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ABSTRACT

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The premolt-postmolt growth of marked or tagged subadult lobsters between 55 and 94 mm carapace length was observed during five experiments spanning a period of 33 yr (1948-80) in waters off Port Maitland, Nova Scotia. Growth increment was greater during 1979-80 than during the four other experiments in 1948-68, but this was probably due to methodological differences. Proportion of prerecruit lobsters molting each year was dependent on the water temperature and on the total degree-days above 5°C. Males were heavier than females at similar sizes.

Key words: Growth, lobster, *Homarus americanus*, length-weight relationship

RÉSUMÉ

Campbell, Alan. 1983. Growth of tagged lobsters (*Homarus americanus*) off Port Maitland, Nova Scotia, 1948-80. Can. Tech. Rep. Fish. Aquat. Sci. 1232: iii + 10 p.

Lors de cinq expériences menées dans les eaux du large de Port Maitland, en Nouvelle-Ecosse, couvrant une période de 33 ans, on a observé la croissance d'avant et d'après-mue de homards subadultes marqués ou étiquetés, et d'une longueur de carapace comprise entre 55 et 94 mm. La croissance a été plus prononcée en 1979-80 que durant les quatre autres expériences de 1948-68, mais ceci est probablement dû à des différences de méthodologie. La proportion des prérecrues muant chaque année dépendait de la température de l'eau et du nombre de jours-degrés au-dessus de 5 °C. Les mâles étaient plus lourds que les femelles de même taille.

INTRODUCTION

An essential part of understanding the population dynamics of an exploited species is the knowledge of growth rates. With growth information on lobster (Homarus americanus) populations mortality rates from catch curves and yield per recruit from a fishery can be estimated (Anthony and Caddy 1980). Estimation of growth rate in lobsters is limited by the absence of annual or seasonal structural marks and the discontinuous nature of the molting process. In this paper, molt increment and proportion molting data from five lobster mark-tag release-recapture experiments are analyzed to determine growth rates near Port Maitland, Nova Scotia, during 1948-80. Wilder (1953) first reported on growth increments of lobsters marked during 1948 off Port Maitland. The present paper reports on four subsequent growth experiments conducted between 1960 and 1980, and compares them with the 1948 data. Length-weight relationships of lobsters during 1979 from this area are also presented.

MATERIALS AND METHODS

Lobsters were caught in baited traps by fishermen from Port Maitland (see Campbell (1982) for location map) during the spring fishing season (Nov.-May) or soon after the fishing season in June (Table 1). Lobsters used for the mark-recapture experiments were purchased from fishermen during 1948-67, but collected by boat charter during 1979. Lobsters were marked with holes punched by a 1/4-in. (6.35 mm) diameter punch in sections of the tail fan during 1948 and drilled with a 3/16-in. (4.76 mm) diameter drill bit during 1960-63. Separate combinations of tail sections were used for each 1/8-in. (3.17-mm) carapace length (L) group: five groups for 1948, ten groups for 1960, five groups for 1963. The marked lobsters were kept in a holding tank for 4-14 h prior to release on the Port Maitland lobster fishing grounds. A detailed account of the tail-punch marking method is given by Wilder (1953).

During 1967 and 1979 the 'sphyrion tag' (Scarratt and Elson 1965) was used by inserting the stainless steel anchor into the dorsal musculature between the carapace and abdomen. The lobsters were tagged and measured at sea and released at the area of capture. The size groups (seven groups of 1/8 in. (3.17 mm) per group in 1967 and 1 mm group for 1979) and numbers of marked or tagged lobsters released in the five growth experiments are shown in Fig. 1 and Table 1. The methods of marking and tagging lobsters were considered not to adversely affect lobster survival and subsequent growth.

Within 1 yr of release, usually during the following fishing season, observers searched for marked/tagged lobsters in most fishermen's catches in Port Maitland and adjoining ports (Cape St. Mary, Short Beach, Sandford). Fishermen were encouraged (with monetary reward) to return tagged legal and sublegal sized lobsters, with information on date and location of recapture, to observers. Tagged or marked 'shorts' (sublegal-sized lobsters) were brought to port (separated from the legal catch), measured by observers, and released. Molt data on 'short' recaptures rely mainly on the fishermen's observations at sea, and thus may not be totally reliable because marked unmolted 'shorts' may have been missed since the fishermen's attention would be mainly on legal lobsters.

