

**Abstract.** – In the summers of 1982, 1983, and 1985, almost 5000 commercial lobsters were transplanted from an area on the northeast coast of Newfoundland to St. Michael's Bay in southern Labrador, about 200 km beyond their reported northern limit of distribution, in an attempt to establish a self-sustaining population. Biological sampling of these lobsters was carried out each summer from 1986 to 1991. A continuous shift to larger sizes and a generally high incidence of new-shell animals indicated molting was a common occurrence in these lobsters. All nonovigerous females had ovaries developing for extrusion that summer, and their seminal receptacles were full. In contrast, percentages of ovigerous females were low and most of these had extruded recently. Many ripe females apparently failed to extrude, and many that did extrude lost the entire clutch before the following summer. Exposure to temperatures near or below 0°C from mid-November to mid-May, and to near-continuous darkness below a layer of ice during most of this period, may cause a high incidence of resorption of ripe ovaries. The incidence of ovigerous females with recently-extruded eggs increased substantially in the later years of the study, indicating a degree of physiological adjustment to the adverse environmental conditions. However, loss of the entire clutch of eggs continued to be prevalent. Prolonged low temperature certainly retarded embryonic development for the females that extruded and retained their eggs. Six of 17 ovigerous females with old, eyed eggs had less than half the yolk remaining. Only one brood would have hatched by early August, long enough in advance of autumn cooling for development to Stage IV and settlement in the area to be possible. Lobsters transplanted to St. Michael's Bay will not likely become a self-sustaining population. Any recruitment that might occur would certainly be too little and too irregular to support a fishery.

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## Reproduction in American lobsters *Homarus americanus* transplanted northward to St. Michael's Bay, Labrador

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The American lobster *Homarus americanus* occurs in the western Atlantic Ocean from the Strait of Belle Isle area of southern Labrador and the northern tip of the island of Newfoundland south to North Carolina (Cooper and Uzman 1980). The species supports commercial fisheries of considerable economic importance throughout most of its range. Its high commercial value led to repeated attempts to establish lobster populations on the Pacific coast of North America, but none of the transplants was successful (Conan 1986). In recent years, the Provincial Government of Newfoundland and Labrador transplanted commercial (mostly adult) lobsters from an area on the northeast coast of the island of Newfoundland to a location ~200 km beyond the reported northern limit of distribution in St. Michael's Bay, Labrador (Fig. 1). The bay extends inland ~28 km from the open coast and contains numerous small islands, features promoting a circulation pattern that would aid retention and eventual settlement in the area of any larvae produced by the transplanted lobsters. This was an important consideration, since the aim of the transplant was to establish a self-sustaining population that would eventually support a fishery.

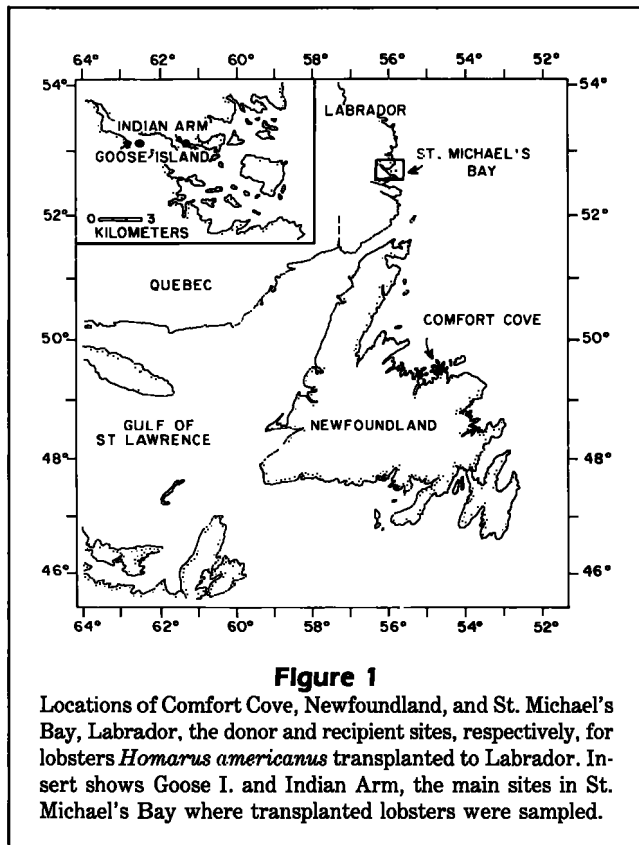
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Lobsters were transplanted to St. Michael's Bay in the summers of 1982, 1983, and 1985. Biological sampling was conducted each summer from 1986 to 1991. Our purpose is to present observations related to various aspects of population biology, in particular, molting, mating, ovary development, spawning and embryonic development, and consider the possibility of this transplanted population being or becoming self-sustaining.

