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Biology of the Polyclad *Prosthiostomum (Prosthiostomum)* sp., a New Coral Parasite from Hawaii[1]

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ABSTRACT: *Prosthiostomum (Prosthiostomum)* sp., a species of polyclad flatworm yet to be described, is an obligate ectoparasitic symbiont of the hermatypic coral *Montipora*. Field and laboratory studies have demonstrated an intimate parasite/host association involving the utilization of host corals as food and substrate by the parasite. Development of larvae is within the immediate host environment; consequently, infections are produced through direct infection. Various aspects of the biology, such as the developmental history, feeding habits, and parasite/host response to thermal environment, are reported. It is concluded that all aspects of the life history of this species show adaptations toward host specificity. This represents a rare example of true coral parasitism since most animals known to feed on coral tissues are considered to be facultative predators. The optimal thermal environment for the parasite appears to coincide with that of the coral host, a phenomenon which may tend to produce a seasonally stable parasite/host interaction. The parasite appears to become a serious coral pest only in disrupted systems such as artificial laboratory situations or in the polluted sections of Kaneohe Bay, Oahu.

UNTIL THE LAST DECADE the Scleractinia and their relatives were believed to be nearly immune to predation and parasitism (Wells 1957). However, records of animals known to feed on living coral tissues and coral mucus have been increasing. It is now recognized that gastropods, polychaetes, crustaceans, and asteroids, as well as bony and cartilaginous fishes, all possess representatives that regularly utilize corals as food sources (reviewed by Robertson 1970). In laboratory experiments on the growth and metabolism on a variety of Hawaiian corals we found that specimens of the perforate hermatypic coral described by Vaughan (1907) as *Montipora verrucosa* (Lamarck) were readily destroyed by a polyclad that has been identified by Jean Poulter as *Prosthiostomum (Prosthiostomum)* sp. This discovery led us to investigate the host specificity, the method and frequency of infection, and various other aspects of its biology. The results of controlled laboratory experiments with various species of corals and other potential food sources and substrates indicate that this polyclad is an obligate ectoparasitic symbiont on its host *Montipora*. To our knowledge this is the first report of a polyclad utilizing coelenterate tissue as a food source.

In this paper we are using the currently accepted definitions for symbiosis and parasitism as employed by Henry (1966) and Cheng (1964, 1970). The original definition of symbiosis employed by DeBary (1879) as the "living together" of two heterospecific organisms, with no type of mutual or unilateral dependency being implied, is retained. Parasitism is accepted as one category of symbiosis and is defined as an intimate and obligatory relationship between two heterospecific organisms. In these associations the parasite (usually the smaller of the two partners) is metabolically dependent on the host. The relationship may be permanent or

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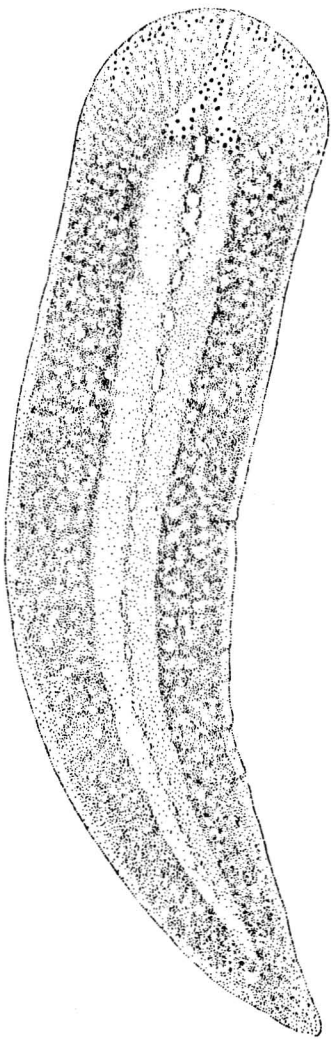

FIG. 1. Drawing of *Prosthiostomum* (*Prosthiostomum*) sp. from living adult animal measuring 12 mm in length.

temporary. Finally, in parasitism the association is obligatory because the parasite cannot survive if it is prevented from making contact with its host. In this paper we show that *Prosthiostomum* (*Prosthiostomum*) sp. is parasitic on its host, and meets the established criteria of the classic definition as well as being consistent with contemporary usage. For example, Bosch (1965) used the term parasitic to describe wentletraps (*Epitonium ulu*) that feed and reproduce on the coral *Fungia scutaria*. Likewise the xanthid crabs *Trapezia* and *Tetralia* which feed on coral mucus have been described as obligate ectoparasites of the coral *Pocillopora* (Knudsen 1967).

Outright host specificity among known coral parasites and predators is uncommon. Most of the animals known to feed on coral tissue and coral mucus have been classified as facultative predators (Robertson 1970). The obligate habits observed in *Prosthiostomum* (*P.*) sp. might be far more widespread than has been suspected, because there are already several indications that other members of this group may feed on coral tissue. Poulter (in press) lists four species of polyclads known to have been collected from corals. Various undetermined species of planarians have been found living on *Montipora*, *Lobophyllia*, *Stylophora*, and *Hydroplana* (Kawaguti 1944). Occasionally these animals were observed to form thick assemblages that covered the coral, causing it to become whitish as a result. The planarians reportedly contained zooxanthellae in fairly large quantities. Although he did not so state in his paper, Kawaguti (personal communication) believes that some of these species were feeding on the coral tissue, and he is presently investigating an acoel that appears to feed on *Acropora* tissue.

