Movement patterns of late-stage ovigerous female lobsters (*Homarus americanus* Milne Edwards) at Jeddore, Nova Scotia.

by

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To the fishermen of Jeddore

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ABSTRACT

A total of 217 late-stage ovigerous female lobsters, *Homarus americanus*, were carapace tagged from May 15 to June 20, 1988, and another 14 tagged with ultrasonic transmitters from June 14 to August 12, 1988, in the Jeddore area of the eastern shore of Nova Scotia. Between May 25 and August 7, 1988, 47 of the carapace tagged lobsters were recaptured. Temperature and salinity were monitored in both Jeddore Harbour and Clam Bay throughout the study.

There was little evidence of migration of carapace or sonic tagged lobsters into the harbour from Clam Bay, although homing was observed for at least one sonic tagged lobster translocated into Clam Bay. A computer model of egg development in a variety of annual temperature regimes suggests that there is no physiological advantage for ovigerous females to either locate in the harbour year-round or to migrate seasonally into the harbour. Late-stage ovigerous females demonstrated 'resident' behaviour in areas with suitable lobster habitat (moving rarely, and only short distances), and 'transient' behaviour on featureless sand or gravel bottoms (where greater distances wre covered, and at faster speeds). There appeared to be specific sites where hatching occurred. The activity of ovigerous females increased with egg development. This increase in movement did not appear to be temperature-related. Movement was not correlated with diel or tidal rhythms. It is suggested that most movement probably occurs due to changes in motivation of the animal based on food and shelter requirements and both intra- and interspecific interactions. Hatching was observed between July 19 and August 23, 1988, requiring 4-7 days. Two sonic tagged females molted in the harbour 4-5 weeks after hatching.

The results of this and other recent studies in the Jeddore area suggest that hypotheses that 1) there exists a "longitudinal recruitment cell" on the Atlantic coast of Nova Scotia, and 2) that protected bays are important areas for larval development, may not be true. The harbour does not appear to be an important brood area. The predicted hatching dates of ovigerous female lobsters in both Clam Bay and Jeddore Harbour appear to leave sufficient time for subsequent larval development . The ovigerous females in the harbour contribute less than 20% of the egg production for the area as a whole. It is suggested that lobsters in Jeddore Harbour may be a largely resident population. In the late fall some lobsters probably migrate out of the harbour, returning in the spring or going to another nearshore area. Many, however, probably remain in the harbour over winter.

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INTRODUCTION

Movements of the American lobster (*Homarus americanus* Milne Edwards), like most animals, are not haphazard or random, but oriented to attaining their needs, and are influenced by external and internal factors (Allen 1966). Migrations involve temporally coordinated and spatially oriented movements of a population (or a distinct component of a population) over relatively long distances, during which movement is typically from one environment or habitat to another (Herrnkind 1980). Herrnkind (1980) has reviewed the movement patterns of spiny lobsters, while more general reviews for marine invertebrates are provided by Allen (1966), Enright (1978) and Herrnkind (1983). A brief examination of some examples of migration in the spiny lobsters (Palinuridae) serves to demonstrate some of the variety and proposed functions of migration.

The migrations of certain palinurids appear to play key roles in recruitment success. In northern New Zealand, *Panulirus verreauxi* migrates against the current to maintain a recruitment cell (Booth 1986). *P. ornatus* adults migrate eastward from the Torres Strait across the Gulf of Papua to spawn so that the larvae will be carried to a juvenile nursery area, after which the juveniles migrate from a nursery area to adult grounds (Moore and MacFarlane 1984). Juvenile *P. cygnus* off western Australia migrate from shallow inshore nursery grounds to deeper water 30-50 km offshore (George 1958, Chittleborough 1970, Morgan 1974). *P. argus* on the Great Bahama Bank migrates from inshore settling areas to areas of soft substrate or reefs where they adopt a "nomadic" life style (Herrnkind 1980).

Migrations may occur for other reasons as well. Throughout its geographical range, adult and late stage juvenile *P. argus* undergo an annual mass migration in single file queues, from the reef shallows to the edge of oceanic channels (Herrnkind 1969, 1970, Herrnkind and McLean 1971). The queuing behaviour and subsequent movement appears to be triggered by abrupt drops in water temperature associated with severe autumnal storms (Herrnkind 1970, Herrnkind and Kanciruk 1978, Kanciruk and Herrnkind 1978).

The migration may serve to remove the lobsters from shallows when the bottom temperatures can drop into the animals lethal range (Herrnkind and Kanciruk 1978, Herrnkind 1980). Finally, inshore-offshore migrations of *P. interruptus* off southern California were correlated with the appearance and disappearance of thermal stratification (Mitchell *et al* 1969, Engle 1979), but may also be due to availability of forage, suitable habitat, and strong surge in shallow waters during winter (Mitchell *et al* 1969).

In contrast with certain species of spiny lobsters, migration by *Homarus americanus* is poorly understood. Inshore lobsters are generally non-migratory, typically moving less than 10-20 km between release and recapture (Templeman 1935, 1940a, Wilder 1954, 1963, Wilder and Murray 1956, 1958, Cooper 1970, Morrissey 1971, Fogarty *et al* 1980, Krouse 1980, 1981, Campbell 1982, Ennis 1983, Maynard and Chiasson 1986a, 1986b, Maynard *et al* 1988, Duggan and Pringle 1988). Some studies have demonstrated seasonal migrations of inshore lobsters into deep water in the autumn and back to shallow water during the spring (Corriveault and Tremblay 1948, Bergeron 1967, Lund 1979), while other studies have demonstrated a lack of seasonal migration (Wilder 1954, Wilder and Murray 1956, 1958). Cooper *et al* (1975) and Ennis (1983, 1984) suggested inshore lobsters movement to deeper water was in response to storm turbulence. They did not equate this movement with a seasonal onshore-offshore migration involving significant horizontal displacement. Seasonal migration by Magdalen Island lobsters was reported by Munro and Therriault (1983). Here, they moved into the shallow lagoons between mid-May and the end of June and then back out to the exposed coast in October.

Seasonal deep-shallow migrations have also been observed for lobsters in the Bay of Fundy (Campbell and Stasko 1986), for ovigerous females off Grand Manan Island (Campbell 1986) and for offshore lobsters on the continental shelf (Cooper and Uzmann 1971, Uzmann *et al* 1977, Lund 1979, Fogarty *et al* 1980, Campbell *et al* 1984, Pezzack and Duggan 1986). These migrations are thought to be maximizing the temperature and

thus the rate of molting, growth, gonadal development, and egg extrusion and development (Cooper and Uzmann 1971, 1980, Uzmann *et al* 1977, Lund 1979, Munro and Therriault 1983, Campbell 1986, Campbell and Stasko 1986).

Clearly, seasonal migration has evolved to place the lobsters in a habitat in which various biological functions will be optimized. In addition, movement patterns can vary between different geographic populations and life stages of the same species (*e.g. P. argus* (Herrnkind 1980) and *H. americanus*(see above)).

Herrnkind (1980) provides an excellent review of the methods used to study movement of palinurids, many of which could be applied to the study of *Homarus americanus*. These include monitoring trends in the commercial catch distribution, tag-recapture programs, direct *in situ* observation by divers and submersibles, ultrasonic telemetry, and laboratory experimentation correlating aspects of behaviour with ecologically significant state variables. Ultrasonic telemetry has been used to study the local movement patterns of *Panulirus argus* in the Caribbean (Clifton *et al* 1970, Herrnkind and McLean 1971, Herrnkind *et al* 1975), *P. cygnus* in Western Australia (Ramm 1980, Phillips *et al* 1984, Jernakoff *et al* 1987), and *Homarus americanus* in the Gulf of St. Lawrence (Maynard and Conan 1984). Additional studies on *H. americanus* using highly accurate fixed arrays of hydrophones coordinated by microcomputer are currently under way in Jeddore (Dr. R. O'Dor, Dalhousie University) and in Newfoundland (Dr. J. Green, Memorial University of Newfoundland)

Two studies tested the effect of attached transmitters on lobster behaviour. Maynard and Conan (1984) found that the presence of non-transmitting tags on *Homarus americanus* had no effect on mortality, but resulted in reduced activity in aquaria. However, they also concluded that the presence of transmitting tags did not seem to affect "behaviour". Jernakoff *et al* (1987) concluded that neither the physical presence of the tags nor the electromagnetic signal affected the number of *Panulirus cygnus* sheltering during the day or foraging at night.

In a review of factors influencing the size of lobster stocks along the Atlantic coast of Nova Scotia, Harding *et al* (1983) suggested that "this region represents a 'fringe' zone for the lobster as the surface temperatures are in general too cool and the prey species too large to allow successful recruitment of the larval stages along the open coast". They suggested further that "it appears that larval refuges exist in protected embayments where a strong thermocline can be developed and where the flushing rates are low".

A study on the ecology of eastern Nova Scotia lobsters was initiated in the early 1980's by Department of Fisheries and Oceans personnel. Duggan and Pringle (1988) found a high incidence of ovigerous females inside the large protected harbour of Jeddore (about 80 km east of Halifax) in 1986-87. They speculated that the harbour may be an important area for both hatching and egg development. Given the continued lobster fishery on the Eastern Shore (Miller *et al* 1987) and an apparent lack of long distance migration (Duggan and Pringle op. cit., also see above), it is likely that successful larval recruitment occurs along this shore. Adult lobsters (or ovigerous females in particular) may have evolved local movement patterns which result in accelerated egg development and/or enhanced larval survival. Local fishermen begin catching lobsters by trap at the start of the season (April 20) in about 40 m depth off Jeddore. They gradually move their traps shoreward until by the end of May, the traps are in shallow water (<10 m) against the shore and over rocky shoals. Many fishermen believe that this progressive change in apparent location of lobsters is due to a spring inshore migration. However, Wilder and Murray (1958) showed that similar trends in the fishery at Port Maitland N.S. were due to the removal of legal-sized lobsters from the shallow areas during the previous season and to warmer temperatures in the deeper waters in early spring.

This study is intended to contribute to our understanding of the ecology and behaviour of late-stage ovigerous female lobsters (*Homarus americanus*). These are female lobsters carrying developing eggs under the ventral surface of the tail (also referred to as "berried"), eggs which are due to hatch within a few months. Specifically, the study was

designed to test the hypothesis that late-stage ovigerous females undertake directed movement from the nearshore coastal zone into the warmer waters of Jeddore Harbour. Ovigerous females were tagged with carapace tags during the spring fishing season and tracked using ultrasonic transmitters after the season. Egg development of all lobsters was monitored throughout the study. Finally, movement is examined in relation to a number of environmental and physiological parameters.

DESCRIPTION OF THE STUDY SITE

The study site was located at Jeddore (44°45'N, 63°00'W) on the Atlantic coast of Nova Scotia, about 80 km east of Halifax (Fig. 1). It consists of an enclosed harbour (Jeddore Harbour, hereafter referred to as 'the harbour') and a coastal area outside the harbour, Clam Bay (Fig. 2). A long narrow channel separates the two arms of the harbour from Clam Bay.

The harbour is about 13 km^2, typical of the many estuaries and harbours along this coast (see Fig. 1). The tides are semi-diurnal with a mean range of 1.5 m. The flushing time of the harbour was estimated at 4.4 tide cycles, or about every 55 hours (DiBacco 1989). The harbour basin bifurcates into two arms, the Eastern Arm and the Western Arm, and is largely characterized by a gently sloping mud-silt bottom 5-10 m deep. There are several extensive mussel (*Mytilus edulis*) and eelgrass (*Zostera marina*) flats inside the harbour which may be exposed at low tide. Lobsters are fished inside the harbour, particularly in the Eastern Arm near reefs along the shoreline. These reefs often have kelp (*Laminaria* spp.) and sea anemones (*Metridium senile*) attached.

The shore of Clam Bay is generally rocky except for stretches of mud and sand with eelgrass or cordgrass (*Spartina alterniflora*) in some shallow inlets. The bottom is typically boulders or bedrock with a dense cover of kelp, interspersed with large expanses of sand (Moore and Miller 1983). *Laminaria longicruris*, *L. digitata*, *Saccorhiza dermatodea*, *Alaria esculenta*, *Agarum cribosum*, *Desmarestia viridis*, and several species of filamentous algae are common. Lobsters shelter under rocks or in cracks and crevices in the bedrock. The Clam Bay area supports a moderate lobster fishery for this coast, with about 20 licensed boats from the communities of East and West Jeddore. The bottom slopes gradually to the Scotian Shelf, levelling off at about 150 m some 60 km offshore. Lobsters are not fished commercially from the inshore grounds to the edge of the continental shelf (Pezzack 1984)

The harbour channel is about 4 km long, 1 km wide, and 10-20 m deep. The walls of the channel are frequently steep (30-50 degrees of slope) and formed of clay and rocks. Numerous burrows in the clay serve as shelters for crabs and lobsters. The habitat appears similar to the "Pueblo Village" habitat described by Cooper and Uzmann (1980) in the submarine canyons of Georges Bank. Similar habitat has been observed in Malpeque Bay, P.E.I. (D. R. Maynard, pers. comm.). Water from the two arms of the harbour feeds into the channel near Brown Island, and from the harbour basin through several breaks in the mussel/eelgrass flats on either side. The principal hydrographic feature of the channel is the strong tidal flow (up to 2-3 knots).

The other area studied, though less rigorously, was seaward of Musquodoboit Harbour (Fig. 3). Musquodoboit was included in one aspect of this study because the fishermen there were eager to participate. Here, lobsters are trapped in a variety of inshore habitats similar to Clam Bay and Jeddore Harbour.

METHODS

221 ovigerous females were sampled during the second half of the lobster fishing season, from May 15 to June 20, 1988. Sampling was conducted from a 6 m enclosed runabout. Lobster fishermen would call by VHF radio when an ovigerous female was captured during their normal fishing activities. The fisherman would pass the ovigerous female to the study personnel, and inform us of the capture location (Loran coordinates), depth, and time-out-of-water. On days we could not be contacted, fishermen with ovigerous females would replace the lobster in the trap until we were available (generally only 1-2 d).

Carapace length, date and location of capture, approximate size of the egg mass (guaged crudely by visual estimate as 0-100% of expected egg mass), depth of capture, and time-out-of-water, and a sample of 15-30 eggs removed. Numbered carapace tags (*sensu* Wilder 1954, Stasko 1980) were applied to 217 of the sampled lobsters [1]. Each lobster was returned to the bottom as close to the capture location as possible using a weighted bucket with a tripline.

A charter was conducted after the fishing season, from July 28 to August 9. One hundred traps were hauled every second day, 40 in Clam Bay and 60 in the harbour. Thirty-six females were caught which were either egg-carrying or had remnants of their egg mass (empty egg cases still attached to setae following larval hatch).

The carapace lengths of 220 ovigerous females sampled during the fishing season and 33 ovigerous females sampled during the charter, were compared between two sample areas (Jeddore Harbour and Clam Bay) and two sampling periods (May/June and July/August) using two-way ANOVA (Sokal and Rohlf 1981).

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[1] Carapace tags were used instead of sphyrion tags (retained through the molt) because of concerns expressed by fishermen about possible mortality to berried females by the sphyrion tagging process.

Movement

Some lobsters tagged during the fishing season were recaptured by fishermen during subsequent weeks of the fishery and during the July charter. When a fisherman recovered a tagged lobster the tag number and Loran coordinates of the recapture location and depth were recorded. A $5 reward was paid to the fisherman for this information. When no Loran coordinates were provided, the recapture location was estimated based on a description of the location and depth. When recaptured lobsters were made available to study personnel, another egg sample was taken.

Beginning June 14, fourteen ovigerous females were fitted with ultrasonic transmitters. Two transmitter models were used, both made by Vemco Ltd. (3895 Shad Bay Rd., R.R.#4 Armdale, Halifax Co., N.S., B3L 4J4, (902) 852-3047): model V3-4HI (65 mm long, 16 mm diameter, 25 g, with a battery life of about 64 d; serial numbers were 6776-6785), and a smaller model with a battery life of over 85 d (serial numbers were 5510-5515). Each transmitter transmitted on one of 5 frequencies (50.00-76.80 kHz) and at one of 2 signal repetition rates (54 or 60 pulses per minute), allowing ten unique combinations of frequency and rate. The transmitter was attached to the dorsal midline of the lobster's carapace with 5-minute epoxy. A cable tie ensured that the transmitter would remain with the lobster if the glue came unstuck (see Figures 4 and 5). A number of these lobsters were held in 1m x 0.7m x 0.5m holding cages near their capture location for periods of up to 12 d when transmitters were not immediately available. Other transmitters (smaller model) were used for 1-3 weeks on three ovigerous females before their assigned transmitters (#6781, #6783, and #6784) were ready for use. Sonic tagged females are identified by the serial number of the transmitter.

Once tagged, the lobsters were released near the site of original capture. They were tracked on a regular basis using a directional vessel-based ultrasonic receiver. The boat was positioned as close as possible to the source of the signal, and the Loran coordinates

recorded. In addition to location, the time, depth, and bottom temperature (taken with a Vemco digital locking thermometer, hereafter referred to as ambient temperature) were recorded.

The accuracy of Loran for positioning the lobsters was estimated by comparing the Loran coordinates of lobsters which were known to be stationary (based on diver observation). None of the Loran coordinates varied from one day to the next by more than 0.2 microseconds for the first Loran coordinate, or by more than than 0.3 microseconds for the second Loran coordinate. The resulting region of uncertainty was an ellipse of about 108 m in the North-South direction and 101 m in the East-West direction (roughly ± 50 m in any direction). This conservative approach avoided consideration of movements which may never have occurred.

Every 1-2 weeks (less frequently at first), each sonic tagged lobster was observed underwater. It was located by a diver-held underwater receiver (Vemco model VUR-455, see Fig. 6). The egg mass was observed for evidence of hatching, and an egg sample removed (Fig. 7). The carapace of females whose eggs had hatched was checked for softness (a sign of approaching ecdysis). In addition, general observations were made on the habitat, including topography, flora, and the presence of other lobsters. The lobster was brought to the surface in most cases only when the transmitter required maintenance. These periodic observations confirmed that the location of the lobster on the bottom was usually within about 20 m of the location determined with the boat-based receiver.

Three extended periods (≥ 24 hours) of tracking were conducted (June 21-23, July 13-14, and July 30-31, 1988) during which the lobsters were tracked at least once every 6 h.

Lobsters were tracked in both the harbour (n=5) and Clam Bay (n=4). If the hypothesized movement of ovigerous females into the harbour occured, then the lobsters in the harbour should remain there while those in Clam Bay would be observed migrating into the harbour. In addition, lobsters were translocated from inside the harbour to Clam Bay

(n=2) and from Clam Bay to inside the harbour (n=3). Given the hypothesized migration of ovigerous females into the harbour, the lobsters translocated into the harbour would be expected to remain there while those translocated from the harbour to Clam Bay would move back into the harbour.

Signals were occasionally lost due to battery or transmitter malfunction, or lobster movement. The signals from 9 of the 14 ovigerous females tracked were lost at least once and later rediscovered. The average and standard deviation of the duration of loss was 12.2 (± 13.8) days. Seven were permanently lost before the predicted end of the battery life. Considerable time was spent searching for lost signals, using an omni-directional hydrophone along a grid search pattern defined by increments in Loran coordinates.

Distance and direction travelled during each interval between release and recapture or between two consecutive locations were determined with the aid of enlarged Loran C charts. Distances travelled were converted into a rate ($m \cdot day^{-1}$), log transformed, and called "activity". No statistical analysis was carried out on the direction of movement because the vector analysis of movement (*e.g.* circular statistics) requires assumptions about topographical constraints, particularly for small-scale movements, and the distribution of fishing effort (in the case of tag returns).

Egg development

Egg samples were taken from 201 ovigerous females during the lobster fishing season and from 17 others captured during the charter. Egg samples were also taken periodically from the 14 sonic tagged ovigerous females. The samples were taken using the methodology of Perkins (1972). Five to ten eggs were taken from 3 different regions of the ventral periphery of the egg mass using forceps and put in a vial. Early in the study, samples were preserved in a 5% solution of formaldehyde buffered with sodium borate. These eggs were often difficult to stage. As a result, all egg samples taken after May 31 were put in seawater and either staged the same day or refrigerated and staged within 2

days.

Five eggs were haphazardly selected from each sample. The width and length of the embryonic eye was measured using a dissecting microscope equipped with an ocular scale calibrated with a micrometer (10 *u*m gradations). The mean axis length of each eye was calculated. The grand mean for the five eggs is the Perkins Eye Index (PEI) value for that sample. All eggs were preserved in the buffered formaldehyde solution following staging.

A number of suspect eye index values were obtained (*i.e.* an ovigerous female recaptured after one month at large with an eye index value substantially smaller at recapture than at release). As a result, all samples were re-staged. The initial value was rejected when it was clearly in error. However, when there was no clear difference between the two values, the initial value was retained.

A number of tests were carried out on the egg staging methodology. These are reported on in detail in Appendix A.

Egg development was compared between two locations (in the harbour and Clam Bay) and three periods of capture (May 31-June 4, June 6-11, and June 13-20) using two-way ANOVA (Sokal and Rohlf 1981). The egg development data of ovigerous females from Musquodoboit, and those sampled during the charter, were not analysed because of small sample sizes.

The estimated hatching date for each of the ovigerous females sampled during the fishing season was predicted using state variables described below. The predicted hatching date was interpreted as the mean date on which hatching was predicted to occur. The empirical model of Perkins (op. cit.) was used to estimate the daily increment in the eye index from the date the sample was taken.

$$X = \frac{-8.3151+2.6019(T)}{7} \qquad (1)$$

where X= increase in eye index ($\mu m \cdot day^{-1}$)

and T= ambient water temperature (°C)

Daily water temperatures from the Eastern Arm thermograph and Big Head thermographs were used for ovigerous females from the harbour and Clam Bay respectively. Hatching was predicted to occur when the eye index reached 560 μm (Perkins op. cit.).

A computer model was constructed to simulate egg development between extrusion and hatching at a variety of ambient temperatures. Details of model development and the results are presented in Appendix B.

Temperature, salinity, and secchi depth measurements

Three fixed hydrographic stations were maintained from May 15 to the end of September (see Fig. 2). Each station was visited at least 3-4 times per week, and the following data collected: time, depth, surface and bottom temperatures, and surface and bottom salinities (using a Nansen bottle to obtain the bottom salinity sample). Salinities were analysed by the Marine Chemistry Division, BIO, using a Gyldline Autosal model 8400 salinometer. Secchi depths were measured periodically at the Clam Bay and Eastern Arm hydro stations. Five thermographs (Ryan Peabody model J180) were deployed as shown in Fig. 2. The location and dates on which the thermographs were deployed and recovered are listed in Table 1. The thermograph near Old Man Rock could not be located at the end of the study.

During the three extended sampling periods (June 21-23, July 13-14, and July 30-31, 1988), salinity and temperature were recorded at each hydro station at high, middle, and low tides for at least two tidal cycles.

Analysis of movement by sonic tagged lobsters

All intervals were combined for the analysis of movement patterns. An interval is defined as the period of time between two consecutive positionings (using the surface-based receiver to obtain Loran coordinates for the lobster). During each interval, distance and direction moved was measured, and a number of quantitative variables (temperature and salinity) and non-quantitative variables (location, translocation, and egg development) and. Intervals were classed as either "active" (those during which the lobster moved) or "inactive" (those during which it did not move).

Data were analysed using a combination of two-way and multi-way contingency tables for the non-quantitative variables, and nonparametric analysis of variance and stepwise multiple linear regression for the quantitative variables (Zar 1974, Legendre and Legendre 1983). Goodness of fit was tested by X^2 or using the log likelihood ratio (G test) for cases with low probabilities (Zar 1974, Legendre and Legendre 1983). Yates correction for continuity was used when testing 2×2 contingency tables.

a) Non-quantitative variables

Handling of lobsters prior to an interval was noted. Handling included any exposure of the lobster to the experimenters. The log likelihood ratio (G test) was used to test for differences in the proportion of active intervals following handling and non-handling (control intervals).

Analysis of the combined movement data (intervals) was carried out to determine if the proportion of active intervals differed between individual lobsters, between locations (the harbour and Clam Bay), between translocated and indigenous (non-translocated) lobsters, or between ovigerous females with different stages of egg development. Among the four non-quantitative variables examined (lobster, location, translocation, and egg development) it was not possible to set up a four-way contingency table due to the small resulting group sizes. As a result, variables were treated singly or in groups of two or

three. First, differences in the proportion of active intervals between lobsters were tested using the log likelihood ratio. Secondly, a 2 x 3 x 2 contingency table was used to test for differences in the proportion of active intervals between two locations (the harbour and Clam Bay) and three stages of egg development (3.0-4.0, 4.0-5.0, and 5.0-6.0, see Table 2). Only non-translocated lobsters were used. Thirdly, differences in the proportion of active intervals between the two locations and whether or not the lobster was translocated were tested with a 2 x 2 x 2 contingency table. In each case where the goodness-of-fit test result for a multi-way table was significant, the factors were tested individually to determine the source of the difference.

b) Quantitative variables

Salinity was estimated for the start and end of each interval by interpolating linearly between the observed salinities nearest in time and location. The salinity value for the interval was taken as the average of the two. Salinities were not assigned to intervals if the sample was taken more than one day before or after the interval. Secchi values were similarly determined for each interval.

Ambient temperature (at the start of the interval) and temperature at the nearest thermograph (Eastern Arm or Big Head) were included in the analysis because they reflect different temperature regimes. The temperature at the thermograph is more a measure of general temperature trends in the study area, and was independent of changes in lobster location.

Differences in temperature and salinity between active and inactive intervals were tested using a Mann-Whitney U test.

Next, relationships between the magnitude of activity ($m \cdot day^{-1}$, transformed and untransformed) during the active intervals and five quantitative variables (day, depth, ambient temperature, temperature at the thermograph, and salinity) were examined with stepwise linear regression.

Changes in activity from one interval to the next were compared with the corresponding changes in salinity and temperature and tested for goodness of fit. This made it possible, for example, to examine whether temperature increase was accompanied by an increase in activity. All intervals were grouped according to the change in activity. These changes could be positive (an increase in activity), negative (a decrease in activity), or zero (no change in activity). Each of the three variables (ambient temperature, temperature at the thermograph, and salinity) were tested independently for goodness-of-fit because of insufficient data for construction of a multi-way contingency table.

c) Activity rhythms

Activity rhythms were examined for intervals which occurred entirely during one part of the day (*i.e.* at sunset, sunrise, entirely at night, or entirely during the day), and the proportion of active intervals in each group tested for goodness of fit. Times of sunset and sunrise were obtained from the Environmental Atmospheric Service (Mr. J. F. Amireault, Climatological Services, Atmospheric Environment Services, Environment Canada, (902) 426-9226) for days on which there were short intervals (primarily the three periods of extended tracking).

Hourly tide heights were obtained for Salmon River Bridge (located at the head of the Eastern Arm) from the Tides Section of the Canadian Hydrographic Service (Mr. C. O'Reilly, Tidal Officer, Canadian Hydrographic Service, Bedford Institute of Oceanography, (902) 426-3846). Intervals occurring entirely during a single flood or ebb tide were examined for tidal activity rhythms. Activity was plotted against mean tide height during intervals (to identify any differences in activity between high and low tides) and against the change in tide height during intervals (to identify any differences in activity between flood and ebb tides).

Trap catch of ovigerous females in the study area

An estimate of the catch per trap haul (CPTH) of ovigerous females in the harbour and in Clam Bay was carried out during the last three weeks of the fishing season. Three volunteer fishermen kept records of the number of traps hauled and the incidence of ovigerous females captured in both locations. In addition, three at-sea sampling trips were carried out on board commercial lobster boats during May. Both CPTH and the proportion of ovigerous females in the catch from different fishing grounds were obtained. Finally, CPTH and the proportion of ovigerous females in the catch were recorded during the fishing charter (July 28-August 9, 1988).

RESULTS

Temperature traces from the four thermographs are shown in Fig. 8. Bottom temperatures at the three thermograph locations outside the harbour (harbour mouth, Big Head, and Cat Rocks) were similar. Trends in the temperature at these three locations tended to occur several days before the corresponding trends inside the harbour. Temperature, salinity, and secchi data from the 3 hydro stations are presented in Appendix C.

