Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, USVI: II Growth and Mortality

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POPULATION DYNAMICS, ECOLOGY AND BEHAVIOR OF SPINY LOBSTERS, *PANULIRUS ARGUS*, OF ST. JOHN, U.S.V.I.:
(II) GROWTH AND MORTALITY

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ABSTRACT: The Von Bertalanffy growth equation was fitted to spiny lobster growth data from St. John, U.S. Virgin Islands. Sexual differences in growth result in male lobsters reaching market size by the end of the second year of benthic life while females may take up to four years. A method for deriving the instantaneous coefficient of mortality is presented and used to derive this information. Survivorship values ranged from 52. 2 percent to 66.1 percent per year.

INTRODUCTION

Management of any living resource is contingent upon knowledge of growth, reproduction, immigration, emigration, and mortality. Once these population characteristics can be defined suggestions for effective management can be made. There is at present little information on the behavioral and ecological mechanisms underlying these basic events for the economicallly valuable spiny lobster, *Panulirus argus*. This paper gives valuable new information about growth and mortality of *P. argus* at St. John, U.S. Virgin Islands.

GROWTH

Data on growth analysis came from three sources. During the two Tektite programs and continued observations during 1970-71, 398 lobsters were tagged with back tags (Cooper 1970), their carapace length (linear distance in millimeters between the posterior margin of the eye socket and the posterior margin of the thorax, measured parallel to the median dorsal line of the thorax) measured, injuries and reproductive state recorded. When these animals were recaptured, the same information was again recorded. Tagging was not feasible for very small animals, so early growth was estimated using the average carapace lengths from four collections of 122 post-larvae which settled out on the floating causeway in Lameshur Bay and which were first noticed in June, 1970. The size-frequency distribution of these animals at each sample date is shown in Figure 11.

The data from the causeway sampled juveniles and from the recaptures (64 males and 38 females ranging in size from 37 to 178 mm carapace length) were analyzed by a computer program (Fabens 1965) to derive the parameters of the Von Bertalanffy growth equation,

$$L_t = L\,(1 - e^{k(t - t_0)}) \qquad (1)$$

where:

L_t = carapace length at time t,
L = asymptotic carapace length,
e = the base of natural logarithms,
t_0 = the time at which carapace length was zero,
k = a coefficient of catabolism.

Results of this analysis are shown in Table 2 and were used to draw the curves shown in Figure 12. The size-frequency distributions (Figure 6) presented in Part I (Olsen, Herrnkind, and Cooper) of this volume, for both males and females, were analyzed by probit analysis (Harding 1949) for the presence of size classes. The

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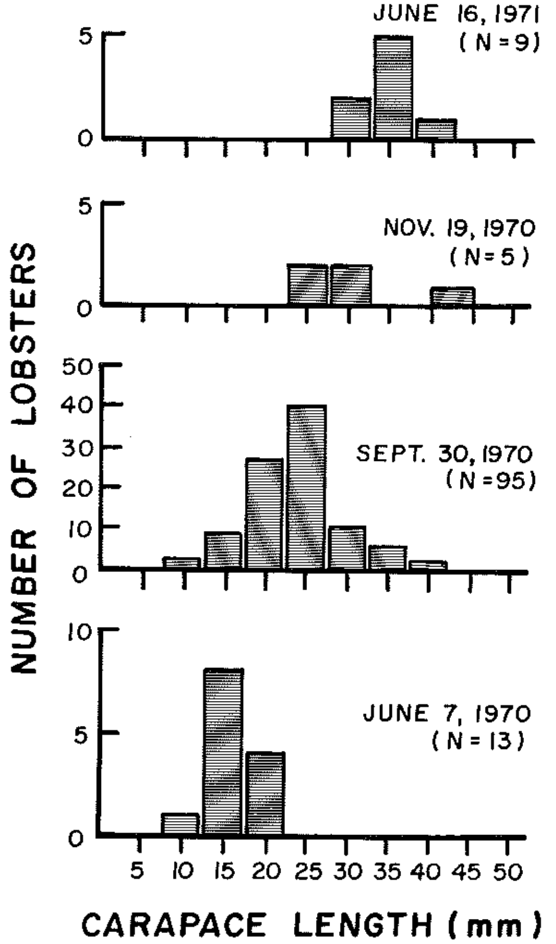

FIGURE 11. Size-frequency distributions of juvenile spiny lobsters from a causeway in Lameshur Bay, St. John, U.S. V.I. Dates of collection are shown.

means for these classes appear to fit the growth curves from the recapture data (Figure 12).

