

Feeding Behavior in the Hawaiian Zoanths *Palythoa* and *Zoanthus*¹

AMADA ALVAREZ REIMER²

ABSTRACT: *Palythoa psammophilia* Walsh & Bowers and *Zoanthus pacificus* Walsh & Bowers are two subtropical, subtidal zoanths closely related phylogenetically but widely different in their feeding methods. *Palythoa* is a predator that feeds on zooplankton, particularly crustaceans. Of a vast array of items offered to *Zoanthus* in the laboratory, only small pieces of freshly killed or frozen fish elicited positive feeding responses. In natural situations *Zoanthus* has never been observed to feed.

Palythoa polyps capture live prey with their tentacles and use these to hold the prey against the peristome. Very few nematocysts are discharged and they do not paralyze the prey. The behavioral response called "tentacle protrusion" allows the polyps to capture additional prey while ingesting one just caught. The optimum density of zooplankton, which causes the fastest response and largest capture, was found to be 200 *Artemia* per m³. This represents approximately 10 times the zooplankton density calculated for the natural environment of *Palythoa*.

After the food has been obtained, either by capture (*Palythoa*) or seizure of items (*Zoanthus*), both animals show the same complex and orderly series of steps which is called the feeding reaction and consists of the following: (1) Lip formation. A group of tentacles seizes the food, the edge of the disc carrying these tentacles first contracts, then rises up and turns inward, thereby folding tentacles and food toward the mouth; (2) Mouth opening. Upon contact with the food, the mouth borders separate and the food is swallowed; and (3) Ingestion response. Food disappears in the coelenteron and the borders of the mouth close over it.

SINCE TREMBLEY PUBLISHED his famous *Mémoires* in 1744, with his observations on the biology of *Hydra*, a large number of papers have dealt with feeding in predatory coelenterates. Reviews covering this work are by Parker (1896, 1917), Jennings (1905), Boschma (1925), Yonge (1930), Pantin and Pantin (1943), and Lenhoff (1968). The nonpredatory group of coelenterates, however, has re-

ceived considerably less attention, the only comprehensive works published being those by Gohar (1940, 1948).

This paper describes and compares the feeding responses of two zoanths: *Palythoa psammophilia* Walsh & Bowers (1971), a predator on zooplankton, and *Zoanthus pacificus* Walsh & Bowers (1971), an animal that has never been observed to feed in nature.

Palythoa is a semicolonial animal found in large numbers on the sand flats of Kaneohe Bay, Oahu, Hawaii. The polyps lie buried in the fine sand to the level of the oral disc and are found solitary or in a small group.

Palythoa belongs to the predatory coelenterates, a large group of animals that utilize complex intracellular secretion products, the nematocysts, in the capture of prey.

Because *Palythoa* is sessile and has very limited movements of the column and oral disc,

¹ This work was supported by a fellowship from the American Association of University Women and a Biomedical Sciences support grant no. FR-07012-02 from the National Institutes of Health. It represents one aspect of the doctoral dissertation presented by the author to the faculty of the University of Southern California in partial fulfillment of the requirements for the Ph.D. degree. Manuscript received November 16, 1970.

² University of Southern California, Department of Biological Sciences, Los Angeles, California 90007. Present address: Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Canal Zone.

the animal depends largely on the natural water movements to carry food within the range of its tentacles. As Crisp (1962) pointed out, the advantage of this system is that food can be derived from a very wide area with minimum effort on the part of the animal. The disadvantage, however, is that the animal must be content with whatever food arrives by chance and cannot afford the luxury of a specialized diet. Hyman (1940) reported that sea anemones eat almost any live animals of suitable size. Yonge and Nichols (1931) made the same observation for corals.

