STOCK AND RECRUITMENT RELATIONSHIPS IN *PANULIRUS CYGNUS*,[1] THE COMMERCIAL ROCK (SPINY) LOBSTER OF WESTERN AUSTRALIA

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ABSTRACT

Abundance of the breeding stock, level of settlement of the puerulus stage, juvenile densities, and recruits to the fishery for *Panulirus cygnus* from 1969 to 1979 are examined.

A dome-shaped relationship between the index of abundance of the breeding stock and subsequent puerulus settlement indicates that stock-dependent effects during the planktonic larval stages apparently control the level of puerulus settlement. However, density-dependent relationships (characterized by more asymptotic relationships between the various life history stages) dominate after settlement of the puerulus on the coastal reefs and control the level of recruitment to the fishery and eventually to the breeding stock. The relationship between the settlement of the puerulus stage and the catch rates of the recruits entering the fishery 4 years later is adequately described by a Ricker's stock-recruitment curve as is the level of puerulus settlement to the subsequent abundance of the breeding stock. The relationship between the level of puerulus settlement and the later abundance of juveniles at various ages is not clear and possible reasons for this are suggested.

The significance of the stock-dependent relationship between breeding stock and puerulus and the density-dependent relationship between puerulus and breeding stock in maintaining recruitment to the fishery is discussed.

The importance of understanding the stock-recruitment relationship in exploited fish populations has been recognized for many years and has been the subject of several workshops and symposia (e.g., Parrish 1973), as well as a great deal of research. While the importance of such relationships in exploited invertebrate stocks has been equally recognized, quantitative data, particularly for crustaceans, has been virtually nonexistent (Hancock 1973).

Like many fish species, crustaceans in general and spiny (rock) lobsters in particular, pass through several distinct stages in their life history and, as Hancock (1973) pointed out, a proper understanding of the overall stock-recruitment relationship can be gained only by considering the relationship between successive stages over a number of years. Hancock's belief is reinforced by the studies of Larkin et al. (1964) and Paulik (1973) who, having considered the theoretical forms of a stock-recruitment relationship involving such multistage life histories, showed that several stable equilibrium points can exist in the overall spawning stock-recruitment curve, depending on the relationships existing between the various life history stages.

The western rock lobster, *Panulirus cygnus* George, the object of an important fishery in Western Australia (Morgan and Barker 1979) passes through several major stages during its life history. These include a series of phyllosoma larvae, a puerulus stage, and juvenile and adult stages. After a planktonic life of 9-11 mo (Chittleborough and Thomas 1969; Phillips et al. 1979), the surviving phyllosoma larvae metamorphose into a puerulus stage and settle between September and January each year in shallow coastal areas. The younger juveniles concentrate on shallow limestone reefs to depths of 10 m, with some larger juveniles to 20 m. At about 4 or 5 yr of age (i.e., 4 or 5 yr from hatching) juveniles migrate from the shallow reef areas onto the continental shelf into depths of 30-150 m where maturity is reached, mating takes place, and the life cycle is completed.

Chittleborough and Phillips (1975) reported that, based on the data available at that time, indices of year-class strengths obtained from the

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[1] The western rock lobster is referred to as *P. longipes* or *P. longipes cygnus* in some of the literature quoted; these are synonymous with *P. cygnus*.

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puerulus at settlement and those derived from measurements of density of juveniles of *P. cygnus* aged 2 or 3 yr were consistent. However, they found survival to recruitment into the fishery did not mirror the pattern of year-class strength at or soon after settlement. The purpose of this paper is to examine the changes that take place in the abundance of the various stages in the life history of *P. cygnus* including data on puerulus settlement and juvenile density and to investigate their interrelationships.

METHODS

The abundance of the several stages in the life history of *P. cygnus* has been measured by various methods over a number of years. The methods used have reflected the practical problems of sampling the different stages and have included catch and fishing effort data from the commercial fishery for the adult stage, collectors composed of artificial seaweed to catch the puerulus stage, and mark and recapture studies of the juveniles using baited traps. All ages and year classes referred to in this paper relate to the year of hatching and so include the 9-11 mo larval phase. For example, the 1969 year class was hatched in January-February 1969 and settled as puerulus larvae between September 1969 and January 1970.

Abundance of the Breeding Stock

The western rock lobster is confined to the western coast of Australia from approximately North West Cape to Cape Naturaliste (Fig. 1). The majority of the commercial catch is taken between lat. 28° and 32°S (Sheard 1962). The coastal fishery operates from 15 November to 30 June of the following year although prior to 1978 the coastal season concluded on 14 August each year. The Abrolhos Islands fishing season which extended from 15 March to 14 August prior to 1978, now also ends on 30 June.

