THE CHEMICAL CONTROL OF FEEDING BEHAVIOUR IN CYPHASTREA OCELLINA AND IN SOME OTHER HAWAIIAN CORALS*

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INTRODUCTION

Since Loomis (1955) first demonstrated that the reduced tripeptide glutathione elicited feeding behaviour in Hydra littoralis, a number of workers have demonstrated a similar phenomenon among other coelenterates. Lenhoff & Schneiderman (1959) found that the siphonophore Physalia physalis and the calypoblastic hydroid Campanularia flexuosa also gave a feeding response to glutathione. On the other hand, Fulton (1963) showed that the feeding behaviour of the gymnoblastic brackish water colonial hydroid Cordylophora lacustris is elicited not by glutathione, but by the imino acid proline. Pardy & Lenhoff (1968) found that proline causes mouth opening in the gymnoblastic marine hydroid Pennaria tiarella. Lindstedt, Muscatine & Lenhoff (1968) found that the amino acid valine initiated feeding in the swimming sea anemone Boloceroides. N. Smith & Lenhoff (unpublished) show glutamine to be a stimulator of feeding in an unidentified acontiate sea anemone. For recent reviews on the chemical mediators of feeding and other behaviour in coelenterates see Lenhoff (1967, 1968).

Nothing is known of the specific feeding stimuli for corals except that mouth opening and feeding behaviour can be elicited by tissue extracts (Abe, 1938). Accordingly, we conducted a comparative study of the stimuli for mouth opening in three Hawaiian corals.

Most of the work involved the colonial encrusting coral Cyphastrea ocellina. Both proline and, to a lesser extent, reduced glutathione were effective in causing mouth opening in this species. Analogues of these compounds, pipecolic acid and S-methyl glutathione, respectively, also caused mouth opening in Cyphastrea.

MATERIALS AND METHODS

The corals were collected from the reefs in Kaneohe Bay, Oahu, Hawaii, and were maintained in running sea-water tables. They were kept without additional food for 24 h. before use, and were used only once in any 24 h. period. Because the animals gave

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similar feeding behaviour in both artificial sea water and natural sea water, the latter
was used almost exclusively.

The pH of the various experimental solutions was similar to that of the natural sea
water in which they were prepared; thus no additional buffer was added. The temper-
ature of the solutions was between 26° and 28° C.

Aqueous homogenates and extracts of either the nauplii of the brine shrimp *Artemia
salina* or of freshly collected plankton were prepared as follows: solid pack suspensions
of a known volume of *Artemia* nauplii were homogenized in a small volume of sea
water. The plankton (consisting mostly of crab megalopa larvae, mysids, caridean
larvae and chaetognaths) was also homogenized in a small volume of sea water. The
homogenates were either used directly or were first centrifuged and only the extracts
tested. Since no differences in feeding response could be detected using either source
of extracts, primarily the *Artemia* were used in the chromatographic analyses.

Extracts of *Artemia* or plankton for chromatographic analysis were obtained by
homogenization in distilled water, centrifuging at about 4500 g, and mixing the
resulting aqueous supernatant with an equal volume of 80% ethyl alcohol. The
alcohol-soluble material was partially dried on a Buchler Rotary Evapo-Mix (Buchler
Instruments, New York, N.Y.), resuspended in 80% ETOH and then recentrifuged.
This procedure was repeated several times, first with 80% ETOH, then 95% ETOH
and finally with absolute ETOH until no further precipitate was formed.

Different concentrations of the alcohol extracts were streaked on Whatman no. 4
filter paper. One-dimensional descending paper chromatograms were prepared using
a butanol-propionic acid solvent after the technique of Benson *et al.* (1950). One strip
was developed with 0.25 M ninhydrin in acetone and its co-chromatogram was retained
for testing. Upon finding a strip which gave both good concentration and separation
of spots, pieces were cut out of the undeveloped portion of the co-chromatogram and
presented directly to the coral polyps. In this way the approximate region of the
chromatogram which elicited mouth opening could be determined. A piece of
blank filter paper which had also been run through the solvent system served as a
control.