Anemones and zoanths use their tentacles to seize food, and, naturally, they are restricted to prey of a size that can be captured by their tentacles. Other coelenterates, such as many siphonophores, possess fishing filaments (Mackie and Boag, 1963). Some species, notably *Physalia*, use these structures to capture large prey such as fish (Wilson, 1947). Other species such as *Nanomia* use their fishing filaments to catch small crustacean larvae (Vogt, 1854). Although very little is known about the natural diet of predatory coelenterates, most of them can be maintained successfully in the laboratory on a diet of *Artemia*, and the general consensus is that, in nature, they feed on crustacean microplankton.

Errington (1967) noted that most predatory species are adapted to do some fasting when necessary and are able to gorge themselves when they have access to an abundance of food. The rate of prey captured is usually proportional to the concentration of the food organisms (Crisp, 1962), but there is a limit to how much the predator can ingest. Crisp (1962) found that barnacles fed *Artemia* ingested only a limited amount of food, the excess material caught by the cirri being returned to the water. He concluded that the rate of ingestion does not depend on the concentration of nauplii in the surrounding water, provided, of course, that it exceeds certain minimal requirements.

Zoanthus is a colonial animal common in surge pools, rocky shores, and coral reefs of all Hawaiian islands. In the areas where it is found, it is strikingly abundant, covering large expanses of the reefs and shores. *Zoanthus* belongs to the group of nonpredatory coelenterates

and seems to survive without any intake of exogenous food.

Von Holt and Von Holt (1968) reported unpublished observations made by Goreau regarding the semicomplete or complete independence of exogenous food and by Goreau and Neuman regarding the lack of typical morphological digestive structures in some tropical *Zoanthus* species.

Gohar (1940), in a comprehensive study of the Xenidiidae of the Red Sea, and later (1948), on the alcyonarian *Clavularia hamra*, reported that these coelenterates will not swallow, or even seize, food of any kind, plant or animal, alive or dead, whole or cut. He also noticed that *Clavularia* has very poorly developed organs of digestion.

The only report of a *Zoanthus* species ingesting particulate food is that of Hadden (1968), who found that *Zoanthus sociatus* can swallow pieces of frozen butterfly fish obtained from the same habitat as that in which the zoanthid is found.

Although I have patiently observed *Zoanthus* for long periods of time, I have been unable to learn how these zoanths feed.

METHODS

Field observations were carried out on the North Reef of Coconut Island, Oahu, Hawaii, during the summer of 1967. Laboratory observations were conducted in Los Angeles during 1969 on specimens that had been collected from the North Reef of Coconut Island and shipped to California by Mr. Ralph L. Bowers. Upon arrival colonies of *Palythoa* and *Zoanthus* (Fig. 1) were placed in well-aerated, 5-gallon aquaria at $25^{\circ} \pm 1.5^{\circ}$ C and 33 ‰ salinity.

Two hours preceding an experiment, colonies were removed from the large aquarium, placed in 250-ml finger bowls containing fresh Instant Ocean (Aquarium Systems, Inc., Wickliffe, Ohio), and were offered the experimental food. *Artemia salina* nauplii were raised in the laboratory from eggs (Bay Shrimp Eggs, San Francisco) in a cone-shaped hatchery. *Artemia* adults, purchased from Los Angeles Aquarium, were rinsed in fresh Instant Ocean and offered to the zoanths. A variety of food materials



FIG. 1. Colonies of *Palythoa psammophila* (P) and *Zoanthus pacificus* (Z).

were cut in pieces small enough to fit into the mouth of the polyps and offered to them.

The reactions of the animals were observed, timed (Cletimer Stop Watch), and recorded.

Observations were completed only when food had been either swallowed or rejected.

FEEDING REACTION

Both *Palythoa* and *Zoanthus* respond to food with a complex and organized series of steps called the feeding reaction. This consists of three major components:

1. Lip formation. A group of tentacles seizes the food (Fig. 2A). The edge of the disc carrying these tentacles first contracts, so that they group together around the food, then rises and turns inward (Fig. 2B), thereby folding tentacles and food toward the mouth. The lip may be localized if it involves a restricted number of tentacles (Fig. 2B) or generalized if it involves all the tentacles (Fig. 2C).

