

Diel Variation in Prey Capture Behavior by the Corallimorpharian *Discosoma sanctithomae*: Mechanical and Chemical Activation of Feeding

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Abstract. The feeding biology of corallimorpharians is poorly understood. This paper describes an envelopment method of prey capture by a Caribbean species, *Discosoma* (= *Rhodactis*) *sanctithomae*, and further examines the stimuli that elicit envelopment and subsequent ingestion of prey. The corallimorpharians exhibited a diel pattern of expansion and contraction of the oral disc margin and tentacles. This was correlated with the density of zooxanthellae in these tissues. The tentacles expanded during the day to expose abundant zooxanthellae. The oral disc margin contained relatively few zooxanthellae and was contracted and turned down in a convex posture during the day. At night the margin was expanded and turned up to give the oral disc a bowl-shaped posture. This allowed effective execution of the envelopment response that was successful in the capture of crustaceans, polychaetes, and small fishes that were most abundant in the plankton at night. The stimuli that elicited this predatory behavior were both mechanical and chemical. Mechanical stimulation elicited envelopment at night but was not as effective during the day. Envelopment was also activated by the imino acid proline and the tripeptide reduced glutathione at low concentrations, and four other amino acids at high concentrations. Continued contraction and ingestion responses required chemical activation. Consistent ingestion responses were caused only by reduced glutathione.

Introduction

Cnidarians typically capture their prey with stinging and adhesive tentacles. However, members of the coralli-

morpharian family Discosomatidae are unusual in that their tentacles do not appear to be adapted for feeding (Den Hartog, 1980). Unlike other cnidarians they have few ectodermal nematocysts in their tentacles, and in contrast to all other taxa in the subclass Hexacorallia they completely lack spirocysts (an important taxonomic character of this group). Spirocysts are usually abundant in the tentacles of hexacorallians, and the adhesive character of these organelles is of major importance in catching and holding prey (Mariscal, 1984). Den Hartog (1980) states that the tentacles of the Discosomatidae are "of a quite unusual character, being non-retractile, non-motile, and practically devoid of musculature. It is difficult to assume that these tentacles are functional catching devices, and bearing in mind that Discosomatidae are invariably associated with extremely numerous zooxanthellae, it seems more likely that this group of Corallimorpharia is primarily, if not entirely, dependant on these associates (and therefore on light) for nutrition." He further notes that the feeding biology of this group is worthy of experimental study.

Indo-Pacific members of Discosomatidae (= Actinodiscidae) have been documented to feed by enveloping prey with their oral discs (Hamner and Dunn, 1980). The purpose of this paper is to describe a similar mode of feeding in a Caribbean member of this family, *Discosoma sanctithomae*. We also examine diel variations in the behavior and experimentally investigate the stimuli involved in eliciting prey capture and ingestion.

Materials and Methods

Field observations

The study was conducted at the Bermuda Biological Station for Research, Bermuda, during August, 1987,

and two weeks in May, 1988. Surveys to determine the distribution and abundance of *D. sanctithomae* were done at many different sites in nearshore and offshore reef areas. Field observations and experiments were conducted at both Whalebone Bay and Coney Island (32° 40' N, 64° 43' W) during the day and night. Feeding behavior was examined by observing the corallimorpharians capture organisms that were attracted to dive lights during night dives. Day feeding observations were made by placing small amounts of live *Artemia* nauplii on the oral discs of the corallimorpharians with a medicine dropper.

Photographs were taken of four different clonal aggregations at Whalebone Bay during the day and night to document feeding behavior, determine maximum population densities, and examine diel variation in size and posture. The photographs were analyzed with a digitizer board (Bioquant digitizer software for IBM PC) to measure surface areas of different portions of the oral disc for patterns of contraction and expansion.

Collection and maintenance

A total of 170 specimens of *D. sanctithomae* were collected at Coney Island by chiselling off the dead coral to which they were attached. The animals were maintained in sea tables supplied with running seawater at temperatures of 22–24°C and a salinity of 36‰. The seatables were indoors where they received indirect ambient lighting from nearby windows as well as artificial lighting from overhead fluorescent lamps producing 15–20 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Observations and experiments were conducted under both ambient and artificial lighting during the day and fluorescent lighting at night. The animals received a variable light/dark cycle, being exposed to 12–18 h of light day⁻¹ depending on the amount of time the fluorescent lights were on during the evening. The 50 individuals used in 1987 were not fed for the two week duration of the study, but the 120 animals used in 1988 were fed *Artemia* nauplii after one week. Some individuals were also used for observations of feeding on whole neroid polychaetes.

Sixty-three specimens of *D. sanctithomae* were collected using the above method at dawn on 17 May 1988. They were immediately placed in plastic bags and then preserved in 10% formalin. The animals were later removed from the coral to which they were attached and the bags were examined for contents that may have been egested during transfer. Each individual was examined under a dissecting microscope for coelenteric contents five days later. Specimens were cut open in a bowl of water and the contents of the coelenteron were removed and measured using an ocular micrometer.

Determination of zooxanthellae densities

The relative densities of zooxanthellae in different portions of the body wall of *D. sanctithomae* were measured using the method outlined by Sebens and DeReimer (1977). Animals were fixed in Bouins, sectioned in a cryostat, and then examined under a compound microscope at 400× magnification. The densities of zooxanthellae (cells · cm⁻³) in the discal tentacle and outer margin regions of the oral disc were measured.

Nematocyst discharge

Experiments were performed to determine if *D. sanctithomae* discharged nematocysts when contacted by a prey item or some other object. Glass coverslips and 1 cm² pieces of parafilm coated with dried *Artemia* homogenate were presented forcefully to the discal or marginal tentacles of the corallimorpharian. Densely packed *Artemia* nauplii in seawater were homogenized, centrifuged for approximately five min at maximum speed on an IEC model C-L tabletop centrifuge (circa: 1500 rpm) and the supernatant used in experiments. Similar nematocyst discharge tests were also done with the anemones *Condylactis gigantea* and *Aiptasia pallida* for comparison. The coverslips were stained in methylene blue then examined for the presence of nematocysts at 400× and 1000× magnifications on a compound light microscope.

