

Fecundity and Reproductive Rates in Indo-West Pacific Spiny Lobsters

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Abstract—The relationship between fecundity and carapace length is analyzed and reproductive rates are calculated for the spiny lobsters *Panulirus versicolor* and *P. penicillatus* at Palau, Western Caroline Islands. *Panulirus versicolor* has more eggs at a given carapace length and is increasingly more fecund at higher carapace lengths than *P. penicillatus*. The size-specific and standardized crude reproductive rates for the two species exhibit similar broad patterns relative to the carapace lengths at which changes occur, but *P. versicolor* attains a much greater overall rate of reproduction than *P. penicillatus*. The great relative importance of females in the larger size classes in maintaining an overall high rate of reproduction is indicated for both species. The information provided has a number of fishery management implications and enables consideration of reproductive tactics in these species.

Introduction

This paper analyzes the relationship between fecundity and carapace length and calculates reproductive rates for the spiny lobsters *Panulirus versicolor* (Latreille, 1804) and *P. penicillatus* (Olivier, 1791) at Palau in the Western Caroline Islands (7°20'N lat and 134°30'E long), where these species contribute to a tropical small-scale fishery (MacDonald, 1982). Artisanal fisheries for these species occur widely throughout this region (George, 1971), and fishing effort and landings have been increasing in recent years (personal communication, Western Pacific Regional Fishery Management Council, Honolulu, HI). The management and development of these fisheries could benefit from a better understanding of these species' reproductive potential.

The estimate of fecundity as a function of size and knowledge of reproductive rates are fundamental factors in defining a species' reproductive potential. In the case of species which are exploited commercially, such as spiny lobsters, this information is useful when considering yield, recruitment, and other population estimates (Gulland, 1977). In particular, estimates of size-specific fecundity have become required data for various mathematical models used to evaluate stock changes of lobsters under varying conditions of exploitation, natural mortality, and regulation (Saila and Flowers, 1966; Caddy, 1977, 1979; Ennis and Akenhead, 1978). However, virtually nothing is known about the fecundity and reproductive rates of Indo-West Pacific spiny lobsters (Morgan, 1980).

Panulirus versicolor is limited in geographic distribution to the oceanic islands of the Indo-West Pacific region, while *P. penicillatus* is distributed more widely and occurs in the western Red Sea, throughout the Indian Ocean, and across the tropical Pacific Ocean as far east as the Galapagos Islands (George, 1968). Within the Indo-West Pacific region, these species occupy distinctly different habitats (George, 1974): *P. versicolor* occupies

relatively sheltered coral habitats, and *P. penicillatus* occupies the exposed wave-swept habitat along the seaward reef margin. These differences in geographic distribution and habitat, together with related inferences about age-specific mortality, form the basis for considering reproductive tactics in these species.

Materials and Methods

FIELD SAMPLING

I collected information on population size structure and reproductive condition for these species by weekly sampling of fishery landings at the Palau Fishermen's Cooperative at the district center of Koror during October 1969 through October 1970. Carapace length (CL) was measured to the nearest millimeter along the mid-dorsal line from the anterior end between the post-orbital spines to the posterior edge. Whether females were bearing eggs (ovigerous) also was recorded.

Both species of lobsters were fished by divers who speared them during the day and at night. The fishery was not regulated, and all but small lobsters were taken without further consideration of size, sex, or reproductive condition. This practice afforded a relatively unbiased sample except that the smaller size classes were probably under-represented. About 40 percent of the females of both species are estimated to be ovigerous throughout the year at Palau (MacDonald, 1979, 1982). A more complete account of these sampling methods and this fishery is presented in MacDonald (1982).

I collected ovigerous females for fecundity analysis from several different areas around the major islands during the same time period. These lobsters were collected apart from fishermen's catches to insure that eggs were not lost due to the customary practice in the fishery of stringing lobsters through the tail upon capture by divers.

FECUNDITY ESTIMATION

Fecundity for each species was estimated over the range of carapace lengths typical of ovigerous females at Palau. Eggs counted were new rather than late stage. The method used to estimate fecundity was similar to the gravimetric methods of Kensler (1967, 1968) and Morgan (1972).

