EXPERIMENTAL MANIPULATION OF POPULATION DENSITY AND ITS EFFECTS ON GROWTH AND MORTALITY OF JUVENILE WESTERN ROCK LOBSTERS, *PANULIRUS CYGNUS* GEORGE

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ABSTRACT

A density manipulation experiment was conducted at Seven Mile Beach, Western Australia, to compare growth and mortality for different density groups of juvenile western rock (spiny) lobsters, *Panulirus cygnus*, inhabiting limestone patch-reefs. Juveniles on a control reef were left at their natural, high densities while those on a treatment reef were reduced to approximately 25% of the original, natural density by trapping and reintroduction, which maintained the original size-frequency distribution. Mark-recapture studies were conducted on each reef at three monthly intervals for a year to estimate size-specific growth rates, population densities, and mortality rates. Direct counts of individuals were made by divers to estimate total numbers of juveniles on each reef. There were no statistically significant differences in growth rates for any age category between the control and treatment reefs, but there were significant differences in size-specific mortality rates between the treatment and control groups, with much lower mortality on the treatment reef. Our results suggest that markedly reduced densities of juveniles on a reef may lead to a corresponding reduction in mortality, but no effect on growth was evident. However, part of the apparently higher mortality on the control reefs may instead have been due to emigration of tagged individuals to other reefs. The difficulties of conducting manipulation experiments in the field on a highly mobile species are discussed.

The western rock (spiny) lobster, *Panulirus cygnus*, occurs on the coast of Western Australia from North West Cape (lat. 22°S) to Cape Naturaliste (lat. 34°S). Juveniles (2–5 years old) inhabit the coastal limestone reefs, primarily at depths of 1–10 m (Chittleborough and Phillips 1975). They remain on the reefs for several years, apparently with little movement from one area to another (Chittleborough 1974a). Joll and Phillips (1984) found that the juveniles feed on a variety of animals and plants associated with the seagrass beds surrounding the reefs. Following the spring molt, larger animals (ages 4–6) move to the adult habitats in depths of 30–150 m (Morgan et al. 1982).

Chittleborough (1970) observed that, near the center of the geographical range, recruitment of small juveniles appeared to exceed the holding capacity of the reef system. He concluded that density-dependent mortality of the juveniles at such sites limits their recruitment to the adult stock. He also observed reduced growth rates of animals at these sites and considered that the available food resources may be inadequate for the maintenance of optimum growth at such high densities.

Although there have been many field studies on the ecology of spiny lobsters (see review by Kanciruk 1980), none have attempted experimental manipulation to elucidate the effects of population density on growth and survival. This paper considers the growth and survival of juvenile *P. cygnus* inhabiting experimental and control patch-reefs at Seven Mile Beach, following a manipulation designed to reduce the density of juveniles of the experimental reef. The hypothesis to be tested was that high population densities of juvenile lobsters limit the growth and survival of the western rock lobsters. Despite its inherent practical problems, a manipulation approach was adopted as the one most likely to yield direct evidence to evaluate the hypothesis.

Manipulation experiments are best done using replicated experimental areas and both increases and decreases in the density of the species under consideration (Connell 1974; Underwood 1979). However, where species (such as lobsters) cannot be transplanted or enclosed effectively, the only practical option is to simply reduce densities (Connell 1983). In the case of the study described here, there are also practical limitations in finding sufficiently

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similar experimental areas to employ as replicates and in selecting control reefs which are equivalent to the premanipulation condition of experimental reefs. In this experiment juveniles on one reef, selected as the control site, were left at natural, high densities, while those on another, selected as the treatment site, were reduced to approximately 25% of their original, natural density. A third reef, also left at its natural high density, was monitored at a lower level to examine the degree of representativeness of the control.

METHODS

Reef Study Sites

Three limestone patch-reefs at Seven Mile Beach, Western Australia (lat. 29°08'S; long. 114°54'E), designated as reefs I, III, and V (Fig. 1), were used as the study sites. These three test reefs are typical of those at Seven Mile Beach in terms of both their structure and biota. Observations by divers also indicated that the size structure of *P. cygnus* on each reef was similar. The patch-reefs occupy a lagoon environment between the beach and a limestone barrier reef approximately 400 m offshore. Each patch-reef is surrounded by a calcareous, sandy substrate and areas of limestone, which both support extensive seagrass beds of mixed species composition, the primary feeding areas for juvenile *P. cygnus* (Cobb 1981; Joll and Phillips 1984). Seagrass species of the genera *Amphibolis*, *Heterozostera*, and *Halophila* dominate in these beds. The reefs themselves are covered by *Amphibolis* spp. and by a variety of algal species.

The approximate area of reef III, the treatment reef, is 0.104 ha, and that of reef V, the main control reef, is 0.103 ha. Reef I, the secondary control reef, has an area of approximately 0.071 ha. Reef I is located approximately 750 m south of reef V, while reef III is located approximately 60 m directly west and offshore from reef V (Fig. 1). Adequate separation of the treatment and control reefs from each other for the purposes of the experiment was assumed, based on maximum foraging ranges of up to 50 m for *P. cygnus* in the Seven Mile Beach area reported by Chittleborough (1974a). Water depths are 2–3 m around reefs I and V and 3–5 m around reef III. The tops of the reefs are nearly exposed at low tide.

Single Molt Increments, Annual and Seasonal Growth

The numbers of juvenile *P. cygnus* from each reef which were sexed, measured, and marked or re-

