

The ecology and feeding biology of two *Polydora* species (Polychaeta: Spionidae) found to ingest the embryos of host hermit crabs (Anomura: Decapoda) from the Philippines

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Abstract

The ecology and feeding biology of two shell-burrowing polydorids associated with hermit crabs from the Philippines were investigated. *Polydora umangivora* and *P. robi* were found in shells of 15 and 28 gastropod species, respectively, occupied by nine hermit crab species. *Polydora umangivora* constructs U-shaped burrows in the outer shell while *P. robi* constructs burrows in the apex of the shell, extending to an opening along the columella of the upper body whorls. *Polydora umangivora* and *P. robi* preyed upon the embryos of three and seven species, respectively, of diogenid hermit crabs collected in the field. In laboratory feeding trials, *P. robi* ingested up to 230 developing eggs and 70 embryos of *Calcinus gaimardii* over a 6-h period. The impact of embryo predation is more apparent in hermit crab species that produce small broods of eggs (*Paguristes runyanae*) than in species that produce large broods of eggs (*Calcinus gaimardii*). *Polydora robi* transports the embryos to the mouth by a combination of muscular and ciliary action of the palps; ingestion follows breakage of the attachment stalk between embryo and pleopod seta. Invertebrates known and suspected to feed on host hermit crab eggs are reviewed and the evolution of polydorid/hermit crab symbioses is discussed.

Key words: Annelida, egg predation, feeding, paguroid, reproduction, symbiosis, *Polydora*

INTRODUCTION

The polydorid polychaete genera *Dipolydora* and *Polydora* contain c. 70 species, of which 14 are known to burrow in gastropod shells occupied by paguroid hermit crabs (Blake & Evans, 1973; Read, 1975; Radashevsky, 1993; Blake, 1996; Martin & Britayev, 1998; Williams & Radashevsky, 1999; Williams, 2000, 2001a). While most polydorid–paguroid associations seem to be facultative, two polydorid species *Dipolydora commensalis* (Andrews, 1891) and *Polydora robi* (Williams, 2000) are obligate commensals of hermit crabs. The shared history of polydorids and hermit crabs is well documented in Pleistocene gastropod shells (Kern, Grimmer & Lister, 1974; Walker, 1988, 1989, 1992, 1995) and a significant amount of work has been completed on the systematics and shell-burrowing activity of polydorids (see Blake, 1996). However, limited research has been directed towards their ecological association with hermit crabs. The purpose of this paper is to provide data on the ecology and feeding biology of two recently described *Polydora* species associated with hermit crabs from the Philippines.

Hermit crabs are conspicuous and ecologically important scavengers of intertidal areas world-wide. Their adaptation to a life in empty gastropod shells has been studied in detail. Shell attributes such as type, weight, and size have been shown to affect the reproduction and development of hermit crabs (e.g. Fotheringham, 1976; Bertness, 1981; Elwood, Marks & Dick, 1995). In addition, shell availability limits hermit crab populations in certain areas (Kellogg, 1976) and may account for the coexistence of multiple hermit crab species in intertidal habitats (Abrams, 1980, 1981, 1987a,b; Gherardi & Nardone, 1997). Hermit crab symbionts found living on, within and burrowing into inhabited shells have been catalogued (Jensen & Bender, 1973; Stachowitsch, 1980; Hoberg, McGee & Feder, 1982; Karlson & Shenk, 1983; Walker, 1992; McDermott, 2001).

The burrowing activity of polydorids reduces the strength of shells occupied by hermit crabs and presumably exposes the hermit crabs to increased risk of predation (LaBarbera & Merz, 1992; Buckley & Ebersole, 1994). In addition to these detrimental effects, Williams (2000) reported that *P. robi* from the Indo-West Pacific ingests the embryos of host hermit crabs. *Polydora robi* occupies a burrow along the columella of gastropod shells similar to that of *Dipolydora commensalis*. Based on the similar burrow morphology and

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biology of the two species, Williams (2000) suggested that *D. commensalis* may also be an egg predator of host hermit crabs and questioned the commensal nature of the symbioses between some polydorids and host hermit crabs. The burrow morphology, feeding behaviour, and reproduction of *D. commensalis* have been investigated (Andrews, 1891; Hatfield, 1965; Blake, 1969; Radashevsky, 1989; Dauer, 1991; Williams & McDermott, 1997). More recently, Williams (2001a) described *Polydora umangivora*, the second polydorid known to ingest the embryos of host hermit crabs from the Philippines.

Polydorids exhibit a variety of feeding methods and have been characterized as suspension feeders, deposit feeders, and both suspension and deposit feeders (see Dauer, Maybury & Ewing, 1981; Williams & McDermott, 1997). These worms have been documented to switch from deposit feeding to suspension feeding mode in the presence of increasing fluid flow (Taghon, Nowell & Jumars, 1980; Bock & Miller, 1997; Qian & Chia, 1997). Various aspects of the feeding biology of spionids have been investigated partly because of their ecological and economic importance (Dorsett, 1961; Self & Jumars, 1978; Jumars, Roberts & Nowell, 1982; Dauer, 1983, 1984, 1985, 1991, 1997; Miller & Jumars, 1986; Muschenheim, 1987; Luckenbach, Huggett & Zobrist, 1988; Hentschel, 1996; Shimeta, 1996; Shimeta & Koehl, 1996; Qian & Chia, 1997; Williams & McDermott, 1997). The worms feed with a pair of peristomial palps containing a median ciliated groove (Dauer & Ewing, 1991). The palps are used to capture food particles and transport them to the mouth for ingestion via a combination of muscular movement and ciliary action of the palps (Qian & Chia, 1997; Williams & McDermott, 1997). Eight functional ciliary groups have been identified on the palps of spionids (Dauer, 1997; Worsaae, 2001). Palp morphology and environmental constraints (e.g. water velocity) can determine the ability of a polychaete to engage in a macrophagous, predatory mode of feeding documented in certain spionids (Dorsett, 1961; Jumars *et al.*, 1982; Williams & McDermott, 1997). In this way, feeding in polydorids can be modified or restricted by environmental and morphological factors.

According to Williams & McDermott (1997), one might expect differences between the feeding behaviour of shell-burrowing polydorids associated with hermit crabs and soft-bottom species due to the distinct habitats of these spionids. Burrow morphology and interactions with host hermit crabs may prevent these worms from feeding at the sediment–water interface. In addition to ecological differences, it is possible that a shared evolutionary history of hermit crabs and certain polydorids has resulted in a change in the feeding behaviour of these worm lineages. Although prevalence of polydorids in hermit crab shells ranges between 12% and 59% in those areas studied (Jensen & Bender, 1973; Stachowitsch, 1980; Walker, 1988; Dauer, 1991; Walker & Voight, 1994) their impacts on host hermit crabs remain largely unknown.

The objective of this paper is to explore aspects of the ecology and feeding biology of *P. umangivora* and *P. robi* from the Philippines. The prevalence of these worms from six provinces of the Philippines and their association with host hermit crab species and their gastropod shells is described. Clutch size of hermit crabs from these regions is calculated and the prevalence of egg predation by the worms is examined with reference to burrow morphology. The mechanics of feeding behaviour (embryo capture, transport, and ingestion) are studied and the results of feeding trials are presented to assess the potential impacts of *P. robi* on host hermit crab reproduction. The nature of the symbioses between polydorids and hermit crabs is discussed and current knowledge of egg predation by other invertebrate symbionts of hermit crabs is reviewed.