The abundance of the breeding stock (i.e., those females carrying external eggs) has been measured since 1966 from research logbook data supplied on a voluntary basis from about 200 boats or 25% of the commercial rock lobster fleet. In addition to catch, fishing effort, and fishing locality information separated into four depth categories, i.e., 0-10, 10-20, 20-30, and over 30 fathoms, each fisherman records his daily catch of numbers of spawning female rock lobsters. However, these data are not available from the Abrolhos Islands for December, January, and February since this area is closed to commercial fishing at this time each year. Consequently, comparable data on the breeding stock had to be obtained from research vessel cruises to each of the four island groups of the Abrolhos during January and February 1979. Sixty commercial wire beehive pots without escape gaps were set each day for a total of 20 d on the fishing grounds where the greatest concentration of spawning females is to be found. The pots had previously been calibrated in the Garden Island area (Fig. 1) by comparison with commercial catch rates of spawning females. During the comparison, catch rates of spawning females were low (mean of 0.05 animals/pot) and the variances relatively large so it is not surprising that no significant difference (at the 5% level) could be detected between the catch per pot lift of spawning females by the research vessel's pots and the catch per pot lift of spawning females by commercial fishermen's pots. However, additional calibration of the research vessel's pots would add confidence to this conclusion.

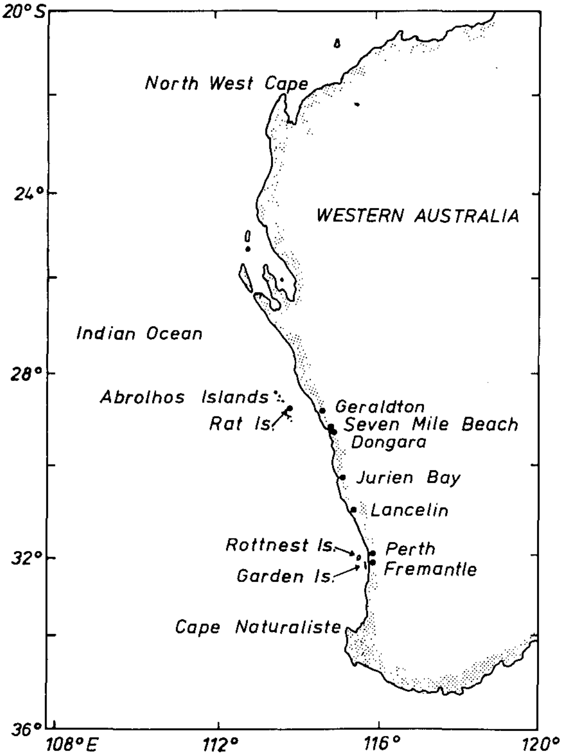

FIGURE 1.—Location of the sites mentioned in the text.

Abundance of the Puerulus Stage

Phillips (1972) showed that the last larval stage, the puerulus, of *P. cygnus* could be captured using collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Subsequent studies by Phillips and Hall (1978) have shown that the catches from these collectors provide a measure of the relative strength of settlement from year to year.

All collectors used in this study were as described by Phillips (1972). The collectors were checked monthly after each new moon period when most puerulus settled. All settlement took place at the puerulus stage. The western rock lobsters were removed from the collectors either as puerulus or after they had molted into very small postpuerulus juveniles. Since the planktonic period is 9-11 mo, settlement occurs between September of the year of hatching and the following January.

Abundance of Juveniles

Density of age groups (ages 2-7 yr) has been measured on shallow test reefs at Garden Island (since 1965) and Seven Mile Beach (since 1970), using the single census trap-mark-recapture method described by Chittleborough (1970). These test reefs are adjacent to the collectors used to catch the puerulus stage.

Abundance of Recruits to the Fishery

During late November of each year, large numbers of immature, newly molted, pale colored rock lobsters migrate into deeper water from the shallow water inshore reefs (which are generally inaccessible to fishermen) where they have spent the previous 4 or 5 yr. This offshore movement normally lasts through December and in all lasts about 6 wk. Since they are newly molted, their food requirements are high (Chittleborough 1975) and consequently their catchability by baited pots is high (Morgan 1974). During this migration the fishermen catch large quantities of these animals which are locally known as the "whites" (George 1958). Although a small number of animals undergo two or perhaps three "white" phases in their life cycle, the "white" phase generally occurs only once during an individual's lifetime (George 1958), and this enables the migrating "whites" to be equated with the recruits to the fishery.

Estimates of the abundance of the potential emigrants from the shallow reefs have been made by Chittleborough (1970), although a better measure of their abundance is available from the catch rate (measured as the catch per pot lift) of the commercial fishery during November and December when practically all of the commercial catch consists of "white" rock lobsters. Information on catch and fishing effort for November and December each year has been taken from the fishermen's monthly returns, which are completed as a condition of the fishing license by all fishermen.

RESULTS

Since there have been several customs adopted in the designation of year classes in *P. cygnus* (e.g., Chittleborough 1970; Morgan 1977) a summary of the convention used in this paper will enable the various relationships presented below to be followed more easily. The convention used and the major events in the life history of *P. cygnus* are as follows:

Hatching of eggs	November, December year $x-1$, January, February, and March year x, with midpoint taken as 1 January of year x.
Settlement of puerulus larvae	September year x to January year $x+1$.
Juveniles on inshore reefs	Year $x+1$ to $x+4$ and $x+5$ (ages 1 to 4 or 5).
Migration of "whites" to offshore areas	November and December year $x+4$ and $x+5$, with the majority being $x+4$.
Maturity and first breeding	January and February year $x+6$ and $x+7$, with the majority being $x+6$.

