught within the hydrophone array, close to several cunner overwintering sites (see Figure 2). Cunner were captured using a baited hoop net. Those selected for tagging were then placed in 20 L buckets, anaesthetized with MS-222 (1:10,000), measured, and equipped with a transmitter holder. This procedure took approximately 2-3 minutes per fish. Dummy transmitters were initially inserted in the housing apparatus so fish could acclimate to the tag before tracking commenced. Dummy transmitters were constructed of epoxy resin and simulated transmitters in size, shape, and weight. Fish were held in a recovery chamber with fresh sea water until they appeared to be functioning normally (~ 10 min). Upon release fish were observed by a diver for several minutes to assess their condition. After a minimum of a 7-day acclimation period, one or more females were recaptured and the dummy transmitter replaced with a real one. This required handling the fish for less than 1 minute. The relative ease with which transmitters could be interchanged minimized the amount of stress and discomfort fish were subjected to.

2.4 DATA COLLECTION

Individual fish were tracked at various times between June 17 and November 24, 1991, providing 107 days of tracking data. During this period 61 cunner were tagged with transmitter holders, 8 of which were equipped with real transmitters and monitored for periods ranging between 4 and 32 days. The females equipped with transmitters ranged in total length from 195 to 250 mm (mean of 225 mm) (Table 1). According to Gravel (1987), fish of this length are sexually mature and between 12-17 years of age.

Although the tracking system operated continuously, positional information could only be obtained on a single fish at any particular 15-second interval. On occasions when two or more fish were being tracked simultaneously, monitoring was switched between fish every 15 minutes. Throughout the tracking period, the number of individuals monitored on a daily basis ranged from 1 to 3 (refer to Table 1 for details).

2.5 ASSESSMENT OF TRANSMITTER ATTACHMENT

Prior to field tracking, three adult cunner were tagged with transmitter holders and held in a running seawater aquarium at the Ocean Sciences Centre, Logy Bay. Fish were observed at various times to assess the effects of transmitter attachment. Assessment of the effects of the transmitter package on equilibrium, swimming, and foraging was based on 10 hours of laboratory observations.

During the field study, observations were made while snorkelling or with SCUBA, on both the behaviour and location of

Table 1 Summary of tracking information on individual female cunner in Broad Cove, Conception Bay.

Fish No.	Total Length (mm)	Tracking Dates	Track Duration (days)
A	194	June17-June30	14
		July5-July6	2
B	215	June18-July4	17
C	250	June28-July21	24
D	235	July12-July21	10
E	195	Aug15-Aug18	4
F	225	Aug30-Sept22	16
G	245	Sept23-Oct20	22
H	240	Oct21-Nov24	32

tagged and untagged cunner. Normally observation dives lasted 60 minutes which resulted in over 40 person-hours of in situ observations. At various times throughout the tracking period feeding stations were also established to compare the feeding behaviour of transmitter-fitted fish and nontagged cunner.

2.6 ENVIRONMENTAL CONDITIONS

Water temperature and sea state were monitored on a regular basis in Conception Bay where tagged cunner maintained positions during daylight hours. Water temperature was measured every 2 hours from the shore station using a thermistor probe located at a depth of 4 m. Sea state was also assessed directly every 2 hours using the following scale: 1 = no wave action, 2 = <.25 m waves, 3 = .25-.50 m waves, 4 = >.50 m waves.

The heights and predicted times of high and low tides were obtained from the Canadian Tide and Current Tables for 1991. The tidal cycle was divided into 4 phases; 1) low-tide (lowest tide ± 90 min.), 2) flood-tide (end of low tide through to start of high tide), 3) high-tide (highest tide ± 90 min.), and 4) ebb-tide (end of high tide through to start of low tide). There is a relatively low tidal amplitude (~ 1 m) at the study site in Conception Bay, Newfoundland.

Information on cloud cover was obtained from the Canadian Climate Centre, Atmospheric Environment Service, Environment Canada at St. John's, Newfoundland. Observations were taken at ground level from the St. John's Weather Bureau. Amount of cloud cover was measured in terms of its degree of opacity on an hourly basis. The scale ranged from 0 to 10, with 0 representing no cloud cover (i.e. 100% sunlight penetrance) and 10, complete cloud cover (i.e. no sunlight penetrance).

2.7 ACTIVITY

Several measures of the daily activity of female cunner were calculated. These were based on positional data taken at 1 minute intervals throughout the day. If a strong signal was received by 3 hydrophones, positional information was obtained. When signal reception was weak, the exact location of a transmitter could not be determined. If signal reception remained poor for more than 12 consecutive intervals (i.e. 3 minutes) fish were assumed inactive under cover. Field observations confirmed that cunner are inactive when they retreat into cracks and crevices or underneath rocks and boulders.

During the night, cunner enter the substrate and undergo a period of nocturnal quiescence. The precise locations where cunner spent their nights were termed night resting sites. These rest sites were the last positional fixes obtained before signal reception was lost for the night. These fixes marked the cessation of daily activity. Similarly, the first positional fixes in the morning depicted the beginning of daily activity. The timing of daily activity was expressed in relation to sunrise and sunset. Onset of activity was calculated as the number of minutes before or after sunrise at which activity first commenced, while cessation of activity was expressed as the number of minutes before or after sunset activity ended. The duration of diurnal activity was defined as the total elapsed time between the onset and cessation of activity (i.e. the elapsed time between when a fish first becomes active during the day until it ceases its activity in the evening).

The computer program Home Range (Ackerman et al. 1988) was used to calculate the distance between consecutive night resting sites to determine whether females exhibit fidelity to the same resting sites each night. The size of the area including all night-rest sites was calculated by connecting the outermost sites by straight lines and using the 100% Convex Polygon Method to calculate the enclosed area (Beckoff and Mech 1984). The types of bottom substrate where night resting sites were located were also recorded for each female.

Cunner were also observed moving under cover at various times throughout the day. The locations of these sites were termed day-rest sites. The length of time between the disappearance and subsequent reappearance of signal reception was calculated. From this data, the amount of time spent inactive was determined for the entire day. This was then expressed as the percentage of a fish's total tracking time. For example, if two fish were tracked at the same time such that each was monitored for 8 hours, the amount of time spent inactive would be expressed as a percentage of this 8-hour tracking period. When only a single fish was tracked, the amount of time spent inactive was expressed as a percentage of its duration of diurnal activity. This measure was defined as percent of time inactive. The mean length of inactivity bouts was also determined.

In describing the activity of female cunner, 5 activity variables were measured: i) percent of time inactive, ii) length of inactivity bouts, iii) onset of activity, iv) cessation of activity, and v) duration of diurnal activity.

2.8 MOVEMENT

Burt (1943) was among the first to define home range as 'the area normally traversed by an animal in its day-to-day activities of food-gathering, mating, and caring for young.' Thus home range can best be defined as an undefended area, to which an animal limits its movements over a period of time. Hayne (1949) recognized that a biological understanding of an animal's home range required information about the intensity of use within the area.

A computer program HOME RANGE (Ackerman et al. 1988) was used to analyze the movement data of individual female cunner. This program was developed to provide home range estimates based on an extension of the harmonic mean utilization distribution (Dixon and Chapman 1980). It calculates a utilization distribution describing the relative intensity of an animal's use of areas within a defined space (Van Winkle 1975) and then specifies the home range boundary by the contour that encompasses a selected percentage of the total space used (Anderson 1982).

In conducting home range studies, one of the most important considerations is to determine an appropriate method for calculating size of the home range area. Most of the earlier research on home range determination in fishes has resulted from tag-recapture studies which provide information on movement between the place at which the fish was tagged and the place at which it was recaptured. However, since no information on the behaviour of fish between the times of tagging and recapture are available, unless the tagged fish are observed directly, it has usually been assumed that the subject remained within the area defined by the points of capture and recapture.

Although telemetric methods allow researchers to repeatedly locate individuals over time, the interpretation of this data is not without problems. Mykytka & Pelton (1988), for example, used 4 standard home range methods to estimate size of black bear home range areas based on radio tracking data. None of the methods employed accurately delineated the area of use of all bears. They were also able to illustrate how the same data can produce different results when different techniques are used. Several other researchers have also identified problems with commonly-used home range estimators which result primarily from a failure to meet assumptions about underlying distributions (MacDonald et al. 1980; Schoener 1981; Anderson 1982; Worton 1987). Thus a careful evaluation of how well the location data conform to the underlying assumptions of various methods is necessary if unbiased estimates of home range are to be obtained.

One of the first methods used to calculate home range size was the Minimum Convex Polygon (Hayne 1949). It involves connecting the peripheral locations of an animal so that the enclosed area represents the home range. Animals have been shown to make occasional excursions outside their normal activity areas which produce extreme locations or outliers that may dramatically affect home range estimates. The Minimum Convex Polygon method is strongly affected by these outliers, and may include large areas not observed to be used by the animal. Also, it does not provide any information on the area potentially used by an animal, only that which was used during the exact times of observation. Furthermore, it provides no information as to how the area within the home range is used. Despite these drawbacks it has been employed by investigators working with a variety of organisms in calculating home range areas (e.g. Dalke and Sime 1938; Lay 1942; Schwartz 1941; Storer et al. 1944; Clark and Green 1990) since it does represent the minimum perimeter of a home range. This method is most appropriate, however, for animals who occupy all parts of their home range with equal intensity, information which is not usually available.