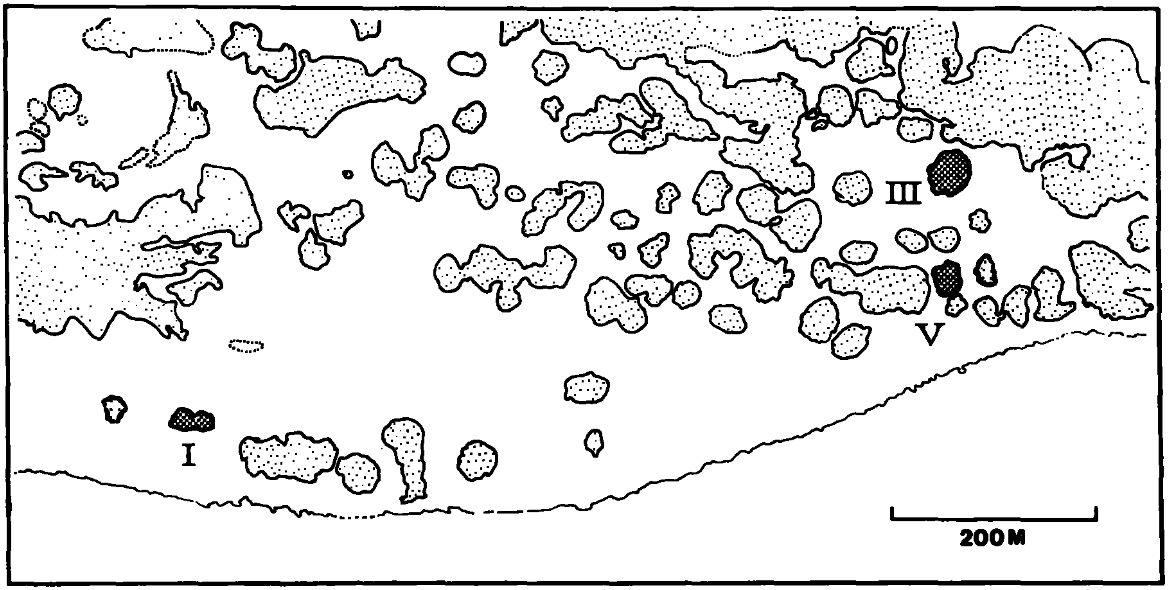

FIGURE 1.—Map of study area at Seven Mile Beach, Western Australia, showing the locations of reefs, I, III, and V (dark shaded) in relation to other reefs (light shaded).

moved in January 1981 at Seven Mile Beach are given in Table 1. Animals with carapace lengths (CL) ⩾40 mm were marked with individually numbered western rock lobster tags (Chittleborough 1974b). Animals with CL <40 mm were marked with individually numbered Floy[4] No. FD-68B spaghetti tags (Davis 1978). Growth data were obtained from tagged individuals recaptured on the three test reefs during resampling in February, March, May, August, and September 1981, and January and February 1982. Growth of tagged *P. cygnus* between recaptures over the period January to May was used to provide data on single molt increments.

Size and Age Structure

Age classes were identified from length-frequency distributions, as described by Chittleborough (1970) and Chittleborough and Phillips (1975). From analysis of the size structure present in January 1981, juveniles up to 38.0 mm CL were judged to be 2 years of age at that time; 38.1–55.0 mm, 3 years of age; 55.1–68.0 mm, 4 years of age; and those >68.1 to be 5 years of age or older. Similarly for January 1982, animals up to 42.5 mm CL were considered to be 2 years of age at that time; 42.6 mm–55.0 mm, 3 years of age; those 55.1–68.0 mm to be 4 years of age; and those >68.1 to be 5 years of age or older.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Population Size, Density, and Mortality Rates

Estimates of the population size, density, and mortality rates of *P. cygnus* juveniles on reef I have been made at Seven Mile Beach since 1970, using recaptures from baited traps (Chittleborough 1970; Chittleborough and Phillips 1975). These estimates for reef I were continued during the period of this study on reef I and, in addition, estimates were also undertaken for reefs III and V, using the same traps and mark-recapture methods. In the present study, 12–13 traps were set around the perimeter of each test reef to ensure catches directly from the area of the reef. At each sampling time an array of 12–13 traps was set simultaneously around reefs III and V in an attempt to reduce attraction by traps of *P. cygnus* from one reef to another.

During the initial tagging in January 1981, trapping was conducted on each reef for four consecutive days, while during each subsequent recapture

TABLE 1.—Numbers of juvenile *Panulirus cygnus* examined on three reefs at Seven Mile Beach, Western Australia.

Reef	Sampling dates							
	1981	1981	1981	1981	1981	1981	1982	1982
	9–10 Jan.	6–7 Feb.	Mar.	May	26–27 Aug.	21–22 Sept.	26–27 Jan.	26–27 Feb.
Reef I								
No. caught	463	447	—	—	362	300	498	419
No. tagged	463	—	—	—	—	—	—	—
No. recaptured	—	103	—	—	98	72	88	[1]5
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef III								
No. caught	1,202	785	475	233	221	359	791	862
No. tagged	304	—	—	—	—	—	—	—
No. removed from reef	898	306	150	—	—	—	—	—
No. recaptured	—	[2]+	+	54	52	55	204	[1]13
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef V								
No. caught	141	682	596	424	599	631	703	696
No. tagged	1,141	—	—	—	—	—	—	—
No. recaptured	—	278	214	154	212	285	140	28

[1]Additional to those recaptured in January 1982.
[2]+ = not scored.

period trapping was conducted for two consecutive days. The single mark-recapture estimate of Bailey (1951) was used to calculate population sizes.

Visual Estimates of Population Size

Direct estimates of the total number of juveniles present on each test reef were made by two divers during the day. Initially the surface of each test reef was mapped, and the map was transferred to acetate writing sheets for use underwater, so that major features such as crevices, holes, and sections of ledges could be recognized and searched in a uniform manner during each census. The two divers moved slowly around and over the reef, counting and recording juvenile *P. cygnus*. Underwater lights were used to aid in this process. Repeated counts were often necessary to obtain consistent results for sections of the reef with large aggregations of juveniles. One diver followed approximately 2–3 m behind the other, and after each section of the reef was censused, the numbers of juvenile *P. cygnus* recorded by the two divers were compared. Only three observers conducted all of the visual censuses and, after experience was gained initially, differences between total counts by any two divers on a reef usually were less than 5%. Counts by the two divers were compared for 12 of these censuses, employing separate Wilcoxon signed-rank tests in which the data recorded by each diver for a given section of the reef were paired. The results for all 12 censuses indicated no significant differences in counts between divers ($P > 0.05$).

There are two primary sources of error in this method. One is that few individuals <40 mm CL can be seen on the surface of the reef or in holes or crevices. The other results from reduced visibility caused by turbidity and water turbulence. This second problem was largely avoided by only doing counts when conditions of turbidity and water turbulence were favorable.

