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FEEDING BIOLOGY AND SYMBIOTIC RELATIONSHIPS OF THE CORALLIMORPHARIAN *PARACORYNACTIS HOPLITES* (ANTHOZOA: HEXACORALLIA)

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***ABSTRACT.* –** Polyps of the corallimorpharian *Paracorynactis hoplites* were studied in coral reefs of the Davao Gulf, the Philippines, between October 2007 and January 2009. Polyps of *Paracorynactis hoplites* preyed mainly on echinoderms. Predation on seven species of echinoderms was observed in the field (four asteroids, two echinoids and one holothurian); an additional ten species were accepted during feeding trials (four asteroids, four echinoids and two holothurians). The echinoids *Diadema setosum*, *Diadema savignyi* and *Echinotrix calamaris*, and the ophiuriod *Ophiomastix* sp. were not adversely affected by the polyps. The opisthobranch *Phyllidiella pustulosa* (Mollusca) was accepted during feeding trials, whereas the gastropod *Cypraea tigris* was not adversely affected. In a feeding experiment, polyps of *Paracorynactis hoplites* (maximum diameter 170 mm) completely ingested crown-of-thorns sea stars (*Acanthaster planci*) of up to 340 mm diameter. The polyps had a mean daily biomass uptake of 24.5 g d^{-1} when having a single-species asteroid diet. Fishes of several species of families Apogonidae, Gobiidae, Labridae, Pomacentridae, and Pseudochromidae as well as the shrimps (*Periclimenes holthuisi*, *Periclimenes lacerate*, *Stenopus hispidus* and *Thor amboinensis*) lived near or among the tentacles of the polyps.

***KEY WORDS.* –** *Acanthaster planci*, Asteroidea, commensalism, crown-of-thorns, Echinodermata, Echinoidea, *Pseudocorynactis*, Teleostei.

INTRODUCTION

Polyps of *Paracorynactis hoplites* (Corallimorpharia) were first recorded from the Torres Strait near Papua New Guinea (Haddon & Shackleton, 1893) and had long been considered to belong to the genus of *Pseudocorynactis*. Recently, the polyps were taxonomically described and added to the new genus *Paracorynactis* (Ocaña et al., 2010). Polyps of *Paracorynactis hoplites* occur in some reefs of Indonesia (den Hartog, 1997), Malaysia (Gosliner et al., 1996), the Marshall Islands (Colin & Arneson, 1995), and the Philippines (Bos et al., 2008a). Little is known about the biology and ecology of this species.

Polyps of *Paracorynactis hoplites* are found at depths between 1–28 m, but the majority lives in water of less than 10 m (Ocaña et al., 2010). Independent of depth, the animals prefer to settle under coral ledges and in reef crevices (Bos et al., 2008a). The diameter of a single polyp can be as small as 2 mm in preserved specimens (Ocaña et al., 2010) and reach an impressive 210 mm in live specimens (Bos et al., 2008a). Den Hartog et al. (1993) inferred from the size of the nematocysts in the acrospheres that the polyps of this corallimorpharian may be highly efficient predators. Bos et al. (2008a) reported that polyps prey on the relatively large asteroids *Acanthaster planci* and *Protoreaster nodosus*, and described how a polyp can quickly extend itself when attacking an asteroid and how the prey is pulled toward the polyp's mouth and fully ingested. In this paper, we provide new information about the feeding biology, behaviour, and symbiotic relationships of *Paracorynactis hoplites*.

Table 1. Species of Echinodermata and Mollusca naturally preyed upon (Prey) and fed to polyps (Fed) of the corallimorpharian *Paracorynactis hoplites* in the Davao Gulf between Oct.2007 and Jan.2009.

