

Reproduction of the Ornate Rock Lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea

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Abstract

Based on the examination of 26 499 female and 17 666 male specimens, the reproductive biology of *P. ornatus* is discussed with spatiotemporal reference to the annual breeding migration from northern Torres Strait to the Gulf of Papua. Migration commences generally in August with ovary development, mating and initial oviposition occurring during migration. Larval release normally commences once the migration has terminated on the reefs of the eastern seaboard in the Gulf of Papua. At the conclusion of the migration, marked segregation of the sexes occurs, with males entering shallow water (< 3 m) before females, who frequent deeper water (3-15 m) until their eggs have hatched. During the breeding season (November-April), females produce up to three broods. Fecundity is determined for 33 females in the carapace size range 75.4-121.0 mm. No significant egg loss during incubation was detected, but there was an indication of a reduction in the size of each subsequent brood. There appears to be a high post-spawning mortality of migratory lobsters. It is likely that the Gulf of Papua is the major source of larval recruitment in the western Coral Sea, including the east coast of Queensland and Torres Strait.

Introduction

Panulirus ornatus (Fabricius, 1798) supports three commercial fisheries on the southern coast of Papua New Guinea and in Torres Strait (Moore and MacFarlane 1980). All three fisheries utilize a common lobster stock (Moore and MacFarlane 1984), which undertakes an annual breeding migration from Torres Strait around the Gulf of Papua to Yule Island, on the eastern seaboard (Fig. 1). The migration commences generally in late August and the lobsters arrive at Yule Island by late November or early December.

Rapson (1962) initially reported the area between Yule Island and Port Moresby as a breeding ground for *P. ornatus*. Later, Pyne (1974) described the biology of *P. ornatus*, based exclusively on the Yule Island fishery.

The reproductive biology of *P. ornatus* in relation to all three fisheries is examined in the present paper. The study formed part of a program undertaken by the Fisheries Division of the Papua New Guinea Department of Primary Industry between 1974 and 1980. The major objectives of this program were to examine the biology of *P. ornatus*, to determine the effects of commercial exploitation, and to advise the Papua New Guinea Government of any management measures necessary to ensure the future rational utilization of the resource.

Materials and Methods

Between December 1974 and May 1980, 26 499 female and 17 666 male *P. ornatus*, obtained from commercial catches and tagging operations [see MacFarlane and Moore (1984) for tagging methods], were examined. These ranged from 15 to 163 mm in carapace length (C.L.). Data recorded included carapace length, sex, the stage of egg development, the state of the spermatophoric mass, and, where possible, the state of ovary maturation. Gonadosomatic index (ovary weight as a percentage of the total body weight) was calculated for 5652 females.

Carapace length was measured to the nearest 0.1 mm along the dorsal midline, between the supra-orbital horns and the median posterior edge of the cephalothorax. Shipboard recording of weights precluded an accuracy of ovary weights better than 1.0 g, and of total body weight, 5.0 g.

Ovary Development

This was classified using four macroscopically distinguishable stages, closely following Berry (1971).

Stage 1. Immature. Ovaries white (2 g or less), flattened dorsoventrally.

Stage 2. Developing. Ovaries pink to pale orange (10–20 g), noticeably enlarged.

Stage 3. Ripe. Ovaries bright orange to red, greatly enlarged (30–80 g).

Stage 4. Spent. Ovaries white, yellow or pale pink, often with a few large ova from stage 3 retained at the extremities of the ovary lobes. This stage was frequently macroscopically indistinguishable from stage 1. Hence, stages 1 and 4 have been combined during analysis of data from the Yule Island reef fishery.

Spermatophoric Mass

This was classified using four macroscopically distinguishable stages.

Stage 0. Absent.

Stage 1. Recently mated. The spermatophoric mass retains the overlying protective matrix in an unscraped condition.

Stage 2. Used. The overlying protective matrix has been removed, exposing the underlying spermatophores, and permitting fertilization to take place.

Stage 3. Old. Spermatophoric mass greatly fragmented.

Egg Development

This was classified using six macroscopically distinguishable stages.

Stage 0. External eggs absent. Ovigerous setae clean, pale yellow and silky.

