

THE BIOLOGY OF LOBSTERS (HOMARUS AMERICANUS
MILNE-EDWARDS) TRANSPLANTED TO
ST. MICHAEL'S BAY, LABRADOR

CENTRE FOR NEWFOUNDLAND STUDIES

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FRANK ALBERT BOOTHROYD, B.Sc



THE BIOLOGY OF LOBSTERS
(*HOMARUS AMERICANUS* MILNE-EDWARDS)
TRANSPLANTED TO ST. MICHAEL'S BAY, LABRADOR.

BY

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ABSTRACT

In 1982, 1983 and 1985 the Newfoundland and Labrador Department of Fisheries transplanted a total of 4484 adult lobsters (*Homarus americanus*) to St. Michael's Bay, Labrador with the intention of creating a self-propagating population. Studies done during the summers of 1986 to 1988 were designed to assess whether or not the population is propagating and were concentrated on the lobsters of the 1982 and 1985 transplants.

The 1985 transplants had few molting events to 1987, and no spawning events to 1988. The stress associated with the transplant caused the paucity of molting and the lack of spawning observed in 1986. Low water temperature is thought responsible for prolonging the effects of the initial stresses. The 1982 transplants were undergoing more molting events than expected. Possible reasons for this are suggested. The percentage of females that were potentially ovigerous was high, but the percentage of ovigerous lobsters was low; of the latter, the fecundities tended to be low and embryo development retarded. Low temperature is probably responsible; however, the possibility of other complicating factors is also discussed.

The potential reproductive output of the St. Michael's Bay lobsters is too low for the population to become self-propagating. This suggests the physiology of *Homarus americanus* dictates the southerly limit for the species.

DEDICATION

This thesis is dedicated to my father, the Reverend Donald Charles Boothroyd, B.A., M.Div. (1916 - 1979).

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Chapter 1

INTRODUCTION

Biogeography texts often refer to the factors which limit the geographic distribution of organisms as "barriers". Within barriers, individuals of a species can survive and reproduce. Beyond them may be habitat which is not colonized by the species, though the habitat may allow its survival and reproduction.

In the case of marine, invertebrate animals, obvious barriers to geographic distribution include inadequate levels of dissolved salts, or water temperatures that are too high or too low. Each of these are barriers only because of limitations of the species' physiology, which is adapted to limited ranges of environmental conditions. Overcoming barriers to colonize new habitat is often a matter of a species' physiological confines expanding by way of evolution. Where the species in question is of commercial importance, mankind has sometimes intervened by deliberately transplanting members to areas not previously colonized. Sometimes the new area is physiologically acceptable to the species; sometimes it is not.

The economic importance of the American lobster, *Homarus americanus* Milne-Edwards, is such that man has tried to make the species more available by artificially extending its range. *H. americanus* is found naturally in only the

western Atlantic Ocean, from the northern tip of the island of Newfoundland and the Quebec shore in the Gulf of St. Lawrence, south to North Carolina (Cooper and Uzman 1980). In attempts to expand this species' range, small populations of adults have been introduced into the Pacific Ocean approximately thirty times (Conan 1986). The earliest attempt was in 1873 and involved transporting 162 lobsters by train from Woods Hole and Massachusetts Bay to the coast of California (Rathbun 1890). More recent transplants have involved much larger numbers of lobsters: just over 2000 adults were shipped by rail from the east coast of Canada to the coast of British Columbia in 1946 (Butler 1964). None of these introductions have established harvestable lobster populations (Conan 1986).

These longitudinal transplants of *H. americanus* were obviously conducted on the assumption that the only barrier to be overcome for the species to survive in the Pacific Ocean was the barrier of the North American continent. That none of these transplant attempts succeeded does not necessarily rule this out, since even 2000 adults may have been inadequate to initiate a viable population there. Recently, another attempt to increase the natural range of *Homarus americanus* has been made; this attempt was not longitudinal in nature, but latitudinal, and involved the shipping of adult lobsters to St. Michael's Bay, Labrador (Fig. 1).

The Newfoundland and Labrador Department of Fisheries undertook the transplant in an attempt to establish a self-propagating lobster population in St. Michael's Bay. During the summers of 1982, 1983 and 1985 a total of almost 4500 adult lobsters were purchased from Newfoundland commercial lobster fishermen and flown north to the bay. It was not clear what factor or factors were causing

the northern limit of distribution of *H. americanus* to be some two hundred kilometers south of St. Michael's Bay. In much the same way the Pacific Ocean transplants were predicated on the assumption of North America being the only barrier to a successful colonization, the St. Michael's Bay transplant was also predicated on assumed barriers. Various people involved in the transplant assumed, hopefully, that the only reasons for the previous lack of lobsters along the southeastern Labrador coast was the Labrador Current, which would carry any larvae produced there south, and the large amount of ice scour incurred there every winter, eliminating overwintering adults. It was hoped that by transplanting adults to sites in the bay relatively far inland, any larvae these lobsters would eventually produce would not be swept south, but remain in the bay. In addition, the bay would protect the adults from the ice scour associated with more coastal locations. These assumed barriers are based not so much on physiology as they are on circumstances: the larval phase of the lobsters' life-cycle being planktonic; and the adult phase occupying a relatively shallow, benthic habitat in the northern part of their range.

The aim of this thesis is to describe the growth, ovary and embryo development of the St. Michael's Bay lobsters in order to evaluate the potential of the St. Michael's Bay transplants to support a commercial fishery. Data were collected on lobsters from three sites in the bay. Two of these sites had lobsters established in them in 1982, and so the data from them were pooled and are compared to data from a site where the lobsters were introduced more recently. The St. Michael's Bay lobsters are also compared to lobsters from three naturally occurring northern populations.

1.1. General Life History of *Homarus americanus*

Lobsters reach sexual maturity at different sizes, depending on their sex and their geographic location. In Newfoundland waters, 100% of females are functionally mature at carapace lengths (CL's) of 90 to 95 mm (Ennis 1980). Males are sexually mature at a considerably smaller size (Ennis 1980).

The following paragraph on lobster reproduction is summarized from Aiken and Waddy (1980b). The reproductive cycle in female lobsters typically covers two years. In late summer, females molt. A male, which has already molted, then copulates with the soft-shelled¹ female. Sperm are transferred to the female's seminal receptacle by paired copulatory appendages, which are the modified first pair of pleopods of the male. The sperm are contained in spermatophores which soon harden in the seminal receptacle, thus acting as a barrier to further matings by the female. The sperm are stored while the female's paired ovaries are developing. As the ovaries develop, they become darker in color and heavier, and individual ova become larger. These characteristics can be used to qualify the degree of development of the ovary as one of six stages ranging from immature to fully mature and ready for extruding the ova (Table 1). The time period for an ovary to develop to stage 6 is approximately two years, though in the autumn and winter months immediately following spawning very little ovarian development occurs.

¹Technically, lobsters do not have shells but "exoskeletons". The term "shell", however, is almost exclusively used in the scientific literature on lobsters and this practice will be continued here.

The pleopods (or swimmerets) of mature female *H. americanus* contain tegumental glands known as "cement glands". It was once thought that these glands released a substance which allowed newly spawned eggs to attach to the lobster's abdomen. It is now known that these glands do not release a "cement" and their role in egg extrusion and attachment is not known (Aiken and Waddy 1982, Chueng 1966). It is known that the cement glands do become engorged prior to spawning. Aiken and Waddy (1982) have qualified their development to four stages based on morphology. Stages 1 and 2 are indicative of lobsters not ready to spawn, either because of sexual immaturity or the time of year. As normal spawning times approach, the pleopods of those lobsters that will spawn develop rapidly through stages 3 and 4.

In the spring or summer following the late summer molting and mating of the previous year, a female lobster extrudes her ova. At this time the sperm, that have been stored by the female since mating, fertilize the ova. The eggs are extruded through her oviducts, located at the base of both third pereopods. The uropods and telson are curled under the rest of the abdomen effectively trapping the extruded eggs within the pocket so created. Within twenty to thirty minutes the full complement of eggs are attached to the pleopods and the abdominal pleura and sterna.

The number of eggs in a brood is proportional to the size of the lobster. Newfoundland lobsters of 81 mm CL (the current minimum legal size for the fishery) may carry 6000 to 10,000 eggs; a lobster of 120 mm CL may carry 20,000 to 35,000 eggs (Ennis 1981). A substantial number of eggs are lost during the

incubation period due to attrition and/or insecure attachment. Perkins (1971) estimated that an average of 38% of the brood of offshore lobsters is lost between the time of extrusion and hatching. The fecundity estimates of Ennis (1981) reported above were calculated after the majority of this egg loss would have occurred.

The incubation period of the embryos is temperature dependent. At a steady temperature of 10°C, the time from extrusion to hatching of an embryo is almost 40 weeks (Perkins 1972). Under normal temperature regimes, lobsters in Atlantic Canada have incubation periods of from 10 to 12 months (Aiken and Waddy 1986).

Most of the thousands of larvae in a brood hatch at night, over a period of 15 to 31 days (Ennis 1975). This hatching period occurs in the summer and has been reported to be synchronized with the period of most rapid temperature increases (Hudon and Fradette 1988). The first appearances of stage I larvae tend to occur with surface temperatures in the range of approximately 11° to 13°C (Harding et al. 1983). Lobsters hatch as prelarvae (Davis 1964) and immediately undergo their first molt to pelagic stage I larvae. Three more molts occur before the larvae become postlarvae and settle to the substrate.

The duration of each larval stage and of the postlarval stage is temperature dependent. At temperatures of approximately 10°C the duration in days of each stage is the following: stage I, 13±1; stage II, 18±4; stage III, 25±3; postlarva, 54±2 (MacKenzie 1988). It is critical that larvae complete their metamorphosis

into postlarvae prior to declining water temperatures in the autumn, since at 5°C, larvae generally die prior to completing the metamorphosis (Templeman 1936).

There are two hypotheses regarding larval recruitment processes in the American lobster (Ennis 1986a): first, that larvae drift passively with currents and settle where they've been carried during their development time; and second, that larvae undergo directed vertical movements and thereby use currents of different directions to allow them to settle at their origin. Other work by Ennis has investigated the swimming abilities of the larvae. Larval stages I to III, although active swimmers, are able to maintain their positions only in weak currents; postlarvae are much stronger swimmers (Ennis 1986b) and can maintain their positions in relatively strong currents.

Soon after becoming postlarvae, they switch from being positively to negatively phototactic and positively thigmotactic (Botero and Atema 1982). It may, however, be quite late in the postlarval stage before actual settlement on a substrate occurs (Cobb et al. 1989).