Data recorded for each marked/tagged lobster included sex, carapace length (in 1/32 in. during 1948-69 and in millimetres during 1979), location and date of release and recapture. Carapace length was measured with Vernier calipers from the inner part of the eye socket to the dorsal posterior margin of the carapace along the mid-line. Variability in measuring L by different observers was empirically estimated to be <1.5 mm. All L measurements are expressed in millimeters in this paper. Release sizes were recorded as the mid-point of each 3.1-mm L group for 1948-69, but actual L for all recaptured individuals during 1948-70 and all released and recaptured lobsters during 1979-80 were recorded.

RESULTS AND DISCUSSION

LENGTH-WEIGHT RELATIONSHIPS

The carapace length (L) and total wet weight (g) relationship of male and female lobsters (Port Maitland, May 1979) were analyzed as a power curve ($wt = aL^b$), using the least squares method after $\log_e$-$\log_e$ transformation:

Males: $\log_e wt = -7.2525 + 3.0233 \log_e L$
(N=135, R=0.9911, L min.-max. = 47-144 mm)

Females: $\log_e wt = -6.7174 + 2.9073 \log_e L$
(N=197, R=0.9895, L min.-max. = 55-118 mm)

Analysis of covariance indicated that the slopes of male and female length-weight relationships were significantly different ($p < 0.01$). For the males, the slope was not significantly greater than 3 ($p > 0.05$), indicating allometric growth. For the females, the slope was significantly less than 3 ($p < 0.01$), suggesting negative allometric growth.

ANNUAL GROWTH

Only a few of the marked/tagged lobsters liberated in the Port Maitland area were recaptured within a year of release: 5% for 1948-49, 6.7% for 1960-61, 3% for 1963-64, 11.9% (only 7.3% were measured) for 1967-68, and 10.8% (only 5.4% were measured) for 1979-80 (Fig. 1). Growth per molt and proportion molting were estimated from these data. Each tagged lobster was considered to have had a chance to molt at least once during the molting period (July-November) in the Port Maitland waters (Wilder 1953). Lobsters were assumed to have molted when the increase in L was ≥5% above the premolt L. Only one molt was assumed to have occurred within the first year of release in this area.

Interpretation of the growth data should be made with caution because three experimental sources of bias may occur: (1) The use of the mid-point of each 3.1-mm L release size group for the 1948-69 data may cause the estimated growth increment of a few individuals to vary up to ± 2% of actual growth. This should not affect the estimation of average molt probability and average growth increments because there were sufficient numbers distributed evenly about the mid-point of each premolt release size group. Consequently, the use of premolt-postmolt regressions and their comparisons, using ANCOVA on similar premolt size ranges, should not be