Our able co-workers Eric B. Guinther and Gerald S. Key provided valuable advice on various aspects of this paper. We are deeply indebted to J. L. Poulter for her identification and description of the animal and for her advice throughout the study. Eric B. Guinther drew the adult flatworm shown as Fig. 1.

GENERAL DESCRIPTION AND BEHAVIOR

The material on which Poulter (in press) based her description of *Prosthiostomum* (*Prosthiostomum*) *montiporae* was obtained from our experiments. This polyclad is a typical prosthiostomid (see Fig. 1). The body is small, much longer than broad. Field specimens were generally from 4 to 8 mm in length, but representatives up to 12 mm long have been collected. Animals grown under optimal conditions in the laboratory are frequently from 12 to 14 mm long, and rarely may reach 18 mm.

Living specimens are translucent, but assume

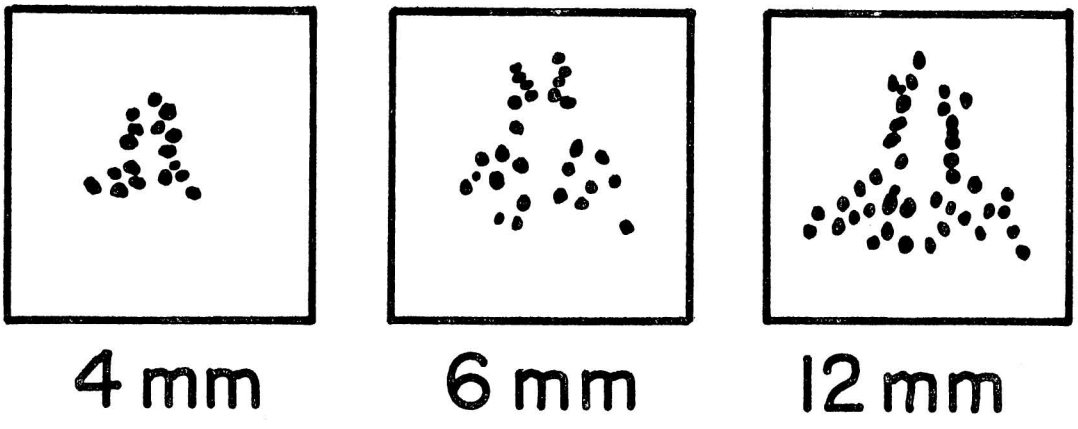

FIG. 2. Cerebral eyespot groups traced from photomicrographs of *Prosthiostomum* (*Prosthiostomum*) *montiporae* specimens measuring 4 mm, 6 mm, and 12 mm in length.

the brownish to terra cotta color of the ingested coral tissue within their gut. The gut contents of feeding animals are concentrated in the lateral digestive diverticula with small amounts in the central intestinal lumen. The living animals thus appear to possess a light brownish medial stripe (intestinal lumen) flanked by dark brown mottling from the lateral digestive diverticula. The mottled pattern grades into the transparent outer periphery of the animal. The ventral surface in living specimens is opaque white.

There is a group of cerebral eyes at the anterior end forming a deltoid pattern, as well as a pair of ventral eyes. The marginal eyes form an irregular pattern along the frontal border; each being approximately one-half the diameter of a cerebral eye. The eyes are distributed behind the anterior margin in the form of an arc with a deltoid cluster of cerebral eyes (Fig. 1).

The larger flatworms possess more eyespots than do smaller individuals. Examples of cerebral eyespots are shown in Fig. 2. We measured flatworm length and number of cerebral eyes for a group of specimens taken from a population grown in a tank and held for 1 month at 26°–27° C. The flatworms were relaxed in a solution of magnesium chloride before being examined under a dissecting scope with ocular micrometer. The smaller individuals could not be handled without damage, and so were relaxed and measured while still on the corals. Length of relaxed specimen and number of cerebral eyes were recorded for each individual, and a least-squares linear regression was performed on these data (see Fig. 3). The F-ratio of the regression is significant ($P < 0.001$), and the coefficient of determination indicates that 75 percent of the variance in the number of eyespots is explained by variation in length.

During the winter (water temperature approximately 23° C) it took several months to grow specimens of the 12-mm size class as opposed to several weeks at 26°–27° C. These animals had as many as 64 eyespots in the cerebral group, whereas the 12-mm animals grown at 26°–27° C had approximately 37 eyespots. Presumably then, the number of eyespots is related more directly to age than to length. Growth in this species is indeterminate, with size of flatworm and number of cerebral and marginal eyespots continuing to increase with time, without a definite maximum.

It is common to find this *Prosthiostomum* in associations of many individuals. Like most polyclads they are cryptic, and are found in the deep recesses of the coral head, wedged into tiny crevices and cracks, or on the underside of the coral. The parasite may tend to enhance the branching growth form of *Montipora* since it prefers to live and feed in the cryptic and lower portions of the coral head, and avoids the more exposed projections.