Phylum/Class	Species	Author	Prey	Fed
Echinodermata				
Asteroidea	*Acanthaster planci*	(Linnaeus, 1758)	×	×
	Archaster typicus	(Müller & Troschel, 1840)		×
	Choriaster granulatus	Lütken, 1869	×	
	Culcita novaeguineae	Müller & Troschel, 1842		×
	Linckia laevigata	(Linnaeus, 1758)	×	×
	Nardoa tuberculata	Gray, 1840		×
	Pentaster obtusatus	(Bory de St. Vincent, 1827)		×
	Protoreaster nodosus	(Linnaeus, 1758)	×	×
Echinoidea	*Diadema setosum*	(Leske, 1778)	not affected	
	Diadema savignyi	Michelin, 1845	not affected	
	Echinometra mathaei	(Blainville, 1825)	×	×
	Echinotrix calamaris	(Pallas, 1774)	not affected	
	Metalia spatagus	(Linnaeus, 1758)		×
	Brissus latecarinatus	(Leske, 1778)		×
	Phyllacanthus imperialis	(Lamarck, 1816)	×	
	Salmacis belli	Döderlein, 1902		×
	Toxopneustes pileolus	(Lamarck, 1816)		×
Holothuroidea	*Holothuria hilla*	Lesson, 1830		×
	Holothuria leucospilota	(Brandt, 1935)		×
	Synapta maculata	(Chamisso & Eysenhardt, 1821)	×	
Ophiuroidea	*Ophiomastix sp.*		not affected	
Mollusca				
Gastropoda	*Cypraea tigris*	Linnaeus, 1758	not affected	
Opisthobranchia	*Phyllidiella pustulosa*	(Cuvier, 1804)		×

MATERIAL AND METHODS

Polyps of *Paracorynactis hoplites* were studied on Samal and Talikud islands, Davao Gulf, the Philippines, during 29 dives to a depth of 37 m between Oct.2007 and Jan.2009. Location and depth of each individual polyp (N = 72) were recorded, and the diameter of each was measured to nearest cm. Prey items and symbionts were recorded and photographed. Froese & Pauly (2008) and Lieske & Myers (2002) were used to identify symbiotic reef fishes. Clark & Rowe (1971) and Colin & Arneson (1995) were used to identify echinoderms, mollusks, and shrimps. For the identification of symbiotic shrimps, we additionally used Bruce (1992).

Feeding behaviour was studied in 11 polyps observed by skin-diving on a patch reef extending to 4 m depth at the western coast of Samal Island (7º0.80'N, 125º43.24'E). The column diameter and length of all polyps were measured before and while they were feeding. To study food preference, polyps were offered common asteroids and echinoids. To study the effect of prey size, from Nov.2007 to Mar.2008, specimens of the asteroid *Acanthaster planci* were offered to the corallimorpharians. The asteroids were collected at a nearby reef because none were found in the patch reef where *Paracorynactis hoplites* was present. Animals of a variety of sizes were offered: the diameter of each was measured before releasing it near a polyp. If it moved away from the polyp, the asteroid was picked up and put back near until it moved toward the polyp. If a sea star was able to free itself from a polyp's tentacles, it was offered to a larger polyp.

To estimate biomass uptake, three polyps were enclosed in individual cages of chicken wire (mesh size 10 × 10 mm^2) with a surface area of about 0.2 m^2. Each polyp was fed asteroids of a single species diet (*Acanthaster planci*, *Linckia laevigata*, or *Protoreaster nodosus*) during 7 wk and had access to no other food. One free-roaming asteroid was available in each cage allowing polyps to feed at any time. Before being offered to a polyp, each asteroid was briefly removed from the water, blotted, measured, and weighed (1 g accuracy). The diameter of *A. planci* and the length of all five rays of *L. laevigata* and *P. nodosus* were measured. For comparison, mean ray length (radius R) was multiplied by two to calculate the diameter for the latter two asteroids.