To determine the identity of the compounds present on the chromatograms of
*Artemia* extract which elicited a feeding response, the $R_p$ of each active spot was com-
pared with those of known amino acids that had been run through the same one-
dimensional chromatography system.

Once an active area on the paper was found, small pieces of clean filter paper were
spotted with known concentrations of various amino acids having similar $R_p$ values.
When one of these pieces of treated filter paper elicited a response, a solution of known
molar concentration of the same compound was prepared and the response of the
entire coral colony to this compound observed and recorded.

The commercially available amino acids which caused positive responses were then
chromatogrammed to determine if any impurities were present. Pieces of paper
obtained from the unsprayed co-chromatograms were tested on the corals to ensure
that the compound in question was responsible for the observed response.

All microscopic observations were made with a Bausch and Lomb Stereozoom
dissecting microscope.

It proved impractical to use the technique of Lenhoff (1961) for quantifying the
mouth-opening response of *Cyphastrea* because of the extremely long time the coral polyp mouths remained open in solution. Three alternative methods were employed.

Method I was a simple plus–minus system to indicate the extent of mouth opening of *Cyphastrea*. Three pluses signified the maximum mouth opening (about 0.5 mm.) of the individual polyps while a minus meant no visible response. Method II involved counting the number of polyps with mouths open in the experimental solution after a fixed interval of time. A 15 min. interval proved convenient for *Cyphastrea* since this allowed a near-maximal response of the coral colony in the highest concentration of compound used (10⁻³M). Lesser concentrations of compounds invariably caused a lesser response after the same time-interval. Method III involved placing the coral in the experimental solution and then counting the number of *Cyphastrea* polyps out of 50 responding with time.

**RESULTS**

*Feeding response to live prey, and to homogenates or extracts of live prey*

Feeding behaviour in *Cyphastrea* (as well as in the other corals investigated) in response to live prey (plankton organisms or *Artemia*), homogenates or sea-water extracts of prey, consisted of a wide mouth opening (Plate 1). Following introduction of any of these stimuli, *Cyphastrea* responded by giving a short, sharp contraction of the tentacles and/or oral disk area. Within 1–3 sec. the mouths of some of the polyps opened, gradually followed by others until, after a period of time dependent upon the concentration of homogenate or extract, or upon the number of prey organisms, nearly all the polyps had responded. Given enough time (i.e. 30–60 min.), all the polyps of a colony generally responded to the aforementioned stimuli. While the mouth was opening, the prey organisms or homogenate particles were worked toward and into it by either ciliary or muscular action or both.

Dilutions as low as one to ten million (10⁻⁷) of the homogenate from a solid pack of *Artemia* nauplii still gave a definite feeding response as measured by method III (Fig. 1). There was, however, a decided difference in the number of polyps responding with time as well as in the extent to which the mouth opened in the various dilutions of homogenate or extract (Table 1).

**Identification of the compounds which stimulate feeding in *Cyphastrea***

Preliminary tests revealed that the stimulus contained in *Artemia* aqueous extract which caused mouth opening of *Cyphastrea* was stable to boiling and soluble in 95% ethyl alcohol. Eluates of chromatograms prepared with alcohol extracts of *Artemia* and tested on *Cyphastrea* showed that the major activity for mouth opening was restricted to a spot having an $R_F$ value of 0.6. Somewhat less activity appeared lower on the chromatographic strip ($R_F$ about 0.3).

Since the upper spot had the yellow ninhydrin colour characteristic of proline as well as having a similar $R_F$ value, several tests were conducted with this amino acid. A piece of filter paper treated with a solution of 10⁻¹M proline directly and a similarly treated piece which had been through the butanol–propionic acid solvent system were both presented to individual *Cyphastrea* polyps. In all the experiments conducted using both of the above types of proline-treated filter paper, a wide mouth opening was
elicited. Other amino acids each having an $R_F$ value close to that of proline and similarly applied to filter paper provoked no response when presented to *Cyphastrea* polyps.