During January–June 1981 and October 1981–February 1982, visual density estimates were obtained monthly or bimonthly in reefs III and V. However, storm conditions and poor visibility during the remainder of 1981 precluded observations. Visual density estimates were conducted on reef I during January 1981 and in January and February 1982, while in January and February 1983 estimates were conducted on all three test reefs.

Density Manipulation Experiment

All of the juvenile *P. cygnus* caught on reefs I and V (the control reefs) in January 1981 were tagged, measured, and released. On reef III (the treatment reef) 1,202 *P. cygnus* were caught during four consecutive days in January 1981 and graded into size categories (5 mm CL size intervals). This was done by measuring the animals and holding them in water in mesh bags suspended from the side of the boat during the 2–3 hours required for processing.

To reduce the population of lobsters on reef III by approximately 75%, three out of each four animals in each size group were removed from the reef and translocated to another locality out of the Seven Mile Beach area. Selection was done by removing the appropriate number of individuals from each size category blindly to avoid bias. This helped to assure that the groups of juveniles returned to reef III had a size frequency and sex ratio similar to those of the original population. The remaining 304 juveniles caught from reef III were remeasured, tagged, and released on that reef. During the next two sampling periods in February and March 1981, any untagged *P. cygnus* caught on reef III were removed (Table 1) to aid in maintaining the density at approximately 25% of its natural level.

Analysis of the Growth Data

Two types of growth data were examined: 1) the single molt increments of animals with <4 legs missing (based on the growth of animals recaptured within four months of a previous capture) (Chittleborough 1976), and 2) the average relative growth rate (Sandland and McGilchrist 1979), which has been shown to be appropriate for analyses of *P. cygnus* growth (Phillips et al. 1983). The data were classified by reef, sex, age class, duration, and time of year at liberty and by the number of legs missing at the time of tagging.

The average relative growth rate data of *P. cygnus* were condensed into a three-factor nonorthogonal experimental design with missing cells. The data were analyzed by examining differences in growth between test reefs for each age and recapture interval, using the Wilcoxon rank sum test, and by examining age, recapture interval effects, and their interaction in a two-factor nonorthogonal analysis of variance.

In addition to *P. cygnus* caught on the reef of original tagging, 75 individuals (12%) were recaptured on both reefs III and V. The data for the 49 of these which showed growth between tagging and recapture were initially analyzed separately.

Chittleborough (1970) found that loss of more than three legs depressed growth. This was confirmed for our data by an analysis comparing the average relative growth rates of *P. cygnus* in the two leg-loss classes (<3 legs missing and ≥4 legs missing), using a *t*-test. There was a significant difference in growth rates between the two leg-loss classes ($P > 0.05$). Although this difference is confounded with differences in the other factors, the result was considered as sufficient evidence, when combined with Chittleborough's findings, to exclude from further analysis data for *P. cygnus* with ≥4 legs missing.

A further analysis was performed to determine if the growth rates of males and females differed. These analyses were done separately for each reef, age class, and recapture interval, using the Wilcoxon rank sum test. The results revealed no significant differences in average relative growth rates between the sexes ($P > 0.05$), so the data for males and females of the same age group were pooled.

RESULTS

Of the 304 tagged *P. cygnus* on reef III, 186 (61.2%; 87 males and 99 females) were never recaptured, while of the 1,141 animals tagged on reef V, 636 (55.7%; 324 males and 312 females) were never recaptured. Similarly, of the 463 *P. cygnus* tagged in January 1981 on reef I, 307 (66.3%; 162 males and 145 females) were never recaptured. Comparison of the size ranges and size-frequency distributions of *P. cygnus* tagged on the three reefs in January 1981 with those not recaptured (Fig. 2) indicated that the "losses" were distributed equally over the full size range and therefore may be assumed to be random. Ratios of males and females in these "losses" did not differ significantly from the male:female ratios in the original tagged population (chi-square test of independence, $P > 0.05$).

None of the tagged *P. cygnus* on reef I were recaptured on reef III or V. However, 75 (12%) of the tagged *P. cygnus* either on reef III or V were subsequently recaptured on the other reef, and some were caught several times on reefs III and V. However, only four of the animals originally tagged on reef III were ever recaptured on reef V, suggesting a general movement of *P. cygnus* from reef V to reef III, i.e., inshore to offshore.

Size and Age Structure

The size-frequency distributions of *P. cygnus* juveniles on reef I in January 1981 and January 1982 and that of the juveniles recaptured in January 1982 are shown in Figure 3. Similarly, the size-frequency distributions of juveniles on reefs III and V in January, May, and September 1981 and in January 1982 are shown in Figure 4. There was change in the composition of the population on reef I between January 1981 and 1982, indicating immigration of 2- and 3-yr-old animals into the population of this reef. Between January and September 1981 there was an indication of immigration of untagged animals to both reefs III and V, principally of animals ≥3 years of age, while in January 1982 there was also an obvious immigration of 2-yr-old animals to both reefs.

Population Size, Density, and Mortality Rates

The estimates of population size, density, and mortality rates for *P. cygnus* juveniles ≥3 years of age on reefs I, III, and V are given in Table 2. The estimate made for the population on reef III in February 1981 assumes that the 304 tagged *P. cygnus* released in January were still within the population in February.

The population densities of ≥3-yr-old juveniles on reef I estimated each January from 1970 to 1982 are shown in Figure 5. The density in January 1981, at the time the study began, was the highest ever recorded. The density in January 1982 was also very high and only exceeded by the levels in January 1974 and January 1981.

The annual mortality coefficient for juveniles aged

TABLE 2.—Population size, population density and mortality-rate estimates for juvenile *Panulirus cygnus* >3 years of age on three test reefs at Seven Mile Beach, Western Australia.

Date	[1]Reef 1 (0.071 ha)		[2]Reef III (0.104 ha)		[3]Reef V (0.103 ha)	
	Population	SD	Population	SD	Population	SD
Jan. 1981	1,990	170	2,192	194	2,644	120
Feb. 1981	—	—	1,879	195	—	—
Aug. 1981	625	38	725	54	1,042	40
Jan. 1982	1,273	93	1,951	92	1,841	101

[1]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.655.
[2]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.302.
[3]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.825.