Stock Definition

Based on similarities in catch rates from the commercial fishery, Morgan (1977) concluded that although some population parameters such as growth rates, size at first maturity, etc. varied between localities, the western rock lobster could, as a first approximation, be considered as a single, genetically coherent, unit stock. This view is reinforced by the studies of Phillips et al. (1979) who demonstrated the wide dispersal of the phyllosoma larvae in the eastern Indian Ocean. Consequently, in the following analyses a single stock has been assumed, although latitudinal differences in some population parameters have necessitated a simple division of the fishery into areas north of lat. 30°S and south of lat. 30°S.

The Breeding Stock

From the research logbook information, it was evident that spawning rock lobsters were concentrated in the 20-30 fathom depth range with an average of 89.9% of the total catch of spawning females each year being taken in this depth range during the period 1966-80. Year-to-year variation was small with the percentage ranging from 86.4% in 1971 to 92.1% in 1967. In addition, the majority of spawning female rock lobsters (average of 81.4% for the period 1966-79) were captured during January and February each year with, again, little year-to-year variation. Accordingly, the catch per pot lift of spawning females taken in 20-30 fathoms in January and February each year has been used as a basis for the calculation of an index of abundance of spawning females. No adjustment for soak time was made since catch per pot lift has been shown to be independent of soak time (Morgan 1977). The use of catch per pot lift data as an index of abundance assumes, of course, that catchability remains constant from year to year. Morgan (1974) has shown that catchability varies during a year in response to molt condition, water temperature, and water salinity. Year-to-year variation in catchability of spawning *P. cygnus* females for January and February is likely to be small, since it would be expected that these animals would be in an intermolt condition, and year-to-year temperature and salinity variation on the spawning grounds in January and February is small (Morgan and Barker 1979).

The average size of the spawning females varies with locality, being larger in southern areas (Morgan and Barker 1979). Average size information on spawning females has been collected on a regular basis since the 1971-72 season from commercial vessels fishing out of the ports of Dongara, Jurien Bay, Lancelin, and Fremantle (Fig. 1). These data have been previously presented in a series of annual reports on the fishery (e.g., Morgan and Barker 1979). Occasional collections of size composition data of spawning females were made prior to the 1971-72 season, particularly at Jurien Bay and Lancelin (B. K. Bowen, unpubl. data). These two sources of data have been used to calculate the average size of spawning female *P. cygnus* for various years. The relationship between size and fecundity (Morgan 1972) has then been used to calculate the number of eggs produced by a spawning female rock lobster of this average size. *Panulirus cygnus* spawns only once per year in most areas in the wild (Morgan 1980b).

Data on the catch rates of spawning female *P. cygnus* taken in 20-30 fathoms in January and February each year, the mean size of these spawning females, and the resultant fecundity are shown in Table 1, separated into two areas: north of lat. 30°S and south of lat. 30°S.

Index of Abundance of Spawning Stock

The most appropriate index of spawning success in *P. cygnus* is the number of first stage phyllosoma larvae released during the hatching period. However, since it has not been possible to measure phyllosoma abundance directly, an indirect measure, utilizing the abundance and fecundity of the spawning females, is necessary. Thus the total number of first stage phyllosoma larvae released is approximately equal to (total number of spawning females) × (their average fecundity).

The number of spawning females in each of the two coastal areas (north and south of lat. 30°S) may be estimated from their catch rate (a measure of density) multiplied by the area of the spawning grounds. The area of the spawning grounds for coastal localities north and south of lat. 30°S is given in Table 2. Thus, for example, a measure of the total number of spawning females north of lat. 30°S in 1966 is given by 0.44 (from Table 1) × 6,690 (from Table 2) = 2,943.6. It should be noted that this measure gives a relative, not an absolute, figure for the numbers of spawning females since a knowledge of the catchability coefficient per unit area, q, would be necessary to convert catch rate (c/g) into absolute numbers (N) by using the relationship

$$c/g = \frac{q \times N}{A}$$

where A = area of the spawning grounds.

Catchability has been measured at the Abrol-

TABLE 1.—Catch (numbers) per pot lift of spawning female *Panulirus cygnus* taken in 20-30 fathoms in January and February each year (*c/g*), the mean size of the spawning females (*S*) (in millimeters carapace length), and the resultant fecundity at this size (*F*), for two coastal areas. The method of calculation of the index of abundance of the breeding stock (I.A.S.) is explained in the text. NA = Not yet available.

	Coastal areas north of lat. 30°S			Coastal areas south of lat. 30°S			All coastal areas	All coastal and Abrolhos areas
Year	*c/g*	*S* (mm CL)	*F*	*c/g*	*S* (mm CL)	*F*	I.A.S. ($\times 10^7$)	I.A.S. ($\times 10^7$)
1966	0.44			0.53			174	198
1967	0.61	92.2	321,710	0.33			179	204
1968	0.50	90.2	302,110	0.65			205	234
1969	0.49			0.28			146	166
1970	0.40			0.34			136	155
1971	0.23			0.23			84	96
1972	0.48	92.9	328,570	0.16	104.3	440,290	125	143
1973	0.22	90.5	305,050	0.15	104.6	443,230	69	79
1974	0.12	91.3	312,890	0.08	106.4	460,870	37	42
1975	0.14	94.5	344,250	0.13	105.0	447,150	49	56
1976	0.16	93.5	334,450	0.13	104.0	437,350	54	62
1977	0.24	92.0	319,750	0.16	103.9	436,370	75	86
1978	0.24	92.8	327,850	0.11	104.6	443,230	67	76
1979	0.27	NA		0.17	NA		83	95
1980	0.19	NA		0.11	NA		56	64

TABLE 2.—Comparison of egg production estimates for coastal areas north and south of lat. 30°S and the Abrolhos Islands area for 1979.