Each egg mass with pleopods attached was removed while the lobster was fresh and was fixed in a 10% formalin and seawater solution. After hardening for about 30 days, eggs were excised from pleopods and dried to constant weight. The dried eggs were then weighed to the nearest mg. Three replicate 0.1 g samples were taken from each mass of dried eggs, rubbed between the fingers to separate the eggs and remove any attached setal material, and counted manually. Egg breakage was negligible. The average of the three samples was used to calculate the total number of eggs for each respective female by simple proportion.

REPRODUCTIVE RATE CALCULATIONS

Reproductive rates were calculated following the methodology of Fleiss (1973). The population sample for each species was divided into I size classes ($i = 1, \text{ to } I$). P_i is the

proportion of females in each sample that fall in size class i . C_i is the reproductive rate specific to each size class i . The reproductive rate is the proportion of females that were ovigerous in each size class adjusted for the size-specific fecundity. The total crude reproductive rate (C) for each population is:

$$C = \sum_{i=1}^I C_i P_i, \text{ where}$$

$$C_i = \frac{\text{n ovigerous in size class } i \times \text{fecundity in size class } i}{\text{n in size class } i}$$

$$P_i = \frac{\text{n in size class } i}{\text{total n}}$$

n = number of females in each respective category.

When crude reproductive rates from two populations are compared, differences can arise in relation to size distribution and size-specific rates. If the two populations are not similarly constituted, a direct comparison of the overall rates may be misleading. The critical relationships are demonstrated as follows.

Given that:

$$1) c = \sum_{i=1}^I c_i p_i \text{ denotes the crude rate of one population;}$$

$$2) C = \sum_{i=1}^I C_i P_i \text{ denotes the crude rate of another population; and}$$

$$3) d = c - C \text{ denotes the difference between the two crude rates, the difference (d) between the two crude rates can be expressed as:}$$

$$c - C = \sum_{i=1}^I \frac{p_i + P_i}{2} (c_i - C_i) + \sum_{i=1}^I \frac{c_i + C_i}{2} (p_i - P_i)$$

difference between difference between
size-specific rates population distributions
(d₁) (d₂)

where p_i , c_i , and P_i , C_i are, respectively, the size class proportions and size-specific rates from the two samples.

For a given summarization of the differences between two schedules of size-specific rates (d_1), the apparent difference (d) between the two populations may vary according to the differences between the two population distributions (d_2). It is therefore important to compare both the size-specific rates themselves and the crude rates "standardized" to remove effects due to differences in population distribution. Direct standardization is applied by choosing a standard population, P_{si} , calculating $c_{si} = \sum_{i=1}^I c_i P_{si}$ and $C_{si} = \sum_{i=1}^I C_i P_{si}$, and comparing. In direct standardization, the standard population is usually the combination of the two samples as employed in this paper.

The term "rate" is used strictly in its statistical sense and as such is kindred to such