MATERIALS AND METHODS

Specimen collection and measurement

Hermit crabs inhabiting gastropod shells were collected by hand, shallow sub-tidally (< 5 m) in Bataan, Batangas, Oriental Mindoro, Aklan, Palawan, and Cebu provinces of the Philippines from June to August 1997 and January to April 1999 (Fig. 1). Hermit crabs were collected from multiple proximate sites within provinces; data from sites were pooled into provinces for analyses. Hermit crabs were either fixed *en masse* in the field (relaxation in 3% magnesium chloride followed by fixation in 10% formalin–seawater solution) or transported to the laboratory and isolated in divided plastic boxes until examination. Isolated hermit crabs were maintained in unfiltered, aerated seawater.

Gastropod shells were identified, measured (total and aperture length), and examined for external burrow openings of *P. umangivora* and *P. robi* ($n=1533$ shells examined). Hermit crabs were removed by cracking the gastropod shells in a mortar and pestle constructed of a galvanized steel pipe (60 mm diameter), which allowed for the containment of shell fragments and associated organisms. Hermit crabs were then identified, sexed, and examined for eggs and parasites. Shield length (rostrum to medial, posterior end of carapace) of the hermit crabs was measured to 0.1 mm using callipers. To determine clutch size, all eggs removed from the pleopods of ovigerous hermit crabs were counted individually under a dissecting microscope. Linear regression analysis was used to examine the relationship between hermit crab size (shield length) and clutch size; single sample *t*-tests were used to test the null hypothesis that the linear relationship of clutch size on shield length was not of predictive value. Analysis of covariance (ANCOVA) was used to test the null hypothesis that there was no difference in clutch size between hermit crabs with and without polydorids after adjusting for shield length. The length and width of hermit crab eggs and embryos were measured from drawing tube sketches; the volume (mm^3) was calculated by the

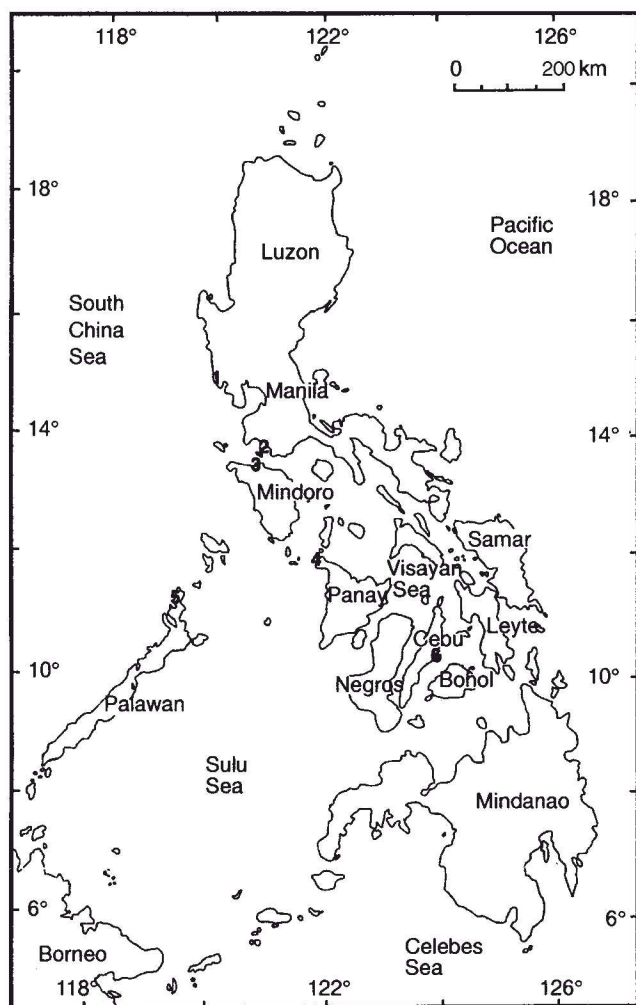


Fig. 1. Map of the Philippines with six provinces indicated in the text: 1, Bataan; 2, Batangas; 3, Oriental Mindoro; 4, Aklan; 5, Palawan; 6, Cebu.

formula $1/6 \pi I^3$ (where I is the mean of the length and width of the eggs or embryos).

The prevalence (percentage of shells infested) and intensity (number of worms/shell) of *P. umangivora* and *P. robi* were calculated after examination of cracked shells. Two-group χ^2 analyses were completed to test for significant deviation from expected values of *P. umangivora* and *P. robi* among sites, hermit crab species, and gastropod shell families. Two-group χ^2 analyses were also used to analyse distribution of hermit crab species and gastropod shells between sites. The null hypotheses in all χ^2 analyses predicted that expected values (e.g. prevalence) were equal among hermit crabs, shells, and sites. A paired *t*-test was used to determine if the difference in mean prevalence of *P. robi* versus *P. umangivora* among the 6 provinces was significant.

Feeding behaviour and trials

After cracking the gastropod shells, *P. robi* were isolated from their natural burrows (by pipetting a

stream of seawater through the opening in the apex) and placed in glass capillary tubes (10–25 mm long, open at both ends; inside diameter between 0.9 and 1.1 mm). Total length and palp length of the worms were measured to 0.1 mm using an ocular micrometer or from drawing tube sketches. The total number of segments of these worms was also recorded and linear regression analysis was used to examine the relation between worm length and number of segments. The worms were maintained at room temperature ($\sim 27^\circ\text{C}$) in 20 ml of artificial seawater (Tropic MarinTM, salinity $\sim 32\text{‰}$) in plastic Petri dishes. The seawater was completely refreshed every 24 h and worms were fed TetraTM fish food (crushed morsels or baby fish food) c. every 48 h. Only worms that exhibited normal feeding and tube maintenance (construction of mucous tube at end of glass tube) were used in the feeding experiments. Worms were not fed 48 h before feeding experiments to ensure that their guts were free of food. The length of *P. robi* specimens used in the feeding trials was $5.1\text{--}30.4$ mm (mean = 12.9 ± 6.0 mm, $n=17$); palp lengths, $1.1\text{--}4.6$ mm (mean = 2.6 ± 1.0 , $n=17$); number of segments, $37\text{--}171$ (mean = 83 ± 32 , $n=17$).

Observations of *P. robi* ingesting embryos *in situ* (attached to the pleopods of hermit crabs) were completed to document the feeding behaviour of the worms. Ovigerous hermit crabs (*Calcinus latens*) removed from their shells were held by the carapace with forceps allowing free movement of abdomen and pleopods with attached embryos. The hermit crab and attached embryos were then positioned within the feeding radius (see Williams & McDermott, 1997) of worms isolated in capillary tubes. Feeding behaviour of 11 worms was examined under a dissecting microscope for 5- to 10-min intervals. The sequence of embryo contact, capture, transfer, and ingestion by the worms was examined and reconstructed from drawing tube sketches.

Additional feeding trials were completed to document maximal number of embryos ingested by isolated worms in a 6-h period. For this work, embryos were removed from the pleopods of ovigerous hermit crabs *Calcinus gaimardii* with forceps and isolated from the pleopod setae in a dish of artificial seawater. The embryos (initially 35–50 embryos) were added within the feeding radius of 17 isolated worms and maintained at room temperature ($\sim 27^\circ\text{C}$) and ambient light for a 6-h period. The worms were examined every hour and additional embryos were added as needed. Following the 6-h feeding trial, uningested embryos were removed via pipette to determine the number of embryos ingested per worm. A second feeding trial used developing eggs dissected from the abdomen of *C. gaimardii* but in all other aspects replicated the first trial. Linear regression analysis was used to examine the relationship between the number of embryos ingested and size (total segments) of the worms. A paired *t*-test was used to determine if the difference in mean number of eggs vs embryos ingested was significant.