Stimuli that elicit the feeding behavior

To determine the factors that elicit the envelopment response and subsequent feeding in *D. sanctithomae*, a series of mechanical and chemical stimuli were tested in both the field and laboratory. The effect of mechanical stimuli was tested in the field by gently passing a pasteur pipette through the discal tentacles of randomly selected specimens every 2 s and recording how many contacts were required to cause the envelopment response and complete closure of the oral disc margin. New pipettes were used for each specimen. This experiment was done during the day (13:00) and night (22:00).

The effect of chemical stimuli in eliciting the envelopment response was tested in the field during the day and night by directing a stream of solution (0.5 ml) from a syringe (5 ml with 18 gauge needle) at the discal tentacles of a specimen from a distance of approximately 3 mm. Individuals separated by more than 1 m were used for each trial. The treatments used were *Artemia* homogenates (prepared as described above), 20 amino acids, 3 proline analogs, the tripeptide reduced glutathione (GSH), and S-methyl glutathione. Carbohydrates and lipids were not tested since they are not effective feeding activators in other cnidarians (Lenhoff and Lindstedt, 1974; Van-Praët, 1985; Sebens, 1987). All other chemi-

cals were dissolved in glass fiber-filtered seawater collected from offshore in the Sargasso Sea. All solutions were used within 6 h to avoid auto-oxidation or loss of amino acids to bacteria. Stock solutions were prepared at 10^{-1} M and then serially diluted to the desired concentrations.

The behavior of the animals in response to the chemical stimuli was recorded as: (1) envelopment and complete closure of the opening to the cavity formed by the margins of the oral disc, (2) partial closure of the opening to the cavity formed by the margins of the oral disc, and (3) presence of mouth opening or extrusion of mesenterial filaments. Each animal was used in a maximum of three trials, and was tested only once in each 24-h period and at least 24 h after feeding.

The effect of mechanical and chemical stimuli in eliciting a continued feeding response was examined by first causing laboratory specimens to close in response to mechanical stimulation from a pipette. Then 0.5 ml of either plain seawater or a test solution was introduced with a pipette into the cavity formed by the margin of the oral disc. The behavior of the animals (amount of oral disc contraction) and the time taken for them to reopen and resume their normal posture was recorded.

To determine which chemicals were effective in causing both closure of the oral disc and ingestion, a piece of Whatman No. 1 filter paper (2×2 mm, with or without chemicals) was positioned 1 cm above the oral disc and dropped onto the discal tentacles. The presence or absence of closure and ingestion and the time taken for the oral disc to reopen and resume normal feeding posture was recorded. All filter papers were soaked in solutions of chemicals dissolved in deionized water and then dried for 12–48 h before being used in experiments. Filter papers that were soaked in chemicals and then dried gave more consistent responses than papers that were not dried before use. To determine if the corallimorpharians would ingest inert items when stimulated with chemicals in solutions, pieces of clean filter paper were dropped onto the oral disc (as described above) and then 0.5 ml of a solution of GSH or proline (10^{-2} M) was directed at the discal tentacles from a pipette to initiate closure.

Results

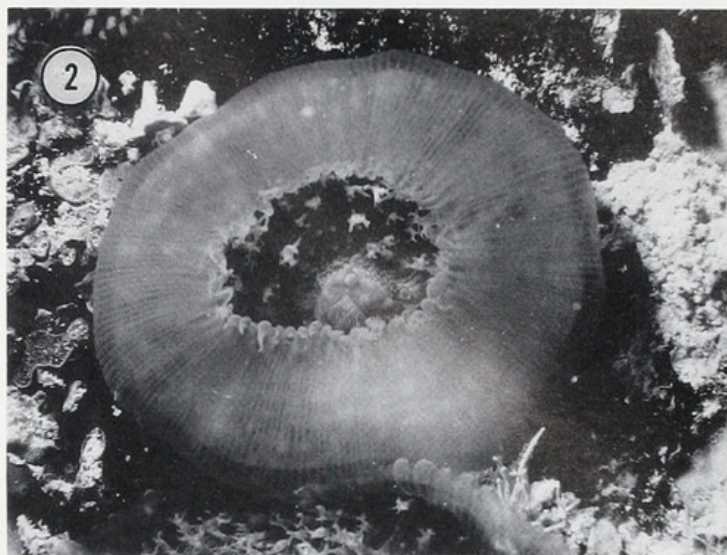
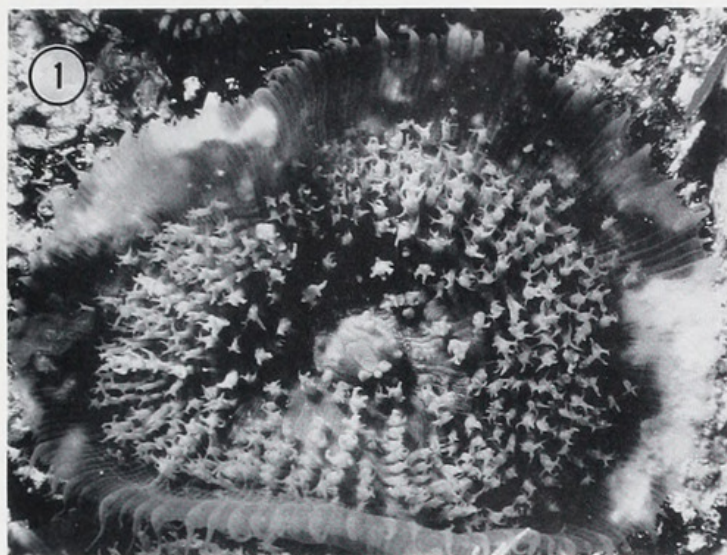
Populations of *D. sanctithomae* were found on all reefs surveyed in Bermuda. This species reached maximum densities of 800 individuals \cdot m $^{-2}$ at Coney Island and Whalebone Bay where it was one of the most abundant sessile invertebrates. Clonal aggregations were generally found on vertical surfaces in well-lighted areas from depths of 1 to 10 m. They were especially common in surge channels in all habitats.