Laboratory and field observations indicate that *Prosthiostomum* (*P.*) sp. is negatively phototactic. In contrast, those animals in which the zooxanthellae are truly symbiotic exhibit

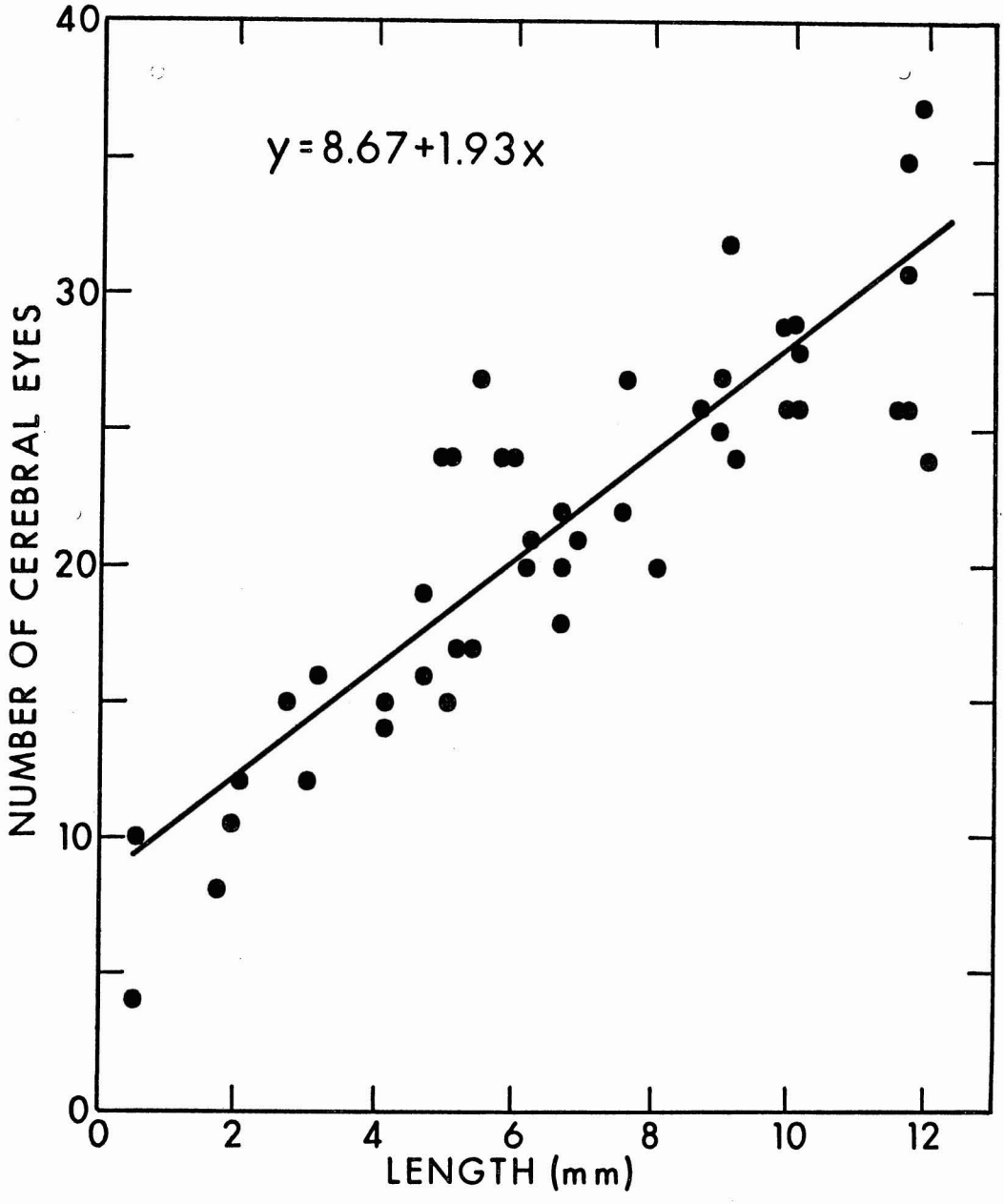

FIG. 3. Number of cerebral eyespots in *Prosthiostomum* (*Prosthiostomum*) sp. vs. length.

positive phototaxis (Kawaguti 1944). This behavior is interpreted as an adaptation that supplies the algal symbiont with the light energy required for photosynthesis. Starvation experiments have shown that the zooxanthellae in this flatworm are present only as a consequence of host utilization and thus no advantage can be ascribed to positive phototaxis. On the other hand, negative phototaxis can be presumed to be advantageous for the avoidance

of predators. Negative phototaxic behavior in animals containing symbiotic algae is potentially a valuable clue for identifying unsuspected predatory or parasitic habits.

Like many polyclads, this *Phosthiostomum* is able to attach itself to a hard substrate by means of a glandular, adhesive organ, or "sucker." We collected the animals by quickly drawing them off the coral with an ordinary household basting pipette. Occasionally, some managed to attach to the host coral by means of their sucker and could not be dislodged even when subjected to jets of water strong enough to rip off their extremities. The ability to withstand such high rate of water movement probably is an adaptation of the worm to wave turbulence. When the worms were exposed for a few moments to strong illumination they began to move toward the underside of the host and, once moving, could be removed.

FEEDING

The host coral *Montipora verrucosa* has widely spaced polyps and comparatively large areas of coenosarc tissue. *Montipora* is a perforate coral, and some tissue and zooxanthellae penetrate deep within the skeleton. The flatworm was observed to ingest circular pieces of superficial coral tissue with its pharyngeal apparatus, producing a small disc-shaped area of exposed coral skeleton. The polyclads attacked the coenosarc first with the polyps initially appearing to suffer less damage. Possibly, this was the result of the polyp's ability to withdraw into the calyx. Furthermore, the polyps are heavily armed with nematocysts, which might render them a less attractive food. Continued feeding resulted in long strips and blotches of host tissue being removed by the animal. Remnants of deeper tissues remain in the skeleton of grazed areas, imparting a pale pink color, which stands out in contrast to the terra cotta color of the surrounding host tissue.