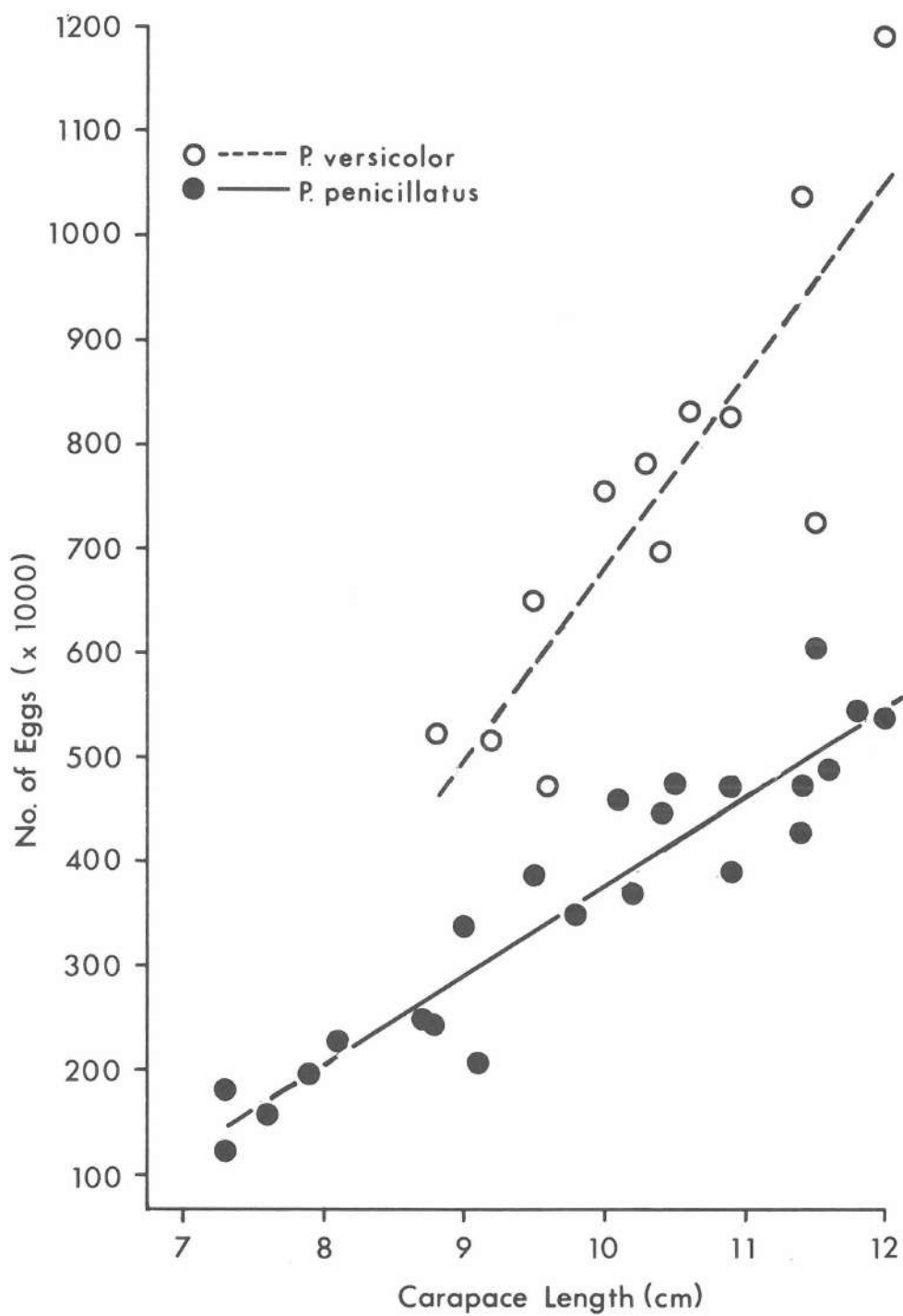


Figure 1. Relationship of total number of external eggs and carapace length for *Panulirus versicolor* (n = 12) and *Panulirus penicillatus* (n = 23) at Palau.

Table 1. Linear regression equations for the relationship of total number of external eggs and carapace length for spiny lobsters at Palau. UL and LL respectively designate the upper and lower limits of the 95 percent confidence intervals for the regression coefficients; n = number of lobsters sampled; r^2 = index of determination.

Species	Regression equation ^a	UL	LL	n	r^2
<i>P. versicolor</i>	$y = -1,169,909 + 185,438x$	192,349	178,527	12	0.7459
<i>P. penicillatus</i>	$y = -481,347 + 85,885x$	87,986	83,785	23	0.8854

^a y = total number of eggs; x = carapace length (cm)

terms as probability, relative frequency and proportion (Fleiss, 1973). What is known in epidemiology and vital statistics as a specific rate is known in probability theory as a conditional probability. In essence, rates are used here to express the degree and likelihood of reproductive output in lobsters of different sizes for each species.