Night diving observations of *D. sanctithomae* in Au-

gust, 1987, revealed that they had a striking feeding behavior in response to being contacted by planktonic organisms (Figs. 1–4). Swarming polychaete epitokes, crustaceans, and small fish that contacted the corallimorpharians' oral disc caused the margins to be quickly pulled up and in (~ 1 –3 s after contact) to form a cavity in which the prey was enveloped. This sequence of behaviors is very similar to that described by Hamner and Dunn (1980) for species of corallimorpharians found in the Indo-Pacific. After prey contact, the radial muscles of the oral disc contract to pull up the margin of the oral disc (Fig. 2) and then the circular muscles of the margin contract to close the opening to the cavity above the mouth (Fig. 3).

Captured prey continued swimming around inside the cavity for a few minutes until continued contraction of the margin reduced the amount of space and trapped the prey against the oral disc tentacles (Fig. 4). There was no adhesion of the prey to the discal tentacles or evidence of nematocyst discharge to cause the prey to be anaesthetized in the captures that were observed. However, since it was difficult to observe the events occurring inside the cavity through the tissue of the oral disc margin there may have been some stinging of the prey by the actinopharynx or extruded mesenterial filaments during ingestion. In laboratory tests no nematocytes were discharged onto coverslips or pieces of parafilm coated in *Artemia* homogenate presented to the discal tentacles, but homotrichs (*sensu*: Den Hartog, 1980) were detected on pieces of *Artemia*-coated parafilm presented to the marginal tentacles. The nematocytes in the marginal tentacles may prevent prey from escaping through the opening above the mouth until complete closure has taken place.

After prey capture the mouth of *D. sanctithomae* opened widely and the actinopharynx became distended. Laboratory observations of feeding showed that large prey (*e.g.*, nereid polychaetes) were moved to the mouth by contraction of the oral disc toward the mouth and by subsequent distension of the actinopharynx toward the prey item. Small prey such as *Artemia* were transported into the mouth by ciliary movement on the actinopharynx. It took approximately 45 min to 1.5 h for *D. sanctithomae* to ingest nereid polychaetes (measuring approximately $30 \times 5 \times 3$ mm) and then reopen and resume a normal feeding posture. Undigested remains of prey were egested 24 to 48 h after ingestion. Of 63 field specimens collected at dawn, only two individuals had any prey items in their coelenterons. One individual contained a gammarid amphipod ($2.3 \times 0.7 \times 0.5$ mm) and the other had an unidentified crustacean appendage ($5.0 \times 1.2 \times 1.2$ mm). Other cnidarians are known to digest their prey within a few hours after capture, with no recognizable items remaining after two to six hours (Porter, 1974; Sebens and Koehl, 1984). Our analysis is probably