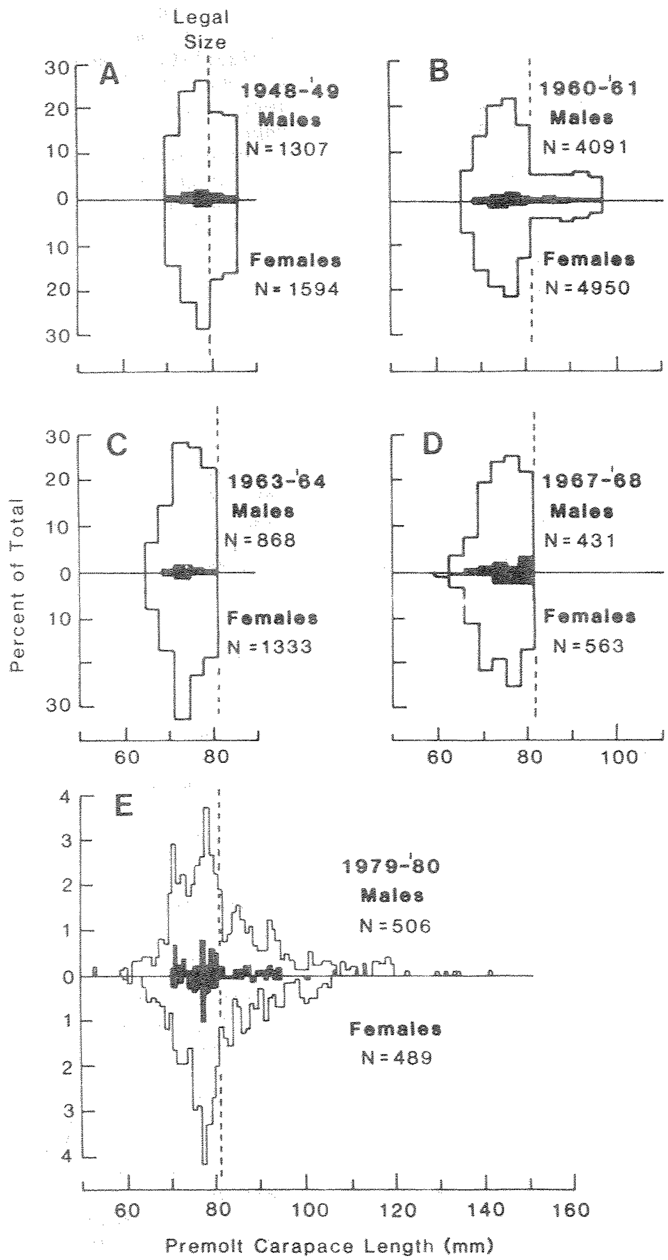

Fig. 1. Size frequencies of marked-tagged male and female lobsters released (clear histogram) and recaptured (shaded) of total lobsters released off Port Maitland during 1948-80.

affected as post-molt lengths are adjusted by using premolt length as a covariate (Snedecor and Cochran 1967). (2) Tag loss during molting and/or mortality due to poor application of tags so that average size-specific growth increment data may be biased downward. Individuals applying tags to lobsters were well trained and experienced so that tag loss was considered minimal. (3) Lobsters molting without a detectable size increase and, in this paper, the exclusion of <5% growth increments may bias the premolt-postmolt regression line and proportion molting data upward. Under field conditions, H. americanus in the 60-95 mm L size range, without significant size increases, are probably rare.

Growth per molt

Growth per molt was expressed by the predictive regression

$$L_{x+1} = A + BL_x,$$

where L_x and L_{x+1} are premolt and postmolt (mm) respectively, and A and B are empirical constants determined by the least squares method (Hiatt 1948). Kurata (1962) suggested that the growth phases of juvenile and mature lobsters were characterized by different growth constants in the premolt-postmolt regression. In this study almost all growth data were obtained from immature lobsters (≤94 mm L) (Campbell 1983) and to a large extent from 'shorts' (Table 1, 2; Fig. 1, 2). As there were so little data on growth of mature (≥95 mm L) lobsters (e.g. Fig. 2), statistical analysis for this size group was not appropriate.

ANCOVA (Snedecor and Cochran 1967) was performed for similar L ranges to determine differences between slopes and elevations of the premolt-postmolt L regressions between sexes within one year and between years. The slopes and elevations of the premolt-postmolt L regression relationship did not significantly differ between males and females and between the four experiments 1948-67 (Fig. 2, Table 2) ($p > 0.05$); consequently, the data were combined to obtain one regression each for the males and females for this period (Table 2). The male and female premolt-postmolt L regression slopes did not differ within the 1979-80 data and between the 1979-80 and 1948-67 data ($p > 0.05$), but there was a significant difference in elevations between 1979-80 and 1948-67 regressions ($p < 0.01$) within a comparable size range of 70-85 mm L for all years (Table 2, Fig. 2). This indicates that lobsters had a greater growth increment (16.9-18.4%) during 1979-80 than during the 1948-68 experiments (13.1-15.7%). In general, lobster growth at molt within an area varies little from year to year (Ennis 1972; Conan 1978). Indeed, methodological differences between experimental years (e.g. tail punching versus tagging, grouping release sizes by 1/8-in. classes versus recording release and recapture size for each individual, low sample sizes in some years, especially in 1979-80, and/or possible differences in measuring techniques by field observers) may be contributing factors to differences in these growth increments. However, if these differences in size increment are real, the cause of growth changes could be due to a number of factors such as changes in: 1) annual mean water temperatures; 2) density-dependent factors; and/or 3) food type availability (Aiken 1980).

