Short Communication

Aust. J. Mar. Freshwater Res., 1991, **42**, 615–23

Occurrence and Influence of Bopyrid Parasites on Female Penaeid Prawns from Coastal Waters of Central Queensland (Australia)

A. J. Courtney

Queensland Department of Primary Industries, Southern Fisheries Research Centre, PO Box 76, Deception Bay, Qld 4508, Australia.

Abstract

The prevalence of bopyrid isopods, parasitic on penaeid prawn hosts, is recorded for the first time from a central Queensland prawn trawl fishery. The bopyrid parasite *Parapenaeon* prox. *expansus* has been recorded for the first time from the red spot king prawn, *Penaeus longistylus*, and the blue-legged king prawn, *Penaeus latisulcatus*. Previous unpublished reports of *Parapenaeon japonicum* parasitizing *P. longistylus* have also been substantiated. Parasite species were not randomly associated with all prawn species but rather were associated with a single prawn host species or species group. The factors that give rise to such specific host–parasite associations, particularly the host-selective behaviour of the parasite and the habitat preferences of the juvenile prawns, are discussed. Bopyrids had no significant effect on the weight of the prawns, but they did have a significant effect on ovary weight and histology, causing sterility in their hosts. High levels of infestation have been recorded from other fisheries (resulting in reduced spawning potential of the host population), but the low prevalence (0·32%) of bopyrid parasites in central Queensland prawns appears to be so low as not to present a concern at present.

Introduction

Bopyrid isopods are parasites that live in the gill chambers of their decapod crustacean hosts, and although they do not physically invade body tissues as adults, they sterilize their hosts. Studies pertaining to bopyrids have been warranted in the past because high infestation levels may threaten host population recruitment (Beck 1979; Owens and Glazebrook 1985; Mathews *et al.* 1988). The suppression of gonad development in host crustaceans, although still not fully understood, has been noted for most of the major decapod groups (Reinhard 1956) parasitized by epicarid isopods, but there has been little research specifically on the influence of bopyrid isopods on their penaeid prawn hosts.

The geographic distribution of the parasites and the prevalence of infestation can be used as biological markers, providing information on migratory behaviour and stock differentiation for host populations (Owens 1983, 1990; Mathews *et al.* 1988). In the eastern Gulf of Carpentaria, Owens (1983) noted that the distribution of infested banana prawns, *Penaeus merguiensis*, was restricted, suggesting limited or restricted mixing of the prawn stocks within the Gulf. Parasites occurred only in the southern region of the eastern Gulf and in salinities greater than or equal to 24. These results supported tagging studies (Lucas *et al.* 1979) showing that movement of adult prawns was limited to a maximum of 85 km. Both studies indicated that stocks of banana prawns in the eastern Gulf of Carpentaria were separate, with little or no migration between populations.

0067-1940/91/060615$05.00

Specific host–bopyrid associations and the prevalence and influence of parasites on individual hosts or host populations are largely unknown in Australian coastal waters. The most significant contribution to this area of research in Australia has been by Owens and Glazebrook (1985), but their work was largely restricted to the Gulf of Carpentaria and northern Australia. Although the Queensland prawn trawl fishery produces 7000–10 000 tonnes of prawns each year, published records on the occurrence of specific bopyrids from the east coast of Queensland are extremely rare. In a description of the zoogeography of prawn parasites from tropical Australian waters, Owens (1990) has used mostly unpublished reports of parasites for the Queensland section of the continent's coastline. The only specific reference to host–parasite associations from Queensland coastal waters was by Nearhos and Lester (1984), and they provided no information on the prevalence.

This short communication is an extension of studies on the reproductive biology and stock dynamics of prawns fished from the central Queensland coast (Courtney and Dredge 1988; Courtney *et al.* 1989; Dredge 1990). Its aim is to describe the prevalence, specific host–parasite associations, and effects the parasites have on their penaeid hosts in this region of Queensland's east coast.

Materials and Methods

Prawns were sampled during 24 consecutive lunar months at predetermined sites in the central region of Queensland's east coast (Fig. 1). Bottom trawl shots of 30 min duration were carried out at each site, using standard commercial trawling gear (Courtney and Dredge 1988). Each sampling trip lasted about 5 days and was planned to coincide with the new moon.