The first visible signs of parasitism were generally observed on the undersides and inner recesses of the coral in those areas occupied by the flatworm. In corals being parasitized by only a few flatworms the small circular patches where the flatworm had removed coral tissue regenerated within a few weeks. In heavily infected corals the grazed, pink-colored coenosarc became extensive and contrasted with the dark-colored polyps. In such cases the tissue remaining in the skeleton as well as the isolated polyps died, and the entire area became white in color. At a later time, the coral skeleton took on a pale green color, resulting from attached algae. Eventually, the area became colored dark gray to black, indicative of dead skeletal material.

A tightly coiled fecal strand was seen being ejected from beneath the anterior edge of a specimen that was being observed under low-power magnification. The strand was spherical when ejected, but when it was released by the worm it rapidly unwound and began spinning. The strand was allowed to unwind fully, and then examined under high magnification. The strand appeared to be composed largely of mucus and fecal material, with a few zooxanthellae and nematocysts. The strand was shaped much like the central lumen and branching lateral diverticula of the worm's digestive tract.

The effects of starvation on the polyclad were tested with approximately 200 individuals that had been removed from living host coral. These animals were placed in a dish covered with fine plankton netting and were supplied only with running seawater. Another group of worms (control) was kept under identical conditions but was also provided with host coral. All containers were kept in full, natural sunlight. Thus, if the zooxanthellae from either group were functional symbionts, they would be provided with equal quantities of radiant energy for photosynthesis.

Within 2 days, the tissues of the starved worms lost the mottled terra cotta color and became entirely opaque white. Microscopic examination of both starved and control flatworms showed that the starved animals were devoid of nematocysts and zooxanthellae. The control specimens that were incubated with fragments of *Montipora* contained large quantities of coral tissue, zooxanthellae, and nematocysts, and retained the characteristic mottled appearance. In the starved specimens the very faint light brown pigmented streak along the mediodorsal line became obvious when there

was no other pigment to obscure it. The pigment of this streak, unlike the pigment from the ingested coral tissue, is insoluble in ethanol or acetone.

Approximately 20 flatworms from the starved group were placed in another dish containing a freshly collected fragment of healthy *M. verrucosa*. A second group of starved worms was placed in a dish containing a freshly collected fragment of the coral *Porites compressa* Dana, while the remaining unfed worms were retained in a dish without coral. The dishes were covered with fine plankton mesh and kept in full, natural light in running seawater. Within 2 hours, many of the specimens in the dish containing the *Montipora* had filled portions of their gut diverticula with coral tissue and had produced scarred areas on the coral surface. The worms in the dish with *Porites* did not invade the coral and were observed wandering randomly about the dish. The worms were retained in the experimental dishes until the following day and then were microscopically examined for ingested material. Fresh squashes of worms taken from the dish containing *Porites* remained colorless, and no indication of host tissues was present. In contrast, all of the specimens from the dish with *Montipora* had filled their gut with coral tissue and were attached to the underside of the host coral. The worms from dishes without *Montipora* were without zooxanthellae and nematocysts.

The above procedure was repeated with various species of coral found in Kaneohe Bay, Oahu. The flatworms did not ingest the tissues of *Fungia scutaria* (Lamarck), *Pocillopora damicornis* (L.), *Porites compressa* Dana, *Pavona varians* Verrill, *Cyphastrea ocellina* (Dana), or *Psammocora* (*Stephanaria*) *stellata* Verrill; but did feed upon the tissues of *Montipora verrucosa* Lamarck, *Montipora patula* Verrill, *Montipora verrilli* Vaughan, and *Montipora flabellata* Studer. Flatworms that fed on *M. flabellata*, a coral having pale blue tissue, became similar in color to their host.

Additional laboratory observations have shown that, when other corals are placed in tanks with infected *Montipora* specimens and maintained together for many months, *Prosthiostomum* (*P.*) sp. would not attack the corals *Fungia scutaria*, *Pocillopora damicornis*, or *Porites lobata* Dana; but would attack *Montipora flabellata*, *M. verrilli*, and *M. patula*. Nevertheless, flatworm infestations were never observed on species other than *M. verrucosa* in the field.

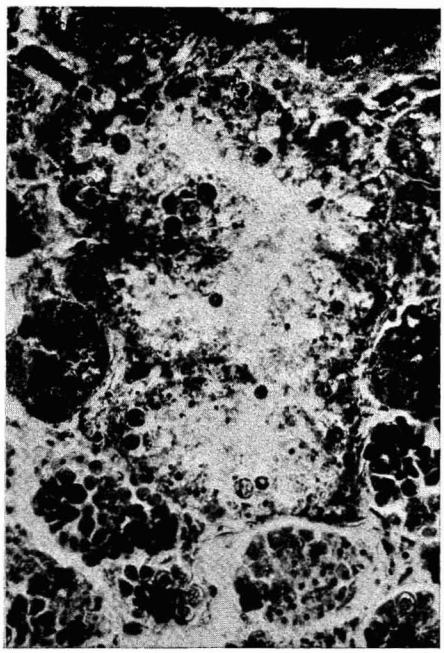

FIG. 4. Sagittal section (10 μ) of continuously fed *Prosthiostomum* (*Prosthiostomum*) sp. showing a digestive diverticulum containing luminal and intracellular zooxanthellae. 40 × magnification.

In examination of large numbers of flatworms no material other than tissue from *Montipora* was ever found in their digestive tracts, although a variety of alternate food sources were available (i.e., other species of coral, detritus, algae, and numerous invertebrate genera).