Since reduced glutathione was thought to have an $R_F$ value similar to that of the lower active spot, pieces of filter paper treated as above for proline were presented to *Cyphastrea* polyps. A definite mouth-opening response, although not quite as strong as that observed with proline, was immediately produced. Filter paper treated with the various amino acids having $R_F$ values corresponding to that of the lower active spot did not cause any distinct mouth-opening response. Reduced glutathione has recently been shown to be abundant in *Artemia* nauplii (R. D. Brown, using the fluorometric assay of Cohn & Lyle, 1966, personal communication).

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**Fig. 1.** The effect of dilutions of *Artemia* homogenate on the number of *Cyphastrea ocellina* polyps giving a feeding response.

**Table 1. Degree of mouth opening of Cyphastrea ocellina in various solutions**

<table>
<thead>
<tr>
<th>(M)</th>
<th>Proline</th>
<th>Pipelic acid</th>
<th>Hydroxy-proline</th>
<th>Reduced glutathione</th>
<th>S-methyl glutathione</th>
<th><em>Artemia</em> homogenate</th>
</tr>
</thead>
<tbody>
<tr>
<td>$10^{-2}$</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ +</td>
<td>+ +</td>
<td>+ +</td>
<td>+ + +</td>
</tr>
<tr>
<td>$10^{-3}$</td>
<td>+ +</td>
<td>+ +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+ +</td>
</tr>
<tr>
<td>$10^{-4}$</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>$10^{-5}$</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>$10^{-6}$</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

**Key:**

+ + +, wide mouth opening; + +, moderate mouth opening; +, slight mouth opening; —, no mouth opening; o, no data.

* Concentrations of *Artemia* extract refer to dilutions of the homogenized packed nauplii.
Chemical control of feeding behaviour of corals

Response of Cyphastrea to analogues of proline and reduced glutathione

Pipecolic acid

A six-membered ring analogue of proline, pipecolic acid, has been found to date only in plant material. It proved to be as effective, and in some cases more effective than proline in causing mouth opening in *Cyphastrea*. With Method I the same concentrations of proline and pipecolic acid elicited similar degrees of mouth opening (Table 1).

Using Method II it was found that pipecolic acid caused a greater percentage response at all three concentrations used than did proline (Table 2). Fulton (1963) reported that the response of the brackish water hydroid *Cordylophora* in pipecolic acid was approximately one-tenth that in proline. Pardy & Lenhoff (1968) found that pipecolic acid was also one-tenth as effective as proline in causing mouth opening in the marine hydroid *Pennaria tiarella*.

<table>
<thead>
<tr>
<th>Table 2. Percentage of mouths open of Cyphastrea ocellina after 15 min. in the test solution</th>
</tr>
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<tbody>
<tr>
<td></td>
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<tr>
<td>----------------------</td>
</tr>
<tr>
<td>No. of polyps</td>
</tr>
<tr>
<td>Mouts open</td>
</tr>
<tr>
<td>Percentage responding</td>
</tr>
</tbody>
</table>

Plotting against time the number of *Cyphastrea* polyps out of fifty responding (method III), a striking difference in the shape of the curves obtained with proline and pipecolic acid was observed (Fig. 2). The curve representing the increase in number of polyps responding with time to proline was hyperbolic, while distinctly sigmoid curves with lag periods of 1–2 min. were obtained at all three concentrations of pipecolic acid tested. Such lag periods were never observed with proline or with the other compounds tested.

Hydroxyproline

Hydroxyproline, which can be considered a proline analogue, was found to be one-hundredth as effective as proline in tests with *Cyphastrea*. In the various tests conducted, a concentration of 10^-3M hydroxyproline elicited a response very similar to that from 10^-3M proline (Tables 1, 2; Fig. 2). As Fulton (1963) warned, however, commercially available hydroxyproline may have a 1% contamination by proline and this could account for the response of *Cyphastrea* to solutions of hydroxyproline.