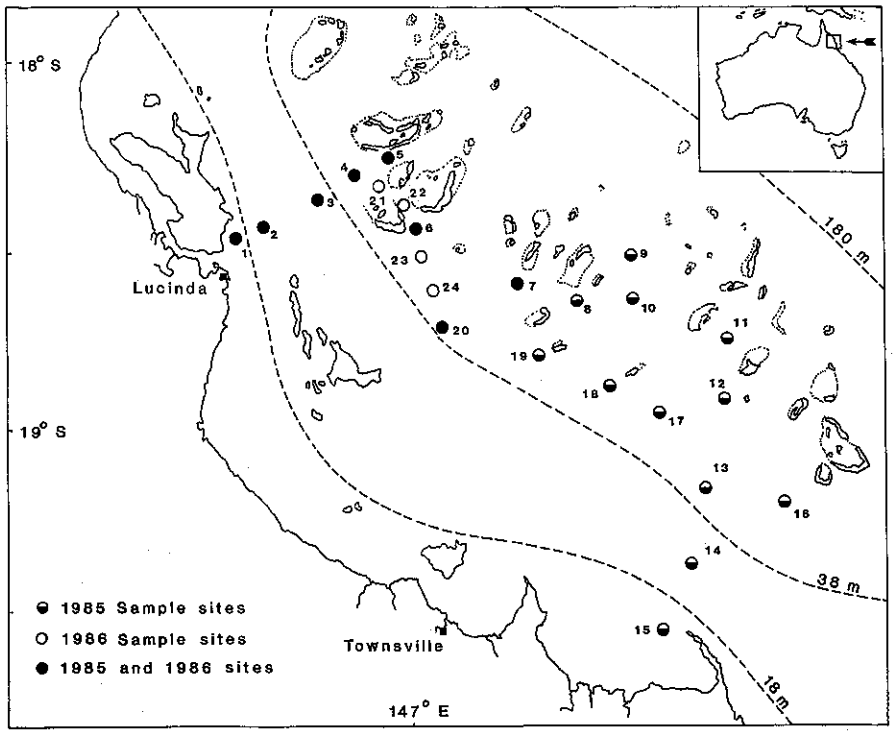

Fig. 1. Sampling sites in the central region of Queensland's east coast.

All penaeid prawns were sorted by species and sex, measured, and frozen on board. In the laboratory, subsamples of female prawns from each site were examined in detail. A maximum of 60 female prawns was examined from each site each month. Total body weight, ovary weight, and location and prevalence of bopyrid parasites were recorded. The effects of the parasites on relationships between host carapace length and body weight and between carapace length and ovary weight were determined statistically, using analysis of covariance (ANCOVA) (Sokal and Rohlf 1981). The histology of ovarian tissue from parasitized and nonparasitized female prawns was compared. Tissue sections were stained with haematoxylin and eosin, and ovary development was staged according to Tuma (1967) and Yano (1984, 1988).

Table 1. Total number of female prawns examined for each species and prevalence of bopyrid isopod infestation from Queensland's central east coast

Prawn species	Number examined	Number parasitized	Percentage parasitized
Penaeus esculentus	296	4	1·35
Penaeus semisulcatus	418	6	1·43
Penaeus longistylus	4042	10	0·24
Penaeus latisulcatus	1138	3	0·26
Metapenaeus endeavouri	613	0	0
Metapenaeus ensis	723	0	0
All species	7230	23	0·32

Table 2. Penaeid prawn species, prawn carapace length (CL), site trawled (see Fig. 1), and attached bopyrid isopod

Prawn species	CL (mm)	Site	Parasite
Penaeus esculentus	24·4	2	*Epipenaeon ingens*
	39·4	2	*Epipenaeon ingens*
	39·9	2	*Epipenaeon ingens*
Penaeus semisulcatus	34·3	1	*Epipenaeon ingens*
	35·3	15	*Epipenaeon ingens*
	38·9	15	*Epipenaeon ingens*
	40·2	15	*Epipenaeon ingens*
Penaeus longistylus	23·4	7	*Parapenaeon japonicum*
	25·4	4	*Parapenaeon* prox. *expansus*
	28·5	20	*Parapenaeon japonicum*
	30·5	7	*Parapenaeon japonicum*
	33·8	5	*Parapenaeon* prox. *expansus*
	38·2	3	*Parapenaeon japonicum*
	40·7	5	*Parapenaeon* prox. *expansus*
	40·8	5	*Parapenaeon japonicum*
	42·9	3	*Parapenaeon japonicum*
Penaeus latisulcatus	34·1	6	*Parapenaeon* prox. *expansus*
	47·9	4	*Parapenaeon* prox. *expansus*

Results

Over the 2-year period, 7254 female prawns were examined in detail. Six species made up 99% (7230) of the prawns examined, and of these 7230 female prawns, 23 (0·32%) were parasitized by bopyrid isopods (Table 1). Of these bopyrids, 18 were successfully removed, preserved in 4% (v/v) formaldehyde solution, and identified to species level (Table 2).