Stage 1. Recently oviposited. Eggs bright orange, no embryonic development visible macroscopically.

Stage 2. Eggs dark orange. No eye-spots visible.

Stage 3. Eggs dark orange to dark red, with noticeable embryonic development and large eye-spots.

Stage 4. Eggs brown. Egg capsules translucent, embryo and eye-spots clearly visible.

Stage 5. Just hatched. Ovigerous setae tangled by egg stalks and empty egg capsules. Within a few days these were detached and this stage was then only distinguishable from stage 0 by the dirtier appearance of the setae.

Determination of Fecundity

Pleopods were removed from ovigerous females, hardened in 10% formalin and then air dried until the eggs could be easily stripped from the setae. Dried samples were passed through a sieve (1-mm mesh) to remove extraneous matter and the whole sample weighed to the nearest microgram.

Duplicated subsamples of approximately 0.1 g were weighed to the nearest microgram and the eggs in each were counted manually, using a $\times 10$ desk magnifier. Fecundity was taken as the mean number of eggs in each sample, calculated from the two subsamples.

Observation of Captive Ornate Rock Lobsters

Lobsters were maintained in groups of two to eight individuals with the sexes being mixed. Each group was held in aquaria or underwater cages at ambient temperatures of 29–30°C. All lobsters were fed daily on a diet of assorted shellfish and whole fin fish. They were examined approximately every 2 days to determine the frequency of mating, oviposition, incubation period and mortality.

Results

Sex Ratio and Size Structure of the Population

Summed data from the Daru reef fishery consistently indicated an excess of males (1♂:0.63♀) in the population before migration (Table 1). This was especially true in the larger size classes (100–160 mm C.L.). In the smaller classes (10–70 mm C.L.), the sex ratio was essentially unity.

By contrast, the trawl and Yule Island reef fisheries both exhibited an excess of females in the population. In the former fishery the sex ratio was 1.52♀:1♂, and 2.86♀:1♂ in the latter. In these two fisheries most females had a carapace length of 90–120 mm and males 100–150 mm.

Hence the migratory population differed markedly from the non-migratory population by having an excess of females, males tending to be larger than females, and with very few small lobsters (less than 70 mm C.L.).

Attainment of Sexual Maturity

Macroscopic examination of the ovaries of 17 657 females (15.2–159.8 mm C.L.) taken from the Daru, trawl, and Yule Island fisheries established that the smallest female with developed ovaries (stage 3) had a carapace length of 67.4 mm. The smallest ovigerous female recorded had a carapace length of 78.6 mm.

It was not possible to determine sexual maturity of males from macroscopic examination of testes.

Table 1. Population structure of *P. ornatus* from the Daru reef fishery, Gulf of Papua trawl fishery and Yule Island reef fishery

Based on commercial catches and tagging data (1974–1980)

Carapace length (mm)	Daru reef fishery			Gulf of Papua trawl fishery			Yule I. reef fishery		
	No. of males	No. of females	Ratio of males to females	No. of males	No. of females	Ratio of males to females	No. of males	No. of females	Ratio of males to females
10.1–20.0	2	1	1:0.50	0	0	—	0	0	—
20.1–30.0	10	7	1:0.70	0	0	—	0	0	—
30.1–40.0	12	8	1:0.67	0	0	—	0	0	—
40.1–50.0	32	20	1:0.63	0	0	—	0	0	—
50.1–60.0	73	87	1:1.19	15	6	1:0.40	0	0	—
60.1–70.0	331	341	1:1.03	57	114	1:2.00	0	0	—
70.1–80.0	1260	1141	1:0.91	282	288	1:1.02	3	4	1:1.33
80.1–90.0	2544	2157	1:0.85	300	591	1:1.97	13	217	1:16.69
90.1–100.0	2541	2242	1:0.88	414	2436	1:5.88	105	1803	1:17.17
100.1–110.0	2291	1442	1:0.63	1533	5070	1:3.31	651	3574	1:5.49
110.1–120.0	2102	819	1:0.39	2184	3327	1:1.52	1163	2067	1:1.78
120.1–130.0	1014	161	1:0.16	1671	813	1:0.49	689	325	1:0.47
130.1–140.0	689	29	1:0.04	1137	69	1:0.06	158	24	1:0.15
140.1–150.0	375	2	1:0.01	615	9	1:0.01	19	1	1:0.05
150.1–160.0	83	1	1:0.01	138	0	1:0.00	6	0	—
Total	13 359	8458	1:0.63	8346	12 723	1:1.52	2807	8015	1:2.85