Movement

Of the 217 carapace tagged ovigerous females, 47 (21.7%) were recaptured during the subsequent weeks of the fishing season (until June 20) or during the charter (July 28-August 9). Of these, 42 (90%) were recaptured once, 4 (8.5%) twice, and 1 (2.1%) four times. The recovery rate of tagged ovigerous females in the harbour was 40.5% (15 of 37 tagged), but only 18.1% (27 of 149 tagged) in Clam Bay. In the Musquodoboit area, 12.9% of the ovigerous females tagged (4 of 31 tagged) were recaptured. Further analysis of data from the latter site was not carried out because the lobsters were frequently released away from the capture location. One tagged lobster, released off the mouth of Jeddore Harbour, was recaptured one year later (on June 12, 1989) off the mouth of Musquodoboit Harbour. The documented movement of carapace tagged lobsters in Clam Bay is shown in Fig. 9.

The probability of recapture varied directly with the amount of time the lobster was kept out of water when it was tagged. The mean and standard deviation of the exposure time for recaptured ovigerous females was 33.4 ($\pm$ 30.5) min, and for ovigerous females not subsequently recaptured, 48.8 ($\pm$ 42.2) min. This difference was determined to be significant using the normal approximation to the Mann-Whitney U test ($z=1.68$, $p=.0465$, Zar 1974).

The mean and standard deviation of the time at large was 21.2 days (± 18.6, n=17) in Jeddore Harbour, 22.2 days (± 17.1, n=32) in Clam Bay, and 12.3 days (± 2.1, n=4) in the Musquodoboit area. There was no observed movement of ovigerous females between the different tagging areas during 1988. The mean and standard deviation of the distance travelled in Clam Bay was 1.2 (± 2.0) km. The only apparent movement pattern by carapace tagged lobsters was based on release location. Movement patterns tended to be local around known lobster grounds off Jeddore Cape, Black Pt., Cat Rocks, Sleepy Head, and the islands and reefs in Clam Bay (Fig. 9). Lobsters released in the area immediately south of the harbour mouth tended to travel further. One ovigerous female released in Clam Bay had moved about halfway into the channel. There was no indication of whether she was still ovigerous when recaptured.

Plots of the movement of 12 of the 14 sonic tagged ovigerous females tracked are shown in Figures 10-13). The size, location, and tracking record of the sonic tagged ovigerous females are listed in Table 2. Detailed descriptions of the movement of the sonic tagged ovigerous females are given in Appendix D. The signals from two of the females (#5513 and #6779) released in the Eastern Arm were lost before any movement was observed. Transmitter malfunction is suspected for #5513.

Three of the sonic tagged lobsters released in Jeddore Harbour moved from their release sites on Dry Ledge (#5515 and #6784) and Rocky Is. (#5510) into the harbour channel (Fig. 10). Once in the harbour channel, #5515 and #6784 both hatched their eggs and then molted. Molting took place during September, roughly 5 weeks after egg hatch. Evidence of molting was the recovery of transmitters with the mount and cable tie still intact, and pieces of cast exoskeleton attached to the epoxy mount.

None of the four sonic tagged lobsters released in Clam Bay moved into the harbour, although #6781 and #6785 moved from one side of the harbour mouth to the other (Fig. 11). Lobster #6781 hatched in 10-20 m of water east of Big Head, and then crossed the mouth of the harbour to Black Pt. #6785 was released off Cat Rocks, and

quickly travelled west across the harbour mouth to Big Head, where she hatched. Much of the movement across the harbour entrance by #6785 occurred during the extended tracking study of July 12-13, and a maximum rate of travel of 190 m·hour $^{-1}$ was observed between 0300h and 0600h on July 13. Lobsters #5511 and #6783 moved little throughout the study, with the exception of a movement of about one kilometre by #5511 after she was brought to the surface on July 9 and a claw accidentally automized.

One of the two lobsters translocated from the harbour to Clam Bay (#6777) returned to the harbour before hatching (Fig. 12). She was about six weeks from hatching (eye index of 373 *u*m) when translocated, and was released near the harbour mouth. The other (#6782) was only three and a half weeks from hatching (eye index of 457 *u*m) when translocated, and was released further from the mouth of the harbour than #6777. She hatched in Clam Bay and then moved near the harbour mouth.

Two of the three lobsters translocated from Clam Bay to the harbour (#6776 and #6780) were lost shortly after being translocated, just before their predicted time of hatching. The third lobster (#6778) moved from Dry Ledge into the harbour channel after translocation, where she hatched her eggs (Fig. 13).

The dates and duration of hatching for sonic tagged ovigerous females are summarized in Table 3. Hatching was observed between July 19 and August 23, 1988. The time required for the bulk of hatching to occur was 4 days for #6778, and 7 days for both #5515 and #6784. Following hatch, empty egg cases were observed attached to the pleopod setae of six females; the period of attachment was from 2-4 weeks.

About 90 dives were made during which sonic tagged lobsters were observed 65 times. Table 4 lists the frequency of observations of these lobsters in different types of shelters in the three areas (Eastern Arm, the harbour channel, and Clam Bay). In the Eastern Arm, they were most frequently observed in natural hollows or crevices in rocky reefs (Fig. 14). They were observed equally in a variety of habitats in the harbour channel, including clay burrows in the channel slope (Fig. 15) and in shallow depressions or

unsheltered on the bottom of the channel (Fig. 7). In Clam Bay, they were observed primarily in hollows or crevices under rocks with a sand or gravel substrate (Fig. 4), although a number were observed on bedrock substrate (Fig. 16).

Egg development

The percentage of ovigerous females carrying new (extruded during summer 1988) and old (due to hatch during summer 1988) eggs are listed in Table 5. During May/June most ovigerous females caught were carrying old eggs (100% in the harbour, 93% in Clam Bay). This changed through the study as the mature eggs hatched and as other females extruded new eggs. By late July (during the charter), 60% and 29% of the egg-carrying females in the harbour and Clam Bay respectively were carrying new eggs.

The frequency distribution of egg development during the May/June samples are presented for inside the harbour (Figure 17) and outside the harbour (Figure 18). Eye index values ranged between 160 and 560 *u*m in the harbour and between 0 and 560 *u*m outside the harbour. The modal egg development was the same in both locations, 420-440 *u*m. Of interest was the occurrence of females with new eggs (no eye pigment visible) in Clam Bay, but not in the harbour.

The mean eye index did not increase significantly over the 3 week period examined ay either location. There was no significant difference in mean egg development between ovigerous females in the harbour and those in Clam Bay ($F=0.172$, $p=.679$), or between sampling periods ($F=0.208$, $p=.812$) (Table 6).

The frequency distribution of predicted hatching dates for sampled ovigerous females are presented for the harbour (Fig. 19) and Clam Bay (Fig. 20). The mean predicted hatching date for lobsters in the harbour (July 27, standard deviation $\pm$ 28.4 days) occured 11 days before that in Clam Bay (August 7, standard deviation $\pm$ 30.1 days). Females sampled in Clam Bay during May and June with newly extruded eggs were

predicted not to have hatched by October 20 (when the thermographs were removed from the water).

The accuracy of the predicted hatching dates were tested using egg samples from sonic tagged ovigerous females whose hatching dates were known. The predicted hatching dates for 20 egg samples were compared with the hatching dates observed in the field. The period of time between when the egg sample was taken and when hatching was observed averaged 26.6 days (standard deviation ± 22.3 days). Over this interval, the mean difference between predicted and observed hatching dates was 8.4 days (standard deviation ± 5.9 days). The difference between observed and predicted eye index values increased with the length of the interval, but not significantly ($r^2=0.176$, $p>.05$). As a result, it was felt the hatching dates were accurately predicted.

Analysis of movement by sonic tagged lobsters

Intervals longer than 4 days were removed from further consideration prior to analysis of the tracking data since, intuitively, a lobster could be expected to change location regardless of hypothesized causal factors given a long enough interval. Four days was selected as the maximum interval length because it was felt that individual changes in salinity and temperature often occurred over periods of up to four days, and a large enough sample size of intervals was maintained to permit subsequent analyses. A number of the analyses carried out on all intervals (see below) were also carried out on intervals of <12 h with no difference in the results. This left a total of 299 intervals, representing data collected from 13 different lobsters for varying periods between June 14 and September 27, 1988.

a) Non-quantitative variables

The different types of handling recorded are listed in Table 7 along with the incidence of movement (number of active and inactive intervals) for each. The amount of

activity varied significantly between intervals where the lobster was handled and control intervals (G=43.562, p=.000). As a result, 121 intervals during which there was any handling were excluded from further analysis, leaving 178 intervals.

The amount of activity varied among individual sonic tagged lobsters (Table 8). This difference was significant (G=67.073, p=.000) even when those with few observations (#5515, #6779, and #6782) were removed. For all subsequent tests, however, data were combined for all lobsters because there were not enough data to maintain individual identity in the analysis and still identify other activity patterns.

Egg development appeared to have a direct impact on activity: ovigerous females carrying more mature eggs tended to be more active than those with less mature eggs (Table 9). The differences in activity between the three stages of egg development were significant both in the harbour (X^2 =16.42, p=.000) and in Clam Bay (G=10.15, p=.006). Females with stage 3 and 4 eggs (corresponding to eggs with eye index values of 300-399 *u*m and 400-499 *u*m respectively) tended to be equally active in both locations, while those with stage 5 eggs (corresponding to eggs with eye index values of 500 *u*m to hatch) were more active in the harbour than in Clam Bay. The differences in activity between the two locations were not significant for egg stages 3 (G=1.88, p=.170) and 4 (G=0.78, p=.378), but were significant for egg stage 5 (X^2=4.06, p=.044).

Translocated lobsters were generally no more active than indigenous (non-translocated) lobsters (Table 10). The differences in activity were not significant in either location (X^2=0.11, p=.744 in the harbour; G=0.00, p=.964 in Clam Bay). Translocated lobsters were equally active in both locations (G=0.70, p=.402), but indigenous lobsters tended to be significantly more active in the harbour than in Clam Bay (X^2=4.14, p=.042).

b) Quantitative variables

There were no significant differences in temperature or salinity between active and inactive intervals. The Mann-Whitney U test statistic was not significant for temperature at the thermograph (p=.827), ambient temperature (p=.097), or salinity (p=.143).

The distance travelled during active intervals was independent of the quantitative variables examined. No descriptors were brought into a linear model by stepwise multiple regression (alpha-to-enter<=.150) using either transformed or untransformed activity.

Activity tended to increase from one interval to the next when ambient temperature increased during the same period, and to decrease when ambient temperature decreased (see Table 11). The changes in activity from one interval to the next were significantly related to changes in ambient water temperature (G=15.69, p=.015), but not to changes in temperature at the thermograph (G=8.023, p=.236) or salinity (G=2.706, p=.608).

c) Activity rhythms

No diel or tidal rhythms in activity were observed. Activity during all intervals less than 9 h is plotted on a polar plot (Fig. 21). The number of active and inactive intervals in different groups (interval occurring at sunset, sunrise, entirely at night, or entirely during the day) are listed in Table 12. There was no significant difference in the proportion of active intervals between groups (G=2.366, p=.55). Similarly, there was no apparent trend in activity with tide height or with the change in tide height during intervals (see Figures 22 and 23).

Trap catch and carapace length

The mean carapace lengths in three sample areas (Jeddore Harbour, Clam Bay, and Musquodoboit) and during two sampling periods (May/June and July/August) are presented in Table 13. Ovigerous females sampled in the harbour were smaller than those in Clam Bay. The carapace lengths were normally distributed and the variance within each

area/period group similar (see Table 13). The differences in carapace length between the harbour and Clam Bay were significant during both sampling periods (F=9.970, p=.002), but did not differ significantly between sample periods at either location (F=1.173, p=.280).

During the present study, ovigerous females were more abundant in Clam Bay than in the harbour during the May sample, with an apparent switch in relative abundance by the July/August sample. The catch per trap haul (CPTH) of ovigerous females (new and old eggs) rose from 0 in May to 0.10 in July/August in the harbour, and from 0.01 in May to 0.03 in July/August in Clam Bay (Table 14). Over the same period, the proportion of ovigerous females in the trap catch varied between 0 and 0.10 in the harbour, and between 0.01 and 0.04 in Clam Bay (Table 15).

DISCUSSION

The distribution of late-stage ovigerous female lobsters and changes in their distribution through movement are key elements in understanding sources of larval recruitment in lobster populations. Despite this, few studies have directly addressed these issues (see Herrick 1895, Templeman and Tibbo 1945, Morrissey 1971, Campbell 1986). On the eastern Atlantic coast of Nova Scotia, the recent increase in landings from historical lows in the late 1970's (Miller *et al* 1987) suggests that either lobsters are immigrating into this region as juveniles (since most recruits into the fishery are juveniles) or successful larval recruitment is occurring. Knowledge of the movement patterns of inshore lobsters suggests the former scenario is unlikely. However, a lack of knowledge regarding both the larval distribution and the source of brood stock render attempts to describe sources of larval recruitment highly speculative. Factors on the eastern shore which may adversely affect larval survival include low summer surface temperatures (Robinson 1979, Harding *et al* 1983, but see Moore *et al* 1986), a prey spectrum too large for larval lobsters (Harding *et al* 1983), and Ekman transport of surface waters offshore due to prevailing longshore (southwest) winds (Robinson 1979). In addition, Dadswell (1979) suggested that the closure of the Strait of Canso in 1954 changed local circulation patterns and caused recruitment mechanisms to fail along the eastern shore.

Evidence against two proposed recruitment mechanisms

Dadswell (1979) hypothesized that a "longitudinal recruitment cell" exists along the Atlantic coast of mainland Nova Scotia. He suggested that there is a continual stepwise movement of lobsters in an upstream direction (against the southwesterly-flowing Scotian Current) during annual seasonal onshore-offshore migrations. Alternately, he suggested a rapid upstream movement of ovigerous females. In either case, the migration was followed by downstream larval drift. Harding *et al* (1983) suggested that larval refuges exist in

protected embayments where there is a strong thermocline and where flushing rates are low. Both hypotheses may be critically examined in light of evidence gathered in this and other recent lobster studies on the Atlantic coast of Nova Scotia.

There is little evidence of the lobster movement on the Atlantic coast of Nova Scotia predicted by Dadswell (1979). The main piece of evidence supporting seasonal inshore-offshore lobster migration in the Jeddore area is the progressive change reported by fishermen in the location of lobsters caught during the fishery. The CPTH data gathered in this study are not relevant in the context of seasonal migration as described by Dadswell (1979), however, since his hypothesis says nothing about migration into embayments. The progressive change in apparent location of lobsters during the fishery may reflect real movement of lobsters into shallower water as temperatures increase, or simply changes in relative abundance and activity of lobsters (*e.g.* Wilder and Murray 1958). However, a recent tagging study in the Jeddore area failed to demonstrate a "continual stepwise movement in an upstream direction" of lobsters released during October 1986 and recaptured during May-June 1987 (Duggan and Pringle 1988). Finally, the present study provides evidence that late-stage ovigerous females do not undertake rapid upstream migration prior to egg hatch. In a study cited by Dadswell (1979), Morrissey (1971) released 232 tagged late-stage ovigerous females July 29-August 1, 1965, off Cape Cod, Mass.. The 38 lobsters recovered had moved an average of 28.2 km during an average time-at-large of 39 days. Since late-stage ovigerous female lobsters in Jeddore were carapace tagged starting May 18 and sonic tagged starting June 14, it seems unlikely that directed movement similar to that observed by Morrissey (1971) would go undetected.

Harding *et al* 's(1983) hypothesized function of protected embayments along the Atlantic coast of Nova Scotia as larval refuges applied only to harbours with low flushing rates. The flushing rate of the Jeddore harbour, once every 55 hours (DiBacco 1989), is sufficiently rapid that newly hatched larvae are probably carried out of the harbour quickly. Tidally coordinated vertical migration by stage I larvae may result in larvae remaining in the

harbour longer (*e.g.* postlarvae of the penaeid shrimp *Penaeus duorarum*, see Creutzberg 1975 for other examples). However, DiBacco (1989) did not find any stage II, III, or IV larvae in the harbour, suggesting that perhaps they have been carried out of the harbour into Clam Bay by the time of their first molt. Since Jeddore Harbour is typical in size of many of the bays and harbours along the eastern shore of Nova Scotia (see Fig. 1), larval refuges probably do not play a significant role in recruitment along this shore.

The role of Jeddore Harbour as a brood area

Duggan and Pringle (1988) suggested that Jeddore Harbour may be an important local brood area. The role of Jeddore Harbour as a brood area can be estimated by examining differences in the predicted hatching time and larval development between the two locations, as well as the relative abundance and egg production of ovigerous females in the harbour.

Differences between the two locations in the time of hatch and subsequent duration of larval stages appeared minimal. During May and June 1988, the eggs of ovigerous females sampled in the harbour and in Clam Bay were equally developed. The mean predicted hatching date for ovigerous female lobsters sampled in Clam Bay during 1988 was August 7, 11 days after that for ovigerous females sampled in Jeddore Harbour. The mean surface temperature during August at the Clam Bay hydro station was 13.9^{o}C (n=6 samples, see Appendix C). At this temperature, the duration of the first 3 larval stages would then be about 30 days (Templeman 1936, MacKenzie 1987). Since the surface water in Clam Bay remains above 10^{o}C through September, this would provide ample time for the completion of the pelagic stages for larvae hatched in Clam Bay as well as those hatched in the harbour and carried out into Clam Bay.

The relative importance of brood stock in the harbour can also be estimated by comparing the abundances of ovigerous females in the harbour and in Clam Bay. Fishing effort in the harbour is around 200 trap hauls·day^{-1}. The average catch rate of ovigerous

females during the fishing season (April-June) is around 0.03 per trap haul (see Table 14), and the overall exploitation rate (for this section of the eastern shore) is about 0.52 (Miller *et al* 1987). Most fishermen only fish on about 40 of the 61 days of the season (Pringle, pers. comm.). As a result, about 240 ovigerous females are caught in the harbour during the season, from a population of some 460 ovigerous females. The catch rate of all lobsters (males and non-ovigerous females included) in the harbour is around 0.50 per trap haul (see Table 14), so the estimated total lobster population is around 7,690.

Of the 20 licenses in Clam Bay, only about 15 fishermen fish each day, hauling about 200 traps each. The average catch rate of ovigerous females here during the fishing season (April-June) is around 0.0075 per trap haul (see Table 14). During the season, about 900 ovigerous females are caught in Clam Bay, representing a population of some 1,730 ovigerous females.With a catch rate for all lobsters (males and non-ovigerous females included) of around 0.60 per trap haul (see Table 14), the estimated total lobster population in Clam Bay is 148,460.

These results suggest that in the Jeddore Harbour/Clam Bay area, only 5% of the lobsters, but over 20% of the ovigerous females, are in the harbour. This is supported by the relative proportions of ovigerous females observed in the catch (see Table 15). The estimates of population size do not take into account differences in trapability between ovigerous females and other lobsters or potentially greater trapability in the harbour where water temperatures are warmer (McLeese and Wilder 1958), and assume an equal exploitation rate in the two locations. However, the higher return rate of carapace tagged lobsters released in the harbour (40.5% vs. 18.1%) suggests that the exploitation rate is greater there than in Clam Bay. As a result, the estimates of the population sizes and contribution to the total egg production in the harbour are probably overestimates.

Ovigerous females in Clam Bay are larger and therefore carry more eggs than those in the harbour, so the relative egg production of larvae in the harbour is less than the relative abundance of ovigerous females. Thus while the harbour appears to have

proportionally more ovigerous females than Clam Bay, they contribute less than 20% of the total egg production of the area.

Movement of ovigerous female lobsters into Jeddore Harbour

In the present study, there was little evidence of migration by ovigerous female lobsters from Clam Bay into the harbour. With the exception of one ovigerous female released in Clam Bay and recaptured in the harbour channel, none of the carapace tagged lobsters were recaptured outside their release area. Similarly, there was no observed exchange of sonic tagged (non-translocated) ovigerous females between Clam Bay and the harbour. One of the sonic tagged females (#6777) translocated into Clam Bay migrated back into the harbour prior to hatching, and the other (#6782) may have been heading in that direction when the signal was lost, after hatching in Clam Bay. None of the three lobsters translocated into the Harbour were observed migrating back to Clam Bay: two were lost shortly after translocation and before hatching, but the other was translocated three weeks prior to hatching and presumably had ample time to return to Clam Bay to hatch. Taken together, the observed movements of the carapace and sonic tagged lobsters do not support a mass movement of late-stage ovigerous females from Clam Bay into Jeddore Harbour prior to hatch.

The return movement of #6777 into the harbour may be homing behaviour, which has been demonstrated for both translocated *Panulirus argus* (*e.g.* Herrnkind *et al* 1975) and *Homarus americanus* (*e.g.* Saila and Flowers 1968, Lund *et al* 1973, Pezzack and Duggan 1986). The lack of apparent homing movement by #6778 (translocated into the harbour) may represent a delay in homing until after egg hatch. Lobster #6778 was five weeks closer to hatching when translocated than #6777 (*i.e.* 3 weeks vs. 8 weeks). Similar delays in homing have been observed for offshore ovigerous females translocated to inshore locations (Saila and Flowers 1968, D. Pezzack pers. comm.).

Observed trends in CPTH suggest that ovigerous females move into the harbour from Clam Bay between May and August 1988. The CPTH in the harbour was 0 in May and 0.10 in August. In contrast, the CPTH of ovigerous females in Clam Bay was 0.01 in May and 0.03 in August. However, few of the tagged lobsters demonstrated the type of movement suggested by the trends in the CPTH over the same period. Only 40 traps were sampled in the harbour in May (catching only one ovigerous female would have resulted in a CPTH of 0.025), so this apparent discrepancy probably occurs because the May sample in the harbour does not reflect the true occurrence of ovigerous females.

More reliable evidence against the movement of large numbers of ovigerous females into the harbour comes from trends in carapace length in the harbour and in Clam Bay. Ovigerous females were significantly larger in Clam Bay than in Jeddore Harbour [2] . This difference increased from the time of the fishing season to the time of the charter (see Table 13). If ovigerous females were migrating into the harbour, the mean sizes would gradually approach each other.

If lobsters migrate into the harbour in the spring, they must do so before mid-May (when ovigerous females were first carapace tagged as part of this study). However, seasonal movements do not usually take place this early. Campbell (1986) observed the seasonal migration of ovigerous females in June-July from deep to shallow waters off Grand Manan, two months after the shallower water became warmer. The seasonal migration of ovigerous females in the Magdalen Islands into shallow lagoons occurred between mid-May and the end of June, after the water in the lagoon had warmed up and once a gradient of increasing temperature entering the lagoon was established (Munro and Therriault 1983). Finally, published records of year-round temperatures on the Eastern Shore indicate that shallow waters (5-10 m) are warmer than deeper waters (40 m) between

[2] Duggan and Pringle (1988) found that the berried females sampled in the harbour in October 1986 and June 1987 were larger than those sampled in Clam Bay. The reason for the discrepancy between their results and those of this study is unknown.

early May and late October (Drinkwater and Trites 1987, Walker *et al* 1987, Gregory *et al* 1988), but only rise above 3.4°C around the end of May. At this temperature, lobsters are only moderately active (McLeese and Wilder 1958).

Finally, there does not appear to be any physiological need for ovigerous females to migrate into the harbour in the spring. Modelled egg development in a number of thermal regimes (see Appendix B) suggests that development time is similar for eggs inside the harbour (3 m), in Clam Bay (10 m), and for ovigerous females migrating seasonally between 40 m in the winter and 3 m in the summer. This result is supported by the similarity in egg development of lobsters sampled in both locations.

A resident or dynamic lobster population in Jeddore Harbour?

The lack of any observed difference in egg development between ovigerous females sampled in the Clam Bay and Jeddore Harbour during May and June suggests that there is no difference in the extrusion date and development rate between the two locations. The computer model (see Appendix B) supports the similarity in egg development rates at the two locations. Alternately, ovigerous females in Clam Bay and Jeddore Harbour may mix sometime after extruding in the fall and before sampling during the spring and early summer.

Although no movement between different areas was observed in this study, Duggan and Pringle (1988) observed a certain amount of movement between Jeddore Harbour and Clam Bay. Fifteen percent of the 1987 recaptures of lobsters released in Jeddore Harbour were from Clam Bay. More recent returns indicate that some non-ovigerous females released in the harbour in June 1987 were recaptured in Clam Bay in 1988, having molted or extruded (Duggan and Pringle, unpub. data). In addition, several ovigerous females released in Clam Bay in 1987 were recaptured in the harbour in 1988, having hatched and molted. This suggests that some lobsters (approx. 15%) either move from the harbour

directly to other areas some time during the year, or that they migrate seasonally to deeper water (>20 m) outside Clam Bay (between September and mid-May).

The results of this and other recent studies do not provide clear evidence of any single life history of lobsters in the harbour. Some ovigerous females (and probably other lobsters as well) may remain in the harbour year-round, with others moving to different areas either directly, or migrating to deeper water during the winter and then to a new area. Overwintering of lobsters in shallow water has been reported in the Bideford River, P.E.I. (Thomas 1968) and in Rhode Island (Stewart 1972). Jeddore Harbour would probably be a suitable location for overwintering: ice covers the harbour for 3 months each winter, preventing the turbulence which is thought to drive lobsters to deeper water in other locations (Cooper *et al* 1975, Ennis 1983, 1984), and the tidal exchange in the harbour channel could prevent oxygen depletion under the ice and procure a supply of food.

Shelter and habitat requirements of ovigerous females

Lobsters are frequently associated with kelp beds (Breen and Mann 1976, Wharton and Mann 1981) although there is no direct evidence that seaweed enhances lobster production (Miller 1985). In Clam Bay, sonic tagged ovigerous females were usually observed in shelters on hard bottom with moderate to dense kelp cover. However, kelp appeared ubiquitous in areas with hard bottom, with the exception of the deep (>20 m) bedrock ridge on which #6782 was observed from August 2-23. In the harbour, lobsters were usually found in shelters provided by reefs (Table 4, see Fig. 14). Otherwise, they were found amongst kelp.

In Clam Bay, shelter did not appear to be a factor limiting local abundance and therefore movement of lobsters. The habitat in which most lobsters were observed (rocks and boulders on a sand or gravel substrate [Fig. 4], also see Table 4) was widespread and appeared to offer an abundance of suitable shelter. The kelp could provide cover for lobsters not actually in burrows (see Figures 4 and 16). In the harbour, the reefs with

which most lobsters were associated varied in size between exposed ridges of bedrock running over 100 m (*i.e.* Dry Ledge) to isolated clumps of rock and kelp less than 5 m across. Both food and shelter may have been limited on some of the smaller reefs, which frequently sheltered other lobsters and numerous crabs (*Cancer* spp.). Lobsters in the harbour channel were observed equally in a variety of habitats, including shallow saucer-shaped depressions on the bottom. The use of this type of shelter may only occur when the density of lobsters is high (McLeese and Wilder 1964, Stewart 1972), suggesting that the availability of shelters in more characteristic habitats in the harbour channel (burrows in the clay slope or under rocks at the base of the slope) is limited. Most burrows in the clay slope large enough to accommodate lobsters were occupied either by lobsters or crabs (*Cancer* spp.). Crabs may compete with lobsters for space, although niche segregation is known to occur in other habitats (Stewart 1972, Cooper and Uzmann 1980, Hudon and Lamarche 1989). Thus shelter appears to be limited in the harbour channel and may also be limited in the reefs of the Eastern Arm. There would probably not be enough suitable habitat for ovigerous females from Clam Bay if they were all to migrate into the harbour.

Observations on reproductive biology

Several unique *in situ* observations on the reproductive biology of *Homarus americanus* were made during this study. Hatching was observed between July 19 and August 23, 1988, although at least two ovigerous females had not yet hatched by September, when their signals were lost. This range in hatching dates is probably similar for the population as a whole since one aim when selecting ovigerous females for sonic tagging was to sample females with a variety of stages of egg development. The main period of hatching was observed for three lobsters, and required 4-7 days. Following hatch, remnants of the egg mass remained attached to the pleopods for 2-4 weeks. This provides a means of identifying female lobsters which have recently hatched. Two sonic

tagged females molted in the harbour 4-5 weeks after hatching, although molting was not observed directly in either case.