There was no significant difference (χ^2 tests) in infestation rates between the two tiger prawn species (*Penaeus esculentus* and *Penaeus semisulcatus*) or between the two king prawn species (*Penaeus longistylus* and *Penaeus latisulcatus*). However, there was a significant difference between the tiger prawn and king prawn groups ($P < 0{\cdot}05$), with the prevalence being about five times greater for tiger prawns. No *Metapenaeus endeavouri* or *Metapenaeus ensis* were parasitized.

ANCOVA revealed that parasitism did not significantly alter the carapace length–body weight relationship for three (*P. semisulcatus*, *P. longistylus* and *P. latisulcatus*) of the four infected prawn species. Generally, the coordinates for parasitized prawns fell very close to or on the normal length–weight regression line (Figs 2*a*–2*d*). Although there was no significant difference among adjusted means (*y*-intercept) for *P. esculentus*, there was a significant ($P < 0{\cdot}05$) difference among slopes, suggesting that parasitism did affect the body weight of this species. ANCOVA also indicated that the parasites had a significant ($P < 0{\cdot}05$) effect on the carapace length–ovary weight relationship; ovaries of parasitized females were relatively lighter in weight (Figs 3*a*–3*d*). These results were consistent for all species of prawns except *P. latisulcatus*, for which the sample size for parasitized females was too small to produce a carapace length–ovary weight regression. Nevertheless, ovaries from the two parasitized *P. latisulcatus* were much lighter than those from nonparasitized females of similar size (Fig. 3*d*).

The histology of ovaries from parasitized females also differed markedly from those of uninfected prawns. Although many of the infected females were larger than the minimum size required for maturation (Courtney and Dredge 1988; Courtney *et al.* 1989), none was

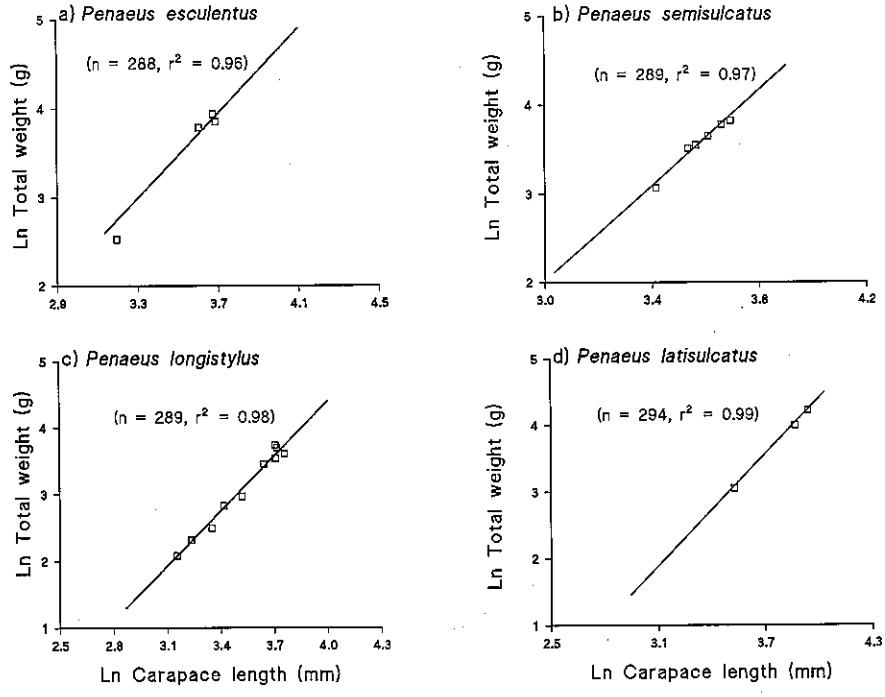

Fig. 2. Relationship between carapace length and total body weight for parasitized and nonparasitized female prawns from the Queensland central east coast fishery. ———, Regression for nonparasitized female prawns (*n*, number of observations; r^2, multiple coefficient of determination); □, coordinates for parasitized females.