Reproductive Development Before Migration

A sample of 9642 females (15–138 mm C.L.) was collected from reefs in northern Torres Strait over 62 consecutive months (1974–1980). Mated and berried females were absent and no females exhibited ovary development beyond stage 1. Concentrated sampling in August, immediately before the commencement of migration, further confirmed that ovary development does not occur until sometime after migration has commenced.

An exception to the general pattern of non-breeding in northern Torres Strait was the consistent occurrence of breeding females at Parama Island, between December and March. Parama Island lies at the eastern extremity of the reef systems in the study area (Fig. 1). Here the number of breeding females was never large.

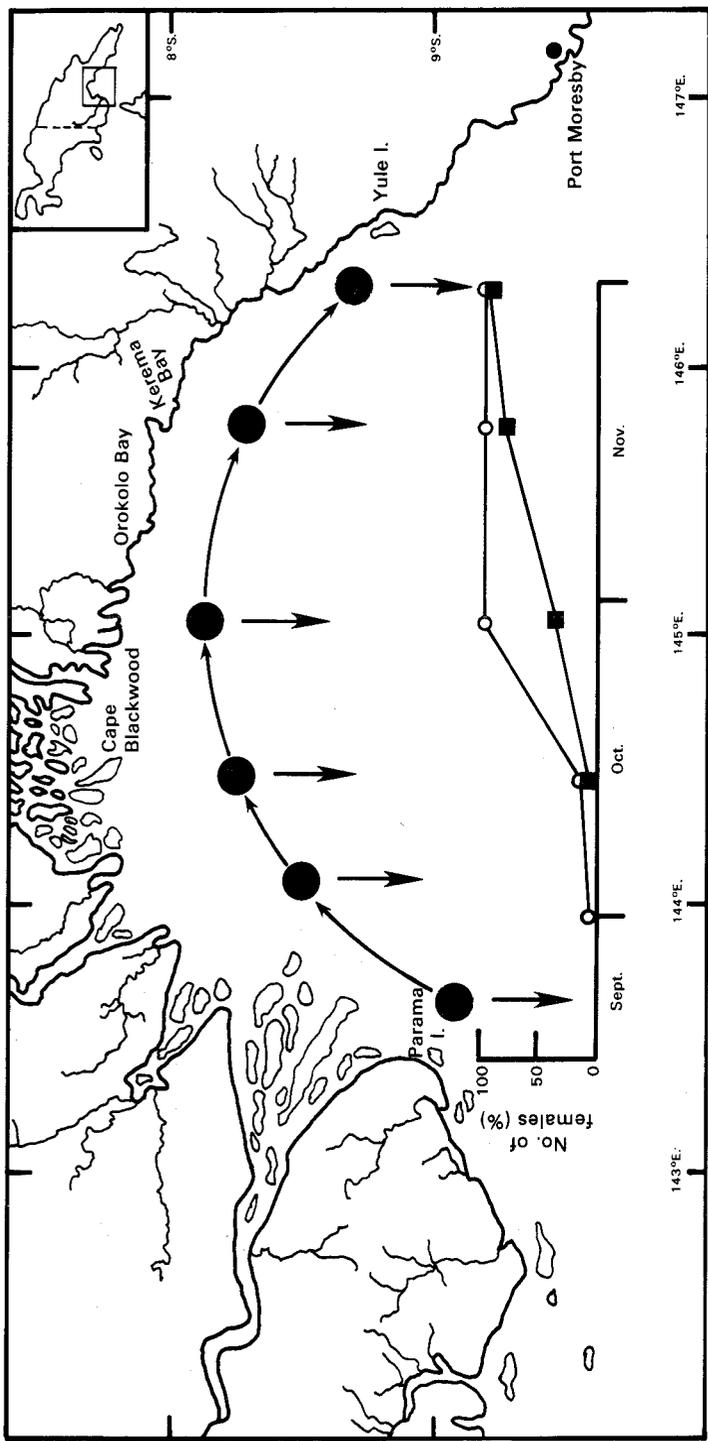


Fig. 1. Schematic representation of the annual breeding migration of *P. ornatus* in the Gulf of Papua, showing the relationship between mating (○) and oviposition (■) relative to the geographical position of the migration. Based on the first migratory wave of the 1977 season.