S-methyl glutathione

S-methyl glutathione is a rare analogue of reduced glutathione which has only recently been described as occurring naturally in bovine brain (Kanazawa, Kakimoto, Nakajima & Sano, 1965). Synthetic S-methyl glutathione (Zion Chemical Co., Yavne, Israel) proved to be as effective in eliciting a mouth opening response in *Cyphastrea* as corresponding concentrations of reduced glutathione (Tables 1, 2; Fig. 3).
The extent of mouth opening of *Cyphastrea* in reduced glutathione (and *S*-methyl glutathione) was one order of magnitude less than it was in the corresponding concentrations of proline or pipecolic acid (Table 1). Although the percentage of mouths opening (Table 2) for the two groups of compounds at $10^{-3} \text{M}$ and $10^{-5} \text{M}$ was roughly similar, both proline and pipecolic acid evoked much stronger responses at $10^{-7} \text{M}$ than did reduced glutathione. Thus proline seems to be more effective than reduced glutathione in causing *Cyphastrea* polyps to open their mouths.

![Graph 1](image1)

**Fig. 2.** The effect of different concentrations of proline, hydroxyproline and pipecolic acid on the number of *Cyphastrea ocellina* polyps giving a feeding response.

![Graph 2](image2)

**Fig. 3.** The effect of different concentrations of reduced glutathione and *S*-methyl glutathione on the number of *Cyphastrea ocellina* polyps giving a feeding response.
Response of Cyphastrea to progressively higher concentrations of glutathione

Cyphastrea polyps showed greater responses to glutathione as the concentration increased (Table 2). Hence, it should be possible to transfer polyps from a lower glutathione concentration to a higher one, with the polyps giving roughly the same response as they would have given had they been initially introduced into the higher concentration. This proved to be the case. Whereas 10.9% of the polyps tested responded to $10^{-7}$M glutathione, an 80.8% response was evoked by the same polyps when transferred to $10^{-5}$M glutathione.

Extrusion of mesenterial filaments

Whereas proline was the primary stimulus for mouth opening in Cyphastrea, glutathione appeared to be more effective in causing extrusion of mesenterial filaments. Although the mouths of the polyps in $10^{-3}$M glutathione did not open as widely as, those in $10^{-8}$M proline, there were many more mesenterial filaments extruded on the surface of the colony in glutathione. We could not find, however, a strong and consistent correlation between the number of filaments extruded and the molarity of the solution. Since this response was not studied in detail, a good deal more work will be necessary to determine not only the relationship of mesenterial filament extrusion to prey capture and feeding in general, but also the influence of the various chemical compounds on the filament extrusion process itself.

Comparative survey of the feeding response in corals other than Cyphastrea

Fungia scutaria

Fungia differs from Cyphastrea in that the mucus may play a greater role in feeding. When small crustaceans contact the oral disk of Fungia, they appear to be trapped in the mucus itself as well as being immobilized by the nematocysts. The mucous sheet with its contained organisms is then carried to the mouth by ciliary action (see Abe, 1938). Within 30–60 sec. of prey capture or the introduction of a food substance, Fungia responds with a wide mouth opening. Depending on the concentration of the stimulatory substance, the mouth may remain open for several hours. In addition, the tentacles bend toward the mouth in concurrence with a general swelling or ‘inflating’ of the tissue immediately surrounding the mouth. The lips of the mouth often bend toward a localized stimulus, such as a small piece of food on the disk.

Small portions of filter paper containing chromatogrammed alcohol extracts of Artemia were presented to Fungia as was done with Cyphastrea. Most mouth-opening activity was caused by spots having $R_F$ values between 0.58 and 0.66. These experiments were not always repeatable, however. Further experiments similar to those conducted with Cyphastrea revealed that proline appeared to be one inducer for mouth opening. In addition, methionine, tyrosine and reduced glutathione caused mouth opening occasionally. It is possible that other compounds may prove to be effective in the case of Fungia, and the above list should not be considered exhaustive.

In the initial experiments with Fungia small (3–6 cm. diameter) isolated polyps were used. However, a good deal of individual variation in response was evident when using small numbers of animals. This variability was present whether the animals were kept in artificial or natural sea water, or whether they were fed or starved for prescribed
periods prior to use. Since relatively large numbers of small stalked *Fungia* were readily available, these were used to provide statistically more reliable data in subsequent experiments. The response of *Fungia* to proline and reduced glutathione in solution was tested for comparison with similar data from *Cyphastrea*. In spite of the variability in response previously observed with *Fungia*, these experiments using larger numbers of animals gave good reproducibility (Table 3).