Results

FECUNDITY

The total number of external eggs increases linearly as carapace length increases for *P. versicolor* and *P. penicillatus* at Palau (Figure 1, Table 1). The total number of external eggs over the range of carapace lengths presented is 467,552–1,189,324 for *P. versicolor* and 127,983–602,807 for *P. penicillatus*. For a given carapace length, *P. versicolor* has more eggs than *P. penicillatus*. The regression coefficients differ significantly between species (Table 1), indicating that *P. versicolor* is increasingly more fecund at higher carapace lengths than *P. penicillatus*.

The number of eggs per sample is not related to body size. There was no significant correlation between carapace length and the mean number of eggs per 0.1 g sample for either *P. versicolor* ($r = 0.4647$, $P = \text{n.s.}$) or *P. penicillatus* ($r = -0.0179$, $P = \text{n.s.}$). However, the number of eggs per 0.1 g sample is significantly greater in *P. versicolor* (LL 2,465 < \bar{x} 2,562 < UL 2,659) than *P. penicillatus* (LL 2,310 < \bar{x} 2,351 < UL 2,392), as evidenced by the sample means and their 95% confidence limits. Accordingly, individual egg weight is significantly less in *P. versicolor* than *P. penicillatus*, the difference being about 10%.

REPRODUCTIVE RATES

The size-specific and standardized crude reproductive rates for *P. versicolor* and *P. penicillatus* at Palau exhibit similar broad patterns relative to the carapace lengths at which changes occur (Figure 2A, B), although the differences in absolute value between the species are considerable. The reproductive rates are relatively low for both species until a carapace length greater than 8.9 cm is attained. At larger sizes, the reproductive rates for *P. versicolor* increase more rapidly and clearly attain a much greater value than do those for *P. penicillatus*. The reproductive rates are greatest in the 10.0–10.9 cm CL class in both species and decrease markedly at larger carapace lengths.