### Methods and materials

Lobsters transplanted to St. Michael's Bay were caught during May–June by commercial fishermen near Comfort Cove, Notre Dame Bay, on the northeast coast of Newfoundland (Fig. 1). They were purchased from a local buyer by the Newfoundland and Labrador Department of Fisheries and transported directly to St. Michael's Bay by float plane. Transplants were made in 1982, 1983, and 1985 and totaled 2174 males, 81–114 mm carapace length (CL), and 2310 nonovigerous females, 81–112 mm CL. Lobsters were released once only at eight widely-separated sites around the bay where the shallow-water habitat appeared quite suitable for lobsters.

The authors conducted biological sampling annually in the summer-



time from 1986 to 1990. In 1991, less detailed sampling was carried out by the Department of Fisheries of the Province of Newfoundland and Labrador. Sampling focused on lobsters in Indian Arm (transplanted in 1982) and at Goose Island (transplanted in 1985) (Fig. 1). These two sites were selected to include lobsters from the earliest and latest transplants. Also, in initial trap sampling in 1986, lobsters were caught more readily at these sites than at others. Lobsters were caught in baited traps in 1986, 1987, and 1991 and by scuba-diving from 1988 to 1990. Samples over the 6 years totaled 295 males and 392 females. Numbers included in sampling for various purposes described below are summarized by year and sampling site in Table 1. Carapace length of each lobster was measured to the nearest mm. Shell condition was determined by external macroscopic examination in 1986 and 1988–90. In over 90% of the lobsters examined for shell condition, those that molted the previous summer (new shell) could be readily distinguished from those that did not (old shell) by general brightness of coloration, sharpness of spines, and the degree of darkening due to abrasion on the leading edges and undersides of the claws. The others could be categorized with reasonable confidence. Each summer from 1987 to 1990, subsamples of nonovigerous females totaling 111 for the 4 years were sacrificed. For each of these, ovary color, ova diameter, contents of seminal receptacles,

**Table 1**

Summary of numbers included in sampling of lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985), 1986–91.

Year sampled	Number and carapace lengths		Shell condition		Setal development		Nonovigerous females			Ovigerous females			
	Male	Female	Male	Female	Male	Female	Ovaries	Seminal receptacles	Cement glands	New eggs	Old eggs	Egg counts	Yolk content of old eggs
<b>Indian Arm</b>													
1986	87	109	87	74	—	—	—	—	—	—	21*	—	—
1987	10	25	—	—	—	—	7	7	7	1	1	2	1
1988	32	48	32	42	—	—	27	27	27	5	2	7	2
1989	24	21	24	21	24	20	8	8	8	7	6	—	6
1990	17	22	17	22	17	21	8	8	8	11	3	—	3
1991	4	9	—	—	—	—	—	—	—	4	3	—	3
<b>Goose Island</b>													
1986	30	32	30	30	—	—	—	—	—	0	0	—	—
1987	7	33	—	—	—	—	23	23	23	0	0	—	—
1988	16	38	10	25	—	—	7	7	7	0	0	—	—
1989	29	20	29	20	29	20	15	15	16	2	2	—	2
1990	23	22	23	22	23	22	15	15	15	7	0	—	—
1991	15	13	—	—	—	—	—	—	—	10	0	—	—

\* In 1986, old- and new-egg ovigerous females were not distinguished.

and the extent of pleopod cement gland development (Aiken and Waddy 1982) were determined. In 1989 and 1990, pleopod setal development (Aiken 1973) was determined for 47 nonovigerous females and 93 males. Eighty-four ovigerous females were included among the 392 females sampled over the 6 years. Egg numbers were determined for nine collected in Indian Arm in 1987 and 1988. Five of these were small egg masses that were counted directly, the other four were estimated by drying and weighing the entire mass, then weighing and counting a subsample representing about 10% of the total. Yolk content of eggs (to the nearest tenth, i.e., 0.1) was determined for 17 ovigerous females carrying old, eyed eggs collected from 1986 to 1991. Perkins Eye Indices (PEI), which provide a measure of embryonic development (Perkins 1972), were determined for four of the latter.