The age at which *P. argus* attained 95 percent of its maximum size is also given in Table 2 and is considered to be an indication of longevity (Taylor 1962). Males attain 95 percent of their maximum size in seven years, females in 10 years in the St. John area. The asymptotic sizes from the analysis for both males and females (153 and 133 mm, respectively) were smaller than the largest-sized animals observed (182 and 162 mm carapace length, CL) and are not an indication of actual asymptotic sizes. In fact, male lobsters have been reported to grow much larger than 182 mm CL. The discrepancy between analysis and observation probably resulted from the fact that none of the larger tagged animals grew in the interval between tag and recapture.

There is also some discrepancy between the estimate of T_0 (time at which length is zero) and length of larval life. This analytical technique indicates a larval life between one and two months, while it is generally recognized that the larval period is six to nine months (Sims and Ingle 1966). The statistic, T_0 , has not generally proven applicable to describe long larval periods.

TABLE 2

Growth parameters of *Panulirus argus* derived from tag-recapture data and fitted from the VonBertalanffy growth equation, $L_t = L\,(1\text{-}e^{-K(t-t_0)})$ after the method of Fabens (1965).

Sex	N	L (mm)	K	T_0 (yrs)	$A_{(95)}$ (yrs)
Male	64	153	.436	.11	7
Female	33	133	.319	.16	10
Combined	97	152	.432	.11	11

Sexual differences in growth parameters have been reported for fishes by Ursin (1967) who attributes it to different energetic requirements for the sexes. Certainly the production of up to 10^6 eggs by a female spiny lobster several times a year must place a higher metabolic load on females than males and this is reflected in differing growth curves.

The relationship between carapace length and body weight in grams was determined so that growth information, taken as linear carapace growth increments, could be converted to changes in weight over time. In order to obtain an adequate sample size, lobsters were weighed in the field on a large triple beam balance, a process which resulted in a loss of some precision, but which still allowed one percent accuracy. Lobsters weighing less than 200 g were returned to the laboratory where they were weighed to the nearest 0.1 g on a triple beam balance.

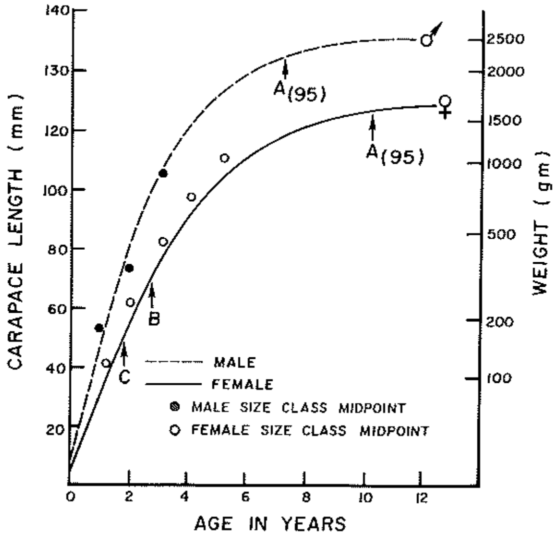

FIGURE 12. Growth curves of *Panulirus argus* derived from tag—recapture data and growth of causeway juveniles after the method of Fabens (1965). Weight is derived from least squares regression of weight on carapace length. (Note, the upper sections of both curves are probably inaccurate due to limited data.)

The total size range was from 18 to 182 mm CL. There were no observable differences in the weight-length relationships for males and females so the data were combined and fitted by a least squares computer program to the standard power function:

$$W = aL^b \qquad (2)$$

where:

W = body weight in grams
L = carapace length in mm
a and b = constants

The analysis suggested that a is equal to 0.0021 while b is 2.788. The index of determination for the regeneration of this regression was 0.954, highly significant.

The growth curves were converted to growth in weight by using the weight-length regression. Figure 12 shows this weight increase as a function of time. Market size (around 700 g) is reached by males in approximately two years of benthic life and females in four years.

MORTALITY

Estimates of the size-dependent mortality coefficient, *m*, from the equation:

$$N_{(t)} = N_{(t-1)}(e^{-mt}) \qquad (3)$$

where:

N_t = the number of animals surviving from the time t − 1 to time t (one year in this case),
e = the base of natural logarithms

can be derived from size-frequency distributions. First the component age classes in a polymodal size-frequency distribution are detected, and their means and standard deviations estimated by probit analysis. This technique, using either graphical (Harding 1949) or computer approaches will give estimates of the mean, X_i, and standard deviation S_i, for each size class *(i)*. If the time interval *t*, between each class is known or can be assumed, mortality estimates can be derived. In the case of these data, the size class means for both sexes fit the growth curves derived independently from tag-recapture data (Fig. 12) allowing the assumption of annual size classes. Use of size class modes is discouraged since they consistently will be skewed towards the smaller sizes if mortality is indeed operating. Assuming that size class overlap is insignificant at X_i so that the frequency at X_i:

$$f(\overline{X_i}) = P\overline{X_i}(N_i) \qquad (4)$$

where:

P = the probability function for a normal distribution found in a table of normal probabilities;
N_i = the total of individuals in the size class.