	Abrolhos	North of lat. 30°S	South of lat. 30°S	Total
Area of spawning grounds from Admiralty charts (km^2) (A)	840	6,690	3,500	11,030
Average size of spawners (mm carapace length (B))	74 (research cruise data)	94 (Morgan and Barker 1979)	105 (Morgan and Barker 1979)	
Fecundity (from Morgan 1972) (C)	143,300	339,300	447,150	
Catch per pot lift of spawning females (D)	1.16 (from research vessel)	0.27 (from fishermen's log books)	0.17 (from fishermen's log books)	
Relative numbers A × D (E)	974	1,906	595	
Egg production × 10^7, E × C (F)	13.99	61.29	26.60	101.88
Percentage egg production	14%	60%	26%	100%

hos Islands (Morgan 1974) but it has not been considered necessary to introduce additional assumptions by converting relative to absolute numbers. From Table 1, it is apparent that for each area the average size of spawning female *P. cygnus* has remained approximately constant for the years for which data are available, although significant differences are apparent between the two coastal areas. Consequently, the mean value of the yearly average sizes for each area has been taken and used to calculate average fecundity for the years 1966-80 using the relationship given by Morgan (1972). These values are north of lat. 30°S, $\overline{\mathrm{CL}}$ 92 mm (fecundity 319,750) and south of lat. 30°S, $\overline{\mathrm{CL}}$ 105 mm (fecundity 447,150). Calculation of an index of abundance of the spawning stock for each coastal area each year can now be made while summation for each year gives the index for all coastal areas. These are as follows:

North of lat. 30°S: Catch rate × 6,690 × 319,750.
South of lat. 30°S: Catch rate × 3,500 × 447,150.
All coastal areas: Catch rate (north of lat. 30°S) × 6,690 × 319,750 + catch rate (south of lat. 30°S) × 3,500 × 447,150.

Annual indices of abundance of the spawning stock for all coastal areas are shown in Table 1. It should be noted that this is a more refined index than that used by Morgan (1980a).

During the research vessel cruises in the Abrolhos Islands area in January and February 1979, the average catch per pot lift of spawning females was 1.16 or about six times that of coastal areas. However, as shown in Table 2, the small geographical area and the smaller average size of spawning female *P. cygnus* reduces the apparent importance of the Abrolhos Islands area, both in terms of the number of spawning females and their egg production, when compared with the coastal areas.

The Abrolhos Islands area, therefore, contributed only about 14% of total egg production in 1979. No data on the catch rates of spawning females at the Abrolhos Islands are available for years other than 1979, so it has had to be assumed that the Abrolhos Islands area contributed 14% of the total egg production in each year from 1966, although year-to-year variation in the geographical distribution of settling puerulus larvae will no doubt change this value to some extent. The index of abundance of the spawning stock for all coastal and Abrolhos Islands areas has therefore been estimated by multiplying the coastal index for each year by 1.14. These values are also shown in Table 1.

Abundance of Puerulus Stage

The relative densities of settlement of the puerulus stage (expressed as the mean number per collector settling between September and January at Rat Island (Abrolhos Islands), Seven Mile Beach, Jurien Bay, and Garden Island) are given in Table 3. The data for the different sites have been pooled as an unweighted arithmetic mean and expressed as the mean number of puerulus settling on the collectors, to provide an annual index of settlement.

Abundance of Juveniles

Estimated densities of various year classes at Garden Island and Seven Mile Beach were calculated as described by Chittleborough and Phillips (1975) (Table 4).

Abundance of Recruits to the Fishery

The catch per pot lift of "white" rock lobsters taken during November and December has varied during the years 1964-78 (Table 5) and has resulted in similar variations in total catch from the fishery (Table 6).

The Relationships

Spawning Stock and Puerulus Settlement

Since the peak of puerulus settlement each year occurs from September to January (Phillips and Hall 1978) and is the result of spawning in the previous January and February (Chittleborough and Phillips 1975), the settlement of pueru-

TABLE 3.—Mean number of puerulus settling per collector. — = not measured.