Grid cell counts (Siniff and Tester 1965) have often been used to calculate the size of home range areas, especially in studies involving live-trapping of animals. In employing this method, the area over which an animal moves is dissected by a grid of cells, or blocks. The number of animal locations is tabulated for each of these cells, and the sum of the areas of cells containing locations is taken as the estimate of the home range area. One advantage of using this technique, as is common for all nonparametric methods, is that no assumptions are made concerning the shape of the area utilized. The greatest problem with the grid cell approach is in selecting grid cell size. Choosing too coarse a grid tends to over-estimate home range size, while too fine a grid results in under-estimating home range area. Furthermore, it provides no measure of the distribution of these fixes.

Bivariate normal models (Jennrich and Turner 1969; Koeppl et al. 1975; Dunn and Gipson 1977; Don and Rennolls 1983; Samuel and Garton 1985) assume an animal's activity is concentrated in the central area of the home range and use of space declines with increasing distance from the center of activity (Metzgar 1973). This method, however, provides no biological reason why animals should be expected to utilize space in this manner. This distribution may be appropriate for sit-and-wait predators or animals supplying a nest, den, or central store (Schoener 1981) in homogeneous environments. Most animals, however, do not move randomly about a central point on a homogeneous surface, since the resources governing animal movements are in many cases not normally distributed in space. For example, mates, food, and predators are all likely to be clumped in distribution. Thus this method does not allow for heterogeneous use of space either because of resource availability or social factors.

Using PROGRAM HOME RANGE (Ackerman et al. 1988), animal locations were tested for bivariate normality using a Cramer-Von

Mises goodness-of-fit test. Since the locational data collected on individual female cunner did not conform to a bivariate normal distribution, a nonparametric method of analysis was chosen as the appropriate home range estimator.

Short sampling intervals are common when movements are recorded via telemetry (Tester and Siniff 1965; Reeve 1982; Harrison 1983) and it has been suggested that such short time intervals between successive observations lead to a lack of independence (autocorrelation), at least between successive points (Tester and Siniff 1965; Dunn and Gipson 1977; Swihart and Slade 1985b). While this may cause problems for probabilistic methods of home range calculation, this is not the case for the Harmonic Mean Method as it does not assume that locational observations are independent of one another i.e. an animal's current position is not influenced by its position during past observations (Dunn and Gipson 1977). Since the shortest time interval common for all fish was 15 minutes, the data was summarized so that a single positional fix was chosen every 15 minutes. Fifteen minute intervals also provided a large enough sample size to calculate the underlying nonparametric distribution.

Recognition that parts of a home range are used with varying intensity raises the question of where the limit of such an area may be drawn. For our purposes the total areas enclosed at two contour levels (e.g. 95% and 75% contours) were calculated on a daily and seasonal basis for each female. Refer to Appendix C for a sample illustration of home range calculations performed by

PROGRAM HOME RANGE (Ackerman et al. 1988). All 15 minute positions obtained during the day were used to calculate daily home range areas, while seasonal home ranges included 15 minute positions taken from all days of tracking. The 95% and 75% contour levels specify the percentage of animal locations used to define home range boundaries. According to Anderson (1982) a 95% home range area refers to the smallest area in which an individual is expected to spend 95% of its time (i.e. the area contains 95% of all positional fixes).

Female locations, taken at 15 minute intervals during the day, were plotted using a Minicad program. This provided a daily map of positions for each female cunner during each day of tracking (Refer to Appendix D for sample illustration). Daily variation in range of female movements was assessed as well as the degree of overlap in home range areas of females tracked during the same time periods. Fifteen minute positions taken throughout the entire tracking period were also plotted to provide a seasonal map of animal positions for each female (Refer to Appendix E for sample illustration). Animal movement plots were then overlaid on a habitat map and the predominant habitat type(s) over which the females were located was recorded. Morning and afternoon locational fixes were plotted separately to determine whether there was temporal variation in habitat use. A similar procedure was carried out for animal locations obtained during different phases of the tidal cycle to determine whether movement patterns were under tidal influence.

Two important home range features (core areas and centers of activity) were calculated using HOME RANGE (refer to Appendix C) to determine whether female cunner use space disproportionately within the boundaries of their home range. The existence of core areas, or areas of intensive use, within an animal's home range was suggested by Kaufmann (1962). Core areas are of particular importance because they are used more frequently than any other areas and probably contain the home sites, refuges, and most dependable food sources (Burt 1943; Kaufmann 1962; Ewer 1968).

Samuel and Green (1988) defined core areas as the maximum area within the home range where the observed utilization distribution exceeded that expected from a uniform distribution. HOME RANGE performs a chi-squared test (Samuel and Green 1988) to determine if observed use is significantly greater than expected. An illustration of the statistical test and further description of the methods are presented in Samuel et al. (1985a) and Samuel and Green (1988). Home range gives the percentage of animal locations included in the core area as well as the percentage of the total home range area comprised by the core area.

Dixon and Chapman (1980) defined the center of activity as the geographical location within the home range of the point of greatest activity. This center of activity represents the true center of activity, therefore depicting the most frequently used point within the home range area. The harmonic mean centers of activity were calculated for each daily home range area. A 100% Convex Polygon Method was used to calculate the total area encompassed when the locations of the outermost harmonic centers of activity were connected for each female. This was performed using PROGRAM HOME RANGE (Ackerman et al. 1988).

2.9 ANALYSIS OF DATA

Statistical analyses of the data were conducted using either Minitab or SPSSX statistical software packages.

2.9.1 Effects of Transmitter Attachment

A series of paired t-tests were run to compare activity the day after transmitter attachment with that of all subsequent tracking days. The activity parameters tested were onset and cessation of activity, duration of diurnal activity, percent of time inactive, and length of inactivity bouts. In carrying out this series of tests, if transmitter attachment was shown to have a significant effect on activity, it was possible to determine how long the effect lasted.

The same procedure was used to see if there were differences between the sizes of home ranges the day following transmitter attachment in comparison with all subsequent tracking days. Three measures were used in assessing home range sizes; 95% and 75% harmonic mean contour levels and core areas.

2.9.2 Inter-individual Comparisons

Females A and B were both tracked between June 28 and July 10, while Females C and D were tracked from July 12-July 21.

Since data on females tracked during the same time periods were limited, a nonparametric analysis was chosen for performing inter-individual comparisons. Wilcoxon matched-pairs signed-ranks tests were carried out on individual female cunner tracked during the same times to determine whether there were significant differences in activity and movement patterns. The activity parameters tested were onset and cessation of activity, duration of diurnal activity, percent of time inactive, and length of inactivity bouts. Movement parameters tested were the sizes of the 95% and 75% harmonic mean contour levels and size of core areas.

2.9.3 Activity

Multiple regression analyses were used to determine whether Julian date, time of day (i.e. morning vs afternoon), and environmental variables (water temperature, cloud cover, and sea state) had a significant effect on activity. The activity parameters tested were onset and cessation of activity, duration of diurnal activity, percent of time inactive, and length of inactivity bouts.

Multiple analyses of variance, within-subjects design for repeated measures, were used to determine whether there were significant differences in percent of time inactive and length of inactivity bouts between the 4 tidal phases.

To assess whether temporal trends exist in female activity, data (e.g. percentage of time spent inactive and the length of inactivity bouts) were divided into morning and afternoon as well as seasonal observations. Twelve noon (Daylight Savings Time) marked the changeover between morning and afternoon observations, while seasonal data were divided into three 2-month periods representing major periods related to feeding and spawning behaviours. The June-July period includes emergence from overwintering torpor and spawning. August-September corresponds to the postspawning period, and October- November represents the period prior to re-entering winter torpor.

Paired comparison t-tests were used to indicate whether the activity patterns of a single female cunner differed during prespawning and spawning periods. (Analyses were based on Fish C since this was the only female tracked during both the prespawning and spawning period). The activity parameters tested were onset and cessation of activity, percent of time inactive, length of inactivity bouts, and duration of diurnal activity.

2.9.4 Movement

Multiple regression analyses were used to determine whether Julian date, time of day (i.e. morning vs afternoon), and environmental variables (water temperature, cloud cover, and sea state) had a significant effect on range of female movements as determined by size of home range. Home range sizes were determined in 3 ways; 95% and 75% harmonic mean contour levels and core areas.

Any temporal differences in size of home range areas were looked at in terms of time of day (morning vs afternoon) and season (June-July, Aug.-Sept., Oct.-Nov.) by combining the data for individual females. For example, data collected on all 8 females were used to calculate the average size of home range areas during the morning.

Paired comparison t-tests were used to indicate whether female cunner have similar movement patterns during prespawning and spawning periods. (Analyses were based on Fish C since this was the only fish tracked during both the prespawning and spawning period). Movement patterns were assessed in terms of size of 95% and 75% home ranges and core areas.

RESULTS

3.1 Transmitter Attachment

3.1.1 Effects on Behaviour

Field observations using SCUBA and snorkelling in conjunction with laboratory studies, indicated that the transmitter package had no observable effect on the fish's equilibrium or swimming ability. Transmitter-fitted fish were observed swimming among groups of nontagged fish and their foraging behaviour was indistinguishable from that of nontagged cunner. Confidence in the results from biotelemetry observations can be increased when transmitter-fitted fish feed normally (Young et al. 1972) or travel in schools of untagged fish (Yuen 1970).