Slopes for the combined data for the 1948-67 male and female premolt-postmolt regressions and those of 1979-80 males were significantly greater than 1 ($p < 0.05$) (Table 2) which meets Kurata's (1962) criteria for progressive growth ($B \geq 1.05$), whereas the slope for females in 1979-80 tended to be regressive ($B < 0.95$), although B was not significantly lower than 1 ($p > 0.05$). In general, the data agree with other studies which indicate that immature lobsters tend to have progressive arithmetic growth although slopes are generally smaller for females than for males (Ennis 1972; Conan 1978; Campbell 1983).

Molt probability

The proportion of individuals molting annually in each size group was calculated for each sex and experimental year. The relationship between proportion molting (Y) and premolt carapace length (L_x) per size was fitted with an exponential curve:

$$Y = ae^{bL_x}$$

where a and b are empirical constants determined by the least squares method after $\log_e$ transformation of Y; only the 1948-49 and 1960-61 data were used where sufficient lobsters > 79 and 81 mm premolt L were recaptured.

The proportion of marked lobsters that molted dropped rapidly from 78 to 85 mm L for 1948-49 and 1960-61, with females molting slightly less than males (Table 3, Fig. 3). There were insufficient data on legal-sized lobsters to estimate proportion molting for the 1963-80 growth experiments (Table 3, 4). The evidence suggests that most lobsters of the size range examined molt less than or equal to once per year. The estimated rapid decline in molt probability is due to a lack of molting data for large lobsters (>100 mm L) because they are not commonly caught in this area during the winter-spring fishery (Campbell 1982) as a result of high exploitation rates and/or trap selectivity for smaller sizes (Ennis et al. 1982; Fogarty et al. 1982).

A combination of proportion molt-premolt L data for the years 1948-49, 1960-61, and 1963-64 resulted in the following relation:

for males

$$Y = 18.25e^{-0.0398L_x} \quad (R=0.794),$$

and females

$$Y = 30.25e^{-0.0469L_x} \quad (R=0.846).$$

Growth curves

Growth curves (Fig. 4) were derived from the product of the annual proportion molting and molt increment. Average proportion molting for 1948-63 was used with the average 1948-67 (Fig. 4C) and 1979-80 (Fig. 4D) premolt-postmolt data (Table 2).

Average von Bertalanffy growth curves for male and female lobsters were fitted to data points of size-at-age (Fig. 4), using