2. Mouth opening. As food is being carried by the tentacles toward the mouth, the borders

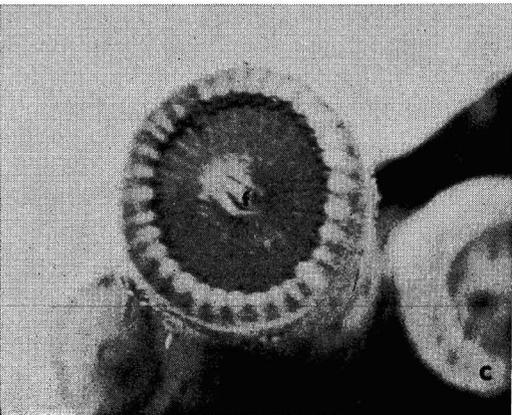
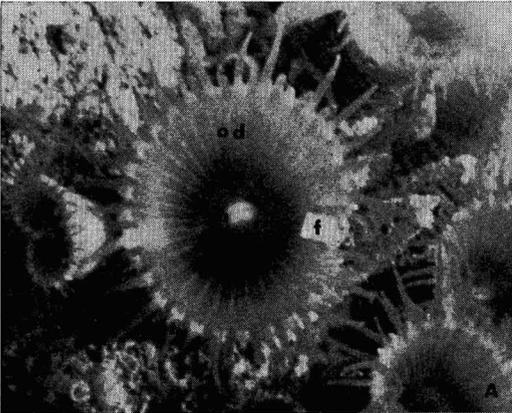


FIG. 2. Feeding reaction in *Palythoa* (m, mouth; od, oral disc; t, tentacles; f, food represented by a small piece of filter paper imbibed in *Artemia* extract). A, seizure of food by a small group of tentacles; B, lip (l) secures and pushes food to the mouth; C, food (f) being ingested.

of the mouth separate so that the food may be ingested (Fig. 2C). Under certain circumstances the mouth-opening response is replaced by a reaction that may be termed "exposure of the actinopharynx." Mariscal and Lenhoff (1968) described a general swelling or "inflating of the tissue immediately surrounding the mouth." The same phenomenon was reported by Lind-

stedt, Muscatine, and Lenhoff (1968) for the sea anemone *Boloceroïdes*. The tissue surrounding the mouth corresponds to the glandular epithelium of the tube, called the actinopharynx, that leads from the mouth into the body cavity. Under certain stimuli this tissue becomes inflated and may protrude as bladderlike lobes.

3. Ingestion of food. The feeding reaction is culminated by the swallowing of food. After the food disappears in the coelenteron the mouth closes and the polyps become relaxed.

RESPONSE OF ZOANTHIDS TO LIVE MATERIAL

Palythoa psammophilia

RESPONSE TO *Artemia salina* (ADULT SHRIMP): On contact with *Artemia* the tentacles of *Palythoa* writhe and discharge very few nematocysts to immobilize the shrimp. Examined prey seldom had more than two nematocysts' tubes piercing their lower abdomen. Once the prey has been secured by the tentacles, it is either pushed by these toward the peristome or enclosed in a lip formed at the point of contact between the prey and the polyp's tentacles. The lip becomes generalized involving all the tentacles. The mouth opens slightly and the oral disc closes over the shrimp (Fig. 3, left), which is swallowed shortly afterward. The entire reaction takes an average of 0.72 minutes. After the

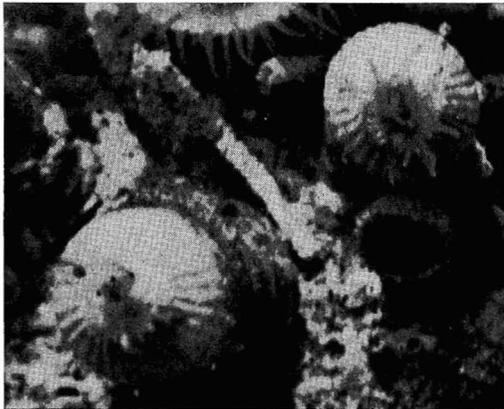


FIG. 3. Response of *Palythoa* to *Artemia salina*. After capturing *Artemia* the polyps close over the prey. Note eyes of *Artemia* on polyp at left. Another polyp shows a group of tentacles protruding, after having ingested shrimp.