Year of hatching	Index annual settlement	Rat Island	SE	Seven Mile Beach	SE	Jurien Bay	SE	Garden Island	SE
1969	9.7	—		15.2	1.90	4.2	1.07	—	
1970	22.4	[1]35.8	8.94	35.0	2.72	17.8	5.00	0.8	0.85
1971	38.8	47.5	3.12	67.3	5.00	34.7	4.50	2.5	1.90
1972	35.7	68.8	3.90	33.7	3.14	39.6	3.12	0.8	0.85
1973	71.4	73.8	6.07	83.2	4.74	117.4	10.96	11.0	3.06
1974	126.3	130.8	8.83	159.8	12.48	209.6	22.04	5.1	2.55
1975	73.2	105.8	8.60	97.3	6.03	79.6	6.07	10.2	2.25
1976	72.3	106.8	7.09	114.3	7.77	65.6	5.67	2.6	0.81
1977	68.4	112.8	7.85	86.0	7.01	72.2	6.81	2.4	0.60
1978	114.5	182.6	19.33	182.8	11.69	82.4	6.53	10.2	2.59
1979	71.0	102.5	7.42	76.2	4.28	94.4	16.74	11.0	2.67

[1] Converted from two collectors to a different set of four collectors to ensure compatability with later samples.

TABLE 4.—Estimates of year-class strength (no./ha) for juvenile western rock lobsters on nursery reefs (in January). — = not measured; NA = not yet available.

Age (yr)	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Garden Island																
2	—	3,800	4,400	1,400	500	1,200	700	150	1,500	2,600	404	1,932	1,246	2,381	957	1,340
3	3,245	1,070	3,324	317	265	875	537	92	971	1,200	274	1,053	765	969	630	1,300
4	921	810	730	174	195	685	333	60	448	813	149	646	311	638	611	NA
5	697	178	401	128	152	424	217	28	304	443	91	366	205	618	NA	NA
Seven Mile Beach																
2	—	—	—	—	—	—	6,200	6,100	5,100	12,100	11,767	29,869	9,952	5,449	40,163	29,503
3	—	—	—	—	—	5,779	3,825	2,318	2,135	7,591	5,460	4,316	5,012	2,828	6,145	4,986
4	—	—	—	—	—	3,540	1,461	978	1,339	3,522	789	2,174	2,598	433	1,039	NA
5	—	—	—	—	—	1,352	616	613	621	509	397	1,127	397	73	NA	NA

TABLE 5.—Catch (kg) per pot lift of rock lobsters taken by the commercial fishery during November and December for the years 1964-79.

Year	Catch (kg)/pot lift	Year	Catch (kg)/pot lift
1964	1.300	1972	1.057
1965	1.344	1973	0.674
1966	1.352	1974	0.997
1967	1.713	1975	1.115
1968	1.304	1976	1.079
1969	0.973	1977	1.238
1970	1.001	1978	1.443
1971	1.029	1979	1.364

TABLE 6.—Total catch for the western rock lobster fishery.

Season	Total catch (kg $\times 10^6$)	Season	Total catch (kg $\times 10^6$)
1965-66	8.120	1973-74	6.780
1966-67	8.635	1974-75	8.877
1967-68	9.853	1975-76	8.731
1968-69	8.078	1976-77	9.281
1969-70	6.918	1977-78	10.742
1970-71	8.013	1978-79	11.429
1971-72	8.171	1979-80	10.698
1972-73	6.809		

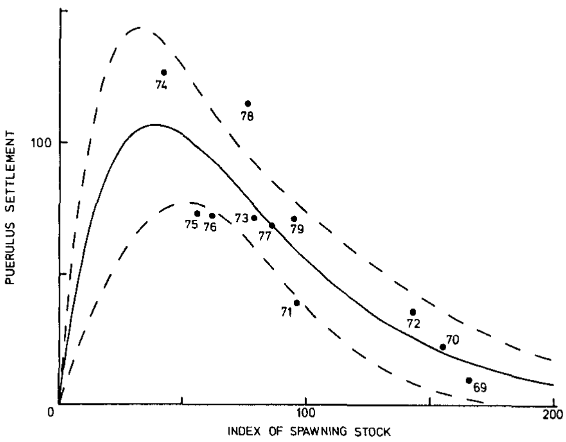

FIGURE 2.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of abundance of spawning *Panulirus cygnus* and the resultant level of settlement of the puerulus stage. The year shown is the season of hatching of the larvae.

lus in year x (plus January of year $x+1$) may be compared directly with the index of abundance of the spawning stock (I.A.S.) in year x.

The Ricker (1958) stock-recruitment relationship of $R = AS\ \exp(-BS)$, where R = recruitment, S = stock size, A = coefficient of density-dependent survival, and B = coefficient of density-independent mortality, was fitted using the method of Cushing and Harris (1973). The relationship is shown in Figure 2 and provides a good fit to the observed data (proportion of sum of squares explained is 0.775). Estimates of A and B with their standard errors (SE) are $A = 7.645$, SE $= 2.193$ and $B = 0.026$, SE $= 0.004$.

Puerulus and Juvenile Densities

The relationship between puerulus and juvenile densities is not clear. In contrast to the statement of Chittleborough and Phillips (1975) that puerulus settlement is a good indicator of subsequent juvenile density, the additional data available for Seven Mile Beach (Table 7) indicate that the correlation between puerulus settlement and the subsequent density of 2-yr-old juveniles is poor ($r = 0.359$, $P > 0.05$). Neither do the data give an acceptable fit to a Ricker (1958) stock-recruitment curve. The same conclusion is reached from examination of Garden Island data (Tables 3, 4) ($r = 0.528$, $P > 0.05$). For example, relatively high settlement of puerulus at Seven Mile Beach in 1974 and 1977 (Table 7) when total juvenile density was also high gave rise to very poor and very high densities, respectively, of 2-yr-olds. Beyond 2 yr of age, however, density-dependent mortality is evident. At both Garden Island and Seven Mile Beach there was a significant ($P < 0.001$)

TABLE 7.—Level of puerulus and subsequent juvenile densities of *Panulirus cygnus* in January and mortality rates at Seven Mile Beach, Western Australia. — = not measured; NA = not yet available; arrows connect individual year classes.