Finally, one of the sonic tagged ovigerous females (#6777) was infected with the ectoparasitic nemertean *Psuedocarcinonemertes homari* (Flemming and Gibson 1981) when sampled on August 26, 1988, in the harbour channel. Although berrried females were not specifically examined for the presence of this parasite when sampled, it's occurrence on the Eastern Shore would appear to be much less than the 31.6% of ovigerous females sampled on the Eastern and South shores reported in Brattey *et al* (1985).

Movement patterns

Two types of movement were distinguished in Clam Bay. Ovigerous females released in shallow nearshore areas and other areas with suitable lobster habitat (see Table 4, also see Cooper and Uzmann 1980) demonstrated 'resident' behaviour, travelling short distances only or not at all (see Fig. 9, also see movement plots for sonic tagged females #5511 and #6783, and #6776 and #6778 prior to translocation). Carapace tagged ovigerous females released over the sand and cobble plains in deeper water (>20 m) south of the entrance to the harbour appeared to travel greater distances (see Fig. 9). Supporting this concept was the rapid movement of sonic tagged ovigerous females across these plains (see movement plots for #6780 and #6785). Thus lobsters in the deep water south of the entrance to the harbour demonstrated 'transient' behaviour, travelling between areas of more suitable habitat. Lund *et al* (1973) showed that sonic tagged lobsters released on a featureless sand bottom travelled further during the first night following release than lobsters released underwater and placed in shelters. Meyer *et al* (1989) showed relatively long movements by lobsters tagged in a midshore area in the central Gulf of Maine with poor lobster habitat and few resident lobsters yet which supported an ongoing trap fishery.

Lobsters frequently remained within a small area in locations with suitable habitat. For example, #5511 was observed on August 2 under a large flat rock in a rugged habitat

with 5 m high bedrock ridges. She was observed on August 11 about 20 m away under a small flat rock supported by two larger rocks. By August 17 and August 22, she had moved into a in a deep horizontal fissure in the bedrock about 15 m away from the previous shelter. Finally, on August 23, she had returned to her August 2 location. Similar behaviour was observed for other sonic tagged females, and has been noted in other *in situ* field studies (*e.g.* Stewart 1972, Lund *et al* 1973).

The observed movement of sonic tagged ovigerous females prior to hatch suggests that specific 'hatching sites' may exist both in Jeddore Harbour and Clam Bay. Ovigerous females observed hatching in the harbour (#5515, #6778, and #6784) moved from the shallow periphery of the harbour into the harbour channel 1-2 weeks prior to hatch. In a coincident study on the distribution of lobster larvae in the harbour, the bulk of stage I larvae were found in the harbour channel, with only a few in the Eastern Arm (DiBacco 1989). This corresponds with the observed distribution of sonic-tagged ovigerous females at time of hatch. In Clam Bay, ovigerous females #6781 and #6785 were observed hatching their eggs in 10-20 m of water east of Big Head. Lobster #6780 moved to this location 2-3 weeks before hatch but was subsequently translocated into the harbour. However, 2 carapace tagged ovigerous females moved away from Big Head prior to hatch, and both the sonic tagged ovigerous females translocated into Clam Bay hatched elsewhere. The hatching sites in the harbour and in Clam Bay are both in moderately deep water (10-20 m). Another possible feature in common may be the presence of current, although the current structure in Clam Bay is unknown.

Movement cues

It was clear in this study that handling lobsters can result in modified behaviour. The effects due to the presence of carapace tags are impossible to assess with data available from this study, however they were probably minimal due to the benign nature of this tag. The weighted bucket and tripline proved to be an effective and rapid method of returning

tagged lobsters to the bottom. In addition to eliminating possible predation on the sinking lobster or its eggs, this method probably also reduced disorientation due to loss of contact with the substrate [3].

The long-term effects of transmitters on the behaviour of lobsters appeared minimal, since normal hatching and molting were observed for several of the ovigerous females tracked in Jeddore Harbour and Clam Bay. This concurs with the views of Lund *et al* (1973), Maynard and Conan (1984) and Jernakoff *et al* (1987). This conclusion was also based on similarities in the behaviour of sonic and carapace tagged lobsters (see Stasko and Pincock 1977). First, movement by both sonic and carapace tagged ovigerous females was limited to each release area (Jeddore Harbour, Clam Bay, and Musquodoboit). Secondly, both types of tagged lobsters in Clam Bay displayed 'resident' behaviour in areas with suitable lobster habitat, and 'transient' behaviour over the featureless sand and gravel habitat south of the harbour mouth.

Lobsters displayed significantly increased activity immediately following handling (see Table 7). Similar results have been reported in other studies with sonic tagged lobsters (Jernakoff *et al* 1987 [*Panulirus cygnus*], Lund *et al* 1973 and Maynard and Conan 1984 [*Homarus americanus*]). The increase in activity was less marked when the lobster was examined or sampled for eggs underwater and replaced in its burrow, rather than brought to the surface. Examination of the data for each of the sonic tagged lobsters suggests that the change in activity following handling is limited to the single interval immediately following the handling (also see Lund *et al* 1973).

The difference in the proportion of active intervals between different sonic tagged lobsters (Table 8) points to one of the drawbacks of ultrasonic telemetry. Individual animals have individual behaviour patterns, but the time and effort required to track sonic

[3] Lobsters and some other decapod crustacea are known to have proprioceptors in their walking legs used for orientation with respect to gravity (Creutzberg 1975, Ache and MacMillan 1980)

tagged animals is such that only a small number of individuals can be followed. Despite this, all individuals in a species are physiologically similar, having the same sensory apparatus and perhaps common behavioural responses to environmental cues. We are a long way from understanding lobster behaviour, but the analysis of grouped movement data may provide insights into some of these cues and their effects on movement.

There were some significant differences in the proportion of active intervals between the two locations, however these differences were not consistent between ovigerous females with different stages of egg development or between translocated and indigenous lobsters, and tended to be only marginally significant ($0.05>p>0.04$). The only consistent and highly significant differences in activity were between lobsters with different stages of egg development. In both Clam Bay and Jeddore Harbour, ovigerous females close to hatch were more active. This may be partly due to the movement of some sonic tagged ovigerous females towards hatching areas (see above). Since there were no significant differences in ambient or thermograph temperature between active and inactive lobsters, the increased activity with late stage eggs does not appear to be simply an artifact of coincident warmer temperatures.

A number of ovigerous females in Jeddore Harbour appear to have left the Eastern Arm following a period of unusually heavy rainfall at the end of July. A bottom salinity of 29.0 ‰ was recorded at the Eastern Arm hydro station on July 30, 1988, the lowest bottom salinity at this location since May (see Appendix C). Lobster #6778 moved into the harbour channel during August 2-12, while #6776 and #6780 were both lost in the Eastern Arm during July 29-August 2. However, there was no significant difference in salinity between active and inactive intervals, and changes in salinity did not appear to affect activity from one interval to the next (Table 11). Since these ovigerous females were all 0-2 weeks from hatch at this time, the movement of the sonic tagged lobsters out of the Eastern Arm may have been due, instead, to the approaching hatch.

An important consideration in this type of analysis is the physiological basis for temperature and salinity perception. Ache and MacMillan (1980) report that antennal chemoreceptors in *Panulirus argus* respond to temperature changes of 1°-2°C. Cooper and Uzmann (1980) point out that offshore lobsters maintain themselves within a temperature range of 8°-14°C , and that seasonal migrations are probably elicited by temperature. There do not appear to be any published estimates of salinity sensitivity of adult lobsters. In the present study, intervals were grouped based on changes in salinity or temperature even though in many cases the magnitude of these changes was small. There were only 12 intervals during which the temperature change was more than ±1°C, and 7 intervals during which the salinity change was more than ±0.2 °/oo. Nevertheless, these may be valid if the smaller changes were part of longer-term changes which continued from one interval to another; behavioural responses to the longer-term changes would be spread through some or all of the individual intervals with the smaller changes.

A further conceptual difficulty in the analysis of behavioural responses to environmental changes is the impact of cyclic, tidally driven variations in temperature and salinity. For example, bottom temperatures and salinities at the Clam Bay hydro station varied by 1°-2°C and 0.4-1.0 °/oo, and at the Eastern Arm hydro, by 1°-3°C and 0.1-0.5 °/oo over 2 complete tide cycles (see Appendix C). Variability appeared to be synchronous with the tidal cycle at the former site, but not the latter. Thus, if temperature and/or salinity cues do modify behaviour, the lobster must have some mechanism for excluding variation from sources such as tides.

Correlations between environmental parameters and movement may be misleading since causality is only inferred. Lobsters are known to change activity patterns in response to environmental cues (Cooper and Uzmann 1980), but there remains the problem of determining whether changes in behaviour are due to changes in orientation cues or to changes in motivation (*e.g.* resting, feeding, avoiding predators, *etc.*) (Stasko and Pincock 1977). In this study, some activity by ovigerous females appears to be explained by

approaching hatch and by location. The larger part, however, is probably due to changes in motivation parameters, which are difficult to address in the field.

Behaviour correlated with diel or tidal rhythms in activity was not observed. Diel activity patterns, particularly nocturnal foraging, have been demonstrated in a number of studies on lobster behaviour (*e.g.* Lawton 1987). This nighttime dispersal is generally less than 300 m, after which the lobsters tend to return to the same or a nearby burrow (see review by Cooper and Uzmann 1980). Ultrasonic telemetry has been used on *Panulirus cygnus* to demonstrate nocturnal feeding forays of 50 m (Phillips *et al* 1984) to an average of 150 m from the den to the farthest point from the den (Jernakoff *et al* 1987), and on *P. argus* of up to 300 m (see review by Herrnkind 1980). Lund *et al* (1973) observed nocturnal movement by *Homarus americanus* of 200 m to 500 m ; movement, however, was infrequent. Maynard and Conan (1984) failed to observe diel periodicity in lobster activity in the Bideford River, P.E.I., but this was probably due to the cold temperature (Cooper and Uzmann 1980). Ennis (1983) observed most activity at night, starting after sunset. Regarding tidal rhythms in activity , Lund *et al* (1973) found a greater tendancy for sonic tagged lobsters to move during the first 3 hours of each tide, particularily the flood tide.

The apparent lack of activity rhythms (particularly diel) in this study is probably a result of the accuracy of the tracking method. The effective spatial resolution of the tracking system was only about 50 m, thus nocturnal foraging less than 50 m would go undetected. The few remaining movements (those > 50 m) would probably be indistinguishable from non-periodic movements. The results show that movement of >50 m can occur at any time during the day or the tide. The more accurate fixed array systems referred to in the introduction may provide a clearer picture of activity rhythms in *H. americanus* in the field.

Conclusions

The results of this and other recent studies suggest that ovigerous females (and probably other lobsters as well) in Jeddore Harbour may be in part resident and in part transient, with some remaining in the harbour year-round and others moving to different areas (either directly or after winter migration to deeper water). This apparent lack of uniformity in behaviour is a trademark of lobster (*Homarus americanus*) populations, and may result from environmental variability on several time scales. Migrations, when they occur, are typically undertaken by only a portion of the population. This "mixed strategy" is characteristic of populations in which the viability of migrants and non-migrants is highly variable (*e.g.* when the variability in winter survival of both groups is high) (Dingle 1980). In addition, mixed migration strategies may be representative of the relative stability of the habitat as a function of generation time (Dingle 1980). Since the current bathymetry of the nearshore coastal region of Nova Scotia is only as recent as the last ice age (*ca.* 10,000 years ago) lobster populations have had only some 1,000 generations to evolve strategies optimizing survival and recruitment.

Jeddore Harbour does not appear to be important either as a larval refuge or a brood area. As a result, successful larval recruitment must occur in Clam Bay and other coastal areas of the Atlantic coast of Nova Scotia. Since little is known about either the nearshore current structure or larval behaviour, it is impossible to speculate on larval recruitment processes. Harbours like Jeddore have abundant habitat for juveniles, so larvae hatched here may have evolved behaviour to avoid being entrained into coastal waters. These would appear to be key areas for future research.

Observations on movement, habitat use, and reproductive biology confirm previously reported aspects of lobster ecology and demonstrate the ability of ovigerous females to adapt to a variety of habitats. *In situ* observations indicate that the duration of hatching and the subsequent period prior to molting was much less variable, despite a wide range in times of hatching onset.

The lack of any clear preference of ovigerous females in location or habitat suggests that identification of movement cues may be difficult or impossible. Indeed, little correlation was observed between the physical parameters measured and activity. Instead, most movement probably occurs due to changes in motivation of the animal based on food and shelter requirements and both intra- and interspecific interactions. An exciting technical aid to future research in this vein is highly accurate fixed arrays of ultrasonic receivers which can position a lobster to ±0.20 m every 5 min. (O'Dor, pers. comm.). Such detailed tracking coupled with an equally detailed knowledge of the locations of food, shelter, and other lobsters in the array may eventually provide the other half of the story.

SUMMARY

The results of this and other recent studies in the Jeddore area (Duggan and Pringle 1988, DiBacco 1989) do not appear to be consistent with hypotheses on larval recruitment on the Atlantic coast of Nova Scotia proposed by Dadswell (1979) and Harding *et al* (1983). The occurence of seasonal inshore-offshore migration by a significant portion of the lobster population remains questionable, while neither gradual movement of lobsters (Duggan and Pringle 1988) nor rapid movement of ovigerous females (this study) in a counter-current direction was observed. In addition, the flushing rate of Jeddore Harbour (4.4 tides, DiBacco 1989) suggests that larvae only remain in the harbour for about two and a half days. Thus the harbour does not appear to be a larval refuge, and since Jeddore Harbour is typical in size of harbours and bays on the eastern shore, larval refuges are probably not an important factor contributing to larval recruitment along this coast.

The harbour does not appear to be an important brood area. Ovigerous females in the harbour and Clam Bay showed no difference in egg development when sampled in May and June, 1988. The predicted hatching dates differed by only 11 days (July 27 in the harbour vs. August 7 in Clam Bay). Both dates appear to leave sufficient time for subsequent development of the larvae. In addition, although there are proportionately more ovigerous females in the harbour than in Clam Bay, they contribute less than 20% of the egg production for the area as a whole.

There was little evidence of migration of tagged late-stage ovigerous females into the harbour from Clam Bay, although homing was observed for at least one sonic tagged lobster carried out into Clam Bay. This conclusion was supported by the distribution of carapace lengths sampled in both locations throughout the study. The results of a sample in May suggest that there were no ovigerous females in the harbour at this time, however this result may be explained in part by the small sample size. In addition, egg development modelled in a variety of annual temperature regimes suggests that there is no physiological

requirement for ovigerous females to either locate in the harbour year-round or to migrate seasonally into the harbour.

The results of this and other recent studies do not identify a single life history for ovigerous females located in the harbour. Instead, they suggest that some lobsters probably migrate out of the harbour in the late fall, returning in the spring or going to other nearshore areas, while others may remain in the harbour over winter.

The lobsters observed in this study were frequently associated with kelp both in Clam Bay and in the harbour. The preferred habitat in Clam Bay was rocks and boulders on a sand or gravel substrate. In the harbour, ovigerous females were usually found around reefs. In the harbour channel, ovigerous females were observed in a variety of habitats including burrows in the clay slope of the channel and in shallow depressions on the bottom (typically observed when lobsters are kept in crowded conditions). The availability of shelters appeared limited in the harbour channel, but may also have been limited on some of the smaller reefs in the Eastern Arm of the harbour.

Several unique *in situ* observations were made during this study. Hatching was observed between July 19 and August 23, 1988, although at least two ovigerous females had not yet hatched by September, when their signals were lost. The main period of hatching was observed for three lobsters, and required 4-7 days. Following hatch, remnants of the egg mass remained attached to the pleopods for 2-4 weeks. Finally, two sonic tagged females molted in the harbour 4-5 weeks after hatching, although molting was not observed directly in either case.

Late-stage ovigerous females demonstrated two types of behaviour. Ovigerous females in areas with suitable lobster habitat demonstrated 'resident' behaviour, moving rarely, and only short distances. These lobsters were frequently observed in a number of different shelters within a small area. In contrast, ovigerous females on featureless sand or gravel bottoms tended to be 'transient', covering greater distances and at faster speeds.

There appeared to be specific sites where hatching occurred; in the harbour channel for females in Jeddore Harbour, and near Big Head for females in Clam Bay.

The activity of ovigerous females increased with egg development. This increase in activity did not appear to be temperature-related or seasonal. Movement did not appear to be correlated with diel or tidal rhythms. Identification of movement cues may be difficult or impossible due to a lack of any clear preference of ovigerous females in location or habitat . Indeed, little correlation was observed between the physical parameters measured and activity. Most movement probably occurs due to changes in motivation of the animal based on food and shelter requirements and both intra- and interspecific interactions.

Figures

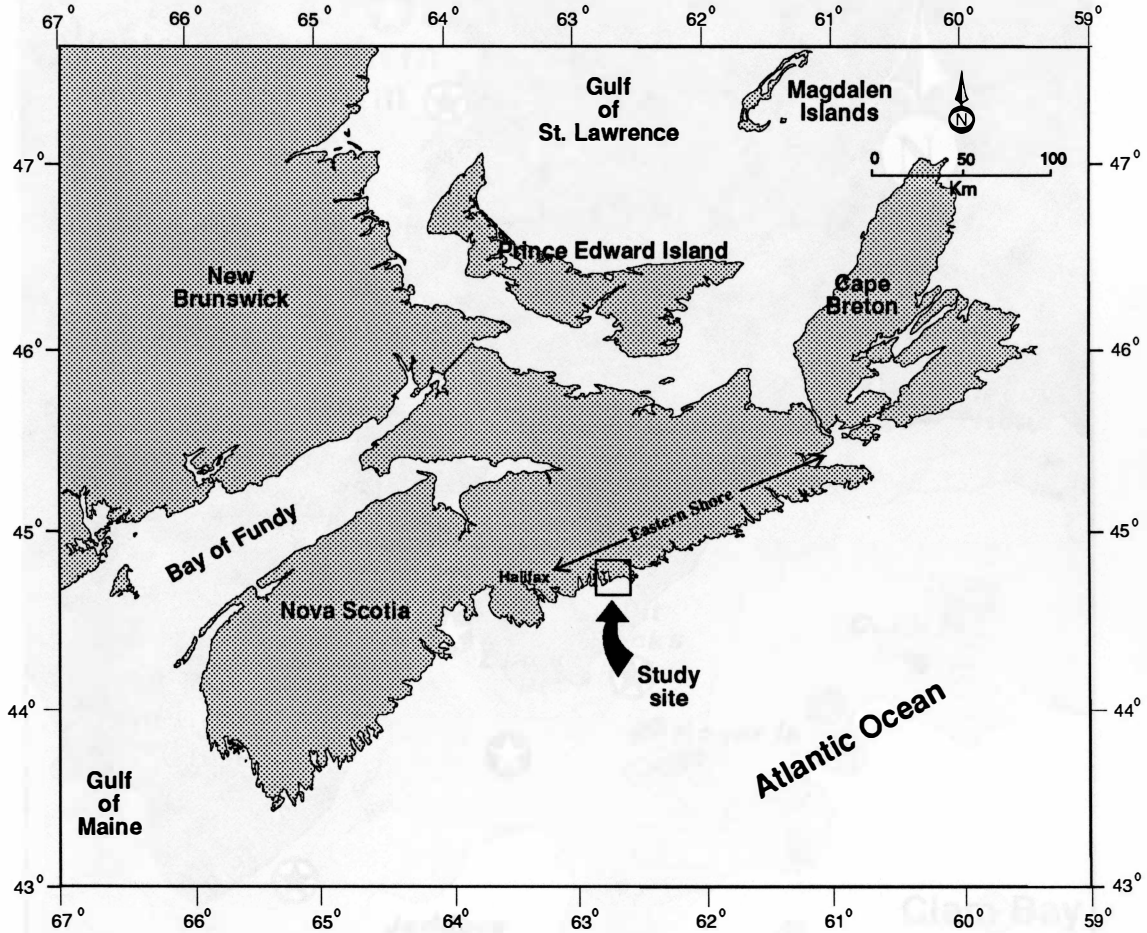


Figure 1: Maritime provinces showing location of study site

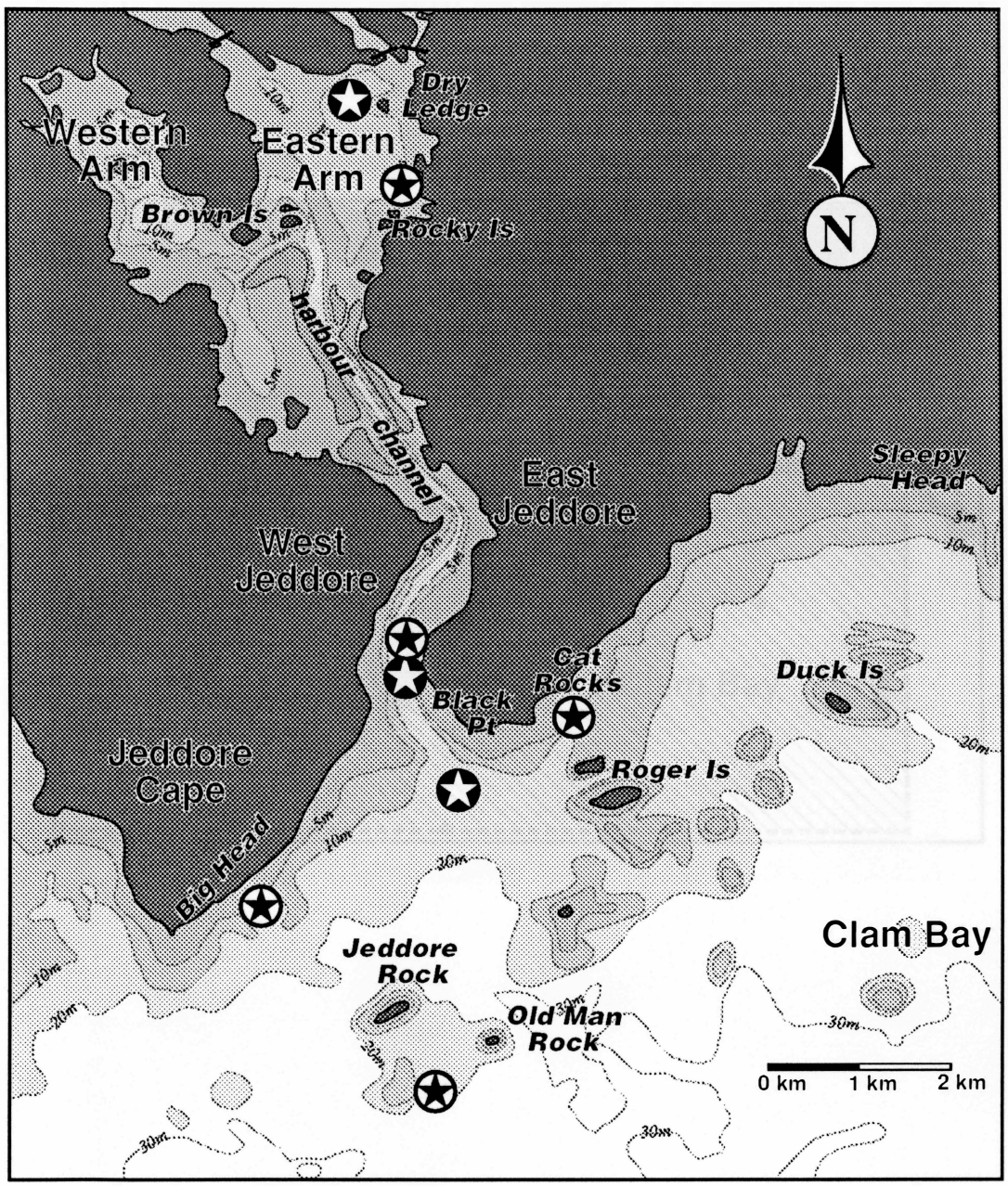


Fig re 2: The study area showing locations of hydrographic stations, ✪, and thermographs, ✪.

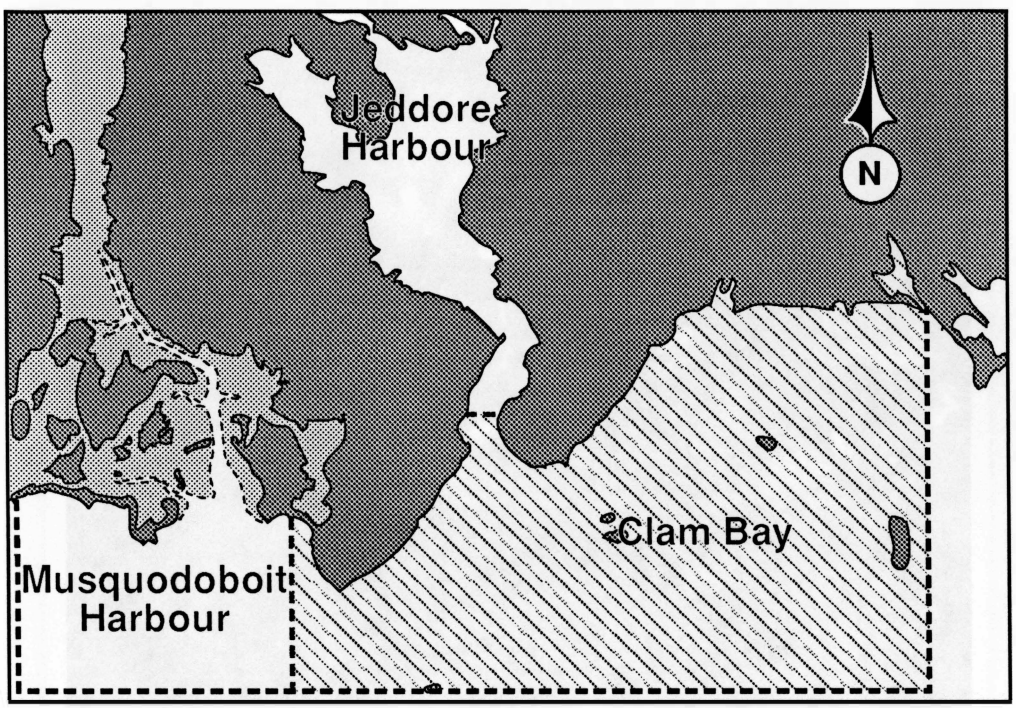


Figure 3: Three areas within the study site in which ovigerous females were tagged

Figure 4: Ovigerous female lobster with transmitter. Habitat is typical of Clam Bay, with macroalgae on rocks, interspersed with sand or gravel.

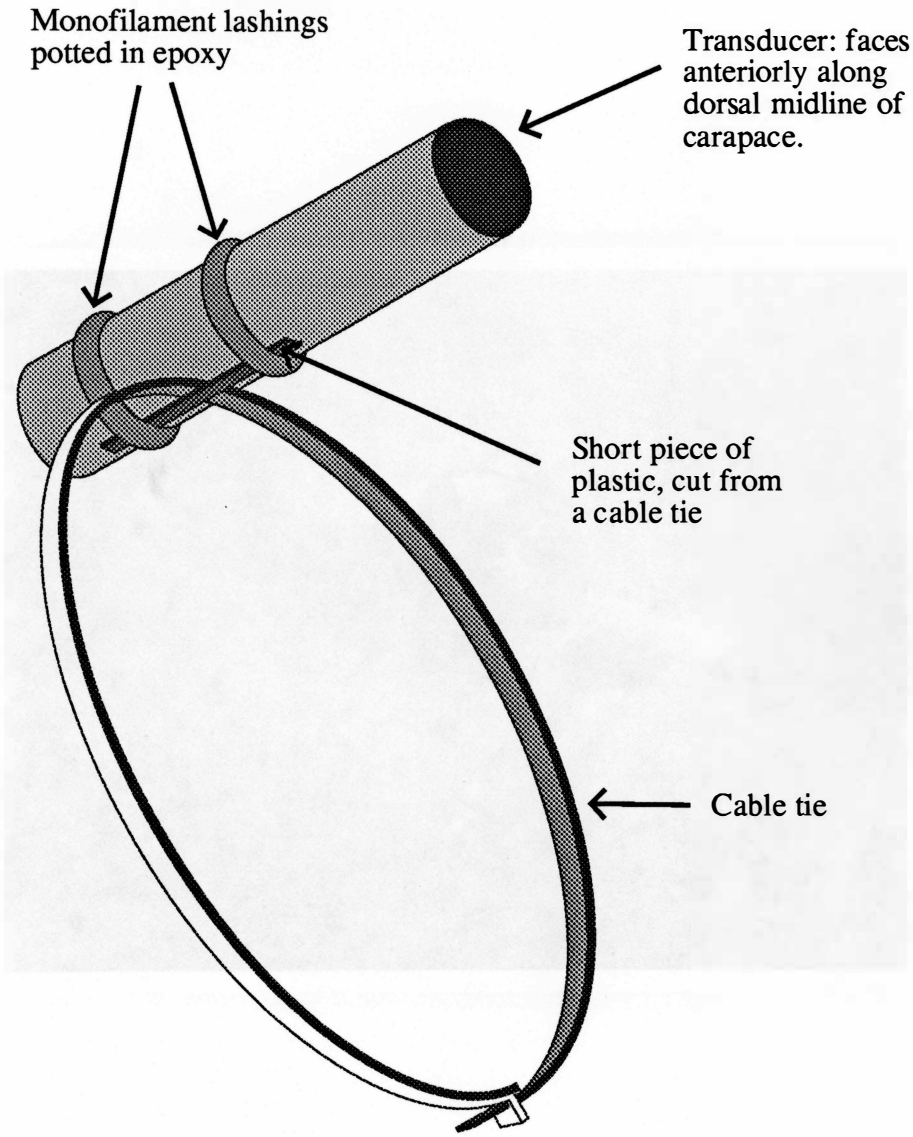


Figure 5: Method of attaching transmitter to lobsters. Cable tie extends around the cephalothorax and connects between the walking legs. Then transmitter is glued to the dorsal surface of the carapace. Actual size.