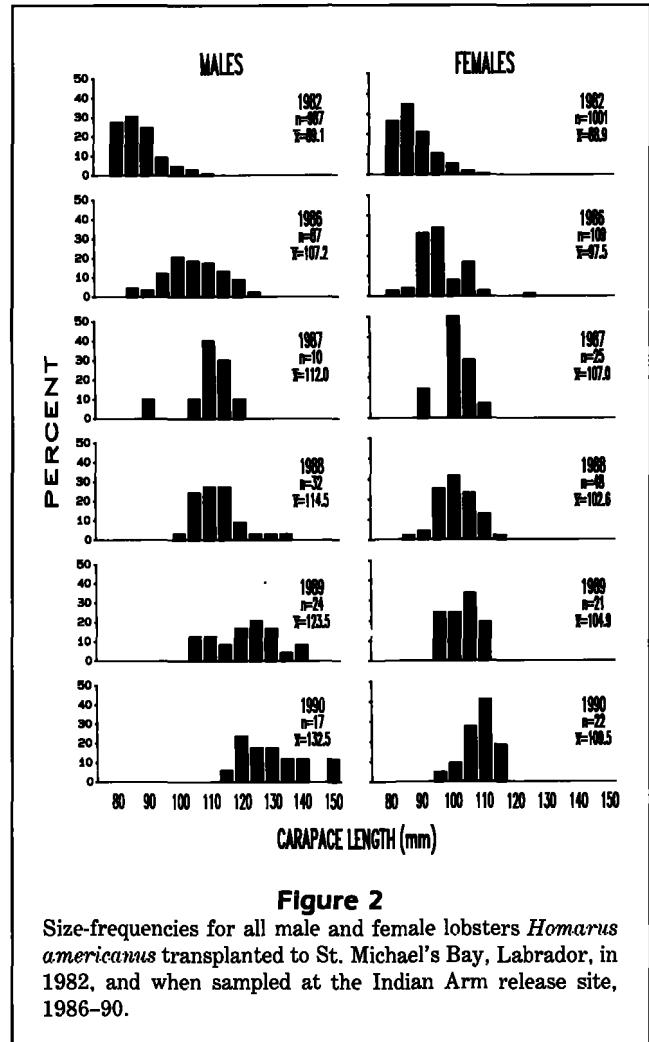
From July 1986 to September 1988, a continuously recording thermograph was maintained in St. Michael's Bay at 7m within the depth range occupied by the transplanted lobsters. Mean daily temperature was obtained from the tapes. These were averaged for the first and second half of each month, with data for the different years combined. Temperature during most of June each year was not obtained because the recording tape expired in 1987 and the instrument malfunctioned in 1988. The June portion of the annual temperature regime was approximated by extrapolating from temperatures which were rising in a near-linear fashion before and after.

## Results

### Changes in size composition

**Indian Arm** Mean CL of all the lobsters transplanted to St. Michael's Bay in the summer of 1982 was 89.1 mm (range 81–114 mm,  $N$  987) for males and 88.9 mm (range 81–112 mm,  $N$  1001) for females (Fig. 2). We assume that these are also representative of the lobsters released at the Indian Arm site. When first sampled in the summer of 1986, mean CL of lobsters in Indian Arm had increased significantly (Tukey test;  $P < 0.001$ ) to 107.2 mm for males ( $N$  87) and 97.5 mm for females ( $N$  109). There were further shifts to larger sizes each year, especially among males, and in the summer of 1990, mean CL was significantly larger ( $P < 0.001$ ) than in all previous years at 132.5 mm (range 116–153 mm,  $N$  17) for males and 109.6 mm (range 98–116 mm,  $N$  22) for females.

**Goose Island** Mean CL of all the lobsters transplanted to St. Michael's Bay in the summer of 1985 was 84.1 mm (range 81–95 mm,  $N$  687) for males and 84.4 mm (range 81–92 mm,  $N$  811) for females (Fig. 3),



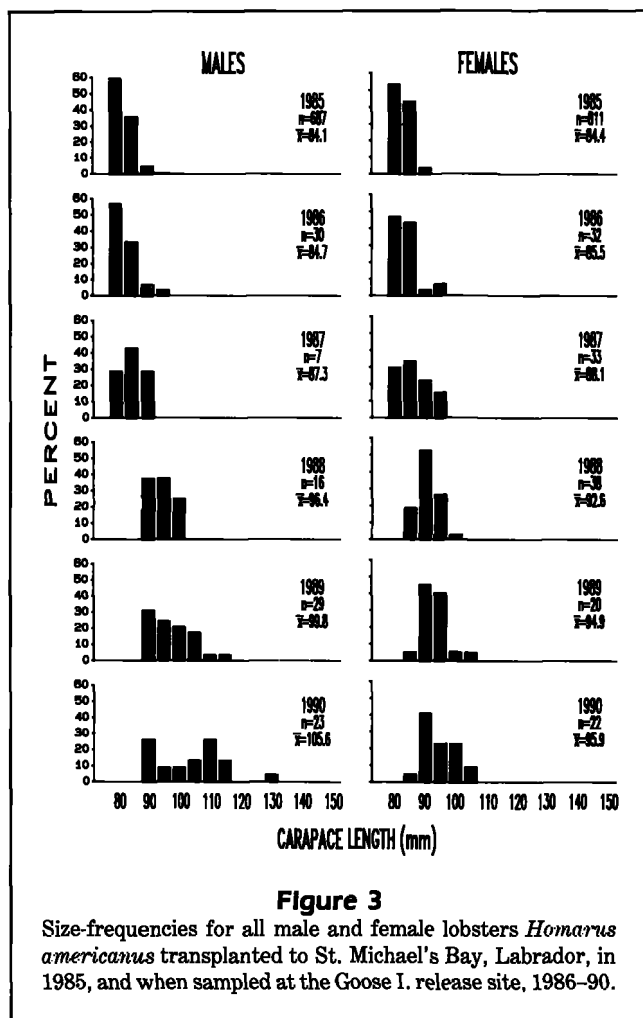
**Figure 2**

Size-frequencies for all male and female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador, in 1982, and when sampled at the Indian Arm release site, 1986–90.

