ספרית אורות

המאמרים במוערבת תדפיסים וז מוגנים על-פי
חוק זכויות יוצרים

הדפסת מאמרים תחת תצריפי לימוד והוראה בלבד

אין לעשוי כל שימוע מסחרי במאמרים.
Sexual Maturity, Reproductive Season and Fecundity of the Spiny Lobster *Panulirus penicillatus* from the Gulf of Eilat (Aqaba), Red Sea

**Itai Plaut**

The Interuniversity Institute of Eilat, The H. Steinitz Marine Biology Laboratory, PO Box 469, Eilat 88103, Israel. Present address: Department of Biology, University of California, Los Angeles, 405 Hilgard Avenue, Los Angeles, CA 90024-1606, USA.

**Abstract**

*Panulirus penicillatus* Olivier (1791) (Decapoda: Palinuridae) is widely distributed in the Indian and Pacific Oceans and is the most common spiny lobster in the Red Sea. Female lobsters (*n* = 234), were collected on four occasions in 1986 from the coral reef of Dahab, 110 km south of Eilat, Israel. Field data and the gonadal index indicated that the reproductive season was from February to October, during which the females spawned 2–4 times. In nature, females became sexually mature at a carapace length (CL) of 50 mm. This result was confirmed by morphometric analysis of the regression between pleopodal exopodite length and carapace length. The number of eggs per spawn (*E*) was related to CL by the equation *E* = 2.715 × (CL)².581. The incubation period of eggs was 35.5 ± 1.0 days (± s.d.) at temperatures of 24–27°C in the aquarium. The results are compared with data on *P. penicillatus* from other parts of its geographic range, and the effect of geographic isolation on reproduction is discussed.

**Introduction**

The plasticity within the genomic pool of widely distributed species (Bayne *et al.* 1976), as well as genetic exchange between populations (Scheltema 1971; Levinton 1982; Rosenblatt and Waples 1986), are key factors enabling these species to occupy a variety of habitats (Plaut and Fishelson 1991). Benthic organisms dispersed by planktonic larvae may experience diverse conditions depending on the specific location of their settlement as larvae. Such diffuse dispersal reduces the probability of their developing highly adapted local populations. A better understanding of this phenomenon requires comparative studies of widespread populations, together with peripherally isolated ones, within a given species.

The spiny lobster *Panulirus penicillatus* is widely distributed in the Indian and Pacific Oceans, from South Africa to the islands in the Galapagos Archipelago between 25°N and 25°S (Fischer and Bianchi 1984). It is the only spiny lobster species with a trans-Pacific distribution (Vermeij 1980). Populations of *P. penicillatus* in the Gulf of Eilat are at the periphery of the species range (Holthuis 1968), and may be partially isolated by the narrow and shallow sills of Bab El Mandab (Plaut and Fishelson 1991).

Although it is widespread and abundant and has potential for commercial development in the Indo-West Pacific (George 1974), knowledge of this species is limited (Ebert and Ford 1986; Junio 1987; Plaut and Fishelson 1991). There is some information on its distribution, ecology and fisheries management (De Bruin 1962, 1969; Holthuis and Loesch 1967; Holthuis 1968; George 1968, 1974; Berry 1971; Bhadia 1974), and on its reproductive biology in Hawaii (Morris 1968; McGinnis 1972; MacDonald 1979) and Palau, Western Caroline Islands (MacDonald 1988). Those studies have revealed high variability between populations with respect to population structure and reproduction.
The population of *P. penicillatus* in the Gulf of Eilat (Aqaba) is composed of small, slow growing individuals (Plaut and Fishelson 1991). This population structure may be an effect of its being at the periphery of the species range and partially genetically isolated from the Indian Ocean by the narrow sill of Bab El Mandab, which might limit import of phyllosoma larvae (Plaut and Fishelson 1991).

In the present study, some aspects of the reproductive biology of *P. penicillatus* females from the field and in captivity are described in order to make a comparison with other populations of this species in the Indian and Pacific Oceans. The possibility of differences in this study population that could be attributed to its partial isolation at the periphery of the species range was also examined.