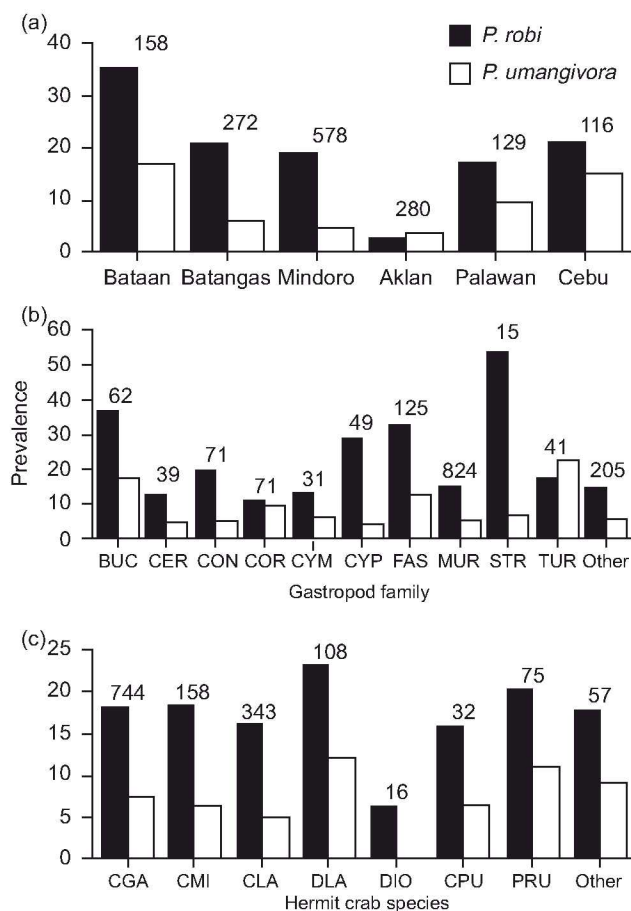


Fig. 2. Prevalence of *Polydora umangivora* (white bars) and *Polydora robi* (black bars) infestation among provinces, gastropod shells, and hermit crabs in the Philippines. (a) Provinces; (b) gastropod families; abbreviations as Appendix 1; Other, unidentified shells or shells represented by ≤ 5 specimens; number of shells given above bars. (c) Hermit crabs; abbreviations as in Appendix 2; Other, unidentified hermit crabs or hermit crabs represented by ≤ 5 specimens; number of hermit crabs examined given above bars.

RESULTS

Ecology of *Polydora umangivora* and *Polydora robi*

No significant difference in prevalence of *P. umangivora* and *P. robi* was found between the 1997 and 1999 samples, therefore the data were pooled to determine prevalence rates for the six provinces (Fig. 2a). The prevalence of *P. umangivora* ranged from 3.6% to 17.1% while *P. robi* ranged from 2.5% to 35.4%; for both species it was highest in Bataan and lowest in Aklan. Over the six provinces, the prevalence of *P. robi* was significantly higher than that of *P. umangivora* ($t = -3.44$, $P < 0.018$, d.f. = 5) (Fig. 2a). The prevalence was significantly different from expected values between provinces for both *P. umangivora* (d.f. = 5, $\chi^2 = 45.18$, $P < 0.0001$, $n = 1533$) and *P. robi* (d.f. = 5, $\chi^2 = 80.68$, $P < 0.0001$, $n = 1533$).

Table 1. Gastropod shell families and hermit crab species distributions among six provinces of the Philippines. Percentage of shells and hermit crabs collected at each province provided; the total number of shells and hermit crabs examined given in parentheses. Abbreviation of shell family names and hermit crab species given in Appendices 1 & 2; Other, unidentified gastropod shells and hermit crabs or those represented by ≤ 5 specimens

	Province					
	Bataan (158)	Batangas (272)	Mindoro (578)	Aklan (280)	Palawan (129)	Cebu (116)
Shells						
BUC	21.5	1.5	0	5.7	0.8	6
CER	1.3	0.7	1.9	1.1	14.7	1.7
CON	1.9	4	2.9	10	4.7	5.2
COR	3.8	2.6	4	12.5	0	0
CYM	1.9	4.8	1.6	1.8	0.8	0
CYP	14.6	3.3	1	2.5	0	3.5
FAS	17.7	9.6	6.8	3.2	8.5	10.3
MUR	24.7	62.5	66.4	48.8	47.3	29.3
STR	0	0	0.9	1.1	1.6	4.3
TUR	3.2	1.5	2.6	1.4	0	11.2
Other	9.5	9.6	11.9	11.8	21.7	28.5
Hermits						
CGA	76	28.7	63.7	55.4	7	12.1
CLA	1.9	30.2	20.1	33.6	10.1	30.2
CMI	15.8	8.5	13.7	9.3	1.6	2.6
DLA	4.4	25	0.9	1.8	5.4	13.8
DIO	0	0	0	0	0	13.8
CPU	0	3.3	0.5	0	1.6	15.5
PRU	0	0	0	0	58.1	0
Other	1.9	4.4	1.2	0	16.3	12.1

Polydora umangivora and *P. robi* were found in 15 and 28 species of gastropod shells, respectively (Appendix 1). The prevalence of *P. umangivora* in shell families ranged from 4.1% to 22% while *P. robi* ranged from 11.3% to 53.3% (Fig. 2b); both species exhibited a statistical difference from the expected distribution among shell species (*P. umangivora*: d.f. = 10, $\chi^2 = 37.27$, $P < 0.0001$; *P. robi*: d.f. = 10, $\chi^2 = 61.57$, $P < 0.0001$). Gastropod shells of the family Muricidae dominated all sites examined, composing 24.7–66.4% of the shells collected (Table 1).

Polydora umangivora and *P. robi* were both found associated with nine species of hermit crabs (Appendix 2). The prevalence of *P. umangivora* with these crabs ranged from 5% to 12% while *P. robi* ranged from 6.3% to 23.2%; neither species exhibited a statistical difference from the predicted distribution among hermit crab species (d.f. = 7, $\chi^2 = 4.65$, $P < 0.7022$; d.f. = 7, $\chi^2 = 9.46$, $P < 0.2213$) (Fig. 2c). *Calcinus gaimardii* was the most abundant hermit crab species found, on average composing 48.5% of the hermit crabs collected at each site (Table 1). *Paguristes runyanae* was only found in Palawan where the species composed 58.1% of those hermit crabs collected (Table 1). The pattern of gastropod shell use by hermit crabs generally followed the distribution of shells among the six sites, with muricids composing 32.4–76.6% of the shells inhabited by the five most common hermit crabs.