Once settled to the substrate, lobsters are referred to as juveniles until they are sexually mature. Larval, postlarval, juvenile and adult lobsters grow by molting. Molting, or ecdysis, involves the removal of the exoskeleton followed by the rapid expansion of the newly exposed, soft exoskeleton before it hardens. The number of molts per unit time and the increase in length per molt varies with the size of the lobster. The percentage length increase at molt decreases and the intermolt time interval increases with increasing carapace length (Aiken 1980).

For areas where lobster populations have a well-defined and relatively short annual molting period, Ennis (1977) has established criteria by which the "shell condition" of lobsters can be determined. Old-shelled lobsters are those that did not molt during the most recent molting period of that population; new-shelled lobsters did molt during the period.

Adult lobsters are territorial (Ennis 1984d), and during the autumn in Newfoundland they move to deeper water (Ennis 1984c). Elsewhere in its range, extensive inshore - offshore migrations have been reported (Campbell 1986, Campbell and Stasko 1986, Pezack and Duggan 1986).

Chapter 2

MATERIALS AND METHODS

The total number of lobsters transplanted to St. Michael's Bay in the three years was 4484. Depending on the shipment, the lobsters had a mean carapace length (CL) of from 84 to 89mm (Table 2). The minimum size of the lobsters was 81mm and the maximum size in each shipment ranged from 92 to 114mm (Table 2). The lobsters were released at eight sites in the bay. No records were kept of the numbers released at each of the sites. The year the lobsters were placed at the individual sites is known.

Results from the preliminary sampling period indicated that only three of the eight sites had lobsters in sufficient density to warrant further study. The sites are Goose Island (1985 transplant year), and Indian Arm and Mussel Tickle (both 1982 transplant year) (Fig. 2). In this thesis both "intra-population" and "inter-population" comparisons are made. Within St. Michael's Bay, the longer established Indian Arm and Mussel Tickle lobsters are compared to the newly established Goose Island lobsters. Data from the former two sites are combined, and the name Indian Arm used in reference to both sites. The Goose Island and Indian Arm data are also compared to data from three naturally occurring lobster populations from insular Newfoundland sites: Comfort Cove, Port au Port, and Pistolet Bay.

A total of 1988 lobsters were transplanted in 1982. The mean CL of the males released that year was 89.1 ± 6.4 mm, and of the females was 88.9 ± 6.2 mm (Table 2). The largest male was 114mm CL and the largest female was 112mm CL.

The 1985 transplant involved 1498 lobsters. The mean CL of the males was 84.1 ± 2.7 mm and the maximum was 95mm (Table 2). The mean CL of the females was 84.4 ± 2.6 mm and the maximum was 92mm (Table 2).

2.1. Biological sampling

The sampling periods in St. Michael's Bay varied both in timing and duration over three study years. In 1986, work was conducted from July 22 to August 25. In 1987, there were two periods of study: July 18 to July 25 and August 26 to September 3. The 1988 study took place from June 25 to July 2. Lobsters from three control sites (Port au Port Bay, Comfort Cove, and Pistolet Bay) were studied in 1987, during the period of May 27 to June 5.

The methods employed to capture the lobsters in St. Michael's Bay varied from year to year. In 1986, all lobsters were caught with standard lobster traps using herring and mackeral as bait. Lobster traps were also used in 1987 as the primary means of capturing lobsters, but some were also collected by diving. In 1988, all lobsters were obtained by scuba divers. The lobsters from the control sites were obtained from local commercial lobster fishermen. Special permits allowed the retention of ovigerous females for study.

The numbers and sizes of lobsters used for each of the procedures described

below varied from year to year and between the study sites (Table 3). Reference to this table should be made at each of the following sections.

2.2. Growth

During the 1986, 1987 and 1988 sampling periods, carapace lengths (to the nearest millimeter) were determined for each lobster caught. Carapace lengths were measured from the base of an eye socket to the posterior edge of the carapace, parallel to the mid-dorsal line. In 1986 and 1988 shell conditions were determined using the criteria of Ennis (1977) to see if the lobsters had molted the previous summer. No shell conditions were determined for lobsters caught in 1987.

Two methods were used to calculate the expected number of new-shelled lobsters. For the Indian Arm lobsters, carapace lengths of new-shelled animals were put into the equations of Ennis et al. (1982) for Comfort Cove lobsters to calculate the premolt CL's. The premolt CL's of new-shelled lobsters were combined with the measured CL's of the old-shelled lobsters and arranged in 5 to 10mm groups with the exception of the largest and smallest size groups. As there were too few lobsters in such groups to be meaningful, broader size classes were ultimately used. The total number of lobsters per group and the percentage of those with new shells were then determined for males and females.

Due to the limited size ranges of the males and females from Goose Island, median carapace lengths for the 1986 and 1988 study years were determined. The expected number of new-shelled lobsters at each median size was then calculated

by substituting the median CL into the equations of Ennis et al. (1982) for Comfort Cove male and female lobsters. The actual number and expected number of new-shelled and old-shelled lobsters from both Goose Island and Indian Arm were compared using the chi-square statistic.

The mean carapace lengths of males and females from Goose Island and Indian Arm were calculated for their respective years of transplant and for the three study years. The mean CL's of the same population for different years were compared using a two-sample t-test (Anon. 1988).

2.3. Ovary Development

Lobster ovaries undergo changes in size and color during their cycles of vitellogenesis and oviposition (Aiken and Waddy 1980a,b). Six stages have been identified for the ovaries of the American lobster (Table 1), and these are believed effective in comparing ovary development among female lobsters (Aiken and Waddy 1980a,b).

At each of the three control sites 30 non-ovigerous female lobsters were obtained from local fishermen during the period of May 27 to June 5. In St. Michael's Bay, the 1987 ovary sampling was done on 30 non-ovigerous lobsters from July 18 to July 25; in 1988, 35 such lobsters were examined from June 25 to July 2. No ovaries were examined in the 1986 St. Michael's Bay study.

All ovaries were examined while still fresh. Each ovary was first weighed and its color noted. Then the membrane of the ovary was torn and a sample of ova examined using a dissecting microscope. Diameters of ten ova were measured

to the nearest 0.1mm using an ocular micrometer. The average ovum diameter was then calculated. The lobster's ovary weight and carapace length were used to calculate an ovary factor (O_f) for each lobster (Aiken and Waddy 1980a,b):

$$O_f = [\text{Ovary weight}(\text{mg}) / \{\text{carapace length}(\text{mm})\}^3] \times 10$$

The color, mean ovum diameter, and ovary factor of each female lobster were then used to determine ovary stage (Aiken and Waddy 1980a,b) (Table 1).

2.4. Fecundity

Fecundity estimates were obtained in 1987 and 1988 to determine whether or not the St. Michael's Bay lobsters were incubating embryos in numbers comparable to lobster in natural populations. All fecundity estimates were made in a manner similar to Ennis (1981). Abdomens with intact broods were fixed with 10% formalin buffered in seawater. At a later date the eggs were removed from the abdomen with forceps and placed in petri dishes containing fresh water. After soaking for 24 to 48h the eggs from each brood were air-dried for 48h and then oven dried at 60-70°C for a minimum of 72h. When repeated weighings of the broods indicated no further desiccation, the eggs were removed from the oven. Eggs were then rubbed manually to remove connective tissue. Whole broods were weighed to the nearest 0.01 g and then subsamples comprising an estimated 10% of the whole brood were also weighed and subsequently counted. The number of eggs in each whole brood was then extrapolated. Several broods were counted entirely and the resultant number of eggs compared to the estimated number. In all cases the differences were less than 5% and the estimated numbers were

considered acceptable. All broods containing less than 1000 eggs were counted manually. Any eggs previously removed from individual broods for other observations were added to the preceding estimate.

Expected fecundity values for each ovigerous lobster from St. Michael's Bay were calculated using Ennis' (1981) equation for Paradise, Placentia Bay lobsters.

2.5. Embryo Development

Embryo development can be monitored by measuring the size of the eye pigment to determine the approximate date of hatching of the embryo. The standard measurement for this is the Perkins Eye Index (PEI) (Perkins 1972):

$$(1) \quad PEI = \frac{\text{greatest length (um)} + \text{greatest width (um)}}{2}$$

The lowest PEI which can be measured is approximately 70; hatching occurs at a PEI of approximately 560 (Perkins 1972). To calculate the number of weeks remaining to hatch for an embryo with measurable eye pigments, the following equation of Perkins is used:

$$(2) \quad T_w = \frac{560 - Y}{-8.3151 + 2.6019(x)}$$

where T_w is the time remaining to hatch in weeks, Y is the embryo's PEI and x is the developmental temperature in degrees Celcius. All eggs to be examined were

taken from the periphery of the brood, just posterior to the left third pleopod (if sufficient numbers were unavailable at that site eggs were taken from proximate areas) and placed in a petri-dish with fresh water. Eye pigment measurements were taken with a dissecting microscope equipped with a camera-lucida and computerized digitizer. The embryos were viewed at 50x magnification.

In the 1986 study, samples of approximately 20 eggs each were taken from three ovigerous lobsters to have PEI's calculated. In the 1987 and 1988 studies (including the control sites) approximately 30 eggs were taken from each ovigerous female and if a brood was comprised of less than 30 eggs, all were examined. The temperature at 7m in St. Michael's Bay ranged between 9 and 11°C during most of July and August and so the time to hatching of eggs was estimated with $x=10^{\circ}\text{C}$.

2.6. Other

Incidence of ovigerous females. To determine the percentages of ovigerous females in St. Michael's Bay, all female lobsters obtained were inspected for the presence of eggs on their abdomens. A total of 285 females from Goose Island and Indian Arm were examined during the three study years.

Cement Gland Development. To determine what percentages of non-ovigerous females would be extruding eggs, the development of pleopod cement glands was assessed. This was done in 1987 and 1988 for the St. Michael's Bay lobsters and in 1987 for the control sites. The endopod of the second pleopod of non-ovigerous female lobsters was severed with scissors. The endopod was then

examined under a dissecting microscope and the cement gland stage determined using the criteria of Aiken and Waddy (1982).

Incidence of Mating. To determine whether or not the female lobsters in St. Michael's Bay had successfully mated, every female which had its ovaries examined or fecundity estimated in 1988 also had its seminal receptacle dissected. The presence or absence of a spermatophoric mass within the seminal receptacle was noted.

Plankton Sampling. Plankton samples were collected for the sole purpose of obtaining lobster larvae and determining their stage of development. Extensive surveys were conducted in St. Michael's Bay during the periods of July 28 to August 22, 1986 and July 18 to August 30, 1987. A plankton net with a mesh size of 350 μm and a mouth aperture of 1 m was towed behind a small boat and just beneath the water's surface during daylight hours in the areas of the lobster release sites. Typically, one 15 minute tow was made per release site per day.