A histological study of flatworms in various stages of feeding and starvation was conducted. Groups of flatworms were removed from corals and placed in separate containers. Four treatments were involved: (1) specimens that were fed on *M. verrucosa* continuously, (2) specimens that were starved for 72 hours, (3) specimens that were starved for 48 hours and placed with *M. verrucosa* for 24 hours, and (4) specimens that were starved for 48 hours and placed with *Porites compressa* for 24 hours. At the end of the 72-hour period the experimental animals and samples of host tissue were fixed with mercuric

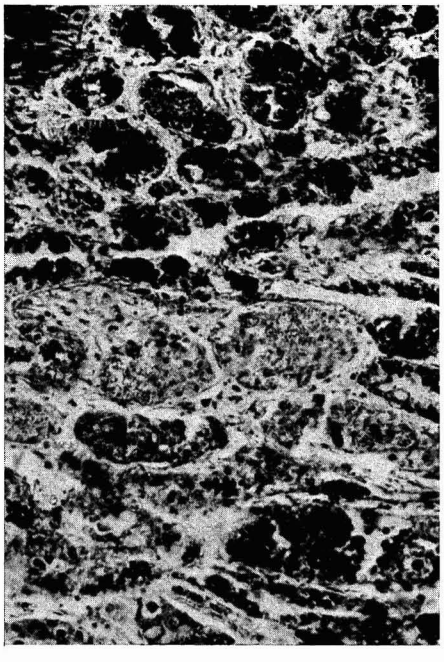

FIG. 5. Sagittal section (8 μ) of *Prosthiostomum* (*Prosthiostomum*) sp. starved 72 hours by being retained in seawater without host coral. Note presence of numerous pycnotic degenerating cells in digestive diverticula and that all zooxanthellae are intracellular. 40 × magnification.

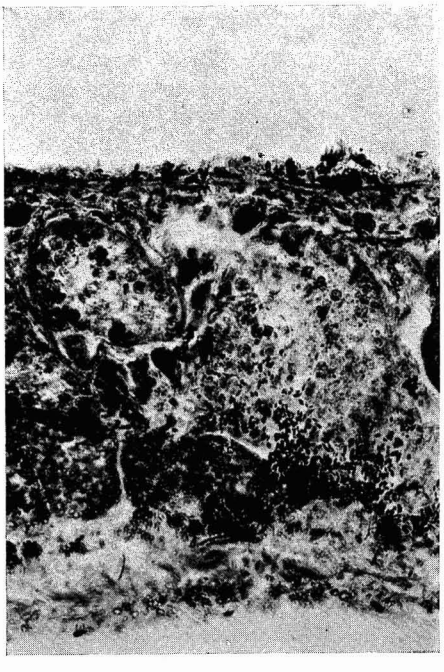

FIG. 6. Sagittal section (8 μ) of *Prosthiostomum* (*Prosthiostomum*) sp. starved for 48 hours and then placed with fresh *Montipora verrucosa* for 24 hours. Large groups of host cells are in lumen of digestive diverticula, and numerous zooxanthellae are being destroyed. 40 × magnification.

chloride solution (Hyman 1953) and were stained with either haematoxylin phloxin, PAS/haematoxylin, or azocarmine. The zooxanthellae and nematocysts found within the flatworm gut and those in the coral tissue were of similar size and morphology and produced similar staining reactions. The nematocysts of *Montipora verrucosa* do not stain and section well with these methods but were recognizable in both the host and parasite tissues. Since all specimens were originally taken from the same population and the treatments were run simultaneously in an identical manner, we attribute the observed differences to feeding history.

Photomicrographs of representative histological sections from animals exposed to the conditions presented above are presented in Figs. 4–6.

Fig. 4 shows zooxanthellae from *M. verrucosa* distributed within the lumen and intracellularly in the digestive diverticulae of a specimen allowed to feed continuously on *Montipora*. The large spherical zooxanthellae with characteristic eccentric pyrenoid (storage body) are easily recognized. The digestive cells contain large inclusion bodies characteristic of feeding flatworms. The histology of the digestive epithelium of these animals closely parallels that for fed and starved specimens of the polyclad *Dugesia dorotocephala* as described by Hyman (1951: 204).

A section from a starved animal is shown in Fig. 5. A few zooxanthellae are recognizable but all are intracellular. There are numerous pycnotic granules near the base of the epithelial cells, and the epithelium is condensed against the basement membrane. The basal portion of the epithelial cells is PAS-positive and also stains with azocarmine. The deeply stained material is assumed to be remnants of host materials in the process of being assimilated or excreted, or possibly even the degenerating cells of the starved flatworm.

A section from a starved animal, subsequently

fed on *Montipora verrucosa*, is shown in Fig. 6. Numerous zooxanthellae are again recognizable, and there are large accumulations of PAS-positive and azocarmine-staining material similar to that seen in the control animals (Fig. 4). The epithelial cells have also become elongated and possess many inclusions. Histological preparations from the group that was starved for 48 hours and placed with *Porites* for 24 hours appeared identical to preparations from animals starved for 72 hours.

DEVELOPMENTAL HISTORY

Reproductive activity occurs continuously throughout the year, resulting in the production of yellowish clusters consisting of from several to hundreds of egg capsules. Each capsule measures approximately 0.2 mm in diameter, a size small enough to be nestled within the perforate skeletal matrix of *Montipora*. The adults lodge the capsules in those areas where they have grazed off the coral tissue or where the skeleton has been exposed by breakage. The number of eggs per capsule is quite uniform within a given cluster, but varies between clusters. We have observed capsules containing from two to six eggs, but four or five is the number most commonly encountered. Each egg is approximately 0.1 mm in diameter. The embryological development of this species closely parallels the general pattern for polyclads described by Hyman (1951: 171–175).