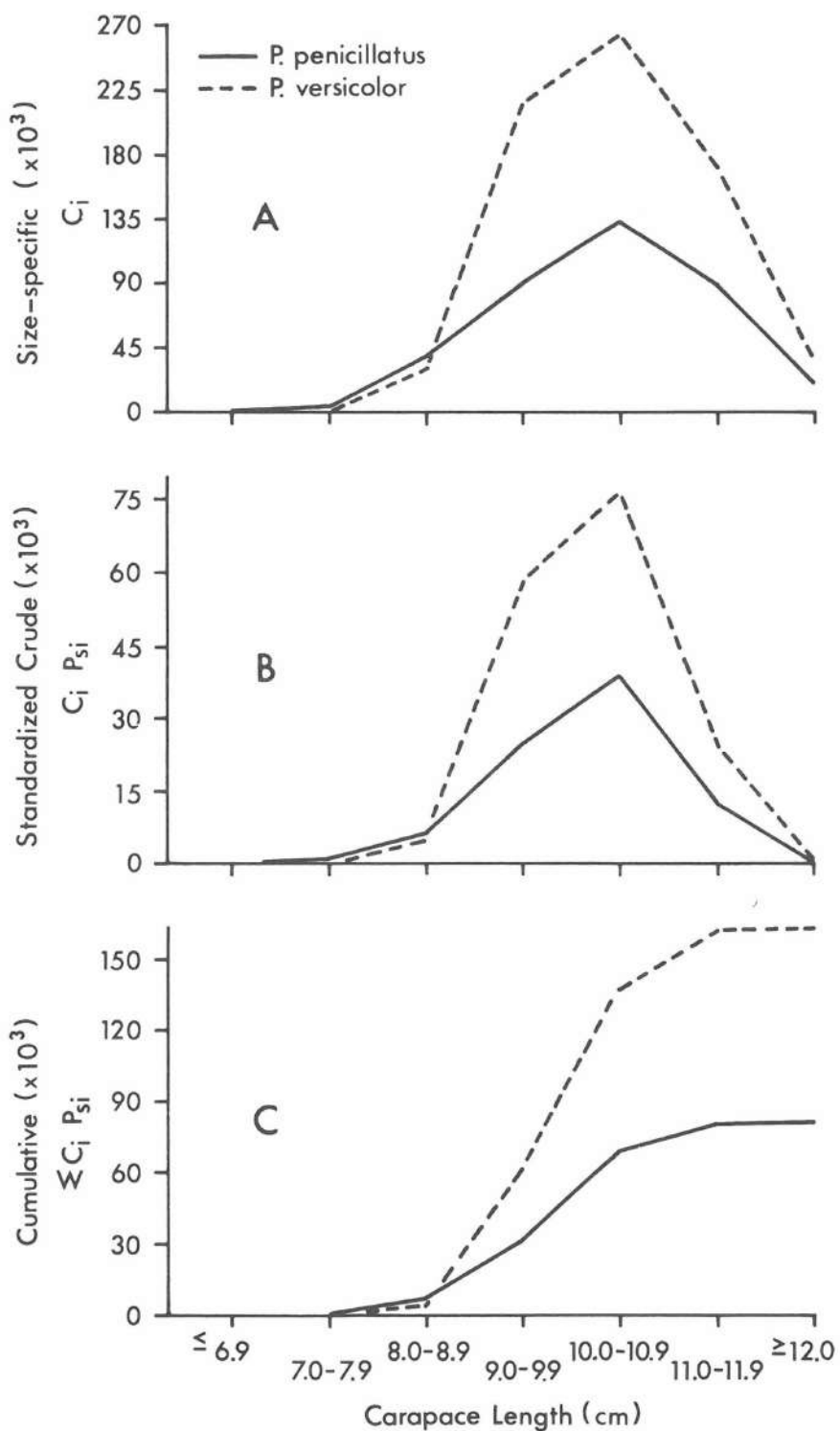


Figure 2. Comparison of (A) size-specific, (B) standardized crude, and (C) cumulative standardized crude reproductive rates for female *Panulirus versicolor* and *Panulirus penicillatus* at Palau.

Table 2. Relationships among size structure and reproductive condition for spiny lobster females at Palau.

Carapace length (cm)	<i>P. versicolor</i>		<i>P. penicillatus</i>	
	Number of females	Number ovigerous	Number of females	Number ovigerous
≤6.9	34	0	9	1
7.0-7.9	42	0	40	8
8.0-8.9	51	8	137	56
9.0-9.9	95	44	216	104
10.0-10.9	92	42	251	119
11.0-11.9	39	21	129	60
≥12.0	6	4	29	9
Total	359	119	811	357

The cumulative size distribution of the standardized crude reproductive rates indicates the great relative importance of females in the larger size classes in maintaining an overall high rate of reproduction within both species (Fig. 2C). Additionally, it emphasizes the particularly large overall difference in reproductive capacity between the two species. A comparison of the standardized crude reproductive rate totals rounded to the nearest thousand indicates that *P. versicolor* attains a significantly much greater rate of reproduction than *P. penicillatus* at Palau ($X^2 = 27.28$, $P \leq 0.001$).

The number of times a female bears eggs is associated with its likelihood of being ovigerous when captured. Because the reproductive rate is the proportion of females that were ovigerous in each size class adjusted for size-specific fecundity, any differences in the number of clutches that lobsters of different sizes produce each year are inherently accommodated by the analysis. Restrictive or simplifying assumptions in this regard are unnecessary.

The relationships among size structure and reproductive condition for these species, which together with the fecundity information formed the basis for the preceding reproduction rate calculations, are provided in Table 2. Females ranged in size from 5.7 cm to 12.8 cm CL for *P. versicolor* and from 5.0 cm to 13.1 cm CL for *P. penicillatus*. The smallest ovigerous female *P. versicolor* was 8.2 cm CL; the smallest ovigerous female *P. penicillatus* was 6.9 cm CL. For purposes of discussion, the size at which females attained reproductive maturity is considered to be the size of the smallest ovigerous female sampled.