$$L_t = L_\infty\ (1-e^{K(t-t_0)})$$

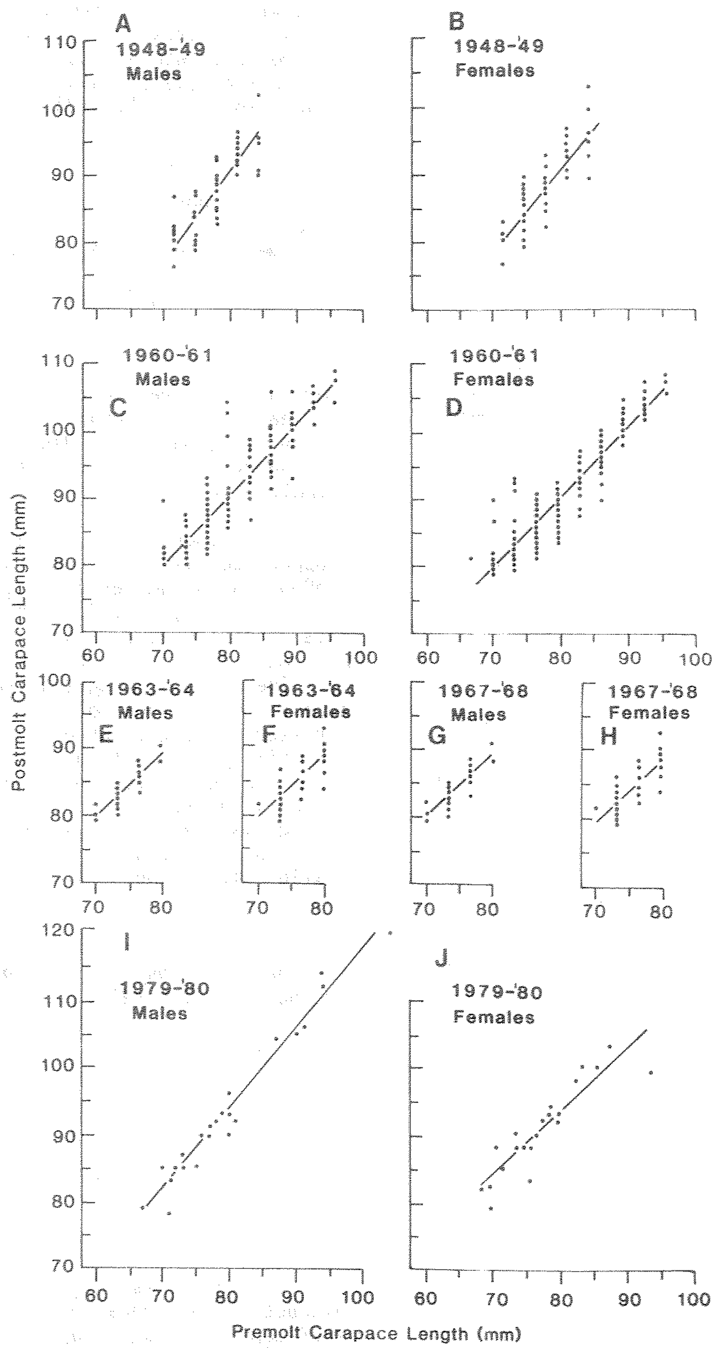

Fig. 2. Premolt-postmolt carapace lengths for male and female lobsters recaptured from the Port Maitland area 1948-80.

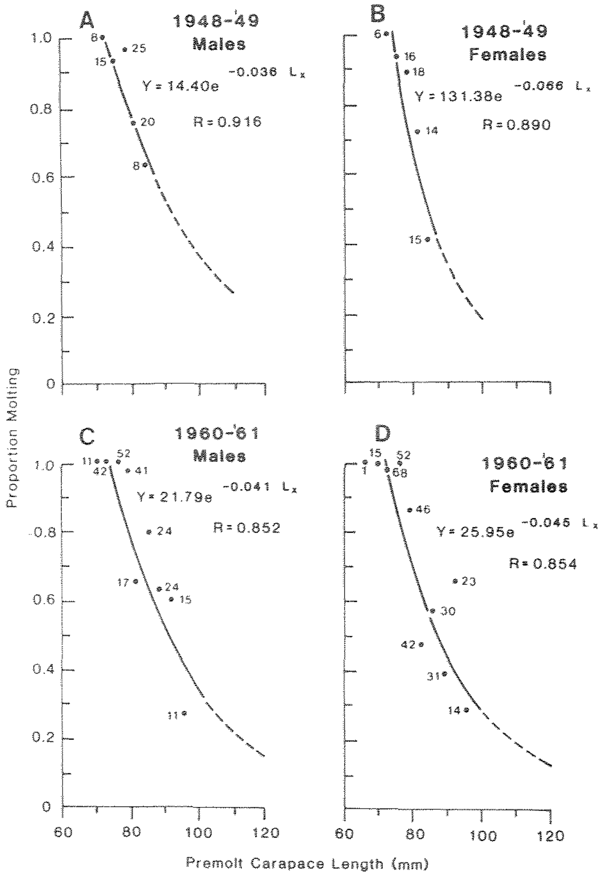

Fig. 3. Proportion molting of marked (A) male, (B) female lobsters during 1948-49 and (C) male and (D) female lobsters during 1960-61 which molted off Port Maitland. The numbers of observations (lobsters recaptured) per carapace length group used to calculate each percentage are shown by each data point.

where t = age in years, L_t = carapace length at t, L_∞ = theoretical maximum L, K = constant determining rate of increase or decrease in length increments, and t_0 = hypothetical age at which the organism would be at zero length, using the method of Allen (1967). Although the age of individual lobsters was not known, the average age of lobsters at 81 mm L, for estimating the von Bertalanffy parameter, was assumed to be 6 yr for both males and females (Aiken 1980; Campbell 1983). The resulting values for each equation are shown in Table 5. The L_∞ values are obviously too low. At larger sizes ($\geq$ 95 mm L), these curves obviously underestimate lobster growth rates (Campbell 1983) but, at the smaller sizes (70-90 mm CL), the growth curves are probably realistic (Fig. 4).