2.7. Water Temperatures

A Ryan thermograph was maintained in St. Michael's Bay from the summer of 1986 to the autumn of 1988. The device was anchored in Indian Arm (proper) (Fig. 2) in approximately 7m of water. The temperature record was periodically removed from the thermograph and daily temperatures were read by eye to $\pm 0.5^\circ\text{C}$. Mean daily temperatures were calculated to obtain a representative annual water temperature regime for St. Michael's Bay. The greatest difference in daily temperatures between years occurred during November of 1986 and 1987, at which time the differences were never more than 1.5 degrees.

No temperature data are available for the period of May 29 to June 27, 1987 due to the recording tape expiring and mechanical failure at that time in 1988. The water temperatures during this period were therefore estimated.

Mean annual water temperatures for *Comfort Cove* and *Port au Port Bay* corresponding to the dates of the *St. Michael's Bay* temperature readings were obtained from G.P. Ennis (unpub. data). Temperature data for *Pistolet Bay* were unavailable.

Chapter 3

RESULTS

3.1. Biological Sampling

3.2. Growth

Mark/recapture techniques were not practiced in this study. Hence, growth is inferred from changes in size composition and from the numbers of lobsters having new and old shells.

The size-frequency distributions of both the Goose Island males and females changed little between 1985 and 1986, but by 1988 a noticeable increase in carapace length had occurred in both sexes (Fig. 3). The Indian Arm male and female sizes increased substantially between the time of their transplant (1982) and the first study year (1986) (Fig. 3). In the latter case the males had reached larger sizes than had the females.

For both the males and females from Goose Island there were significant differences between the observed and expected numbers of new-shelled lobsters. In 1986 there were significantly fewer male and female lobsters found with new shells than expected ($P < .005$ for both males and females) (Table 4). In 1988 the opposite was true: more new shelled lobsters found than expected ($P < .05$ males, $P < .005$ females) (Table 4).

The percentages of Indian Arm lobsters with new shells ranged from 13.0% (males) and 6.3% (females) to 62.5% and 75.0% respectively for all years combined (Fig. 5). The smallest of the 1986 Indian Arm male size classes (90mm CL) had the same numbers of lobsters with new and old shells as predicted (Table 5). The three larger size classes had significantly more new-shelled lobsters than predicted ($P < .005$ for each) (Table 5). Again in 1988 these same three size classes all had significantly more new-shelled lobsters than expected ($P < .005$ for each) (Table 5). For the 1986 Indian Arm females, only the 85mm size class had significantly more new shells than predicted ($P < 0.025$) (Table 5). In 1988 the 93mm and 98mm size classes were significantly greater than the expected values ($P < 0.005$ for both). The largest size class (105mm) showed no significant difference ($P < 0.975$).

The mean carapace length of the Goose Island males was 84mm when transplanted in 1985 and had increased by 12mm during the three years they were at liberty in St. Michael's Bay (Fig. 4). The Goose Island females also had a mean carapace length of 84mm when introduced; their average carapace length increased by 9mm during the three years (Fig. 4). There was no significant difference in the mean carapace lengths of the Goose Island males between 1985 and 1987 ($T = -2.15$; $df = 6$; $P = 0.075$) but there was between 1987 and 1988 ($T = -5.22$; $df = 11$; $P < 0.01$). The Goose Island females had significantly different mean CL's between 1985 and 1987 ($P < 0.01$) and between 1987 and 1988 ($P < 0.01$).

The mean carapace lengths of the Indian Arm males was 89mm when

transplanted in 1982, and during their six years in St. Michael's Bay increased by 27mm (Fig. 4). The females originally averaged 89mm CL and increased by 14mm during the 6 years. The mean CL's of the Indian Arm males and females were all significantly different ($P < 0.01$) for the years tested (1982 and 1986; 1986 and 1988).

3.3. Ovary Development

In 1987 and 1988 53% of the Goose Island lobsters had stage 4 ovaries. Stages 3, 5 and 6 were nearly equally represented at 13% to 17% (Fig. 6). The Indian Arm lobsters had stages 3 to 5 in 11% to 20% of the lobsters examined; stage 6 ovaries were found in 51% of the lobsters (Fig. 6). The lobsters from both Port au Port and Pistolet Bay had predominately stage 4 and 5 ovaries; the Comfort Cove lobsters had predominately stage 5 ovaries (Fig. 7).

None of the ovaries of the St. Michael's Bay lobsters or the lobsters from the three control sites had ovaries in stages 1 or 2, indicating all lobsters examined would have been expected to spawn in the upcoming summer. Of the stage 6 ovaries, none had ova "free in the ovary", a state which, along with the characteristics of a stage 6 ovary, indicates impending extrusion of the ova (Aiken and Waddy 1980a,b) (Table 1).

3.4. Fecundity

Only nine ovigerous lobsters were included in St. Michael's Bay samples in 1987 and 1988. One female 102mm CL and another 95mm CL carried nearly 18,000 eggs each which represented 84% and >100% respectively of the expected

fecundities (Table 6). The other seven had brood sizes ranging from $<0.1\%$ to 45% of the expected number.

3.5. Embryo Development

Egg samples were obtained from twelve ovigerous females caught in St. Michael's Bay from 1986 to 1988. In only four of these was development sufficiently advanced for the eye pigment to be measured and Perkins Eye Indices (PEI's) to be determined (Table 7). The highest mean PEI was 470 for an egg sample taken on June 29, 1988 for which the projected date of hatching, at a developmental temperature of 10°C , was August 4, 1988. The lowest mean PEI was 108 for a June 30, 1988 sample for which the projected date of hatching was December 26, 1988. For the two samples taken on July 19, 1987 and August 1, 1986, the mean PEIs were 127 and 431, respectively for which projected hatching dates were January 6, 1988 and September 21, 1986 (Table 7).

PEI values from the three control sites ranged from <70 to 419 PEI for Port au Port, 148 to 429 for Comfort Cove and <70 to 308 for Pistolet Bay, all obtained over an eight day period (Fig. 8). The estimated time of hatching of eggs from Port au Port using the Perkins Eye Index and based on a 13°C development temperature was from July 3 to July 15 for six out of ten broods (Table 7). The other Port au Port broods were calculated to begin hatching around September 20, 1987. The Comfort Cove broods were calculated to hatch from July 19 to November 7, 1987 based on a 10°C developmental temperature (Table 7). At the same temperature, eight of ten broods from Pistolet Bay were calculated to hatch from September 10 to November 14, 1987. The other two broods were calculated to hatch some time after November 14 (Table 7).

3.6. Other

Incidence of ovigerous females. The incidence of ovigerous females in the Indian Arm sample ranged from 8.0% in 1987 to 19.3% in 1986 (Table 8). None of the 103 females examined from Goose Island during the three study years was ovigerous. There was no clear association of female size with incidence of ovigerous females; the smallest ovigerous female was 81mm CL.

Cement gland development. In all cases the pleopod cement glands were stage 1 or stage 2.

Incidence of mating. A spermatophoric mass was present in all lobsters for which it was searched.

Plankton surveys. No lobster larvae were found in any of the plankton samples. Crab larvae, copepods, and gelatinous zooplankton were common in the samples.

Anecdotal reports. The fishermen of St. Michael's Bay have provided some information relevant to the lobster transplant. Small-scale scallop dragging is conducted in St. Michael's Bay and on several occasions what were thought to be juvenile lobsters have been caught in the drags. I have examined two such specimens and in both cases the organism in question was *Schlerocrangon boreas*, a benthic crangonid shrimp species. Many of these anecdotal accounts of "small lobsters" have been, and undoubtedly will be, received. That these reports persist is probably due to the size of these shrimps (~10 cm total length), their red

coloration and the desire of the local people to find proof of recruitment to the initial lobster population.

Other information provided by fishermen has proven more valuable. Five lobsters have been retrieved from areas not stocked with lobsters. The closest of these areas to the transplant sites is off Square Island, at the mouth of St. Michael's Bay. The farthest site is near Rigolet, Labrador, over three hundred kilometers north of St. Michael's Bay.

3.7. Water Temperatures

The annual water temperature regime of St. Michael's Bay is slightly colder than that of Comfort Cove and substantially colder than Port au Port temperature regime. In St. Michael's Bay, bottom temperatures at 7 m are below 0°C from mid-November through to mid-May (Fig. 9). In later May, temperature increases rapidly to a peak of about 11°C in August. By mid-September it begins to decrease rapidly and reaches sub-zero values by mid-November (Fig. 9).

The mean annual minimum and maximum bottom temperatures at Comfort Cove (9 m depth) are similar to those of St. Michael's Bay at 7 m depth (Fig. 9). A peak temperature of approximately 11°C occurs in mid-August in both areas. At Comfort Cove, temperature begins to decline later in September but does not fall below 0°C until February. By April, temperature begins to rise more or less steadily until the peak in mid-August.

The bottom temperature (9 m depth) at Port au Port both increases and declines less rapidly than that of St. Michael's Bay (Fig. 9). The spring increase

occurs at approximately the same time (May), but the Port au Port temperature has reached 11°C in July. The peak temperature is approximately 15°C, and occurs in late August to September. In later September the temperature begins a rapid decline.

Chapter 4

DISCUSSION

4.1. Molting and Growth

Goose Island lobsters

The low proportion of molting in the early fall of 1985, as indicated by the low number of new-shelled lobsters recovered from Goose Island in 1986 (Table 4) and the small change in size-frequency distribution (Fig. 3), may have been due to stress just prior to, and during, the lobsters' transplant to St. Michael's Bay in the spring of 1985. Stresses, such as confinement and handling have previously been credited with decreasing growth rates in lobsters. Stewart and Squires (1968) found that under restrictive conditions (such as those commonly found in the boxes used by lobster fishermen to hold their catch) the incidence of molting dropped to 70% or more of that of a free population. Even repeated handling of lobsters, such as occurs with sub-legal sized lobsters during the fishing season, serves to inhibit molting (Ennis 1971). Such conditions would have been experienced by the St. Michael's Bay lobsters prior to and during their capture in Comfort Cove and subsequent transplant to Labrador.

Following the 1986 study some molting events did occur, as indicated by the

slight rise in the mean CL in 1987 (Fig. 4) and the change in size frequencies (Fig. 3). Similar findings in 1988, and the high percentages of new-shelled males, suggest that by 1988 the Goose Island males had recovered from the stresses imposed on them during the transplant.