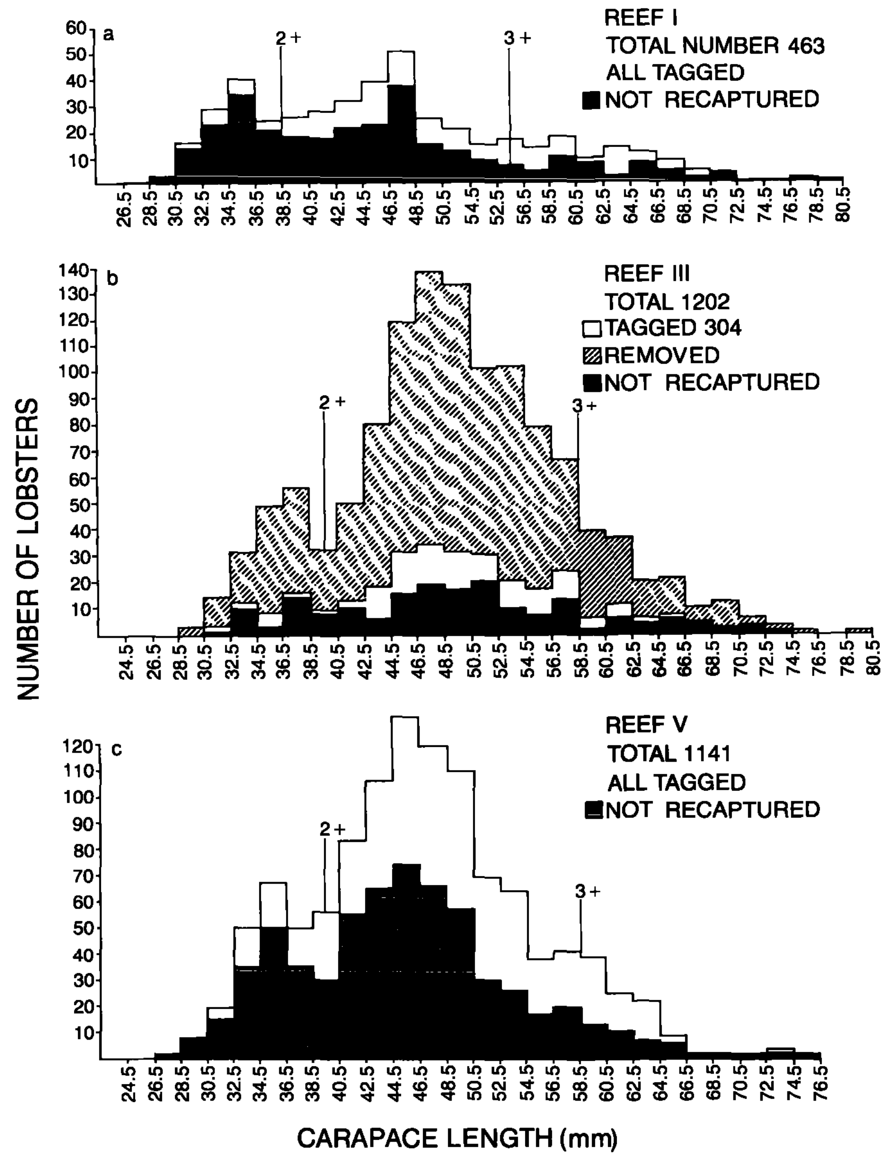

FIGURE 2.—Size-frequency distributions of juvenile *Panulirus cygnus* in January 1981 on three test reefs (reefs I, III, and V) at Seven Mile Beach, Western Australia and size-frequency distributions of animals removed or tagged. Size-frequency distributions of tagged animals not subsequently recaptured also are indicated.

≥3 years on reef III was slightly lower than that for juveniles on reefs I and V. Comparison of the estimates of population size on which these mortality coefficients were based showed that annual survival of animals ≥3 years old was significantly higher on reef III than on reef V (chi-square test of independence, $P < 0.005$).

The numbers of juveniles tagged and released on each test reef in January 1981 are shown in Table 1, while the numbers and percentages of those same individuals recaptured on the same reef in January or February 1982 are summarized in Table 3 for each age group. These data were used, in part, to provide more specific estimates of age-specific survivorship over the 1-yr period, based on assumptions considered later in this paper. A striking feature of the data for reef III is the very high percentage of recaptures, ranging from 97.4 to 100% for 3-, 4-, and ≥5-yr-old individuals, and with a somewhat lower value of 58.1% for 3-yr-old animals. Percentage recaptures for all age groups combined were 71.4% on reef III, as compared with much lower values on reef V (14.7%) and reef I (20.1%). Separate comparisons employing chi-square tests of independence indicated that the number of juveniles recaptured were significantly higher on reef III than on reef V for each of the four age groups ($P < 0.005$).

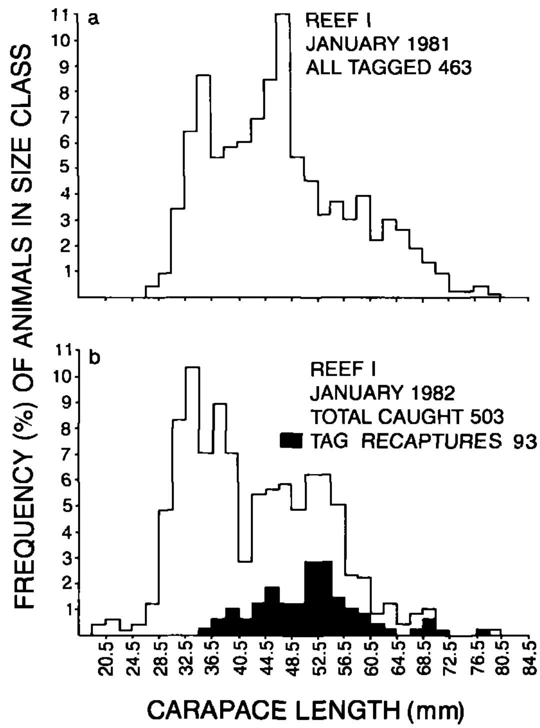

FIGURE 3.—Size-frequency distributions of juvenile *Panulirus cygnus* on Reef I at Seven Mile Beach, Western Australia, in January 1981 and 1983.

Visual Estimates of Population Size

Estimates of the mean total numbers of *P. cygnus* juveniles on the three test reefs, based on visual sampling by two divers, are summarized in Table 4.