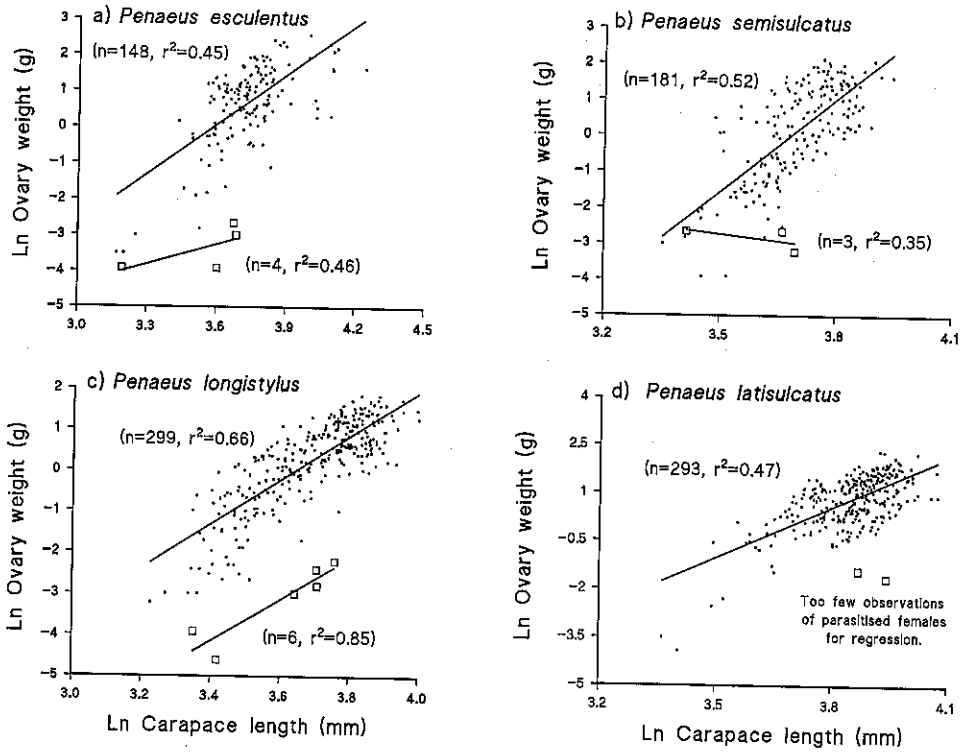

Fig. 3. Relationship between carapace length and ovary weight for (□) parasitized and (●) non-parasitized female prawns from the Queensland central east coast fishery. ———, Regressions for both groups (*n*, number of observations; r^2, multiple coefficient of determination).