During the spawning season at least two tagged females were observed spawning with territorial males. Fish C was observed spawning on July 8 with a territorial male at 220,85 near a cluster of small boulders. Fish A was also observed engaging in spawning behaviour on July 11, after its tracking had ended, in the same general area it had been located during tracking.

At least two males bearing attached transmitter holders were successful at acquiring and maintaining territories. Both were observed actively patrolling their territories on numerous occasions and were seen chasing other cunner from their territories.

3.1.2 Effects on Activity

Results from the paired t-tests indicated there were no significant differences between the day after transmitter attachment and subsequent tracking days in any of the activity parameters, with the exception that females had significantly shorter bouts of inactivity the day after transmitter attachment. By the second day after transmitter attachment, length of inactivity bouts were no different than they were during other tracking days.

3.1.3 Effects on Movement

Using a series of paired t-tests, no significant differences in the size of home ranges were found between the day after transmitter attachment and all subsequent tracking days.

3.2 Activity

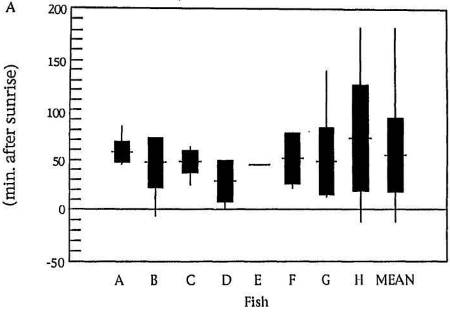
3.2.1 General Observations

All fish tracked were active during the day and inactive at night. Tagged female cunner commenced activity on average 55 minutes after sunrise (s.d. = $\pm$ 36.8 min.) and ceased activity 49 minutes after sunset (s.d. = $\pm$ 36.3 min.). There was considerable daily variation among individuals in the timing of this activity though (Figure 4).

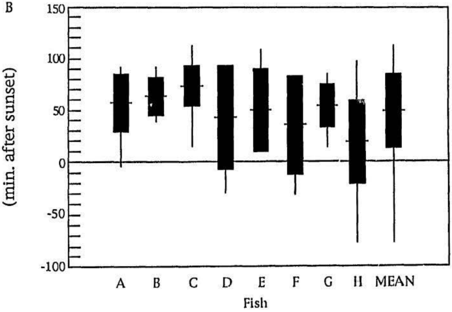
Throughout the day, the active period was interrupted by periods of inactivity which usually lasted between 5-15 minutes, but could last in excess of an hour. During this time, cunner were

Figure 4 A) Daily variation in the onset of activity (relative to sunrise) of 8 female cunner (A-H) in Broad Cove. The vertical line gives the total observed range; the black rectangle gives an interval of one standard deviation on either side of the mean; and the mean is shown as a horizontal crossbar. B) Daily variation in the cessation of activity (relative to sunset) of 8 female cunner (A-H) in Broad Cove.

A


200
150
100
50
0
-50
(min. after sunrise)
A
B
C
D
E
F
G
H
MEAN
Fish

B


150
100
50
0
-50
-100
(min. after sunset)
A
B
C
D
E
F
G
H
MEAN
Fish

under rocks, boulders, or other bottom relief structures providing shelter. Throughout the day, females exhibited variation in the locations of their day-rest sites. The locations of day-rest sites were also shown to vary on consecutive days, although some rest sites were occupied on more than one occasion.

3.2.2 Inter-Individual Comparisons

Wilcoxon matched-pairs signed-ranks tests were carried out on female cunner tracked during the same time periods. No significant differences were found between fish in any of the activity parameters measured (i.e. percent of time inactive, length of inactivity bouts, onset and cessation of activity, and duration of diurnal activity). The complete size range of female cunner was represented in these paired comparisons: Fish A had the shortest total body length (194 mm) and Fish C, the largest (250 mm) (Table 1).

3.2.3 Effects of Environmental Variables

Results from multiple regression analyses indicated that all parameters (i.e. Julian date, time of day, and environmental variables) taken together accounted for between 8.6 and 93.4% of the variation in activity variables (Table 2).

i) Water Temperature

Water temperature accounted for 0.9% of the variation in duration of diurnal activity (Table 2). In general, duration of

Table 2 Summary table for a multiple regression analysis on the effects of Julian date, time of day, and environmental variables (water temperature, sea state and cloud cover) on activity and movements of female cunner in Broad Cove. The analysis was based on 62-229 days of tracking collected on 8 female cunner. (Percentage of variation accounted for by each variable is given as well as the level of significance).

Behavioural Parameter	n	Time of Day	Julian Date	Water Temperature	Sea State	Cloud Cover	Combined Variables
Percent of Time Inactive	205	0.4	59.5 ***	0.4	0.3	0.3	60.9 ***
Length of Inactivity Bout	229	0.1	11.1 ***	1.5	1.1	0.4	14.2 ***
Onset of Activity	75	NA	6.6 *	1.9	0.0	0.1	8.6
Cessation Of Activity	83	NA	22.3 ***	0.2	0.0	0.5	23.0 ***
Duration of Diurnal Activity	62	NA	92.3 ***	0.9 **	0.1	0.1	93.4 ***
95% Home Range Area	204	1.1 *	14.2 ***	3.3 *	0.0	2.2 *	20.8 ***
75% Home Range Area	206	0.8 *	13.3 ***	2.5 *	0.0	2.4 *	19.0 ***
Size of Core Areas	178	6.2 **	13.3 ***	3.3 **	0.1	0.8	23.7 ***

* Significant at 0.05 level
** Significant at 0.01 level
*** Significant at 0.001 level

diurnal activity was shown to increase with increasing water temperature. Water temperatures above 5°C had no significant effect on the onset or cessation of activity, the percent of time spent inactive, or the length of inactivity bouts.

At temperatures below 5°C cunner sought shelter and remained inactive. On June 23-24, for example, strong north-westerly winds forced a body of cold water into the study area causing the water temperature to drop from 6°C to 3°C. This resulted in cunner being inactive for 2 days. The two fish (Fish A and Fish B) tracked during this time, responded differently when the water temperature rose above 5°C on June 25. Fish A spent a significantly smaller percentage of its time inactive the day following this 48-hour period of inactivity, while Fish B was found to occupy a significantly larger home range area.

During the morning of June 26 the water temperature again dropped to 3°C resulting in cunner being inactive for the remainder of the day. On June 27 when the water temperature increased above 5°C, Fish B covered its largest daily home range area. The duration of its diurnal activity was also significantly longer. Neither the activity nor size of home range of Fish A changed the day following this inactivity period.

ii) Sea State

Sea state did not have a significant effect on any of the activity variables (ie. onset or cessation of activity, percent of time inactive, length of inactivity bouts, or duration of diurnal activity). There was a trend, however, for length of inactivity bouts to increase on days having high surface waves.

iii) Cloud Cover

Cloud cover had no significant effect on any of the activity variables (i.e. percent of time inactive, length of inactivity bouts, duration of diurnal activity, or onset and cessation of activity). There was a trend, however, for females to remain inactive for longer periods of time (i.e. percent of time inactive and length of inactivity bouts increased) as amount of cloud cover increased. There was also a tendency for the duration of diurnal activity to decrease with increasing cloud cover.

iv) Tidal Phases

The multiple analyses of variance showed that percent of time inactive and length of inactivity bouts were not significantly different during the 4 tidal phases.

3.2.4 Temporal Effects

i) Time of Day

Results from multiple regression analyses showed there were no significant differences between morning and afternoon observations in either the percentage or length of time spent inactive.

ii) Season

Julian date accounted for 59.5% of the variation in percent of time inactive (Table 2). Specifically, cunner were shown to spend an increasing proportion of their time inactive from June through November. Julian date accounted for only 11.1% of the variation in length of inactivity bouts which increased over time as well (Table 2). Julian date accounted for 6.6% and 22.3% of the variance in onset and cessation of activity, respectively (Table 2). The trend was for activity to start later in the morning and end earlier in the evening as time progressed. Julian date accounted for 92.3% of the variation in duration of diurnal activity (Table 2). As the seasons progressed and the number of daylight hours became progressively shorter, there was a corresponding decrease in the duration of diurnal activity (Figure 5).

Thus the duration of diurnal activity, percent of time inactive, and length of inactivity bouts all varied across seasons. By combining the data collected on individual female cunner, the average elapsed time between onset and cessation of activity (i.e. duration of diurnal activity) was 16.5 hrs during June and July, 13.5 hrs in August and September, and only 11.0 hrs during October and November. Between June-July 22.9% of the active period was spent inactive, 47.0% in August-September, and 71.8% during October and November (Figure 6), while length of inactivity bouts increased from an average of 6.4 min. in June-July, to 9.3 min in Aug.-Sept., and 12.7 min. in Oct.-Nov.

Figure 5 Relationship between seasonal changes in daylength (i.e. elapsed time between sunrise and sunset) and duration of diurnal activity (i.e. elapsed time between onset and cessation of activity) of 8 female cunner in Broad Cove.