RESULTS

***Prey species.* –** Polyps of *Paracorynactis hoplites* were observed to prey largely on members of Echinodermata: four species of Asteroidea and one species of Holothuroidea (Table 1). They were inferred to prey on two species of Echinoidea from tests and spines found under or beside the polyps (Fig. 1). A feeding trial with the echinoid *Echinometra mathaei*

confirmed it to be an appropriate prey. In further feeding trials, polyps of *P. hoplites* ingested other echinoderms common in the vicinity, which increased the prey inventory of members of the Echinodermata to a total of 17 species (Table 1). However, three echinoids, *Diadema setosum*, *Diadema savignyi*, and *Echinotrix calamaris* were not preyed upon. Spines of these urchins could touch the tentacles of a polyp without adverse effects (Fig. 2). Similarly, the arms of a brittle star from the genus *Ophiomastix* could touch the tentacles unaffected. One species of Opisthobranchia, *Phyllidiella pustulosa*, was accepted as prey when offered to the polyps, whereas the gastropod *Cypraea tigris* was not affected (Table 1).

Polyps of *Paracorynactis hoplites* naturally prey on the crown-of-thorns sea star, *Acanthaster planci* (Table 1). A polyp can ingest a sea star larger in diameter than itself: the larger the polyp, the larger the sea star it ingested (Fig. 3). The largest sea star we observed to be ingested was 340 mm in diameter (Fig. 3). Maximum diameters of *Linckia laevigata* and *Protoreaster nodosus* ingested were 244 and 172 mm, respectively. In the feeding experiments, the daily biomass uptake was 29.5, 19.0, and 25.0 g d^{-1} for the prey species *Acanthaster planci*, *Linckia laevigata*, and *Protoreaster nodosus*, respectively. The mean daily biomass uptake of a polyp was 24.5 g d^{-1}.



Fig. 1. Extended polyp of *Paracorynactis hoplites* pulling a partly whitened asteroid (*Linckia laevigata*) toward its mouth. Note test of echinoid *Echinometra mathaei* beside base of polyp (A. R. Bos).

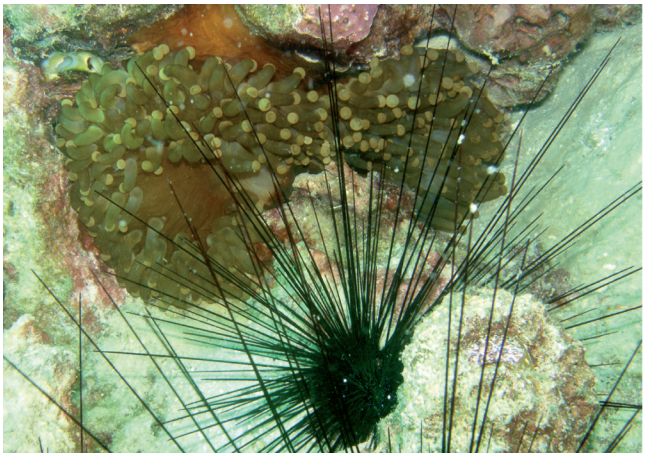


Fig. 2. Echinoid *Diadema savignyi* not adversely affected by polyp of *Paracorynactis hoplites* (A. R. Bos).

***Prey capture.* –** Polyps actively moved their tentacles to detect potential prey. When acrospheres touched the surface of prey items, they immediately stuck to the prey and remained firmly attached. Subsequently the polyps expanded to bring as-yet unattached acrospheres closer to the prey items. Some polyps extended toward prey even before contact was made. After extension and attachment of most acrospheres to prey items, polyps slowly retracted, pulling the prey toward themselves. Simultaneously, the polyp mouth opened and enveloped the nearest parts of the prey item. Acrospheres continued to attach, further entangling the prey. However, some prey items escaped the pull of the tentacles, especially if they were large or relatively fast moving, or if few acrospheres had adhered to them. In cases where the prey had been moving across a sandy bottom near the polyp, this appeared to be an advantage to the polyp, because prey had relatively poor traction on sandy substrate. About 50% of the polyps had settled near sandy substrate.