The Müller's larvae, which measured approximately 0.1 mm in diameter, were small enough to move freely into the spongelike skeleton of the coral which surrounded the egg sacks. Occasionally, we observed Müller's larvae within the skeletal material of *Montipora*, along with small flatworms of less than 0.5 mm length. These animals moved deep within the coral skeleton when exposed to the bright light needed to observe them under magnification. Flatworms longer than 0.5 mm were too large to get into the skeleton and remained on the surface. These observations led us to speculate that *Prosthiostomum* (*P.*) sp. undergoes metamorphoses and early development within the *Montipora* head. This environment would afford protection from larger predators and contains a ready source of coral tissue which extends to a depth of several mm under the surface of the skeleton. Infection of the coral from within the head would allow larvae and juveniles to avoid the nematocyst defenses of the coral.

OBSERVATIONS ON *Prosthiostomum* (*P.*) sp. IN NATURAL AND DISTURBED SYSTEMS

The discovery of the flatworms on *Montipora* in our laboratory tanks and observations on the appearance of corals infected with the parasite provided information needed for subsequent recovery of the flatworm from Kaneohe Bay, Oahu. A large parasitized head of *M. verrucosa* was observed on the Coconut Island reef, near the channel leading to the Hawaii Institute of Marine Biology. Although the animals were not noticeable, evidence of infection was recognized in the form of the characteristic denuded areas of coral tissue. A small section of approximately 300 g wet weight was removed from the head and taken to the laboratory for inspection. From the cryptic areas of this fragment, six *Prosthiostomum* (*P.*) sp. specimens, each measuring from 6 to 8 mm in length, were recovered. Careful observations on the infected head from which the original field specimens were recovered were made in the months following its discovery. Initially, only the cryptic areas within the head were infected, but as the coral tissue was removed from these inner regions the parasites apparently were forced to move into the more peripheral areas to feed, probably during the night. Ultimately the damaged and dead areas became larger and spread outward from the initial site of infection. Within 6 months most of the tissue had been grazed off the coral head. Only a few isolated pinnacles of exposed living coral were unaffected. At this point grazing appeared to cease and the remaining living areas continued to grow.

Specimens of *Prosthiostomum* sp. were found throughout 1972 in the southern sector of Kaneohe Bay. Infected corals were recognized by the characteristic pink splotches which result from the removal of coral tissue. In nearly all cases we were able to recover flatworms from

such heads. All of the flatworms recovered from the field were taken from the eutrophic south basin of the bay, where water quality and the once magnificant reefs have recently undergone considerable degradation due to rapid urbanization and the discharge of sewage into the area (Banner and Bailey 1970; Caperon, Cattell, and Krasnick 1971).

We were unable to recover specimens from the relatively unpolluted northern part of the bay where extensive beds of *M. verrucosa* are present. The cryptic areas of the *Montipora* colonies from the nothern part of the bay were covered with living tissue, and evidence of heavy infestation could not be detected.

In the south basin of Kaneohe Bay the population of *Prosthiostomum* appears to fluctuate widely. In June 1972, nearly half of the *Montipora* heads on the Coconut Island reef were infected by the flatworm, this being evidenced by heavy tissue damage and the presence of numerous flatworms in the cryptic areas of the damaged heads. By September, signs of flatworm grazing were no longer evident, and it was difficult to find specimens. By December, damage produced from infections was again widespread enough to cause death to large areas of *Montipora* tissue.

In Kaneohe Bay, flatworm infections cooccur with various forms of urban pollution. The cryptic and lower portions of the corals found in polluted areas of the bay tend to be without tissue, although the uppermost areas of these corals may continue to survive. It is impossible to differentiate areas killed by intermittent flatworm infections from areas killed by other agents such as sedimentation or algal overgrowth unless one is fortunate enough to observe the infestation in progress. However, in view of the relatively high percentage of heavily infected heads observed in the south basin, it would appear that under certain conditions *Prosthiostomum* (*P.*) sp. can be a significant factor in limiting the distribution and abundance of its host.

The parasite was originally discovered in laboratory tanks when it became a serious pest and began to kill coral heads of 50–300 g wet weight. It appeared that such outbreaks could be the result of the overly simplified biotic environment of our tanks, which normally contained only corals and those organisms introduced incidentally with the running seawater. To test this possibility a series of four tanks of the same type described in the following section was established with natural coral rubble substrate taken from the reef, along with all associated benthic biota and a number of characteristic reef fish (*Scarus* sp., *Acanthurus sandvicensis*, *Asteropteryx semipunctatus*). When heavily infected *Montipora* heads were transferred to these tanks, the parasites ceased to be a threat. The damaged heads recovered within a week and further severe damage did not occur during the course of the subsequent 10-week experiment. It is likely that a predator of the flatworm was among the many species introduced with the material added from the reef.