The probability $\overline{PX_i}$ is derived from the mean and standard deviation of each size class and found in a table of normal probabilities. First the difference, *d*, between the upper and lower limits of the interval containing the mean X_i, and the mean itself is calculated.

$$d = (X_i - X_1) \qquad (5)$$

where:

X_1 = the limit of the size interval containing the mean. A *d* value is calculated for both the upper and lower limits of the size interval.

Then a *z*-score, z_i, is calculated by dividing the absolute value of this difference for both upper and lower limits by the size class standard deviation S_i.

absolute value:

$$z_i = \frac{d}{S_i} \qquad (6)$$

When the *z* score for both limits is calculated, a probability function is looked up for each in a table of normal probabilities and summed. This sum, $\overline{PX_i}$ is used to calculate N_i, the number of individuals in that size class, by simple algebra from equation (2) so that:

$$N_i = \frac{f(X_i)}{P\overline{X_i}} \qquad (7)$$

The mortality coefficient is derived from equation (3) (when t = 1) by simple algebra since:

$$N = -m + LnN_{t-1} \qquad (8)$$

and

$$m = LnN_{t-1} - LnN_t \qquad (9)$$

In order to assess the efficiency of this technique, the size-frequency distribution with characteristics shown in Table 3 was constructed using means and standard deviations approximating the lobster data. The results of the analysis (Table 3) shows that the first two classes were estimated within 1.5 percent, but thereafter the estimated values depart markedly from the actual values. This is due to overlap between size classes caused by the variance characteristics of the distribution. If the size class variance decreases with the mean, then this technique will be

TABLE 3
Estimation of size class numbers from an artificial polymodal size-frequency distribution of known characteristics.

Size Class Mean	Size Class S.D.	Frequency at mean	Actual Number in class	Derived Number in class
40	4.0	465	1000	998
60	6.0	66	200	203
80	8.0	32	150	131
100	10.0	29	110	149
120	12.0	22	90	127

TABLE 4
The coefficient of instantaneous mortality, *m*, as derived from spiny lobster size-frequency distributions. Computational steps are shown in test.

Source	Size[1] Class Mean (mm)	Size[1] Class S.D. (mm)	Frequency[1] in Mean Interval	Estimated Size Class	Mean[2] Weight in Interval	m (yr^{-1})	% survival/ yr
Reef Females	42.0	4.0	2	5	—[3]	—	—
	60.0	7.0	18	64	—	—	—
	81.0	9.0	26	119	—	—	—
	98.0	9.0	81	370	958	0.651	52.2
	116.0	8.0	18	71	1320	0.413	66.1
	132.0	8.0	10	47			
Reef Males	60.0	12.0	10	60	265	0.483	61.7
	77.0	11.0	7	37	—	—	—
	105.0	10.0	28	142			
Mangrove Males	36.5	13.0	14	95	114	0.427	65.2
	59.0	7.0	17	62			

[1] From probit analysis (Harding 1949) of size-frequency distribution.

[2] Derived from weight-length distribution and growth curves (Fig. 12).

[3] Omitted values represent complex mortality estimates including recruitment, and/or emigration.

more discriminating. Variance proportional to the mean was tested here because the lobster data suggested proportional variance. A later examination of some other lobster data from Bimini (Herrnkind, personal communication) suggests that this proportionality was a function of combining collections over the period of study and therefore variance reflected growth. Unless variance characteristics of the size-frequency distribution are known, it is suggested that this technique be used with caution.

The results from the lobster data are shown in Table 4 and Figure 13, and agree with values derived from Buesa (1969b). The coefficient of instantaneous mortality, *m*, ranges from 0.413 to 0.651 with yearly survival from 52.2 percent to 66.1 percent.