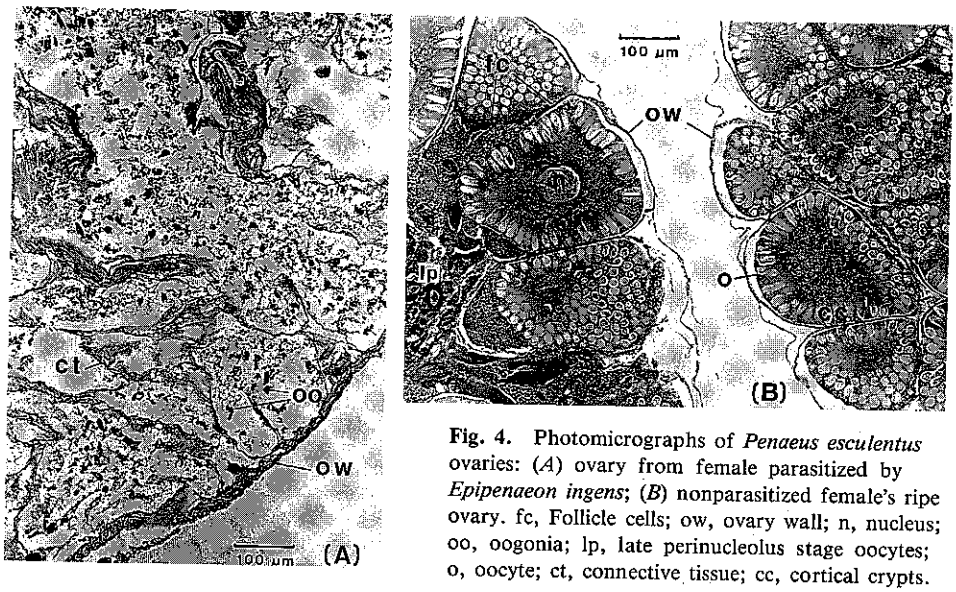

Fig. 4. Photomicrographs of *Penaeus esculentus* ovaries: (*A*) ovary from female parasitized by *Epipenaeon ingens*; (*B*) nonparasitized female's ripe ovary. fc, Follicle cells; ow, ovary wall; n, nucleus; oo, oogonia; lp, late perinucleolus stage oocytes; o, oocyte; ct, connective tissue; cc, cortical crypts.

found to have mature ovaries. Macroscopically, ovaries from parasitized females appeared pale and flaccid. Histological development (Fig. 4*A*) appeared to be suspended, with ovaries lacking developing oocytes. Connective tissue, which partitions the ovary into sections, was apparent, but egg development was halted at a very early stage and was not observed beyond the oogonia stage (Yano 1988). Generally, the internal structure of the ovary was vacuolated in appearance, with a complete absence of oil globules and yolk granules. Darkly staining follicle cells were scattered throughout the tissue. No vitellogenic, mature or ripe oocytes, which can be found in nonparasitized females (Fig. 4*B*), were observed in any of the infected prawns.

Discussion

Bourdon (1979) has described *Parapenaeon* prox. *expansus* parasitizing 'tiger prawns' in coastal waters near Darwin, northern Australia. This bopyrid is similar in appearance to both *P. expansus* and *P. secundum* but differs from them taxonomically on the morphology of its posterior lateral plates (Bourdon 1979). It has not been recorded previously from the king prawns *P. longistylus* and *P. latisulcatus*. This is also the first published record of *Parapenaeon japonicum* from Australian coastal waters and parasitizing the red spot king prawn, *P. longistylus*, although Owens (1987, 1990) has cited unpublished reports of this parasite from the north-eastern Queensland coast. All *P. japonicum* reported from Australian waters have been parasitizing only the king prawns *P. longistylus* or *P. latisulcatus* and have been found only from areas east or south-east of Torres Strait. *Parapenaeon japonicum* has been recorded previously on *Parapenaeopsis sculptilis* from the Gulf of Martaban (Bourdon 1979) and *P. latisulcatus* in the Sudanese Red Sea (Branford 1980).

Both the brown tiger prawn, *Penaeus esculentus*, and the grooved tiger prawn, *P. semisulcatus*, from the central Queensland coast were parasitized by a single bopyrid isopod, *Epipenaeon ingens*. This is the same, and only, parasite found infesting these two tiger prawn species in the Gulf of Carpentaria (Owens and Glazebrook 1985). *Epipenaeon ingens* has also been found on *P. semisulcatus* from the south-eastern Indian coast (Thomas 1977) and the Sudanese Red Sea (Branford 1980). Owens and Glazebrook (1985) suggested that such globally distributed (Grey *et al.* 1983) prawn species as *P. semisulcatus* may have introduced bopyrid parasites to endemic Australian prawns and that *E. ingens* is 'adapting' to the endemic brown tiger prawn, *P. esculentus*.

Epipenaeon ingens is one of only two bopyrid species that have been recorded previously from the Queensland coast. It was found on the grooved tiger prawn, *P. semisulcatus*, near Maryborough and on the banana prawn, *P. merguiensis*, in Rosslyn Bay (Nearhos and Lester 1984). The other bopyrid recorded by Nearhos and Lester (1984) was *Parapenaeon expansus* parasitizing the eastern king prawn, *Penaeus plebejus*, in Moreton Bay.

Infestation rates in the present study were highest (1·43%) for *P. semisulcatus*, which was also the most commonly parasitized species (at 2·9%) in the Gulf of Carpentaria (Owens and Glazebrook 1985). The infestation rate (1·35%) for *P. esculentus* was only slightly less than that for *P. semisulcatus* but was much higher than that found in the Gulf (0·0007%). Data from the present and other studies indicate that the blue endeavour prawn, *Metapenaeus endeavouri*, is far less subject to bopyrid parasitism than are other prawns. None of the 6923 *M. endeavouri* examined by Owens and Glazebrook (1985) was parasitized. Buckworth (unpublished data) also found a very low prevalence of bopyrid infestation for *M. endeavouri* in th western Gulf of Carpentaria. He examined 67 557 *M. endeavouri* and found a bopyrid infestation rate of only 0·006% (four prawns). This endemic prawn species contributes significantly to mixed prawn trawl fisheries in Torres Strait (Somers *et al.* 1987; Watson *et al.* 1990), on the north-eastern coast of Queensland (Coles *et al.* 1985), and in the western Gulf of Carpentaria (Buckworth 1989). On the basis of the limited number of observations dealing with bopyrid infestations in Australian coastal waters, it would appear that *M. endeavouri* is the least infested of the commercially significant endemic penaeids.