Small and flexible prey items were completely enveloped by the mouth, then swallowed, which generally stretched the polyp. After feeding, the polyp's tentacles hung downward, and when a potential prey item was touched to the tentacles, the acrospheres had little adhesiveness. Asteroids that escaped the pull of the tentacles after short contact with the polyps were partly whitened on those parts that had been in the mouth of the polyp (Fig. 1). Large prey species, especially those with stiff skeletons (e.g. *Protoreaster nodosus*), that were not able to escape the pull of the tentacles were only partially eaten and were usually released with a single arm missing. After digestion of the soft tissues, indigestible parts were regurgitated through the mouth and fell onto the sediment near the polyp (Fig. 1). Although spines of the asteroid *Acanthaster planci* were also regurgitated, nothing was found from *Linckia laevigata*.

Mean length of non-feeding polyps was 40 mm (N = 17), but when feeding (N = 55) polyps extended up to 5 times normal

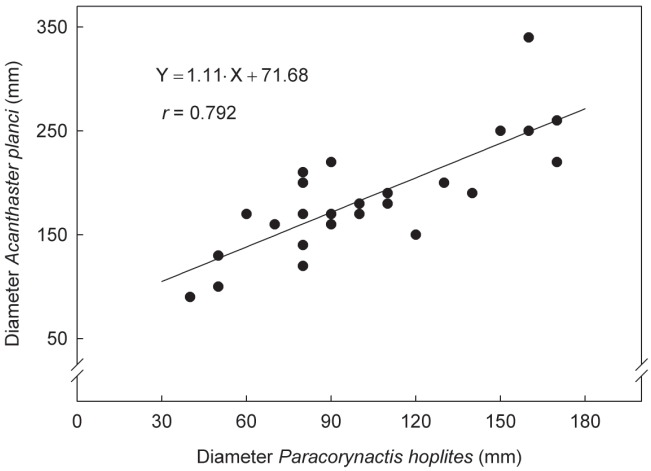


Fig. 3. Diameter of fully digested crown-of-thorns sea stars (*Acanthaster planci*) as a function of polyp diameter of *Paracorynactis hoplites*.

length (Fig. 1). One non-feeding polyp with a diameter of 90 mm and a length of about 45 mm stretched to 240 mm in length when catching and enveloping a specimen of *Linckia laevigata* (radius = 103 mm). The period from prey detection to full ingestion usually lasted >1 h, but if conditions were favorable to the polyp (i.e. small prey or poor traction on sandy substrate), prey could be ingested in <1 min.

Symbiotic species. **–** Some fishes took refuge among the tentacles or hovered over the mouth of polyps of *Paracorynactis hoplites*. Specimens of the cardinal fishes *Apogon multilineatus*, *Apogon nigrofasciatus*, and *Cheilodipterus quinquelineatus*, and the gobies *Eviota pellucida* and *Trimma nasa* swam among the tentacles of the polyps, and appeared to contact them, apparently without being adversely affected. Specimens of the dusky dottyback *Pseudochromis fuscus* commonly swam about the column of the polyp hiding underneath the crown of tentacles possibly avoiding direct contact to the acrospheres. Less often, we observed juveniles of the wrasse *Halichoeres purpurescens* and the damselfishes *Plectroglyphidodon lacrymatus* and *Pomacentrus grammorhynchus* near the tentacles without actually touching the acrospheres, also apparently without negative effects. The goby *Trimma striata* visited the column of entirely closed polyps only (Fig. 4), when the risk of being touched by tentacles was nil.

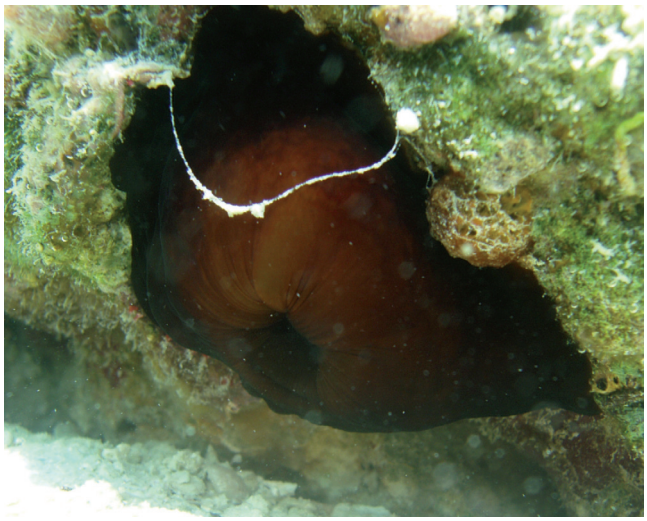


Fig. 4. Entirely closed polyp of *Paracorynactis hoplites* where tentacles are not visible (A. R. Bos).

