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DEFENSIVE STRATEGIES OF SOFT CORALS (COELENTERATA: OCTOCORALLIA) OF THE GREAT BARRIER REEF. II. THE RELATIONSHIP BETWEEN TOXICITY AND FEEDING DETERRENCE

STEPHANE C. LA BARRE[1,**], JOHN C. COLL[1,*], AND PAUL W. SAMMARCO[2]

[1]*Department of Chemistry and Biochemistry, James Cook University of North Queensland, Townsville, Qld, 4811, Australia, and* [2]*Australian Institute of Marine Science, P.M.B. No. 3, M.S.O., Townsville, Queensland, 4810, Australia*

Abstract

Thirty-six specimens of soft corals (Coelenterata, Alcyonacea) were tested for toxicity by exposing *Gambusia affinis* (Vertebrata, Pisces) to aqueous extracts of coral macerate and assessing mortality. Fifty percent of the soft coral extracts were determined to be ichthyotoxic to the fish, supporting earlier studies. In another experiment, commercial fish food was immersed in the same aqueous soft coral extracts, dried, and offered to *G. affinis* at three concentrations with appropriate controls. The study of feeding deterrence showed that 88% of the 36 extracts produced negative feeding responses at the highest concentration. At intermediate concentrations, 75% of the extracts acted as feeding deterrents; 48% showed detectable deterrence at lowest concentrations. Levels of toxicity and feeding deterrence, however, were not correlated; *i.e.*, feeding deterrence was as common among non-toxic corals as among toxic ones. This finding may help to explain why some soft corals, which apparently lack toxic defense substances, do not exhibit signs of predation in the field.

Introduction

One of the most important selective factors influencing the evolution of living organisms is predation. The specific morphological (*e.g.*, Kettlewell, 1956), chemical (Whittaker and Feeny, 1971), and behavioral (Harvey and Greenwood, 1978) adaptations which have evolved in plants and animals and which clearly serve an anti-predatory function are extremely numerous and diverse in nature. Common anti-predatory adaptations include (1) feeding deterrent properties, involving olfaction and taste, whereby an organism is avoided by a predator or receives a low food preference, and (2) toxicity, whereby an animal may ingest the prey and become ill, experience physiological stress, or die (*e.g.*, Brower, 1969). These behavioral responses in the predator can be chemically mediated by secondary compounds either produced by the prey itself (Eisner, 1970; Gerhart, 1983) or acquired by the prey in turn from its own food (Brower *et al.*, 1970; Eisner *et al.*, 1974; Schulte *et al.*, 1980; Thompson *et al.*, 1982; Carte and Faulkner, 1983; Jensen, 1984).

Evidence for co-occurrence of feeding deterrent properties and toxicity is variable. Some studies have demonstrated a positive correlation between toxicity and the presence of feeding deterrents (West, 1976; Picman *et al.*, 1982; Camazine, 1983; Camazine *et al.*, 1983; Gerhart, 1984, 1986). By contrast, Rowell *et al.* (1983) found that

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* Address reprint requests to Dr. John C. Coll.

** Present address: Laboratoire National de la Recherche Scientifique, Laboratoire des Plantes Medicinales, Parc Forestier-Montreal, B.P. 643, Noumea, New Caledonia.

certain ferns were differentially palatable to two species of tropical grasshoppers, and that the presence of this palatability was not correlated with the presence of known plant toxins, such as phenolics and tannins. Toxicity of soft corals (Coelenterata: Alcyonacea) on the Great Barrier Reef has been demonstrated (Bakus, 1981; Coll *et al.*, 1982b; Coll and Sammarco, 1983), but the presence or absence of feeding deterrent properties has not been examined.

Soft corals can be quite common on coral reefs in the Indo-Pacific, and particularly in certain areas of the Great Barrier Reef (Dinesen, 1983). Although common species of soft coral are potentially rich sources of protein, carbohydrate, and especially lipids (Coll, 1981) and are easily accessible to predators such as fish because of their exposure, they suffer relatively low levels of predation (P.W.S., unpub. data; work in progress). Certain predators are specialized in such a way as to be able to consume highly toxic soft coral tissues. For example, *Ovula ovum* Linnaeus, 1758 (Mollusca, Prosobranchia) feeds almost exclusively on soft corals and possesses mechanisms for disposal or storage of toxins (Coll *et al.*, 1983). Certain chaetodontid fish have been observed to pick soft coral polyps from expanded colonies (Tursch and Tursch, 1982; also Sammarco, Coll, and Alino, work in progress). Most fish, however, appear to ignore the soft coral as prey; this has been attributed to their tissue toxicity (Bakus, 1981; Coll *et al.*, 1982b). In several recent studies, we have shown that approximately half of the common exposed soft corals from several regions of the Great Barrier Reef exhibit significant ichthyotoxic properties (Coll *et al.*, 1982b; Coll and Sammarco, 1983). It thus seems probable that non-toxic soft corals have some alternate or additional defensive mechanism against predation. The presence of feeding deterrents has been suggested by Tursch (1976) who pointed out that some crude soft coral extracts were highly unpalatable to fish. Stoecker (1980) also found that many tropical ascidians exhibit similar properties.