The data for reef I are incomplete but show a dramatic decrease from 265 on 10 January 1981 to 66 on 19 January 1981. There was also an overall reduction from 265 in January 1981 to 181 in January 1982 and 173 in January 1983.

The data for reef III (Table 4) indicate that removal of *P. cygnus* by trapping on 11–15 January 1981 reduced the number of juveniles from 705 present on 10 January to about half of that number, with 395 (56%) observed on 19 January and 346 (49%) on 3 February. Further removal by trapping on 4 and 5 February 1981 reduced the number of juveniles to approximately 29% of the original 10 January level (205 observed on 18 February).

From March through June 1981 the mean estimated numbers of juveniles on reef III varied from 189 to 260, representing approximately 27–48 ($\bar{x}$ = 36%) of the original, natural population level observed on 10 January 1981 (Table 4). By January 1982, the number of juveniles on reef III had increased to 430, or approximately 61% of the level observed in January 1981 and by January 1983 the number had increased to 590 or approximately 84% of the natural level two years before.

The numbers of juveniles on reef V were rather more variable, ranging from a low of 72 (25 March 1981) to a high of 780 (October 1981). Of special im-

TABLE 3.—Number and percentage of juvenile *Panulirus cygnus* tagged in each age class on three reefs at Seven Mile Beach, Western Australia, in January 1981, and the numbers present and recaptured in January and February 1982.

	Reef I				Reef III				Reef V			
Age class (Yr)	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%
2	117	260	12	10.3	38	227	37	97.4	192	338	12	6.3
3	245	196	62	24.4	203	375	118	58.1	777	267	102	13.1
4	77	36	14	18.2	57	109	56	98.2	149	112	45	30.2
≥5	15	6	5	33.3	6	92	6	100.0	23	14	9	39.1
Total	463	503	93	20.1	304	804	217	71.4	1,141	731	168	14.7

[1]In January 1981

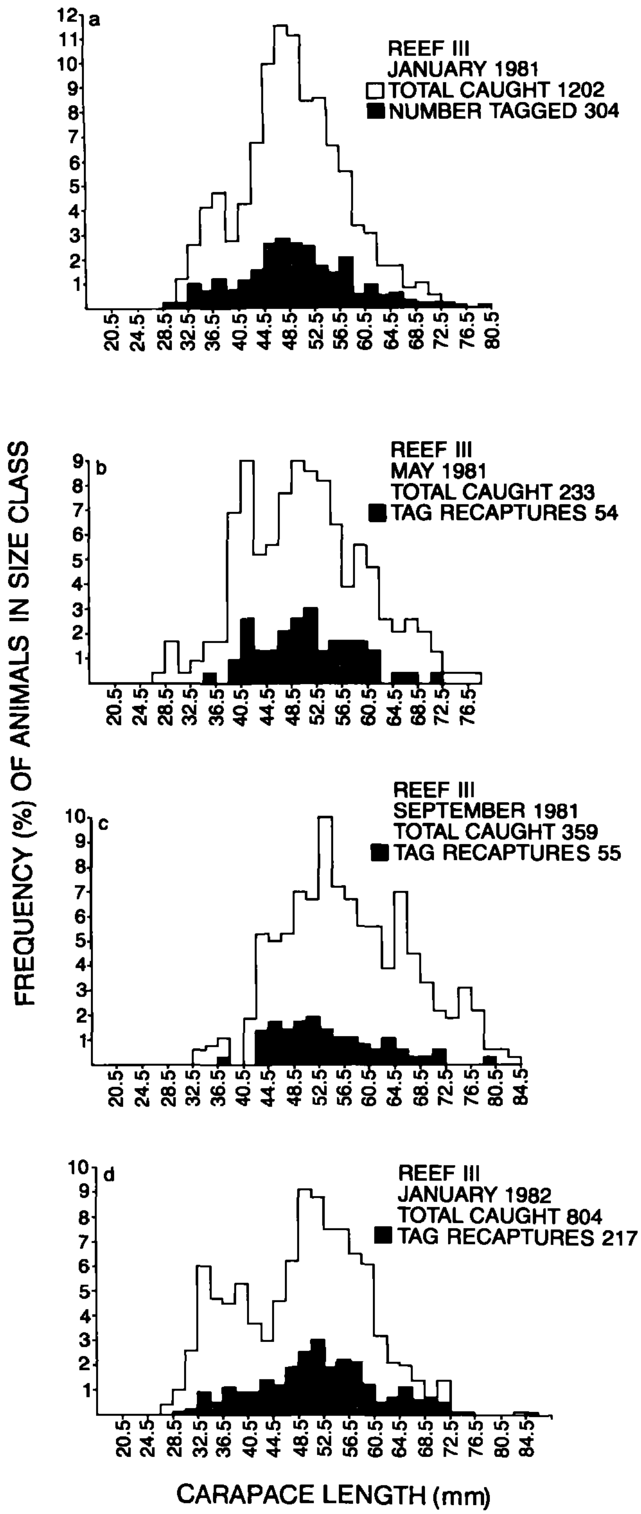

FIGURE 4.—Size-frequency distributions of juvenile *Panulirus cygnus* on reefs III and V at Seven Mile