significantly smaller ( $t$ -test;  $P < 0.001$ ) than for those transplanted in 1982. We assume that these means are representative of the lobsters released at Goose I. At Goose I., annual shifts to larger sizes were small until 1988, when mean CL had increased significantly (Tukey test;  $P < 0.001$ ) to 96.4 mm for males ( $N$  16) and 92.6 mm for females ( $N$  38). By summer 1990, mean CL had increased significantly again ( $P < 0.001$ ) to 105.6 mm (range 90–131 mm,  $N$  23) for males and to 95.9 mm (range 89–105 mm,  $N$  22) for females.

### Incidence of new-shell lobsters

The donor population at Comfort Cove is subjected to a very intensive fishery each spring which removes most of the commercial lobsters (nonovigerous and  $\geq 81$  mm CL). Following the summer molting period, the vast majority of commercial-size animals in the population had molted and grown from smaller sizes



during the summer. As a consequence, the incidence of new shells among commercial sizes averaged 96% and 94% for male and female lobsters, respectively, in autumn samples from 1986 to 1990 (Ennis, unpubl. data). These are much higher percentages than could be expected for the transplanted lobsters in St. Michael's Bay. There has been no lobster fishing in St. Michael's Bay and, because of their larger sizes, lobsters there are less likely to molt. Old-shell lobsters are therefore likely to be much more prevalent.

Among Indian Arm lobsters, the incidence of new shells (indicating lobsters molted the previous summer) ranged from 40.2% in 1986 to 62.5% in 1989 for males and from 21.6% in 1986 to 47.6% in 1989 for females (Table 2). In 1986, the incidence of new shells was very low among Goose I. lobsters (3.3% for males and 6.7% for females) indicating few molted in summer 1985 when they were transplanted. However, in 1988 and 1989 the incidence of new shells was quite high (75.0-92.0%) for males and females (Table 2).

**Table 2**

Percentage with new shells (molted previous summer) among lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1986 and 1988-90. Number sampled in parentheses.

Year sampled	Indian Arm		Goose Island	
	Males	Females	Males	Females
1986	40.2 (87)	21.6 (74)	3.3 (30)	6.7 (30)
1988	53.1 (32)	42.9 (42)	80.0 (10)	92.0 (25)
1989	62.5 (24)	47.6 (21)	75.9 (29)	75.0 (20)
1990	52.9 (17)	31.8 (22)	52.2 (23)	63.6 (22)

**Table 3**

Pleopod setal development stages for male and nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1989-90.

Year sampled	Setal development stages* (%)					
	N	Males		N	Females	
		0-2.0	2.5-5.0		0-2.0	2.5-5.0
<b>Indian Arm</b>						
1989	24	70.8	29.2	8	62.5	37.5
1990	17	47.1	52.9	8	0	100
<b>Goose Island</b>						
1989	29	69.0	31.0	16	81.2	18.8
1990	23	39.1	60.9	15	0	100

\* From Aiken (1973). Stages 0-2.0 indicate molting is unlikely, and stages 2.5-5.0 that molting is probable in the current summer.

Pleopod setal development was determined in 1989 and 1990 only. Percentages with advanced stages (2.5 and higher), which indicated molting would occur later in the summer, varied between years and sexes at both sampling sites. Among males, advanced stages increased from 29.2% to 52.9% and from 31.0% to 60.9% in Indian Arm and Goose I. samples, respectively, between 1989 and 1990 (Table 3). Among females, it increased from 37.5% in the Indian Arm sample and 18.8% in the Goose I. sample in 1989, to 100% in both in 1990 (Table 3).

### Reproductive condition of nonovigerous females

Ovaries of 110 nonovigerous females from Indian Arm and Goose Island combined were examined from 1987 to 1990 and all were found to be medium- to dark-green

**Table 4**

Ovary color and ova diameter among nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1987–90.