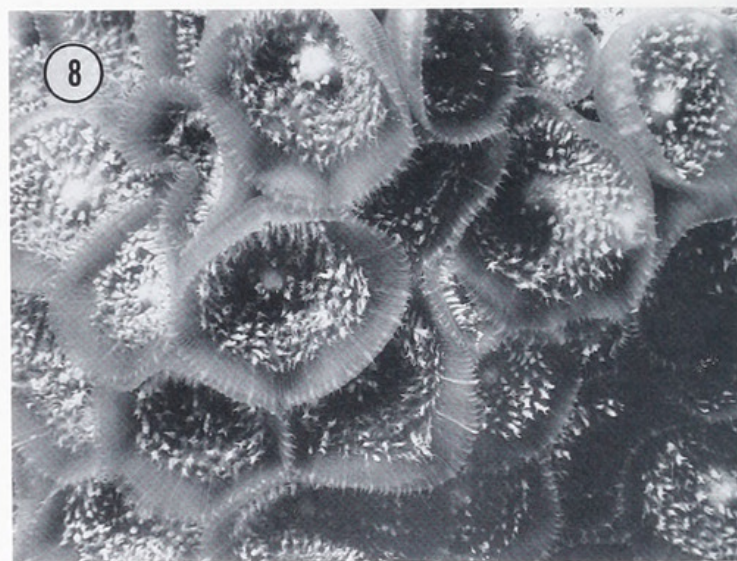
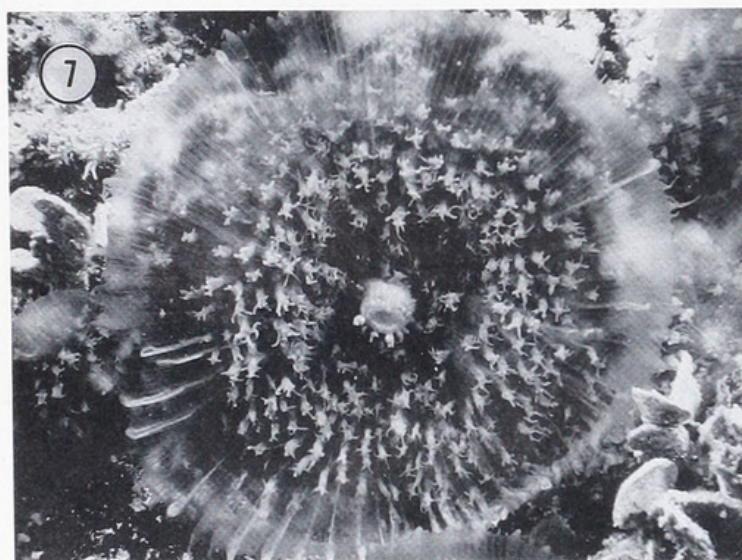
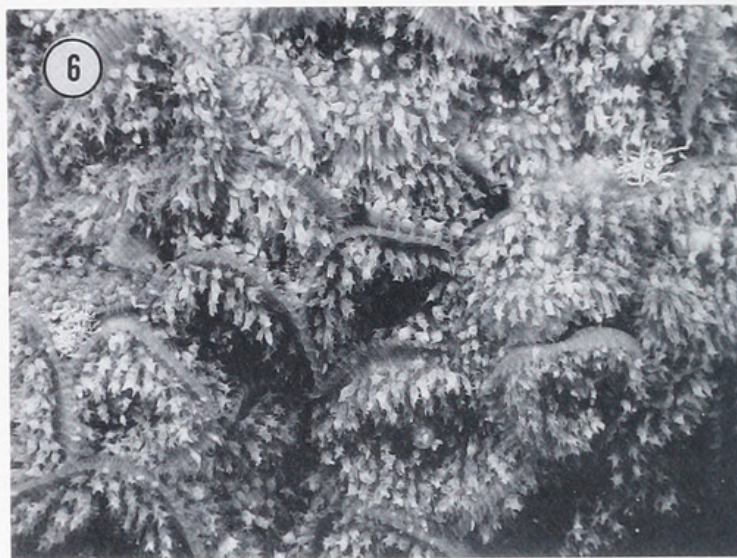
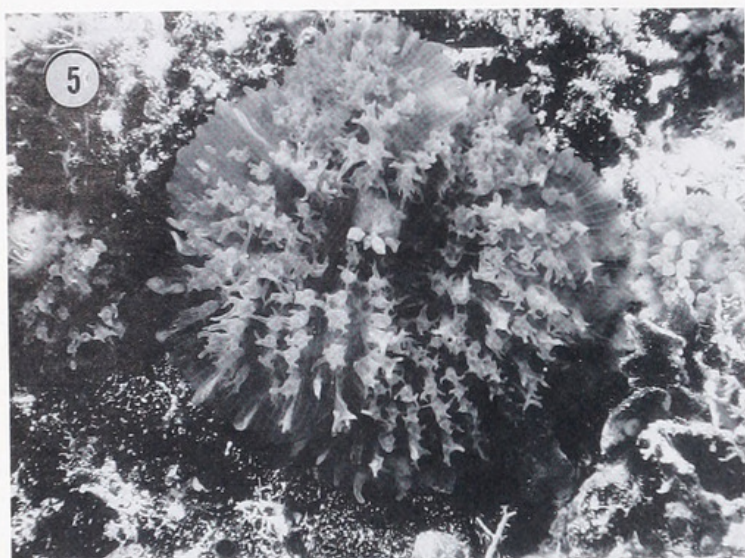
Figures 1–4. Prey capture sequence of *Discosoma sanctithomae*. (1) Feeding posture at night. Margin of the oral disc expanded and turned up to form a bowl-shaped structure. (2) After stimulation the margin of the oral disc contracts forming a cavity with a restricted opening above the mouth that is fringed by the marginal tentacles. (3) Complete closure of the opening above the mouth. (4) Photograph of a different specimen of *D. sanctithomae* that has captured a small fish. Refer to text for a more detailed description of the behavior.

a reasonable estimate of the numbers of prey captured during dawn but underestimates the number of prey captured throughout the night.

No *D. sanctithomae* were observed feeding in the field during the day. However, field specimens did feed on *Artemia* nauplii presented to them from a medicine dropper. The feeding response was not as fast or as effective compared to the same trials done during the night. This was related to the animals change in posture between day and night. During the day the margin of the oral disc was turned down in a convex posture (Figs. 5, 6), but at night the margin of the oral disc expanded and was turned up forming a bowl-shaped structure (Figs. 7, 8). This posture facilitated the capture of prey. When *Artemia* were presented to the oral disc of *D. sanctithomae* during the

day, most individuals did not perform an effective envelopment response and few prey were captured. This was because the margin of the oral disc was not expanded and turned upwards allowing the engulfment of a large volume of water when the margin contracted. Instead, when the oral disc margin contracted it was pulled in across the surface of the discal tentacles, or in some individuals the turned-down oral disc margin contracted around the column.

The surface area of the oral disc was significantly smaller during the day than during the night (Figs. 5, 7). Individuals that were separated by open space during the day often overlapped neighboring individuals at night with their expanded oral disc (Figs. 6, 8). Digitized measurements of oral disc surface area (in the plane of the



Figures 5–8. Diel change in posture and pattern of contraction and expansion of the oral disc and tentacles of *Discosoma sanctithomae*. (5) Day-time posture of a single individual with contracted oral disc margin that is turned down toward the substratum and the discal tentacles expanded. (6) Colony of *D. sanctithomae* during the day. (7) Posture at night of the same individual as in Figure 5. Oral disc margin is expanded and is turned up to form a bowl-shaped structure. The discal tentacles are contracted. (8) Same colony of *D. sanctithomae* as in Figure 6 at night.

photograph) taken during the day and night demonstrated no diel difference in the surface area covered by the discal tentacles ($P > 0.05$; Paired t -test), but the disc margin expanded to cover a much wider surface area at night (Fig. 9; $P < 0.001$). The discal tentacles were also expanded during the day and contracted at night (Figs. 5–8). This was correlated with the densities of zooxanthellae in the tissues of these different body regions. There were high densities of zooxanthellae in the discal tentacle region (54.5 ± 8.9 cells \cdot mm $^{-3}$; $n = 6$), but low densities in the disc margin (15.5 ± 1.4 cells \cdot mm $^{-3}$; $n = 6$). This pattern was correlated with the amount of pigmentation in these two regions. The central portion of the oral disc and the discal tentacles were dark green and

brown and the margin was relatively transparent when expanded at night (Figs. 5–8).

Animals kept in the laboratory under a varying light/dark cycle of both ambient and fluorescent lighting did not display a distinct diel difference in expansion and contraction or posture. There was a variety of responses by different individuals, with some remaining in an expanded state throughout the day and night and other specimens varying their shape over time.