Reproductive Development During Migration

The annual migration into the Gulf of Papua commences in mid to late August. This generally takes the form of several, usually two to three, waves of migratory lobsters moving around the gulf from west to east. Each wave migrates with a temporal separation of approximately 2 weeks.

The reproductive events occurring during the migration were determined from the examination of commercial catches and experimental trawling. In 1977 considerable experimental trawling was carried out so that migratory waves could be followed throughout the migration. Data obtained for other years between 1975 and 1980 are somewhat fragmentary but are generally consistent with the pattern established in 1977.

Fig. 1 illustrates the migration, and relates the geographic position of the first migratory wave of 1977 to the events of mating and oviposition. Ovary maturation was first noted in early September when 48% of females examined had ovaries developed to stage 2. By mid to late September 6% of females had ovaries developed to stage 3 but mating or oviposition had not as yet occurred. By early October, with the migration passing approximately 20 nautical miles south of Cape Blackwood, 53% of females had ovaries developed to stage 3, 42% at stage 2, and 5% remained at stage 1. At this point in the migration, 6% of females had mated and 2% were berried. With the migration passing through Orokolo Bay, in late October to early November, 100% of females had mated, 32% were berried and 80% had ovaries at stage 3.

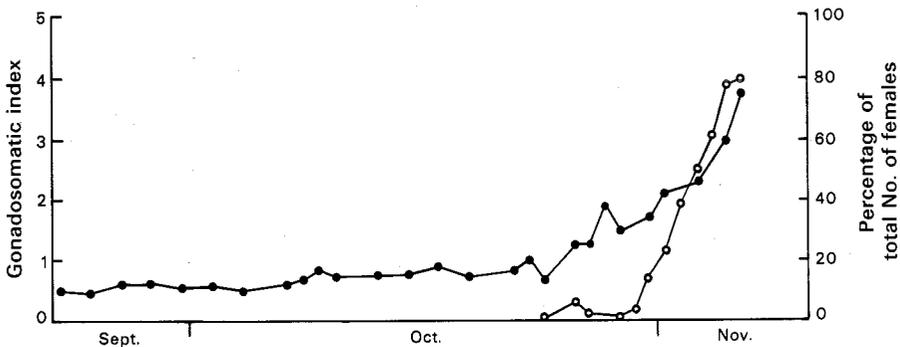


Fig. 2. Relationship between the mean gonadosomatic index (●) and the occurrence of first mating (○) for female *P. ornatus*, during the annual breeding migration across the Gulf of Papua. Based on data from the 1976 season, *N* = 2006.

Fig. 2 illustrates the close relationship between ovary development and the occurrence of first mating. Mating occurs at a time when ovary maturation is proceeding rapidly from stage 2 to stage 3. Hence, when females have fully ripe ovaries they will already have been mated. As the migration continued towards Yule Island the percentage of egg-bearing females steadily increased to 100%. By early December, with the migration approximately 20 nautical miles to the north-west of Yule Island, 4% of females had already hatched their first brood. By early December the first migratory group had reached Yule Island where the lobsters moved into the reef systems and thus became inaccessible to the trawl fishery.

Although some variation occurred from season to season and even between different migratory waves in the same season, the general trend was quite consistent. Characteristically some mating had occurred by the time the migration had reached Cape Blackwood but as yet little or no oviposition had occurred. By Orokolo Bay most females had mated and a substantial proportion were berried. As the migration approached Yule Island virtually all females had mated and were berried. A small percentage of females shed eggs before Yule Island but most did not hatch their eggs until they had reached Yule Island. Hence, larval release occurs mainly after the lobsters have entered the reef systems.