Year sampled	N	Ovary color		Ova diameter (mm)	
		Med. green	Dark green	$\bar{x}$	Range
<b>Indian Arm</b>					
1987–88	34	11 <sup>a</sup>	23	1.4	0.9–1.5
1989	8	0	8 <sup>b</sup>	1.0	0.9–1.3
1990	8	1	7	1.0	0.8–1.2
<b>Goose Island</b>					
1987–88	30	21 <sup>a</sup>	9	1.3	0.9–1.5
1989	15	1	14	1.0	0.8–1.3
1990	15	0	15	1.1	0.9–1.2

<sup>a</sup>The high proportion with medium-green ovaries in the 1987–88 sample is probably due to a different observer than in 1989–90.

<sup>b</sup>Includes one specimen with yellow specks throughout the ovary, indicating resorption underway.

in color, with ova 0.8–1.5 mm in diameter (Table 4). All these ovaries were developing for extrusion in the summer they were sampled; one had yellow specks characteristic of an ovary being resorbed. However, of these nonovigerous females, only 2 of 24 sampled in 1989 (2 out of 111 overall) had sufficient pleopod cement gland development (Stage 3) to indicate egg extrusion would occur (Table 5). The seminal receptacles of all of the nonovigerous females examined from 1987 to 1990 were full, which means each had mated at the last molt and was capable of fertilizing a clutch of eggs. Pleopod setal development indicated 25% of 24 and 100% of 23 nonovigerous females sampled in 1989 and 1990, respectively, would molt (Table 3). While molting does not preclude egg extrusion in the same summer, this is unlikely to occur among lobsters in St. Michael's Bay. This phenomenon probably involves only animals extruding for the first time and <81 mm CL (Ennis 1984a).

### Incidence of ovigerous females

The reproductive cycle in female lobsters normally covers 2 years. Molting and mating occur one summer, egg extrusion one year later, followed by hatching of eggs, molting, and mating again in the third summer (Aiken and Waddy 1980a). Departures from this 2-year cycle known to occur in the wild include molting, mating, and extrusion in the same summer (mentioned in the preceding section) and resorption of ripe ovaries just before extrusion (Aiken and Waddy 1976 and

**Table 5**

Pleopod cement gland stages for nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1987–90.

Year	N	Cement gland stages*			
		1	2	3	4
<b>Indian Arm</b>					
1987	7	7	0	0	0
1988	27	27	0	0	0
1989	8	7	0	1	0
1990	8	8	0	0	0
<b>Goose Island</b>					
1987	23	23	0	0	0
1988	7	7	0	0	0
1989	16	15	0	1	0
1990	15	15	0	0	0

\* From Aiken and Waddy (1982). Stages 3 and 4 indicate extrusion will occur in the current summer.

1980ab, Ennis 1984b). While variability in the incidence of these phenomena may contribute somewhat, the intensity of the commercial fishery and its timing in relation to the spawning season exert by far the greatest impact on the incidence of ovigerous females in a lobster population.

At Comfort Cove, most of the nonovigerous commercial-size females in the population are removed by the spring fishery just before the summer spawning period. In autumn sampling from 1986 to 1990 an average 6% of commercial-size females were ovigerous, excluding those that molted and grew from subcommercial sizes and extruded as well during the summer (Ennis, unpubl. data). Not being fished and being more likely to spawn as well because of their larger size, the percentage of females ovigerous among St. Michael's Bay lobsters by comparison should be quite high.

In St. Michael's Bay, the percentages of females that were ovigerous with old eggs each summer (i.e., extruded previous summer) were very low, particularly in 1986–88 samples, considering all nonovigerous females examined the previous summer had ripe ovaries. In the 1986 Indian Arm sample, 19.3% of the females were ovigerous, including both new- and old-egged females which were not distinguished at the time. In subsequent years, the incidence of ovigerous females with old eggs increased from 4.0% in 1987 to 33.3% in 1991 (Table 6). No ovigerous females were included in Goose I. samples until 1989, when 10% of the females carried old eggs. In 1990 and 1991 samples, however, there were none with old eggs (Table 6).

**Table 6**

Percentage of females that were ovigerous among lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1986–91.

Sampling dates	Indian Arm				Goose Island			
	No. females	% new eggs	% old eggs	% ovigerous	No. females	% new eggs	% old eggs	% ovigerous
22 July–25 Aug. 1986	109	—	—	19.3*	32	0	0	0
18–25 July								
26 Aug.–3 Sept. 1987	25	4.0	4.0	8.0	33	0	0	0
25 June–2 July 1988	48	10.4	4.2	14.6	38	0	0	0
19–25 July 1989	21	33.3	23.8	57.1	20	10.0	10.0	20.0
13–20 Aug. 1990	22	50.0	13.6	63.6	22	31.8	0	31.8
14–19 Aug. 1991	9	44.4	33.3	77.8	13	76.9	0	76.9

\* In 1986, old- and new-egg ovigerous females were not distinguished.