Discussion

FISHERY MANAGEMENT IMPLICATIONS

The data and results of analyses presented in this paper constitute important baseline information which can serve principally as a benchmark to assess directly the impact of fishing and management regulations on the reproductive rates of *P. versicolor* and *P. penicillatus* at Palau. In concept, this approach is one of the central precepts in managing the spiny lobster fishery for *P. marginatus* in the Northwestern Hawaiian Islands (Polovina

et al., 1988). The results presented here have the same general utility for managing the fishery for *P. versicolor* and *P. penicillatus* at Palau. As of 1969–70 when the data were collected, these species had sustained relatively little fishing pressure and much of that had been of a subsistence nature.

Fecundity in *P. versicolor* and *P. penicillatus* is of the same order of magnitude as in other species of *Panulirus* studied; the number of eggs per spawning generally ranging between about fifty thousand to one million depending upon carapace length (Morgan, 1980). Direct comparison of reproductive rates with other species of spiny lobster is hindered by the lack of appropriate studies or by the use of different methods of analysis. However, reproductive rates generally are low at small carapace lengths, peak towards the mid-range, and decrease at large sizes (Morgan, 1972; Lyons et al., 1981; Gregory et al., 1982). This general pattern apparently does not vary much with fishing pressure, although the total reproductive rate of a population clearly does (Lyons et al., 1981).

The method of analysis (Fleiss, 1973) used to calculate the reproductive rates for *P. versicolor* and *P. penicillatus* is a standard technique for comparing rates and proportions. However, the smaller size classes may not have been fully represented in the population samples drawn. Such bias would tend to underestimate the true size class proportions (p_i) of the smaller lobsters and would lower estimates of the crude reproductive rates ($c_i p_i$) as a consequence. Whereas the size-specific rates (c_i) tend to be relatively free of bias, the crude rates likely are not and the total contribution to reproduction provided by the smaller size classes might have been underestimated as a result. Related methods used to calculate reproductive potential in other spiny lobster species also would seem to be susceptible to the same form of bias (e.g. Morgan, 1972; Kanciruk and Herrnkind, 1976; Lyons et al., 1981; Gregory et al., 1982).

Within the limits just described, certain aspects of the reproductive rate analyses for *P. versicolor* and *P. penicillatus* are pertinent to consideration of minimum legal sizes for these species. Although *P. versicolor* attains a significantly much greater overall rate of reproduction than *P. penicillatus*, it has an appreciably greater size at first maturity (see also MacDonald, 1982). Further, the degree of under-representation of the smaller size classes is proportionately less for *P. versicolor* than *P. penicillatus* (Table 2). As a result, the crude reproductive rates calculated across the smaller size classes are probably more representative of actual values for *P. versicolor* than *P. penicillatus*. The combination of these factors suggests that *P. versicolor* might require a larger minimum legal size than *P. penicillatus* to maintain comparable levels of reproductive capacity in instances of increased fishing pressure.

Because of the very long time period (6–11 months) during which spiny lobster phyllosoma larvae are transported by ocean currents (Phillips and Sastry, 1980), fishing at Palau probably has very little to do with the level of recruitment to that fishery per se. Consequently, a minimum size based on a biological premise probably would have very little effect on the conservation of the stock at that single island location. Alternatively, if stocks of these lobsters become widely fished down at numerous locations across the Pacific, multilateral agreements between island states may become necessary to prevent recruitment overfishing on a regional basis. In that eventuality, results of reproductive rate analyses such as presented here become highly relevant to fishery management decisions involving minimum size restrictions for these species.

Evaluation of reproductive rates, however, is but one consideration of setting mini-

imum legal size. Other factors include estimates of lobster growth and mortality which help define a fishery's yield characteristics (Saila et al., 1979; Ebert and Ford, 1986), economic considerations that bear on differential marketability of various tail sizes (Samples and Gates, 1987), and fishing methods that relate to the practicality of compliance with the regulation by fishermen and enforcement by government. Also, exploitation may effect a decrease in size at maturity in lobsters (Polovina et al., 1988) through genetic pressure (Aiken and Waddy, 1980) or by modifying individual growth rates of the remaining stock (Chittleborough, 1976; Davis and Dodril, 1980), which can profoundly influence reproductive rate structure.