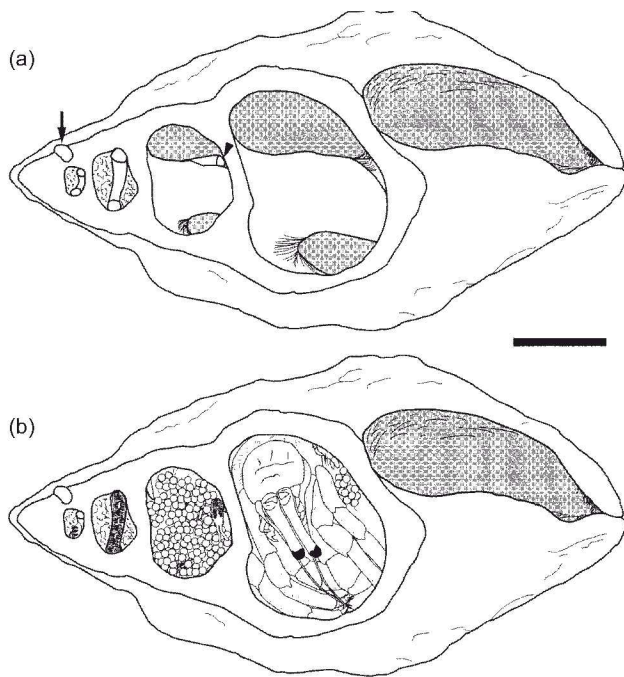


Fig. 3. Burrow morphology of *Polydora robi* in *Drupella cornus* shell. Shell sectioned longitudinally to show lumen (shaded area) of shell. (a) Shell with hermit crab and worm removed, showing burrow with opening at apex (arrow) and along columella of upper body whorl (arrowhead); (b) shell inhabited by ovigerous *Calcinus gaimardii*, showing *Polydora robi* extended from the burrow opening along columella among the embryos of the host hermit crab. Scale = 5 mm.

Burrow morphology of *Polydora umangivora* and *Polydora robi*

Polydora umangivora forms U-shaped burrows typical of other well-known members of the genus (e.g. *P. websteri*). The burrows are found in a variety of areas, particularly in the area surrounding the aperture and in the columella near the siphonal canal. A mean number of 1.6 ± 1.6 worms were found per shell ($n = 205$ shells examined). Fifteen shells were occupied by greater than two worms per shell, the maximum number of worms found in one shell was 10.

Polydora robi occupies burrows that extend from an opening in the apex of the shell, and wind around the columella to an opening in the lumen of the shell (Fig. 3a). The worm forms a tube of detrital material and effectively blocks off the upper lumen of the shell, leaving only the tube ending open. The worm can project from the burrow opening along the columella and contact the embryos of the hermit crab when it is fully or partially retracted in the shell (Fig. 3b). Worms reverse direction in their burrows and suspension feed by extending their palps from the opening at the apex.

Polydora robi was found in the apex of 85% of inhabited shells (246 of 290 shells examined), the additional 15% were usually observed in the outer or inner lips surrounding the aperture. A mean number of 1.1 ± 0.4 worms was found per shell ($n = 281$ shells

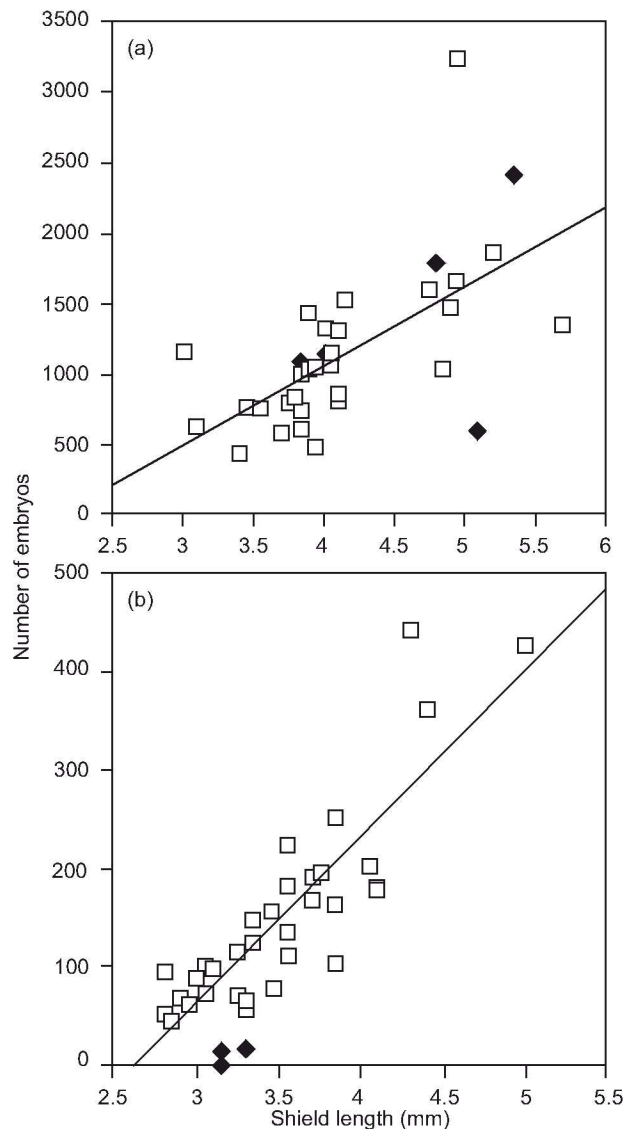


Fig. 4. Reproduction of *Calcinus gaimardii* and *Paguristes runyanae*. Open squares, hermit crabs free of *Polydora* spp.; black diamonds, hermit crabs which had embryos removed by *Polydora* spp. (a) Relationship between shield length and numbers of embryos in broods of *Calcinus gaimardii* collected from January to April 1999. (b) Relationship between shield length and numbers of embryos in broods of *Paguristes runyanae* collected from January to April 1999. Regression lines shown for hermit crabs without *Polydora* spp. only; for regression equations see Table 2.

examined). When two worms were found, typically one large female was accompanied by a smaller specimen. In three instances, more than two worms were found per shell, with a maximum of five worms being found in one shell.

Reproduction of host hermit crabs and occurrence of egg predation

A summary of the clutch sizes of four hermit crab species collected in the Philippines is provided in Table 2. Early

Table 2. Clutch size of ovigerous hermit crabs collected from the Philippines from January to April 1999. Mean shield length (SL) and mean number of embryos per brood of hermit crabs without *Polydora* spp. or with *Polydora* spp. present (P) and ingesting embryos. n = sample size

Species	n	Ovigerous crabs SL (mm) \pm SD	Embryos \pm SD	Regression equation	r^2	P -value
<i>Calcinus gaimardii</i>	31	4.1 \pm 0.6	1115 \pm 536	$y = 554.60x - 1152.26$	0.39	< 0.01
P	6	4.5 \pm 0.7	1295 \pm 682	$y = 541.60x - 1132.84$	0.29	0.27
<i>Calcinus minutus</i>	4	3.4 \pm 0.6	747 \pm 330	$y = 464.25x - 843.07$	0.67	0.17
P	5	2.9 \pm 0.7	536 \pm 350	$y = 371.68x - 549.29$	0.58	0.13
<i>Calcinus latens</i>	5	2.7 \pm 0.6	571 \pm 190	$y = 247.52x - 104.53$	0.54	0.15
P	4	3.6 \pm 1.1	1248 \pm 499	$y = 303.42x - 166.55$	0.44	0.34
<i>Paguristes runyanae</i>	34	3.5 \pm 0.5	153 \pm 100	$y = 164.35x - 425.76$	0.73	< 0.01
P	3	3.2 \pm 0.1	11 \pm 10	$y = 73.33x - 224.00$	0.45	0.53

Table 3. Sizes of developing eggs and embryos of *Calcinus gaimardii* and *Paguristes runyanae* collected from the Philippines. Mean length, mean width, and volume of developing eggs (DE) dissected from the abdomen and embryos (EM) attached to the pleopods. n = sample size

Egg size Species	Stage	n	Length (mm) \pm SD	Width (mm) \pm SD	Volume (mm ³)
<i>Calcinus gaimardii</i>	DE	24	0.41 \pm 0.02	0.38 \pm 0.02	0.033 \pm 0.004
<i>Calcinus gaimardii</i>	EM	25	0.46 \pm 0.02	0.41 \pm 0.01	0.044 \pm 0.004
<i>Paguristes runyanae</i>	EM	50	0.68 \pm 0.03	0.54 \pm 0.03	0.120 \pm 0.015

in this study it was found that boring acrothoracican barnacles of the family Trypetesidae also ingest the eggs of host hermit crabs (Williams, 1999). Therefore, their presence in the shells of hermit crabs was recorded and clutch size of hermit crabs with trypetesids were removed from the present analyses. A significant positive correlation was found between the clutch size of *C. gaimardii* without the presence of polydorid egg predators and shield length (Fig. 4a, Table 2). There was no significant difference in clutch size between hermit crabs with and without egg predation by polydorids (ANCOVA: F -ratio = 0.034, P = 0.855). Recently deposited embryos of *C. gaimardii* are slightly ellipsoid with a total volume of 0.044 mm³ (Table 3).