TABLE 1
INFLUENCE OF A BEHAVIORAL RESPONSE*
ON THE ABILITY OF *Palythoa* TO MAKE
SUCCESSIVE CAPTURES OF *Artemia*

NUMBER OF POLYPS TESTED	PERCENTAGE OF POLYPS WITH TENTACLES PROTRUDING AFTER CATCH	PERCENTAGE OF POLYPS MAKING SUCCESSIVE CAPTURES
69	66	73
50	0	25

* A group of tentacles protrude after the animal, having captured live *Artemia* (Fig. 3a), closes its oral disc.

shrimp has been ingested, a group of expanded tentacles protrudes above the rim of the contracted disc (Fig. 3, right). This proved to be a behavioral response that allows consecutive capture of prey. Table 1 shows that 73 percent of the polyps that maintain a clump of protruding tentacles after capturing the first prey do capture a second time. Of those that do not show the tentacle protrusion, only 25 percent achieve consecutive captures.

The results presented in Table 2 suggest that shrimp density may have an effect in producing the tentacle-protrusion response. Polyps exposed to either low (5 or 15 per 250 ml) or high (90 per 250 ml) densities of shrimp tend to show higher incidence of tentacle-protrusion than do polyps exposed to intermediate (50 or 70 per 250 ml) densities. *Artemia* density also seems to have an effect on the frequency with which the shrimp escapes after being captured by *Palythoa*. Table 3 indicates that, only when the shrimp density is 16 or less per 250 ml, can

TABLE 2

PERCENTAGE OF POLYPS OF *Palythoa* WHICH LEAVE TENTACLES PROTRUDING AFTER CAPTURING *Artemia*

SHRIMP DENSITY PER 250 ML	NUMBER OF POLYPS TESTED	PERCENTAGE OF POLYPS WITH TENTACLES PROTRUDING AFTER FIRST CAPTURE
5	5	100
16	16	100
30	20	50
50	20	46
70	20	30
90	20	78

TABLE 3
FREQUENCY OF ESCAPE OF *Artemia salina*
FROM *Palythoa*

SHRIMP DENSITY PER 250 ML	NUMBER OF POLYPS TESTED	PERCENTAGE OF SHRIMP ESCAPING AFTER CAPTURE
5	20	50
16	20	22
30	20	0
50	20	0
70	20	0
90	20	0

Artemia escape after capture. Such inability to escape, however, may occur only in enclosed containers such as used in the experiments. Many shrimp swimming actively about in a finger bowl may well interfere with each other's free movements and lower the overall oxygen supply in the bowl, thus making the shrimp less able to escape after being captured. *Palythoa* requires a somewhat longer time to capture shrimp in the lower densities (Table 4). The reason for this may be that, in containers crowded with shrimp, chemicals released by *Artemia* lower the threshold of response in *Palythoa* and cause the polyps to react much faster when a shrimp collides with their tentacles. It seems logical to assume that the density at which the largest number of shrimp is captured in the shortest time represents the optimum prey density for *Palythoa*. Such density was found to be 50 shrimp per 250 ml. However, the experiments were discontinued after the second capture in densities of 70 shrimp per 250 ml and after the first capture

in densities of 90 shrimp per 250 ml, for the number of shrimp swimming about the polyps made it extremely difficult to record accurately the number of shrimp being caught or the sequence of captures by a particular polyp. For this reason it is not possible to say that 50 shrimp per 250 ml represents the optimum concentration, but only that this is the minimum concentration of shrimp at which *Palythoa* can acquire food rapidly and efficiently. After 1.33 minutes the polyps captured 74 percent of the shrimp present in the dish. In densities of 30 *Artemia* per 250 ml, the polyps require 1.64 minutes to capture 74 percent of the shrimp present in the dish. Although the times of capture are not very different, the number of shrimp caught is significantly higher in densities of 50 per 250 ml than in 30 per 250 ml.