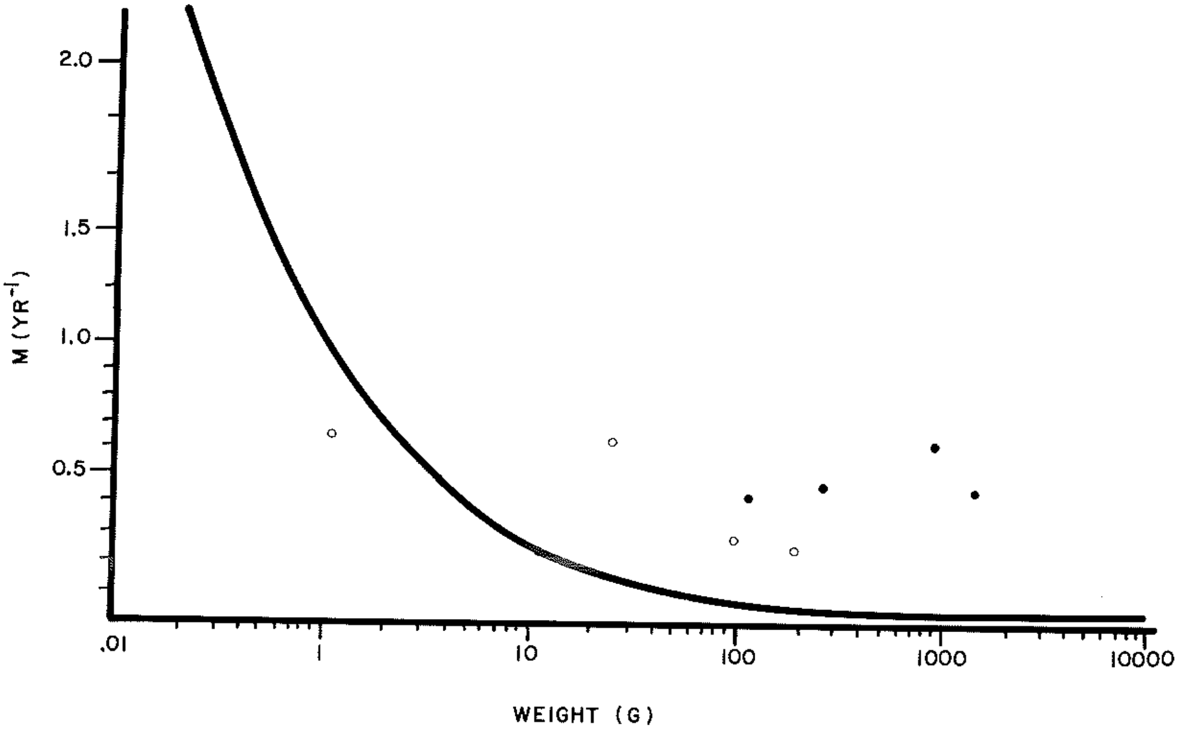

FIGURE 13. Instantaneous coefficient of mortality, *m*, from the present study (solid circles) as compared to values derived from Buesa's (1969) Cuban lobster study (open circle). The solid line represents a theoretical value of metabolic natural mortality ($W^{-1/3}$) from Ursin (1967).

The lobster data analysis (Table 4) also points out several significant aspects of population dynamics. Our sampling of the juvenile populations in the magrove and *Thalassia* habitats suggested that recruitment to the reef population takes place in the second year of benthic life, but is not complete until the animals are almost 80 mm CL. There may be sexual differences in this phenomenon since two size classes of males were found in the mangroves and only one of females. Prerecruitment size classes show increasing numbers in the reef population. In this case mortality coefficient estimates greater than unity represent a complex of immigration and mortality.

When these mortality values are compared to a theoretical value for natural (metabolic induced) mortality, weight$^{-1/3}$ (Ursin 1967), the effects of fishing and pressure can be assessed. Figure 13 suggests small animals are nearly free from externally induced mortality. As they grow, mortality from predation and fishing pressure increases as expected. In St. John, where strict catch limits are enforced by the National Park Service, the population still shows the effect of fishing, although not as great as in Cuba's intensively fished populations (derived from Buesa 1969b). The results of this analysis also suggest that attempts to increase juvenile settlement and survival, perhaps using the methods of Witham, Ingle, and Joyce (1968) would effect a definite increase in the population.

SUMMARY AND CONCLUSIONS

The coefficient of mortality derived from size-frequency distributions of Virgin Islands lobsters was in close agreement with values derived from Buesa's (1969b) long term study of the Cuban lobster fishery. The results suggest, as might be expected, that fishing (or possible predation induced) mortality increases as the animals grow in size.

Both growth and mortality results presented herein offer encouragement for management of the resource. Any attempts to increase juvenile survival of the type underway in Florida (Sweat 1968; Witham et al. 1968) should result in an almost direct increase in the fished size classes within two to three years.

Aquaculture of the type proposed by Ingle and Witham (1969) may also be supported by the present study. Mortality from post larval to market size may be below 70 percent of the starting population. In natural populations most of this mortality may be externally induced, and this figure could probably be bettered in captivity. Growth also appears to be closer to the faster estimates in the literature (Sutcliffe 1957; Witham et al. 1968). It may be that those authors suggesting slower growth rates (Buesa 1969b; Smith 1948) have not accounted for the sexual differences in growth rate documented here. The animals in these latter studies may also have come from areas where there are cooler temperature regimes with consequently slower growth rates.