The present results and those of Owens and Glazebrook (1985) suggest that individual bopyrid species are not randomly associated with numerous prawn species but rather with individual prawn species or species groups. Although the underlying conditions that give rise to such specific host (or host group)–parasite relationships are still largely unknown, there is evidence that prawns are infected early in their life cycle as postlarvae or juveniles by the cryptoniscan larval stage of the isopod (Anderson 1975, 1990). Correlations between host and parasite sizes (Owens 1983; Abu-Hakima 1984) support this and suggest that both host and parasite grow concurrently.

Most juvenile penaeid prawns have specific habitat requirements (Young and Carpenter 1977; Coles and Lee Long 1985; Staples *et al.* 1985; Coles *et al.* 1987), and because infestation most likely occurs when the prawns are postlarvae or juveniles, it is likely that the infecting cryptoniscan larvae also occur in these nursery areas. The formation of host–parasite associations could be at least partly explained if the infecting larvae also displayed specific habitat preferences. At present, however, it is unknown whether bopyrid cryptoniscan larvae display such habitat preferences.

There is evidence that host–parasite associations are at least partly determined by the host-selective behaviour of the infecting cryptoniscan larvae. Anderson (1990) has shown under laboratory conditions, and others (Thomas 1977; Owens and Glazebrook 1985) have implied from field observations, that bopyrid cryptoniscan larvae display host-species selectivity. Alternative host species may be parasitized in the absence of a first-preference host species (Owens and Glazebrook 1985).

It is reasonable, although speculative, to assume that host–parasite associations are determined by a combination of host-species selectivity and habitat preference displayed by the infecting cryptoniscan larvae. Such a combination of factors would explain why the tiger prawns *P. esculentus* and *P. semisulcatus*, which co-inhabit coastal seagrass meadows as juveniles (Staples *et al.* 1985; Coles *et al.* 1987), were parasitized by the same bopyrid, *Epipenaeon ingens*, and why *E. ingens* was not associated with *P. longistylus*, which inhabits shallow reef platforms during its juvenile stage (Racek and Dall 1965; Coles *et al.* 1987). Similarly, such a combination of factors influencing selection would explain why *P. japonicum*, parasitic on *P. longistylus*, was not found parasitizing either of the tiger prawn species.

Although the parasites did not affect the body weight of most host species, there was a significant difference among the slopes for parasitized and nonparasitized *P. esculentus*. This significance was due to the influence from one of the four observations of parasitized *P. esculentus* (the small (Ln CL = 3·19) prawn in Fig. 2*a*). When the results for this individual were removed from the analysis, there was no longer a significant difference between slopes. Because the significance observed for *P. esculentus* was largely dependent on one observation and because the other species showed no significant effects on body weight, it is likely that the results for *P. esculentus* were due either to a single outlier coordinate or to an error in recording the length or weight of this single observation. If this was the case, then the data imply that the parasites have no significant effect on the carapace length–body weight relationship.

The results from the present study, based on measured changes to ovary weight and histology in infected females, support macroscopic observations (Tuma 1967; Thomas 1977) and other histological observations (Abu-Hakima 1984) suggesting that bopyrids sterilize their prawn hosts. The histology of ovary tissue from the infested females was similar to that described by Abu-Hakima (1984) for *P. semisulcatus* infected with *Epipenaeon elegans* in Kuwaiti waters. Oocytes in parasitized *P. semisulcatus* females from Kuwait were found to 'lie in a loose meshwork of connective tissue and scattered cells' (Abu-Hakima 1984, p. 57) and did not progress beyond previtellogenesis. Although the mechanism underlying sterilization in penaeids by boprids is still unknown, Abu-Hakima (1984) has suggested that it is by way of the parasite producing a factor (or factors) that act upon the host system, inhibiting maturation.