Both mechanical and chemical stimuli were effective in eliciting the envelopment response. There was a significant diel difference in the number of contacts to the discal tentacles required to elicit envelopment (Fig. 10; $P < 0.001$, Mann-Whitney). In field trials done during

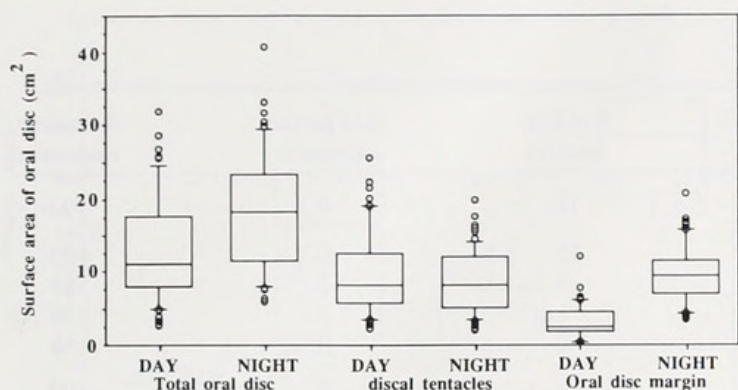


Figure 9. Boxplots for the surface areas of different portions of the oral disc during the day and night. There are significant differences in surface area between day and night for the total oral disc ($P < 0.001$) and the oral disc margin ($P < 0.001$), but not for the discal tentacle region ($P > 0.05$; Paired t -tests for each comparison). The central box part of the display (the hinges) indicates the interquartile range, the absolute difference between the 25th and 75th percentiles. The central horizontal line is the median, and the "whiskers" that extend out from the central box indicate the main body of the data and are calculated using the formula: hinge ± 1.5 (interquartile range). Any data values that extend out beyond these limits are plotted with a circle ($n = 61$).

the day, more than two contacts to the discal tentacles with a pasteur pipette were usually required to elicit the response, but some individuals did not close after even 20 contacts or forceful blows. At night most individuals closed after the first few contacts and exhibited a typical envelopment response. The sensitivity of the animals appeared to be related to their degree of expansion of the oral disc and their posture. In the laboratory, those individuals displaying a typical feeding posture were most sensitive to mechanical stimuli, while animals that were in a normal daytime posture rarely responded, independent of the ambient light levels.

A forceful stream of sea water (approximately $1 \text{ ml} \cdot \text{s}^{-1}$) directed at the oral disc from a pipette or syringe was also capable of eliciting the envelopment response. However, gentle streams of seawater (approximately $0.1 \text{ ml} \cdot \text{s}^{-1}$) that only lightly swayed the discal tentacles did not elicit envelopment. This allowed the presentation of chemicals in the stream of seawater. In field tests *Artemia* homogenate was very effective at eliciting the envelopment behavior (Table I). Of the 20 amino acids tested, 15 did not cause a response: glycine, serine, threonine, cystine, arginine, tyrosine, lysine, histidine, aspartic acid, valine, leucine, isoleucine, methionine, phenylalanine, and tryptophan. Five amino acids were effective at high concentrations ($10^{-1} M$). However, only proline elicited a consistent response at $10^{-2} M$ and a less strong response at $10^{-3} M$. The strongest reaction was caused by the tripeptide reduced glutathione (GSH) that was effective to concentrations of $10^{-4} M$. Both proline and GSH also caused mouth opening, distension of the actinopharynx, and extrusion of mesenterial filaments through the

mouth or body wall of the oral disc. We point out that these are the concentrations in the stream of water directed at the animals so that the actual effective concentrations are much lower.

Two chemical analogs of proline, pipecolic acid, and L-hydroxyproline were also effective in eliciting the closure response and subsequent mouth opening behavior at the same concentrations (Table II). Azetidine carboxylic acid was not effective. The glutathione analog, S-methyl glutathione, was effective at approximately the same concentrations as GSH and elicited both closure of the oral disc and mouth opening.

Previous tests demonstrated that mechanical and chemical stimuli elicit oral disc closure. The control of subsequent feeding behaviors was investigated in the laboratory by presenting one or both of these stimuli. Animals that closed in response to being contacted with a pipette and sea water control reopened and resumed their typical posture after two to three minutes. This same behavior was observed for field specimens that closed in response to being contacted by a prey item but were not successful in capturing it. When a solution of proline or GSH was released into the cavity instead of plain seawater, the animal responded by contracting the margin fully, opening its mouth, and distending the actinopharynx as in a typical feeding reaction. The amount of time the animals remained closed before resuming their open posture was significantly greater with GSH or proline than with the seawater control (Fig. 11; $P < 0.05$, Mann-Whitney). The stronger the chemical stimulus the stronger the contractions of the oral disc. Thus it took a longer time for the animal to re-expand and resume a normal feeding posture. In both field and laboratory tests done with GSH ($10^{-2} M$) all animals extruded many

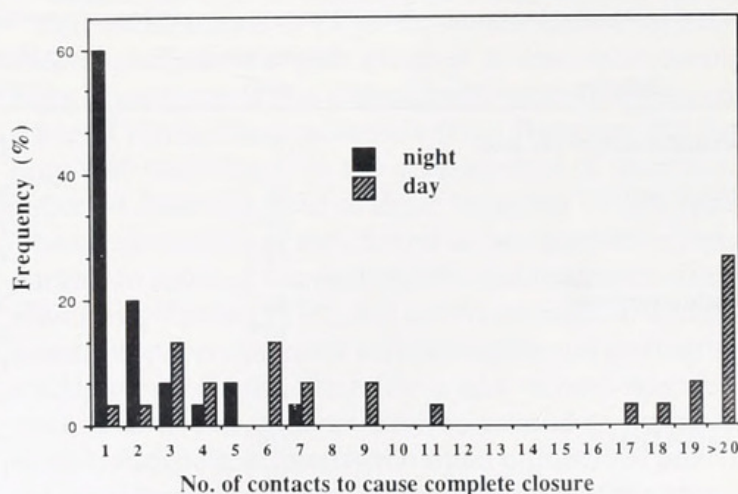


Figure 10. Frequency histograms for the number of contacts to the discal tentacles with a glass pipette that are required to cause complete closure of the oral disc. There was a significant difference in the number of contacts required between the night and day ($P < 0.001$; Mann-Whitney, $n = 60$).