The clutch size of *Paguristes runyanae* was also significantly positively correlated with shield length (Fig. 4b, Table 2). Three hermit crabs in this population were associated with *Polydora umangivora* and the worms were found with host hermit crab embryos in their guts. The worms had reduced the clutch sizes to 18, 14, and 0 embryos (Fig. 4b). Based on shield length of the hermit crabs (3.3, 3.15, and 3.15 mm) and the regression equation, their clutch sizes would be predicted to be 114, 89, and 89 embryos. There was a significant difference in clutch size between hermit crabs with and without egg predation by polydorids (ANOVA: F -ratio = 7.47, P = 0.01). Recently deposited embryos of *Paguristes runyanae* are ellipsoid with a volume of 0.12 mm³ (Table 3).

In total, *Polydora umangivora* was found to ingest the embryos of *C. gaimardii*, *Dardanus lagopodes*, and *Paguristes runyanae* while *Polydora robi* was found to ingest the embryos of *C. gaimardii*, *C. latens*, *C. minutus*, *C. pulcher*, *Clibanarius cruentatus*, *C. englaurus*, and *D. lagopodes*.

Feeding behaviour of *Polydora robi*

In the presence of ground fish food, *P. robi* moved to the capillary tube opening and exhibited an increase in the rate of palp movement. Worms were often found with their anterior body segments (~ 5–10 segments) and palps extended beyond the tube opening while feeding. The palps moved through the water and along the bottom of the Petri dishes, contacted food particles and transported them to the mouth for ingestion by a combination of ciliary and muscular action. After ingestion of all deposited particles, palps were irregularly lashed through the water and along the bottom before the worms withdrew into the capillary tubes.

The main components of the feeding mechanics of *P. robi* on host hermit crab embryos are shown in Fig. 5. After placement of the pleopods and attached embryos within the feeding radius of the worms, the palps of the worms usually extended from the tube within 1 min (Fig. 5a). Contact with the embryos resulted in the worm either withdrawing into the tube or immediately beginning the feeding process (Fig. 5b). Feeding was initiated by orientation of the palps to top or sides of the embryos, allowing contact between the embryo surface and the oral groove of the palps. A combination of ciliary action along the oral groove and muscular manipulation by the palps was utilized to transport the embryos to the mouth as the worm advanced from the tube opening (Fig. 5b, c). The palps of the worms were observed to wind around the embryo. Typically both palps were used to transport a single embryo to the mouth, although on occasion multiple embryos were also transported. During transport, worms often extended further from the tube opening toward the embryo. After transport to the mouth, the

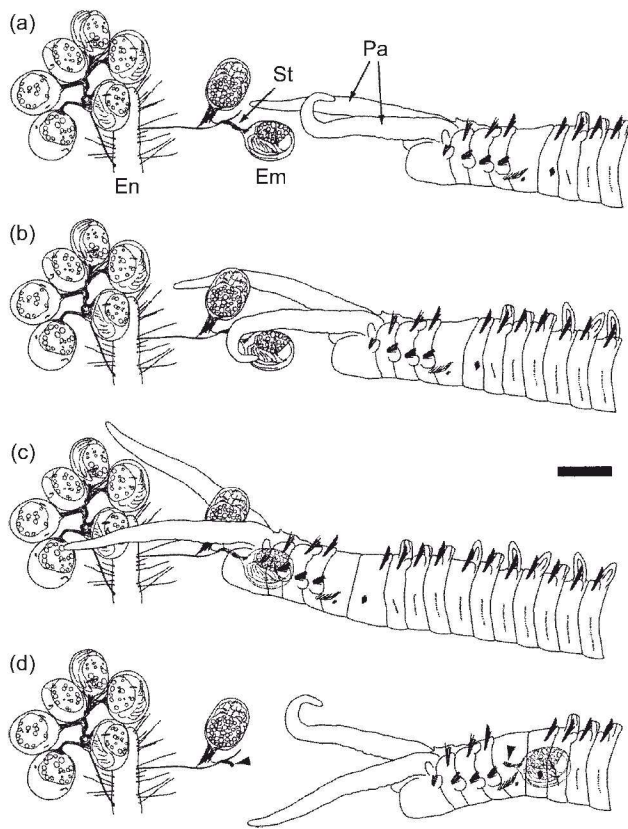


Fig. 5. *Polydora robi* predation on embryos of *Calcinus latens* in lateral view. Endopod (En) of *C. latens* with embryos (Em) attached to pleopod hairs via attachment stalks (St); many embryos have been removed to see details of the feeding behaviour. (a) Pre-contact of embryo, palps (Pa) extended; (b) contact and transport of the embryo by ciliary and muscular action of the palps; (c) engulfment of embryo (note: attachment stalk is still intact); (d) ingestion of the embryo following breakage of the attachment stalk (arrowheads, ends of broken stalk). Arching of the anterior body segments. Scale = 500 µm.

embryos were engulfed by the lateral lips of the mouth and partially ingested into the pharynx (Fig. 5c). The attachment stalk between embryo and pleopod seta of the hermit crab remained unbroken as ingestion progressed. Breakage of the attachment stalk occurred as the worms moved away from the pleopod and partially withdrew in the tube. The attachment stalks were observed to break both at the embryo surface and across the stalk. Following breakage of the stalk, the embryos were fully ingested and transported down the digestive tract (Fig. 5d). Arching of anterior body segments (segments 1–8) was observed as the embryo moved down the anterior portion of the digestive tract. The abdomens of the hermit crabs were not observed to move in response to the removal of embryos from their pleopods. After a feeding event, worms would partially withdraw into their burrows or immediately resume feeding. The feeding sequence required 1–4 min from time of contact to embryo ingestion.