Mathews *et al.* (1988) studied the distribution of *P. semisulcatus* parasitized by *E. elegans* in Kuwaiti waters. They found that infestation rates peaked in April for both years of the study and that in some of the fishing grounds just outside Kuwait Bay, rates were as high as 37%. Owens and Glazebrook (1985) also found the prevalence of *E. ingens* on *P. semisulcatus* in northern Australian waters to be seasonal. Again, some areas were associated with particularly high rates of infestation (up to 30%), which would almost certainly have a deleterious effect on spawning potential in those particular areas. The seasonal variation in infestation levels in the present study cannot be determined because of the relatively small sample size of prawns each month. However, the overall infection rate for all species was only 0·32% and as such is unlikely to pose a threat to the spawning potential, future recruits, or populations of commercially important prawns in the Queensland fishery. Even the most frequently parasitized prawn, *P. semisulcatus*, was not infected with a frequency likely to threaten future recruitment.

Acknowledgments

All bopyrid specimens from this study have been lodged with the Queensland Museum (Accessions QM W17082 to QM W17099). Drs S. Nearhos and L. Owens helped identify the parasites, and Mr G. Smith aided with the photomicrographs. The work was funded mainly by the Australian Fishing Industry Research and Development Council.

References

Abu-Hakima, R. (1984). Preliminary observations on the effects of *Epipenaeon elegans* Chopra (Isopoda; Bopyridae) on reproduction of *Penaeus semisulcatus* de Haan (Decapoda; Penaeidae). *International Journal of Invertebrate Reproduction and Development* **7**, 51–62.

Anderson, G. (1975). Larval metabolism of the epicaridean isopod parasite *Probopyrus pandalicola* and metabolic effects of *P. pandalicola* on its copepod intermediate host *Acartia tonsa*. *Comparative Biochemistry and Physiology* **A50**, 745–51.

Anderson, G. (1990). Postinfection mortality of *Palaemontes* spp. (Decapoda: Palaemonidae) following experimental exposure to the bopyrid isopod *Probopyrus pandalicola* (Packard) (Isopoda: Epicaridea). *Journal of Crustacean Biology* **10**, 284–92.

Beck, J. T. (1979). Population interactions between a parasitic castrator, *Probopyrus pandalicola* (Isopoda: Bopyridae), and one of its freshwater shrimp hosts, *Palaemontes paludosus* (Decapoda: Caridea). *Parasitology* **79**, 431–49.

Bourdon, R. (1979). Sur le taxonomie et l'éthologie de quelques Orbionines. (Iospoda: Epicaridea). *Internationale Revue der Gesamten Hydrobiologie* **64**, 425–35.

Branford, J. R. (1980). Bopyrid parasites of penaeid shrimp from the Tokar Delta (Red Sea). In 'Proceedings of the Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical West Indian Ocean'. Vol. 11, pp. 275–9. (Red Sea and Gulf of Aden Environmental Programme: Jeddah.)

Buckworth, R. C. (1989). Movements and growth of tagged *Metapenaeus endeavouri* (Schmitt) 1926, in the western Gulf of Carpentaria. M.Sc. Thesis, University of New South Wales, Kensington, Australia.

Coles, R. G., and Lee Long, W. J. (1985). Juvenile prawn biology and distribution of seagrass prawn nursery grounds in the southeastern Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 55–60. (NPS2: Cleveland, Queensland.)

Coles, R. G., Lee Long, W. J., Mellors, J. E., and Goeden, G. B. (1985). An assessment of the 1985 Queensland east coast prawn trawling closure. Queensland Department of Primary Industries Information Series No. QI85023.

Coles, R. G., Lee Long, W. J., Squire, B. A., Squire, L. C., and Bibby, J. M. (1987). Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. *Australian Journal of Marine and Freshwater Research* **38**, 103–19.

Courtney, A. J., and Dredge, M. C. L. (1988). Female reproductive biology and spawning periodicity of two species of king prawns, *Penaeus longistylus* Kubo and *Penaeus latisulcatus* Kishinouye, from Queensland's east coast fishery. *Australian Journal of Marine and Freshwater Research* **39**, 729–41.

Courtney, A. J., Dredge, M. C. L., and Masel, J. M. (1989). Reproductive biology and spawning periodicity of endeavour shrimps *Metapenaeus endeavouri* (Schmitt, 1926) and *Metapenaeus ensis* (de Haan, 1850) from a central Queensland (Australia) fishery. *Asian Journal of Fisheries Science* **3**, 133–47.