Table I

Field tests with Artemia extract and chemicals at various concentrations

Solution	Concentration (M)	Number of trials	# of full closures	# of partial closures	% closure responses
Artemia homogenate		18	18	0	100
Asparagine	10 ⁻¹	15	15	0	100
	10 ⁻²	12	5	2	58
	10 ⁻³	8	1	2	38
	10 ⁻⁴	10	0	0	0
Glutamine	10 ⁻¹	12	12	0	100
	10 ⁻²	10	0	0	0
Glutamic acid	10 ⁻¹	10	10	0	100
	10 ⁻²	10	1	2	30
	10 ⁻³	8	2	0	25
	10 ⁻⁴	12	0	0	0
Alanine	10 ⁻¹	10	10	0	100
	10 ⁻²	10	1	5	60
	10 ⁻³	10	0	0	0
Proline	10 ⁻¹	15	15*	0	100
	10 ⁻²	20	20	0	100
	10 ⁻³	10	7	2	90
	10 ⁻⁴	10	0	2	20
	10 ⁻⁵	10	0	0	0
GSH	10 ⁻¹	18	18*	0	100
	10 ⁻²	10	10*	0	100
	10 ⁻³	11	11	0	100
	10 ⁻⁴	7	2	2	57
	10 ⁻⁵	12	0	0	0

* Extrusion of mesenterial filaments in some individuals.

Responses of *Discosoma sanctithomae* to a gentle stream of test solution (0.5 ml) from a 5-ml syringe directed at the discal tentacles from a distance of approximately 3 mm. Full closure refers to a complete envelopment response in which the margin of the oral disc was fully contracted closing the aperture to the cavity above the mouth. Partial closures were only slight contractions of the oral disc margin. Other amino acids tested that did not cause a response were glycine, serine, threonine, cystine, arginine, tyrosine, lysine, histidine, aspartic acid, valine, leucine, isoleucine, methionine, phenylalanine, and tryptophan.

Table II

Tests with analogs of proline and glutathione (GSH) in the laboratory

Solution	Concentration (M)	Number of trials	# of full closures	# of partial closures	% closure responses
L-azetidine carboxylic acid	10 ⁻²	10	0	0	0
Pipicollic acid	10 ⁻²	10	10	0	100
	10 ⁻³	10	9	0	90
	10 ⁻⁴	10	0	0	0
L-hydroxyproline	10 ⁻²	20	20	0	100
	10 ⁻³	10	8	1	90
	10 ⁻⁴	10	0	0	0
	10 ⁻⁵	10	0	0	0
S-methyl GSH	10 ⁻²	10	10	0	100
	10 ⁻³	10	6	3	90
	10 ⁻⁴	10	0	0	0

Responses of *Discosoma sanctithomae* to a stream of filtered sea water (0.5 ml; with and without dissolved chemicals) at various concentration from a glass pipette directed at the discal tentacles from a distance of approximately 3 mm.

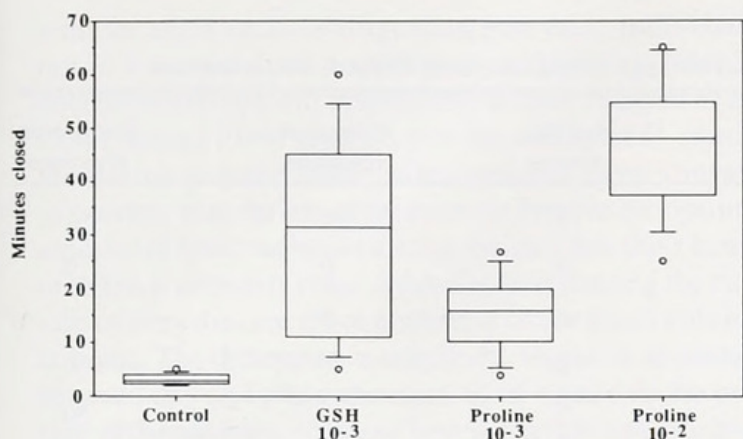


Figure 11. Boxplots for the number of minutes the oral disc of *Discosoma sanctithomae* remained closed after being stimulated with a light touch of a glass pipette and then 0.5 ml of solution being injected into the cavity formed by the margin of the oral disc. The control was plain seawater and the treatments were solutions of glutathione and proline. Ten trials were performed for the control and each treatment in laboratory tests. Each treatment was significantly different from the control ($P < 0.001$; Mann-Whitney tests), and proline (10^{-2} M) was significantly different from the other two treatments ($P < 0.05$; Mann-Whitney tests). Proline (10^{-3} M) was not significantly different from GSH (10^{-3} M) ($P > 0.05$; Mann-Whitney test).

mesenterial filaments and did not reopen for several hours. The time specimens remained closed was greater for animals stimulated with proline (10^{-2} M) than for proline (10^{-3} M) and GSH (10^{-3} M) ($P < 0.05$, Mann-Whitney tests). There was no significant difference between GSH (10^{-3} M) and proline (10^{-3} M) ($P > 0.05$, Mann-Whitney test).

Tests were done with filter papers (with and without chemicals) to determine which chemicals elicited the envelopment response and subsequent ingestion (Table III). Most animals did not respond to plain pieces of filter paper that were dropped onto the oral disc (>93% of trials), and the papers were rarely ingested (<2% of trials). All trials were done by first dropping a plain piece of filter paper onto the oral disc and if there was no response then a treated piece of paper was tested. Chemicals effective only at high concentrations in the field syringe tests did not elicit consistent closure or ingestion in these tests. Proline and GSH-treated filter papers caused immediate closure of the oral disc, but GSH was effective at lower concentrations. Only GSH elicited consistent ingestion. Some filter papers with GSH that were not ingested were covered with mesenterial filaments extruded through the mouth or body wall of the oral disc. Similar responses occurred in tests using plain pieces of filter paper and then eliciting closure with 0.5 ml of GSH or proline from a pipette.