CONSIDERATION OF REPRODUCTIVE TACTICS

Life history strategies are theorized to evolve as adaptations to suites of selective pressures associated with species' habitats (Southwood, 1977), and reproductive success notably is dependent upon habitat characteristics. Based on these species' use of habitat, George (1974) considers *P. versicolor* and *P. penicillatus* to be distinctly different. *Panulirus versicolor* occupies relatively sheltered areas within the lagoon and along the reef face at depths well below which surge commonly is felt. *Panulirus penicillatus* occupies the exposed, wave-swept area along shallow, seaward reef margins where surf commonly breaks. The pronounced dichotomy of habitat type characteristic of these species probably is associated with very different selective pressures including the number of predators.

Natural mortality is thought to strongly influence the evolution of life history strategies (Stearns, 1970), and natural mortality in spiny lobsters is believed to be caused largely by predation (Munro, 1974). Although there are insufficient data to determine the extent to which predation on spiny lobsters differs between these two reef habitats, the seaward reef margin may have the lower risk of predation. Goldman and Talbot (1976) have demonstrated that both the number of species and total biomass of fishes generally are lowest in this habitat. Personal observations at Palau indicate that this finding includes species potentially predaceous on spiny lobsters. The adaptation of robust pereopods characteristic of *P. penicillatus* enables this species to forage in strong surge and probably provides the selective advantage that allowed this species to penetrate and successfully occupy this habitat, which may serve as a refuge from predation.

Age-specific differences in the magnitude and variability of natural mortality are particularly important in the evolution of life history strategies, and may provide a plausible ultimate explanation of why reproductive rates differ between these species. In general, poorer adult survivorship should select for higher reproductive rates (Stearns, 1976, 1977; Horn, 1978). Predation pressure on adults conceivably might be greater in *P. versicolor* than in *P. penicillatus* based on the habitat differences noted above, and may explain in part why reproductive rates in *P. versicolor* are significantly greater than in *P. penicillatus*. Other factors that may select for the reproductive rates of these species include the magnitude and variability of prereproductive mortality (e.g. Murphy, 1968; Schaffer, 1974; Horn, 1978).

Larval mortality in *P. versicolor* may be lower and less variable than in *P. penicillatus*. The dispersal of larvae of *P. versicolor* does not extend beyond distances of about 1,600 km based upon the geographic distribution of adults (George, 1968), whereas there is direct evidence that the dispersal of larvae of *P. penicillatus* may exceed distances of

about 3,300 km (Johnson, 1974). One would expect diminishing and more variable survivorship due to the increasing pelagic period that probably accompanies increases in the dispersal of the larvae (Strathmann, 1974). Since both greater mortality and increased variability in survival of prereproductives should select for low reproductive rates (Murphy, 1968; Schaffer, 1974; Stearns 1976, 1977; Horn, 1978), lower reproductive rates conceivably might be favored in *P. penicillatus* than in *P. versicolor*, as evidenced by this study. A corollary of lower reproductive rates is greater investment per progeny, which is manifested in this study by the significantly greater weight per egg in *P. penicillatus* than in *P. versicolor*.

The essence of the foregoing discussion is that adult mortality and prereproductive mortality have opposite effects on the evolution of reproductive tactics. In the terminology of life history theory (MacArthur and Wilson, 1967), adult mortality biases toward r-selection, but prereproductive mortality biases toward K-selection (Horn, 1978). Thus, there are two central hypotheses that require testing to determine why reproductive rates differ between these species: (1) adult mortality is higher in *P. versicolor* than *P. penicillatus*, and (2) prereproductive mortality is higher and more variable in *P. penicillatus* than *P. versicolor*. Growth rate information, size-specific age estimates and knowledge of population size structure are needed to test the first hypothesis based on species differences in adult mortality. Direct estimates of prereproductive mortality and its variability both of larvae and juveniles, are needed to test the second hypothesis. Notably, this latter information may prove difficult to acquire due to sampling problems associated with (1) the extremely low density of phyllosoma larvae and pueruli in the open ocean and (2) the virtual inaccessibility of juveniles of these species amid the physical complexity of their benthic habitats.

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