Here we report the results of a detailed study of 36 soft corals for ichthyotoxic and feeding deterrent properties as determined by tests on the mosquito fish *Gambusia affinis* (Baird and Girard) (Vertebrata, Pisces). We also examine the co-distribution of these two characters among these soft coral species and demonstrate that they do not appear to be related.

Materials and Methods

Thirty-six common soft coral specimens (9 genera, 32 species) were collected from Britomart Reef (18°14′S, 146°45′E) (herein referred to as the BRI-series) at depths of 1–12 m, Rib Reef (18°15′S, 145°45′E) (RIB-series) at depths of approximately 5 m, and from Myrmidon Reef (18°16′S, 147°24′E) (MYR-series) at depths ranging from 2–10 m. Sampling was performed between August to October, 1982. Specimens used for toxicity and feeding deterrence studies (>20 g wet weight) were placed in labeled plastic bags and frozen. Corresponding samples were preserved in 70% ethanol and used as reference specimens for taxonomic identifications. Identifications were made using information published in Bayer (1956, 1961), Verseveldt (1980), Tixier-Durivault (1966, 1972), and references cited by these authors.

Toxicity tests

Ichthyotoxicity tests were performed according to the techniques described by Yamanouchi (1955) and Bakus and Thun (1979), using similar dosage levels. These have been described in Coll *et al.* (1982b), but a summary will be provided here.

Aqueous extracts were prepared from each soft coral as follows. Fifteen g of frozen tissue was blended with fresh water (30 ml), and the macerate were centrifuged at 10,000 RPM for 10 min. The supernatant was divided into three equal portions, two of which were used for the ichthyotoxicity study; the third was reserved for the palatability study.

The test organism used to determine the toxicity was the common mosquito fish *Gambusia affinis*. The cosmopolitan distribution of the species, its ability to survive environmental fluctuations, and its abundance make it attractive for laboratory work, especially for toxicity studies (Cornman 1968; Birkhead 1972; Spiegelstein *et al.,* 1973; Ne'eman *et al.,* 1974; Fernandez Bernaldo de Quiros, 1978). *Gambusia affinis* was chosen as the test organism because it can be trained to feed under experimental conditions in the laboratory, is discriminating in its feeding behavior, and is sensitive to feeding deterrents. These qualities have made it the preferred test organism in similar palatability tests conducted by both chemists (Rideout *et al.,* 1979) and vertebrate physiologists (Strieck, 1924; Glaser, 1966; Atema, 1977; Herbert and Atema, 1977) in studies examining the molecular basis of chemoreception in teleost fish. In addition, this extant freshwater species most likely has had no exposure to soft corals through evolutionary time and does not possess adaptations of resistance to soft coral toxins or tolerance to associated feeding deterrents.

The mosquito fish were collected from a creek at least 24 hours prior to testing and acclimatized in a large storage aquarium containing dechlorinated tap water. Only the apparently healthiest individuals of both sexes were selected for the experiment.

Extracts were added to small duplicate test aquaria, each containing fresh water (200 ml) and three randomly selected specimens of the test fish. Mortality counts were taken after 22, 45, 90, 180, 360, and 720 min for each of the extracts.

Palatability determinations

A commercial fish food in the form of dried flakes (Tetra Min^{R}) was used in the preparation of test foods and controls. Preliminary tests were performed to determine a concentration range for the experimental food. Concentrations were selected by determining the levels at which several randomly selected extracts could be minimally detected by the test organism. Once these levels were determined, the flakes were ground to a fine powder, from which 120 portions of 100 mg each were weighed out. Three replicate portions of fish food were prepared for each of the 36 soft coral extracts. One ml of extract was added to the first, 2 ml to the second, and 4 ml to the third. The suspensions were mixed, freeze-dried, and ground using a mortar and pestle. The food preparations were stored in the absence of moisture to prevent rehydration. Controls were prepared in a similar manner using the addition of 1, 2, and 4 ml of fresh water (instead of extract). This provided 108 test and 12 control preparations.

The method used here was particularly efficient for testing large numbers of crude extracts. Particles were clearly accepted or rejected by the fish.

Ten to twenty fish were used in the palatability tests and were conditioned to accept a small amount of untreated ground fish food from the experimenter for between 7–10 days. The test and control food preparations were presented to the fish several times per day by holding a few particles with dissecting tweezers, and releasing them just beneath the surface of the water. A small trail of dissolving chemicals was visible around each sinking particle. Responses of fish to the food were recorded only for particles detected by the fish between the surface and the mid-depth of the aquarium. Test samples and controls were presented at random, using three different samples and a control of the same concentration per feeding session.