The low number of female lobsters from Goose Island that underwent a molt in the fall of 1985 was not unexpected. Since these females were all originally caught in Comfort Cove by the commercial fishery, the majority of them would be at the same stage in their reproductive cycles: the ovaries would be completing vitellogenesis in preparation for spawning in the summer of 1985 (Aiken and Waddy 1980b). Ennis (1980) reports twenty percent of non-ovigerous females ≥ 81 mm CL have not reached sexual maturity when caught. Since the minimum size of the lobsters sent to St. Michael's Bay was 81mm CL, most of the females would, then, be preparing to spawn that summer. A minority of the females may have been preparing to molt and then spawn that same summer. This latter case is most common in warmer-water populations (Aiken and Waddy 1980b, Ennis 1984b, Attard and Hudon 1987). Hence, for the majority of these females, no molt was expected, but they would have been expected to extrude eggs after arriving in St. Michael's Bay and did not (Table 8).

Shell conditions were not determined in 1987, and hence the percentages of females (or males) that had molted in 1986 could not be estimated. The small change in size-frequencies between 1985 and 1986 (Fig. 3), however, suggests a very low incidence of molting. It is clear that in 1987 these lobsters did not extrude eggs (Table 8) and the majority molted, as indicated by the high number

of new-shelled females found in 1988 (Table 4). This suggests that, as seems the case for the males, the females tended to finally overcome the stresses of the transplant by 1988. This is only apparent in their growth, however, and not in reproduction.

Of the many factors which affect growth of lobsters, temperature is considered the most important (Aiken and Waddy 1986). Temperature affects both the time of molting and the number of lobsters of a given size undergoing a molt. The shorter the period of warm, summer water temperatures, the shorter the period available for successful molts to occur in a population (Aiken and Waddy 1986). When water temperatures drop below approximately 5°C the molting process is usually blocked until they again rise above 5°C (Aiken 1980). Clearly, the temperatures experienced by the St. Michael's Bay lobsters are not so low so as to prevent molting; the temperatures may, however, be such that they prolong the stressful affects experienced by the lobsters shipped to the bay.

Indian Arm lobsters

The Indian Arm lobsters have much higher percentages of new-shells throughout their size classes (Fig. 5) than those expected from the proportion molting curves of Ennis et al. (1982). Although the curves of Ennis et al. do underestimate the proportions of large lobsters molting, it is unlikely that it would be to the high degree suggested by the high proportions of large lobsters molting in St. Michael's Bay. The broader size classes used in this study compared to Ennis et al. (1982) would serve to increase the proportion molting in each size

class. However, Aiken and Waddy (1986) reported that the proportion of lobsters of a given size that molt each year is higher in warm-water areas. Ennis (1983) observed higher proportions of lobsters molting in Placentia Bay than in Comfort Cove, where they are subjected to a colder temperature regime. Since the water temperatures in St. Michael's Bay tend to be lower than those of Comfort Cove, the high proportion of animals molting in St. Michael's Bay may be related to factors other than temperature. Consideration must, of course, be given to yearly variations in the proportions molting (Ennis et al. 1982, Ennis 1983, Aiken and Waddy 1986), but of the seven chi-square tests done on the 1986 and 1988 Indian Arm males with new and old shells, six were significantly different, of which all had a higher proportion of new shells than expected.

What factors may be influencing the molting process? One possible factor is prey. Prey items may be more available to the St. Michael's Bay population than to lobster populations elsewhere. However, even if greater food intake does increase molt frequency (see Aiken 1980), it is not clear that there is more food available to the St. Michael's Bay lobsters. Also, there is no indication from the literature that food availability might limit lobster growth in the wild.

A more plausible explanation involves the abiotic conditions of St. Michael's Bay. Aiken and Waddy (1976) found increased molt frequency with long photoperiod in colder water compared to the same in warmer water. Photoperiod has recently been implicated in molting and reproduction in female lobsters (Nelson et al. 1983, 1988a,b; Nelson 1986), but this relationship is now thought to apply only to lobster populations experiencing little seasonal variation in

temperature (and, therefore, not in St. Michael's Bay) (Aiken and Waddy 1989). The high proportion of St. Michael's Bay lobsters molting may be due to a synergistic effect of temperature and photoperiod. Aiken and Waddy (1976) reported lobsters held at 10°C on a short photoperiod took nearly four times as long to complete a molt than those held at 20°C with the same photoperiod. Under a long photoperiod at 10°C, days to molting decreased by almost 50%; at 20°C days to molting decreased by less than 15% (Aiken and Waddy 1976). Yet, the absolute time to molting was longer at the lower temperature. Photo-intensity may also be implicated, depending on the ability of lobsters to perceive light, the amount of snow and ice cover St. Michael's Bay gets every winter, and the depths at which lobsters live. Some work has been done on light perception in *H. americanus* (see Ache and Macmillan 1980), but the relationship among photoperiod, light perception and molting is not clearly understood.

My data are insufficient to show that the high proportion of molting in St. Michael's Bay is a product of the environmental characteristics of the bay. The data do show, however, that molting does occur, and that at least one of the conditions required for successful fertilization of ova is met there: the presence of soft-shelled (i.e. recently molted) females. The data also indicate St. Michael's Bay is within the limits imposed by *H. americanus*' physiology regarding molting. This suggests that the northern limit of lobsters is not due to their inability to complete molting events in areas further north.

4.2. Reproduction

The ovaries of *Homarus americanus* undergo a two-year seasonal cycle of development. Aiken and Waddy (1980b) describe the cycle as being composed of two phases: primary and secondary vitellogenesis. Primary vitellogenesis occurs over many months during the warming of the water in spring. In the winter there is little ovarian development. During the following spring, secondary vitellogenesis occurs and culminates in spawning that summer or autumn (Aiken and Waddy 1980b). In the spring of the second year, then, non-ovigerous female lobsters have ovaries which are in stage 4, 5 or 6, depending on the proximity to egg extrusion.

The timing of the studies in St. Michael's Bay and the control sites was such that the ovaries were examined prior to the spawning period for the population in question and also prior to the hatching period of the embryos that were spawned the previous summer. It would have been preferable to examine the ovaries earlier in the spring of each year and the ovigerous females the following autumn. This would have allowed direct comparisons between the number of lobsters with developing ovaries and the numbers that subsequently spawned that same summer. As it is, those data are available for only one year, 1987, and during the interval between spawning and sampling the next spring, an unknown number of lobsters may have lost their broods.

Goose Island ovary development

Because the females sent to St. Michael's Bay were non-ovigerous and

captured during the spring fishery, the majority should have spawned soon after being transplanted. As mentioned previously, the stress the transplant had on the lobsters was associated with very low incidences of both molting and spawning. It is clear that unfavourable holding conditions near the expected time of spawning (such as was experienced by the St. Michael's Bay females) results in massive ovary resorption (Templeman 1940b, Templeman and Tibbo 1945, Squires 1970; Ewart and Fulton 1888, Farmer 1974, Herrick 1909 *in* Aiken and Waddy 1980b). The lack of ovigerous lobsters from Goose Island in 1986 (Table 8) suggests this was the case. Resorbed ovaries, however, are capable of developing to stage 6 by the next summer (Aiken and Waddy 1980b) and thus extrude eggs shortly thereafter. This did not occur. The lack of ovigerous females in the Goose Island population in 1987 (Table 8) suggests their ovarian development is being retarded. This retarded state of development is made evident by comparing the ovary stages of the Goose Island lobsters with those of the control sites. The Goose Island lobsters had ovaries which were predominantly stage 4. This contrasts sharply with the ovaries of lobsters from the control sites, especially when the timing of the sampling is considered. The Port au Port and Comfort Cove lobsters have the highest percentages of their ovaries in stage 5; only the Pistolet Bay lobster ovaries are predominately stage 4, like those of the St. Michael's Bay lobsters. Yet for each control site, the sampling period was ~1 month earlier than for St. Michael's Bay.

If, as assumed for the discussion on molting and growth, the Goose Island lobsters represent what happened to the Indian Arm lobsters the first three years

following their transplant, then the converse would also be true, and the Indian Arm lobsters represent what *should* happen to the Goose Island lobsters. This being so, at least some of the Goose Island females should eventually spawn.

Some Newfoundland lobster populations do not spawn biennially. Squires et al. (1971) found the normal biennial reproductive cycle in the warmer of two areas of the Bay of Islands, and a three year cycle in the colder area. Ennis (1971) found that lobsters in the Bonavista Bay area had a four to five year reproductive cycle which Aiken and Waddy (1986) felt was temperature related. Both Squires et al. (1971) and Ennis (1971) based their conclusions on comparisons of the percentages of female lobsters that were potentially ovigerous in the autumn to the percentage of ovigerous females the next spring.

It is not clear whether these slow reproductive cycles are due to retarded ovarian development or to an inability to spawn the developed ova. Since the ovaries of the "potentially ovigerous lobsters" were examined in the autumn, primary vitellogenesis should have been completed. This, presumably, would make the ova appear "ripe for the next spawning season". How long vitellogenesis (both primary and secondary) actually takes in these populations is unknown. For St. Michael's Bay, the ovary development of the Goose Island lobsters is occurring very slowly. It is unclear whether or not the transplant stress was the sole cause of the deficiency of ovigerous females from Goose Island. The extreme photo-period regime in St. Michael's Bay during winter (caused by ice and snow cover effectively limiting much of the available light) combined with the low temperatures may also play a role in limiting the numbers of ovigerous females.

It is clear, however, the ovaries of the Goose Island lobsters were less developed than those of the Indian Arm lobsters (Fig. 6). Besides possible transplant-related stress, two other factors might contribute to differences in ovary development among sites: the lobsters of the different sites might be subjected to differing temperature regimes or ovary development time might increase with the size of the lobster.

The temperature conditions at Goose Island, although not measured, were not likely to be dissimilar to those at Indian Arm, thus the first explanation appears untenable. Regarding the ovary development time: I have found no records in the literature of lobsters lengthening their reproductive cycles as they grow. Indeed, Waddy and Aiken (1986) has shown that in females of ~ 120 mm CL or greater, successive spawnings over two years without an intervening molt is not uncommon, and is possible because a single mating can effect multiple fertilizations (Aiken and Waddy 1980a,b, Waddy and Aiken 1986).

Indian Arm ovary development

The ovaries of the Indian Arm females were predominantly in stage 6 (Fig. 6), a more developed state than found concurrently at Goose Island or one month earlier at the control sites. Because of this one month lag, comparing ovary development of the Indian Arm lobsters with that of the control sites is difficult.

The purpose of examining the lobsters' ovaries was to qualify relative development by comparing ovary development to the numbers of ovigerous

females found. The "potentially ovigerous" lobsters referred to by Squires et al. (1971) and Ennis (1971) are lobsters which, in the autumn, had ova developed to the extent that the ova should be extruded the following summer. Since these studies were done, Aiken and Waddy (1980a,b) have established criteria (Table 1) by which to qualify ovary development. In the following discussion, "potentially ovigerous lobsters" will be those with ovaries in stages 4, 5 and 6.