**Materials and Methods**

In all, 234 females and 143 males of *Panulirus penicillatus* were collected in February, May, August and October 1986 by snorkelling at night at the coral reef in Dahab, Sinai Peninsula (28°30'N, 34°32'E). Specimens were brought to the H. Steinitz Marine Biology Laboratory and kept in tanks of 140–3000 L (50–70 cm depth) with a water exchange rate of 10–40 L min⁻¹ in an open sea-water system. The density of lobsters in the tanks was up to 15 small individuals (≤ 50 mm carapace length, CL) or 3 large individuals (≥ 90 mm CL) per m² surface area of the tank. Water temperature ranged from 21°C in winter to 27°C in summer. Lobsters were fed *ad libitum* with fish, shrimp, sea urchin and squid, and were checked daily for mating, spawning and hatching.

Measurements of CL were taken along the mid-dorsal line from the anterior end between the post-orbital spines, not including the tip of rostral carapace spines, to the posterior edge of the carapace. Leg length was measured from the tip of the dactyl to the proximal margin of the ischium. Pleopodal exopodite length was also measured. All lengths were measured using mechanical calipers (± 0.1 mm). Reproductive state, as determined by the presence of spermatophore or eggs, was recorded on the day of collection.

Every month from February 1986 to January 1987, 7–10 mature females (50–120 mm CL), based on preliminary observations that minimum size at onset of maturity is about 50 mm CL) from the latest collection were dissected. A gonadal index was calculated as the ovary wet weight as a percentage of total body wet weight.

In an attempt to find a reliable non-destructive method to determine the onset of sexual maturity by morphological characters, the lengths of the longest intact appendage of the pair from the first and fifth legs (George and Morgan 1979), and the pleopodal exopodite were measured. For three groups—males, females <50 mm CL and females ≥50 mm CL—the length of each appendage was related to the CL. The relationships were tested for equality of slopes to determine differences between males and females and between sexually immature and mature females. Statistical analyses were made using a test for equality of slopes in regression analysis (Sokal and Rohlf 1981).

To estimate the number of eggs per spawn, eggs were removed from the eight pleopods of 15 females, dried on blotting paper for 1 min and weighed. The mean weight of a single egg was calculated by weighing a known number of eggs (15–50).

The number of eggs on the pleopod was then calculated by dividing the weight of the egg mass of each pleopod by the mean weight of a single egg. The sum of eggs on all eight pleopods provided the total number of eggs in the spawn.

**Results**

**Annual Reproductive Cycle**

Females collected from the coral reef at Dahab were in various reproductive stages (Fig. 1). In February, only 14·0% of females showed reproductive activity by carrying spermatophore. In May, all the collected females were reproductively active, carrying uneroded spermatophore or eggs, with 79·0% of them carrying both. In August, 97·2% of the collected females were reproductively active, but only 14·3% carried both eggs and uneroded spermatophore. In October, only 9·4% of the females carried eggs, 90·6% carrying neither eggs nor spermatophores.
Reproduction of *Panulirus penicillatus* from the Red Sea

![Graph showing reproductive state of *P. penicillatus* females](image)

Fig. 1. Reproductive state of *P. penicillatus* females $\geq 50$ mm CL (see 'Onset of Sexual Maturity' in Results) during each collection period from Dahab, Gulf of Elat (Aqaba), Red Sea, in 1986. White bars, females not carrying eggs or uneroded spermatophore; stippled bars, females carrying uneroded spermatophore only; striated bars, females carrying eggs only; solid bars, females carrying both eggs and uneroded spermatophore.

The gonadal index of females in captivity (Table 1) showed that ovarian development occurred in March. By April, the gonadal index was about 4 times its initial value. By September, it had decreased toward non-reproductive levels. By November, all ovaries were white and in a non-reproductive state (Stage 1 according to Junio 1987). In the non-reproductive season (November–February) the gonadal index averaged 0.57±0.18%, whereas during the reproductive season it increased to an average of 2.01±1.73%. The high standard deviation of the gonadal index during the reproductive season represents differences in reproductive state: some females carried spermatophores before spawning, and others that had already spawned were producing new eggs. In captivity, egg incubation measured for 11 females at temperatures of 24–27°C required 35.5±1.0 days. Most females in captivity spawned 2–4 times between February and September. Three out of 50 females collected in February 1986 (78.2, 79.3 and 93.4 mm CL) spawned 5 times during this period in captivity. These findings support the conclusion from field data (Fig. 1) that the reproductive season occurs from February to October and that females regularly spawn 2–4 times during this season.