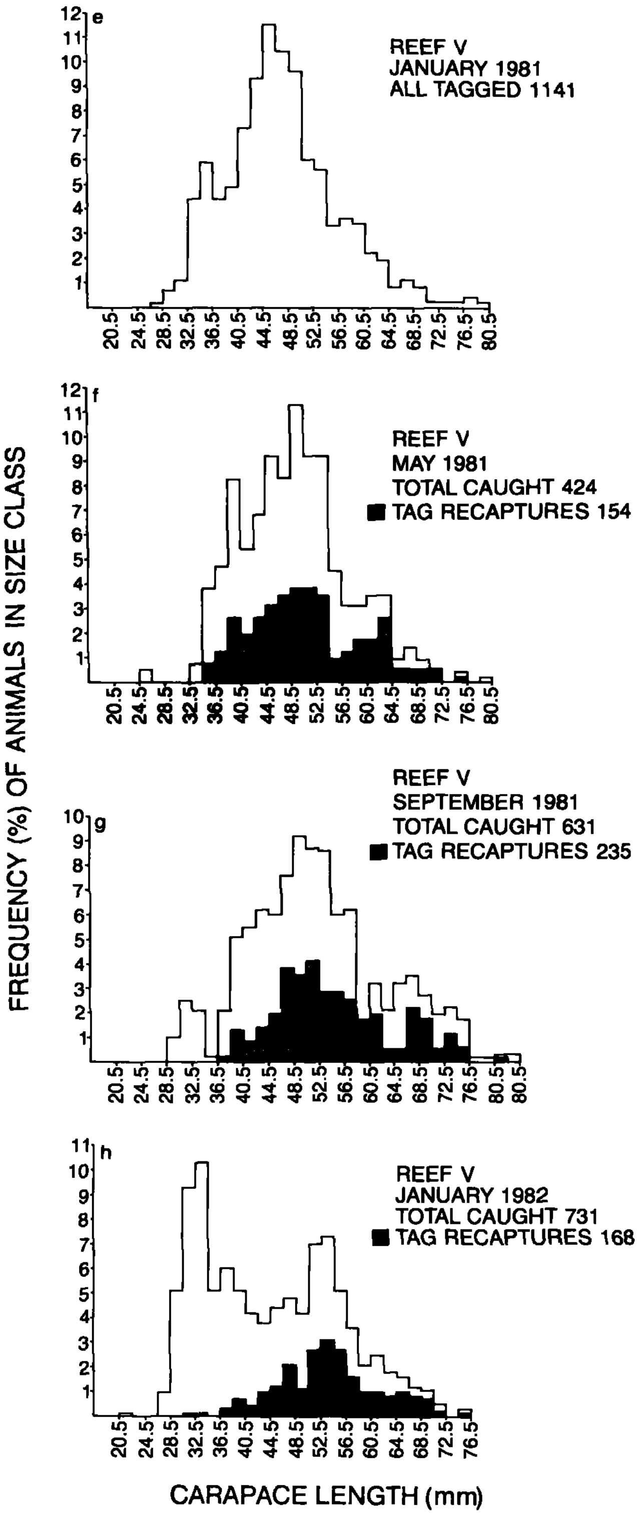

FIGURE 4.—*Continued*—Beach, Western Australia, during the period January 1981 through January 1982.

portance was the 34% decline in numbers between 10 January and 18 February on reef V. By mid-February 1981 the estimated population on reef V was below that on reef III. The mean number of animals for reef V in February 1982 (401) was 71% of that observed in January 1981 (563), although in October, November, and December 1981 it exceeded the January 1981 level. In January 1983, the number of juveniles (537) was essentially the same as that observed two years before (Table 4).

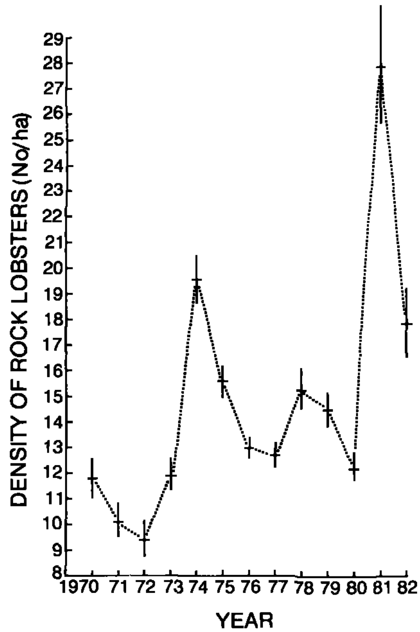

FIGURE 5.—Densities of 3-yr-old juvenile *Panulirus cygnus* in January on reef I at Seven Mile Beach, Western Australia, for the period 1970 through 1982. Mean and 95% confidence limits are shown. Data for 1970–80 from Morgan et al. (1982).

TABLE 4.—Mean total numbers of juvenile *Panulirus cygnus* on three test reefs at Seven Mile Beach, Western Australia, based on visual estimates made by two observers. — = no visual estimate made.

Date	Reef I	Reef III	Reef V
10 January 1981	265	705	563
19 January 1981	66	395	286
3 February 1981	—	346	235
18 February 1981	—	205	191
9, 13 March 1981	—	335	227
25 March 1981	—	189	72
23 April 1981	—	233	220
15, 17 June 1981	—	260	451
15 October 1981	—	374	780
19 November 1981	—	424	680
10 December 1981	—	321	647
29 January 1982	181	430	—
23 February 1982	42	474	401
11 January 1983	173	590	537
16 February 1983	121	521	501

Growth

Single Molt Increments

Mean single molt increments of male and female *P. cygnus* on reefs III and V, the treatment and control reefs, (Table 5) showed no significant difference within either the 2-, 3-, or 4-yr-old age-classes (t-test, $P > 0.05$). Only four animals estimated to be ≥5 years of age were recaptured and these were all from reef V. After pooling the molt increment data for the two sexes there were no significant differences between the mean single molt increments of 2-, 3-, or 4-yr-old animals on reefs III and V (t-test, $P > 0.05$).

TABLE 5.—Mean molt increments in carapace length (mm) for sex age-class groups of juvenile *Panulirus cygnus* from three test reefs at Seven Mile Beach, Western Australia during January–May 1981. Data are mean SE (n).

Age class	Reef I		Reef III		Reef V	
	Males	Females	Males	Females	Males	Females
2	—	—	2.58(0.40) (5)	1.84(0.11) (5)	1.75(0.28) (4)	2.41(0.20) (10)
3	2.85(0.56) (6)	1.74(0.21) (9)	2.01(0.33) (16)	1.76(0.15) (16)	2.27(0.14) (76)	2.17(0.26) (60)
4	—	—	2.75(0.61) (4)	1.94(0.26) (5)	3.17(0.26) (16)	2.88(0.19) (18)

The data from reef I, the secondary control reef, were only sufficient for an examination of the single molt increments of 3-yr-olds. Within this age class there was no significant difference in mean molt increment between the two sexes and the data for the whole age class were pooled. There were no significant differences between the mean single molt increment for 3-yr-olds from reef I and the mean single molt increment for this age class on either reefs III or V (t-test, $P > 0.05$).