The percentages of females that were ovigerous with new eggs (i.e., extruded within the preceding 2 or 3 weeks) ranged from 4% in 1987 to 50% in 1990 in the Indian Arm samples, and increased from 10% in 1989 to 32% in 1990 in the Goose I. samples (Table 6). Of 64 ovigerous females included in the combined 1987–91 samples, 73% had new eggs and, overall, there was a substantially higher incidence of ovigerous females among St. Michael's Bay lobsters in 1989–91 than previously.

The low incidence of ovigerous females in samples up to 1988 indicates most of the nonovigerous females, all of which had ripe ovaries in summer, failed to extrude eggs. In subsequent years, however, the proportion of nonovigerous females extruding increased substantially. There was no evidence of hatching of old eggs prior to our sampling each summer, which might have accounted for the scarcity of old-egged relative to new-egged females. This indicates that many females that extruded lost their entire clutch of eggs sometime prior to the following summer.

### Fecundity and egg development

Egg numbers were determined for 9 ovigerous females included in the 1987 and 1988 samples from Indian Arm. Four of these egg counts were <0.1% of expected numbers as determined from a size-fecundity relationship for a population on the south coast of Newfoundland, one had 2%, and the others had 30–105% of the expected number of eggs (Table 7). The extremely low numbers in 5 of the 9 specimens cannot be attributed to high variability generally associated with such data, but rather indicate a high incidence of massive egg loss. Although egg numbers were not determined for any of 21 ovigerous females included

**Table 7**

Egg numbers for nine ovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador, included in 1987 and 1988 samples from Indian Arm.

Carapace length (mm)	No. of eggs	% of expected number*
97	15	<0.1
97	7	<0.1
101	122	<0.1
102	186	<0.1
94	334	2.0
103	6588	30.0
104	10122	45.0
102	17878	84.0
95	17854	105.0

\* Expected number of eggs was calculated from a CL–fecundity relationship ( $\log_{10} F = 3.0984 \log_{10} CL - 1.8963$ ) for a population in Placentia Bay on the south coast of Newfoundland (Ennis 1981).

in the 1989 and 1990 samples, cursory examination indicated that most had what appeared to be full clutches, although one had just a few hundred eggs.

The extent of embryonic development for 17 ovigerous females with old, eyed eggs collected from 1986 to 1991 ranged from 0.8 to 0.3 yolk content (Table 8). Only 6 had less than half the yolk remaining when examined. Perkins Eye Indices (PEI) were determined for four specimens. One with 0.3 yolk content had a mean PEI of 470 on 29 June 1988. At an assumed constant developmental temperature of 10°C, it was estimated, using Perkin's (1972) formula, that hatching would have occurred by 4 August. Another with 0.4 yolk content had a mean PEI of 431 on 1 August 1986, for which hatching by 21 September was estimated.

**Table 8**

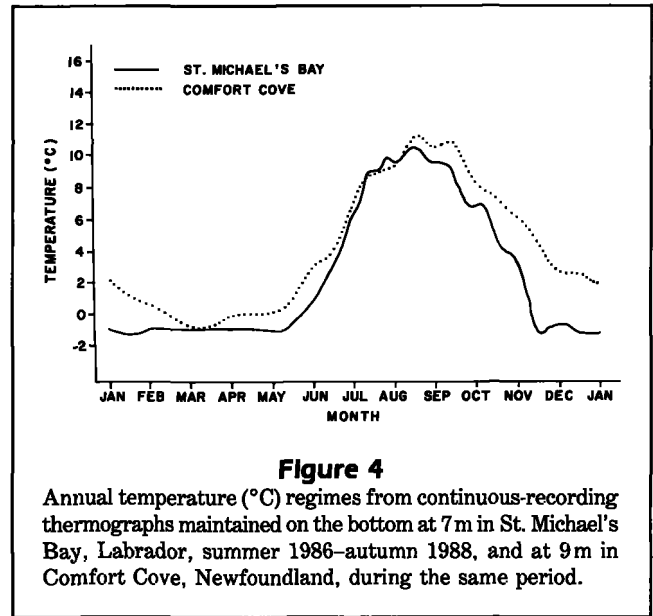
Yolk content of eggs for 17 ovigerous females with old, eyed eggs included in 1986–91 samples of lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador. Yolk content to the nearest tenth.

Sampling date	Carapace length (mm)	Yolk content
1 Aug. 1986	94	0.4
19 July 1987	92	0.7
29 June 1988	95	0.3
30 June 1988	97	0.8
20 July 1989	88	0.4
21 July 1989	110	0.6
21 July 1989	108	0.6
21 July 1989	103	0.7
21 July 1989	109	0.6
21 July 1989	106	0.5
22 July 1989	92	0.7
16 Aug. 1990	116	0.3
16 Aug. 1990	111	0.4
16 Aug. 1990	104	0.5
19 Aug. 1991	101	0.5
19 Aug. 1991	114	0.5
19 Aug. 1991	107	0.4

The other two PEIs were 108 and 127 (0.8 and 0.7 yolk content, respectively). Even at 10°C, well above the temperature in St. Michael's Bay beyond September, it was estimated these broods would not be ready to hatch until late December–early January.