Figure 6: Diver searching for sonic tagged lobster using underwater receiver in Clam Bay. Note the dense kelp.

Figure 7: Sonic tagged ovigerous female lobster being sampled for eggs in the middle of the harbour channel. The substratum shown is typical for the channel bottom.

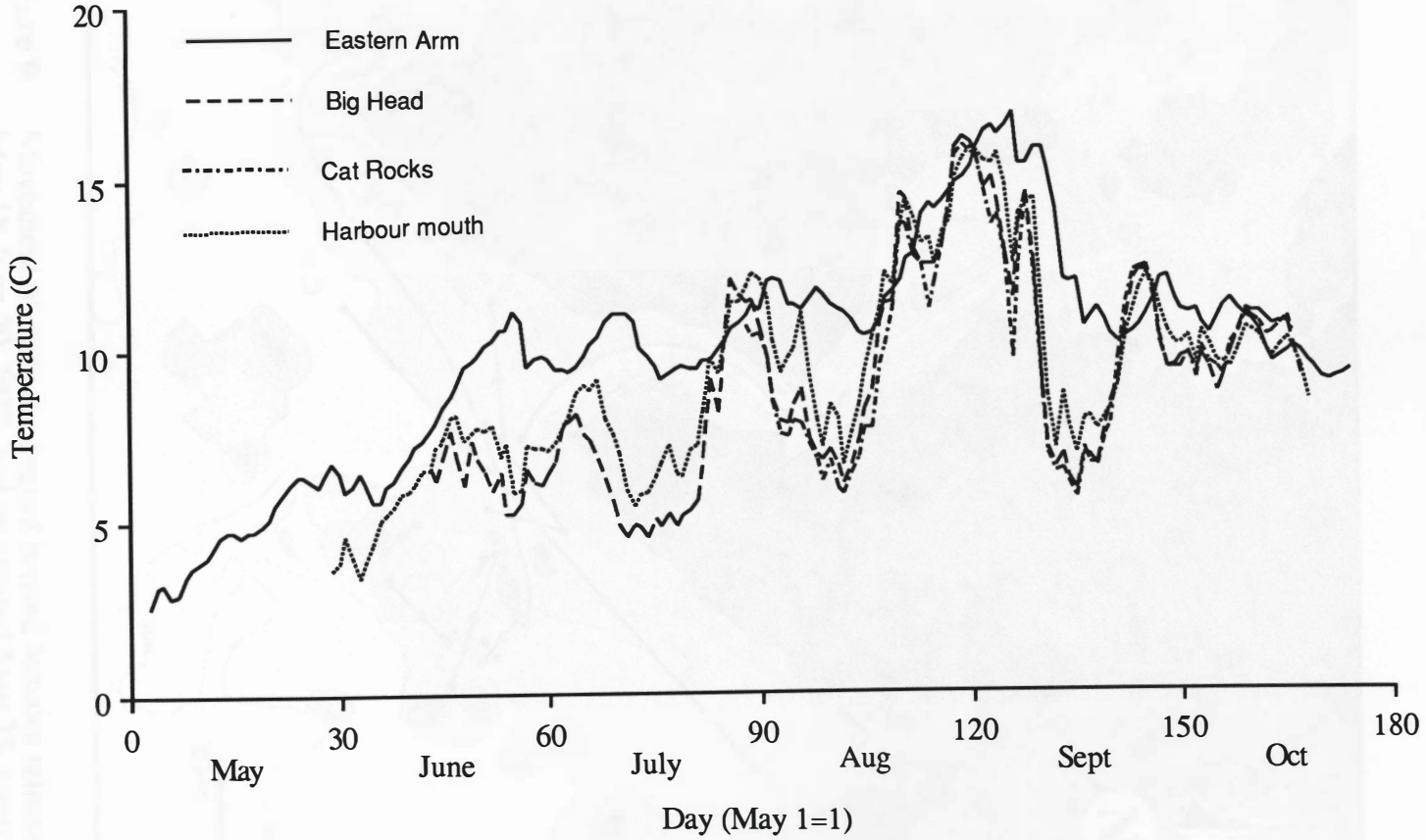


Figure 8: Bottom temperatures from the four thermographs at the study site, 1988.

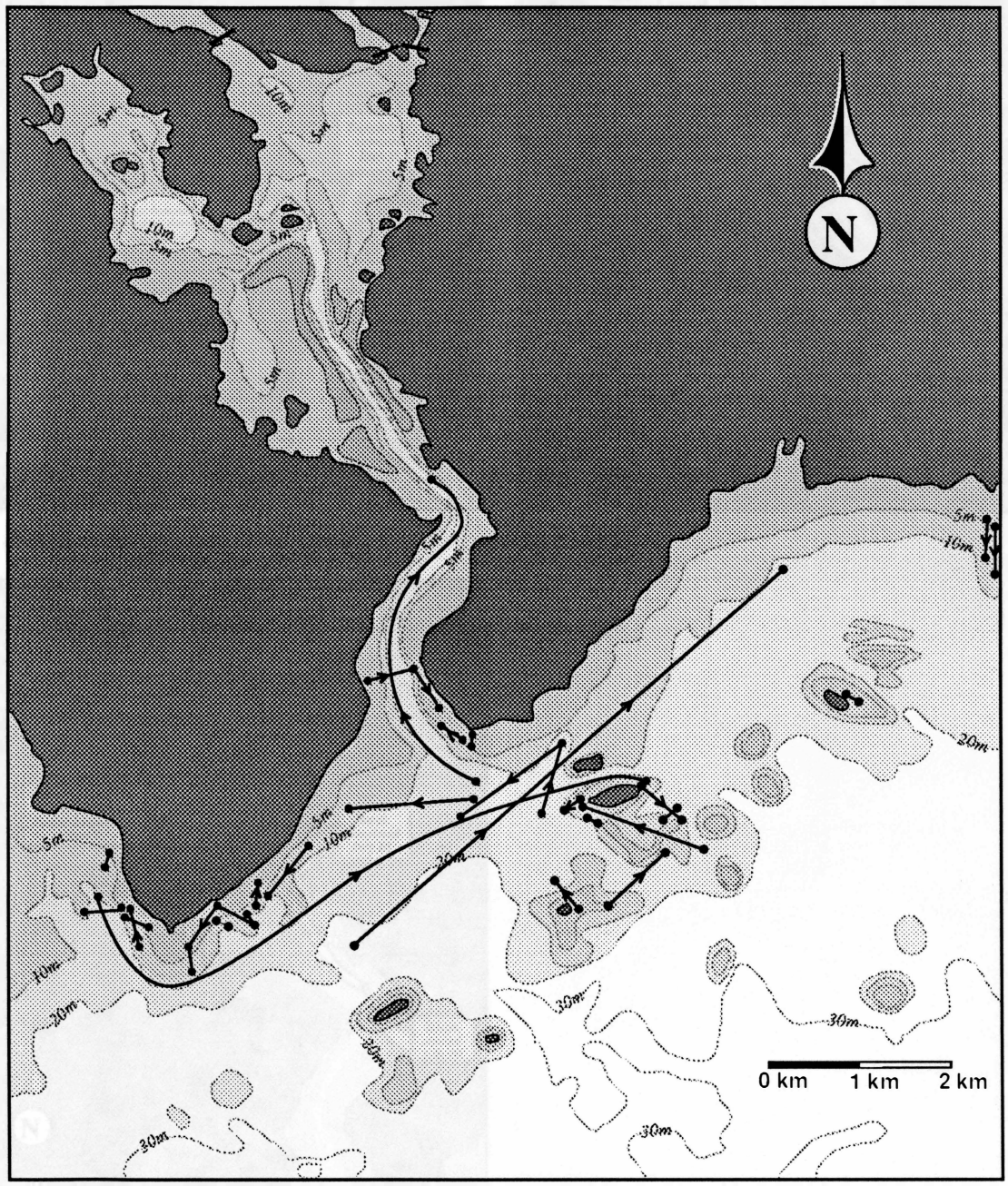
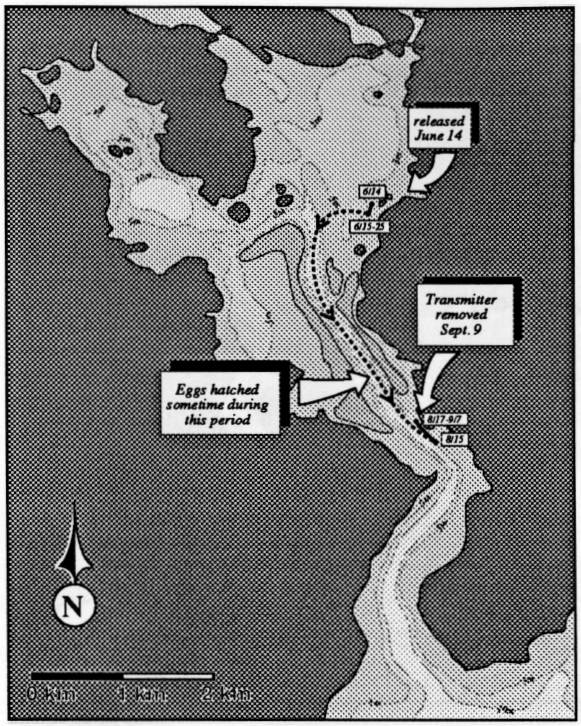
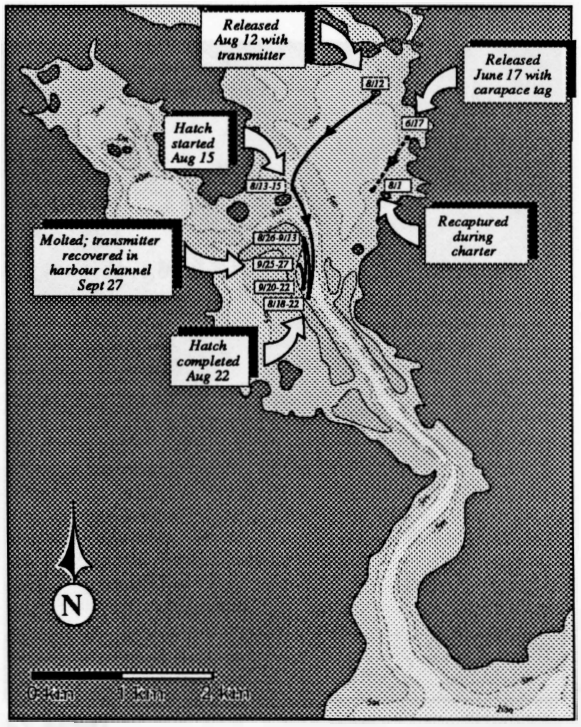


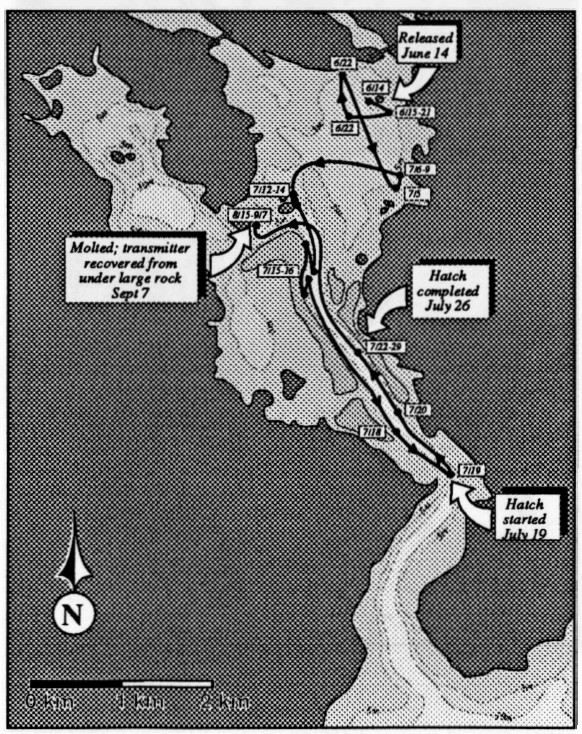
Figure 9: Movement of carapace-tagged berried females released in Clam Bay, May 18-June 20, 1988, and recaptured May 25-August 7, 1988.



a) #5510



b) #5515



c) #6784

Figure 10: Movement of sonic tagged ovigerous female lobsters released in Jeddore Harbour: a) #5510; b) #5515; c) #6784. #5513 and #6779 were lost from Dry Ledge (see Fig. 2) before movement was recorded

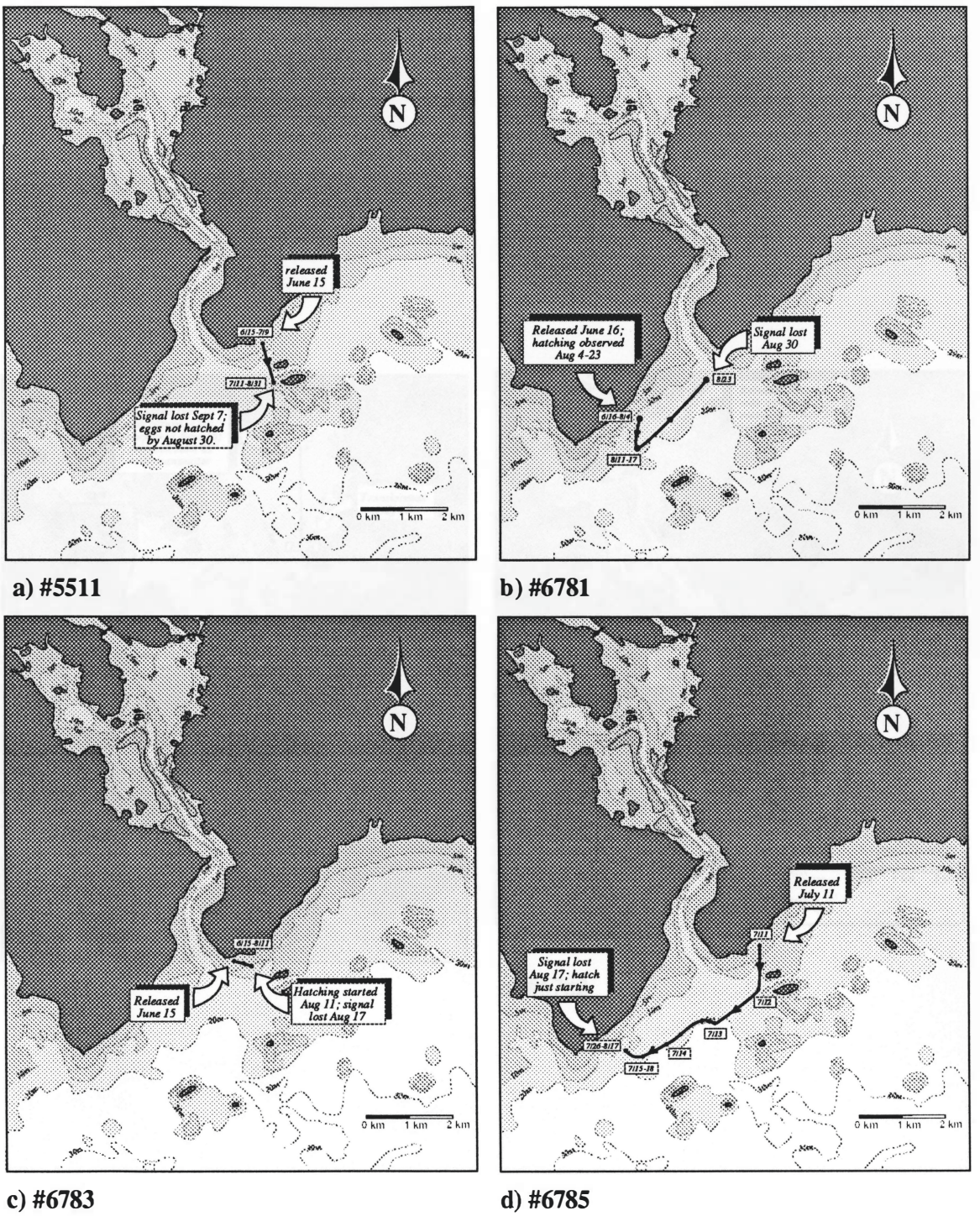
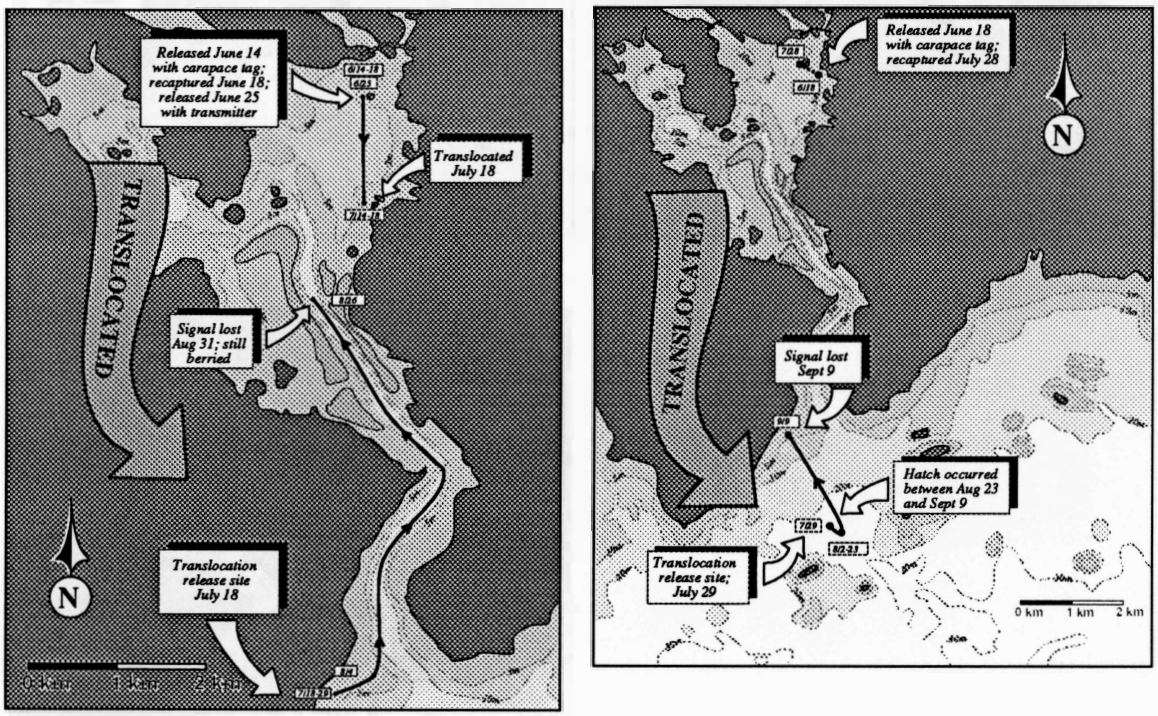
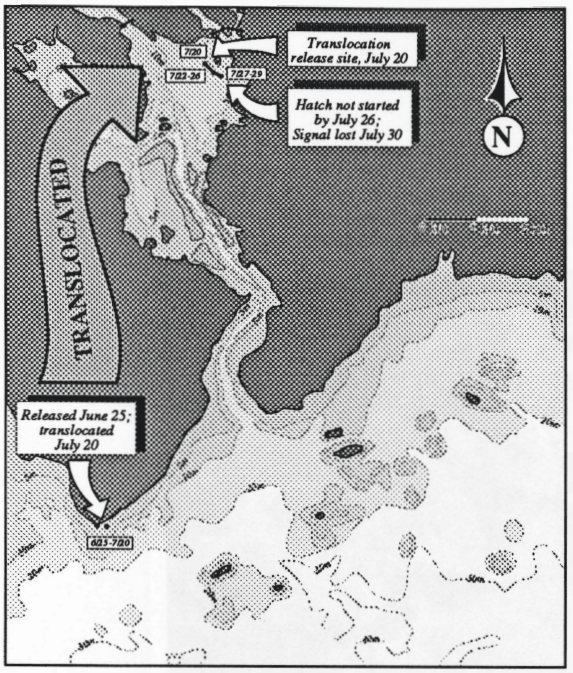


Figure 11: Movement of sonic tagged ovigerous female lobsters released in Clam Bay: a) #5511; b) #6781; c) #6783; d) #6785.

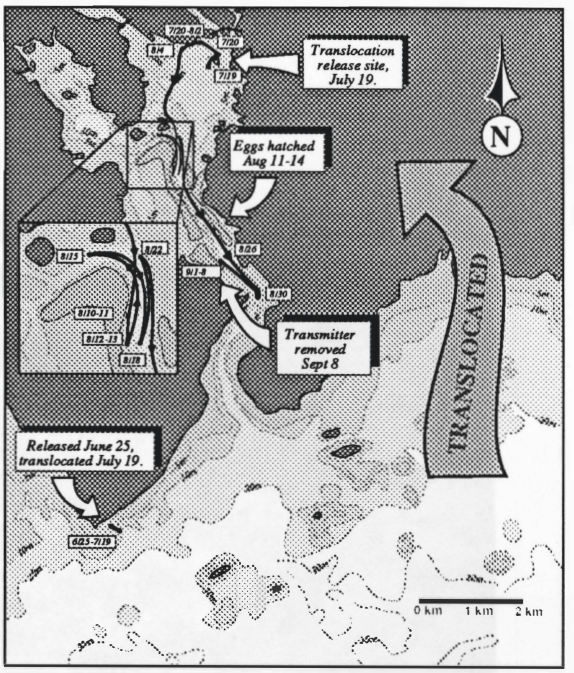


a) #6777 **b) #6782**

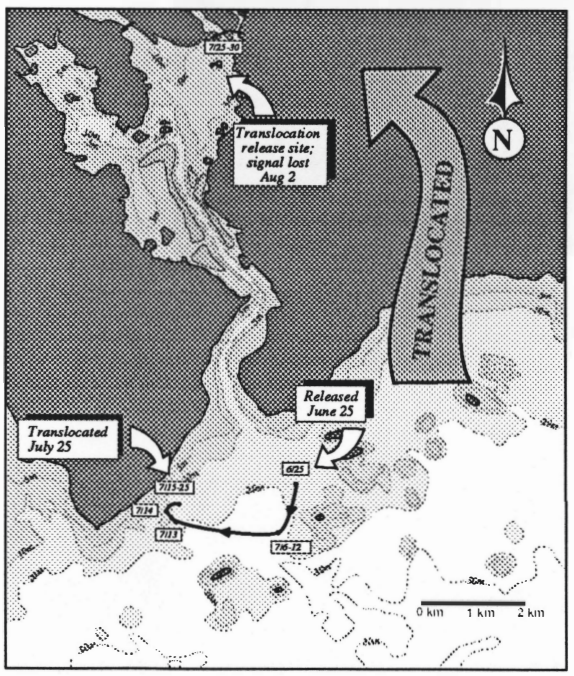
Figure 12: Movement of sonic tagged ovigerous females lobsters translocated from Jeddore Harbour to Clam Bay: a) #6777; b) #6782.



a) #6776



b) #6778



c) #6780

Figure 13: Movement of sonic tagged ovigerous female lobsters translocated from Clam Bay to Jeddore Harbour: a) #6776; b) #6778; c) #6780.

Figure 14: Reef in Eastern Arm, Jeddore Harbour, with sea anemones (*Metridium senile*) on rocks. Bottom substrate is soft mud.

Figure 15: Sonic tagged ovigerous female lobster at the mouth of a burrow in the clay slope of the harbour channel. The angle of the slope is about 50°.

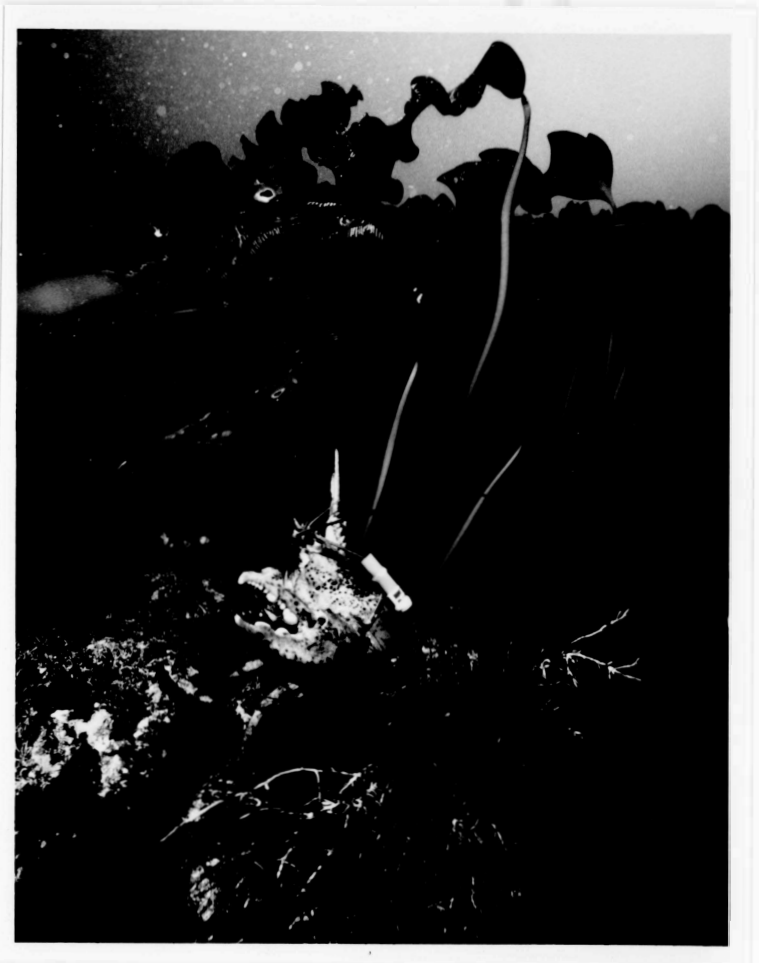


Figure 16: Sonic tagged ovigerous female lobster on a bedrock ridge in Clam Bay, near Roger Is.