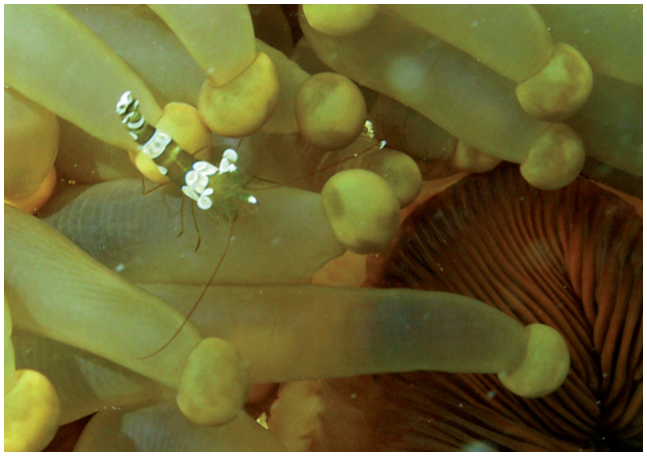


Fig. 5. Symbiotic shrimp *Thor amboinensis* among tentacles of a polyp of *Paracorynactis hoplites*. Mouth of polyp is visible at lower right (A. R. Bos).

Specimens of the cleaner shrimps *Periclimenes holthuisi* and *Periclimenes lacertae* lived among the tentacles, at an abundance of one specimen per polyp. The shrimps *Thor amboinensis* also lived among the tentacles (Fig. 5) with up to five individuals per polyp. Furthermore, two specimens of the larger cleaner shrimp *Stenopus hispidus* were observed to share a small crevice with a polyp of *Paracorynactis hoplites*. *S. hispidus* antennae touching polyp tentacles did not adhere to each other and did not appear to adversely affect either party.

We regularly found injured polyps and sometimes just some tissue of the mesenterial filaments. One polyp of *Paracorynactis hoplites* survived repeated attacks by an unknown predator during two months of observation, and one polyp was eaten by two *A. planci* specimens.

DISCUSSION

Asteroids and echinoids appear to be major prey items of *Paracorynactis hoplites*, because acrospheres easily attach to these animals. Echinoids preyed upon were mainly species with relatively short spines; this anatomy may allow acrospheres to attach to soft tissue and explains why the echinoids *Diadema setosum*, *Diadema savignyi*, and *Echinotrix calamaris*, which have relatively long spines (Coppard & Campbell, 2004), were unaffected. Excluding the long-spined sea urchins, all echinoderms have surfaces or relatively soft bodies to which acrospheres easily attach. The acceptance of a nudibranch as prey (Table 1) may suggest that all slow-moving, soft-tissue animals are potential prey for polyps of *P. hoplites*. Only those with long spines and smooth surfaces (e.g. shells) seem to be safe from acrosphere attacks. However, only one species of shelled mollusk was examined here, so further studies are needed on reactions to a wider variety of potential prey items to determine the diet specificity of these corallimorpharians. Many coral reef cnidarians are known to consume almost any animal material that falls upon their oral disks, including zooplankton (e.g. Fabricius & Metzner, 2004). The ability of this corallimorpharian to consume large echinoderms is interesting, especially consumption of the major cnidarian predator *Acanthaster planci*, and may be a special trait of this species.

Bos et al. (2008a) observed polyps of *Paracorynactis hoplites* to prey upon specimens of *Acanthaster planci* with maximum diameter of 250 mm. We found asteroids as large as 340 mm consumed by polyps up to 170 mm diameter. The polyps of *P. hoplites* did not feed differently and were not adversely affected by consuming *Acanthaster planci*, which is considered toxic to humans (Shiomi et al., 1985; Moran, 1990; Sato et al., 2008) and may also be toxic to some marine

predators. Also, the echinoid *Toxopneustes pileolus*, known to be toxic to fishes (Frey, 1951), was eaten by the polyps without being adversely affected.