The percentage of potentially ovigerous females for 1987 and 1988 combined was 88 (stage 4, 20%; stage 5, 18%; stage 6, 50%) (Fig. 6). Yet the percentages of lobsters found to be ovigerous in 1986, 1987, and 1988 was below 20. Squires et al (1971) and Ennis (1971) both based their reproductive cycles on the large differences found between the percentages of potentially ovigerous and ovigerous lobsters. Comparing similar percentages for a northern Alaskan population of the snow crab, *Chionoecetes opilio* O. Fabricius, Jewett (1981) made the following statement: "This high proportion of [female *C. opilio*] with advanced ovarian development and low proportion of egg-bearing females seems paradoxical". Jewett hypothesised an environmental cause but could not support it with his data. This "paradox" of Jewett (1981) for the snow crabs is similar to the situation of the St. Michael's Bay lobsters and so makes Jewett's suggestion of physical environment as the causative factor very plausible. In that case, temperature must be considered foremost.

The rate of ovary development is governed by temperature. Due to the relatively brief period of warm "summer" water temperatures in St. Michael's Bay, ovary development may take a much longer time than in the more southern,

natural populations of lobsters. Due to natural variations in, especially, secondary vitellogenesis, we would expect to find the ovary stages normally distributed in the spring. Only those lobsters with the most advanced ovaries would be able to spawn during the brief summer period. The lobsters having ovaries in stages 4, 5, and perhaps early 6, may not spawn that year. Are these ovaries then resorbed or does secondary vitellogenesis continue at a decreasing rate with the declining water temperatures in the autumn? Ennis (1984a) indicates that in a given year 20% of the physiologically mature females in Comfort Cove fail to spawn. Ennis cites resorption of the mature ovary at the expected time of extrusion as the main reason. Also, Aiken and Waddy (1980a) state there are indications that final ovary maturation may be disrupted should it occur during a certain period of the molt cycle. The long periods of cold water in St. Michael's Bay may cause this conflict between molt and reproductive cycles to occur relatively often.

The large differences between potentially ovigerous and ovigerous lobsters reported by Squires et al. (1971) and Ennis (1971) may not be due entirely to prolonged reproductive cycles. The annual spring fishery reduces the relative abundance of mature non-ovigerous females just prior to the spawning season. This depletion of mature females, combined with the release of ovigerous lobsters by the fishery, artificially reduces the percentage of potentially ovigerous females. Since there is no commercial lobster fishery in St. Michael's Bay, this would not affect the proportions of ovigerous and non-ovigerous females.

Fecundity

The fecundities of those lobsters that do spawn suggest that complicating factors must still be at work. There are two possible reasons for the low fecundity values: the lobsters are extruding very few ova, or, the lobsters are extruding the normal number of ova, but they are subsequently being lost.

Knight (1918) reported that *H. americanus* females maintained in pounds often extruded only a few hundred eggs, and where post-mortem ovary examinations were done, spawning had been completed. In studies by Talbot et al. (1984) on spawning and egg retention, one out of 44 lobsters held in captivity spawned an "unusually small number of eggs [(800)]". Other lobsters that spawned seemed to also have low initial fecundity values, but the results of Talbot et al. (1984) do not allow the calculation of percentages of the expected brood size. Knight's (1918) data suggest the impoundment of the lobsters caused the low numbers of spawned eggs.

Perkins (1971) estimated an average of 36% egg loss during the period of October to June for offshore *H. americanus* females. He attributed the losses to normal attrition over the course of the eggs' incubation. Waddy (pers. comm.) raised the possibility of the broods of the St. Michael's Bay lobsters taking more than one year to develop and hatch. This would act to increase the percentage of eggs that are lost during incubation. However, many of the broods having very few eggs also showed very little development of the embryos. If the eggs were being lost due to normal attrition but over a much longer period, the most developed broods would be expected to have the fewest eggs and vice versa.

Aiken and Waddy (1986) observed that eggs were lost from the pleopods of ovigerous *H. americanus* and died when conditions, presumably including temperature, were "unfavorable". Recent work on the embryos of the crab *Cancer anthonyi* has shown that while development is prolonged at 10°C, substantial mortalities of embryos occur in broods incubated at 4°C (Shields and Kuris 1988). This is obviously not the case in embryos of *H. americanus* (see Perkins 1972); however, it does pose the possibility of some low critical temperature existing. Wear (1974) suggested that at very low temperatures the tolerance limits were determined more by a slowing of development than by any directly harmful effects *per se*.

Talbot et al. (1984) showed extensive loss of embryos from laboratory-maintained females. From the data presented for 17 ovigerous *H. americanus*, 14 had lost $\geq 80\%$ of their broods within 130 days of spawning. Of these 14, 10 had lost the $\geq 80\%$ within the first month of spawning. These data conflict with the results of Aiken and Waddy (1986), who reported very low levels of egg loss from their laboratory-maintained females. The differences may be due to the experimental procedure used by Talbot et al. (1984) which involved "periodic" photographing of the brood. This presumably required a periodic removal of the ovigerous female (and her brood) from water, which may have affected the attachment of the eggs.

Talbot and Harper (1984) concluded that, although many of the factors responsible for egg loss during brooding in laboratory-maintained lobsters are undefined, improper formation of the egg stalk, that portion of the egg connecting

it to other eggs or to the brooding lobster, is a major contributor. Regrettably, no examinations of the egg stalks of the St. Michael's Bay lobster embryos were made.

Other causes of severe egg loss include parasitism of the brood by nemertean worms, molting before the eggs are hatched, and lack of fertilization. The nemertean worm, *Pseudocarcinonemertes homari*, is known to be a micropredator on egg masses of *Homarus americanus* and can cause the female lobster to strip her eggs in an attempt to remove the worms (Wickham 1986). There are, however, no reports of *P. homari* infesting ovigerous females in Newfoundland waters and none were observed in St. Michael's Bay.

Ovigerous lobsters have been known to molt and thereby lose their brood (Aiken 1980a, Ennis 1975). Though this may help explain the paucity of ovigerous females in St. Michael's Bay (there are no data available to substantiate it) it does not account for the low fecundity since molting effectively removes the whole brood from the female.

Knight (1918) first noted that unfertilized eggs do not remain affixed to the female. The reasons for this are unclear (see Aiken and Waddy 1980b). Since all the St. Michael's Bay females that had their seminal receptacles examined contained spermatophores, it is unlikely that unfertilized eggs are a common occurrence in the bay.

Whatever the cause of the low percentage of ovigerous females in St.

Michael's Bay and their low fecundities, it is clear that these phenomena seriously compromise the extent to which this population can become self-propagating.

Many eggs must be incubated to ensure that some of the embryos will not suffer natural mortality before they reach sexual maturity and can contribute to the population's reproductive effort. The low egg production in St. Michael's Bay suggests no such contribution will be made.

4.3. Embryonic and Larval Development

The embryos of lobsters from St. Michael's Bay tend to be less developed than those from the three control sites, given the dates they were sampled (Fig.8). Subsequently their predicted dates of hatching are generally later than those of the control sites (Table 7). Embryo development is regulated by temperature (Templeman 1940; Perkins 1972; Branford 1978). The shortness of the period of warm temperatures in St. Michael's Bay will cause the embryos there to develop more slowly than in warmer areas, just as the Comfort Cove embryos develop more slowly than the Port au Port broods (Fig.8). The predicted dates of hatching of embryos from the control sites seem late compared to what has been observed; old-egged females do not occur after the middle of August in these areas (G.P. Ennis, Pers. Comm.). This may be an artifact of the development temperatures or the formulae used to calculate the dates of hatching.

The normal schedule is for eggs to be extruded during the summer, incubated through the winter and hatched the following summer. The earliest predicted time of hatching of any of the St. Michael's Bay broods is August 4 (Table 7). Though this is important insofar as the subsequent larval survival is concerned, it creates the possibility of conflict with the molt cycle, resulting in the loss of the whole brood (see previous section). Prolonged development also increases the number of embryos that are lost by natural attrition (Perkins 1971).

Two of the four broods for which Perkins Eye Indices (PEI's) could be calculated had advanced development (Table 7). Larvae from these broods may be able to complete their larval development prior to the water temperatures

falling below 5°C, at which point larvae generally die (Templeman 1936). The percentages of the St. Michael's Bay larvae to survive may be very low, however. The survival rate of larvae from stage I to postlarvae has been reported at between 0.1% and 2.5% (Scarratt 1964, 1973). Aiken and Waddy (1986) report the survival to postlarvae of broods hatched in August and September, and incubated at a constant 20°C, was only 30% and 20% of the respective broods. With the much lower water temperatures of St. Michael's Bay at those times, the percentage of larvae surviving to postlarvae would be much lower. No larvae were found during any of the plankton sampling conducted in St. Michael's Bay, but this does not indicate that there were none in the bay. Some of the St. Michael's Bay embryos may be surviving their larval phases and settling to the substrate.

Since there are few females extruding eggs in St. Michael's Bay (Table 8) and those that are tend to have low fecundities (Table 6), a low percentage of larval survival (compared even to the situation in natural populations) will result in very few lobsters being recruited into the population each year. Their numbers will not be sufficient to make up for the natural mortality these lobsters will invariably suffer. The St. Michael's Bay lobster population, then, will not increase in size by natural means, let alone reproduce itself.

The few embryos being produced and the retarded development of those that are produced indicates the distributional confines of *H. americanus* that are imposed by reproduction have been exceeded. This suggests the northern limit of the lobster is due to an inability to maintain an initial population beyond one generation in more northerly areas.

4.4. Conclusions

The lobsters that were introduced to St. Michael's Bay should continue to survive there for many years. This population will not, however, become self-propagating. The conditions of St. Michael's Bay are such that adult growth is not likely to be seriously compromised, but they do not favor the production and extrusion of ova. The few embryos that are being produced are characterized by retarded development with an extremely high, if not total, mortality of the embryos and/or larvae.

A small percentage of the embryos may survive and hatch successfully. The numbers of these that would complete metamorphosis successfully in any given year, however, would not adequately compensate for natural mortality of juveniles and adults.

The *Homarus americanus* population introduced to St. Michael's Bay, Labrador, is unable to increase or maintain its size by naturally occurring recruitment. Therefore, the population is unable to support a commercial fishery. The limitations of the lobsters' physiology in more northern environmental conditions seem the paramount barriers to extending their distribution further north.