<table>
<thead>
<tr>
<th>Table 1. Gonadal index of captive <em>Panulirus penicillatus</em> from Dahab, Gulf of Elat (Aqaba), Red Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gonad wet weight as a percentage of total body weight</td>
</tr>
<tr>
<td>Month</td>
</tr>
<tr>
<td>--------</td>
</tr>
<tr>
<td>February</td>
</tr>
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<td>March</td>
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<tr>
<td>April</td>
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<tr>
<td>December</td>
</tr>
<tr>
<td>January</td>
</tr>
</tbody>
</table>
Onset of Sexual Maturity

According to field observations, females <50 mm CL did not carry eggs or spermatophores. In the 51–60 mm CL size class, 94% of the females carried eggs or spermatophores when collected in May and August, the peak of the reproductive season (Table 2). In the larger size classes, 80–100% of the females were reproductively active.

<table>
<thead>
<tr>
<th>Size class (mm)</th>
<th>n</th>
<th>Reproductive females (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤50</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>51–60</td>
<td>31</td>
<td>94</td>
</tr>
<tr>
<td>61–70</td>
<td>34</td>
<td>97</td>
</tr>
<tr>
<td>71–80</td>
<td>21</td>
<td>100</td>
</tr>
<tr>
<td>81–90</td>
<td>11</td>
<td>100</td>
</tr>
<tr>
<td>91–100</td>
<td>6</td>
<td>100</td>
</tr>
<tr>
<td>≥100</td>
<td>5</td>
<td>80</td>
</tr>
</tbody>
</table>

Table 2. Percentage of *Panulirus penicillatus* females in reproductive state (carrying eggs and/or spermatophores) in samples collected in May and August 1986 from Dahab, Gulf of Elat (Aqaba), Red Sea

Fig. 2. The relationship between (A) the first limb length and carapace length and (B) the fifth limb length and carapace length, for males and females of *P. penicillatus* from Dahab, Gulf of Elat (Aqaba), Red Sea.

Analysis of the regression of CL v. first limb length and CL v. fifth limb length (Fig. 2) failed to produce a morphological index enabling distinction between immature and mature females as in the case of *P. versicolor* (George and Morgan 1979). The regression lines were constant for all sizes and no difference was found between females either under or above
50 mm CL. However, analysis of the regression of CL v. pleopodal exopodite length (PEL) showed different slopes for males, females <50 mm CL, and females >50 mm CL (Fig. 3). Since each of these three groups has a significantly different slope in this regression (Table 3), there seems to be an acceleration in growth of the pleopodal exopodite in females from about 37 to 54 mm CL, and a subsequent deceleration. From this point on, the slope of the regression between CL and PEL is constant and higher than the slope of this regression for males. As in Templeman (1935), George and Morgan (1979), and Jayakoby (1989), the inflection points in Fig. 3 were estimated by eye.

![Graph showing the relationship between pleopodal exopodite length and carapace length for males, females <50 mm CL, and females >50 mm CL.](image)

**Fig. 3.** The relationship between the pleopodal exopodite length and carapace length for males, females ≤50 mm CL and females ≥50 mm CL of *P. penicillatus* from Dahab, Gulf of Elat (Aqaba), Red Sea.

### Table 3. Significance of the differences between slopes in the regression between carapace length (CL) and pleopodal exopodite length (PEL), which represent different growth rates of the pleopodal exopodite in males, females <50 mm CL, and females >50 mm CL

<table>
<thead>
<tr>
<th>Test</th>
<th>$F_s$</th>
<th>d.f.</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males v. females &gt;50 mm CL</td>
<td>177.7</td>
<td>115</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Males v. females &lt;50 mm CL</td>
<td>158.5</td>
<td>60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Females &gt;50 mm CL v. females &lt;50 mm CL</td>
<td>36.4</td>
<td>89</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**Fecundity**

The fecundity of *P. penicillatus* is size dependent (Fig. 4). The relation between the number of eggs in each spawn ($E$) and CL of the female is described by the equation:

$$
E = 2.715 \times (CL)^{2.581}
$$

($n = 15$, $R^2 = 0.853$).
Loss of eggs during the incubation period was negligible or not observed at all.

The first pair of the pleopodal endopodites possessed 12.08 ± 2.24% of the eggs. The second, third and fourth pairs of pleopodal endopodites possessed 30.19 ± 1.38%, 30.65 ± 2.76% and 27.08 ± 2.68% of the eggs respectively.