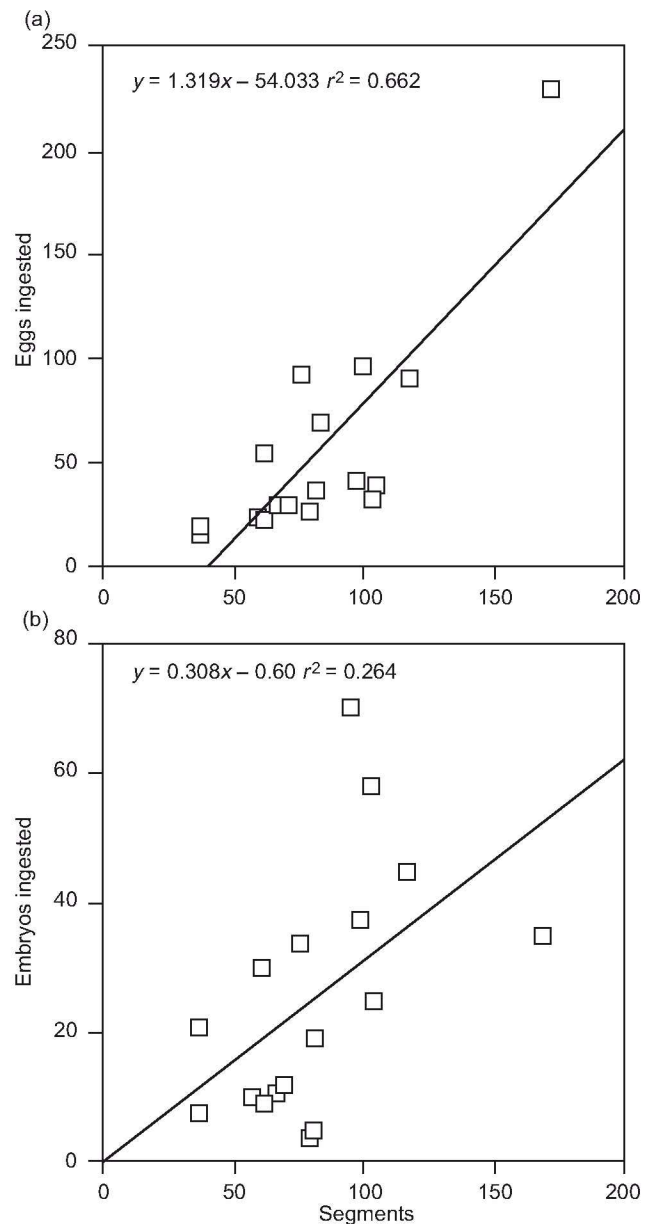


Fig. 6. Results of laboratory feeding trials of *Polydora robi* on developing eggs and embryos of *Calcinus gaimardii*. Relationship between size of *Polydora robi* in total number of segments and: (a) numbers of developing eggs ingested (the positive relationship between segments and number of developing eggs ingested is significant ($t = 5.42$, $P = 0.001$, d.f. = 15)); (b) numbers of embryos ingested (the positive relationship between segments and number of embryos ingested is significant ($t = 2.32$, $P = 0.025$, d.f. = 15)). See Table 3 for sizes of eggs and embryos of *Calcinus gaimardii*.

Feeding on hermit crab eggs and embryos

The two feeding trials using *Calcinus gaimardii* eggs and embryos revealed that all worms ingested both eggs and embryos. A significant correlation was found between length and number of segments of worms used in feeding trials ($y = 4.95 + 20.6x$, $r^2 = 0.81$, $t = 7.49$,

$P < 0.01$, d.f. = 15). The range of eggs ingested was 16–230 (mean = 55.6 ± 52 , $n = 17$) (Fig. 6a), while the range of embryos ingested was 4–70 (mean = 25.5 ± 19.2 , $n = 17$) (Fig. 6b). A significant positive relationship was found between both numbers of eggs and embryos ingested compared to worm size (Fig. 6a, b). The number of eggs ingested was significantly greater than the number of embryos ($t = -2.52$, $P = 0.0227$, d.f. = 16). The worms deposited orange faecal pellets 6–12 h after feeding. The yolk content of the ingested eggs and embryos was visibly reduced and these eggs and embryos were not viable.

DISCUSSION

Polydora umangivora and *P. robi* are widely distributed in the Philippines and both species are associated with a variety of hermit crab and gastropod shell species. The gastropod shells utilized differed greatly in morphology from high-spined shells (e.g. *Drupella cornus*) to low-spined shells (e.g. *Conus* sp.) and cowries (*Cypraea* sp.) (Appendix 1, Fig. 2b). The prevalence of the worms reached high percentages (17% and 35% for *P. umangivora* and *P. robi*, respectively) in some provinces; samples from all provinces yielded both species. *Polydora umangivora* and *P. robi* were documented to ingest the embryos of three and seven hermit crab species, respectively, collected in the field. However, the worms have been found associated with nine hermit crab species and it is likely that they also ingest the eggs of these and additional hermit crab species.

Loss of eggs and embryos during oviposition and brooding has been documented in hermit crabs and other decapod crustaceans (Kuris, 1991). The present study showed that *P. robi* is able to remove the embryos attached to the pleopods of hermit crabs by breaking the attachment stalk. In addition, it is possible that these worms ingest embryos detached from pleopod setae by natural mechanical loss later in embryogenesis. Embryos in both the early (composed of ~80% yolk) and late stages of development (exhibiting eye pigmentation) have been found ingested by the worms. Hermit crab eggs may also be susceptible to polydorid predation as they are extruded from the gonopores during oviposition. Feeding trials indicate that *P. robi* is able to ingest large numbers of eggs at this stage (a maximum of 230 eggs in 6 h). Further behavioural studies of worms feeding in their natural burrows are required. Video-endoscopy techniques, used to examine particle processing inside bivalve species (Ward, 1996), could be adapted to examine the feeding of polydorids *in situ*. It is unknown how the worms are able to detect the presence of embryos. Dauer (1991) suggested that the papillae covering the palps of *Dipolydora commensalis* are sensory. The presumed sensory papillae and nuchal organs of *P. umangivora* and *P. robi* could allow for the detection of hermit crab embryos.

Fotheringham (1976) found that a variety of commensal species may have detrimental effects on the

clutch size of host hermit crabs as a result of embryo predation or competition for internal shell space. In feeding experiments, he showed that nine commensal species (polychaetes, gastropods, hydroids, and crustaceans) associated with hermit crabs from Texas were able to feed on eggs or embryos removed from hermit crabs and isolated in cups. Under natural conditions *Nereis fucata* Savigny, a non-burrowing commensal polychaete, and the cnidarians *Adamsia palliata* (Müller) and *Podocoryne carnea* (Sars) have been found to ingest the embryos of *Pagurus prideauxi* Leach and *Pagurus bernhardus* (Linné) (Matthews, 1959; Goerke, 1971). Cerrano *et al.* (1998) showed that *Podocoryne carnea* also ingests the recently released larvae of *Diogenes pugilator* (Roux). The cnidarian *Hydractinia echinata* (Fleming) has been found to ingest the embryos of *Pagurus bernhardus* (Christensen, 1967).

Hermit crab egg predation was shown in the turbellarian flatworm *Stylochus zebra* Verrill, which ingests the embryos of *Pagurus pollicaris* (Lytwyn, 1979). In the Philippines a large unidentified flatworm is found in the apex of gastropod shells inhabited by hermit crabs (J. D. Williams, pers. obs.). The species represents another unidentified egg predator as evidenced by the purple colour of the gut, the same colour as host hermit crab eggs (this phenomenon was documented in *Stylochus zebra*: Lytwyn, 1979). *Dipolydora commensalis* has been found to ingest the embryos of *Pagurus longicarpus* Say from Rhode Island (J. D. Williams, pers. obs.) although McDermott (1999) reported no effect of the polychaete on the brood size of *P. longicarpus* from New Jersey. Finally, an unidentified acrothoracican boring barnacle of the genus *Trypetesa* is found in the columella of shells inhabited by hermit crabs from the Philippines, and predation on host hermit crab embryos has been documented (Williams, 1999). In total, there are presently at least 9 species (representing four phyla) known to be egg predators of hermit crabs (Table 4).