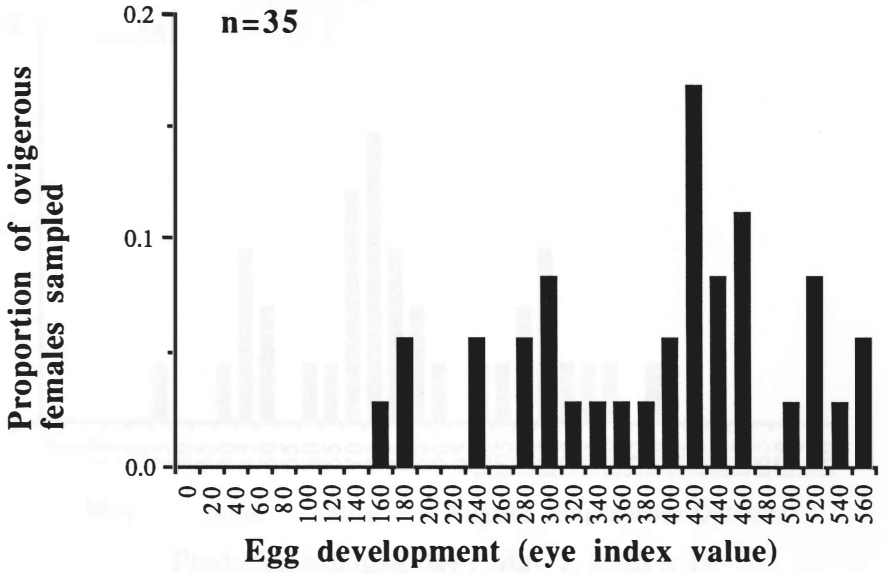


Figure 17: Frequency of egg development of ovigerous female lobsters in Jeddore Harbour, May 15-June 20, 1988

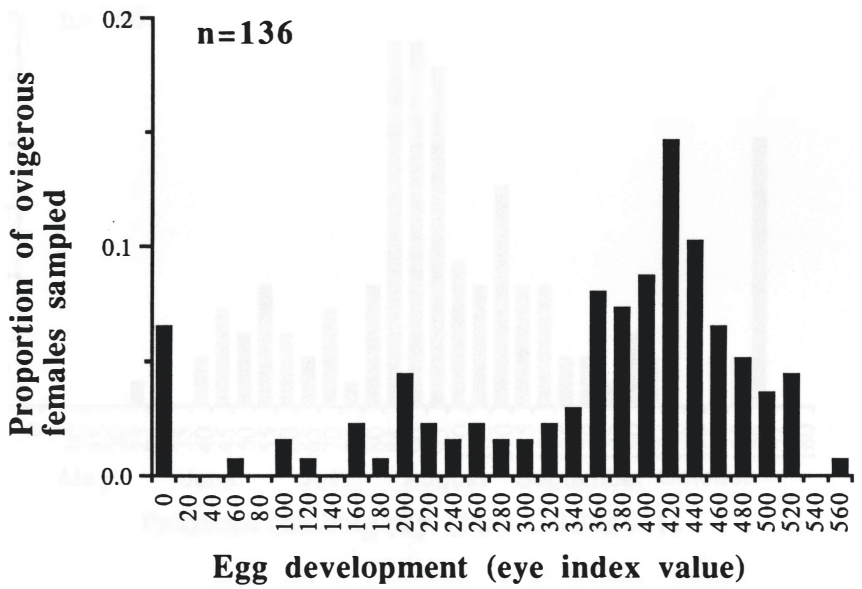


Figure 18: Frequency of egg development of ovigerous female lobsters sampled in Clam Bay, May 15-June 20, 1988

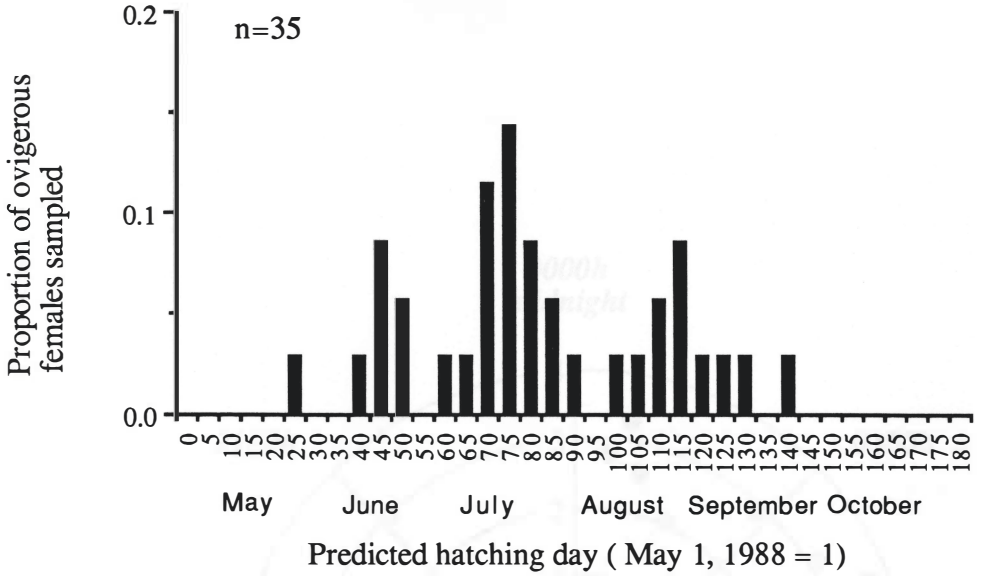


Figure 19: Predicted hatching days of ovigerous females sampled in Jeddore Harbour, May 15-June 20, 1988. Mean hatching date is July 27.

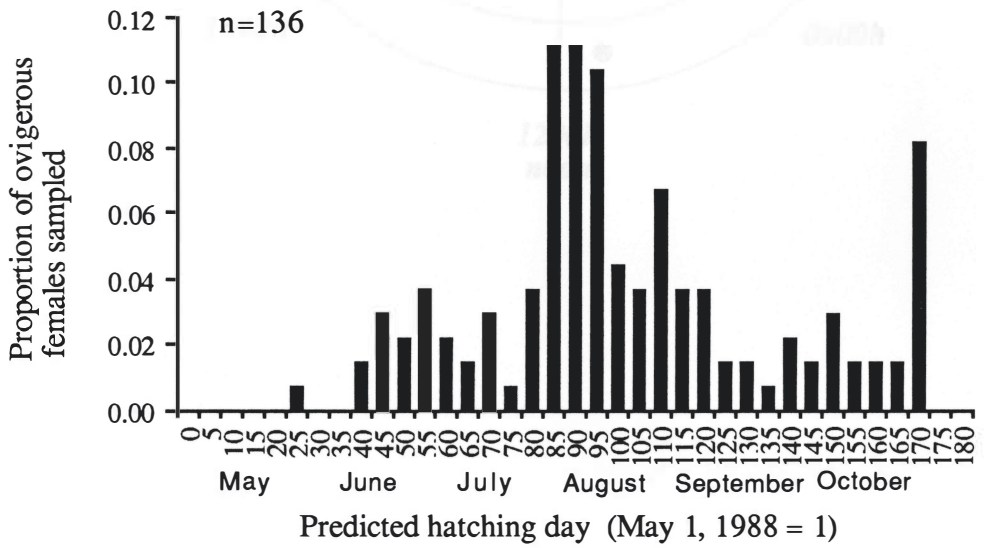


Figure 20: Predicted hatching days of ovigerous females sampled in Clam Bay, May 15-June 20, 1988. Mean hatching is August 7.

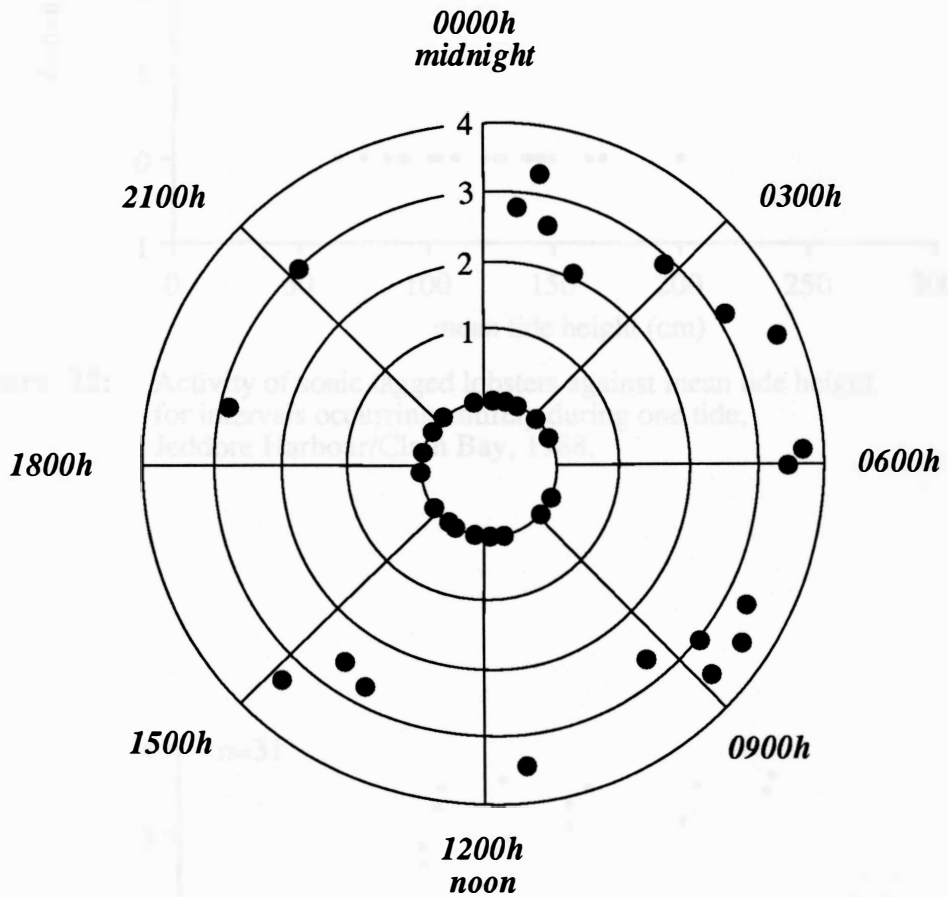


Figure 21: Activity during intervals less than 9 hours duration. Time corresponds to midpoint of the interval. Distance from the center indicates the amount of activity during the interval ($\log_{10}$(m/day)+1).

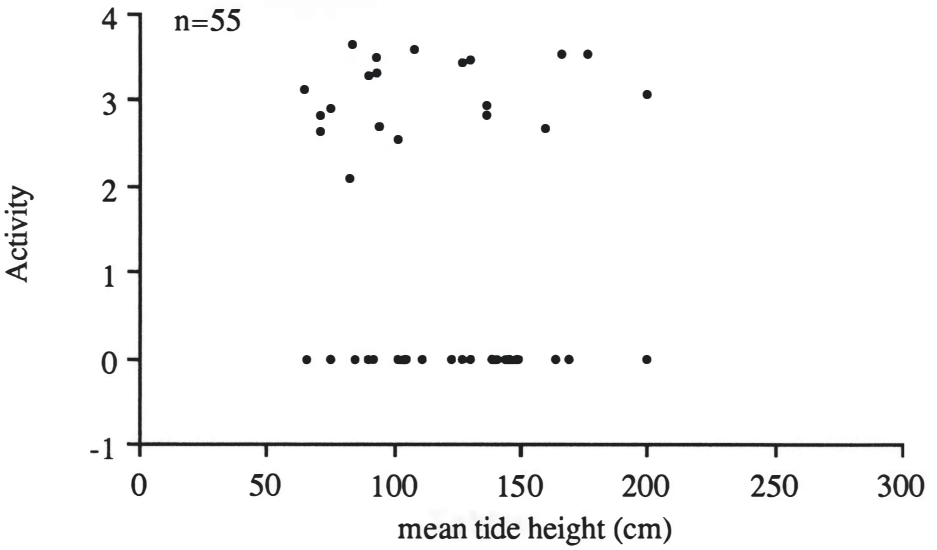


Figure 22: Activity of sonic tagged lobsters against mean tide height for intervals occurring entirely during one tide, Jeddore Harbour/Clam Bay, 1988.

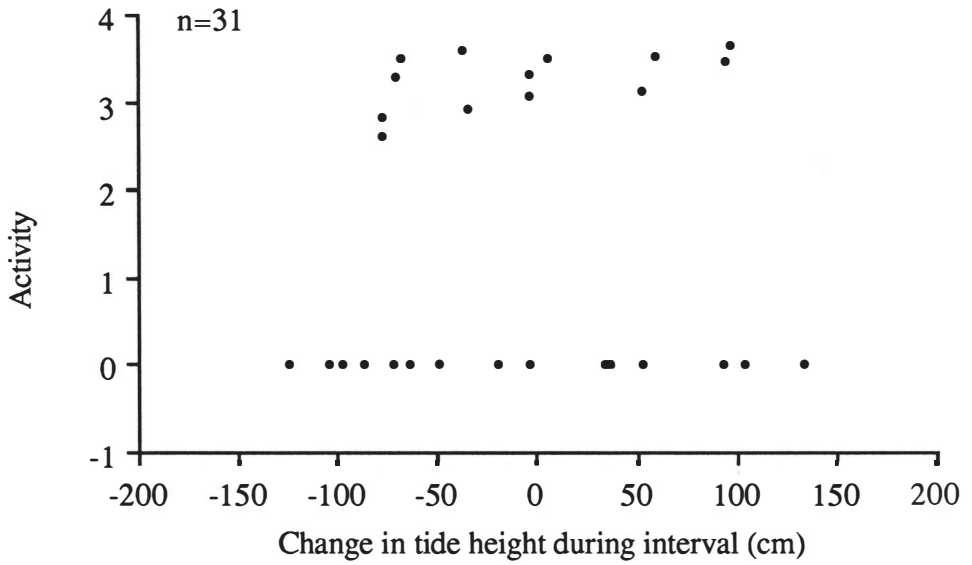


Figure 23: Activity of sonic tagged lobsters against change in tide height over intervals occurring during a single tide, Jeddore Harbour/Clam Bay, 1988. Positive changes are during flood tides, negative changes during ebb tides.

Tables

Table 1: Thermograph data collected from Jeddore Harbour/Clam Bay area, May-October 1988. Bottom depth (m) is shown . All thermographs were 1 m above the bottom.

Location	Bottom depth (m)	Date deployed	Date recovered
Eastern Arm (NE of Rocky Is)	8	May 3	October 22
harbour mouth	10	May 28	October 16
Big Head	9	June 18	October 16
Cat Rocks	10	July 26	October 16
The Old Man	20	May 19	not recovered

Table 2: Size and tracking summary of sonic tagged ovigerous females, Jeddore Harbour and Clam Bay, 1988

Transmitter number	Carapace length(mm)	Location	Tracking start	Tracking end	Tracking duration(d)	Reason ended
5510	102	Eastern Arm	June 14	Sept 7	85	transmitter removed
5511	110	Clam Bay	June 15	Sept 7	84	signal lost (battery died?)
5513	110	Eastern Arm	Aug 12	Aug 12	0	signal lost (transmitter malfunction?)
5515	98	Eastern Arm	Aug 12	Sept 20	39	molted
6776	101	Clam Bay, later translocated to Eastern Arm	June 25	July 29	34	signal lost
6777	111	Eastern Arm, later translocated to Clam Bay	June 25	Aug 26	62	signal lost (battery died?)
6778	101	Clam Bay, later translocated to Eastern Arm	June 25	Sept 8	75	transmitter removed
6779	112	Eastern Arm	June 25	July 6	11	signal lost
6780	115	Clam Bay, later translocated to Eastern Arm	June 25	July 27	32	signal lost
6781	108	Clam Bay	June 16	Aug 23	68	signal lost
6782	110	Eastern Arm, trans-located immediately to Clam Bay	July 29	Sept 9	41	signal lost
6783	120	Clam Bay	June 15	Aug 11	57	signal lost
6784	114	Eastern Arm	June 14	Sept 1	78	molted
6785	115	Clam Bay	July 11	Aug 17	37	signal lost

Table 3: Summary of hatching by sonic tagged ovigerous lobsters, Jeddore Harbour and Clam Bay, 1988. Predicted hatching dates included for ovigerous lobsters lost while hatching [1].

Lobster	date [2] started	date [3] ended	predicted hatching date	duration (days)
5510	>June 25	<Aug 15	July 14	<51
5511	>June 23	—	Sept 17	—
5513	>Aug 12	—	Aug 14	—
5515	Aug 15	Aug 22	—	7
6776	July 29	—	—	—
6777	>Aug 26	—	Sept 12	—
6778	Aug 11	Aug 15	—	4
6779	>June 17	—	July 18	—
6780	July 25	—	—	—
6781	Aug 4	<Aug 23	—	<19
6782	Aug 23	<Sept 9	—	<17
6783	Aug 11	—	—	—
6784	July 19	July 26	—	7
6785	Aug 17	—	—	—

1. see Methods (p.12) for method of predicting hatching date.
2. > indicates that hatching began after the date indicated.
3. < indicates that hatching was completed before the date indicated.

Table 4: Frequency of observed dwelling places of sonic tagged ovigerous lobsters in Jeddore Harbour and Clam Bay, June-September 1988.

Habitat and dwelling place		frequency of observations
A. Eastern Arm (mud bottom with scattered rock reefs)		
i)	In natural hollows or crevices in the reef	8
ii)	Under kelp blade, in vicinity of reef	2
iii)	Under kelp blade, on open mud bottom	2
iv)	unsheltered on mud bottom, walking	2
B) Harbour channel (clay wall sloping at 30-50 ^{o}, descending to flat silt/sand bottom with occasional boulders, and with narrow field of rocks on gravel at bottom of slope)		
i)	In burrow in clay wall of slope	2
ii)	In burrow or hollow under boulders, gravel substrate	3
iii)	In burrow or hollow under boulders, sand/silt substrate	3
iv)	Against small rocks or under kelp, sand/silt substrate	3
v)	In shallow depression on sand/silt substrate, otherwise unsheltered	3
vi)	Unsheltered, sand/silt substrate	2
C. Clam Bay (rocks and boulders on sand, gravel, or bedrock base)		
i)	In hollows or crevices under rocks, sand or gravel substrate	28
ii)	In hollows or crevices under rocks, bedrock substrate	4
iii)	In hollows or crevices in bedrock	2
iv)	Sheltered against rock, mixed bottom	1

Table 5: Percentage of ovigerous lobsters with new and old eggs in the Jeddore Harbour/Clam Bay area during May 15 to June 20 and July 28 to August 9, 1988. Ovigerous lobsters with old eggs includes those with remnants of their egg masses, indicating recent hatching. (n= number of ovigerous females)

location		n	% with new eggs	% with old eggs
in Jeddore Harbour				
	May 15 to June 20	35	**0**	**100**
	July 28 to August 9	10	**60**	**40**
Clam Bay				
	May 15 to June 20	137	**7**	**93**
	July 28 to August 9	7	**29**	**71**

Table 6: Egg development of ovigerous females in the Jeddore Harbour/Clam Bay area between May 31 to June 20, 1988 (n=number of ovigerous females sampled). Data are mean eye index value ± standard deviation. An ANOVA indicated no significant difference in mean egg development between ovigerous females in the harbour and those in Clam Bay (F=0.172, p=.679), or between sampling periods (F=0.208, p=.812).

	May 31- June 4	June 6- June 11	June 13- June 20
Jeddore Harbour	**408.8** ± 118.4 (n=9)	**390.6** ± 108.2 (n=13)	**399.8** ± 116.6 (n=13)
Clam Bay	**393.0** ± 129.6 (n=41)	**380.8** ± 84.7 (n=70)	**396.1** ± 88.7 (n=7)
Musquodoboit	**522.9** ± 0 (n=1)	**362.1** ± 95.3 (n=26)	—

Table 7 : Proportion of active and inactive intervals following different types of experimental intervention of sonic tagged ovigerous lobsters, Jeddore, 1988. A G test for differences between different types of intervention and control intervals was significant (G=43.562, p=.000).

		Intervals	
Type of intervention	n	Active	Inactive
Brought to surface	21	0.67	0.33
Handled underwater	12	0.50	0.50
Observed underwater	16	0	1.00
Holding cage	4	1.00	0
Translocated	4	0.75	0.25
Control (no experimental intervention)	178	0.28	0.72

Table 8: Proportion of active and inactive intervals for sonic tagged lobsters, Jeddore, 1988. A G test for differences between lobsters was significant (G=67.073, p=.000) even when those with few observations (#5515, #6779, and #6782) were removed.

	Intervals		
Lobster	n	Active	Inactive
5510	12	0	1.00
5511	17	0	1.00
5515	4	0	1.00
6776	12	0	1.00
6777	15	0.07	0.93
6778	19	0.32	0.68
6779	4	0.50	0.50
6780	11	0.36	0.64
6781	19	0.11	0.89
6782	2	0.50	0.50
6783	23	0.26	0.74
6784	30	0.63	0.37
6785	10	0.80	0.20

Table 9 : Proportion of active and inactive intervals for 3 stages of egg development in Jeddore Harbour and Clam Bay, 1988. Egg stage 3 corresponds to eye index value of 300-399, egg stage 4 corresponds to eye index value of 400-499, egg stage 5 corresponds to eye index value of 500 to hatch.

Location	Stage of egg devel	Intervals n	Active	Inactive
Jeddore Harbour	**3**	12	0.08	0.92
	4	15	0.13	0.87
	5	30	0.63	0.37
Clam Bay	**3**	18	0	1.00
	4	60	0.23	0.77
	5	18	0.33	0.67

Table 10 : Proportion of active and inactive intervals for translocated and indigenous (non-translocated) sonic tagged ovigerous lobsters, Jeddore Harbour and Clam Bay, 1988.

Location	Trans-located	Intervals n	Active	Inactive
Jeddore Harbour	**no**	62	0.35	0.65
	yes	15	0.40	0.60
Clam Bay	**no**	96	0.21	0.79
	yes	5	0.20	0.80

Table 11 : Changes in activity (decrease, no change, increase) of sonic tagged lobsters from one interval to the next, with changes (decrease, no change, increase) in ambient temperature, temperature at thermograph, and salinity over the same interval.

Variable	Change in variable	Change in activity		
		Decrease	No change	Increase
ambient temperature	decrease	14	36	3
	no change	1	1	0
	increase	8	33	17
Temperature at thermograph	decrease	12	40	8
	no change	0	6	1
	increase	16	32	12
Salinity	decrease	3	16	3
	no change	0	0	0
	increase	9	27	7

Table 12 : Number of active and inactive ovigerous lobsters during different periods of the day. All intervals used were less than 9 hours in length. G test for differences between groups not significant (G=2.366, p=.55).

	Intervals		
Period of day	n	Active	Inactive
entirely during daylight hours	28	0.32	0.68
including sunset	8	0.25	0.75
entirely during dark hours	7	0.57	0.43
including sunrise	12	0.42	0.58

Table 13: Carapace length (in mm) of ovigerous females from three locations in the Clam Bay/Jeddore Harbour area and two sample periods (May 15 to June 20 and July 28 to August 9, 1988) (n=total number of lobsters sampled).

	May 15 to June 20			July 28 to August 9		
Location	mean CL	st dev	n	mean CL	st dev	n
in Jeddore Harbour	**103.9**	±10.66	58	**103.4**	±14.41	20
Clam Bay	**109.7**	±16.35	151	**116.8**	±15.42	13
Musquodoboit	**107.6**	±12.53	31			

Table 14: Catch per trap haul (**CPTH**) of ovigerous females and of all lobsters from available sources and data from this study (n=number of traps sampled during sample period). Continued on next page.

		CPTH (ovigerous females)		CPTH (all lobsters)	
Sample period	Source of data	Jeddore Harbour	Clam Bay	Jeddore Harbour	Clam Bay
October 1986	1	**0.05** (n=300)	**0.01** (n=828)	**0.87** (n=300)	**1.22** (n=828)
April/June 1987	2	no sample	**<0.01** (n=18,314)	no sample	**0.51** (n=9,172)
late June 1987	1	**0.05** (n=106)	**0.02** (n=679)	**0.55** (n=106)	**0.74** (n=679)
April/June 1988	2	no sample	**<0.01** (n=18,837)	no sample	**0.47** (n=9,890)
May 1988	3	**0** (n=40)	**0.01** (n=590)	**0.50** (n=40)	**0.86** (n=590)
June 1988	4	**0.05** (n=951)	**<0.01** (n=5,406)	no sample	no sample
July/August 1988	5	**0.10** (n=211)	**0.03** (n=407)	**0.77** (n=211)	**0.88** (n=407)

Table 14 (continued):

Sources of data

1. Duggan and Pringle (1988) and J. D. Pringle (unpublished data), from tagging study in Jeddore Harbour, 1986 and 1987
2. R. E. Duggan (unpublished data), from fishermans logbook
3. three sea samples, data from this study
4. records of CPTH of ovigerous lobsters kept by 3 fishermen, data from this study
5. fishing charter, July 28 to August 9 1988, data from this study

Table 15: Proportion of ovigerous females in total catch in the Clam Bay/Jeddore Harbour area during the present study (May-Sept 1988) and from other sources (n=total number of lobsters caught).

sample period	source of data	Jeddore Harbour		Clam Bay	
October 1986	1	**0.06**	(n=261)	**0.01**	(n=8)
April/June 1987	2	no sample		**<0.01**	(n=4,689)
late June 1987	1	**0.09**	(n=58)	**0.04**	(n=502)
May 1988	3	**0**	(n=40)	**0.01**	(n=537)
April/June 1988	2	no sample		**0.01**	(n=4,712)
July/August 1988	4	**0.13**	(n=163)	**0.04**	(n=374)

Sources of data

1. Duggan and Pringle (1988) and J. D. Pringle (unpublished data), from tagging study in Jeddore Harbour, 1986 and 1987
2. R. E. Duggan (unpublished data), from fishermans logbook
3. three sea samples, data from this study
4. fishing charter, July 28 to August 9 1988, data from this study

Appendices

Appendix A

Detailed tests of egg staging methodology

INTRODUCTION

Since its publication in 1972, Perkins' formalized method of estimating the development of lobster embryos has been used in numerous studies on the reproductive ecology of berried female lobsters (*e.g.* Campbell 1986, Attard and Hudon 1987). Despite this, there has not been any critical assessment of the methodolgy. This would seem to be especially relevant given that the original publication is lacking in details concerning optimal sample size, the method of selecting eggs, the effect of preservation, and repeatability. As a result, a number of tests were carried out to determine the effect of various aspects of the sampling methodology on eye index values.

METHODS

A sample of 30 eggs was taken from each of seven berried females. Normal probability plots of the eye index values of all 30 eggs were constructed for each sample. These plots showed an approximately normal distribution of eye index values within each sample. Based on this, parametric tests were used when testing hypotheses comparing egg development between samples.

Different samples were used for each test

1) Effect due to sample size

The thirty eggs from each sample were randomly included in groups of 5, 10, or 15 eggs. A two-way ANOVA was used to test for differences in the eye index between the three size groups for each of the 7 lobsters.

2) Effect due to method of selecting eggs from egg sample

The usual method of selecting eggs to stage from the sample was to place the entire

sample in a Petri dish and haphazardly choose 5 individual eggs. Generally, it was noted that there was a selection for eggs oriented with the embryonic eye facing up, or which could readily be moved into that position. To test this selection method, the eggs were staged using the usual method of selecting eggs, and then replaced into the sample. Then 5 eggs were selected using a randomized selection method on a gridded Petri dish. A two-way ANOVA was used to test for differences in the eye index between the methods of egg selection for 9 samples.

3) Effect due to preservation in formaldehyde

Perkins (1972) stated that preservation of the eggs in a 5% solution of formaldehyde (buffer unspecified) prior to staging caused significant swelling in the eggs themselves, but had no determinable effect on the size of the eyes. To test this, 5 berried females were sampled twice. One of the samples was placed in seawater, and the other in a 5% solution of buffered formaldehyde. Both samples were staged within 2-3 days. A two-way ANOVA was used to test for differences in the eye index between the two methods.

4) Difference between replicate samples

Replicate samples were taken from 9 berried females sampled on June 11. In each case, the same method of sampling the eggs from the female was strictly adhered to for each of the two samples. The paired samples were then staged, and the eye index values plotted and the correlation coefficient determined.

RESULTS

There was no significant effect due to sample size ($F=0.569$, $p=.567$, see Table A1) or due to the method of selecting eggs from the sample ($F=1.983$, $p=.163$, see Table A2).

The difference in mean eye index between preserved and not preserved samples was significant ($F=14.105$, $p=.001$, see Table A3). In each case, the eye index was smaller for the samples preserved in formaldehyde than for those kept in seawater.

Finally, the eye index values of the replicates were highly correlated (see Fig. A1 and Table A4).