Another important feature of the prey-predator relationship between *Artemia* and *Palythoa* is the number of shrimp that can be captured at any one time (Table 5). Here again the density of shrimp is very important in determining the number of shrimp caught. The highest density gives the highest number of prey caught at any one time. The maximum observed was six shrimp captured simultaneously by a single *Palythoa* polyp. However, *Palythoa* most often captures only one *Artemia* at a time and ingests this before capturing a second one. Only a few polyps capture more than three shrimp at any one time (Table 5).

The shrimp captured is ingested and digested, for, after 10 to 12 hours, the clean exoskeletons of *Artemia*, together with some brown-yellow material and some granular, red material, are extruded through the mouth.

TABLE 4
FREQUENCY* OF SHRIMP (*Artemia salina*) CAPTURE BY *Palythoa*

SHRIMP DENSITY PER 250 ML	TIME OF FIRST CAPTURE (min.)	TIME OF SECOND CAPTURE (min.)	TIME OF THIRD CAPTURE (min.)	TIME OF FOURTH CAPTURE (min.)
5	1.91 ± 1.23 (5)**	None	None	None
16	0.86 ± 0.64 (16)	None	None	None
30	0.42 ± 0.19 (20)	2.75 ± 0.69 (6)	43.83 (3)	55.66 (1)
50	0.33 ± 0.15 (20)	0.94 ± 0.68 (6)	1.02 ± 0.48 (6)	1.33 ± 0.77 (5)
70	0.28 ± 0.19 (20)	10.91 ± 6.58 (6)	Not observed	Not observed
90	0.76 ± 0.65 (20)	Not observed	Not observed	Not observed

* Rates are expressed as mean values with standard deviation.

** Number in parenthesis indicates number of polyps tested.

TABLE 5
EFFECTS OF SHRIMP DENSITY ON THE ABILITY OF *Palythoa* TO PERFORM
CONSECUTIVE CAPTURE OF *Artemia salina*

SHRIMP DENSITY PER 250 ML	NUMBER OF POLYPS TESTED	PERCENTAGE OF POLYPS ACHIEVING CONSECUTIVE CAPTURES	PERCENTAGE OF POLYPS CAPTURING SHRIMP, AT ANY ONE TIME						
			1	2	3	4	5	6	
5	5	0	100						
16	16	0	100						
30	20	20	80	20					
50	20	20	80	10	10				
70	20	40	60	20	20				
90	20	50	50	30	5	5	5	5	5

RESPONSE TO SYLLID POLYCHAETES, NEMERTEANS, AND *Tubifex* WORMS: Tentacles of *Palythoa* writhe, the mouth opens, and food is ingested within 1 minute.

Zoanthus pacificus

RESPONSE TO *Artemia* NAUPLII AND ADULTS: There was no reaction to shrimp moving about the polyps or colliding with their tentacles.

RESPONSE TO SYLLID POLYCHAETES, NEMERTEANS, AND *Tubifex* WORMS: No reaction was observed.

RESPONSE OF ZOANTHIDS TO DEAD MATERIAL

Palythoa psammophila

RESPONSE TO FISHSTICKS (CERTI-FRESH BREADED COD), FROZEN COD, AND FRESHLY KILLED *Gambusia* (ALL CUT IN PIECES 1×2 mm IN SIZE: All the polyps tested showed a characteristic feeding reaction. When food is placed on its peristome, the polyp first responds with mouth opening; then the area surrounding its mouth becomes depressed so that its oral disc resembles the upper portion of a funnel. At the same time its tentacles curl up and move toward its mouth, enclosing the food, which is ingested within 1 to 3 minutes. When the food is placed on the margin of the oral disc, the animal first forms a lip which encloses the food and literally pushes it toward its mouth; when the food reaches the peristome, the mouth opens and the food is ingested.