Dredge, M. C. L. (1990). Movement, growth and natural mortality rate of the red spot king prawn, *Penaeus longistylus* Kubo, from the Great Barrier Reef lagoon. *Australian Journal of Marine and Freshwater Research* **41**, 399–410.

Grey, D. L., Dall, W., and Baker, A. (1983). 'A Guide to the Australian Penaeid Prawns.' (Northern Territory Department of Primary Production: Darwin.)

Lucas, C., Kirkwood, G., and Somers, I. (1979). An assessment of the stocks of banana prawns *Penaeus merguiensis* in the Gulf of Carpentaria. *Australian Journal of Marine and Freshwater Research* **30**, 639–52.

Mathews, C. P., El-Musa, M., Al-Hossaini, M., Samuel, M., and Abdul Ghaffar, A. R. (1988). Infestations of *Epipenaeon elegans* on *Penaeus semisulcatus* and their use as biological tags. *Journal of Crustacean Biology* **8**, 53–62.

Nearhos, S. P., and Lester, R. J. G. (1984). New records of Bopyridae (Crustacea: Isopoda: Epicaridea) from Queensland waters. *Memoirs of the Queensland Museum* **21**, 257–9.

Owens, L. (1983). Bopyrid parasite *Epipenaeon ingens* Nobili as a biological marker for the banana prawn, *Penaeus merguiensis* de Man. *Australian Journal of Marine and Freshwater Research* **34**, 477–81.

Owens, L. (1987). A checklist of metazoan parasites from Natantia (excluding the crustacean parasites of the Caridea). *Journal of Shellfish Research* **6**(2), 117–24.

Owens, L. (1990). Maricultural considerations of the zoogeography of parasites from prawns in tropical Australia. *Journal of Aquaculture in the Tropics* **5**, 35–41.

Owens, L., and Glazebrook, J. S. (1985). The biology of bopyrid isopods parasitic on commercial penaeid prawns in northern Australia. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 105–13. (NPS2: Cleveland, Queensland.)

Racek, A. A., and Dall, W. (1965). Littoral Penaeinae (Crustacea: Decapoda) from northern Australia, New Guinea, and adjacent waters. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, 2de Reeks* **56**, 1–116.

Reinhard, E. G. (1956). Parasitic castration of Crustacea. *Parasitology* **V**, 79–107.

Sokal, R. S., and Rohlf, F. J. (1981). Linear regression. In 'Biometry: The Principles and Practice of Statistics in Biological Research'. 2nd edn, pp. 454–560. (Freeman: New York.)

Somers, I. F., Poiner, I. R., and Harris, A. N. (1987). A study of the species composition and distribution of commercial penaeid prawns of Torres Strait. *Australian Journal of Marine and Freshwater Research* **38**, 47–61.

Staples, D. J., Vance, D. J., and Heales, D. S. (1985). Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 47–54. (NPS2: Cleveland, Queensland.)

Thomas, M. M. (1977). A new record of *Epipenaeon ingens* Nobili (Bopyridae, Isopoda) parasitic on *Penaeus semisulcatus* de Haan from Palk Bay and Gulf of Mannar. *Indian Journal of Fisheries* **24**(1–2), 258–61.

Tuma, D. J. (1967). A description of the development of primary and secondary sexual characteristics in the banana prawn, *Penaeus merguiensis* de Man (Crustacea: Decapoda: Penaeinae). *Australian Journal of Marine and Freshwater Research* **18**, 73–88.

Watson, R. A., Channells, P., and Blyth, P. J. (1990). Commercial prawn catches in Torres Strait. In 'Torres Strait Prawn Project: A Review of Research 1986–88'. (Ed. J. E. Mellors.) pp. 13–20. Queensland Department of Primary Industries Information Series No. QI190018.

Yano, I. (1984). Rematuration of spent kuruma prawn, *Penaeus japonicus*. *Aquaculture* **42**, 179–83.

Yano, I. (1988). Oocyte development in the kuruma prawn *Penaeus japonicus*. *Marine Biology (Berlin)* **99**, 547–53.

Young, P. C., and Carpenter, S. M. (1977). Recruitment of postlarval penaeid prawns to nursery areas in Moreton Bay, Queensland. *Australian Journal of Marine and Freshwater Research* **28**, 745–73.

Manuscript received 22 April 1991; revised and accepted 5 August 1991