DISCUSSION

The only significant negative result obtained was an effect due to preservation of the sample in formaldehyde prior to staging. This suggests that differences in the eye index values between berried females sampled prior to about June 1 (when all egg samples where preserved prior to staging) and those sampled after June 1, may be due to the preserving technique. It may be that the results of this test were confounded by the use of paired (but independent) samples. Perkins (1972) stated that preservation of the egg samples in formaldehyde prior to staging caused the eggs to swell but had no effect on the dimensions of the eye pigment. This result now appears questionnable.

A more general difficulty with preserved eggs sample is that they are usually more difficult to stage than fresh eggs. Frequently the corneal layer of the embryonic eye becomes cloudy, or the pigmented layer is bleached or becomes stained and diffuse. Thus, when possible it is preferable to stage fresh eggs. Eggs will remain fresh for 3 or 4 days if immediately refrigerated.

While there was no significant difference in the mean eye index between samples of 5, 10, and 15 eggs, there is one aspect of sample size which should be considered. This is the effect of sample size on the width of the confidence interval around both the mean and the standard deviation of the eye index for that sample. The mean eye index can be thought of as the average development of the eggs. If a hatching date is predicted from the mean, then this is the date around which hatching will occur. Similarly, the standard deviation of

the sample can be thought of as a measure of the distribution of development around the mean. Samples with high standard deviation will begin and end hatching well before and after the peak of hatching. Thus both the mean and standard deviation of the egg sample are useful parameters.

Figures A2 and A3 show the effect of sample size on the width of the 95% confidence interval around the mean eye index and the standard deviation respectively. Clearly the width of the both intervals is reduced by increasing the sample size. This is a useful property when testing inferences concerning both parameters. As a result, it is recommended that 10 eggs be staged from egg samples rather than the 5 suggested by Perkins (1972).

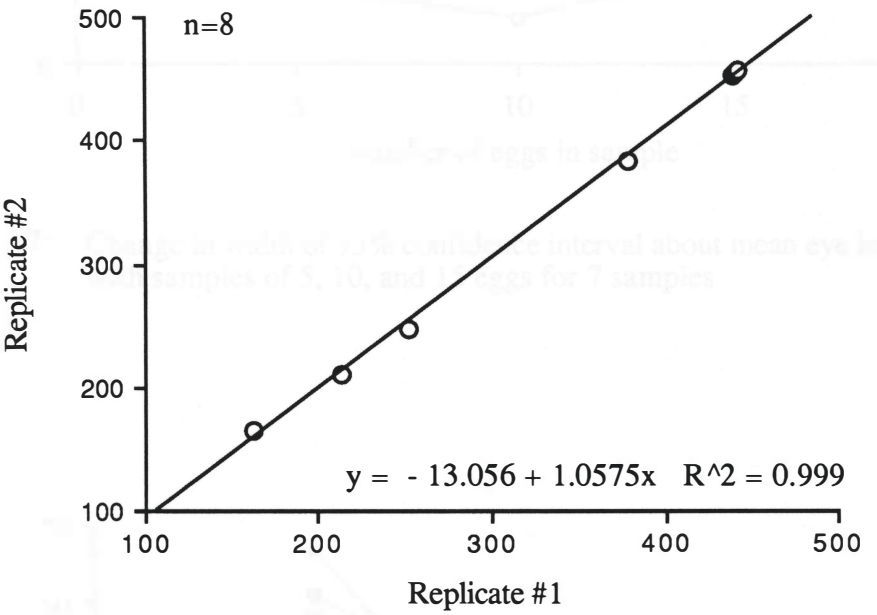


Figure A1: Perkins eye index values of replicate samples from 8 ovigerous femlaes, Jeddore, 1988. Correlation coefficient highly significant ($p<.001$)

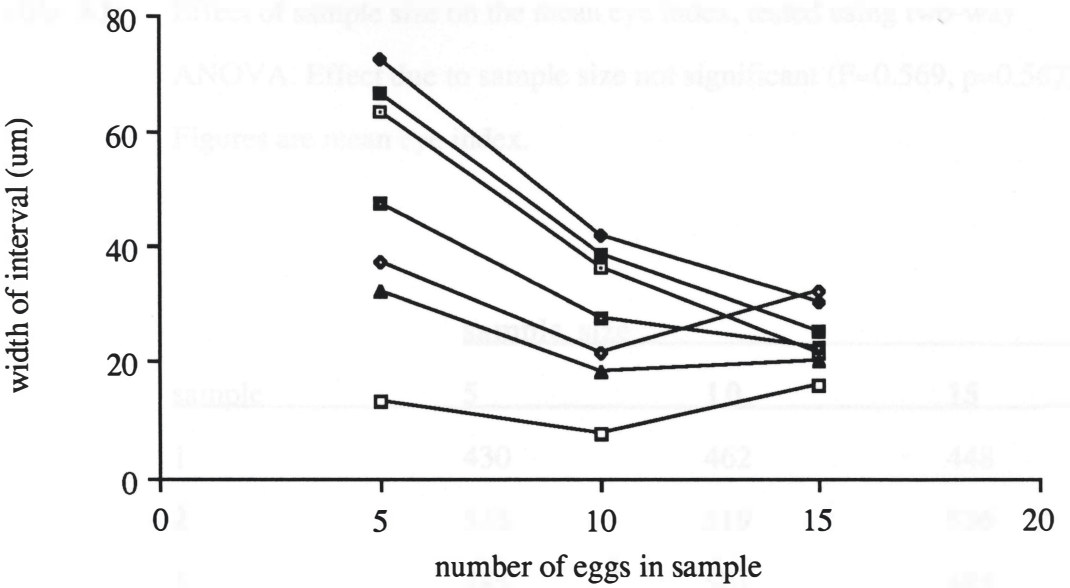


Figure A2: Change in width of 95% confidence interval about mean eye index with samples of 5, 10, and 15 eggs for 7 samples

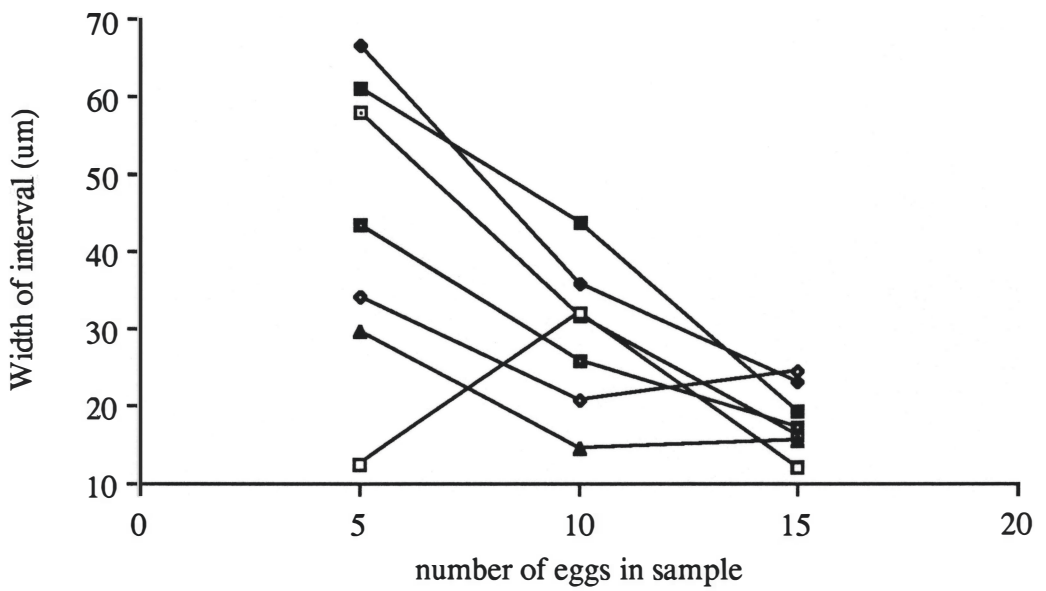


Figure A3: Change in width of 95% confidence interval about standard deviation of eye index with 5, 10, and 15 eggs in sample for 7 samples

Table A1: Effect of sample size on the mean eye index, tested using two-way ANOVA. Effect due to sample size not significant (F=0.569, p=0.567). Figures are mean eye index.

	sample size		
sample	**5**	**10**	**15**
1	430	462	448
2	535	519	536
3	485	501	485
4	523	524	515
5	551	559	560
6	533	536	552
7	455	438	452

Table A2: Effect of method of selecting eggs from sample on the mean eye index, tested using two-way ANOVA. Effect due to selection method not significant (F=1.983, p=0.163). Figures are mean eye index.

	selection method	
sample	normal	randomized
1	477	463
2	395	404
3	408	412
4	457	469
5	412	414
6	187	198
7	434	434
8	361	375
9	174	182

Table A3: Effect of preservation of egg sample on the mean eye index, tested using two-way ANOVA. Effect due to preservation method significant (F=14.105, p=0.001). Figures are mean eye index.

	preservation medium	
sample	seawater	formaldehyde
1	455	418
2	509	497
3	431	394
4	284	258
5	296	278

Table A4: Mean eye index determined from two replicates, tested using two-way ANOVA. Difference between replicates not significant (F=3.462, p=0.067). Figures are mean eye index.

	replicate	
sample	1	2
1	162	164
2	440	453
3	252	248
4	443	457
5	213	211
6	441	455
7	379	383
8	441	455

Appendix B

A computer model for *in situ* egg development

INTRODUCTION

A complete reproductive cycle requires a minimum amount of heat (frequently measured as degree days). As a result, the feasibility of any hypothesized behaviour of ovigerous lobsters can be tested using a model which inputs the temperatures to which the lobster will be exposed. The similarity between the modelled egg development and that observed in nature then provides a basis for judging the validity of the hypothesis.

One compelling reason for modelling egg development is to estimate whether there is a physiological need for berried females inshore to migrate into deeper water during the winter. The water over the Scotian Shelf consists of three main layers which are distinguished by their temperature and salinity characteristics (Hachey 1942, McLelland 1954a). The bottom layer is warm and saline, with salinities greater than 33.5‰ and temperatures above 5°C year-round. It is formed from intermediate and deep slope waters which lay along the continental slope and enter the shelf basins through channels and gullies (McLelland 1954a, and Smith *et al* 1978). Over eastern portions of the shelf (Sable Island Bank and eastward) the bottom configuration prevents direct communication with the warm slope waters (Hachey 1942, Drinkwater pers. comm.). Here, the cold intermediate layer extends to the bottom (McLelland 1954a), and bottom temperatures are cold, between 0°C and 3°C (McLelland 1954b, see figures in same). However, west of Sable Island Bank the shelf edge is open to the slope, allowing communication between the shelf basins and the slope water. Here, bottom temperatures are substantially warmer, typically between 5°C and 9°C (McLelland 1954b, see figures in same). By migrating from Jeddore Harbour or Clam Bay roughly 40 km offshore (to a depth of about 150 m) in November and then back in late May, berried females could remain in water >5°C year-round. Despite favourable temperatures, though, lobsters do not appear to be abundant on the interior Scotian Shelf (Pezzack 1984, Pringle unpub. data).

Campbell (1986) calculated the number of degree days (above 3.4°C) in shallow water (0-5 m) and deep water (182 m) around Grand Manan. He then used this data to infer a temperature requirement for seasonal migration by berried females based on Perkins (1972) estimate of 1832 degree days (above 3.4°C) required for complete egg development. Campbell and Stasko (1986) did likewise for lobster migrations in the upper Bay of Fundy. However, Perkins (1972) estimate of the degree days required for complete egg development does not take into account several factors brought up elsewhere in his paper, and there is no estimate of the accuracy of this figure. As a result, the model developed here uses data from several sources to develop empirical formulas modelling the daily development of the embryo at each stage between extrusion and hatching.

METHODS

A series of starting (extrusion) dates was generated using a normal pseudo-random numbers generator with a mean extrusion date of August 1 and a standard deviation of 15 days. Thus, roughly 95% of the 100 extrusion dates generated lay between July 1 and September 1, with the peak around August 1. The same generated extrusion dates were used for each run of the model.

Time of extrusion varies between areas with different temperature regimes (Aiken and Waddy 1986). In Grand Manan, extrusion has been observed from July 15 to August 5 (Templeman 1940b) and from mid-August to late September (Campbell 1986). McLeese and Wilder (1964) reported extrusion in the Maritime provinces occurred between June and September. Finally, Herrick (1895) reported extrusion in Maine between July and August, peaking during the first half of August. In the Jeddore area, the occurence of numerous berried females with new eggs during the charter (July 28 to August 9, 1988) suggests that extrusion was already well under way by August 1.

Egg development was considered in two phases, based on descriptions in Herrick (1895), Templeman (1940b), and Perkins (1972). These were 1) the initial embryonic development following extrusion and prior to the appearance of eye pigment, and 2) that following the appearance of pigment, and prior to hatching.

The development rate of the eggs between extrusion and the appearance of eye pigment is temperature dependant (Perkins 1972). An empirical relationship between ambient temperature and pre-pigment development was determined using data from several published sources (see Table B1).

$$Y = 2.108 - 0.0324(T) \qquad (2)$$

where $Y = \log_{10}$(days required for onset of pigment)

and T = temperature (°C)

The data for 5°C were not used in developing equation (2) because of an apparent discrepancy in the original published results which gave this point undue influence. Each of the 100 hypothetical egg masses was assigned a "pre-pigment value" of zero on the starting date (date of extrusion). The daily increment in this value was determined using equation (2). For example, if the ambient temperature was 15.0°C, equation (2) gives a predicted pre-pigment development time of 41.87 days. For that day, the "pre-pigment value" would be incremented by $\frac{1}{41.87}$.

When the "pre-pigment value" reached 1.000, then the pre-pigment stage of development was considered finished, and development proceeded using equation (1) (see Methods p.12). When the pigment first appears, it is already crescent-shaped (Herrick 1895, Templeman 1940b), and when first clear enough to be staged, has an eye index of

about 70 *u*m (Perkins 1972). As a result, the starting eye index for this second phase of embryonic development was 70 *u*m rather than 0 *u*m.

Another characteristic of the model was to compensate for differential rates of development (*sensu* Perkins 1972). Perkins stated that "lobster embryos develop differentially under the same thermal conditions, depending on their age or extent of development when they are subjected to a given thermal environment". Specifically, he provided data to show that during cold periods (less than 3.4°C) when equation (1) predicts no increase in the eye index, some development may actually occur, and that the rate of this development is a function of the development of the embryo at that time. As a result, minimum development rates of 2.52 *u*m·week^{-1} and 0 *u*m·week^{-1} were set for embryos with eye index values ≤200 *u*m and ≥400 *u*m respectively, and based on a linear relationship for embryos with eye index values between 200 *u*m and 400 *u*m. The values of 200 *u*m and 400 *u*m were selected based on Perkins description of the age of the embryos in his paper. The differential development relationship was described by

$$Z = (2-(PEI)/200) * \frac{2.52\ u\text{m}\cdot\text{week}^{-1}}{7\ \text{days}\cdot\text{week}^{-1}} \qquad (3)$$

where Z= minimum development rate (*u*m·day^{-1})

and PEI= eye index (*u*m)

The computer model was tested against data for 17 berried females kept under seasonal thermal conditions during 3 years in the lobster culture facility in St. Andrews, N.B.[4] . In each case, the extrusion and hatching dates were known, and a daily temperature record of the water temperature provided. Data were provided for 6 female

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4 Data kindly supplied by S. Waddy, Fisheries Biological Station, DFO, St. Andrews, N.B., Canada, E0G 2X0, (506) 529-8854.

lobsters extruding during summer 1981 and hatching in 1982, for 5 female lobsters extruding during summer 1982 and hatching in 1983, and for 6 female lobsters extruding during summer 1983 and hatching in 1984.

Embryonic development was modelled for berried females in three different temperature regimes corresponding to discrete depths, and for berried females migrating to take advantage of the maximum temperatures at each depth. Temperature data were not available from the study site for a full 12 month period, and so were obtained from published data for Port Bickerton (about 90 km east of Jeddore) from April 1986 to September 1987, from depths of 3 m, 10 m, and 40 m (Walker *et al* 1987, Gregory *et al* 1988). In several cases, there were gaps in the temperature data of several days to several months duration. The missing temperatures were estimated either by linear interpolation between two endpoints of existing data or by using empirical relationships between the temperatures at different depths. The sources of the daily temperature data used in the model are summarized in Table B2.

The temperature data for 3 m are interpreted as representative of temperatures in Jeddore Harbour, while those from 10 m are interpreted as representative of Clam Bay. Temperature data for 40 m are interpreted as representative of temperatures in the deep water outside of Clam Bay. These data appear representative of annual inshore temperatures along the Eastern Shore of Nova Scotia (Ken Drinkwater, pers. comm.).

The first three runs of the model were for development at 3 m, 10 m, and 40 m respectively for the entire period of embryonic development. The fourth was for berried females remaining at 3 m from the date of extrusion to October 27, the day on which the temperature at 3 m cooled to less than that at 40 m. At that time, migration to 40 m until May 4 was simulated, after which the water at 3 m was once again warmer.

RESULTS

Tests of the model

When initially tested, the hatching dates predicted by the model were substantially later than the observed hatching dates (mean difference of 33.5 days, s.d.=16.2 days). With all known quantifiable factors affecting embryonic development included in the model, the difference between predicted and observed hatching dates was considered due to unexplained factors. One potential source of error is that temperatures used were measured in the intake line at the St. Andrews lab, and the actual temperature in the tanks may have been an average of 0.5°C warmer (S. Waddy, pers. comm.). Since most aspects of embryonic development are temperature dependent, the difference for each of the three years was fitted to the mean temperature for that year (the average of the mean monthly temperatures between July in the year of extrusion and July in the year of hatching, inclusive). The resulting curve (see Fig. B1) is described by

$$F = 143.59 - 128.53(\log_{10} T) \qquad (4)$$

where F= estimate of difference between observed and predicted hatching dates

and T= temperature (°C)

This relationship was assumed to be logarithmic since it represents a cumulative estimate of the effects of unknown factors on egg development. It was incorporated into the model as a correction factor, and used in all subsequent applications of the model. With the correction factor, the mean magnitude of the difference between observed and predicted hatching dates was 0.1 days (±15.6 days).

The model is shown in Exhibit B1.

Modelled embryonic development

The distribution of randomly generated starting (extrusion) dates is shown in Fig. B2. The model assumes that ovigerous females in the two thermal environments extrude at the same time, an assumption which may not be valid (see Aiken and Waddy 1986).

The mean monthly temperatures of the data used are shown in Fig. B3. This figure also demonstrates how shallow water (*i.e.* 3 m) is warmer during the summer and autumn than deeper water (*i.e.* 40 m), but colder during the winter and spring. These are compared with the mean monthly temperatures recorded by the thermographs in Jeddore Harbour and in Clam Bay (at Big Head) during this study (Fig. B4). Temperatures recorded in the harbour and in Clam Bay were slightly colder than the temperatures at 3 m and 10 m (respectively) used in the model.

The modelled hatching dates are shown in Fig. B5. The predicted mean hatching dates for berried females sampled in Jeddore Harbour and in Clam Bay are included for comparison. The predicted mean hatching date modelled at 40 m was not included because only 20 of the 100 berried females in the "sample" were predicted to have hatched their eggs by October 26, which differs greatly from the predicted mean hatching dates for sampled berried females.

DISCUSSION

Several conclusions may be drawn from the results presented in Fig. B5. First, the predicted hatching dates of the berried females sampled in this study could have resulted from exposure to the temperature regimes at 3 m, 10 m, or by undergoing a seasonal migration. In fact, the only possibility which the model appears to eliminate is year-round development at 40 m. Secondly, the model does not predict any significant benefit to

undergoing seasonal migration. This is probably due to the term for differential development in the model. Finally, the standard deviation of predicted hatching dates is much greater for sampled lobsters than for the randomly generated starting dates. This suggests that extrusion is not as temporally coordinated as assumed here, and perhaps that the effect of differential development suggested by Perkins is not as important as the model assumes.

The results of the modelling also suggest that there is no reason (from the perspective of egg development) to undertake seasonal migrations to the Scotian Shelf. This may explain in part why lobsters appear scarce in this habitat (see above).

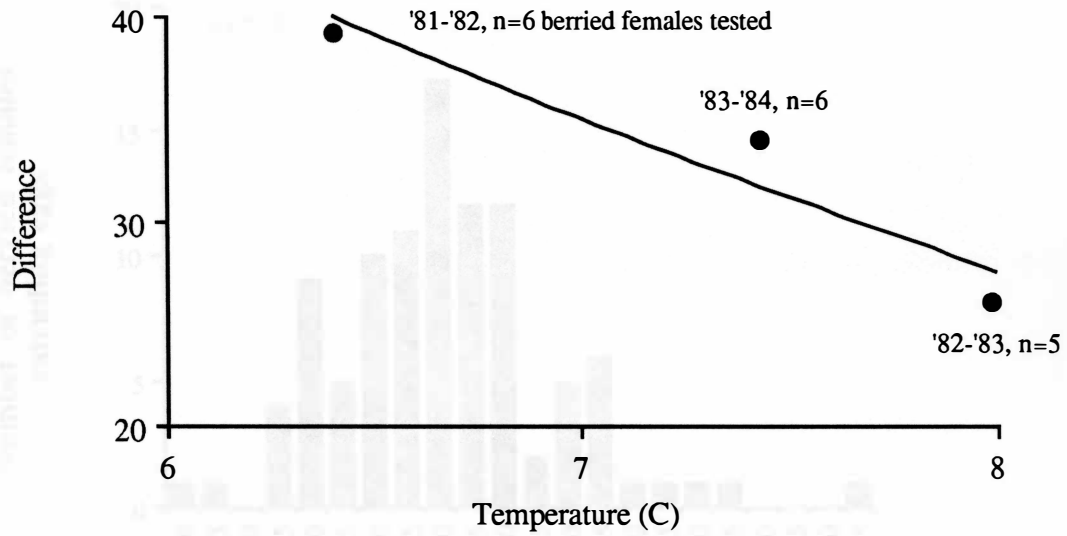

Figure B1: Difference between observed and predicted hatching dates for berried females in the St. Andrews culture facility. Temperatures are mean annual temperatures (C) for berried females, July to July.

Difference = 143.59 -128.53*log(Temperature) R^2 = 0.902

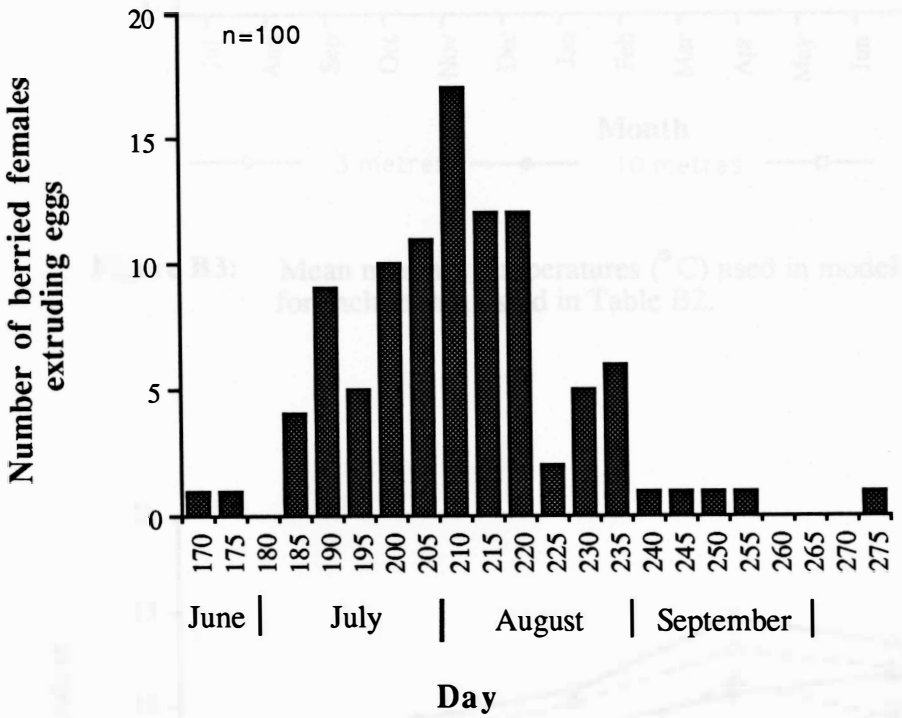

Figure B2: Randomly generated extrusion dates. Mean extrusion date is August 1, with about 95% of extrusion dates between July 1 and September 1.

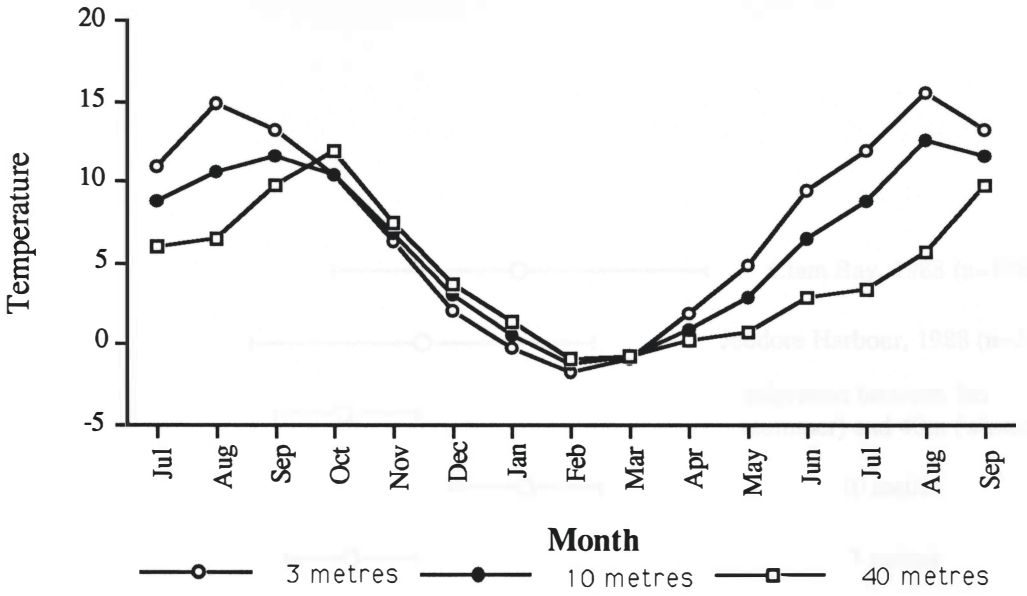

Figure B3: Mean monthly temperatures (°C) used in model. Sources of data for each month listed in Table B2.

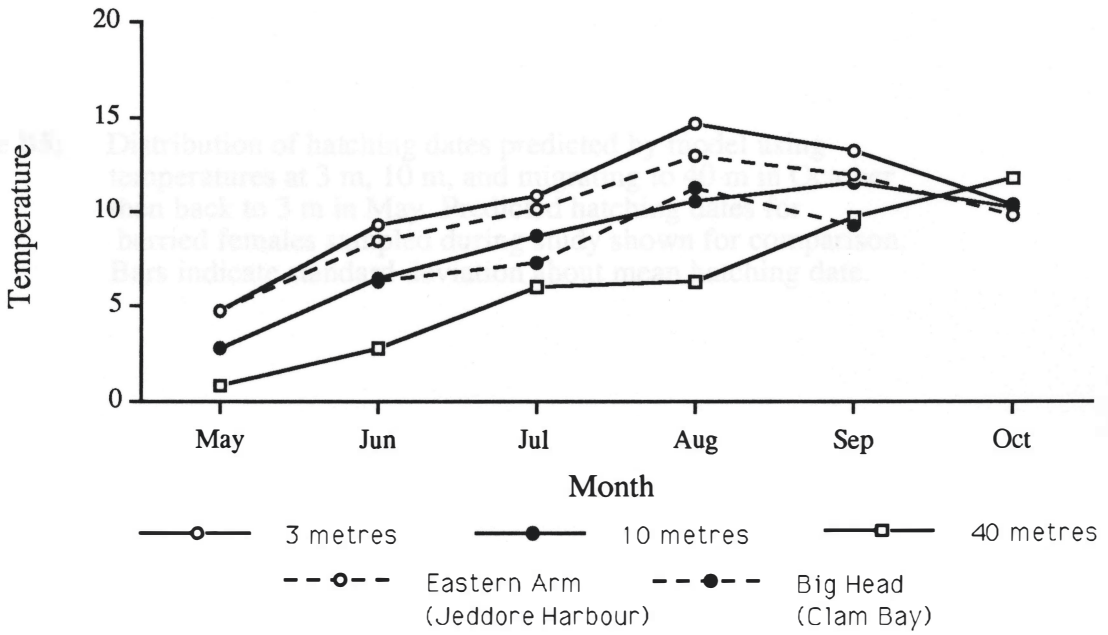

Figure B4: Mean monthly temperature (°C) used in modelling egg development (from Port Bickerton, 1986/87) and mean monthly temperatures from Jeddore Harbour and Clam Bay, 1988.