After ingestion the polyps begin to relax and within 8 to 10 minutes they are expanded and capable of responding to more food.

RESPONSE TO FRESHLY KILLED *Artemia salina*: Regardless of where the shrimp is placed on the oral disc, a lip is formed. This encloses the food and carries it to the mouth, which opens within 30 seconds. The shrimp is ingested within 2 to 3 minutes.

All food offered and ingested by *Palythoa* remained in the animal for 10 to 12 hours. After this period pellets containing clean exoskeletons of *Artemia* mixed with a greenish-brown material and with red granules were eliminated through the polyp's mouth.

RESPONSE TO FILAMENTOUS GREEN AND BLUE-GREEN ALGAL MASS: Rejected by all the polyps tested.

Zoanthus pacificus

RESPONSE TO FISHSTICKS (CERTI-FRESH BREADED COD, CUT IN 0.5×1 mm PIECES: All the polyps tested showed a definite positive reaction. Their response consisted of curling down the tentacles, raising the mouth, exposing the actinopharynx, and ingesting the food. After a small piece of fishstick had been kept on the exposed lining of the actinopharynx for 1 to 3 minutes, the process of ingestion took about 30 minutes. The column of the polyps contracted repeatedly and somewhat rhythmically during swallowing. On several occasions 12 to 24 hours after ingestion of a fishstick piece, a greenish-brown mass was eliminated through the polyp's mouth. The mass contained red granules and is regarded as a product of digestion.

RESPONSE TO FRESHLY KILLED *Artemia salina* (ADULT SHRIMP CUT IN 0.5-mm-LONG

PIECES): When deposited on the peristome or on the margin of the oral disc, dead specimens of *Artemia* caused a weak lip formation in 10 percent of the polyps tested. The rest of the animals rejected the food by creating a ciliary current which moved the material to the margin. Here several tentacles collapsed, the edge with the shrimp sank, and the food slid downward off the oral disc.

RESPONSE TO FILAMENTOUS GREEN AND BLUE-GREEN ALGAL MASS: Rejected by all the polyps tested.

DISCUSSION

The seemingly inactive polyps of *Palythoa* show quick and predictable responses to zooplankton. The steps of the feeding reaction, although somewhat modified, are essentially those described for most predatory coelenterates (Lenhoff, 1968). When *Artemia* contacts *Palythoa's* tentacles, the polyp discharges nematocysts which pierce the prey, a grasping lip secures and pushes the food toward the mouth, the mouth opens, and the prey is ingested. *Palythoa* captures prey with the tentacles by discharging few nematocysts. This zoanthid relies more on the grasping action of a localized lip which secures and pushes the prey toward its mouth than on immobilizing its prey with toxins injected upon contact with it, such as occurs in *Hydra* (Ewer, 1947) and in *Pennaria* (Pardy and Lenhoff, 1968).

The clasping of food by tentacles and disc has been described previously for sea anemones such as *Anemonia sulcata* (Pantin and Pantin, 1943). Torrey (1904a, b) described similar behavior in *Sagartia* and in the hydroid *Corymorpha*.

Because *Palythoa* is sessile, it undoubtedly is dependent for its food on the available supply at particular times of the year. Feeding thus becomes a fortuitous and discontinuous process.

According to Peterson (personal communication), the waters near the reef where *Palythoa* was collected contain microzooplankton overwhelmingly dominated by one of two copepod genera and their respective naupliar and copepodite stages. The animals are *Pseudocalanus* sp. and *Oithona* sp. Peterson estimated that the

copepodites of these crustaceans numbered 40,000/m³. If expressed as density per milliliter this could represent six copepodites per 250 ml, which compares to the lowest density of *Artemia* used in this study. Given the size of the copepodites, 0.18 to 0.5 mm for *Pseudocalanus* and 0.40 mm for *Oithona* (cephalothorax length on both) and their density, they do not seem to represent much food for *Palythoa*. The polyps probably capture not only microcrustaceans but also macrozooplankters such as barnacle nauplii, crab zoea larvae of *Lucifer chacei* (pelagic decapod shrimp), and *Alpheus* (snapping shrimp) mysis stages. According to Peterson's estimates of the macrozooplankters named above, only 212 animals occur per cubic meter. The food available to *Palythoa* in the natural environment does not seem to amount to much but it is impossible to decide how significant it is for *Palythoa* without knowing the metabolic requirements of the polyps and the ways in which they might fulfill them.