Post-migratory Reproductive Activity

After approximately 2 weeks on the deeper reefs, the lobsters moved inshore onto the shallow reef top, generally in late December to early January. At this time they became vulnerable to the local artisanal fishery.

Initially catches taken from the shallow reef areas (< 3 m) were characterized by an excess of males (1♂ : 0.6♀). However, as the season advanced females began to predominate in commercial landings (Table 2). By contrast there was no excess of males in deeper water (3–15 m) at any time during the season. Two trawl catches made in 6 m of water, 2 nautical miles to the north of Yule Island, further suggested a marked segregation of the sexes after the completion of migration. These catches were taken in January and March 1978 and resulted in sex ratios of 1♂ : 30♀ ($N = 63$) and 1♂ : 44♀ ($N = 91$), respectively.

Table 2. Monthly sex ratios in the fished *P. ornatus* population at Yule Island
Summed data (1975–1980) are from commercial landings taken in shallow water (< 3 m), and from deep water (3–15 m) taken during tagging operations

Month	From shallow water			From deep water		
	No. of males	No. of females	Ratio of males to females	No. of males	No. of females	Ratio of males to females
November	0	0	—	20	20	1:1
December	174	11	1:0.06	24	42	1:1.8
January	1588	2473	1:1.6	11	65	1:5.9
February	762	2508	1:3.3	18	90	1:5
March	255	2913	1:11.4	0	0	—
April	28	110	1:3.9	0	0	—
Total	2807	8015		73	217	

Berried females were more common in deep water (3–15 m) than on the shallow reef tops (Fig. 3). Of 66 berried females tagged in deep water, six inshore movements were recorded. When recaptured, four females had shed their eggs and two carried eggs close to hatching. Of the 154 females trawled in January and March 1978, none was berried and six showed signs of having recently shed eggs. As the population structure of these catches is not typical of the migratory population, these females were probably part of a local inshore movement between reefs. It therefore seems likely that there is inshore movement of females after hatching has occurred.

Duration of the Breeding Season

Berried females were taken at Yule Island from November to April (Fig. 3) but most reproductive activity occurred between November and February. As the season progressed there was a steady decline in mating activity and ovary development (Fig. 4).

The non-migratory breeding lobsters observed at Parama Island (Fig. 5) bred during the same period (November–April) as those at Yule Island. Although the numbers of breeding females were never large, the percentage of berried females was often as high as 25% in January, declining to zero by April. The percentage of recently mated females followed the same trend, reaching a maximum of 8% by January and declining to zero by March.

Repetitive Breeding and Incubation Period

During the migration it was possible to obtain consistent trawl by trawl samples on a daily basis and thus assess the progress of ovary development, egg production and breeding potential of the migratory population up to the point where the lobsters entered the reef systems around Yule Island and thus became inaccessible to the trawl fishery.

Using these data from the trawl fishery, east of Kerema Bay (Fig. 1) all migratory females were first berried by mid to late November. To determine if these females would produce a second brood, a sample of 1852 egg-bearing females was examined in detail to establish the stages of egg development, ovary development and the state of the spermatophoric mass.

Of those females that carried external eggs in stages 1 and 2, only 57% had developed stage-3 ovaries and only 1% of these had recently remated. Of those females that carried external eggs in stages 3, 4 and 5, 100% had ripe ovaries (stage 3) and had recently mated for a second time. Therefore, all females once their first brood of external eggs was well developed were preparing to produce a second brood. Thus it was concluded that 100% of migratory females produce a minimum of two broods per season.

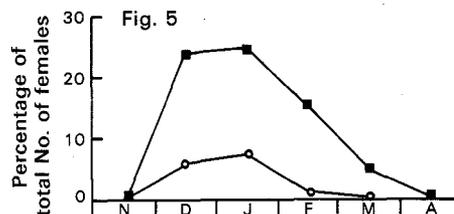
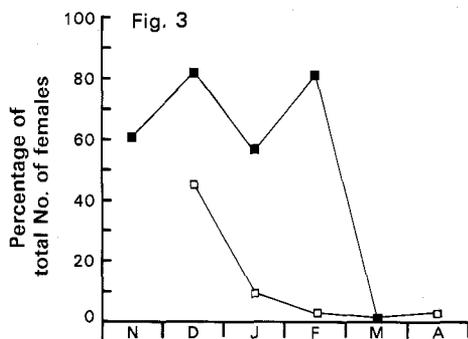


Fig. 3. Percentage of berried female *P. ornatus* recorded from Yule Island in commercial landings taken in shallow water (<3 m; $N = 5876$) (□) and tagging operations in deep water (3–15 m; $N = 343$) (■). Based on summed data from 1975 to 1978.