Pipecolic acid treated filter papers caused closure and were ingested at a concentration of 10^{-1} M but were not effective at 10^{-2} M (Table IV). Hydroxyproline and aze-

tidine carboxylic acid treated papers did not elicit any consistent response. The responses to S-methyl GSH were much similar to GSH and resulted in closure, ingestion, and extrusion of mesenterial filaments.

Discussion

Many cnidarians use the products of their endosymbiotic zooxanthellae as a major source of nutrients. It has been suggested that the Discosomatidae of the Caribbean may be primarily, if not exclusively, dependent on these associates for nutrition (Den Hartog, 1980). However, cnidarians also require exogenous sources of nitrogen, phosphorus, essential amino acids, and trace elements not provided by their symbionts. These are usually obtained through feeding on benthic or planktonic prey (Muscatine and Porter, 1977; Van-Praët, 1985; Sebens, 1987). The disc-shaped morphology of the Discosomatidae is probably adaptive for the collection of solar radiation (Den Hartog, 1980), but their flattened shape is also effective in allowing the capture of prey by envelopment.

Indo-Pacific Discosomatidae (= Actinodiscidae) have a similar morphology and utilize the same type of prey capture technique as *D. sanctithomae* (Hamner and Dunn, 1980). The largest Indo-Pacific species, *Amplexidiscus fenestrafer*, can envelop prey almost as quickly as *D. sanctithomae* (within 3 s after contact). Two smaller species (*Actinodiscus fungiformis* and *Rhodactis howesii*) close much more slowly (10 s–1 min). Colonies of these three species are found in well-lit reef areas on vertical walls, much like populations of *D. sanctithomae* in Bermuda. This orientation may facilitate the capture of large planktonic organisms that are swept into contact with the oral disc. An engulfment feeding method may be more effective in the capture of large, active prey than tentacular adhesion.

Our observations of *D. sanctithomae* capturing polychaetes and fish that were attracted to dive lights during night dives suggests that these corallimorpharians are capable of capturing large mobile prey. However, the few prey that were found in the coelenterons of specimens collected from the field at dawn were not of this type. The small number of prey found in our samples is comparable to some of the analyses of coral coelenterons examined by Porter (1974), but on the average he found a higher proportion of coral polyps feeding and containing multiple prey items. The relative lack of food items encountered in our analysis may be related to the small sample size (63 specimens), the small numbers of prey in the plankton during May, or be an artifact of the morning collection time. Further coelenteron analyses from animals collected at different times of the year and night are required to better establish the natural diet of *D. sanctithomae*.

Table III

Responses of *Discosoma sanctithomae* to filter papers (saturated with solutions with and without chemicals) dropped onto the oral disc

Filter paper	Concentration (M)	Number of trials	# of full closures	# ingestion responses	% ingestion responses
Control (no chemicals)		185	12	2	1
Asparagine	10 ⁻¹	5	0	0	0
Glutamine	10 ⁻¹	5	0	0	0
Glutamic acid	10 ⁻¹	5	0	0	0
Alanine	10 ⁻¹	6	3	3	50
	10 ⁻²	5	0	0	0
Proline	10 ⁻¹	5	5	0	0
	10 ⁻²	10	3	1*	10
	10 ⁻³	5	0	0	0
GSH	10 ⁻¹	5	5	4*	80
	10 ⁻²	22	22	16*	73
	10 ⁻³	10	10	7*	70
	10 ⁻⁴	10	8	1	10
	10 ⁻⁵	10	0	0	0

* Extrusion of mesenterial filaments in some specimens.

Many coral reef anthozoans have diel patterns of expansion and contraction that are related to both light and prey availability (Porter, 1974; Gladfelter, 1975; Sebens and DeReimer, 1977). Structures that have high densities of zooxanthellae are expanded during the day and are retracted at night. Those with few or no zooxanthellae are retracted during the day and are expanded at night when demersal zooplankton are most abundant. Sebens and DeReimer (1977) did not report that *Discosoma* (= *Rhodactis*) *sanctithomae* had a change in posture or a diel pattern of expansion and contraction of the margin of the oral disc and discal tentacles. However, the pattern observed in our study supports their general observa-

tions. The oral disc and discal tentacles have high densities of zooxanthellae and are expanded during the day. The margin of the oral disc, which has relatively few zooxanthellae, is greatly expanded at night compared to during the day. Expansion at night is adaptive for the capture of prey and contraction during the day may be a strategy to reduce metabolic costs or shading of clone-mate neighbors when the probability of capturing prey is low (Sebens and DeReimer, 1977).

These differences in expansion and contraction may not be as conspicuous as in other species of cnidarians that have been studied (Sebens and DeReimer, 1977), but a slight change in the posture of *D. sanctithomae* had

Table IV

Responses of *Discosoma sanctithomae* to filter papers saturated with solutions of proline and glutathione analogs

Filter paper	Concentration (M)	Number of trials	# of full closures	# ingestion responses	% ingestion responses
L-azetidine carboxylic acid	10 ⁻²	6	0	0	0
Pipelicolic acid	10 ⁻¹	10	9	8	80
	10 ⁻²	5	1	0	0
L-hydroxyproline	10 ⁻¹	5	1	1	20
	10 ⁻²	5	0	0	0
S-methyl GSH	10 ⁻²	10	10	7*	70
	10 ⁻³	9	7	1	11
	10 ⁻⁴	10	6	0	0
	10 ⁻⁵	10	0	0	0

* Extrusion of mesenterial filaments in some specimens.

a major effect on its ability to capture prey. Individuals not in a bowl-shaped posture were unable to exhibit an effective envelopment response or did not respond at all. Den Hartog (1980) suggests that the ability of *D. sanctithomae* to vary the shape of the oral disc from concave to convex may be an adaptation to receive an optimal amount of solar radiation during the day, but this change in shape is probably more related to maximizing the capture of prey that are more abundant in the water column at night. The difference in sensitivity to physical contact between day and night appeared to be related to the posture of the animals. Animals kept in the laboratory under a varying light regime did not exhibit a diel pattern of expansion and contraction. Independent of the time of day or light intensity, only those individuals that were in an expanded feeding posture displayed a consistent envelopment response. There may be a certain physiological state associated with the feeding posture that increases the sensitivity of the animals to mechanical stimuli. Other cnidarians are more sensitive toward feeding stimuli when they are in a normal feeding posture (Williams, 1972). Further neurophysiological studies of the diel behavior patterns of corallimorpharians may prove to be interesting.