The number of zooplankters consumed by *Palythoa* will depend on the number of collisions of their tentacles with the plankters: it would seem that the higher the density of zooplankton the higher the possible number of collisions. But if the density increases beyond a certain point the collisions would be so numerous that *Palythoa* would spend more time contracted and capture less prey. There is an indication of this in the experiments where 90 shrimp per 250 ml were offered, but the information gathered was too scant to place much importance on it. This observation agrees with the information reported by Cushing (1968), who found that prey mortality decreases with prey density because the time spent capturing and eating increases. Cushing worked with grazing herbivorous copepods which obtain their food by tactile encounter as they move steadily through the water. This method, according to Crisp (1962), represents an inverted system with respect to that of sessile animals that are static and spread out as a surface layer, while their food material is carried past them by the movement of the water. In both systems, however, the same rules seem to operate for both involve prey-predator relationships.

The optimum density of zooplankton, that

which causes the fastest response and largest capture, was found to be 50 shrimp per 250 ml. This is about 10 times that calculated for the natural environment of *Palythoa*.

Although the information obtained on the feeding behavior of *Zoanthus* is rather scant, one very important observation made was that this zoanthid has a feeding reaction similar to that of *Palythoa*. This reaction can be elicited in experimental polyps by offering them small pieces of freshly killed *Gambusia* or frozen cod. Hadden (1968) found *Zoanthus sociatus* would take pieces of butterfly fish collected from the same environment as that in which the polyps were found. This information suggests that species of *Zoanthus* may feed on particles proceeding from fish.

ACKNOWLEDGMENTS

I wish to thank Dr. Ralph L. Bowers of the University of Hawaii for the collection and shipment of the zoanths from Hawaii to Los Angeles; Mr. William T. Peterson of the University of Hawaii for valuable information on the diversity and abundance of zooplankton in Kaneohe Bay, Hawaii; and Mr. Roger D. Reimer for the photographs presented in this paper.