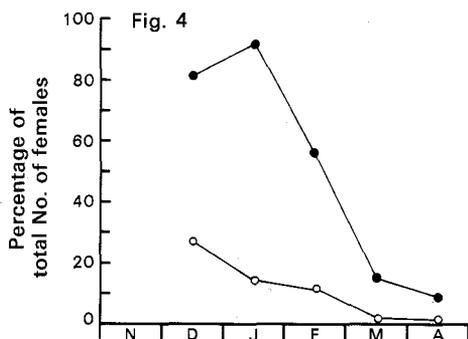


Fig. 4. Percentage of female *P. ornatus* at Yule Island with developed ovaries (stages 2 and 3; $N = 6940$) (●) and females recently mated (spermatophoric mass at stage 1; $N = 5184$) (○). Based on commercial landings from 1975 to 1980.

Fig. 5. Percentage of berried (■) and recently mated (○) female *P. ornatus* taken in each month of the breeding season at Parama Reef. Based on summed data from 1975 to 1980, $N = 76$.

At the conclusion of the migration it was not possible to apply the same criteria to determine if a female would produce a third or subsequent brood as it was impossible to determine the number of broods produced after females had entered the reef systems. Breeding capacity was assessed indirectly from observation of 29 captive females maintained in aquaria tanks over 7 months (November 1977 to March 1978). These females ranged in size from 92.5 to 125.2 mm C.L., and were obtained from both the trawl fishery ($N = 3$) and the Yule Island fishery ($N = 26$). The three females obtained from the trawl fishery successfully produced three broods between November and March. Eleven females obtained from Yule Island produced two broods between January and April, while the remaining 15 females produced only one brood between February and April.

The mean incubation period, at an ambient water temperature of 29°C, was 35 days with a range of 30–51 days. The mean period between hatching and subsequent oviposition was 4 days (range 3–12 days). The size of individual females did not appear to affect the period for hatching or brooding within the size range of females observed in this study.

It therefore appears likely that most migratory females do produce three broods during the season. Females of the first migratory group were berried by late October with hatching occurring in late November to early December, at or close to Yule Island. The second brood would be

hatched on reefs in the Yule Island area in early January, with a third brood being hatched in early to mid February. The arrival of subsequent migratory groups would result in the breeding season being prolonged through to late March or early April.

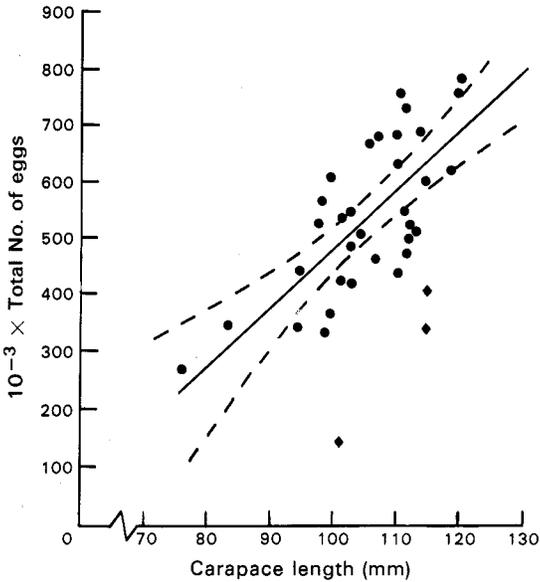


Fig. 6. Fecundity of *P. ornatus*. Based on 33 females from the trawl and Yule Island fisheries (●), taken between November 1979 and January 1980. These are compared with three females (◆) taken from Yule Island at the end of the breeding season in April 1980. ----- 95% limits of confidence.