Furthermore, use of natural coral rubble substrate and associated fauna reduced detrital buildup in the tanks and allowed coral tissue to completely cover the skeleton. When the corals were kept on glass plates, organic sediment accumulated near the base, killing the coral tissue in contact with the glass and possibly increasing chances of infection by *Prosthiostomum* larvae. This may provide a clue as to why the parasite achieves higher populations in the polluted areas of Kaneohe Bay. The coral of this region has been damaged by sedimentation and algal overgrowth and may be more vulnerable to successful settlement of the parasite larvae. At the north end of the bay single *Montipora* colonies covering several square meters are common. The tissue of these heads is continuous, possibly presenting a barrier that cannot be penetrated by the larvae. Alternative explanations for the success of the parasite in the south basin could be the restricted circulation and unstable plankton community of the area (Clutter 1969) which might enhance the success of the parasite larvae. Unlike the other common corals, *M. verrucosa* shows tolerance to physical factors associated with sewer discharge (Maragos 1972), but is still being eliminated from polluted regions. This may indicate that biotic factors such as parasitism may be of importance in controlling the distribution of this species in Kaneohe Bay.

TABLE 1

DATA FROM THERMAL TREATMENT TO TEST EFFECTS ON HOST–PARASITE RELATIONSHIP

TREATMENT	TEMPERATURE °C				ALTERATION FROM AMBIENT °C	
	$\bar{X}$	SD	MIN	MAX	$\bar{X}$	SE
Heated	28.1	1.2	22.5	30.6	+4.45	0.03
Heated	25.8	0.9	22.4	28.5	+2.12	0.02
Ambient	23.6	1.1	21.4	27.2	0	0
Chilled	19.8	1.2	17.5	24.7	−3.89	0.03

NOTE: Data based on hourly sampling rates, 1 March to 25 April 1972. N = 1,248.

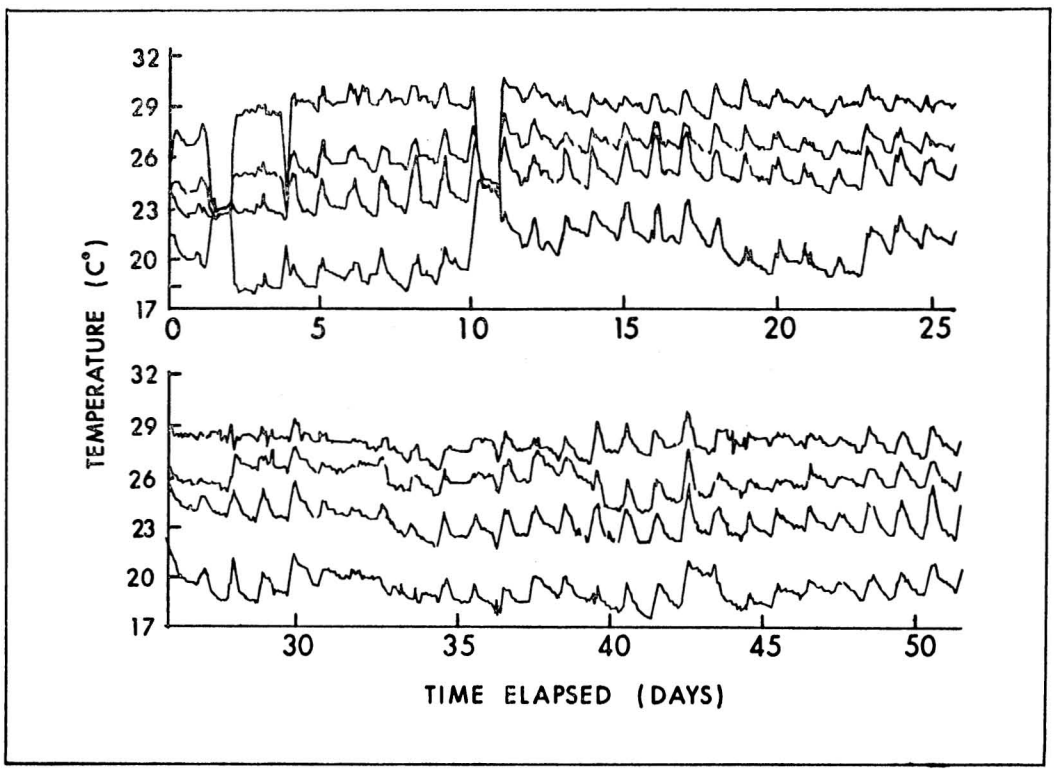

FIG. 7. Plot of temperatures in the tanks during the period of the experiment.

PARASITE/HOST RESPONSE TO ALTERED THERMAL CONDITIONS

A controlled laboratory experiment designed to test the effect of thermal environment on the host/parasite relationship was conducted in a series of tanks having inner dimensions of 115 cm × 119 cm × 45 cm deep and filled to a depth of 35 cm. The tanks were maintained outdoors in full natural light and supplied with temperature-regulated, nonrecirculating, unfiltered seawater pumped from Kaneohe Bay at a rate sufficient to flush the tanks in less than 1 hour. Only inert materials contacted the seawater; pump and piping surfaces were of polyvinyl chloride plastic and heat exchange surfaces were of titanium. Tank temperatures were recorded for 5-minute periods at hour

TABLE 2

EFFECT OF TEMPERATURE ON THE GROWTH OF *Montipora verrucosa*, 1 MARCH TO 25 APRIL 1972

MEAN TEMPERATURE (°C)	MEAN % INCREASE IN SKELETAL WEIGHT	NET CALCIFICATION RATE (mg g^{-1} day^{-1})
28.1	16.7	2.85
25.8	20.2	3.36
23.6	19.5	2.98
19.8	6.53	1.01

TABLE 3

NUMBERS OF *Prosthiostomum* (*P.*) SP. REMOVED FROM TANKS DURING THE EXPERIMENT

MEAN TEMPERATURE (°C)	DAY OF EXPERIMENT									TOTAL
	16	19	21	25	28	33	37	43	51	
28.1	82	46	21	41	7	9	10	11	8	235
25.8	100	120	53	110	32	35	10	23	38	531
23.6	15	84	21	65	38	30	42	73*	53	421
19.8	4	21	8	34	14	15	10	26*	80	212

* Wet weights of 26 specimens removed from tank held at 19.8° C = 28 mg. Average = 1 mg. Largest specimens from tank held at 25.8° C weighed approximately 10 mg each.

intervals by means of a scanning thermistor telethermometer.