TABLES AND FIGURES

Table 1: Ovary staging criteria for the American lobster,
Homarus americanus.¹

Stage	Ovary Color	Oocyte Size (mm)	Ovary Factor*
1 immature	white	<0.5	<100
2 immature developing	yellow, beige pale green	<0.8	<100
3 developing	light to medium green	<1.0	<200
4 developing	medium green	1.0 - 1.6	<325
5 developing	dark green	1.0 - 1.6	>325
6 ripe	dark green	1.4 - 1.6	>400
6A	oocytes free in ovary		
Spent/ Resorbing	white or yellow with dark green residual ova		

* Ovary factor (O_F) = $\frac{\text{ovary weight}}{(\text{carapace length})^3} \times 10$ weight in mg
length in mm

Table 2: Numbers of male and female lobsters transplanted to St. Michael's Bay and their size characteristics for each transplant year. All sizes in millimeters.

Year	Sex	Number	Mean CL	Std.Dev	Range
1982	Males	987	89.1	6.4	81.0 - 114.0
1982	Females	1001	88.9	6.2	81.0 - 112.0
1983	Males	500	89.0	6.2	81.0 - 120.0
1983	Females	498	86.5	4.9	81.0 - 112.0
1985	Males	687	84.1	2.7	81.0 - 95.0
1985	Females	811	84.4	2.6	81.0 - 92.0

Table 3: Summary of numbers and carapace lengths (in millimeters) of lobsters caught and examined by place and year.

	Goose Island			Indian Arm			Control Sites (1987)		
	1986	1987*	1988	1986	1987*	1988	PP	CC	PB
No. caught	(M) 30	7	16	86	10	33			
	(F) 32	33	38	109	25	48	40	40	40
	(tot) 62	40	54	195	35	81			
Mean CL (S.D.)	(M) 85(4)	86(3)	96(4)	108(9)	112(8)	115(7)	85(4)	90(8)	82(5)
	(F) 86(4)	88(5)	93(3)	98(7)	107(8)	102(6)			
Minimum CL	(M) 81	83	90	85	92	100	76	70	74
	(F) 81	81	86	81	91	89			
Maximum CL	(M) 96	92	102	125	122	138	98	90	105
	(F) 99	99	100	126	122	116			
No. ovigerous	0	0	0	21	2	7	10	10	10
No. ovaries examined	0	23	7	0	7	27	30	30	30
No. pleopods examined	0	23	7	0	7	27	30	30	30

* The first sampling period in 1987 was intended for ovary, fecundity and embryo studies only. Records of males caught during this period were not kept.

Table 4: Actual (act) and expected¹ (exp) numbers of Goose Island lobsters with new and old shells and the corresponding chi-square statistics.

Year	Sex	Shell Condition		Total No. Lobsters	Chi-sq	df	P
		<u>New</u> act exp	<u>Old</u> act exp				
1986	Males	1 18	29 12	30	42.1	1	<.005
1988	Males	8 4	2 6	10	5.2	1	<.05
1986	Females	2 13	28 17	30	16.3	1	<.005
1988	Females	23 12	2 13	25	19.6	1	<.005

1. Calculated using the probit equations of Ennis et al. (1982):

Proportion molting = $15.615 - 0.123 \text{ CL(mm)}$ males
 Proportion molting = $14.604 - 0.113 \text{ CL(mm)}$ females

Table 5: Actual (act) and expected¹ (exp) numbers of Indian Arm lobsters with new and old shells and the corresponding chi-square statistics.

FEMALES												
CL	1986				chi-sq	P	1988				chi-sq	P
	New		Old				New		Old			
act	exp	act	exp	act	exp	act	exp	act	exp	act	exp	
85	12	7	5	10	6.07	<.025	-	-	-	-	-	-
93	1	3	21	19	1.54	<.50	11	2	4	13	46.7	<.005
98	2	.8	15	16.2	1.89	<.50	6	.6	7	12.4	50.9	<.005
105	1	1.3	17	16.7	.075	<.50	1	.98	13	13.02	.0004	<.975

MALES												
CL	1986				chi-sq	P	1988				chi-sq	P
	New		Old				New		Old			
act	exp	act	exp	act	exp	act	exp	act	exp	act	exp	
90	4	4	9	9	0	1.0	-	-	-	-	-	-
97	13	2	11	22	66	<.005	9	1	1	9	71.1	<.005
105	16	.4	22	37.6	587	<.005	7	.1	4	10.9	395	<.005
115	2	.01	10	11.99	330	<.005	1	.01	10	10.99	89	<.005

1. Calculated using the probit equations of Ennis et al. (1982):

Proportion molting = $15.615 - 0.123 \text{ CL(mm)}$ males
 Proportion molting = $14.604 - 0.115 \text{ CL(mm)}$ females

Table 6: Actual and expected¹ fecundity values of ovigerous lobsters from St. Michael's Bay.²

Year	CL(mm)	Number of Eggs		Percent of Expected
		Actual	Expected	
1987	103	6588	21891	30
1987	94	334	16491	2
1988	102	17878	21240	84
1988	95	17854	17040	>100
1988	102	186	21240	<0.1
1988	104	10122	22557	45
1988	97	15	18177	<0.1
1988	97	7	18177	<0.1
1988	101	122	20601	<0.1

1. Calculated using the equation:

$$\log \text{ fecundity} = 3.0984 \log \text{ CL} - 1.8963 \quad (\text{Ennis 1981}).$$

2. Ovigerous females from 1986 study are not included.

Table 7: Perkins Eye Indices, estimated number of days to hatching¹, and projected dates of hatching of lobster embryos from St. Michael's Bay (SMB), Port au Port (PP), Comfort Cove (CC), and Pistolet Bay (PB).

Place	Date	No.	Mean PEI	Estimated Days to Hatch	Projected Date of Hatching
SMB	25 June, 1988	30	< 70		
SMB	29 June, 1988	30	470	36	August 4
SMB	29 June, 1988	30	< 70		
SMB	29 June, 1988	30	< 70		
SMB	30 June, 1988	10	108	179	December 26
SMB	30 June, 1988	30	< 70		
SMB	02 July, 1988	30	< 70		
SMB	19 July, 1987	32	127	171	January 6
SMB	31 July, 1986	20	< 70		
SMB	01 August, 1986	13	431	51	September 21
SMB	06 August, 1986	20	< 70		
SMB	30 August, 1987	30	< 70		
PP	25 May, 1987	30	131	118	September 20
PP	25 May, 1987	30	374	51	July 15
PP	25 May, 1987	30	377	50	July 14
PP	25 May, 1987	30	419	39	July 3
PP	25 May, 1987	30	402	43	July 7
PP	25 May, 1987	30	411	41	July 5
PP	25 May, 1987	30	419	39	July 3
PP	25 May, 1987	30	< 70		
PP	25 May, 1987	30	< 70		
PP	25 May, 1987	30	< 70		
CC	28 May, 1987	30	394	66	August 2
CC	28 May, 1987	30	368	76	August 12
CC	28 May, 1987	30	148	163	November 7
CC	28 May, 1987	30	429	52	July 19
CC	28 May, 1987	30	398	64	July 31
CC	28 May, 1987	30	326	93	August 29
CC	28 May, 1987	30	362	78	August 14
CC	28 May, 1987	30	375	73	August 9
CC	28 May, 1987	30	400	63	July 30
CC	28 May, 1987	30	321	94	August 30
PB	02 June, 1987	30	142	165	November 14
PB	02 June, 1987	30	145	164	November 13
PB	02 June, 1987	30	308	100	September 10
PB	02 June, 1987	30	238	127	October 7
PB	02 June, 1987	30	185	148	October 28
PB	02 June, 1987	30	184	149	October 29
PB	02 June, 1987	30	187	147	October 27
PB	02 June, 1987	30	250	123	October 3
PB	02 June, 1987	30	< 70		
PB	02 June, 1987	30	< 70		

1. Based on developmental temperature of 10°C, except PP (13°C).

Table 8: Numbers of non-ovigerous (non-ovig) and ovigerous (ovig), and percent ovigerous female lobsters found in Indian Arm (IA) and Goose Island (GI) for each study year.

Date	Place	Number of Females			% Ovigerous
		Non-ovig.	Ovig.	Total	
1986	IA	88	21	109	19.3
1987	IA	23	2	25	8.0
1988	IA	41	7	48	14.6
1986	GI	32	0	32	0.0
1987	GI	33	0	33	0.0
1988	GI	38	0	38	0.0

Figure 1: Locations of the experimental site, St. Michael's Bay (SMB), and the three control sites: Port au Port (PP), Comfort Cove (CC), and Pistolet Bay (PB).

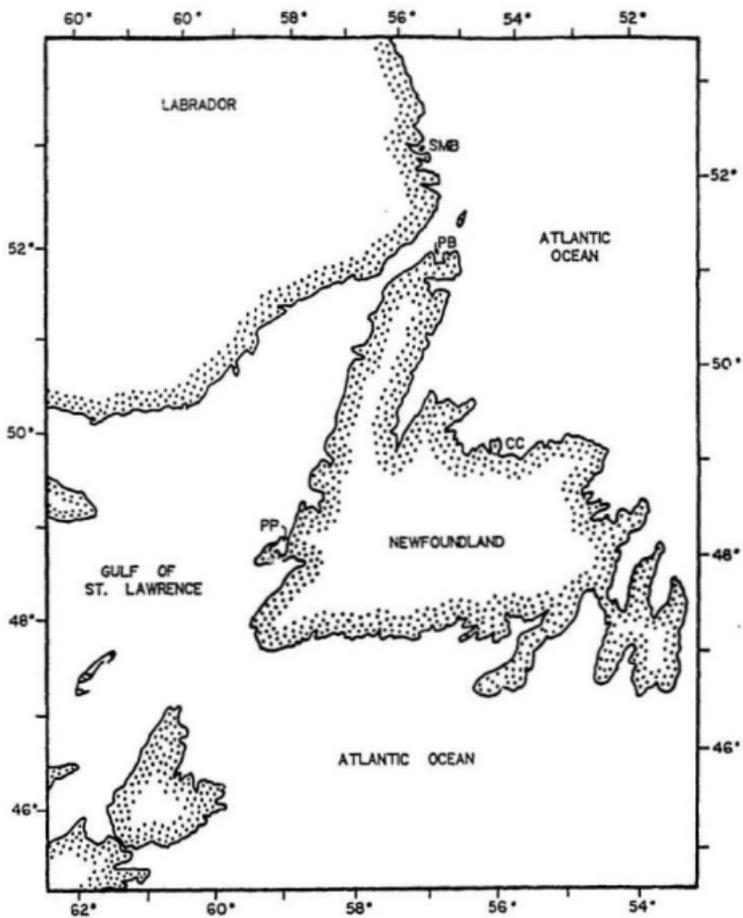


Figure 2: Locations of three study sites in St. Michael's Bay: Indian Arm (IA), Mussle Tickle (MT), and Goose Island (GI).



Figure 3: Size frequency histograms of male and female lobsters from St. Michael's Bay by study site for the years of transplant and the three study years.