Additional associates of hermit crabs, particularly members of the Platyhelminthes, are suspected to feed on the eggs of host crabs. For example, the large turbellarian flatworm *Emprosthopharynx rasae* Prudhoe is found associated with *Calcinus latens* from Hawaii (Prudhoe, 1968). The flatworm is found in the upper lumen of gastropod shells and wraps around the abdomen of host hermit crabs (Prudhoe, 1968), where embryos of ovigerous hermit crabs are located. Other polydorids and polychaetes associated with hermit crabs should be examined to determine their effects on host reproduction. In particular, *Polydora biocipitalis* Blake & Woodwick forms burrows similar to *Dipolydora commensalis* and may ingest the embryos of host hermit crab *Pagurus hirsutiunculus* (Dana) from California. Free-living polychaetes belonging to the families Polynoidae, Nereididae, and Syllidae have been observed as associates of hermit crabs and their predatory nature would allow for ingestion of embryos (Jensen & Bender, 1973; Stachowitsch, 1980; Hoberg *et al.*, 1982). Nemertean worms are well documented egg predators of decapod crustaceans, but have not been found

Table 4. List of invertebrate species known to feed on embryos attached to the pleopods of host hermit crabs.

Egg predator species	Host hermit crab	Authors
Cnidaria: Hydrozoa		
<i>Adamsia palliata</i>	<i>Pagurus bernhardus</i>	Matthews, 1959
	<i>Pagurus prideauxi</i>	
<i>Podocoryne carnea</i>	<i>Pagurus bernhardus</i>	Matthews, 1959;
	<i>Diogenes pugilator</i>	Cerrano <i>et al.</i> , 1998
<i>Hydractinia echinata</i>	<i>Pagurus bernhardus</i>	Christensen, 1967
Platyhelminthes: Turbellaria*		
<i>Stylochus zebra</i>	<i>Pagurus pollicaris</i>	Lytwyn, 1979
Annelida: Polychaeta		
<i>Nereis fucata</i>	<i>Pagurus bernhardus</i>	Matthews, 1959;
	<i>Pagurus prideauxi</i>	Goerke, 1971
<i>Dipolydora commensalis</i>	<i>Pagurus longicarpus</i>	J. D. Williams, pers. obs.
<i>Polydora umangivora</i>	<i>Calcinus gaimardii</i>	Williams, 2001a, present study
	<i>Dardanus lagopodes</i>	
	<i>Paguristes runyanae</i>	
<i>Polydora robi</i>	<i>Calcinus gaimardii</i>	Williams, 2000,
	<i>Calcinus latens</i>	2001a, present study
	<i>Calcinus minutus</i>	
	<i>Calcinus pulcher</i>	
	<i>Clibanarius cruentatus</i>	
	<i>Clibanarius englaucus</i>	
	<i>Dardanus lagopodes</i>	
Crustacea: Cirripedia		
<i>Trypetesa</i> sp.	<i>Calcinus gaimardii</i>	Williams, 1999
	<i>Calcinus latens</i>	

* In addition to the flatworm listed, there is evidence of an unidentified species that preys on the embryos of hermit crabs from the Philippines, see Discussion.

associated with hermit crabs (e.g. Wickham & Kuris, 1985, 1988; Wickham, 1986; Kuris, 1991).

The impact of egg predation of *P. umangivora* and *P. robi* on hermit crab reproduction is difficult to evaluate fully because the reproduction of Indo-West Pacific hermit crab species is poorly known. Although reproduction in a number of diogenid hermit crabs has been examined (see Asakuri & Kikuchi, 1984; Imazu & Asakura, 1994; Mantellatto & Garcia, 1999), the present report is the first to provide data on the reproduction of *Calcinus gaimardii*, *Calcinus minutus*, and *Paguristes runyanae*. Additionally, a variety of factors including shell type, size, and weight has been shown to influence clutch size of hermit crabs (e.g. Childress, 1972; Fotheringham, 1976; Bertness, 1981; Elwood *et al.*, 1995). In species such as *C. gaimardii*, which produces large broods of small eggs (up to 3200), variation in brood size and the factors noted above may mask the effects of egg predation. However, feeding experiments showed that *P. robi* was able to ingest up to 230 eggs and 70 embryos of *C. gaimardii* over a 6-h period. Assuming a brooding period of < 1 week, the worms could ingest > 60% of the brood of this hermit crab species (based on feeding experiments and

the average clutch size of *C. gaimardii*). There is no evidence that female hermit crabs are able to detect the removal of embryos by the worms; in feeding experiments the abdomen of the hermit crab was not withdrawn from *P. robi* as they fed on attached embryos. However, other hermit crab associates have been shown to influence the shell selection behaviour of hermit crabs (Conover, 1976).

In hermit crabs species such as *Paguristes runyanae* which produces smaller broods (generally < 300 eggs) the impact of egg predation is more evident. *Polydora umangivora* was found to remove all or nearly all the embryos within clutches of this species. Interestingly, *Paguristes runyanae* has a brood pouch that covers the pleopods and attached embryos. It is unknown how the worm is able to invade the pouch and remove the embryos, but the worms may gain access to the embryos when the hermit crabs extend from the aperture of occupied shells.

Regardless of the mechanics of embryo removal, the effect of this predation indicates a need to re-examine the nature of the symbiotic relationship between polydorids and hermit crabs. In addition to their negative impact on the reproduction of hermit crabs species, polydorids reduce shell strength because of their burrowing behaviour (Buckley & Ebersole, 1994). Based on this research, Buckley & Ebersole (1994) suggested that the symbiotic relationship may shift from commensalism to parasitism depending on the presence of predators. Similarly, the present findings may indicate a shift from commensalism to parasitism based on the deleterious impacts on hermit crab reproduction.

Polydorids derive a variety of positive benefits from their association with hermit crabs. As indicated by Conover (1976) and Stachowitsch (1980) the worms are removed from risk of burial while inhabiting shells carried by hermit crabs. In addition, their feeding is enhanced in two ways. First, as hermit crabs scavenge for food they provide access to areas of high flow and may re-suspend or transport of food particles to worms by the branchial currents (Dauer, 1991; Radashevsky, 1993). Second, when associated with an ovigerous female crab, the worms are able to ingest the embryos of the host. The large caloric content of such eggs and embryos (4.78–6.05 cal/g dry wt in *Pagurus bernhardus*; Pandian & Schumann, 1967) indicates that the benefit of this predation is considerable. While suspension or deposit feeding the worms may predominately ingest detrital particles of considerably less caloric content (1.65–4.62 cal/g dry wt; Tenore, 1981). Studies on the reproduction of *Polydora robi* have indicated that members of this species exhibit the highest fecundity of any polydorid examined to date (Williams, 2001b). Whether this high fecundity is partly the result of the nutritional benefits derived from embryo predation remains unknown. It would be interesting to determine if the worms display synchrony of reproduction when associated with female hermit crab hosts, such as that demonstrated in nemertean brood parasites of decapod crustaceans (McDermott & Gibson, 1993).

In addition to nutritional benefits, hermit crabs may also provide the worms with a refuge from predators (Conover, 1976; Stachowitsch, 1980). It seems that the association between polydorids and hermit crabs initially evolved predominately based on factors related to the benefits of shelter, and this association was reinforced by the mode of feeding, as suggested in turbellarian symbionts (Jennings, 1974). Spionids exhibit a long fossil association with hermit crab hosts, as displayed by the *Dipolydora commensalis*-type burrows of *Helicotaphrichnus commensalis* dating to the Eocene (Walker, 1992). While such long-term associations seem to be based on the advantages to polydorids (i.e. shelter, food, protection from predators), negative impacts on hosts lead to questions of why hermit crabs do not exhibit behavioural or morphological adaptations to reduce or avoid association with the worms? One explanation is that hermit crabs have no choice; shells are limited in many areas and therefore hermit crab populations may be controlled by the number of free shells available (Fotheringham, 1976; Kellog, 1976). As a result hermit crabs are often forced to inhabit sub-optimal shells (broken shells or those occupied by other associates). Based on these observations, egg predation may have little or no overall impact on hermit crab populations where shells act as the limiting resource. It is possible that even when clutch size is reduced because of egg predation, there may be more juveniles produced than shells available. However, impacts may be detectable and biologically significant in areas that exhibit high polydorid infestation rates or where multiple egg predator species are present. Further studies on the ecology and biology of polydorids and other invertebrate egg predators of hermit crabs should be initiated to define more accurately their symbiotic relationships and influence on hermit crab populations.