### Temperature

Bottom temperature at 7 m in St. Michael's Bay drops below 0°C in late November, remains around -1°C throughout the winter, and rises above 0°C in early June (Fig. 4). Summer warming is rapid. Temperature reaches 9°C between mid- and late-July and peaks at just over 10°C in late August. By mid-September, autumn cooling is underway and temperature starts to drop rapidly around the end of September. At Comfort Cove, where the transplanted lobsters originated, sub-zero temperatures prevail for only about 2 months in late winter (Fig. 4). Summer warming begins in late April–early May and reaches a slightly higher peak at around 11°C in late August. Autumn cooling begins somewhat later and proceeds more slowly. In St. Michael's Bay, transplanted lobsters are exposed to a similar range in temperature as at Comfort Cove, but to a substantially lower mean temperature during most of the year.

**Figure 4**

Annual temperature (°C) regimes from continuous-recording thermographs maintained on the bottom at 7 m in St. Michael's Bay, Labrador, summer 1986–autumn 1988, and at 9 m in Comfort Cove, Newfoundland, during the same period.

### Discussion

The very low incidence of new-shell lobsters in the 1986 Goose I. sample indicates few molted in summer 1985 when they were transplanted. This was most likely due to molt inhibition caused by handling-induced stress, possibly including wide temperature fluctuations, during transplant. The high incidence of new-shell lobsters at Goose I. in 1988, and the substantial shift to larger sizes among the Indian Arm lobsters (transplanted in 1982) by 1986, indicate the transplanted lobsters acclimated over time and resumed molting despite the lower temperatures in St. Michael's Bay.

All nonovigerous females examined during the study had advanced ovaries developing for extrusion in the summer they were sampled. All of these had full seminal receptacles indicating they mated at the last molt. However, only 1.8% (2 out of 24 examined in 1989) had advanced pleopod cement gland development indicating extrusion was imminent. Some ovigerous specimens with recently-laid eggs were observed each year. This suggests most nonovigerous females that were going to extrude each summer had done so by the time our samples were collected. These amounted, however, to only 23% (*N* 104) of the females (excluding old-egg ovigerous) examined at Indian Arm from 1987 to 1990, and 22.5% (*N* 40) of those examined at Goose Island in 1989 and 1990. In 1991, this percentage increased to 66.7% (*N* 6) and 77% (*N* 13) in the Indian Arm and Goose I. samples, respectively. Advanced pleopod setal development among the ripe nonovigerous females that were examined in 1989 and 1990 indicated 62% would soon molt.

Based on the foregoing observations, it appears that up until 1990 at least most of the mature, nonovigerous females in St. Michael's Bay did not extrude. Rather, they resorbed the lipovitellin accumulated in the ripening oocytes, and many then proceeded to molt. Resorption of the ripe ovary has been associated with unfavorable holding conditions near the expected time of extrusion (Templeman 1940) but appears to be common in the wild as well (Ennis 1984b). Resorption occurs when the molting and reproductive cycles are out of phase, and molting is due to occur within 3 or 4 months after egg extrusion (Aiken and Waddy 1976, 1980ab). These cycles are normally synchronized by temperature and photoperiod regimes to ensure that when a female lobster extrudes eggs in one summer, it will not molt until after the eggs have hatched sometime the following summer.

In their experiments on the effects of winter temperature and photoperiod on spawning, Aiken and Waddy (1989) found a high incidence of resorption among mature females held at high temperature throughout the winter, particularly when a short-day photoperiod was maintained throughout the summer (55% resorbed). Onset of a long-day photoperiod in spring was necessary to trigger spawning among females held at high winter temperature. The incidence of spawning was high ( $\geq 90\%$ ) among those held at low winter temperature, even without onset of a long-day photoperiod in spring, and only a few resorbed.

These results do not explain the high incidence of resorption among female lobsters in St. Michael's Bay where they are exposed to environmental conditions well outside the foregoing experimental treatments. From mid-November to mid-May, the bottom temperature is near or below  $0^{\circ}\text{C}$  and the bay is frozen over for most of this period. Visual acuity of lobsters at very low light intensity has not been described. It seems unlikely, however, that sufficient light would penetrate a layer of snow-covered sea ice underlaid by low-salinity water (from continuous river discharge and slow mixing under the ice) for lobsters to detect a light:dark cycle. This combination of very low temperature and near continuous darkness for 5–6 months from late autumn to spring is probably the main cause of the high incidence of ovary resorption that has prevailed among female lobsters in St. Michael's Bay.