Table 3. Percentage of mouths open of *Fungia scutaria* after 2 min. in test solution

<table>
<thead>
<tr>
<th></th>
<th>Proline (m)</th>
<th>Pipecolic acid (m)</th>
<th>Reduced glutathione (m)</th>
<th>S-methyl glutathione (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10^{-3}</td>
<td>10^{-5}</td>
<td>10^{-7}</td>
<td>10^{-3}</td>
</tr>
<tr>
<td>No. of polyps</td>
<td>103</td>
<td>103</td>
<td>103</td>
<td>103</td>
</tr>
<tr>
<td>Mouts open</td>
<td>97</td>
<td>42</td>
<td>41</td>
<td>86</td>
</tr>
<tr>
<td>Percentage responding</td>
<td>94.2</td>
<td>40.8</td>
<td>39.8</td>
<td>83.4</td>
</tr>
</tbody>
</table>

Note in Table 3 that 10^{-3} M proline caused the highest percentage of animals to open their mouths (94.2%). At this concentration the mouths occasionally remained open for several hours. A concentration of 10^{-3} M glutathione elicited only a 70.4% response (Table 3), and the mouths stayed open about 12 min. at most.

*Pocillopora damicornis*

A feeding stimulus caused a sharp contraction and partial withdrawal of individual *Pocillopora* polyps, followed by a wide mouth opening similar to that of *Cyphastrea*. Both the contraction and mouth opening seemed important for the full feeding response.

Pieces of a filter-paper chromatogram of *Artemia* alcoholic extract gave results similar to those obtained with *Cyphastrea*. Because of the difficulties in observing these small polyps, only a few experiments were conducted with *P. damicornis*. These revealed that proline and reduced glutathione seemed to be the main stimuli for mouth-opening (Table 4). In addition, there were occasional responses to methionine and possibly phenylalanine. Note that the percentage of response was similar in both 10^{-3} M proline and 10^{-3} M glutathione. Proline, however, elicited a stronger contraction and wider mouth-opening response than did a similar concentration of glutathione spotted on filter paper, implying that proline was more effective than glutathione in the mouth-opening response of *Pocillopora*. Unlike *Cyphastrea*, *Pocillopora* extruded more mesenterial filaments in proline than in glutathione.

Table 4. Percentage of mouths open of *Pocillopora damicornis* after 15 min. in test solution

<table>
<thead>
<tr>
<th></th>
<th>Proline (m)</th>
<th>Reduced glutathione (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10^{-3}</td>
<td>10^{-5}</td>
</tr>
<tr>
<td>No. of polyps</td>
<td>311</td>
<td>240</td>
</tr>
<tr>
<td>Mouts open</td>
<td>295</td>
<td>202</td>
</tr>
<tr>
<td>Percentage responding</td>
<td>94.8</td>
<td>84.2</td>
</tr>
</tbody>
</table>
DISCUSSION

The general pattern of prey capture in *Cyphastrea* can be summarized as follows: a small crustacean such as a crab megalopa larva either bumps into the tentacle of an expanded polyp or blunders into the skeletal cup of a partially contracted one. Contact with the tentacles causes them to infold sharply, partially entrapping the prey as well as bringing it into close contact with the mouth of the polyp. Simultaneously, the contact with the tentacles causes the nematocysts there to discharge and puncture the crustacean, thereby releasing the body fluids, which contain numerous compounds including proline and glutathione. Such chemical stimulators of feeding cause the mouth to begin to open. Often the side of the mouth nearest the prey bends toward it. This orientation of the mouth to the prey cannot be evoked by strictly mechanical stimuli, such as contact with a small piece of clean filter paper. A similar sized piece of filter paper soaked in crustacean extract, proline or glutathione, however, always evoked a mouth-opening response like that caused by live prey.