TEMPERATURE AFFECTING PROPORTION MOLTING

Table 6 shows the relationship between mean temperature and total degree-days above 5°C (June-November) and percentage molting of prerecruit lobsters (69.9-80.0 mm L) during the five growth

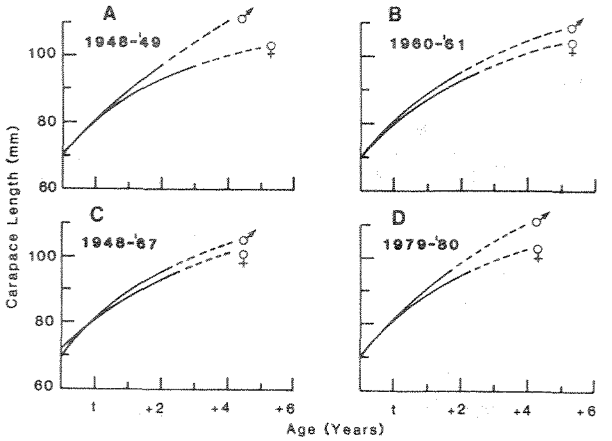

Fig. 4. Growth curves for male and female lobsters off Port Maitland during (A) 1948-49, (B) 1960-61, (C) 1948-67 all experiments combined, (D) 1979-80. Broken lines are extrapolated beyond available data. Growth curves derived from product of proportion molting and growth increment.

experiments, 1948-79. Temperatures were obtained from Prince Station #5 temperature records (St. Andrews Biological Station, N.B.) and extrapolated with Lurcher Lightship temperatures (Lauzier and Hull 1969). Temperatures $\geq$5°C are assumed to be required for most lobsters to molt (Aiken 1980) in this area. The period when most lobsters molt in this area is between June and November (Wilder 1953). There were sufficient degree-days during the summers of 1948, 1960, 1963, and 1979 for over 90% of all prerecruits to molt into the fishery. During 1967, however, summer temperatures were low and, with only 212 degree-days accumulated, only 50% of prerecruits molted (Table 6). The data illustrate how lobsters are highly dependent on sufficient heat units to molt each season in this area.

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Table 1. Summary of mark-tag lobster growth experiments at Port Maitland, Nova Scotia, 1948-80. During 1948-67 lobsters were released in 1/8-in. groups measured in 1/32 in. of the carapace length (L) whereas, during 1979, lobsters were released in 1-mm L groups. All L data are converted to millimeters.

Release			Recapture		Type mark-tag	Legal minimum size L, mm
Period	Number	Size range L, mm	Period	Number		
19 April-31 May, 1948	2,901	69.8-85.7	4 Nov., 1948-13 May, 1949	145	Tail-punch marking	79.4
11 April-28 May, 1960	9,041	65.1-96.0	1 Nov., 1960-31 May, 1961	560	"	81.0
14-24 May, 1963	2,201	65.1-80.2	4 Nov., 1963-1 June, 1964	66	"	81.0
24 May-8 June, 1967	994	58.7-61.1	3 Nov., 1967-4 June, 1968	119	Sphyrion	81.0
4-13 June, 1979	995	59.0-141.0	Nov., 1979-31 May, 1980	108	"	81.0

Table 2. Constants for predictive linear regressions comparing the relationship between premolt (L_x) and postmolt (L_{x+1}) carapace lengths (in mm) obtained from mark-tag data (see Fig. 2) off Port Maitland. A and B are empirical constants of the regression $L_{x+1} = A + BL_x$; R = correlation coefficient; and N = number of individuals. Slopes significantly different from 1 are shown as * $p < 0.05$ and ** $p < 0.01$.

Year	Sex	Regression constants A	B	R	N
1948-49	male	-16.681	1.340*	0.845	65
	female	- 4.217	1.183	0.825	53
1960-61	male	6.759	1.049	0.908	185
	female	6.332	1.048	0.938	232
1963-64	male	13.434	0.953	0.867	21
	female	10.347	0.990	0.806	38
1967-68	male	- 1.712	1.166	0.943	13
	female	- 0.081	1.139	0.931	23
1948-67 combined					
	male	3.865	1.083**	0.899	284
	female	5.592	1.057*	0.927	346
1979-80	male	- 1.633	1.192**	0.982	26
	female	18.651	0.927	0.902	24
	male[a]	4.361[a]	1.111[a]	0.914	20
	female[a]	2.818[a]	1.136[a]	0.909	21

[a]Restricted size range of 70-85 mm carapace length.