Parts of prey items that had been in the mouths of polyps for a short while, were whitened and showed signs of digestion, possibly because their relatively stiff skeletons escaped the pull of the tentacles, but they lost soft tissue from their body. In areas where polyps of *P. hoplites* were abundant, a relatively high proportion of specimens of the sea star *Protoreaster nodosus* had shortened or missing rays (Bos et al., 2008b). Thus polyps of *P. hoplites* may, together with other predators, be responsible for high numbers of irregular sea stars in the Davao Gulf (Bos et al., 2008c; Bos et al., 2011). Moreover, polyps of *P. hoplites* were not observed at the remote Tubbataha reefs in the Philippines and their apparent absence or low density may have contributed to a recent outbreak of *Acanthaster planci* in this UNESCO world heritage site (Bos, 2010).

Although polyps of *Paracorynactis hoplites* appeared to mainly prey on echinoderms, they may additionally be able to prey on planktonic organisms. Other corallimorpharians (Chadwick, 1991) and actinian sea anemones (Fautin et al., 1995) prey on zooplankton, and the corallimorpharian *Amplexidiscus fenestrafer* feeds on a wide range of food items including zooplankton (Hamner & Dunn, 1980). However, because polyps of *P. hoplites* were usually not willing to take up more food after capturing prey (reduced adhesiveness of acrospheres), the biomass uptake estimates reported here may be fairly accurate, in that polyps were satiated and did not otherwise feed. Feeding on zooplankton may be of importance only when larger prey are not trapped by these polyps.

Several fish species of different genera hovered near or lived within the polyps of *Paracorynactis hoplites* without adversely being affected. Anemones are known to host fishes and provide them with shelter and other benefits (Fautin & Allen, 1997). Typical anemone fishes are those of the genera *Amphiprion* and *Premnas* (Fautin & Allen, 1997), but these did not inhabit the polyps of *P. hoplites*. Also Hamner & Dunn (1980) observed the relatively large corallimorpharian *Amplexidiscus fenestrafer* not to be inhabited by these genera and under laboratory conditions fish were even captured and eaten. This may explain why none of the common anemone fishes were observed to inhabit polyps of *P. hoplites*.

Randall & Fautin (2002) observed other fish species than anemone fishes to associate with anemones, representing some of the families that we observed to live about the corallimorpharian polyps. These fishes may be very cautious in avoiding contact with the polyps or may have adjusted to life with nematocysts by developing a mucus layer to protect themselves against nematocyst attacks (Fautin, 1991). Anecdotal evidence suggested that the polyps of *Paracorynactis hoplites* prey on fish, but such observations were only done in aquaria. We fed a polyp with a dead specimen of the scorpion fish *Pterois volitans*, which was immediately ingested (personal observation). This confirms that *P. hoplites* accepts fish as prey.

The shrimps that live on the polyps of *Paracorynactis hoplites* are cleaners of fish and other marine animals (Becker & Grutter, 2004) and commonly live on anemones (Guo et al., 1996). Some symbiotic shrimps collect trapped planktonic organisms on anemone tentacles and remove mucus secretions on their hosts' columns (Fautin et al., 1995). Some shrimps are highly selective in terms of their association with hosts, but the shrimp *Thor amboinensis* is considered a generalist symbiont with sea anemones (Guo et al., 1996). Although the symbiotic shrimp *Periclimenes holthuisi* is generally considered selective (Becker & Grutter, 2004), Khan et al. (2003) suggested that it does not exhibit high host specificity. The observation of *P. holthuisi* in polyps of *P. hoplites* provides further evidence of lack of selectivity. The circumtropical cleaner shrimp *Stenopus hispidus* does not usually live symbiotically with anemones (Chockley & Mary, 2003), but was observed to share a crevice with a polyp of *P. hoplites* without being affected.

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