LITERATURE CITED

- BOSCHMA, H. 1925. On the feeding reactions and digestion in the coral polyps *Astrangia danae* with notes on its symbiosis with zooxanthellae. *Biological Bulletin*, Woods Hole, vol. 49, pp. 407-439.
- CRISP, D. J. 1962. An assessment of plankton grazing by barnacles. In: *Grazing in terrestrial and marine environments*, pp. 251-264. Blackwell Scientific Publishing Company, Oxford, England.
- CUSHING, D. H. 1968. Grazing by herbivorous copepods in the sea. *Journal de Conseil Permanent International pour l'Exploration de la Mer*, vol. 32, no. 1, pp. 70-82.
- ERRINGTON, P. L. 1967. *Of predation and life*. The Iowa State University Press, Ames, Iowa. 277 pp.
- EWER, R. F. 1947. On the functions and mode of action of the nematocysts of *Hydra*. *Proceedings of the Zoological Society, London*, vol. 117, pp. 365-376.
- GOHAR, H. A. F. 1940. Studies on the Xenidiidae of the Red Sea. *Publications of the Marine Biological Station, Ghardaqa*, vol. 2, pp. 25-118.
- . 1948. A description of some biological studies of a new alcyonarian species *Clavularia bamra* Gohar. *Publications of the Marine Biological Station, Ghardaqa*, vol. 6, pp. 1-33.
- HADDEN, E. M. 1968. The relationship between *Zoanthus sociatus* and its zooxanthellae. Unpublished Ph.D. dissertation, Yale University.
- HYMAN, L. H. 1940. *The invertebrates: Protozoa through Ctenophora*. Vol. 1. McGraw-Hill Book Company, New York.
- JENNINGS, H. S. 1905. *Modifiability in behavior*. I. Behavior of sea anemones. *Journal of Experimental Zoology*, vol. 2, pp. 447-472.
- LENHOFF, H. M. 1968. Chemical perspectives on the feeding response, digestion, and nutrition of selected coelenterates. In: M. Florin and B. Scheer, eds., *Chemical zoology*. II. Porifera, Coelenterata and Platyhelminthes, pp. 157-221. Academic Press, New York.
- LINDSTEDT, K. J., L. MUSCATINE, and H. M. LENHOFF. 1968. Valine activation of feeding in the sea anemone *Bolocerooides*. *Comparative Biochemistry and Physiology*, vol. 26, no. 2, pp. 567-572.
- MACKIE, G. O., and D. A. BOAG. 1963. Fishing, feeding and digestion in Siphonophores. *Pubblicazione della Stazione Zoologica di Napoli*, vol. 33, no. 3, pp. 178-196.
- MARISCAL, R. N., and H. M. LENHOFF. 1968. The chemical control of feeding behavior in *Cyphastrea ocellina* and in some other Hawaiian corals. *Journal of Experimental Biology*, vol. 49, no. 3, pp. 689-699.
- PANTIN, A. M. P., and C. F. A. PANTIN. 1943. The stimulus to feeding in *Anemonia sulcata*. *Journal of Experimental Biology*, vol. 38, pp. 685-694.
- PARDY, R. L., and H. M. LENHOFF. 1968. The feeding biology of the gymnoblastic hydroid, *Pennaria tiarella*. *Journal of Experi-*

- mental Zoology, vol. 168, no. 2, pp. 197-202.
- PARKER, G. H. 1896. The reaction of *Metridium* to food and other substances. Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge, vol. 29, pp. 102-119.
- 1917. Actinian behavior. Journal of Experimental Zoology, vol. 22, pp. 193-230.
- TORREY, H. B. 1904 *a*. On the habits and reactions of *Sagartia davisi*. Biological Bulletin, Woods Hole, vol. 6, pp. 203-216.
- 1904 *b*. Biological studies on *Corymorpha* and its environment. Journal of Experimental Zoology, vol. 50, pp. 395-422.
- TREMBLEY, A. 1744. Mémoires pour servir a l'histoire d'un genre de polypes d'eau douce à bras en forme de cornes. Verbeek, Leiden.
- VON HOLT, C., and M. VON HOLT. 1968. Transfer of photosynthetic products from zooxanthellae to coelenterate hosts. Comparative Biochemistry and Physiology, vol. 24, pp. 73-81.
- VOGT, C. 1854. Recherches sur les animaux inférieures de la Méditerranée. I. Sur les Siphonophores de la Mer de Nice. Mémoires de l'Institut des Naturalistes de Genoeis, vol. 1, pp. 1-164.
- WALSH, G. E., and R. L. BOWERS. 1971. A review of Hawaiian zoanthids with descriptions of three new species. Zoological Journal of the Linnean Society, vol. 50, no. 2, pp. 161-180.
- WILSON, D. P. 1947. The Portuguese Man-of-War *Physalia physalis* L., in British and adjacent seas. Journal of the Marine Biological Association, United Kingdom, vol. 27, pp. 139-172.
- YONGE, C. M. 1930. Studies on the physiology of corals. Feeding mechanisms and food. Scientific Reports of the Great Barrier Reef Expedition, vol. 1, no. 2, pp. 13-57.
- YONGE, C. M., and A. G. NICHOLLS. 1931. Studies on the physiology of corals. II. Digestive enzymes. Scientific Reports of the Great Barrier Reef Expedition, vol. 1, no. 3, pp. 8-81.