Discussion

In *Panulirus penicillatus* from Dahab, there appears to be no reproductive activity from November to January, as indicated by the lack of females with spermatophores in October and the lack of females with eggs in February. Other populations of *P. penicillatus* in the Northern Hemisphere are actively reproductive throughout the year with an acceleration in the summer (Morris 1968; MacDonald 1979, 1988; Ebert and Ford 1986; Juniao 1987); this increase in reproductive activity in the summer is related to the increased water temperature. Unfortunately, recordings of water temperature in the sites studied are not available for comparison with those of the Red Sea. In the Gulf of Eilat (Aqaba), Red Sea, the surface water temperature ranges from 20 ± 2°C in the winter to 28 ± 2°C in the summer (Edwards 1987). Since the reproductive season of *P. penicillatus* in the Gulf of Eilat (Aqaba) occurs from February to the end of October, it is most likely that the factor that stimulates reproductive activity of mature *P. penicillatus* in this region is the increase in water temperature. A similar trend was suggested for *P. cygnus* (Chittleborough and Thomas 1969). The lack of reproductive activity in the winter at Dahab is attributable to low water temperatures which fell to 20 ± 2°C in December and January.

Between March and August, most of the females larger than 50 mm CL carried eggs and/or new spermatophores. The finding that a female can spawn immediately after the carried eggs have hatched suggests that the time needed for redevelopment of the ovary is not longer than the incubation period. A similar estimate was reached by Juniao (1987) in the Philippines. Since the incubation period is 35.5 ± 1.0 days, and captive females spawned
continuously up to five times during a season, *P. penicillatus* females could potentially do the same in the field. However, there are insufficient field data to estimate reliably the number of spawns per female in a year. Observations on females in captivity, together with the field data (Fig. 1), suggest that mature females spawn regularly 2-4 times a year in nature. The ability to spawn up to four times in a year was reported for *P. homarus* (Berry 1971) and for *P. penicillatus* (Junio 1987).

The minimum size at sexual maturation was 50 mm CL for *P. penicillatus* females from Dahab, as indicated by the field observations and by the morphometric examination of the relation between pleopodal exopodite length and CL. A similar result for the minimum size at sexual maturity of *P. penicillatus* females was reported by Junio (1987) in San Vicente, Cagayan, Philippines (45-49-5 mm CL), and by Ebert and Ford (1986) in Enewetak Atoll, Marshall Islands (62 mm CL). In other populations, females were reported to become sexually mature at a size as large as 100 and 98 mm CL at Palau and Oahu respectively (MacDonald 1979), and 69 mm CL in the Western Caroline Islands (MacDonald 1988). As minimum size at sexual maturity is a function of age (Fielder 1964), it is possible that *P. penicillatus* in the Gulf of Eilat grows more slowly than some other conspecific populations in the Indo-Pacific Ocean, as previously suggested (Plaut and Fishelson 1991).

Unlike other lobsters, palinurid lobsters produce a remarkably large number of eggs per spawn which is theoretically inversely correlated to the survival of the planktonic larvae (Aiken and Waddy 1980). Although the sample size is small, the relationship between CL and the number of eggs per spawn in females of *P. penicillatus* from Dahab is consistent with the data from conspecific populations in Enewetak Atoll (Ebert and Ford 1986), in San Vicente (Junio 1987) and in Palau, Western Caroline Islands (MacDonald 1988). This indicates that the relationship is constant in *P. penicillatus* over a wide range of environmental conditions.

The first pair of pleopodal exopodites carries only 12.08 ± 2.24% of the eggs, and each of the three posterior pairs of exopodites carries about 30% of the eggs. Since lobsters swim by moving the abdomen strongly towards the ventral part of the carapace, eggs on the anterior part of the abdomen are vulnerable to mechanical damage by the escape response. Location of the eggs on the exopodites enables free movement of the abdomen for swimming during the incubation period and possibly prevents damage to the eggs.

There is a high variability between distinct populations of *Panulirus penicillatus* in different parts of the geographical range in terms of the duration of the reproductive season and the minimum size at sexual maturity. One source of this variability may be the differences in water temperature between different sites. No significant variability was found in fecundity. The similarity in size at onset of sexual maturity between the *P. penicillatus* population in the Gulf of Eilat and in San Vicente, Cagayan, Philippines (Junio 1987) suggests that geographical isolation does not influence this aspect of reproductive biology for *P. penicillatus* in the Red Sea directly, and could be explained as a result of low growth rate as indicated by Plaut and Fishelson (1991).

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