Year of hatching	Puerulus mean no. settling/ collector	Age in years of juveniles arising from puerulus 2 No./ha	3 No./ha	4 No./ha	5 No./ha	Juveniles present on reef at time of puerulus settlement Total no./ha 2-5 yr	Mortality rate/yr of animals aged $\geq$ 3 yr
1969	15.2	6,200	—	—	—	—	—
1970	35.0	6,100	3,825	3,540	—	—	—
1971	67.3	5,100	2,318	1,461	1,352	10,231	0.863
1972	33.7	12,100	2,135	978	616	15,829	0.466
1973	83.2	11,767	7,591	1,339	613	21,310	0.768
1974	159.8	29,869	5,460	3,552	621	39,472	1.934
1975	97.3	9,952	4,316	789	509	15,566	0.686
1976	114.3	5,449	5,012	2,174	397	13,032	0.657
1977	86.0	40,163	2,828	2,598	1,127	46,716	1.879
1978	182.8	29,503	6,145	433	397	36,478	1.780
1979	76.2	NA	4,986	1,039	73	NA	NA

correlation between total density of juveniles on the test reefs and annual mortality rate.

Puerulus Settlement/Juvenile Densities and Recruitment to the Fishery

Chittleborough and Phillips (1975) examined the relationship between the density of larger juveniles on the coastal reefs during the latter part of the year and the success of the commercial white fishery in adjacent waters. They found that, although density-dependent mortality during the juvenile phase ensures reasonably constant recruitment to the fishery over a wide range of initial year-class strengths, in some years the level of puerulus settlement may be inadequate (i.e., below the holding capacity of the shallow-water reefs), and poor recruitment to the fishery may result. They reported that from the data available at that time only the incidence of particularly poor year classes could be used to predict the relative success of the "white" fishery, i.e., to forecast poor future recruitment to the fishery.

Thus, as reported by Hancock (1971), following the low settlement of puerulus larvae on the collectors in 1969-70 (the hatchings of January-March 1969) and low density of early juveniles, it was predicted by Chittleborough and Phillips in 1971 (Anonymous 1974) that low catch levels would be likely in 1972-73 and even lower levels likely at the opening of the 1973-74 season (i.e., the "whites" of November and December 1973). This prediction was borne out by the catches of these 2 years (Anonymous 1974), the white season of 1973 being the poorest on record, particularly in the Fremantle area (reflecting trends observed in the Garden Island research area).

It was pointed out by Chittleborough and Phillips (1975) that the appearance of a very strong settlement, such as that resulting from the hatchings of 1974 at Seven Mile Beach, did not necessarily mean that a high level of recruitment to the fishery could be predicted for the 1977-78 and 1978-79 seasons. The preceding year classes were relatively strong so that the year class of 1974 faced intense competition and high mortality while on the "nursery" reefs. Nevertheless, the 1978 "white" catch rate was the second highest on record.

Figure 3 shows that in fact a good relationship does exist between the level of settlement of the puerulus and the subsequent catch rate (measured as the catch per pot lift) of the "whites" 4 yr later. (Proportion of sum of squares accounted for is 0.574.) The relationship is well described by a Ricker (1958) stock-recruitment curve, fitted by the method of Cushing and Harris (1973). Parameter estimates and their standard errors (SE) are $A = 0.048$, SE $= 0.0066$ and $B = 0.012$, SE $= 0.0018$. A similarly good relationship is achieved by using the puerulus settlement data from Seven Mile Beach only; this is to be expected because of their close correlation with the annual index of settlement ($r = 0.966$, $P<0.01$).

Since the "whites" catch contributes about 40% of the total catch of any one season, it follows from Figure 3 that there should also be a good relationship between the level of puerulus settlement in year x and the total commercial catch rate of the season beginning in November, year $x + 4$, despite the inevitable confusion of year classes in catches taken after December (i.e., after the "whites") each season. The total commercial catches for 1965-66 to 1978-79 are shown in Table 6. The influence of the poor white catch rate of 1973 and the high white catch rate of 1978 on total catches of these years can be clearly seen.