Annual and Seasonal Growth

The mark-recapture data from reefs I, III, and V are considered within four time periods: From January 1981 to May 1981 (the "summer–autumn" period), from May 1981 to September 1981 (the "winter" period), from September 1981 to February 1982 (the "spring–summer" period) and from January 1981 to January–February 1982 (the "annual" growth period). As described in Methods section above, average relative growth rates (ARGRs) of males and females were not significantly different and therefore the data were pooled. Because of the small number of ≥5-yr-old lobsters, their growth data were combined with the data for the 4-yr-old individuals. The ARGRs of the different age groups from all three reefs over each of the four time periods are given in Figure 6.

Comparison of growth data for the test reefs for each age group and recapture interval were made using Wilcoxon rank sum tests. The primary purpose was to evaluate whether growth data for the three reefs could be pooled for later analysis. The comparisons are of interest in their own right, but caution is required in interpreting some of the differences established because of small sample sizes in some cells.

The results showed no significant differences in ARGRs of any age group between reefs III and V ($P > 0.05$), the treatment and the principal control reefs respectively in the density manipulation experiment. There were significant differences in ARGRs between reefs I and III for individuals 3 years of age in January–May 1981, May–September 1981, and January 1981–January 1982 and for individuals ≥4 years of age in January–May 1981. There also were significant differences in ARGRs between reefs I and V for individuals 3 years of age in January–May 1981 and May–September 1981, and for individuals ≥4 years of age in January–May 1981 ($P < 0.05$). The significant differences all showed consistently higher ARGRs on reef I than on reefs III and V.

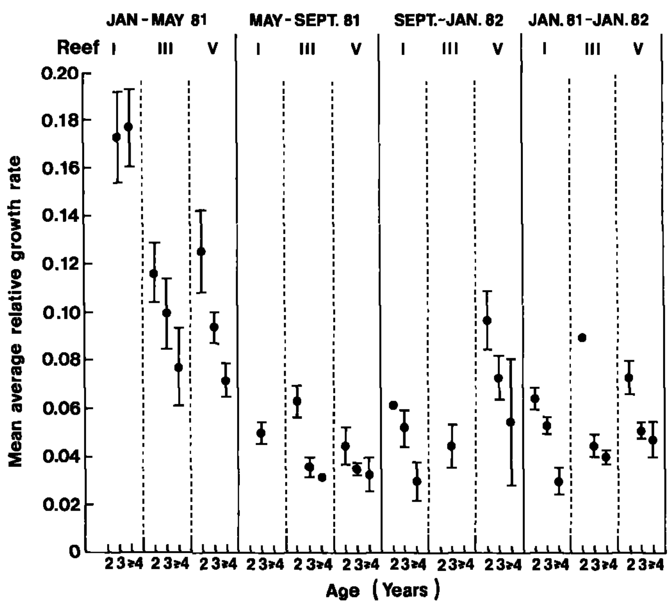

FIGURE 6.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs at Seven Mile Beach, Western Australia.

The data for both reefs III and V were then pooled. The data for 49 *P. cygnus* which were recaptured on reefs III and V were included in this set (Fig. 7). Comparisons of these combined data were made with the data for reef I, and the results indicate that all of the significant differences in growth described above were maintained except that for 3-yr-old individuals in January 1981–January 1982. The lack of a consistent significant difference between reefs at all ages and recapture intervals suggests that the effect is not a simple response to a superior environment, but rather that interactions between reef and age and between reef and recapture interval are present.

DISCUSSION

The density manipulation described in this paper is an attempt to use an ecological field experiment in a nonbenign, subtidal habitat to study the population processes of a spiny lobster. Practical limitations within this environment related to wave effects on drifting plant material and the need to enclose enough area to adequately provide for the foraging range of juvenile *P. cygnus* precluded the use of large enclosures which would have effectively prevented migration. Also, because of the potential mobility of *P. cygnus*, it was not possible to increase and maintain the density of juveniles above natural levels on a reef without such an enclosure. Therefore, only an experimental reduction in density was attempted:

1. Data from the visual estimates show that we were successful in reducing the number of juvenile *P. cygnus* on reef III to approximately 30% of the original, natural level by removing animals in January, February, and March 1981. Following the last removal, the estimated numbers of animals varied, but showed a slow increase over the 1-yr period of the manipulation experiment, with a mean of 36% of the original January level during March through June 1981 and a mean of 55% of the original level during October 1981 through January 1982. However, the number of juveniles on both reefs I and V, the control reefs, also declined during this period, and the population on reef V was estimated to be below that of reef III on 18 February 1981. Therefore, it is difficult to separate the effects of the systematic removals from a general decline in numbers indicated by what was observed on reefs I and V.

The size and age structures and the sex ratios of *P. cygnus* juveniles on reefs I, III, and V in January 1981 were very similar. Size and age structures and the sex ratios of these juveniles

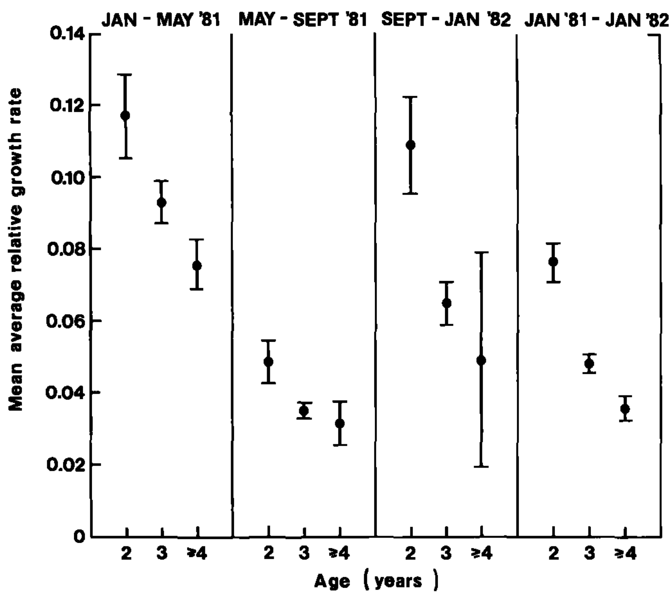

FIGURE 7.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs III and V (combined) at Seven Mile Beach, Western Australia.

also were very similar among the reefs at all subsequent sampling times, suggesting that the drastic reduction in the density of *P. cygnus* on reef III, and the method of reconstituting the population, did not have an evident effect on these characteristics over the 1-yr period of the experiment.