Actual physical contact with the mouth is not necessary to cause mouth opening. Generally, the closer the captured prey to the mouth, the more rapid the mouth opening. As the mouth opens, ciliary currents as well as muscular action seem to aid in directing the prey towards and into it. When the lips contact the prey they appear to work their way up and around it as it is being drawn into the coelenteron.

This study presents the first instance in which the feeding behaviour of a single coelenterate, *Cyphastrea*, has been shown to be controlled by either a specific amino acid or a specific peptide (as well as their respective analogues). To date, all coelenterates investigated have been shown to respond to glutathione alone (e.g. various species of *Hydra, Physalia*) or to a specific amino acid (e.g. *Cordylophora, Pennaria, Boloceroides*) but not to both. Although additional compounds may be found to induce feeding in other corals, *Cyphastrea ocellina* seems to respond primarily to proline or reduced glutathione, with proline being the more effective activator at low concentrations.

The response curve of *Cyphastrea* to pipecolic acid (Fig. 2) was unusual in that it was sigmoid, while those to proline, glutathione, and S-methyl glutathione were hyperbolic (Figs. 2, 3). The initial 1–2 min. lag period in responsiveness does not reflect a lowered sensitivity of *Cyphastrea* to pipecolic acid, because a greater percentage of polyps responded to this compound than to proline at all concentrations tested (Table 2). The sigmoid curve suggests that the polyps are responding to pipecolic acid in a facilitated fashion, perhaps nervous, throughout the colony. Alternatively, the pipecolic acid might be involved in an allosteric activation of the receptor sites like that described by Monod, Wyman & Changeux (1965).

As Fulton (1963) pointed out, although the proline and glutathione molecules are markedly different, some glutathione molecules in solution may take a form having a heterocyclic α-amino acid moiety (see Calvin, 1954; Wieland, 1954; Isherwood, 1959). Possibly this form of glutathione might be recognized by the proline receptors of *Cyphastrea*. Because only a small proportion of the glutathione molecules might have an α-amino structure at any one time, we might expect higher concentrations of glutathione to be necessary to give a response as effective as that given by proline alone. Such is the case. Another possibility is that two different receptor sites are involved, one for proline and one for glutathione.
The number of mesenterial filaments extruded in various concentrations of proline and glutathione was checked for *Cyphastrea* and *Pocillopora damicornis*. *Cyphastrea* extruded a greater percentage of filaments in glutathione than in proline. *Pocillopora*, however, extruded more filaments in proline than in glutathione and always extruded a relatively greater number than did *Cyphastrea* in either solution. In high concentrations of proline (10^-3M), *Pocillopora* extruded approximately one filament for each two polyps observed. Concentrations of 10^-5M and 10^-7M proline caused *Pocillopora* to extrude only about 10% of its filaments. With either species, however, there seemed to be no fixed correlation between the concentration of compounds which induced mouth opening and the number of mesenterial filaments extruded. Some filaments were extruded in feeding experiments with live crustaceans, but these did not seem essential for prey capture. It is possible that the mesenterial filaments are more important for feeding at night when the reef waters contain much more plankton. However, based on the present study, little more can be said concerning the role of these filaments.

**SUMMARY**

1. The feeding response of the Hawaiian coral *Cyphastrea ocellina* was elicited by alcoholic extracts of *Artemia* nauplii and of plankton.
2. Chromatographic analysis of these extracts revealed that the imino acid proline was primarily responsible for the observed mouth opening and feeding behaviour.
3. Somewhat less feeding activity was also caused by the reduced tripeptide glutathione.
4. Analogues of these compounds, pipecolic acid and S-methyl glutathione, respectively, were as effective as the naturally occurring compounds.
5. Some data are also presented for the feeding responses of two other Hawaiian corals, *Pocillopora damicornis* and *Fungia scutaria*.

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**REFERENCES**


**EXPLANATION OF PLATE**

(a). Photograph of a colony of *Cyphastrea ocellina* in natural sea water in the absence of any feeding activator. (Photo by R. N. Mariscal.)

(b). Photograph of the same colony of *Cyphastrea ocellina* in 10^{-3}M proline prepared in natural sea water. Note the wide mouth opening of each of the polyps. (Photo by R. N. Mariscal.)