Puerulus Settlement and Subsequent Spawning Stock

Whereas the relationships between the other stages in the life history of *P. cygnus* are not influenced by the effects of fishing mortality, the rela-

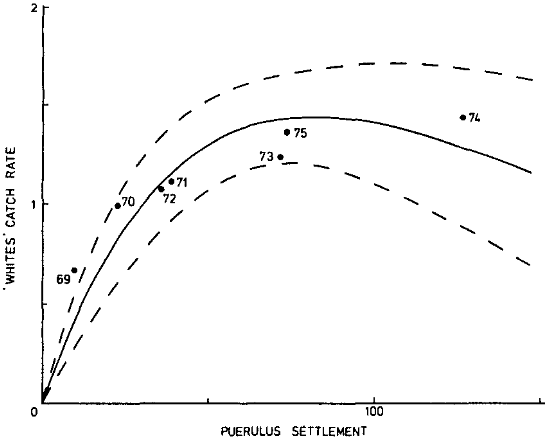

FIGURE 3.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent catch rates of *Panulirus cygnus* at recruitment into the fishery 4 yr later. The year shown is the season of hatching of the larvae.

tionship between puerulus settlement and the subsequent spawning stock will inevitably be confused by the effects of variable amounts of fishing pressure on the commercial stocks between the time the rock lobsters are recruited to the fishery as whites and the time that they become mature. In addition, the mature females will be subjected to fishing pressure when they are not carrying eggs. When they are carrying eggs, the fishermen are required by law to return these mature females to the sea.

This fishing pressure on the mature and immature stocks will lead to a reduction in the abundance of the spawning females compared with their potential abundance if there was no fishing pressure. Moreover, the degree of reduction will be a function of the fishing effort (f) since

$$N_t = N_0 e^{-(M+qf)t}$$

where N_t = numbers present at time t
N_0 = numbers present at time 0
M = instantaneous natural mortality rate
q = catchability coefficient.

If the growth rate of *P. cygnus* is considered (Morgan 1977), it will take approximately 1 yr in coastal areas north of lat. 30°S for female rock lobsters to grow from the legal minimum length of 76 mm to the average size of a mature female of 92 mm (Table 1) and approximately 2 yr in areas south of lat. 30°S to grow from 76 mm to the average size of a mature female of 105 mm. Therefore, as a first approximation and neglecting the apparently small influence of the Abrolhos Islands area, it will be assumed that female *P. cygnus* are subjected to fishing pressure for an average of 1.5 yr during their life in the fishery. The indices of abundance of the spawning stock for all areas (Table 1) can now be adjusted to take into account the probable effects of fishing pressure by assuming the index for any year, i, is not only a result of puerulus settlement in previous years but has been reduced by the effect of fishing effort in year $(i - 1)$ and one-half the fishing effort in year $(i - 2)$.

Using the effective fishing effort data given by Morgan (1979) and Hancock (1981), a relative index, R.I., for later years can be calculated so that it takes into account the effects of fishing effort prior to maturity. This will be given by

$$\text{R.I.}(i) = \text{I.A.S.}(i)/\exp\left(-q(f(i-1) + 0.5\, f(i-2))\right)$$

where $f(i-1)$ = fishing effort in year $i - 1$
$f(i-2)$ = fishing effort in year $i - 2$
$\text{I.A.S.}(i)$ = index of abundance of the breeding stock in year i.

Using the values of fishing mortality rate F and effective effort, f, given by Morgan (1977) a value of q may be calculated from

$$q = \frac{F}{f}\,.$$

This gives an average value of q for the period 1967-73 of 1.4×10^{-7}.

Using the above formula and value of q, relative indices of abundance have been calculated and are shown in Table 8.

The spawning stock will inevitably comprise a number of year classes each of which is the result of puerulus settlement some 6 yr earlier. However, at the high levels of fishing effort which have been characteristic of the fishery in recent years (Morgan 1979) the breeding stock will be dominated by the younger year classes. Using the value of q of 1.4×10^{-7} and the value of the natural mortality rate M of 0.226 (Morgan 1977), it can readily be shown that during the 1978-79 season, the total instantaneous mortality rate Z was about 1.54. At this level of mortality, only about 21% of spawning females may be expected to survive for a second year's spawning and about 5% for a third year.

The relative indices of the spawning stock

TABLE 8.—The relative index of the breeding stock (R.I.) calculated from the index of abundance of the breeding stock (I.A.S.), and adjusted for fishing effort. The method of calculation is explained in the text. NA = not yet available.

Fishing season	I.A.S. ($\times 10^7$) from Table 1	Fishing effort ($\times 10^6$)	R.I. ($\times 10^7$)
1963-64		4.798 (assumed)	
1964-65		4.798	
1965-66	198	5.036	542
1966-67	204	5.147	578
1967-68	234	5.173	684
1968-69	166	4.292	491
1969-70	155	5.771	406
1970-71	96	7.888	291
1971-72	143	7.536	646
1972-73	79	7.253	394
1973-74	42	7.127	196
1974-75	56	8.035	252
1975-76	62	8.100	314
1976-77	86	8.339	469
1977-78	76	9.765	431
1978-79	95	9.357	668
1979-80	64	NA	470

shown in Table 8 will therefore represent a majority of 6-yr-old spawning females with relatively minor contributions from older year classes. The relative index (R.I.) of the spawning stock may then be directly related to the puerulus settlement 6 yr earlier. This relationship is shown in Figure 4 where again, a Ricker (1958) stock-recruitment relationship provides a good description of the data. (Proportion of sum of squares accounted for is 0.845.) Parameter estimates and their standard errors (SE) are A = 21.17, SE = 2.43 and B = 0.013, SE = 0.0016. This relationship however may be less apparent at lower levels of fishing effort where the spawning stock would not be so dominated by the younger year classes.