Figure 4: Mean carapace lengths and standard deviations of male and female lobsters from St. Michael's Bay by study site, Indian Arm (IA), Mussel Tickle (MT), and Goose Island (GI), for the years of transplant and the three study years. Mean lengths of Indian Arm lobsters for the period 1983 to 1985 based on percent length changes of the Goose Island lobsters during the period 1985-1987.

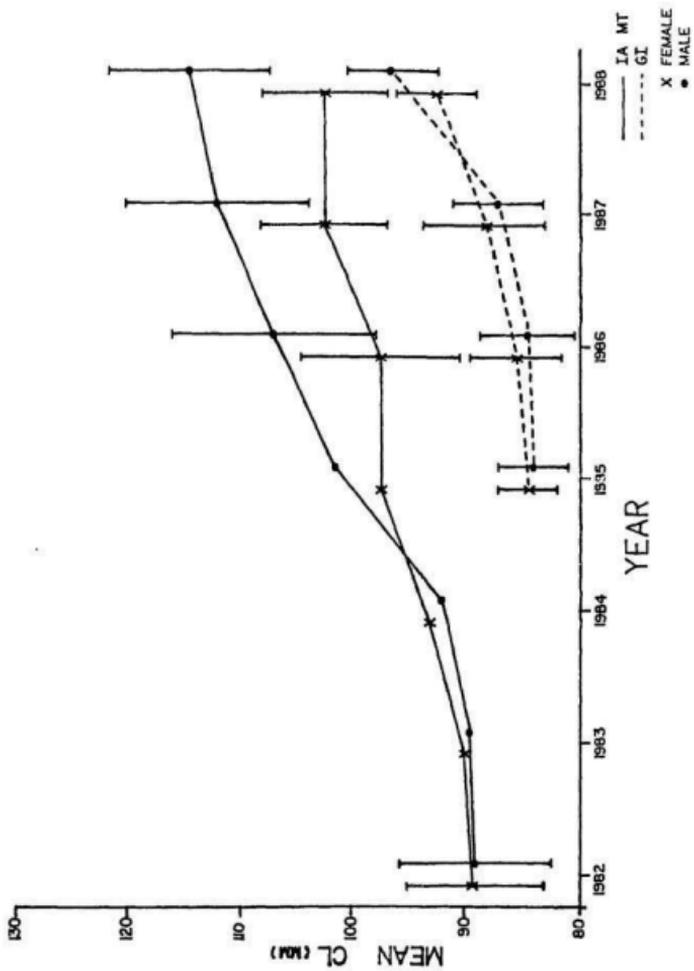


Figure 5: Percent of Indian Arm lobsters with new shells.
Data from all study years combined. Lines drawn by hand.

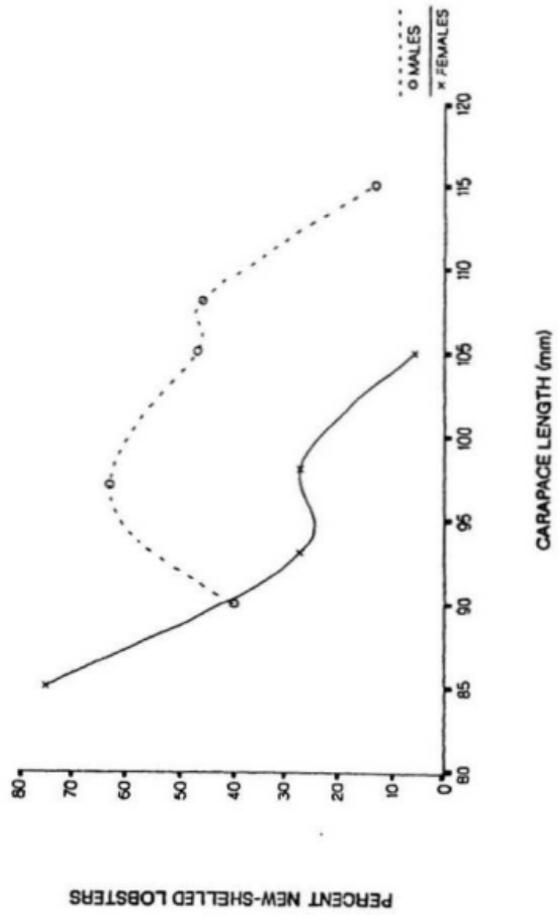


Figure 6: Percentage of Goose Island and Indian Arm lobsters with ovary stages 1 to 6. Data from 1987 and 1988 studies combined.

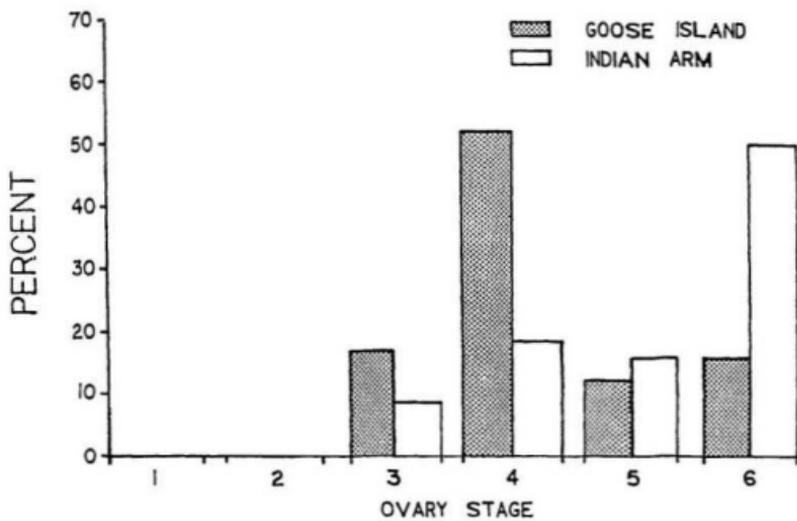


Figure 7: Percentage of Port au Port, Comfort Cove, and Pistolet Bay lobsters with ovary stages 3 to 6.

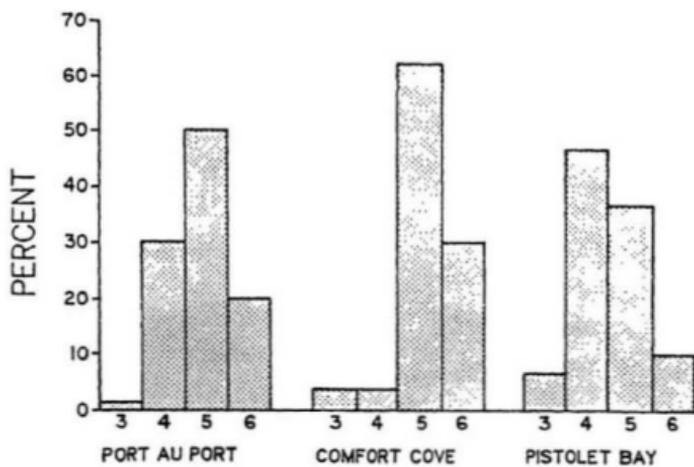


Figure 8: Mean Perkins Eye Indices of embryos from St. Michael's Bay (SMB), Port au Port (PP), Comfort Cove (CC), and Pistolet Bay (PB) by date of capture.

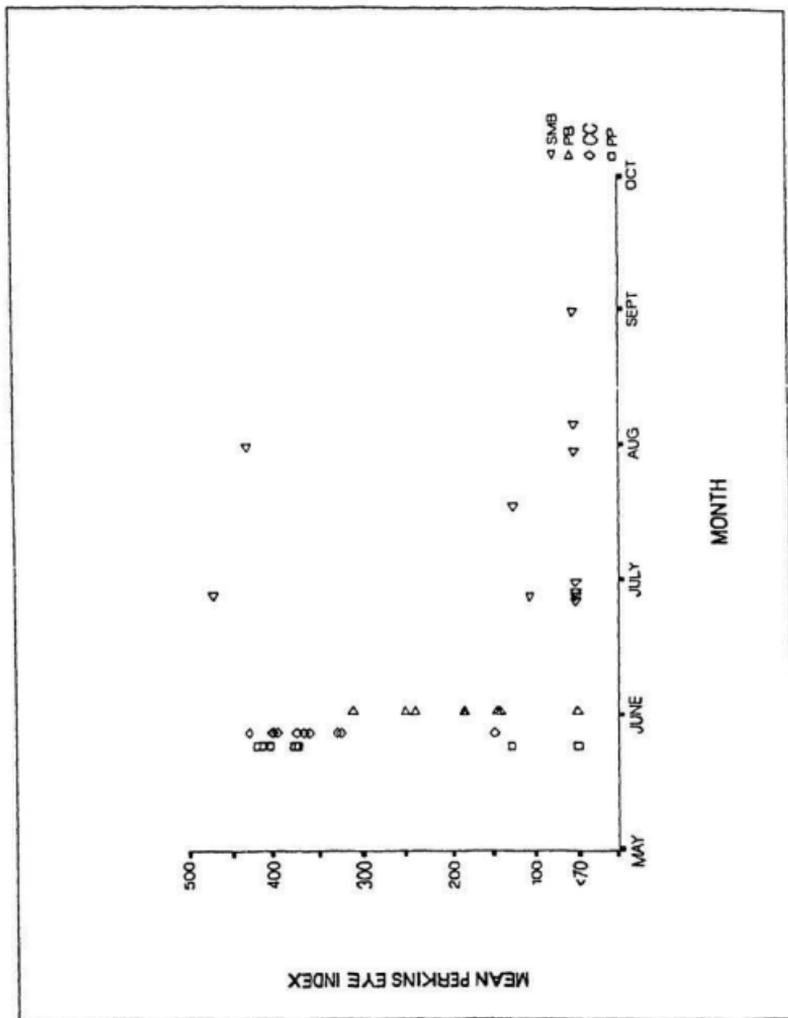
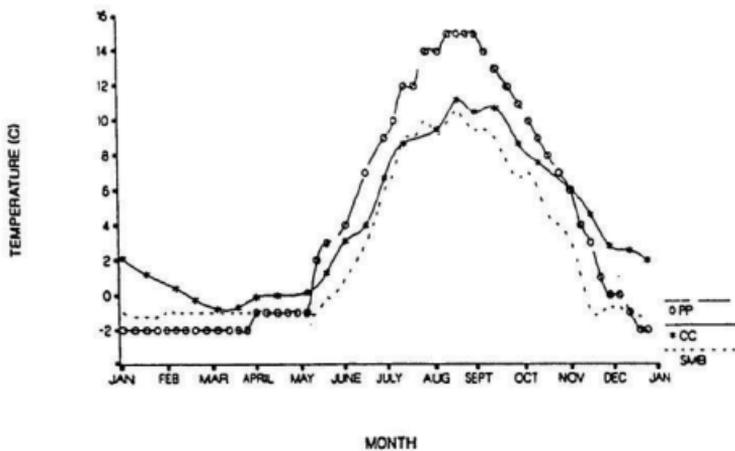


Figure 9: Mean annual temperature regimes of
St. Michael's Bay (SMB), Port au Port (PP), and
Comfort Cove (CC).