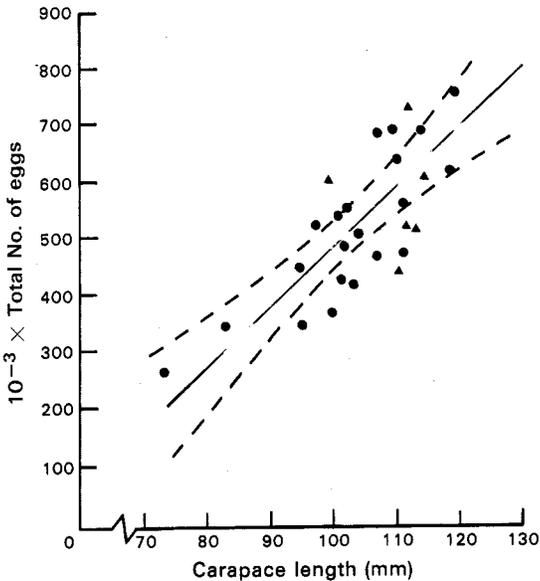


Fig. 7. Comparison of fecundity between 21 female *P. ornatus* with stage-1 eggs (●) and six females with stage-4 eggs (◆). Based on samples taken from the trawl and Yule Island fisheries between November 1979 and January 1980. ----- 95% limits of confidence.

Fecundity

Fecundity was determined for 33 females (75.4–121.0 mm C.L.) collected from the trawl and Yule Island fisheries between November 1979 and January 1980 (Fig. 6). The linear regression is given by the equation:

$$y = 10\,416.68x - 56\,1793.71, \quad r = 0.76 \quad (1)$$

where y is total number of eggs produced and x is carapace length (mm). At the 95% limits of confidence, fecundity was directly related to carapace length.

Fecundity was also determined for three ovigerous females (102.3–115.6 mm C.L.), collected towards the end of the breeding season (April 1980). Brood size was reduced by 47.6–70.0% (Fig. 6) with a mean of 51.3%.

It was only possible to compare broods produced early in the season (November–January) and those produced at the conclusion of the season (April). It was not possible to determine reduction in size between first, second and subsequent broods for individual females. Hence, progressive reduction in brood size may account for the observed variation in fecundity determined from samples collected between November 1979 and January 1980.

A further comparison was made between the fecundity of females bearing eggs at stages 1 and 4 to determine egg loss during incubation. Based on a sample of 21 stage-1 females (72.15–119.9 mm C.L.) the regression line

$$y = 10\,578.95x - 56\,6703.32, \quad r = 0.81 \quad (2)$$

was obtained (Fig. 7). The fecundity of six stage-4 females (99.5–115.0 mm C.L.) was not significantly different from that of stage-1 females at the 95% limits of confidence. Hence there appears to be no significant egg loss during incubation.

Table 3. Estimate of relative fecundity for each size class in the female population, taking into account the proportion each size class constitutes within the migratory population, the relationship between size and fecundity, and the number of broods produced per season

Size class (mm)	70–80	80–90	90–100	100–110	110–120	120–130	130–140
Percentage of total No. of females in each size class (N = 12 723) ^A (A)	0.05	2.65	22.00	45.00	26.00	4.00	0.30
10 ⁻³ × No. of eggs produced (B)	225	325	425	530	635	735	840
Average No. of broods produced per season (C)	3	3	3	3	3	3	3
10 ⁻³ × Total fecundity (A × B × C)	34	2583	28 050	71 550	49 530	8820	757
Relative fecundity (% of total fecundity)	0.02	1.60	17.30	44.35	30.70	5.46	0.46

^A Based on summed data from the trawl and Yule Island fisheries (1977–78).

The relative fecundity of the breeding population was calculated (Table 3), based on equation (1). It was assumed that all females produce an average of three broods but it does not take account of any reduction that may occur in the size of each successive brood. Females in the 100–200 mm C.L. range contributed the most (75.05%) to total egg production.

Post-spawning Activity

Towards the end of the Yule Island season (April), lobster stocks in the area were negligible and there was a steady decline in the condition of the lobsters as the season progressed. This loss of condition has been discussed in detail by Moore and MacFarlane (1984).