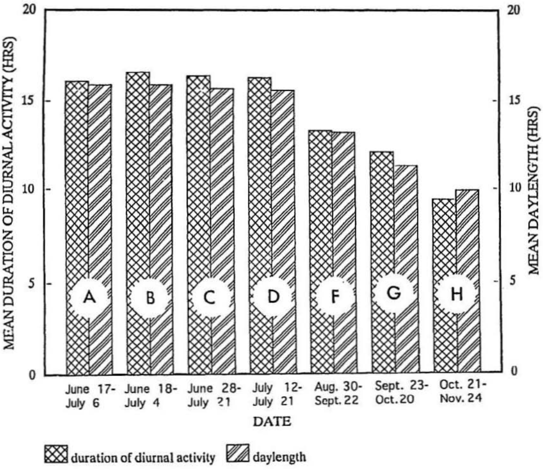
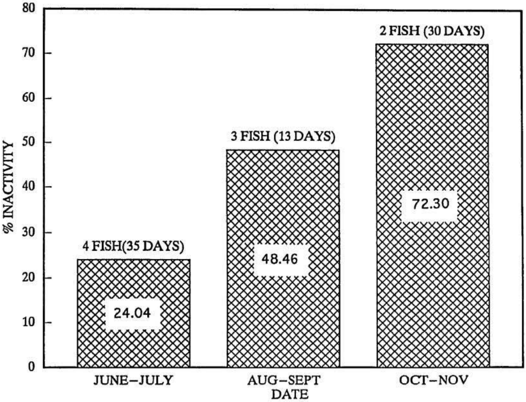

MEAN DURATION OF DIURNAL ACTIVITY (HRS)
MEAN DAYLENGTH (HRS)
20
15
10
5
0
A
B
C
D
F
G
H
June 17-
July 6
June 18-
July 4
June 28-
July 21
July 12-
July 21
Aug. 30-
Sept. 22
Sept. 23-
Oct. 20
Oct. 21-
Nov. 24
DATE
duration of diurnal activity
daylength

Figure 6 Seasonal changes in percentage of time spent inactive by female cunner in Broad Cove.


% INACTIVITY
80
70
60
50
40
30
20
10
0
4 FISH(35 DAYS)
24.04
3 FISH (13 DAYS)
48.46
2 FISH (30 DAYS)
72.30
JUNE–JULY
AUG–SEPT
OCT–NOV
DATE

By combining the data in this manner, effects of individual variability were ignored, although such effects still contribute to the total variance in the data set. However, this should not invalidate the results since the effect of ignoring inter-individual variation is to reduce the amount of variance that will be explained, effectively decreasing the actual "Type I error" and making tests more conservative. Limited data collected on females tracked during the same time periods also seems to suggest females do not differ substantially from one another in terms of their activity. Since the data were limited, however, we should be careful in any interpretation of these results.

To calculate the average number of hours a female cunner spends inactive each day, the percent of time inactive was expressed in terms of duration of diurnal activity (i.e. the elapsed time between when a fish first becomes active during the day until it ceases its activity in the evening). On average, during June and July female cunner were active for 12.5 h/day, 7 h/day during August and September, and only 3 h/day during October and November.

Paired comparison t-tests carried out on Fish C between June 28 and July 21 showed there was no significant difference between prespawning and spawning periods in any of the activity parameters (i.e. percent of time inactive, length of inactivity bouts, onset and cessation of activity, and duration of diurnal activity).

3.3 Movement

3.3.1 General Observations

Cunner exhibited variation in their choice of night-resting sites. Tagged cunner returned to the same general areas each night (that is, within an area of 973 m^2, on average), but did not use the same sites (Table 3). Despite this generalization, however, on several occasions 7 of the 8 females tracked returned to the same exact sites on successive nights. All night rest sites had the common characteristic of being located near bottom structures. The locations of night resting sites occupied by Fish A, C, and D throughout their tracking periods are shown in Figure 7.

Fish G occupied the smallest night-rest site area (~ 146 m^2) and moved the shortest distance between consecutive night-rest sites (8.7 m) (Table 3). Fish B covered the greatest distance in moving between consecutive night-rest sites, on average rest sites were located 21.6 m apart. The night-rest site locations of Fish H encompassed the largest area (~ 2897 m^2) (Table 3).

Cunner have been shown to have restricted home ranges remaining in close association with bottom relief structures affording cover (Green 1975; Olla et al. 1975). For all eight fish the mean daily 95% home range area was between 299.6 m^2 and 2253.6 m^2. Although females exhibited considerable variation in the size of their home ranges (i.e. 95% and 75% contours) and core areas on successive days (Table 4), the general areas over which females ranged remained fairly consistent. The 95% home range areas of Fish A on 4 consecutive days are shown in Figure 8. The seasonal home

Table 3 Summary of night-rest site fidelity of female cunner in Broad Cove. The mean distance between consecutive night rest sites, the total area in which night-rest sites were located, and the types of bottom substrates over which the sites were situated are provided for each individual female. Refer to Appendix B for a description of bottom substrate types. (The method for measuring areas is described in the text).

Fish No.	Number of Rest Sites	Mean Distance Between Consecutive Rest Sties (m)	100% Rest Site Area (m^2)	Type of Bottom Substrate
A	14	16.13	658.50	Boulder/Outcrop II
B	15	21.57	1799.00	Boulder/Outcrop II
C	24	10.36	617.00	Boulder/Outcrop I Rock Outcrop
D	9	15.03	814.00	Boulder/Outcrop I Boulder/Outcrop II
E	4	18.63	286.50	Boulder/Outcrop II
F	6	20.55	569.00	Boulder/Outcrop II
G	21	8.68	146.00	Rock Outcrop Boulder/Outcrop II
H	31	15.70	2896.50	Mixed Boulder/Outcrop I Boulder/Outcrop II

Figure 7 Locations of night resting sites occupied by Fish A, C, and D during their entire tracking periods. (Location of the original capture site is included).

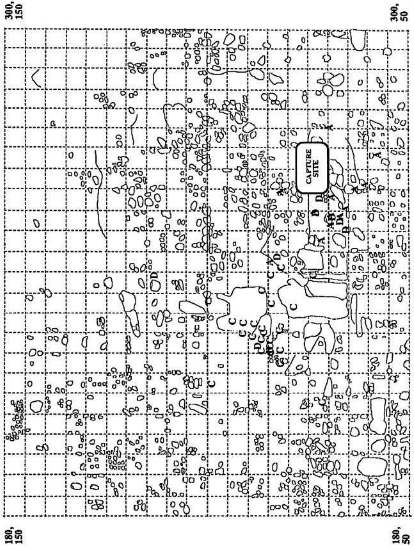

300, 150
300, 50
180, 150
180, 50
CAPTURE SITE

Table 4 Summary of daily and seasonal movements and home range areas of 8 sonic-tagged female cunner in Broad Cove. (Refer to methods for a description of area calculations).

Parameters	Fish A	B	C	D	E	F	G	H
Average size of 95% home range (m²)	1559.7	2252.6	2248.3	1560.7	960.4	905.4	299.6	1158.2
Range in 95% home range area (m²)	598.6-4605.9	543.6-3811.3	752.1-4950.5	79.3-2987.7	271.5-1332.6	102.4-1869.8	148.4-530.2	150.9-3217.1
Average size of 75% home range (m²)	655.4	1033.1	1077.5	846.3	601.0	401.6	138.9	377.7
Range in 75% home range area (m²)	186.9-1027.2	160.6-1663.3	192.7-2373.2	181.2-1510.8	185.6-925.0	11.0-891.1	53.2-241.4	99.7-1307.5
Average size of core areas (m²)	387.8	593.0	687.8	566.7	427.7	261.2	63.5	377.7
Range in size of core areas (m²)	172.3-572.5	147.9-1123.7	96.9-1603.4	398.1-786.1	425.8-429.6	11.0-516.0	11.0-120.7	36.8-1075.9
Average % of time spent in core area	62.0	63.0	62.1	57.6	57.4	62.9	62.2	60.1
Average % of home range encompassed by core area	29.26	24.52	28.37	28.96	31.53	31.21	31.73	28.23
Size of seasonal home range area (m²)	6841.00	7449.90	6414.07	6550.87	2024.98	2851.25	4112.81	11743.31
Area encompassing 100% harmonic mean center of activity (m²)	172.50	119.50	876.00	1422.50	0.50	73.50	163.00	3538.00
Track Duration (Days)	16	17	24	10	4	16	22	32

Figure 8 Home range areas of Fish A on 4 consecutive days between June 27 and June 30. Home range areas were drawn by connecting the outermost points depicting the 95% harmonic mean contour levels. Refer to Appendix C for illustration of home range calculations. (Location of the original capture site is included).