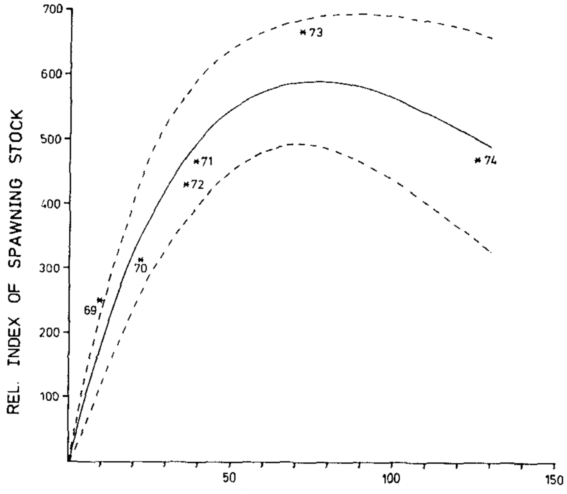

FIGURE 4.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent relative abundance of the breeding stock (i.e., adjusted to the same level of fishing effort as explained in the text) of *Panulirus cygnus*. The year shown is the season of hatching of the larvae.

DISCUSSION

During the period 1969-79, it has been possible to measure abundance of the various life history stages of the rock lobster *P. cygnus* using a variety of methods. The subsequent preliminary analysis of the interrelationships, shown in Figures 2-4 and Table 7, has provided information both on the regulatory strategies of the *P. cygnus* population and on the effect of fishing pressure on the stocks.

A dome-shaped relationship is apparent in Figure 2 which is indicative of strong stock-dependent effects (following the terminology of Harris 1975) operating during the planktonic larval stages of *P. cygnus*. This results in the greatest abundance of puerulus being produced by an initially small number of spawning females and a very much lower abundance of puerulus being produced by a large number of spawning females. Cushing (1971) and Cushing and Harris (1973) have shown that such dome-shaped relationships are characteristic of fish with high fecundities, whereas those with low fecundities have more asymptotic relationships. In this respect, the western rock lobster is highly fecund (Morgan 1972), a characteristic which confers upon the species a greater capacity for stabilization and resistance to environmental perturbations. The mechanism by which this stock-dependent mortality occurs is not known, although Harris (1975) and Cushing and Horwood (1977) have shown that such pronounced dome-shaped stock-recruitment relationships can only occur when the number of predators (or cannibals) is explicitly related to the number of eggs or larvae released. Chittleborough (1979) suggested that low levels of zooplankton off the west coast of Australia impose density-dependent (stock-dependent in Harris terminology) mortality upon *P. cygnus* larvae.

Once the puerulus have settled in the coastal reef systems, more asymptotic relationships are apparent which are indicative of density-dependent, rather than stock-dependent, processes (Harris 1975). This results in more asymptotic relationships between the level of puerulus settlement and the subsequent abundance of recruits to the fishery (Fig. 3) and to the breeding stock (Fig. 4). The intermediate relationship between the level of puerulus settlement and the abundance of juveniles of various ages (Table 7) does not appear to be as clear. This may be a result of the juvenile abundance being measured on small areas of reef which may, or may not, be representative of the abundance of juveniles over a wider area. It is possible, at times of high puerulus settlement, that reef areas underutilized or not normally used by juveniles may be occupied. Alternatively the area available to juveniles for either shelter or food supply may vary over a period of years because of changing reef siltation or seagrass bed development. Dramatic changes in reef occupancy by juvenile and adult *Panulirus homarus homarus* (Linnaeus) caused by siltation have been observed at Durban in South

Africa by Smale (1978), and similarly Booth (1979) suggested that varying survival and possible changes in location of juveniles may occur in *Jasus edwardsii* (Hutton) at Castlepoint in New Zealand as a result of periodic sand movement in the area. Chittleborough (1975) has pointed out that the availability of food on the coastal reefs is probably the predominant factor limiting the survival of juveniles. Studies in progress should provide further data to examine this hypothesis. The role of competitors and predators also requires further examination.

Because of the close relationship between the level of puerulus settlement and subsequent abundance of recruits to the fishery, the level of puerulus settlement can be taken as an indicator of the likely level of the future fishery. The data for Seven Mile Beach, which is near the center of the range of population, appears to provide a satisfactory basis for this prediction up to the present time. However, its use as the sole measure of puerulus settlement would introduce assumptions regarding the future puerulus distribution. The densities of juveniles on small test reefs do not appear at this time to provide a good basis for estimation of the future recruitment to the fishery.

The combination of a stock-dependent relationship between breeding stock and puerulus settlement and a density-dependent relationship between puerulus and breeding stock will result in a population which has only one stable equilibrium point of abundance (Paulik 1973), the location of this point being dependent upon the fishing mortality rate on spawning and prespawning animals. If fishing effort is high the number of spawning female rock lobsters will be reduced, which, from Figure 2, will lead to a higher level of puerulus settlement. This higher level of puerulus settlement will then result in a good recruitment of "whites" to the fishery. The possibility of incorporating the relationships between these various life history stages into a production model of the fishery is therefore feasible and warrants further investigation. However since the results presented here are preliminary, in the sense that a longer time series of data would be needed to add confidence to the relationships shown in Figures 2-4, such a production model may at present be premature.

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