Discussion

Moore and MacFarlane (1984) have noted that migratory groups of *P. ornatus* are characterized by an excess of females and by males migrating at a greater age and size than females. Berry (1970) reported that for *P. homarus*, males must be larger than females before successful mating can take place. The extreme elongation of the second and third walking legs, which accompanies the onset of physical maturity in the male, enables the males to manipulate a female of similar or smaller size during courtship and mating. MacFarlane and Moore (unpublished data) have shown that for *P. ornatus* this elongation is most pronounced in males

of 110+ mm C.L., which includes most migratory males. It therefore seems probable that the size differential observed between the sexes of *P. ornatus* at migration is a strategy developed to maximize breeding potential for the population.

The consistent presence of ovigerous females at Parama Reef (Fig. 1) during the breeding season (November–March) suggests that extensive migration is not a necessary component of reproduction for *P. ornatus*.

The extra energy expended in a migration of 511 km across the Gulf of Papua may account for the wasted or 'spent' condition noted by Moore and MacFarlane (1984) at the conclusion of the breeding season. This 'spent' condition is typified by gross atrophy of the tail musculature, often up to 50% by volume after cooking. Lobsters are also lethargic in reaction when captured and the ventral surface of the tail feels soft, not turgid as in lobsters taken from the pre-migratory and pre-spawning populations. Non-migratory breeding lobsters caught on Parama Reef have never been found in a 'spent' condition. The results of cage experiments are suggestive of a high post-spawning mortality in migratory lobsters. The almost total disappearance of *P. ornatus* from Yule Island reefs at the conclusion of the breeding season has been described by Moore and MacFarlane (1984). The loss cannot be accounted for by offshore movements into deeper water or by return migration to Torres Strait. However, this disappearance can probably be accounted for by a high natural post-spawning mortality in the migratory population.

The inshore movement of females, at Yule Island, after hatching has occurred is consistent with the observations of Olsen *et al.* (1975) for *P. argus*, who noted different behavioural patterns between the sexes during the breeding season.

The fecundity of *P. ornatus* is similar to that of other members of the genus *Panulirus*, e.g. *P. homarus* (Berry 1971) and *P. cygnus* (Morgan 1972). Ino (1950) reported a reduction of 50% between first and second broods for *P. japonicus*, which is similar to the mean of 51.3% for *P. ornatus* in the present study.

The phyllosoma larvae hatched at Parama Reef are probably carried westward by currents into northern Torres Strait (MacFarlane 1980) and could account for the juvenile recruitment on Saibai, Sigabaduru and Boigu reefs noted by Moore and MacFarlane (unpublished data). Larval dispersion from Yule Island is probably to a much more extensive area. MacFarlane (1980) demonstrated that currents adjacent to Yule Island dispersed surface drifters widely throughout the Coral Sea but major recoveries were recorded along the Queensland coast from Double Island Point (25°58'S., 153°11'E.) in the south to Prince of Wales Island in Torres Strait (10°24'S., 142°16'E.) in the north. Recoveries were particularly concentrated from Princess Charlotte Bay (14°14'S., 143°13'E.). In view of the close correlation noted between areas of drifter recovery and major juvenile occurrence in Princess Charlotte Bay, Shelburne Bay (11°45'S., 142°59'E.) and southern Torres Strait (10°19'S., 142°15'E.), MacFarlane (1980) suggested that a part of the recruitment to the Queensland east-coast reefs probably originates from Yule Island in the Gulf of Papua. Local breeding does occur along the Queensland east coast and the authors have collected breeding females from Hedge Reef (13°50'S., 144°00'E.) in the south to Wallace Reef (11°27'S., 143°02'E.) in the north. However, the number of lobsters recorded is small ($N = 35$). Berried females ($N = 5$) have also been observed at Murray Island (9°44'S., 144°03'E.) at the northern extremity of the Great Barrier Reef.

Larval dispersion around the Coral Sea is undoubtedly complex and the relative contribution to recruitment from any of the sources mentioned previously probably varies considerably from year to year, depending on prevailing currents and weather patterns. However, as the Gulf of Papua appears to be the major breeding ground for *P. ornatus* in the area, it seems likely that it is the major source of larvae in the western Coral Sea.

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