Sixty *M. verrucosa* colonies were added to each of the experimental tanks, care being taken to make all four groups as similar as possible. Only colonies of 15 to 45 g wet weight that were completely covered with living tissue and relatively free from crevices were selected. Neither flatworms nor signs of their presence were evident when the corals were collected, although it is possible that individuals of less than 1 to 2 mm in length were present. Since the seawater being supplied to the tank was unfiltered, we assume constant larval recruitment. Associated organisms were removed from the corals so as to prevent predation on the flatworms, and the corals were placed on glass plates supported 10 cm from the tank bottom.

Four thermal treatments were used (see Table 1), with one approximating natural (ambient) reef temperatures, one chilled by 4° C, one heated by 2° C and one heated by 4° C. All tanks followed the diurnal temperature curve (Fig. 7) during the 2-month experimental period. The corals held at the highest and lowest thermal treatments lost some zooxanthellar pigment and areas of tissue, indicating that such temperatures are suboptimal. The corals in the tanks held at mean temperatures of 25.8° C and 23.6° C remained healthy throughout the experiment.

Coral growth, expressed as change in coral skeletal weight, was determined by measuring the change in buoyant weight during the experiment (Franzisket 1964; Maragos 1972). Coral growth data for the experiment are presented in Table 2. Corals held at a mean temperature of 25.8° C showed the highest skeletal growth rate. A detailed analysis of the coral growth rate data taken during this experiment has been presented elsewhere (Coles 1973). Growth rate in the 26° C treatment was found to be significantly greater than at 28° C and substantially (but not significantly) greater than at 24° C. Growth at 20° C was significantly less than at all other temperatures.

On the 16th day of the experiment evidence of coral parasitism was noted. At this point and at 2- to 4-day intervals thereafter, the corals were carefully inspected and all *Prosthiostomum* (*P.*) sp. encountered were removed from the coral specimens and their underlying glass

TABLE 4

MEAN WET WEIGHTS FOR *Prosthiostomum* (*P.*) SP. RECOVERED ON LAST DAY OF EXPERIMENT (AFTER 24 HOURS IN 70-PERCENT ETHANOL)

MEAN TEMPERATURE (°C)	NUMBER OF INDIVIDUALS	TOTAL WET WEIGHT (g)	MEAN WEIGHT (mg)
28.1	8	0.035	4
25.8	38	0.191	5
23.6	53	0.223	4
19.8	80	0.203	3

plates. Data on numbers of animals harvested are presented in Table 3.

Throughout the experiment the flatworms recovered from the 25°–27° C regime were considerably larger than specimens recovered from other temperatures, with some reaching a length of 14–18 mm. In contrast, the specimens recovered from the chilled tank (18°–20° C) were generally in the 1–4 mm size range as were specimens from the warmest tank. For example, on the 43rd day of the experiment the combined weight of the three largest flatworms removed from the 25.8° C treatment exceeded the entire weight of all 26 specimens removed from the coldest tank (Table 3). Mean weights for the flatworms recovered on the last day of the experiment are reported in Table 4, showing the same pattern. In addition, the 25.8° C treatment consistently produced larger harvests of parasites throughout the experiment (Table 3). The total number of flatworms removed from the 25.8° C treatment was over twice that of the tanks held at the highest and lowest temperature. We estimate that the 25.8° C treatment produced at least four to five times the parasite biomass of the tanks held at the temperature extremes and at least twice the biomass of the 23.6° C treatment.

It is evident that the temperature favoring parasite tissue production rate coincided with the optimal temperature for the host. Food was not limiting to the flatworm because most of the corals remained covered with tissue throughout the experiment. Furthermore, all potential predators of the flatworms had been removed from the tanks, and, except for temperature, all conditions were nearly identical in the four tanks. In view of the extremely high rate of parasitism among the corals held at 25.8° C, it is surprising that the host could still maintain the highest growth rate in the series.

The basic mechanisms involved in regulating the observed parasite/host thermal optima are probably physiological and related to the intimate evolutionary association of these two species. Such thermal regulation of the relationship, whether coincidental or the result of selective pressure, will tend to produce a more stable parasite/host interaction in areas such as Kaneohe Bay where temperatures vary seasonally between 21° and 28° C. If other factors in such a system remain constant, maximum parasitism would tend to occur when thermal conditions were optimal for the coral and would tend to diminish under less favorable temperatures. Obviously such a relationship will produce the maximum parasite biomass over the course of the year with least damage to the host.

SUMMARY

1. *Prosthiostomum* (*Prosthiostomum*) sp. probably represents the first polyclad known to feed on coelenterate (coral) tissue and is one of the few animals that can be described as an obligate coral parasite.
2. This species will attack only *Montipora verrucosa* and its conspecifics.
3. The flatworm appears to become a serious pest only in disturbed coral systems such as the polluted area of Kaneohe Bay, Oahu, and in simplified laboratory situations.
4. The parasite/host relationship appears to be physiologically regulated to allow maximum parasitism under thermal conditions that are optimal for the host.

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