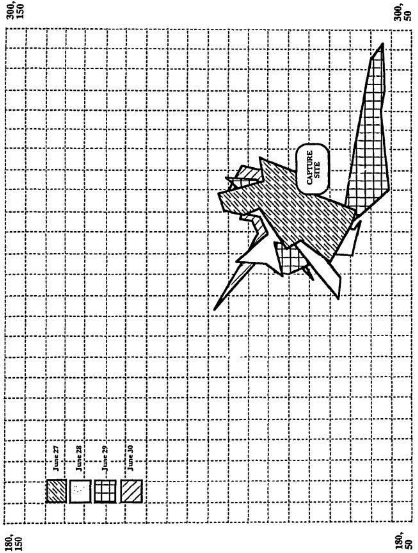
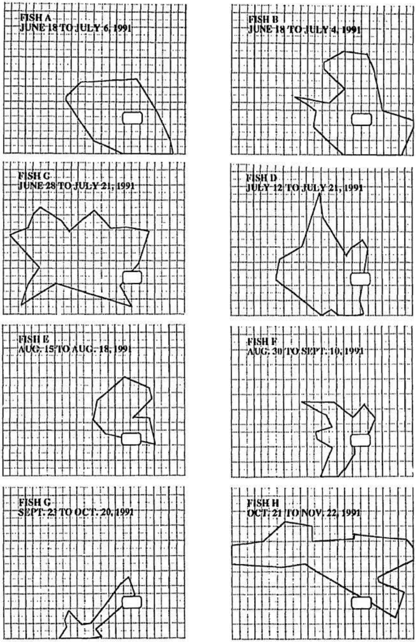

300,
150
300,
50
180,
150
180,
50
CAPTURE
SITE
June 27
June 28
June 29
June 30

Figure 9 Seasonal home ranges of 8 female cunner tracked in Broad Cove, Conception Bay. (For illustrative purposes home range areas were drawn by connecting the outermost points).


FISH A
JUNE 18 TO JULY 6, 1991
FISH B
JUNE 18 TO JULY 4, 1991
FISH C
JUNE 28 TO JULY 21, 1991
FISH D
JULY 12 TO JULY 21, 1991
FISH E
AUG. 15 TO AUG. 18, 1991
FISH F
AUG. 30 TO SEPT. 10, 1991
FISH G
SEPT. 21 TO OCT. 20, 1991
FISH H
OCT. 21 TO NOV. 22, 1991

ranges of 8 female cunner are shown in Figure 9. On average seasonal home range size varied from 2025.0 m^2 (Fish E) to 11,743.3 m^2 (Fish H) (Table 4).

Cunner, like most animals, do not utilize their entire home range area with equal intensity. This was evident from the presence of core areas where females were found to concentrate most of their daily activity. Mean daily core areas for all eight females were between 64-688 m^2 in size and usually encompassed 25-30% of the home range area. The high percentage of time females spend occupying these relatively small areas illustrates how restrictive females are in their movements.

The harmonic mean centers of activit · calculated for each daily home range varied over the course of the study. The area encompassed when the outermost centers of activity were connected to form polygons, ranged in size from 0.5 m^2 to 3538.0 m^2 (Table 4). Thus while some females concentrated their activity centers in a confined area (i.e. the points of greatest activity remained fairly consistent on successive days), others appeared to shift their centers of activity over time. The degree of shifting among females varied considerably.

3.3.2 Inter-Individual Comparisons

Analyses carried out using Wilcoxon matched-pairs signed-ranks tests showed no significant differences between females tracked during the same time in the size of their home ranges. (The interpretation and usefulness of these results has been addressed above). Although the size of female home ranges were similar, some variation existed among females in the locations of their home range areas.

Two females (Fish A & B) tracked during the same time period, exhibited some degree of overlap in their range of movements (Figure 9). However, because of the nature of data collection (while tracking two fish at the same time the position of only one female was monitored during a 15-minute interval), the exact degree of overlap could not be determined. These females were often found in close association with other similar-sized cunner as well so they did not maintain exclusive use of their home range areas. Direct underwater observations showed these females followed the same types of movement patterns each day; they were often found out over the drop-off region in deeper water during the days and then moved further inshore during the evenings. Not all fish showed this pattern of movement.

3.3.3 Effect of Environmental Variables

Multiple regression analyses indicated that Julian date, time of day (i.e. morning vs afternoon), and environmental variables taken together accounted for 19.0 to 26.4% of the variation in size of 95% and 75% home range areas and core areas (Table 2).

i) Water Temperature

Water temperature accounted for 3.3% and 2.5% of the variation in the size of 95% and 75% home range areas, respectively, while

3.3% of the variation in size of core areas was accounted for by water temperature (Table 2). As water temperature increased, size of 95% and 75% home range areas and core areas decreased. Thus females seemed to become more restrictive in their movements at higher temperatures.

ii) Sea State

Sea state had no significant effect on size c˙ home range or core areas (Table 2).

iii) Cloud Cover

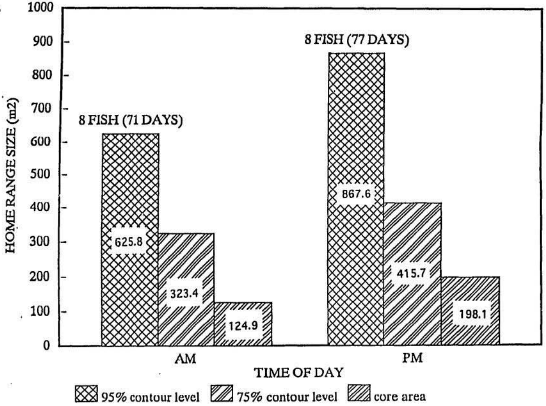
Cloud cover accounted for 2.2% and 2.4% of the variation in the size of 95% and 75% home ranges, respectively (Table 2). As cloud cover increased size of 95% and 75% home ranges increased. Cloud cover had no significant effect on the size of core areas (Table 2).

3.3.4 Temporal Effects

i) Time of Day

Time of day accounted for between 0.8 and 6.2% of the variation in the sizes of 95% and 75% home ranges and core areas. All three home range measures (95% and 75% contour levels and core areas) were significantly larger in the afternoons than in the mornings. On average, 95% home range areas were 867.6 m^2 in the afternoon and only 625.8 m^2 in the morning (Figure 10). Thus in the mornings females occupied home range areas 28% smaller than those

Figure 10 Temporal changes in size of home range areas of female cunner. Mean size of 95% and 75% contour levels and core areas are shown for morning and afternoon observations.


1000
900
800
700
600
500
400
300
200
100
0
HOME RANGE SIZE (m2)
8 FISH (71 DAYS)
8 FISH (77 DAYS)
625.8
323.4
124.9
867.6
415.7
198.1
AM
PM
TIME OF DAY
95% contour level
75% contour level
core area

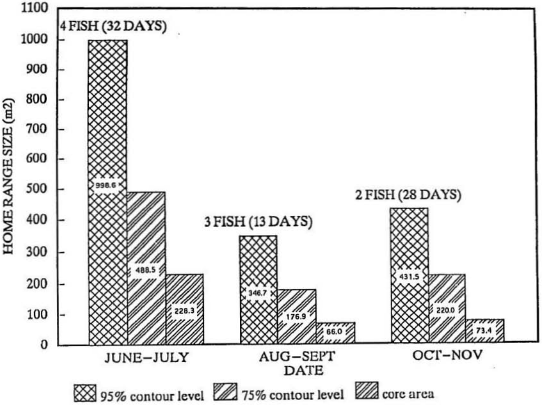
occupied in the afternoons, while activity levels remained the same. The 75% home range contours encompassed an area of 415.7 m^2 in the afternoon and 323.4 m^2 in the morning (Figure 10), a 22% increase in the size of the home range area from morning to afternoon. Females occupied core areas in the afternoon covering 198.1 m^2 while only covering an area of 124.9 m^2 in the morning (Figure 10). Thus females increased the size of their core areas by about 37% in the afternoon.

ii) Season

Julian date accounted for 14.2% and 13.3% of the variation in the size of 95% and 75% home range areas, respectively (Table 2). In general, size of the 95% and 75% home ranges decreased over time. Julian date accounted for 13.3% of the variance in size of core areas (Table 2). Again, size of core areas decreased over time.

Home range areas were greatest during June-July, followed by Oct.-Nov., and lastly Aug.-Sept. On average, during June-July females spent 95% of their time in an area 998.6 m^2, in Oct.-Nov., 431.5 m^2, and Aug.-Sept only 346.7 m^2 (Figure 11). Thus females had their largest range of movement during the months of June and July. During Aug.-Sept., females occupied home range areas almost three times smaller than those occupied in June and July, while during October and November the size of female home ranges was little less than half the area females had covered in June and July. Similar differences in home range size were found with 75% contour levels;

Figure 11 Seasonal changes in size of home range areas of female cunner. Mean size of 95% and 75% contour levels and core areas are shown for June-July, August-September, and October-November.



1100
1000
900
800
700
600
500
400
300
200
100
0
HOME RANGE SIZE (m2)
4 FISH (32 DAYS)
3 FISH (13 DAYS)
2 FISH (28 DAYS)
998.6
488.5
228.3
346.7
176.9
66.0
431.5
220.0
73.4
JUNE–JULY
AUG–SEPT
DATE
OCT–NOV
95% contour level
75% contour level
core area

June-July (488.5 m^2), Oct.-Nov. (222.0 m^2), and Aug.-Sept. (176.9 m^2) (Figure 11). Size of core areas were also greatest in June-July (228.3 m^2), followed by Oct.-Nov. (73.4 m^2), and Aug.-Sept. (66.0 m^2) (Figure 11). There was no significant difference, however, between the Aug.-Sept. and Oct.-Nov. periods in the size of core areas. For both periods, core areas encompassed only about one-third of the area females had covered in June and July.