Both mechanical and chemical stimuli are generally required to elicit a complete feeding response in most cnidarians (Lenhoff and Lindstedt, 1974). Strictly mechanical stimuli do not elicit consistent mouth opening and ingestion (Williams, 1972). Contact with a glass pipette to the oral disc of *D. sanctithomae* caused only closure and specimens reopened after a few minutes to resume a normal feeding posture. Purely mechanical stimuli will also cause envelopment by *A. fenestrafer* (Hamner and Dunn, 1980).

Chemical stimuli elicited both closure and further feeding behaviors in *D. sanctithomae*, but the source of these activators is not readily explained. Most studies of cnidarian feeding behavior assume that mouth opening and ingestion are a response to the release of body fluids (which contain numerous compounds including various feeding activators) from the prey liberated from puncture wounds made by nematocyst discharge during capture. There are few nematocysts in the tentacles of *D. sanctithomae*, and no nematocysts were discharged onto items that were put in contact with the discal tentacles. Prey did not appear to be stung by these tentacles after capture but they may be stung by extruded mesenterial filaments, nematocysts on the actinopharynx, or the marginal tentacles if they try to escape through the constricted opening of the cavity formed by the margins of the oral disc. Nematocysts were discharged onto objects presented to the marginal tentacles and they could be involved in releasing feeding activators from the prey. External digestion by mesenterial filaments extruded out of

the mouth or other regions of the oral disc has been described for *Rhodactis howesii* (Hamner and Dunn, 1980) and was observed for treated filter papers in *D. sanctithomae*. These filaments have high densities of holotrichous nematocytes (Den Hartog, 1980) that could puncture prey and liberate body fluids. There may only need to be a few nematocysts discharged to puncture the prey enough to create a point source of chemical to elicit feeding. Reimer (1971) suggests that the concentrations required for many feeding activators to elicit a response (10^{-4} M and higher) are too high to be ecologically significant since they are not likely to occur under natural conditions. However, if these chemicals are being released into a confined space, such as the cavity formed by the contraction of the oral disc in the Discosomatidae, then high concentrations may occur. Other sources of feeding activators may be components of prey excretory products or the epidermal covering of the prey (e.g., fish mucus). Lubbock (1980) has shown that the mucus of some fish species can elicit prey capture and ingestion by sea anemones.

The concentrations of chemicals tested in our experiments were similar to those used in other studies. In filter paper tests both corals (Lehman and Porter, 1973) and sea anemones (Reimer, 1973) respond to filter papers soaked in solutions of chemicals as dilute as 10^{-3} M, much the same as the responses of *D. sanctithomae* to both proline and GSH. In tests where whole animals are placed in solutions, responses have been recorded to concentrations as low as 10^{-7} M (Mariscal and Lenhoff, 1968). We did not perform this type of experiment, but the effective concentrations of both GSH and proline may be comparable in our experiments in which solutions were released from syringes in the general direction of the corallimorpharians. The concentrations of the chemicals would have been much lower once they reached the animals because of rapid dilution in the surrounding seawater.

The imino acid proline and the tripeptide GSH are widespread feeding activators in cnidarians (reviews by Lenhoff and Lindstedt, 1974; Lenhoff *et al.*, 1976; Van Praët, 1985; Sebens, 1987). These activators, along with various other amino acids and chemicals, cause both preparatory feeding and ingestion responses in different groups of anthozoans. In some species different activators cause different parts of the feeding response (Lindstedt, 1971; Reimer, 1971, 1973; Williams, 1972; Nagai and Nagai, 1973; Bursey and Guanciale, 1977). This was also observed for *D. sanctithomae*. Proline, GSH, and some other amino acids elicited envelopment at high concentrations, but only GSH caused a complete feeding sequence ending in ingestion. Proline and GSH have been reported to cause ingestion behaviors in both corals and sea anemones (Lenhoff and Lindstedt, 1974; Van-

Praët, 1985). Mesenterial filaments were extruded only at high concentrations of proline ($10^{-1} M$), whereas GSH elicited mesenterial filament extrusion at concentrations as low as $10^{-3} M$. Similar differences in response to these chemicals have been reported for corals (Mariscal and Lenhoff, 1968). The differences in behavior elicited by proline and GSH, along with the knowledge that proline has a distinctly different chemical structure from GSH, suggests that these activators have different receptors and different connections to the neuronal network involved in the feeding response.

Trials with proline and GSH analogs revealed some characteristics of the receptor(s) for these chemicals. Two proline analogs, pipecolic acid and L-hydroxyproline, were as effective at causing envelopment as the naturally occurring compound. The proline analog L-azetidine carboxylic acid did not elicit any behavior. This suggests that the size of the ring structure is important, but additional side chains do not alter the recognition of this group of compounds. Reimer (1971) reported a different result for the zoanthid *Palythoa*, in which changes in the size of the ring structure did not alter its activity. Also, Reimer (1973) found that addition of an OH-group (hydroxyproline) caused a response in the sea anemone *Calliactis polypus*. The analog S-methyl glutathione also reacted in the same fashion as GSH. To better establish the structural requirements of the receptor(s) involved in these feeding behaviors further tests should be conducted for inhibition and competition with particular chemical analogs.

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