Chapter 5

LITERATURE CITED

- Ache, B.W. and D.L. Macmillan. 1980. Neurobiology. Pp.165-213 In J.S. Cobb and B.F. Phillips [eds.]. *The Biology and Management of Lobsters*. Vol. 1. Academic Press, New York, N.Y.
- Aiken, D.E. 1980. Molting and growth. Pp.91-163 In J.S. Cobb and B.F. Phillips [eds.]. *The Biology and Management of Lobsters*. Vol. 1. Academic Press, New York, N.Y.
- Aiken, D.E. and S.L. Waddy. 1976. Controlling growth and reproduction in the American lobster. *Proc. Annu. Meet. - World Maricult. Soc.* 7:415-430.
- Aiken, D.E. and S.L. Waddy. 1980a. Maturity and reproduction in the American lobster. *Can. Tech. Rep. Fish. Aquat. Sci.* 932.
- Aiken, D.E. and S.L. Waddy. 1980b. Reproductive biology. Pp. 215-276 In J.S. Cobb and B.F. Phillips [eds.]. *The Biology and Management of Lobsters*. Vol. 1. Academic Press, New York, N.Y.

- Aiken, D.E. and S.L. Waddy. 1982. Cement gland development, ovary maturation, and reproductive cycles in the American lobster *Homarus americanus*. *J. Crust. Biol.* 2(3):315-327.
- Aiken, D.E. and S.L. Waddy. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. *Can. J. Fish. Aquat. Sci.* 43(11):2258-2270.
- Aiken, D.E. and S.L. Waddy. 1989. Interaction of temperature and photoperiod in the regulation of spawning by American lobsters *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 46:145-148.
- Anonymous. 1988. Minitab Statistical Software Reference Manual - Release 6.1. Minitab, Inc., U.S.A. 341 pp.
- Attard, J. and C. Hudon. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobsters (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 44(6):1157-1164.
- Botero, L. and J. Atema. 1982. Behaviour and substrate selection during larval settling in the lobster *Homarus americanus*. *J. Crust. Biol.* 2(1):59-69.
- Branford, J.R. 1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. *Mar. Biol.* 47:363-368.
- Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. *Can. J. Fish. Aquat. Sci.* 43:2197-2205.

- Campbell, A. and A.B. Stasko. 1986. Movements of lobsters (*Homarus americanus*) tagged in Bay of Fundy, Canada. *Mar. Biol.* 92:393-404.
- Cheung, T.S. 1966. The development of egg membranes and egg attachment in the shore crab, *Carcinus maenas*, and some related decapods. *J. Mar. Biol. Ass. U.K.* 46:373-400.
- Cobb, J.S., D. Wang and D.B. Campbell. 1989. Timing of settlement by post-larval lobsters (*Homarus americanus*): field and laboratory evidence. *J. Crust. Biol.* 9(1):60-66.
- Conan, G.Y. 1986. Summary of session 5: recruitment enhancement. *Can. J. Fish. Aquat. Sci.* 43(11):2384-2388.
- Cooper, R.A. and J.R. Uzmann. 1980. Ecology of juvenile and adult *Homarus*. Pp. 97-142 In J.S. Cobb and B.F. Phillips [eds.]. *The Biology and Management of Lobsters*. Vol.II. Academic Press, New York, N.Y.
- Davis, C.C. 1964. A study of the hatching process in aquatic invertebrates. XIII. Events of eclosion in the American lobster, *Homarus americanus* Milne Edwards (Astacura, Homaridae). *Amer. Midl. Natur.* 72:203-210.
- Ennis, G.P. 1971. Lobster (*Homarus americanus*) fishery and biology in Bonavista Bay, Newfoundland 1966-70. *Fish. Res. Board Can. Tech. Rep.* 209:46pp.
- Ennis, G.P. 1973. Food, feeding, and condition of lobsters *Homarus americanus*,

throughout the seasonal cycle in Bonavista Bay, Newfoundland. *J. Fish. Res. Board Can.* 30(12):1905-1909.

Ennis, G.P. 1975. Observations on hatching and larval release in the lobster *Homarus americanus*. *J. Fish. Res. Board Can.* 32:2210-2213.

Ennis, G.P. 1977. Determination of shell condition in lobster *Homarus americanus* by means of external macroscopic examination. *Proc. Nat. Shellfish. Assoc.* 67:67-70.

Ennis, G.P. 1980. Size-maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 37(6):945-956.

Ennis, G.P. 1981. Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters. *Fish. Bull.* 79(4):798-800.

Ennis, G.P. 1983. Variation in annual growth in two Newfoundland lobster *Homarus americanus* populations in relation to temperature conditions. *Int. Council. Explor. Sea. C.M.1083/K:24*. Shellfish Committee.

Ennis, G.P. 1984a. Comparison of physiological and functional size-maturity relationships in two Newfoundland populations of lobsters *Homarus americanus*. *Fish. Bull.* 82(1):244-249.

Ennis, G.P. 1984b. Incidence of molting and spawning in the same season in female lobsters, *Homarus americanus*. *Fish. Bull.* 82(3):529-530.

- Ennis, G.P. 1984c. Small-scale seasonal movements of the American lobster *Homarus americanus*. *Trans. Am. Fish. Soc.* 113(3):336-338.
- Ennis, G.P. 1984d. Territorial behaviour of the American lobster *Homarus americanus*. *Trans. Am. Fish. Soc.* 113(3):330-335.
- Ennis, G.P. 1986a. Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*: a review. *Can. J. Fish. Aquat. Sci.* 43(11):2072-2084.
- Ennis, G.P. 1986b. Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water. *Can. J. Fish. Aquat. Sci.* 43(11):2177-2183.
- Ennis, G.P. In Press. Annual variation in egg production in a Newfoundland population of the American lobster, *Homarus americanus*.
- Ennis, G.P., P.W. Collins and G. Dawe. 1982. Fisheries and population biology of lobsters (*Homarus americanus*) at Comfort Cove, Newfoundland. *Can. Tech. Rep. Fish. Aquat. Sci.* 116:45 pp.
- Harding, G.C., J.D. Pringle, W.P. Vass, S. Pearre Jr., S.J. Smith. 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. *Mar. Ecol. Prog. Ser.* 41:29-41.
- Herrick, F.H. 1896. The American lobster: a study of its habits and development. *Bull. U.S. Fish. Comm.* 15:1-252.

- Hudon, C. 1987. Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Iles de la Madeleine (Quebec). *Can. J. Fish. Aquat. Sci.* 44(11):1855-1869.
- Hudon, C. and P. Fradette. 1988. Planktonic growth of larval lobsters *Homarus americanus* off Iles de la Madeleine (Quebec), Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 45(5):863-878.
- Hudon, C., P. Fradette and P. Legendre. 1986. La repartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des Iles de la Madeleine, golfe de Saint-Laurent. *Can. J. Fish. Aquat. Sci.* 43(11):2164-2176.
- Jewett, S.C. 1981. Variations in some reproductive aspects of female snow crabs *Chionoecetes opilio*. *J. Shellfish Res.* 1(1):95-99.
- Knight, A.P. 1918. Lobster investigations at Long Beach Pond, N.S. *Cont. Can. Biol.* 1917-1918:53-71.
- Mackenzie, B.R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory reared *Homarus americanus* Milne Edwards larvae. *J. Exp. Mar. Biol. Ecol.* 116:87-98.
- Nelson, K. 1986. Photoperiod and reproduction in lobsters (*Homarus*). *Amer. Zool.* 26:447-457.

- Nelson, K., D. Hedgecock, and W. Borgeson. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). *Can. J. Fish. Aquat. Sci.* 40:940-947.
- Nelson, K., D. Hedgecock, and W. Borgeson. 1988a. Effects of reproduction upon molting and growth in female American lobsters (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 45:805-821.
- Nelson, K., D. Hedgecock, and W. Borgeson. 1988b. Factors influencing egg extrusion in the American lobster *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 45(5):797-804.
- Perkins, H.C. 1971. Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). *Fish. Bull.* 69:451-453.
- Perkins, H.C. 1972. Development rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). *Fish. Bull.* 70(1):95-99.
- Pezzack, D.S. and D.R. Dugga. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 43:2206-2211.
- Rathbun, R. 1890. The transplanting of lobsters to the Pacific coast of the United States. *Bull. U.S. Fish. Comm.* 8:453-472.
- Shields, J.D. and A.M. Kuris. 1988. An *in vitro* analysis of egg mortality in

- Cancer anthonyi*: the role of symbionts and temperature. *Biol. Bull.* 174:267-275.
- Squires, H.J. 1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. *Proc. Nat. Shellfish Assoc.* 60:22-30.
- Squires, H.J., G.E. Tucker and G.P. Ennis. 1971. Lobsters (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963-65. *Fish. Res. Board Can. Man. Rep. Ser.* 1151:58pp.
- Stewart, J.E. and H.J. Squires. 1968. Adverse conditions as inhibitors of ecdysis in the lobster *Homarus americanus*. *J. Fish. Res. Board Canada.* 25(9):1763-1774.
- Talbot, P. and R. Harper. 1984. Abnormal egg stalk morphology is correlated with clutch attrition in laboratory-maintained lobsters (*Homarus*). *Biol. Bull.* 166:349-356.
- Talbot, P., C. Thaler and P. Wilson. 1984. Spawning, egg attachment and egg retention in captive lobsters (*Homarus americanus*). *Aquaculture* 37:239-249.
- Templeman, W. 1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). *J. Biol. Board Can.* 2(5):485-497.
- Templeman, W. 1940a. Embryonic developmental rates and egg-laying of Canadian lobsters. *J. Fish. Res. Board Can.* 5:71-83.

- Templeman, W. 1940b. The life history of the lobster. *Newfoundland Dept. of Natural Resources, Service Bull. (Fisheries) 15*. 42pp.
- Templeman, W. and S.N. Tibbo. 1945. Lobster investigations in Newfoundland 1938 to 1941. *Newfoundland Government Research Bull. No. 16 (Fisheries)*. 00pp.
- Waddy, S.L. and D.E. Aiken. 1986. Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 43:2291-2294.
- Wear, R.G. 1974. Incubation in British decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. *J. mar. biol. Ass. U.K.* 54:745-762.
- Wickham, D.E. 1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. *Can. J. Fish. Aquat. Sci.* 43(11):2295-2302.