Using paired comparison t-tests, data collected on Fish C between June 28 and July 21 indicated there was no significant difference between prespawning and spawning periods in the size of home range areas or core areas.

3.4 General Underwater Observations

The first spawn of the 1991 season was recorded on July 8, the last on August 10. No courtship behaviour was observed after August 12. Two of seven females assessed on August 10 were spent. The remaining females were nearly spent, the eggs being stripped with difficulty. All 29 females assessed on August 17 were spent.

Fish A and B were observed on numerous occasions during July and August maintaining positions in the same general areas they had been located during their tracking period (i.e. from June 17 to July 6).

On days experiencing a lot of turbulence and heavy surge, few cunner were visible during dives. Of those observed most were under rocks or in crevices, while some were found further offshore, relatively close to the substrate where there was less water movement. In general, under these conditions few fish were seen inshore of the drop-off region where water depths were less than 6m. (General location of the drop-off can be seen in Figure 2).

3.5 General Weather Observations

Temperature variations of up to 2.5°C occurred on a daily basis as weather conditions changed. Overall there was an upward trend in temperature from mid-June until the end of August, after which the temperature declined until it reached 5°C in late November.

DISCUSSION

4.1 Response to Transmitter Attachment

The stationary tracking system used in this study permitted continuous data collection on the movements of individual cunner. The biological usefulness of these studies, however, depends on whether the technique employed provides unbiased results. In some studies externally attached transmitters have been shown to affect the fish's equilibrium and swimming performance. McCleave and Stred (1975), for example, found transmitters reduced swimming stamina in Atlantic salmon (Salmo salar) smolts, while Shepherd (1973a) found attachment through the dorsal musculature of cutthroat trout, Salmo clarki, created a wound at the site of attachment and appeared to alter the fish's behaviour. Temporary effects on buoyancy have also been observed in several fish species having transmitters inserted internally (Gallepp and Magnuson 1972; Hawkins et al. 1974; Fried et al. 1976).

Our findings suggested that the attached transmitter package had no adverse effect on the fish's equilibrium or swimming ability nor produced significant changes in female activity or movements during the course of the tracking period. Careful design of the transmitter package coupled with the use of dummy transmitters to habituate the experimental subjects prior to tracking were probably important factors in minimizing effects of transmitter attachment. Olla et al. (1975) also found externally attached transmitters had no detectable effect on the behaviour of cunner, Tautogolabrus adspersus.

In tracking studies it is often difficult to monitor the movements of individuals for long periods of time. Even with a stationary array system as used in this study, there was the problem of recapturing individual fish for battery replacement once a transmitter had expired. The size of the fish precluded the use of larger transmitters with longer battery life. While the location of a tagged fish was always known, we were not successful in recapturing the same individuals for battery replacement more than twice. After tagging, fish became very wary of all attempts to recapture them. Therefore, most information obtained during tracking consisted of 2-3 weeks of data on individual female cunner.

While the behaviour of individuals tracked during different times of the year showed significant variation, there were no significant differences among fish tracked during the same time periods. The information gained by tracking individual females appears, therefore, to be representative of female cunner in Broad Cove.

4.2 Use of Time and Space

The Harmonic Mean Measure Method (Dixon and Chapman 1980) was used to analyze movement data collected on individual female cunner. This method provided information on the intensity of space use (ie. core areas and centers of distribution) within the home range area. Furthermore, since the data collected did not conform to a bivariate normal distribution, a nonparametric method of analysis provided the best unbiased estimate of home range size.

Cunner in Conception Bay have been shown to occupy small home range areas (Green 1975). Pottle (1979) reported that tagged female cunner remained within 25 m of their initial tagging site during the spawning season, although some ranged considerably further afterwards. Thus while past studies have indicated cunner are restrictive in their movements, no specific data have been collected on the size of home ranges or temporal (i.e. daily or seasonal) variation in the range of cunner movements or use of space within the home range area.

All female cunner tracked had relatively small mean daily home ranges (ranging from 299.6-2252.6 m^2) in relation to the habitat available to them. Females clearly utilize space disproportionately within the boundaries of their home ranges. Individual female cunner were shown to spend a significant proportion (60%) of their time occupying a small fraction (30%) of their home range area. Other species have also been shown to utilize their home range area with variable intensity (e.g. Adams and Davis 1967; Van Ballenberghe and Peek 1971; Metzgar 1973; Leuthold 1977; Nursall 1977; Inglis et al. 1979; Dixon and Chapman 1980; Georgii 1980; Nursall 1981; Whitten 1982; Springer 1982). The Harmonic Mean Measure Method (Dixon and Chapman 1980) used to calculate home ranges identified intensively used areas. Generally central portions of the home range areas were occupied more intensively than other areas, with relatively little time spent on outside excursions. The function of these excursions and their importance to female cunner could not be estimated by a simple analysis of movement. This pattern of movement, however, would be expected from an animal making occasional visits to the periphery of its range for such purposes as resource assessment and assessment of a neighbour's reproductive condition.

Five female cunner had daily activity centers (i.e. points of greatest activity) at fairly consistent locations over the period of study (i.e. centers of activity were located within an area ranging from 0.5-172.5 m^2 as determined by the Minimum Convex Polygon Method). From this it seems some females not only remain in the same general areas over long periods of time, but their distribution of activity around central areas also appears to be maintained. Other females exhibited considerable variability in the daily locations of their centers of activity, which ranged in area from 876-3538 m^2.

Female cunner tracked during the same time period occupied overlapping home ranges, as well as overlapping core areas. Ewer (1968) found most organisms having overlapping home ranges did not have overlapping core areas. Nontagged cunner were often found within the home range areas of tagged females as well. Thus female cunner did not maintain exclusive use of their home range areas, or core areas, against other conspecifics.

The Harmonic Mean Measure Method (Dixon and Chapman 1980) employed 95% and 75% contours as home range estimators in calculating home ranges of female cunner. The boundaries described by these contours did overestimate the area of use. Bands of varying widths where no activity was recorded surrounded the outer locations of each of the females. The boundaries describing core areas corresponded well to the area of observed use and included a relatively small band of no activity.

The physical characteristics of the environment of Broad Cove are not limiting for females. The structural complexity, although variable, throughout most of the area provides suitable refuge sites and availability of food. Despite this, females were still found to occupy restricted home ranges within a limited area of the study site. By restricting their movements to familiar areas females may be able to quickly find shelter in known refuges during times of danger (i.e. under adverse weather conditions or when threatened by predators) and may also know the locations of the best feeding areas. It has also been suggested that fish remain in the one place as a means of maintaining a stable social structure (Sale 1971). Thus it seems likely the distribution and abundance of resources (i.e. food, mates, and shelter sites) should determine the size of home range areas.

The current study confirmed the importance of various bottom topographical features in determining the locations of female home range areas. In general, females spent most of their time over areas having bottom relief structures. No fish were found in the portion of the hydrophone array over sandy open substrate and very few positional fixes placed fish over sand. Although we speculate cunner occupy areas having suitable availability of resources (i.e. food, mates, and shelter), further study may identify other factors responsible for differential habitat utilization.

Seeking shelter under rocks during the night is a common characteristic of many labrids including cunner (Hobson 1965; Hobson 1972; Olla et al. 1975). All tracked females selected night-resting sites under rocks or in crevices, where signal transmission from the sonic transmitters was partially or completely blocked. It would be energetically beneficial for females to take shelter during nonforaging periods as well as providing a means of avoiding predators.

Night rest-site fidelity, which involves fish returning to the same exact resting locations each night, has been demonstrated in several fish species (Edmundson et al. 1968; Ehrlich et al. 1977; Hobson 1972; Hobson 1973; Olla et al. 1974; Clark and Green 1990). In general, Hobson (1972) found low fidelity to nocturnal refuges in tropical labrids. He stated, however, that at least one labrid, Thalassoma duperrey, was observed occupying a given resting spot on several consecutive nights, but this specific behaviour lasted only a week or so (Hobson 1972). In Conception Bay, although some females returned to the same resting locations on more than one occasion, females typically occupied different night-resting sites on consecutive nights. The locations of these rest sites, however, were always in the same general areas where females maintained positions during the day and were usually located within the most frequented portion of their home range (i.e. core areas).

Although it is known cunner are active only during daylight hours (Green et al. 1984; Olla et al. 1975), very little is known about how female cunner spend their time during the day. Some diurnal fishes alternate periods of activity with periods of rest during the day (Gibson 1986; Erlinge 1979; Olla et al. 1978; Pottle 1979; Whoriskey 1983). Under laboratory conditions, adult tautog (Tautoga onitis), a temperate labrid, have active periods interrupted by intermittent periods of resting on the bottom of the tank (Olla et al. 1978). Whoriskey (1983) observed cunner in Massachusetts remaining underneath boulders during the day when they were not foraging. Pottle (1979) reported that territorial male cunner in Conception Bay, Newfoundland, undergo periods of daylight quiescence. Quiescent males were normally found under cover, but on occasion were seen immobile on the substrate in exposed positions.

Because of the effect on signal transmission of cunner moving under rocks and into crevices, it was possible to quantify rest periods both temporally and spatially. Female cunner in Conception Bay experienced periods of inactivity during which they took shelter beneath rocks or in crevices. The locations of these day-rest sites were shown to vary over the course of the day. On average, bouts of inactivity lasted between 5 to 15 minutes, but some lasted in excess of an hour. The length and frequency of inactivity bouts were shown to vary on a seasonal basis, increasing from June to November.