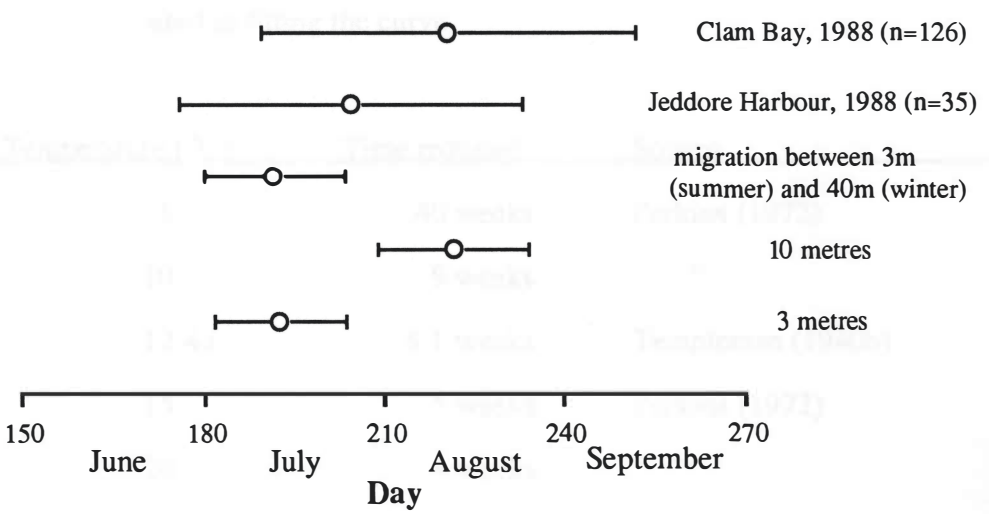

Figure B5: Distribution of hatching dates predicted by model using temperatures at 3 m, 10 m, and migrating to 40 m in October then back to 3 m in May. Predicted hatching dates for berried females sampled during study shown for comparison. Bars indicate standard deviation about mean hatching date.

Table B1: Time required between extrusion and the onset of eye pigment. Data were fit to a logarithmic curve described by **Y= 2.108-0.0324(T)** (r^2 =0.948) where Y= $\log_{10}$(days required for onset of pigment) and T= temperature (°C). The development time at 5°C was not used in fitting the curve.

Temperature (°C)	Time required	Source
5	40 weeks	Perkins (1972)
10	9 weeks	"
12.45	8.1 weeks	Templeman (1940b)
15	5 weeks	Perkins (1972)
20	4 weeks	"
21.0	3.9 weeks	Herrick (1895)
25	3 weeks	Perkins (1972)

Table B2: Sources of daily temperature data used in modelling egg development at 3 different depths (summarized by month), based on published thermograph records for Port Bickerton, N.S.

Month	Depth 3 m	10 m	40 m
July	1	1	1
August	1	5	1
September	1	5	1
October	3	3	1
November	1	1	1
December	1	1	1
January	2	5	2
February	2	5	2
March	2	4	4
April	2	4	4
May	2	2	2
June	6	2	2
July	6	2	2
August	6	2	2
September	1	5	1
October	3	3	1
November	1	1	1

KEY TO SOURCES OF TEMPERATURE DATA

1. Port Bickerton, 1986, from published thermograph records.
2. Port Bickerton, 1987, from published thermograph records.
3. linear decrease between two endpoints in published thermograph records.
4. linear increase between two endpoints in published thermograph records.
5. average of temperatures at 3 m and at 40 m.
6. temperature at 10 m + 3.0°C

Exhibit B1: Simplified GW-BASIC program modelling egg development. Actual version of model used allows choice of temperature from 3m, 10m, or 40m, or migration from 3m to 40m on a user-specified date in late-autumn, and back to 3m on a user-specified date the following spring. Extrusion dates are taken from a file containing the 100 randomly generated extrusion dates

```
10   OPEN "R",#1, "TESTTEMP",13          Opens file with daily temperature
                                         records (see Table C2).
20   FIELD #1,4 AS YEAR$,3 AS DAY$,4 AS TEMP$
30   !
40   INPUT "ENTER DATE (JULIAN DAY) OF EXTRUSION";START
50   INPUT "ENTER YEAR IN WHICH EXTRUSION OCCURRED";YEARX
60   INPUT "ENTER MEAN ANNUAL TEMPERATURE FOR THAT
                                         YEAR";AVTEMP
70   !
80   N=1;INIT=1;PEI=70                   Initializes development prior to onset of eye
                                         pigment at 0, eye index following onset of
                                         eye pigment at 70.
90   !
100  GET #1,N
110  YEAR=VAL(YEAR$):DAY=VAL(DAY$):TEMP=VAL(TEMP$)
120  IF YEARX>YEAR THEN 150 ELSE 130
130  IF START>DAY THEN 150 ELSE 170      Finds appropriate temperature
                                         records in temperature file
140  !
150  N=N+1:GOTO 100
160  !
170  IF INIT<1 THEN 190 ELSE 230         Terminates development prior to onset of eye
                                         pigment at 1
180  !
```

```
190   Y=2.1077-0.032382*TEMP          Equation for development between extrusion
                                      and onset of eye pigment (Equation 2)
200   Y=10^Y
210   INIT=INIT+(1/Y):GOTO 150
220   !
230   PEIINC=(-8.3151+2.6019*TEMP)/7      Equation for daily increment in eye
                                      index value between onset of eye pigment
                                      and hatch (Equation 1)
240   !
250   PEIMIN=(2-PEI/200)*0.36         Equation 3
260   IF PEIMIN<0 THEN PEIMIN=0
270   IF PEIMIN>0.36 THEN PEIMIN=0.36
280   IF PEIINC<PEIMIN THEN PEIINC=PEIMIN ELSE      Sets minimum daily
                                      increment in eye index based on differential
                                      development rates (see text)
290   !
300   PEI=PEI+PEIINC                  Adds daily increment in eye index
310   IF PEI<560 THEN 150 ELSE 330    Terminates development following onset of
                                      eye pigment at 560 (hatch)
320   !
330   X=LOG(AVTEMP)
340   DAY=DAY-(143.59-128.53*X)       Correction factor (Equation 4)
350   !
360   PRINT "LOBSTER EXTRUDING ON DAY";START;YEARX;"PREDICTED TO
                                      HATCH ON DAY";DAY;YEAR
370   GOTO 40
380   END
```

Appendix C

Temperature, salinity, and secchi data from
Jeddore Harbour, harbour mouth, and Clam Bay
hydro stations, May-September 1988.

Temperature, salinity, and secchi depth measurements at hydro stations.

Temperatures and salinities at the three hydrographic stations are shown in Figures C1-C6 (Clam Bay: Fig. C1 (temperature) and Fig. C2 (salinity); harbour mouth: Fig. C3 (temperature) and Fig. C4 (salinity); Jeddore Harbour: Fig. C5 (temperature) and Fig. C6 (salinity))

Surface temperature in Clam Bay varied between 3.4 °C (June 2) and 17.2 °C (August 31), and in the Eastern Arm between 7.0 °C (June 2) and 18.4 °C (August 13, although there was no surface temperature taken at the end of August). The bottom temperature in Clam Bay varied between 2.6 °C (June 2) and 15.8 °C (August 27), and in the Eastern Arm between 2.2 °C (May 3) and 16.7 °C (September 3). Records from the hydro stations show that peak surface and bottom temperatures are reached at the same time.

Salinities in Clam Bay varied between 29.2 ‰ and 31.2 ‰ at the surface and between 30.3 ‰ and 31.5 ‰ on the bottom. In the Eastern Arm, salinities varied between 20.1 ‰ and 30.0 ‰ at the surface and between 28.4 ‰ and 30.5 ‰ on the bottom (see Figures C2, C4, and C6).

Temperature and salinity values at the harbour mouth tended to lie between those in Clam Bay and those in the Eastern Arm. The harbour mouth station was located on the east side of the channel, near the slope. As a result, depth varied between 5-15 m depending on where the bottom temperature/salinity cast was made relative to the slope

The secchi depth in Clam Bay varied between 5-11 m, and was typically 2-4 m shallower in the harbour (Figure C7). Secchi depths tended to decrease in both locations through the summer.

Tidally induced variability in temperature and salinity.

Salinities and temperatures observed during the three extended sampling periods (June 21-23, July 13-14, and July 30-31) are plotted in Figures C8, C9, and C10. Severe

weather prevented sampling in Clam Bay on July 30-31, and reduced the number of samples elsewhere. Tide heights are based on hourly estimates for Salmon River Bridge (located at the head of the Eastern Arm) provided by the Tides Section of the Canadian Hydrographic Service.

Tidally induced variability differed between stations. The harbour mouth showed the strongest impact of the tides with the influx of cold, saline shelf water during flood tide, and the efflux of warmer, less saline harbour water during ebb tide.

Temperatures and salinities at the Clam Bay and Eastern Arm hydro stations showed only occasional deviation with the tides. Temperatures and salinities in Clam Bay (particularily on the bottom) remained relatively constant through all extended sampling periods. At all three hydro stations, fluctuations in temperature and salinity were more pronounced at the surface than on the bottom.

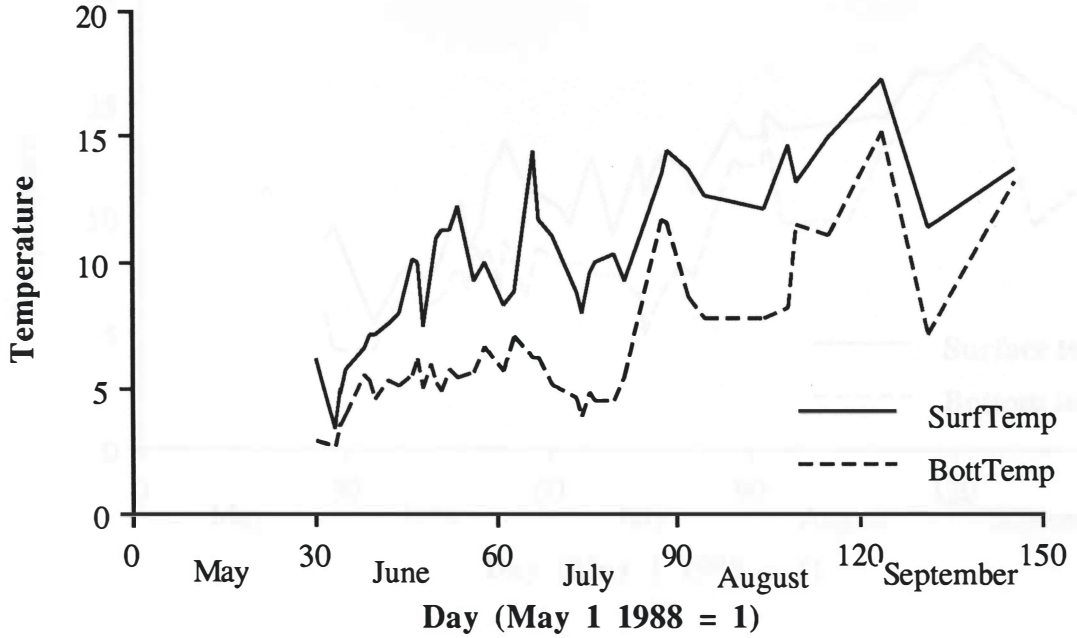

Figure C1: Surface and bottom (15m) temperatures (C), Clam Bay hydro station

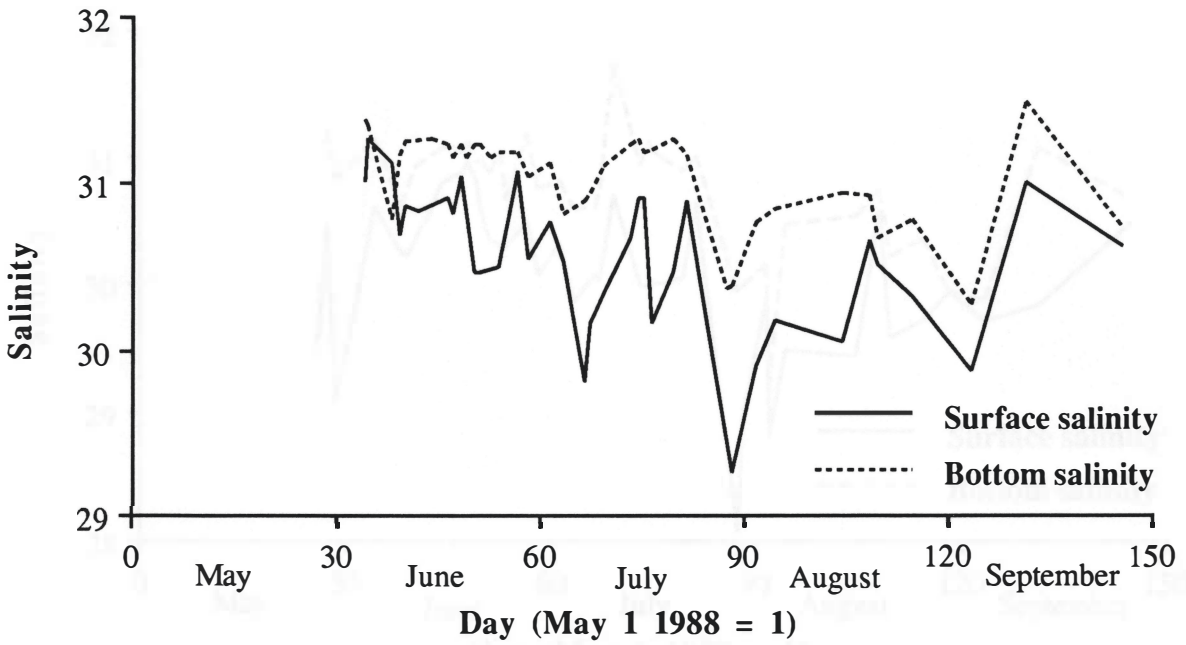

Figure C2: Surface and bottom (15m) salinities, Clam Bay hydro station

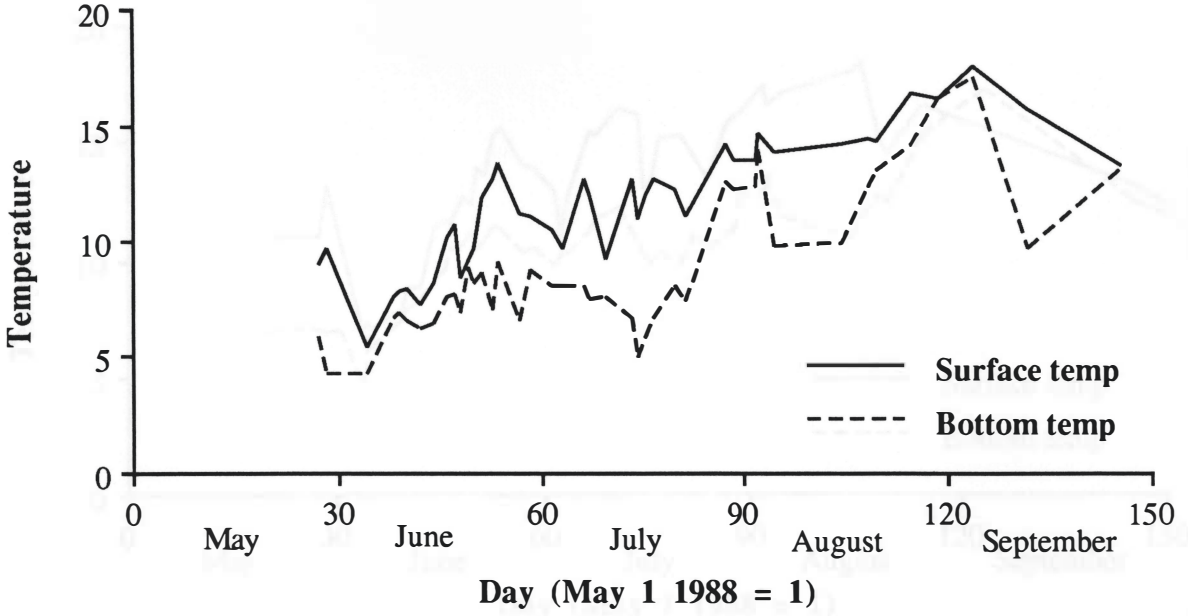

Figure C3: Surface and bottom (10m) temperatures (C), harbour mouth hydro station

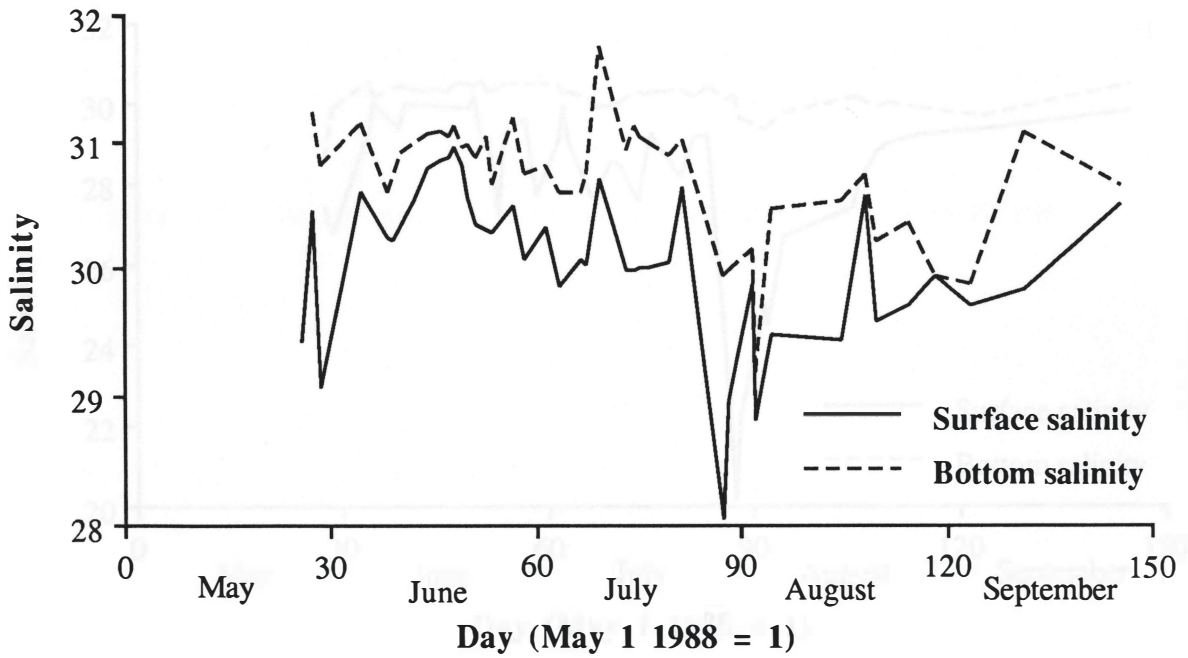

Figure C4: Surface and bottom (10m) salinity, harbour mouth hydro station

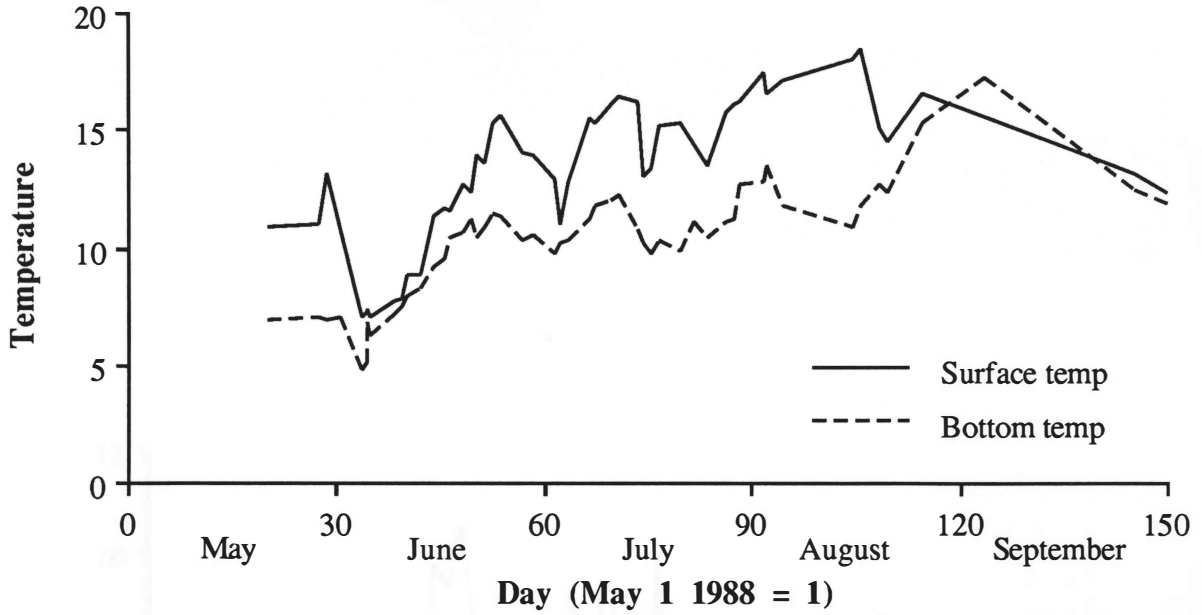

Figure C5: Surface and bottom (8m) temperature (C), Eastern Arm hydro station

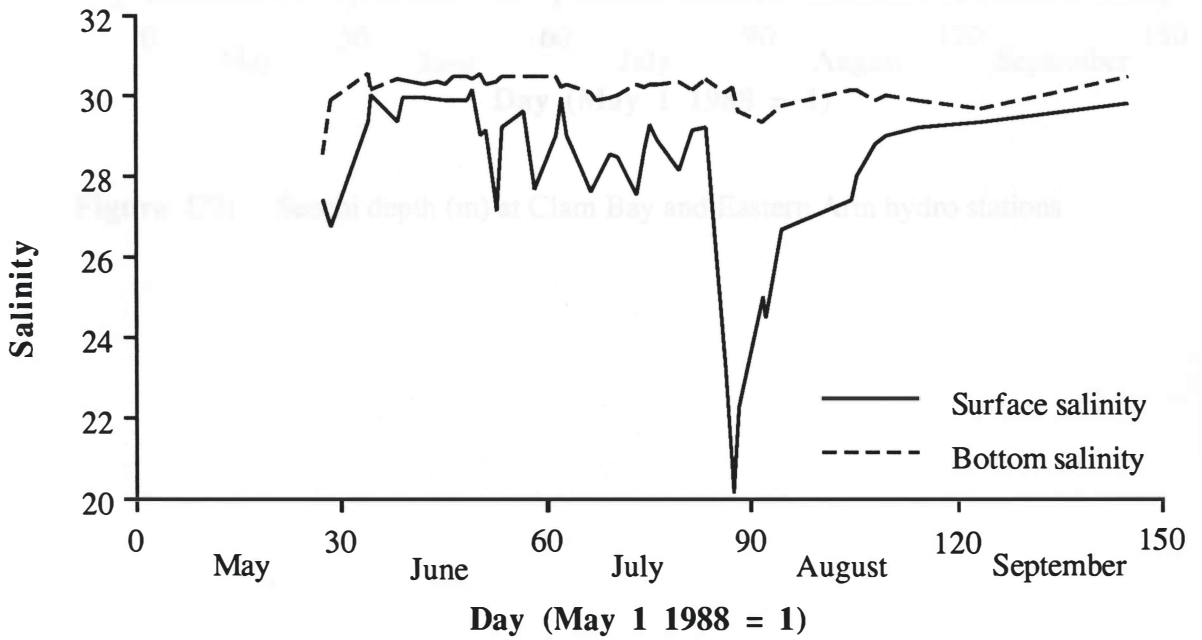

Figure C6: Surface and bottom (8m) salinity, Eastern Arm hydro station

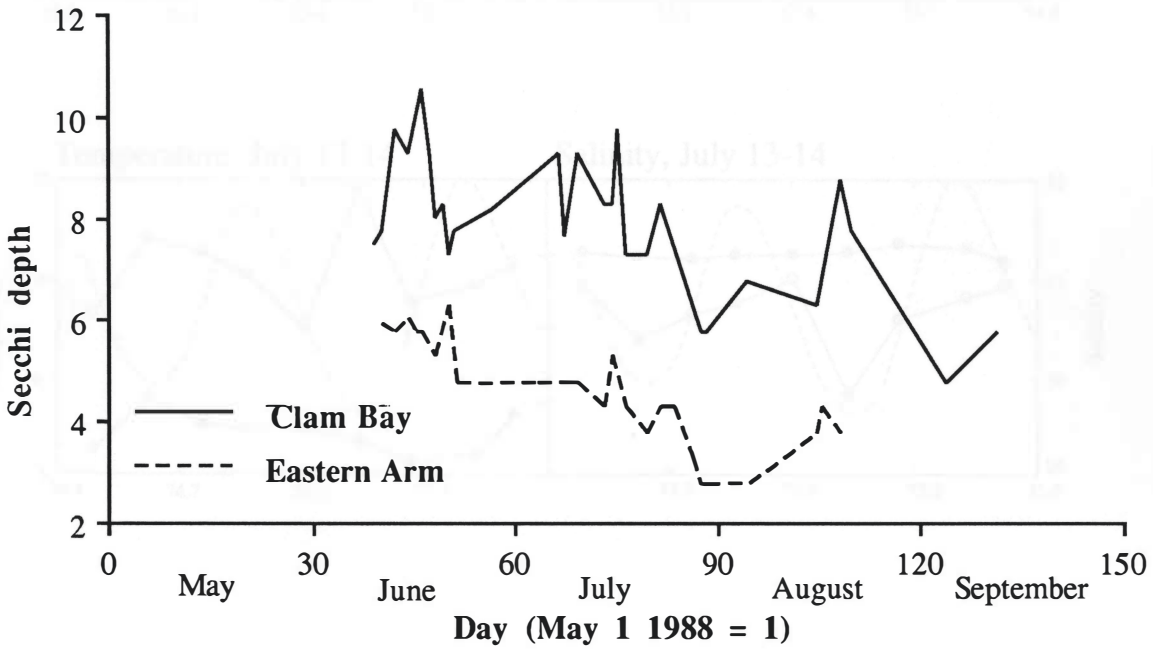

Figure C7: Secchi depth (m) at Clam Bay and Eastern Arm hydro stations

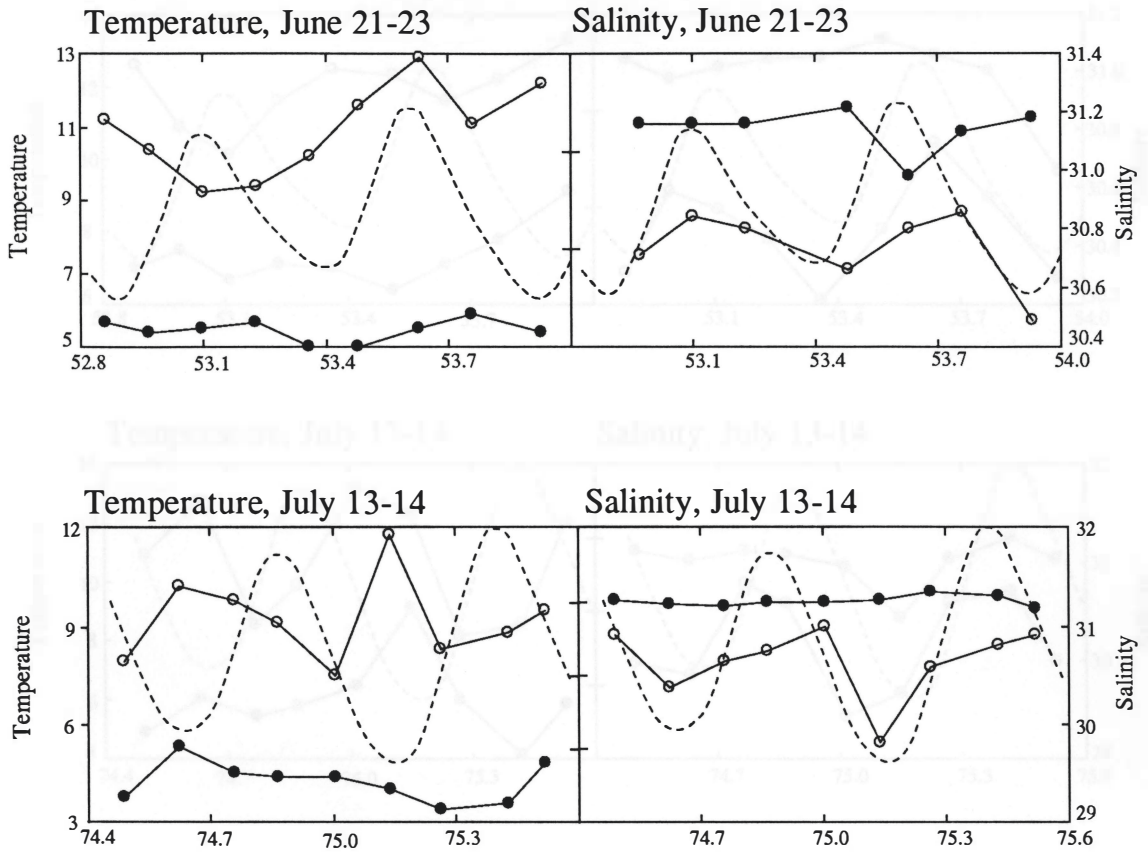

Figure C8: Temperature and salinity profiles at Clam Bay hydro station shown with tidal amplitude (dotted line) during three extended observation periods. Open symbols are for surface samples, closed symbols for bottom samples.
Horizontal axes are days (May 1, 1988 =1). Tidal amplitude 0.5-2.0 m on June 21-23, 0-2.0 m on July 13-14,