Most of the ovigerous females collected in St. Michael's Bay had extruded quite recently. The remainder were old-egged females that spawned the previous summer. Apparently, many females that extruded lost the entire clutch of eggs before the following summer. Massive but incomplete loss of eggs was also observed. Of 9 ovigerous females collected in Indian Arm in 1987 and 1988, 5 had numbers of eggs ranging from 7 to 334. Only one of the 21 ovigerous

females collected in 1989 and 1990 had just a few hundred eggs. The overall incidence of ovigerous females, particularly those with new eggs, increased substantially in 1989 and 1990 and especially in 1991. At Goose I., no ovigerous females at all were included in samples until 1989, 4 years after they were transplanted. This indicates a high degree of acclimation or physiological adjustment to environmental conditions in St. Michael's Bay on the part of females, resulting in much less resorption of ripe ovaries and much more extrusion in recent years. However, loss of the entire clutch of eggs appeared to be still quite prevalent. Ovigerous females sometimes lose their entire clutch of eggs by molting (Ennis 1984b). This may have been a more common occurrence in later years, which could explain the near absence of tiny clutches compared with the high incidence observed in 1987 and 1988, and would also be consistent with a high incidence of new shells and advanced setal development among females in 1989 and 1990. Despite some physiological adjustment resulting in more extrusion, for most females the molting and reproductive cycles continued to be out of phase.

Embryonic development in lobsters proceeds slowly at temperatures below  $6^{\circ}\text{C}$ , and hatching can be delayed by as long as 6 months if temperature remains at  $2\text{--}3^{\circ}\text{C}$  throughout spring, summer, and autumn, although it will eventually occur, even at that temperature (Aiken and Waddy 1986). Perkins (1972) found that advanced embryos will develop more slowly than less advanced ones when held at the same temperature. In one specimen with 29-week-old eggs on 10 January held at the Boothbay Harbor Laboratory under local water conditions, there was no measurable development for an 18-week period starting in early December. Over most of the period, temperature ranged from  $0.1^{\circ}\text{C}$  to  $1.5^{\circ}\text{C}$ .

In St. Michael's Bay, bottom temperature drops below  $6^{\circ}\text{C}$  by mid-October, below  $3^{\circ}\text{C}$  by mid-November, and below  $0^{\circ}\text{C}$  by late November. Of the old-egged ovigerous specimens from there, which are presumed to have extruded the previous summer, there was one with 0.8 yolk remaining when examined at the end of June, three with 0.7 remaining around 20 July, and three with 0.5 remaining in mid-August. Possibly some of these females carry their eggs through a second winter and may represent the ones observed in our samples with sufficiently advanced development for hatching to occur before the end of summer (i.e., hatching 2 years after extrusion rather than the usual 1).

Only 6 of the 17 old-egged ovigerous females collected in St. Michael's Bay from 1986 to 1991 had less than half the yolk remaining in the eggs when examined. Four of these would likely have been ready for



hatching by sometime in September, around the time autumn cooling begins. The other, which had 0.3 yolk remaining and a PEI of 470 at the end of June, would probably have hatched by early August. This was the only specimen for which hatching as much as 4 or 5 weeks in advance of autumn cooling was a possibility. However, extensive plankton sampling (130 15-min tows with a 1 m diameter net) conducted near the sites where lobsters were released in St. Michael's Bay, from 28 July to 22 August 1986, and from 18 July to 30 August 1987, failed to produce lobster larvae.

Bottom temperature at 7 m in St. Michael's Bay during August ranged from around 9°C to 10.5°C. Assuming temperature in the surface layer was around 15°C, at which lobster larvae will reach Stage IV in 25 days (Templeman 1936), it is possible that larvae hatching in early August would be in Stage IV at the end of August and ready to settle by mid-September. Larvae hatching in late August would be exposed to temperatures below 10°C well in advance of reaching Stage IV. At 10°C, it takes 2 months from hatching to Stage IV; and at 5°C, larvae generally die without reaching Stage IV (Templeman 1936). Caddy's (1979) consideration of the influence of seasonal temperature regime on survival of lobster larvae indicates poor chances of survival if larvae have not reached Stage IV by the end of August. Any larvae hatching in St. Michael's Bay in late August-early September appear to have little chance of reaching Stage IV and settling in the area. The 1988-90 diver-collected samples involved 12 dives totaling about 30 diver hours searching at the Indian Arm and Goose I. sites. Not a single small lobster was found, suggesting there had been very little if any recruitment since lobsters were transplanted in 1982.

The possibility that the lobsters transplanted to St. Michael's Bay will become a self-sustaining population is remote. While the portion of females with ripe ovaries that actually extrude has increased substantially during this study, many of these lose all or most of their clutch of eggs before the following summer. Of those females that carry their eggs for at least a year, very few have eggs ready for hatching sufficiently early in the summer that any larvae are likely to settle in the area. Any local recruitment that might occur would be too little and too irregular to support a fishery for lobsters in St. Michael's Bay.

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