Cunner may seek cover for several reasons. Researchers have assumed temperate wrasses use cover to avoid predation (Olla et al. 1979; Hobson et al. 1981), although predation threat has not been well-documented. In Newfoundland, cunner of the size tagged do not have any known predators so it is unlikely that predation risks have a strong influence in shaping this shelter-seeking behaviour. A more plausible explanation stems from the fact that females are often harassed by other conspecifics, especially territorial males, in the form of courtship or chasing behaviours. Females may seek shelter to avoid such harassment. Most importantly, perhaps, it is less energetically expensive to maintain one's position under cover than it would be to remain stationary near the substrate or up in the water column, particularly during periods of rough sea conditions. Sea state was shown to have a significant influence on the amount of time spent under shelter. Digestive processes impose significant metabolic costs and it would be interesting to determine whether longest periods of diurnal quiescence follow the most intense or successful bouts of foraging.

4.3 Factors Affecting Activity and Movement

4.3.1 Daily Effects

In many diurnal species the onset and cessation of activity coincides closely with the rising and setting of the sun (Hobson 1972; Hobson 1973; Hawkins et al. 1974; Olla et al. 1974; Olla et al. 1975; Maurel 1979; Mauget 1979; Clark and Green 1990). Female cunner became active on average 55 minutes after sunrise and ceased activity about 49 minutes after sunset.

Cloud cover and sea state, both of which affect light penetration, were not shown to affect the activity of female cunner, except on days having heavy surge females were found to remain inactive for longer periods of time. Although cloud cover did not significantly affect the onset or cessation of activity, the trend was for activity to begin later in the morning and end earlier in the evening on days having increased cloud cover.

Cunner occupied basically the same home range areas irrespective of amount of cloud cover, but the size of these home ranges were shown to increase with increasing cloud cover. Water movement from turbulence and heavy surge, however, was shown to affect the distribution of some cunner, while the size of home range areas remained unchanged. Water disturbances can easily displace fish thus increasing their chance of injury. In addition, maintaining position and carrying out normal daily activities, such as foraging, under these circumstances presumably requires increased energy expenditure.

According to the energy constraint hypothesis (Allen 1969), if the potential benefits (e.g. food availability, absence of predators and competitors) of different habitats are equal, fish should prefer locations that minimize the metabolic cost required to hold position. By minimizing the amount of energy required to maintain position, this would result in more energy being available for growth and/or reproduction.

Underwater observations made at the study site, during adverse sea conditions, showed that some cunner took shelter under bottom relief structures while others remained close to the bottom in deeper, offshore waters where the effects of water movement were reduced. Although female cunner tracked during these periods did not show any offshore movement, they did tend to remain in areas offering shelter.

Numerous inshore fish species synchronize their activities with the tidal cycle (Williams 1957; Zander 1967; Green 1971; Tyler 1971; Healey 1971; Gibson 1973; Kuipers 1973; Thomson and Lehner 1976; Gibson et al. 1978; Gibson 1986). The maximum tidal amplitude in Broad Cove, Conception Bay is less than 1 m and cunner in this area do not use or have access to an extensive intertidal feeding area. Therefore it is not surprising female activity is not significantly influenced by the tidal cycle. Distribution of cunner does not seem to be affected by the tides either, since cunner were observed occupying the same areas during all phases of the tide. Similar findings were found by Olla et al. (1975) who observed cunner remaining in the subtidal region throughout the tidal cycle. Whoriskey (1983), on the otherhand, demonstrated that while some cunner remained in the subtidal region during both high and low tides, others would leave their subtidal sites and forage in the intertidal zone during high tide.

Temperature is an important factor influencing the activity of cunner (Green and Farewell 1971; Olla et al. 1975; Dew 1976). When the temperature dropped below 5°C at various times throughout the tracking period, cunner became inactive. This occurred on June 23-24 and again on June 26. Following these periods of inactivity, females might be expected to compensate for lost foraging opportunities by increasing their level of activity. In fact, the day following these periods of inactivity, one fish (A) had a decrease in the amount of time it spent inactive, while the other (B) occupied a larger home range area. Given a uniform distribution of food, females could presumably increase their food consumption by foraging for longer periods of time or over larger areas.

4.3.2 Seasonal Effects

Cunner in Newfoundland are active only during summer and fall and then overwinter in a torpid state for the remaining 6 months of the year (Green and Farewell 1971). Upon emergence from overwintering torpor, cunner must consume energy to replenish energy reserves depleted during winter, prepare for reproduction, and increase somatic growth. According to Jones (unpublished data), between emergence from torpor and spawning, most food energy in female cunner is devoted to the maturation and development of gonads. Although gonadal recrudescence begins shortly after spawning, most occurs after emergence from torpor approximately 9 months later. Thus while some energy has already been put into gonadal development prior to emergence from torpor, the majority of investment occurs after emergence. Wootton (1977; 1979) found female threespine stickleback spent virtually no energy on somatic growth during the spawning season, but invested between 15-20% of their energy income on egg development.

In fishes, females are more likely to be energy-maximizers than time-minimizers since the amount of egg production is positively correlated with food uptake (Scott 1962; Bagenal 1969; Bagenal 1978; Perrone 1978). Green et al. (1984) provided some evidence that female cunner are energy-maximizers as compared to territorial males. During the spawning season, females feed throughout their entire active period, mostly on prey of high energy content (e.g. blue mussels and capelin), while territorial males forage primarily in the morning (Green et al. 1985).

To meet the energy requirements of the post-torpor and reproductive period (i.e. during the June-July period), it was hypothesized that female cunner would exhibit high levels of activity. Apart from having these high energy requirements following emergence from torpor, females are also exposed to increases in water temperature. Metabolic rate increases with temperature, thus increasing maintenance costs (Brett et al. 1969; Brett and Groves 1979; Jobling 1988), but also increasing the rate at which food can be processed (Elliot 1975; Brett and Groves 1979; Elliot 1976b). Thus as temperature increases (up to some maximal level), females are able to acquire energy at a faster rate as long as food is available. Energy excess to metabolic requirements can then be used for reproduction and/or growth.

During June and July, cunner did have their highest activity levels (i.e. females were active for about 12.5 hours of the day) and were also shown to occupy the largest home range areas. Several other tracking studies have provided evidence that the spawning season, compared with other times of the year, is a period of high activity (Diana et al. 1977; Diana 1980; Mackay and Craig 1983; Cook and Bergersen 1988; Lucas et al. 1991).

Several investigators have shown that home range size is determined by an animal's energy needs (McNab 1963; Schoener 1968; Turner et al. 1969; Milton and May 1976; Harvey and Clutton-Brock 1981; Gittleman and Harvey 1982; Mace et al. 1982), and since energy needs may vary over time this may result in temporal changes in the size of home range areas.

Schoener (1971) showed that as food availability increased, food requirements could be attained at a faster rate. If this were true for cunner, when food availability is low, they would need to spend more time foraging over a larger area to obtain their energy requirements.

Benthic sampling of the distribution and abundance of food organisms within the study site at Broad Cove was conducted over a depth range of 2.5-10.0 m by Martel (1983). His results indicated that food availability increased with depth. Within a given depth range, however, food organisms appeared to be uniformly distributed, with the exception of mussels, Mytilus edulis, (Linnaeus). Mussels are patchily distributed in groups of individuals of varying sizes (Kautsky 1982). Keats (1986) also found the density of invertebrates increased with depth at other sites in Conception Bay, reaching peak abundance between 6-9 m. Apart from gastropods being most abundant in shallow water during late August through September, no other seasonal shifts in abundance were observed (Keats 1986). It seems reasonable, however, that other invertebrate species probably reach their peak abundance during this period as well.

If food availability is lowest during June and July (i.e. prior to recruitment of invertebrates), females might be expected to cover the largest areas during this period in obtaining food resources as was found. During August-September, when food availability is expected to be highest, females also occupied the smallest home range areas and spent more time inactive.

Cunner are opportunistic feeders and a seasonally abundant food resource at the study site is capelin, Mallotus villosus, (Muller 1777) (Pottle 1979). Following spawning, capelin remains are often found on the substrate where they are available to cunner. According to Pottle (1979), capelin appeared to be a major food source for a 2-3 week period. In 1991, capelin were available at the study site for a 2 week period in mid-July. During this period no significant changes were observed in the size of home range areas.

Not all of the cunner activity may be directed towards acquiring energy. Other factors such as habitat quality, risk of predation, mate acquisition, inter- and intraspecific competition, and population density (Covich 1976) might influence the size of home range areas.

Martel and Green (1987) suggested that some degree of female choice exists in Tautogolabrus adspersus's mating system, but it could not be clearly separated from male-male competition. Minor and Crossman (1978) found muskellunge females moved over greater areas during the spawning season and they were observed to spawn in several areas. It was suggested that this might result from a polygynous mating system whereby females sequentially search for and attempt to mate with several males. Gibson (1986) suggested that selectivity imposes an energetic cost as well as being time-consuming and possibly increases vulnerability to predators.