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Appendix 1. Use of gastropod shells by *Polydora umangivora* and *P. robi* in the Philippines during June 1997 to April 1999. Family, shell length, and prevalence (%) of *P. umangivora* and *P. robi* in each shell species recorded. *Polydora umangivora* and *P. robi* are reported as absent (A) or present (P) for shell species collected in low abundance (≤ 5 shells); n = number of shells examined. Abbreviation of family names indicated for cross reference with Table 1 and Fig. 2. Other indicates unidentified gastropod shells

Gastropod shell species	Family and (abbreviation)	Shell length (mm) mean \pm SD (n)	n	<i>P. umangivora</i> %	<i>P. robi</i> %
<i>Astrarium rhodostoma</i> (Lamarck, 1822)	Turbinidae (TUR)	20.1 \pm 4.8 (8)	12	A	8.3
<i>Cantharus undosus</i> (Linnaeus, 1758)	Buccinidae (BUC)	28.8 \pm 5.4 (66)	51	19.6	39.2
<i>Cerithium tellenum</i> Sowerby, 1855	Cerithidae (CER)	—	4	P	P
<i>Clypeomorus bifasciatus</i> (Sowerby, 1855)	Cerithidae (CER)	27.1 \pm 5.6 (12)	17	A	11.8
<i>Clypeomorus moniliferus</i> (Kiener, 1841)	Cerithidae (CER)	26.0 \pm 0.0 (2)	15	A	A
<i>Conus</i> sp.	Conidae (CON)	29.5 \pm 8.9 (47)	57	3.5	19.3
<i>Coralliophila neritoidea</i> Lamarck, 1816	Coralliophilidae (COR)	25.0 \pm 3.3 (54)	70	10	11.4
<i>Cymatium rubeculum</i> (Linnaeus, 1758)	Cymatiidae (CYM)	39.3 \pm 6.1 (6)	5	A	P
<i>Cypraea</i> sp.	Cypraeidae (CYP)	26.5 \pm 8.4 (39)	38	5.3	31.6
<i>Drupa grossularia</i> Röding, 1798	Muricidae (MUR)	21.3 \pm 1.9 (13)	12	A	8.3
<i>Drupa ricinus ricinus</i> (Linnaeus, 1758)	Muricidae (MUR)	18.9 \pm 3.2 (9)	8	A	A
<i>Drupa rubusidaeus</i> Röding, 1798	Muricidae (MUR)	32.1 \pm 5.1 (4)	8	12.5	25
<i>Drupa</i> sp.	Muricidae (MUR)	—	15	20	6.7
<i>Drupella cornus</i> (Röding, 1798)	Muricidae (MUR)	27.9 \pm 3.4 (225)	453	5.5	17.2
<i>Drupella rugosa</i> (Born, 1778)	Muricidae (MUR)	22.4 \pm 2.9 (113)	136	5.2	8.8
<i>Fasciolaria trapezium</i> (Linnaeus, 1758)	Fascioliariidae (FAS)	—	1	A	P
<i>Gyrineum</i> sp.	Cymatiidae (CYM)	21.4 \pm 9.7 (4)	5	P	P
<i>Latrolagena smaragdula</i> (Linnaeus, 1758)	Fascioliariidae (FAS)	35.5 \pm 4.3 (29)	31	35.5	67.7
<i>Latirus belcheri</i> (Reeve, 1847)	Fascioliariidae (FAS)	—	4	A	P
<i>Latirus polygonus</i> (Gmelin, 1791)	Fascioliariidae (FAS)	33.6 \pm 13.3 (7)	7	28.6	57.1
<i>Latirus turritus</i> (Gmelin, 1791)	Fascioliariidae (FAS)	26.3 \pm 4.3 (15)	18	11.1	16.7
<i>Morula granulata</i> (Duclos, 1832)	Muricidae (MUR)	—	26	A	7.7
<i>Peristernia incarnata</i> (Kiener, 1840)	Fascioliariidae (FAS)	15.5 \pm 3.9 (7)	1	A	P
<i>Peristernia nassatula</i> Lamarck, 1822	Fascioliariidae (FAS)	26.1 \pm 6.3 (15)	23	4.4	21.7
<i>Rhinoclavis fasciata</i> (Bruguère, 1792)	Cerithidae (CER)	—	6	A	16.7
<i>Strombus labiatus labiatus</i> Röding, 1798	Strombidae (STR)	—	8	A	62.5
<i>Thais armigera</i> (Link, 1807)	Muricidae (MUR)	27.3 \pm 5.7 (15)	14	A	14.3
<i>Thais mancinella</i> (Linnaeus, 1758)	Muricidae (MUR)	28.4 \pm 9.1 (12)	6	50	33.3
<i>Thais</i> sp.	Muricidae (MUR)	—	1	A	P
<i>Turbo chrysostomus</i> Linnaeus, 1758	Turbinidae (TUR)	29.3 \pm 3.5 (8)	6	A	A
<i>Vexillum</i> sp.	Costellariidae (COS)	—	1	A	P
Other	—	—	130	4.6	14.6

Appendix 2. Hermit crab species associated with *Polydora umangivora* and *P. robi* in the Philippines during June 1997 to April 1999. Hermit crab shield length, number of hermit crabs examined (n), and prevalence (%) of *P. umangivora* and *P. robi* recorded. *Polydora umangivora* and *P. robi* are reported as absent (A) or present (P) for hermit species collected in low abundance (≤ 5 hermit crabs). Abbreviation of hermit crab species indicated for cross reference with Table 1 and Fig. 2. Other, unidentified hermit crabs

Hermit crab species	Abbreviation	Shield (mm) mean \pm SD (n)	n	<i>P. umangivora</i> %	<i>P. robi</i> %
<i>Calcinus gaimardii</i> (H. Milne Edwards, 1848)	CGA	4.4 \pm 1.1 (432)	744	7.4	18.2
<i>Calcinus latens</i> (Randall, 1839)	CLA	3.3 \pm 0.8 (172)	343	5.0	16.1
<i>Calcinus minutus</i> Buitendijk, 1937	CMI	3.3 \pm 0.7 (76)	158	6.3	18.4
<i>Calcinus pulcher</i> Forest, 1958	CPU	3.7 \pm 0.6 (11)	32	6.3	15.6
<i>Ciliopagurus strigatus</i> (Herbst, 1804)		4.7 \pm 1.2 (5)	5	A	P
<i>Clibanarius englaucus</i> Ball & Haig, 1972		—	1	P	P
<i>Clibanarius merguiensis</i> De Man 1888		—	1	P	A
<i>Dardanus lagopodes</i> (Forskål, 1775)	DLA	4.0 \pm 1.8 (74)	108	12.0	23.2
<i>Dardanus pedunculatus</i> (Herbst, 1804)		—	1	P	A
<i>Diogenes</i> sp. ^a	DIO	—	16	A	6.3
<i>Paguristes runyanae</i> Haig & Ball, 1988	PRU	3.6 \pm 0.8 (61)	75	10.7	20.0
Other		—	48	8.3	16.7

^a Probably represents an undescribed species from Cebu, Philippines (P. Cassidy, pers. comm.).