2. The population sizes of ≥3-yr-old *P. cygnus* juveniles, estimated from catches with baited traps, were significantly lower on reef III than on reef V in January 1981 and August 1981, but were similar (i.e., not significantly different) in January 1982. However, these data, and the estimates of mortality derived from them, are subject to the usual problems associated with mark-recapture techniques. Phillips (unpubl. data) has found in more recent studies that the baited traps are capable of attracting juveniles from over a wide area and hence the population size and density estimates applied to individual reefs probably are inaccurate. However, the trends in the population estimates from the mark-recapture data are supported by the visual estimates of population size, indicating that they reflect what was actually happening on these two reefs.
3. Clearly, the visual estimates provide a more specific set of information about population levels of juveniles living on the reef. The method also allows direct estimates of numbers over short time intervals and with minimal disturbance of the western rock lobsters. However, although there is no doubt about the drastic decline in the numbers of tagged lobsters on reefs I and V after the period of initial tagging, it is not possible to determine if this was as a result of tagging mortality, an emigration as a response to handling and tagging or part of the normal behavior pattern.

Despite the attempts to select directly comparable reefs for the experiment, it is possible that reefs III and V do provide different environments for the resident *P. cygnus*. The movement of 71 individuals from reef V to reef III may be part of a typical movement from shallower to deeper reefs. It seems unlikely that water depth, per se, is the primary factor involved, because the difference in depth between the two reefs is no more than 2 m. The reefs used by Chittleborough (1970) at Garden Island, on which he found *P. cygnus* juveniles remained for several years with little movement even from one part of the reef to another, were similar in depth to reef III.

Observations during sampling indicated that on reefs I and V, which are both located close to the beach, relatively large amounts of plant detritus build up around the base of the reef and under ledges and that turbidity of the water is sometimes quite high. These effects also occur on reef III, but are less pronounced. This suggests that less favorable conditions on the shallower, inshore patch-reefs may cause some *P. cygnus* to seek reefs slightly farther offshore which have more suitable conditions. It also may help to explain the higher variability in numbers of juveniles from the visual estimates made on reef V compared with reef III. Some individuals may temporarily emigrate from areas such as reef V during periods of adverse conditions.

Survival and mortality data, which were obtained from both the mark-recapture estimates of population size and the numbers of tagged animals recaptured on the same reef, indicate that survival of *P. cygnus* juveniles was significantly higher on reef III than on reef V over the 1-yr period of the experiment. This was evident for individuals of all four age groups. It suggests that the experimental reduction in numbers of juveniles on reef III, resulting in relatively low population densities (29–61% of the original, natural number) during the 1-yr experimental period, led to significantly higher survival than on reef V, where *P. cygnus* juveniles were present at natural density levels. One explanation for this is that reduced densities of juveniles on a reef may lead to a corresponding reduction in predation mortality and adverse interspecific effects of crowding. An alternative explanation for the very high survival of *P. cygnus* juveniles estimated on reef III, relative to reefs I and V, is that the tagged juveniles on reef III remained for the entire year while many of those tagged on reef I and V emigrated to other reefs.

These mortality data are subject to several sources of error, including the basic problems associated with mark-recapture sampling to obtain population estimates (Bailey 1951). The age-specific estimates of survival obtained from comparisons of numbers of tagged individuals released on each reef in January 1981 and recaptured there in January or February 1982 requires a major assumption. It is that all of the tagged individuals not recaptured on a particular reef after one year have died. This undoubtedly is not the case because some of those individuals probably moved to other reefs at Seven Mile Beach after their release. To the extent that this occurred, the survivorship estimates are low.

No quantitative information is available to correct the estimates for this effect.

The analyses of the growth data, including both the single molt increments and the ARGRs, clearly indicated high variability in growth rates between age groups, and that site (reef) and season variations (recapture interval) were compounding factors. Estimates of growth made during the 1-yr period of the study were similar to those obtained on reef I in previous studies at Seven Mile Beach (Chittleborough 1970, 1975, 1976; Chittleborough and Phillips 1975; Joll and Phillips 1984). However, despite the fact that the population densities in 1981 were the highest ever recorded, the molt increments of the 3-yr-old *P. cygnus* were significantly higher than at the low densities in 1971–74.

Comparisons of the growth data for *P. cygnus* juveniles showed no significant differences in growth within any age group between reefs I, III, and V. The reduced densities of juveniles on reef III had no apparent effect on either their overall growth rates or their molt increments. This suggests that the food resources on the surrounding seagrass beds may not limit growth within the range of *P. cygnus* densities present on these reefs during the field experiments. However, other factors may be involved. The foraging ranges of juveniles on reef III may overlap those animals from reef V and other nearby patch-reefs. More recent acoustic tracking studies by Jernakoff (unpubl. data) suggest that this is probably the case. If so, then reducing the density of *P. cygnus* on reef III might not produce a significant increase in their growth rates, because they could still be sharing their food resources with animals from nearby reefs.

The best tests of hypotheses about the effects of limited resources are those where the densities of *P. cygnus* are experimentally manipulated in replicated experimental areas and which incorporate appropriate controls (Connell 1974; Underwood 1979). This attempt has highlighted a number of problems. Nevertheless, it may be useful to conduct modified manipulation experiments of this kind in the future. Obviously, one of the problems with the present experiment was the lack of replication, and replication should be incorporated in the design of any future experiments. This was not possible in the present study because of high time and manpower requirements associated with the use of trapping and mark-recapture techniques. Furthermore, our observations indicate that it will be extremely difficult to find a series of patch-reefs similar enough in size, structure, and other features to serve as true replicates. As has been shown in this study, even small differences in water depth, or as yet unidentified characteristics, make the selection of reefs as equivalents very difficult. Selection of such reefs also will not be easy because often several reefs are within the known foraging range of the juveniles.

Evaluation and refinement of the visual estimation technique also will be necessary before further manipulation experiments are undertaken, as the usefulness of mark-recapture techniques is dubious. Without the development of such a refined method which would permit rapid and frequent estimates of population size, the effect of subsequent changes in population levels cannot be properly monitored. Without such a method it also would not be possible to determine the extent to which migrations of *P. cygnus* juveniles to and from the reefs are induced by the use of the baited traps or by handling and other disturbances during the mark-recapture process.

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