Since no territorial females were tracked during the present study, no females were restricted to a few square meters of a male's territory during the spawning season (Pottle and Green 1979a; Pottle and Green 1979b). If females exhibit choice in their selection of mates, this presumably involves movement from one territory to another in search of potential mates, resulting in an increase in range of female movements. Based on an average size of 40-45 m^2 for male territories in Broad Cove (Pottle and Green 1979a; Martel and Green 1987), a single female would be expected to encounter between 30-45 territorial males in its home range. While females were found to occupy the largest home range areas during June and July, no significant difference was found between the spawning and prespawning period in the home range size of the single female tracked during both periods.

Furthermore, if female assessment does involve an increase in movement, females might be expected to cover larger areas during the afternoon when spawning occurs. While females did occupy larger home ranges in the afternoon during the spawning season, this was true for all tracking periods, not just the spawning season.

Thus at least two factors may be governing the greater range of female movements observed during June and July (i.e. food acquisition and searching for potential mates), but energy acquisition is probably the most important.

During August and September females occupied the smallest home range areas and spent a considerable amount of time inactive. Since spawning is complete, energy requirements may be lower so females do not have to spend as much time foraging or forage over as large an area in obtaining food resources. However, it may be, as stated above, that an increase in food abundance combined with high water temperatures at this time may enable females to consume the same amount of energy, or more, by foraging over a shorter time period in a smaller area.

The increase in size of home range areas during October and November may be related to decreasing food abundance or to females searching for potential overwintering sites. Females occupied approximately the same size core areas during October and November as they did during August and September, so the increased range of movement (i.e. home range) would be consistent with females making occasional excursions outside the main activity areas to either assess possible overwintering sites or take advantage of opportunistic feeding situations. Since swimming may not represent a large energetic cost (Brett 1964; Brett and Sutherland 1965; Soofiani and Priede 1985), the increase in swimming activity may not be expensive in terms of energy expenditure. More detailed observations on the behaviour of females will be required to determine the reasons for this increased movement at this time of year.

Cunner exhibited a marked decrease in the duration of their diurnal activity (from 16.5 hours in June-July to 13.5 hours in August-September to 11.0 hours in October-November) as the number of daylight hours decreased. As the seasons progressed, females also spent an increased percentage of their time inactive. During October and November, cunner were active for only 3 hours of the 11.0 hour daylight period (measured as elapsed time between sunrise to sunset) as compared to the 12.5 hours spent active of a possible 16.5 hours during June and July.

Although temperature is an important factor influencing the activity of cunner, seasonal changes in water temperature alone cannot account for this dramatic difference in activity. Mean daily water temperatures during June-July and October-November were approximately the same (8.2°C and 9.2°C, respectively), yet there were significant differences in activity.

If females are energy maximizers, it is not clear why females spend significantly fewer hours of the day active as time progresses. Clearly more field observations need to be made on the activity of female cunner, specifically in terms of their foraging behaviour. It would be important, for example, to know what percentage of the active period is actually spent in foraging-related behaviours. By combining tracking, which provides the specific location of a subject, with direct observations, it should be possible to resolve some of the questions pertaining to changes in female activity and size of home range areas which occur over time.

According to D. Jones (Department of Biology, Memorial University, St. John's, Newfoundland-unpublished data) female cunner continue to acquire energy throughout their entire active period. More information on the energetics of cunner as well as factors affecting energy acquisition is required to gain a fuller understanding of the observed changes in the behaviour of female cunner over time. For many animals there is often a trade-off between growth rate and mortality which might explain some of the seasonal changes in female activity and movement. By spending less time active (i.e. spending a greater percentage of their time under cover) as the seasons progress this could result in a decrease in energy expenditure as well as any associated risks of predation during a time when little is gained through increased foraging in terms of future reproductive success.

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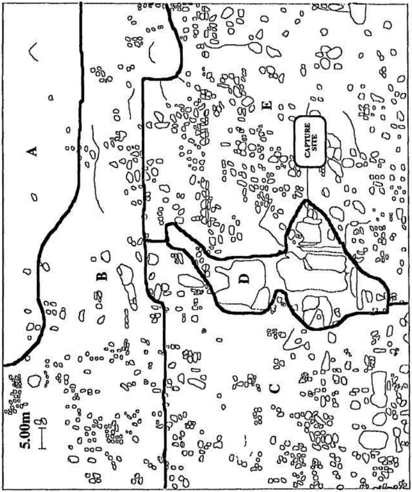
APPENDIX

Appendix A Hydrophone array showing 5 major subdivisions based on predominant substrate types. (For a description of substrate types refer to Appendix B).


A
B
C
D
E
CAPTURE SITE
5.00m

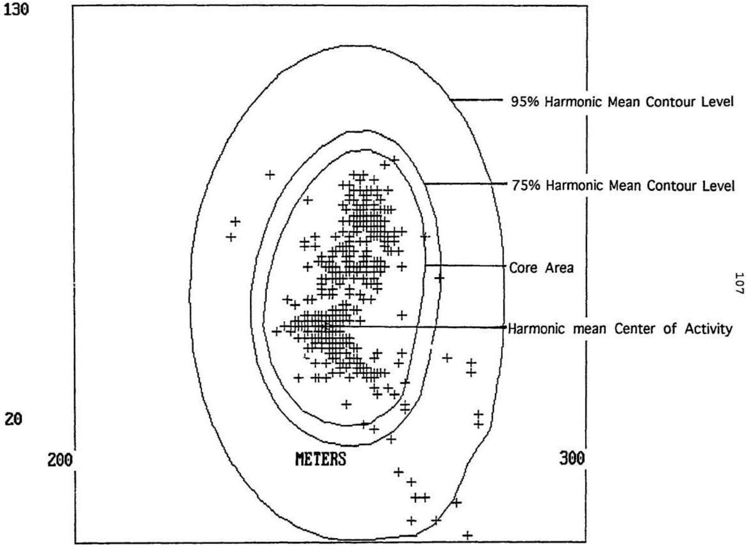
Appendix B Description of bottom substrate types within the hydrophone array in Conception Bay, Newfoundland. Definitions were obtained from Hunt and Grooves 1965; Tver 1979. (Relative proportions of substrate types contained in the 5 major subdivisions are included).

	Bottom Substrate Type	Description	Total Area Enclosed (m^2)	Percentage of Array Covered
A	Sand	85% sand 15% mixture of sand, cobble, boulder, and outcrop	1400	12
B	Mixed	23% boulder and outcrop 14% sand and boulder 13% sand and outcrop 50% mixture of all bottom types	3100	26
C	Boulder/Outcrop I	80% boulder and outcrop 20% outcrop combinations	3100	26
D	Rock Outcrop	100% outcrop	600	5
E	Boulder/Outcrop II	90% boulder and outcrop 10% outcrop combinations	3800	31

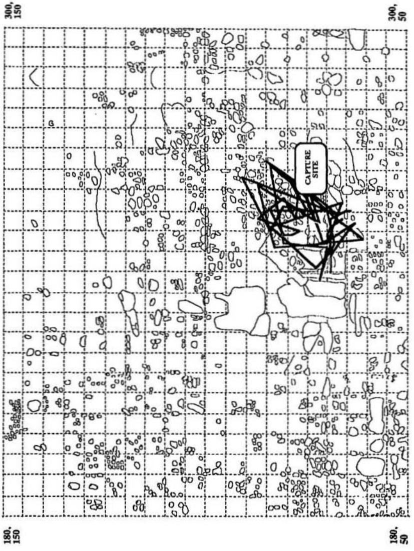
NOTE:

Sand - Loose materials consisting of grains ranging between 0.0625 and 2.0000 mm in diameter.
Cobble - Rock fragment between 64 and 256 mm in diameter which is rounded or otherwise abraded.
Boulder - Solid rock greater than 256 mm in diameter.
Outcrop - Naturally protruding rock bed or formation mostly covered by outlying material.

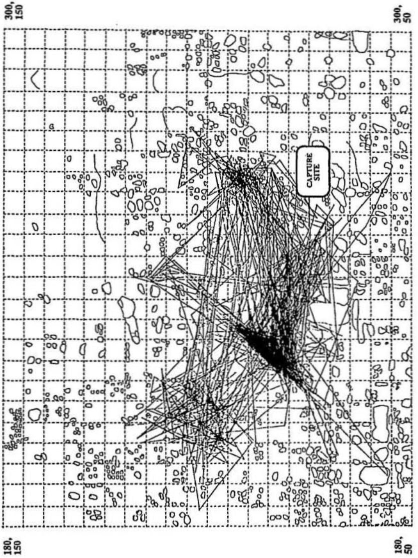
Appendix C Sample illustration of home range calculations carried out by Program Home Range. 95% and 75% harmonic mean contour levels, core areas, and harmonic mean center of activity are depicted.


130
20
200
METERS
300
95% Harmonic Mean Contour Level
75% Harmonic Mean Contour Level
Core Area
Harmonic mean Center of Activity

Appendix D Movements of Fish A taken at 15-minute intervals on June 24, 1991.


300, 150
300, 50
CAPTURE SITE
180, 150
180, 50

Appendix E   Movements of Fish C taken at 15-minute intervals during its entire tracking period from June 28 to July 21, 1991.


300, 150
300, 50
CAPTURE SITE
180, 150
180, 50