Table 3. Percentage molting of marked-tagged lobsters in first year of recapture in growth experiments at Port Maitland 1948-68.

Mid-point premolt groups	1948-49						1960-61						1963-64						1967-68					
	male		female		total		male		female		total		male		female		total		male		female		total	
L, mm	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
63.5																					1	100	1	100
66.7							0	-	1	100	1	100							2	0	2	0	4	0
69.9							11	100	15	100	26	100	3	100	1	100	4	100	6	66.67	4	25.00	7	42.86
71.5	8	100	6	100	14	100																		
73.0							42	100	68	98.53	110	99.09	11	90.91	20	100	31	96.77	6	50.00	14	71.43	20	65.00
74.7	15	93.33	16	93.75	31	93.55																		
76.2							52	100	53	100	105	100	7	100	11	81.82	18	88.89	3	66.66	13	69.23	16	68.75
77.9	25	96.00	18	88.89	43	93.02																		
79.4							41	97.56	46	86.96	87	91.95	3	100	10	90.00	13	92.31	12	41.67	13	15.38	25	28.00
81.0	20	75.00	14	71.43	34	73.53																		
82.6							17	64.71	42	47.62	59	52.54												
84.2	8	62.50	15	40.00	23	47.83																		
85.8							24	79.17	30	56.67	54	66.67												
88.9							24	62.50	31	38.71	55	49.09												
92.1							15	60.00	23	65.22	38	63.16												
95.4							11	27.27	14	28.57	25	28.00												
Total	76	86.84	69	76.81	145	82.07	237	85.23	323	75.54	560	79.64	24	95.83	42	92.86	66	93.94	26	46.15	47	48.94	73	47.95
Total no-molt	10	13.16	16	23.19	26	17.93	35	14.77	79	24.46	114	20.36	1	4.17	3	7.14	4	6.06	14	53.85	24	51.06	38	52.05

Table 4. Percent molting of tagged lobsters in first year of recapture of growth experiments at Port Maitland, 1979-80.

Size class L, mm	male N	male %	female N	female %	Total N	Total %
66-70	1	100	4	100	5	100
71-75	7	100	6	100	13	100
76-80	11	90.91	11	100	22	95.45
81-85	1	100	2	100	3	100
86-90	2	100	2	100	4	100
81-95	3	100	1	100	4	100
96-100						
101-105	1	100			1	100
Total	26	96.15	26	100	54	98.15
Total no-molts	1	3.85	0		1	1.85

Table 5. von Bertalanffy growth parameters for recaptured lobsters tagged off Port Maitland, 1948-80, based on empirical growth curves calculated from the product of annual molt increment and proportion molting. Values in brackets are approximate 95% confidence intervals. Only the available data in size range 60-95 mm L were used to estimate parameters.

Sex	Year	K	L_∞	t_0
Males	1948-49	0.110 (±0.013)	164.7 (±9.2)	-0.122 (±0.244)
	1960-61	0.242 (±0.029)	118.9 (±3.7)	1.247 (±0.280)
	1948-67	0.229 (±0.008)	118.4 (±1.1)	0.963 (±0.086)
	1979-80	0.193 (±0.043)	135.3 (±10.2)	1.244 (±0.459)
Females	1948-49	0.389 (±0.065)	102.9 (±2.8)	2.064 (±0.376)
	1960-61	0.288 (±0.026)	109.3 (±2.1)	1.324 (±0.228)
	1948-67	0.288 (±0.026)	109.1 (±2.0)	1.303 (±0.226)
	1979-80	0.372 (±0.023)	108.0 (±1.3)	2.262 (±0.128)

Table 6. Mean summer bottom temperatures (°C) and degree-days above 5°C from 1 June-30 November and percentage molting of prerecruit lobsters (69.9-80 mm L) for each growth experiment off Port Maitland, 1948-79.

Year	Mean temperature	Degree-days >5°C	% molt	N
1948	6.82	352.4	94.3	84
1960	8.10	574.3	97.6	328
1963	7.59	485.9	93.9	66
1967	6.01	212.0	50.0	61
1979	9.50	816.9	97.5	40