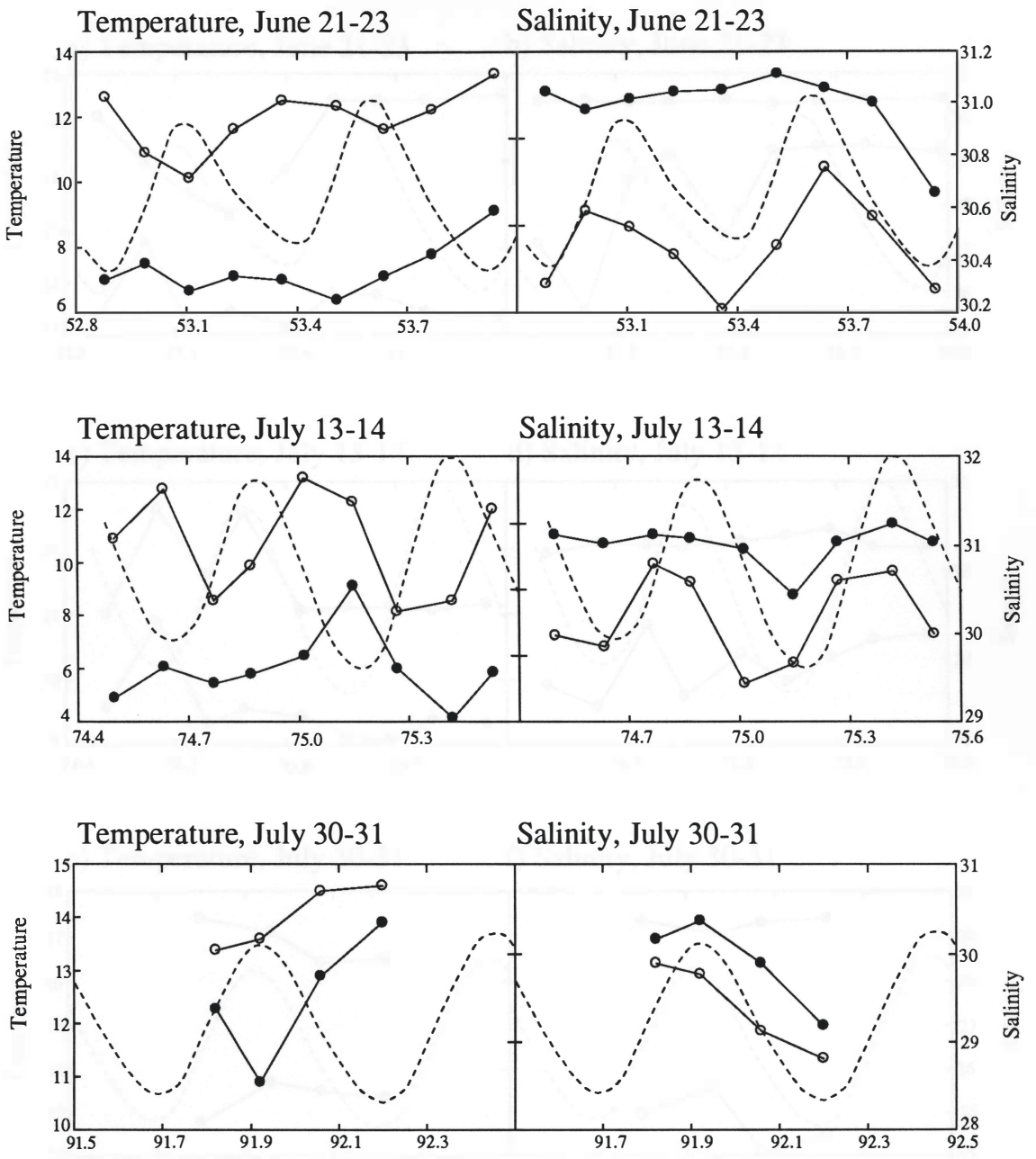

Figure C9: Temperature and salinity profiles at harbour mouth hydro station shown with tidal amplitude (dotted line) during three extended observation periods. Open symbols are for surface samples, closed symbols for bottom samples. Horizontal axes are days (May 1=1). Tidal amplitude 0.5-2.0 m on June 21-23, 0-2.0 m on July 13-14, and 0-3.0 m on July 30-31.

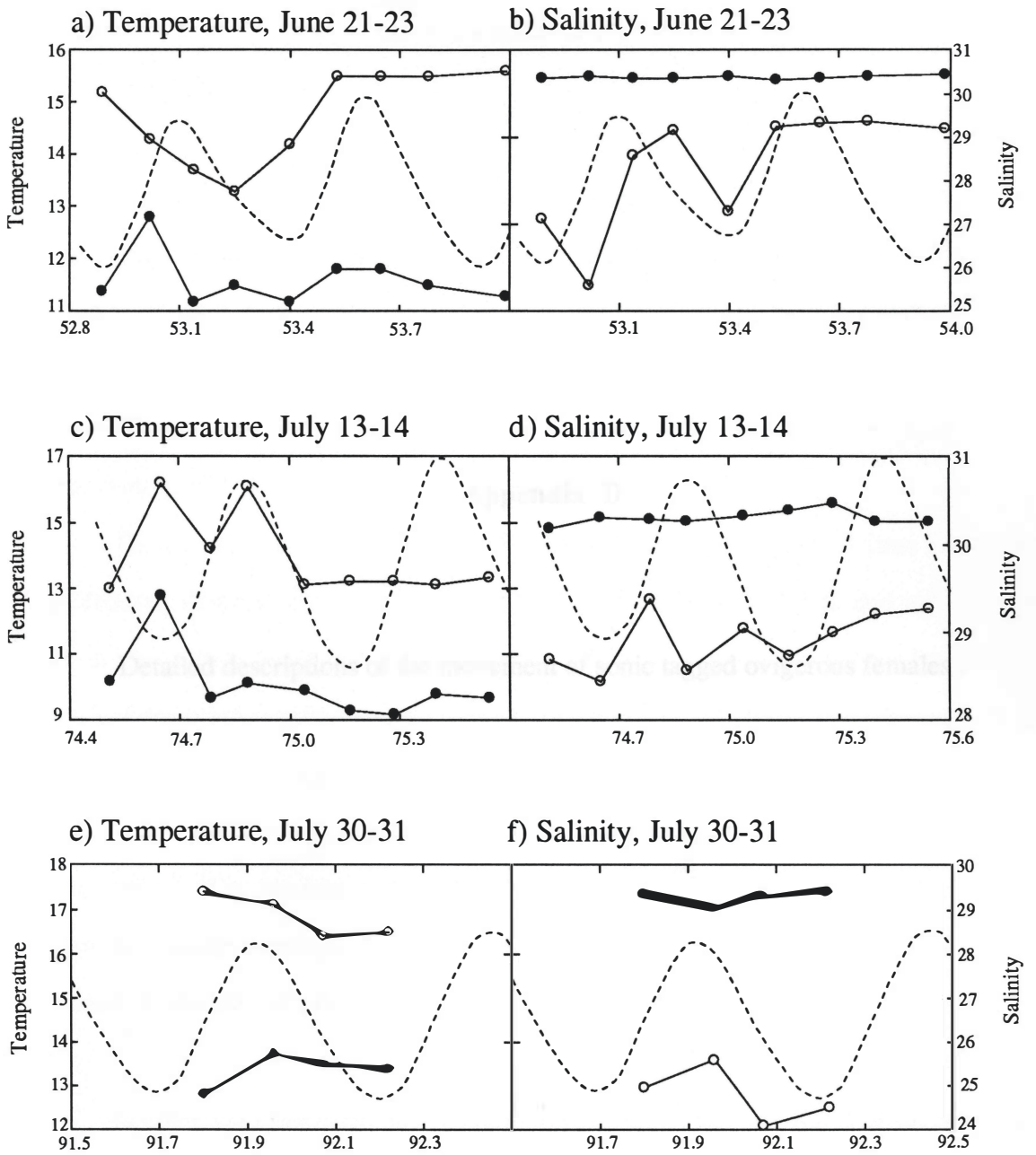

Figure C10: Temperature and salinity profiles at Eastern Arm hydro station shown with tidal amplitude (dotted line) during three extended observation periods. Open symbols are for surface samples, closed symbols for bottom samples. Horizontal axes are days (May 1=1). Tidal amplitude 0.5-2.0 m on June 21-23, 0-2.0 m on July 13-14, and 0-3.0 m on July 30-31.

Appendix D

Detailed descriptions of the movement of sonic tagged ovigerous females .

The lobsters in this portion of the study are identified by the serial number of the transmitter. Plots of the movement of each animal are included in the main bidy of the text (Figures 10-13).

Lobster 5510 was caught by a fisherman in the Eastern Arm of the harbour on June 12, and put into a holding cage at a fisherman's wharf near Rocky Islands. After 2 days in the holding cage, a transmitter was attached, an egg sample taken, and the lobster released near Rocky Islands. The lobster was located on 13 subsequent occasions prior to June 25. During this time she remained on the same reef, in about 4 m of water. After June 25, the signal was lost.

The lobster was relocated almost two months later, on August 15, near the town of East Jeddore. She had travelled roughly 3.5 km up the harbour channel, and was in a rocky area on a gravel/silt bottom near the edge of the channel. The glue holding the transmitter in place had detached, and the transmitter had slipped underneath the cephalothorax, held on by the cable tie. All her eggs had hatched. There were a few remnants, indicating that hatching had probably occurred less than 4 weeks previously (see Results, p. 20). The lobster remained in this area until at least September 15. At this time, the signal from the transmitter became weak, so the transmitter was removed from the lobster and the lobster released. At the time of release, her carapace was still hard.

Lobster 5511 was captured off Cat Rocks on June 16. She had been on board the fishing boat for four hours and ten minutes when we received her, but had been kept cool and moist during that time. An egg sample was taken and the transmitter attached immediately, and the lobster released at the location of capture. She remained in the same location for the next three weeks, sometimes in the same burrow on consecutive days, and sometimes in a different burrow less than 50 m away. This area was characterized by large boulders and ridges overgrown with dense kelp. On July 4 an attempt was made to recover

her so that the transmitter could be replaced. She was deep in a burrow under a 2 m wide rock and could not be recovered by hand, so baited traps were placed in front of the mouth of the burrow. Trapping was tried unsuccessfully on 5 consecutive days.

The lobster was finally recovered by hand on July 9. Unfortunately, one of the claws was pulled off in the process. The lobster was temporarily placed in a holding cage, however she escaped from this and was 1 km away when located next, two days later. She had moved to an area of extremely rugged bottom topography, with a series of 3-5 m high ridges gradually dropping to 20 m. The lobster was located in a shallow rock burrow in dense kelp at the base of one of the ridges. She remained there until August 31, and was observed in three different burrows, each within about 20 m of each other. Several additional egg samples were taken during this period. The signal was not heard after August 31, indicating that either the lobster had moved or the transmitter battery had died. When she was lost on August 31, 5511 still had not hatched her eggs.

Lobster 5513 was initially captured on July 28 in a lobster trap on Dry Ledge, in the Eastern Arm of Jeddore Harbour. At that time, an egg sample was taken and the lobster placed in the holding cage near Rocky Islands. She was kept in the holding cage for two weeks during which she was fed several times. On August 12, another egg sample was taken and the transmitter attached, and the lobster released on Dry Ledge. She could not be located the following day or on any subsequent occasions. Tansmitter malfunction is suspected since the transmitter was an old one that had been used earlier on another lobster and removed.

Lobster 5515 was caught in the Eastern Arm on June 16. She was kept in a holding cage at the fisherman's wharf overnight, then tagged with a carapace tag and released the following day. She was subsequently recaptured during the charter, on August 1, near Rocky Islands. Her eggs had not hatched, and were estimated to be about two weeks away

from hatching at that time (eye index value of 513.7 *u*m).

She was kept in the holding cage until August 12, at which time a transmitter was applied and the lobster released near Dry Ledge. She was located the following day in a burrow on the steep clay wall of the harbour channel east of Brown Islands, about 1.5 km from the release site. There was evidence that the eggs had started hatching when she was examined underwater two days later, on August 15. She was at the base of the channel slope in a burrow under a small rock. One week later, on August 22, she was re-examined: her eggs had all hatched, and the remnants of about half of the egg cases remained. The remnants were gone September 7, when she was next examined. At this time she was in a burrow in the clay slope of the channel. The burrow was located above the thermocline in the channel, and there was a large recently-molted female in a nearby burrow. 5515 was next recovered on September 13, at which time a scar was seen in the integument under the posterior margin of her carapace which appeared to have been caused by a sphyrion tag (prior to her involvement with the current study).

She was last observed on September 20, at which time her carapace was noted as being soft around the edges. One week later, on September 27, the transmitter was recovered from the bottom in mid-channel, attached to the carapace. Apparently, she had molted.

Lobster 6776 was captured in shallow water east of the tip of Jeddore Cape on June 18. She was kept in a holding cage near Big Head with several other lobsters until June 25. She was released near the same location, within 0.5 km of the site of capture, in a shallow (4 m) cove with dense kelp on the bottom. She remained in the same cove until she was translocated on July 20. It required several dives to remove her from this habitat because of the dense kelp, numerous suitable burrows to hide in, and strong wave surge. She was released at Dry Ledge inside the harbour after being on the surface for about three hours. An egg sample taken at this time suggested that the eggs would hatch in about one month

(eye index value of 447.3 *u*m). She did not remain on Dry Ledge, moving eastward to a cove inside the harbour with a flat muddy bottom 10 m deep. Here, she sheltered in a small reef. Her eggs were sampled on July 26 and again on July 29. There was evidence of her eggs having started to hatch on July 29. That was the last time she was located.

Lobster 6777 was caught inside the harbour near Dry Ledge on June 13. She was released the following day with a carapace tag after being kept in the fisherman's holding cage overnight. She was recaptured again on June 18, and returned once again to the holding cage. An egg sample taken at that time suggested that her eggs would only hatch at the end of August (eye index value of 275.4 *u*m). She was released on Dry Ledge with a transmitter on June 25. She was next located near Rocky Islands on July 4, remaining there until July 18. During that time, she remained sheltered in a shallow (3-4 m) reef extending out from one of the islands.

She was translocated on July 18, to a location near the entrance to the harbour. The first release location proved to be unsuitable (sand bottom with no shelter), so she was returned to the surface and taken to another location nearby, where the bottom provided more shelter (rocks with a sand substrate). She remained near the release location until the end of July, at which time she appeared to begin moving towards the harbour mouth. After August 4, she was lost.

She was located next on August 26 well inside the harbour, in a shallow depression in the sand/silt bottom, near several clumps of mussels. She was still berried. An egg sample taken at that time suggested that her eggs were still about three weeks from hatching (eye index value of 466.8 *u*m). Three nemerteans (*Psuedocarcinonemertes haomari*) and some egg cases were found in the egg sample. After this, she was not seen again. An erratic signal was heard in the channel near Brown Islands on August 31, and the transmitter battery appears to have run down.

Lobster 6778 provided considerable data, with 39 observations covering 76 days. She was initially caught on June 18, kept in a holding cage off Big Head for one week, and then released west of Big Head. She remained near the release location until July 19, when she was recovered from a shallow cave under a rock with a garvel substrate. She was translocated to the harbour and released on Dry Ledge.

From Dry Ledge, 6778 moved north to the shore of the Eastern Arm. Here, she remained in rock reefs on the mud bottom, usually sheltered under a piece of kelp. Frequently other lobsters were found in the same reef. She remained in this area for about two weeks, during which her eggs were sampled several times. On August 2, empty egg cases were noted in the egg mass, indicating that some hatching had started (eye index value of 541.0 *u*m).

On August 4, she was located on a flat mud bottom apparently heading across the Eastern Arm towards the harbour channel. Six days later, she was located in the harbour channel south of Brown Island. Only about 40% of the eggs remained, those on the periphery of the egg mass having hatched. By August 15 all of her eggs had hatched, and by August 22, only half of the remnants of the egg mass remained. During this period she was usually found stationary in shallow depressions in the sand/silt channel bottom, or completely unprotected.

She remained in this part of the channel until August 22, after which she headed towards the mouth of the harbour. By September 8, the signal from the transmitter was barely audible. She was recovered from the bottom at the base of the channel slope, nestled against a large rock. Only about 10% of the remnants remained, and her carapace was quite brittle, and soft around the edges. The transmitter was removed, and the lobster released.

Lobster 6779 was released in the Eastern Arm during the fishing season with a carapace tag, and recaptured twice during the following two weeks. After the second recapture, on June 17, when it had become abundantly clear that she wanted a starring role

in this study, she was placed in the fisherman's holding cage for one week. At this time, an egg sample suggested that she was about 4 weeks away from hatching her eggs (eye index value of 449.2 *u*m). She was released on June 25 on Dry Ledge. After two weeks with little activity, the signal was lost, and was never relocated.

Lobster 6780 was originally caught approximately 1.5 km west of Big Roger Island, on June 18. She was placed in a holding cage at the capture location for one week, then fitted with a transmitter and released. At the time of capture, she was estimated to be within 6 weeks of hatching (eye index value of 466.8 *u*m).

She remained near the release location for 2 weeks. Then, from noon on July 12 to 2200h on July 13, she travelled about 2 km west across the approaches to the harbour. This area is roughly 20 m deep with an open sand bottom. She moved to an area about 0.5 km east of Big Head with a typical hard bottom: boulders and rocks on a substrate of mixed stones, gravel, and cobble, and dense kelp. She was recovered on July 25 from under a 1.5 m diameter boulder in a cave open from two sides, and translocated into the harbour. The glue holding the transmitter in place had detached, and the transmitter had slipped sideways down the carapace, held on by the cable tie.

Upon recovery, the transmitter was reattached (the tail of the cable tie was accidentally left on, protruding dorsally underneath the lobster). An egg sample showed that hatching was either imminent or had already started (eye index value of 566.4 *u*m). She was released on Dry Ledge. An attempt to recover her on July 27 to cut the tail off the cable tie failed. She was still on Dry Ledge, inaccessible under a large boulder. Three days later, she remained in the same location. However, on August 2, the signal could not be located, and she was not found subsequently.

Lobster 6781 was caught on June 16 near Big Head. A transmitter was attached immediately, and she was returned to the water within 30 minutes. An egg sample indicated

that hatching was 5 weeks away (eye index value of 478.5 *u*m).

On July 4 an attempt was made to recover her. She was in a cave under a large boulder, and was able to retreat deep enough into the cave that she could not be grabbed. The bottom had large boulders and smaller rocks with dense kelp. A baited trap borrowed from a fisherman was placed in front of the mouth of the cave. The following day, the trap was recovered with the lobster in it. The original transmitter was approaching the end of its battery life, and was replaced with another transmitter. An egg sample showed that she still had 4 weeks to go before hatching (eye index value of 485.1 *u*m). After the new transmitter had been attached, she was replaced by a diver in the same cave from which she had been trapped.

During the next month, she remained in roughly the same location, in 10-15 m of water. She was observed under a 3 m diameter boulder on July 29, and under the same rock on August 2. She was finally recovered on August 4, again using a lobster trap. At this time, the transmitter was worn on the upper leading edge from contact with the roof of the cave. Her eggs had just started to hatch, (eye index value of 566.4 *u*m), and some remnants were visible in the egg mass.

She was next located on August 11, and had moved to deeper water (19-20 m). On August 16, an attempt to recover her failed because she was once again under a large boulder on a rocky bottom. On August 17 a trap was placed in front of the same boulder. The following day, the trap was recovered, but without 6781.A large male lobster was observed in the cave that had contained 6781 the previous day. An ovigerous female from Georges Bank (released south of Jeddore Rock on June 25, 1988) was found in the trap (D. Pezzack, unpub. data).

6781 was located on August 23 about 2 km northeast of her previous location, near the entrance to the harbour. The bottom was 6 m deep, with rocks and boulders on a gravel substrate, and thick *Laminaria* spp. and *Alaria. esculenta.* She was brought to the surface and some epoxy applied to the upper leading edge of the transmitter where it was worn.

Only 5% of the remnants of the egg mass remained. She was replaced in the same burrow from which she had been taken. She was not located on any subsequent occasions.

Lobster 6782 was originally caught in the Eastern Arm on June 17, held in the fisherman's holding cage overnight, and released the following day with a carapace tag. The eye index of an egg sample at this time was 355.9, indicating that she was over 2 months from hatching.

She was recaptured on July 28. Both claws were banded, and one claw had a 1 cm^2 perforation in the propodus. She was put in the holding cage overnight, and the following day fitted with a transmitter and translocated outside the harbour. She was released in 21 m of water about 1 km northeast of Jeddore Rock. An egg sample was taken at this time indicating that she still had 3-4 weeks to go before hatching (eye index value of 457.0 *u*m).

She remained near the release location in 20-27 m of water for one month. Several egg samples were taken underwater during this time. The lobster was located on a bedrock ridge near the edge of a gravel/cobble plain. Macroalgae were sparse at this depth, consisting primarily of *Agarum cribosum*, *Laminaria longicruris*, and *L. digitata.* An egg sample taken on August 11 indicated that the eggs would hatch about one week later (eye index value of 529.3 *u*m), and another sample on August 23 confirmed that there were many remnants in the egg mass (eye index value of 534.8 *u*m).

She had moved about 110 m to the west by August 31 when she was next located. After that, she was lost. On September 9 she was relocated 2 km to the northwest, just off the mouth of the harbour. All her eggs had hatched, and the remnants of about 20% of the egg mass remained. The claw with the perforation was still attached and appeared functional. She was not located again after this.

Lobster 6783 was caught on June 15 off Black Point. She had been on board the fishing boat for about 5 hours when we received her, but had been kept cool and moist

during that time. An egg sample indicated that the eggs still had about two months to go before hatching (eye index value of 392.6 *u*m). She was released off Black Point and remained in roughly the same location for the entire time she was tracked (until the signal was lost on August 17).

She was recovered from a cave under a 2 m diameter rock on June 30 and another egg sample taken (eye index value of 410.2 *u*m). The bottom consisted of large boulders and rocks on a substrate of gravel and stones, with dense kelp. She was recovered again on July 4 and the transmitter replaced with a new one. When she was observed next on July 26, the glue holding the transmitter in place had detached but the transmitter was held in place by the cable tie.The transmitter was reattached and an egg sample taken (eye index value of 492.2 *u*m, about 3 weeks from hatch). In each case when the lobster was brought to the surface, she was returned either to the same burrow or to a nearby one.

On August 11 she was again brought to the surface to reattach the transmitter. By this time she was within one week of hatching her eggs (the eye index was 541.0 *u*m). She was not located on any subsequent occasions.

Lobster 6784 was caught in the Eastern Arm on June 12 and placed in the fisherman's holding cage. Two days later a transmitter was applied and the lobster released on Dry Ledge. An egg sample indicated that hatching would occur in about three weeks (eye index value of 492.2 *u*m).

During the week following her release, she travelled several hundred metres eastwards to a reef leading off a point on the shore. She remained there for several days. Then, during the extended observation period of June 21-23 she wandered around the upper Eastern Arm, moving roughly 1 km between 1500h on June 21 and 0920h on June 22. After this, the signal was lost.

She was next located on July 5 near Rocky Island walking over an open mud bottom, apparently going from one rock reef to another. She was recovered and the original

transmitter replaced with a new one. An egg sample indicated that hatching would occur in about one week (eye index value of 539.1 *u*m).

On July 9 she was located in the same location, but by July 12 had crossed the Eastern Arm and was in the channel east of Brown Island. During the extended observation period of July 13-14 she travelled up and down the channel, ending up at 0920h on July 14 about 100 m south of Brown Island. After this, she continued moving down the channel towards the mouth of the harbour.

When she was observed on July 19, she was at the bend in the channel, past the towns of East and West Jeddore. She was stationary on a highly sculpted bottom of coarse sand in the middle of the channel, where tidal currents are high. This is an area where the fish plants in Jeddore dump their offall, and there were numerous piles of fish carcasses on the bottom. Although there was no evidence of empty egg cases in the egg mass, about 20% of the eggs in the egg sample hatched in the vial before the sample was staged (eye index value of 566.4 *u*m).

She was next observed one week later, having travelled about half the distance back to Brown Island. She was recovered from 14 m in the middle of the channel under a large (3 m diameter) flat rock on a sand/silt bottom. Her eggs had all hatched, and there remained a large mass of the remnants of the eggs. Three days later, on July 29, she was located under the same rock, but most of the remnants were now gone. After this, the signal was lost for two weeks.

6784 was relocated two weeks later, on August 15, west of Brown Island on the edge of the channel which branches into the Western Arm. She was to remain in this area for the rest of the time she was tracked. She was under a kelp frond in the vicinity of a rock reef on a mud/silt substrate. All of the remnants of the egg mass were now gone.

One week later, on August 22, she was observed under a large boulder with a large male lobster. The following day she was under the same boulder, but the large male was gone. Her carapace was still hard around the edges.

On September 1 she was located under a huge boulder (5 m in diameter, 5 m high), again with a large male. She was not observed directly. Six days later, on September 7, the transmitter was recovered from under the same rock with several fragments of the carapace attached, held on by the epoxy. It appears that she moulted. No other shell fragments were seen.

Lobster 6785 was caught off Cat Rocks on July 5 in one of the traps being used to recapture lobster 5511. An egg sample indicated that hatching would occur in about six weeks (eye index of 459.0 μm). She was kept in the trap for 6 days, then fitted with a transmitter and released on July 11. During the two days following her release she travelled about 2 km, first south and then southwest towards the tip of Jeddore Cape. Her progress across the approaches to the harbour continued during the extended observation period of July 13-14, during which she was travelling at the rate of 190 $m \cdot hour^{-1}$ during at least one 3 hour period (between 0305h and 0554h on July 14, 1988). She finally stopped on July 15, east of Big Head, in about 20 m of water.

During the following month she remained near Big Head, moving in to slightly shallower water. She was observed on July 29, and an egg sample taken (eye index value of 498.0 μm, indicating that hatching would occur in about three weeks). She was on a hard bottom, under a rock overhang, in moderate kelp cover. Two weeks later, on August 11, she was observed again and another egg sample taken. She was deep in a cave under a rock, and unfortunately both claws were pulled off in the attempt to extricate her. The egg sample indicated that hatching would occur in one week (eye index value of 533.2 μm). On August 17 she was observed in the same burrow. There was evidence of a few remnants in her egg mass, and some larvae were found in the egg sample (eye index value of 513.7 μm). She was not located again after this.

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