The response of any test fish to the experimental food was classified as follows:

(1) *Acceptance:* The fish detected a food particle, seized it, and ingested it—an indication of lack of feeding deterrence;
(2) *Rejection:* The fish detected a food particle, ingested it, and expelled it immediately—an indication of feeding deterrence via taste; unpalatability;
(3) *Avoidance:* The fish detected the food and moved towards it, but turned away upon approaching it, and failed to ingest it—an indication of the presence of an olfactory deterrent.

For the purposes of this study, the term "feeding deterrence" will refer to responses including both avoidance (olfaction) and rejection (taste).

Ten unambiguous responses were recorded for each sample at a given concentration. Occasionally the fish did not detect the food (usually towards the end of an experimental feeding session). Detection could be enchanced, however, if samples and controls were presented in small quantities at different sites, decreasing the potential local build-up of food particles and their associated chemicals.

Numerical methods

Data were analyzed by non-parametric tests of association. The Kendall's Rank Correlation Coefficient (Sokal and Rohlf, 1981) yielded an indication of the level of association between toxicity and palatibility (also see Siegel, 1956).

Toxicity rankings were assigned according to relative mortality levels of test fish, using primarily the 720-min samples. Within these mortality categories, tied ranks were further split using data from successively earlier sample times. Ties unresolvable by this method were assigned according to the conventions of the Kendall's Rank Correlation Analysis (Sokal and Rohlf, 1981). Unpalatability ranks were assigned in a similar fashion, primarily using data from the most highly concentrated test preparations and ranking further on the basis of data from successively less concentrated preparations.

Results

One half of the 36 soft coral aqueous extracts were found to be non-toxic; *i.e.*, they were indistinguishable from controls in their effect on *Gambusia affinis* and caused no mortality in test fish at the concentrations used (Table I). Twenty-two percent of the extracts killed all fish in 12 hours and were categorized as 100% lethal. The remainder (28%) elicited intermediate levels of mortality and were considered to be toxic. The majority of soft coral extracts examined in this study (89%, n = 36) had detectable deterrent effects on feeding in test fish at the highest concentration utilized. Seventy-five percent of the extracts elicited at least some avoidance or rejection responses by fish at the intermediate concentration, and about one-half (47%) elicited such at the lowest concentration.

The four samples (constituting 11%) showing the lowest acceptance levels were *Efflatounaria* sp. a, *Lemnalia* sp. c, *Sinularia capillosa,* and *S. flexibilis;* each showed high rejection rates at all concentrations. Two-thirds (24/32) of the samples were found to be avoided or rejected by test fish, with 50–100% rejection rates at the highest concentration. Among the least palatable of these, *Sarcophyton glaucum, Sarcophyton* sp. c, *Lemnalia* sp. a and b, and *Sinularia* sp. a, were rejected at the lowest concentration (at levels of ≥30%). Only eight out of 36 samples showed evidence of avoidance by the fish, including *Lemnalia* sp. a and c and *Sinularia* sp. a, which elicited avoidance responses even at the median concentration (Table I).

Two-thirds of the samples were found to be unpalatable, with high rejection scores occurring at highest concentrations. Of the 12 least palatable extracts, 5 were found to be within the "non-toxic" category, including the least palatable specimen—*Efflatounaria* sp. a (RIB-10). In addition, four of the most palatable soft coral extracts were found to fall within the lethal or toxic categories—namely *Sinularia* sp. 3 (RIB-23), *S. polydactyla*, *Sinularia* sp. c (RIB-5), and *S. peculiaris* (RIB-21). The extracts of four (4) soft corals were accepted at all concentrations; these included *Capnella* sp. a (RIB-24, -25; two specimens), *Capnella* sp. b (RIB-14), and *Sinularia* sp. c (RIB-5).

Some soft coral genera exhibited different levels of interspecific variability in palatability. For example, species of *Sinularia* were among the most variable. Various species of *Capnella* tended to elicit little feeding deterrence, while all *Lemnalia* species elicited at least some response.

There was no significant correlation between ichthyotoxicity and feeding deterrence for the 36 samples studied ($P > 0.05$, Kendall's Coefficient of Rank Correlation). Thus, no evidence was found to indicate that these two characters generally co-occur in this group of organisms.

Discussion

With respect to toxicity, the mortality data lent further support to earlier conclusions that crude aqueous extracts of some soft corals are potentially lethal to the test fish *Gambusia affinis* (see Coll *et al.*, 1982b; Coll and Sammarco, 1983). These aqueous extracts have been shown to contain suspended lipid-soluble toxins, including terpenes (Coll *et al.*, 1982b). Three very toxic samples came from alcyonacean species already found to be toxic in earlier studies: *Lemnalia* sp. c. (RIB-15), *Sinularia flexibilis* (BRI-1), and *Sarcophyton glaucum* (BRI-5) (Coll *et al.*, 1982b). The genus *Sarcophyton* was consistently found to be lethal, whereas representatives of the genus *Lemnalia* ranged from 100% lethal to non-toxic. These results are in accordance with our earlier findings.

Toxicity offers an important adaptation for organisms otherwise defenseless against predation (see Ehrlich and Raven, 1964; Eisner and Meinwald, 1966; Whittaker and Feeny, 1971; Faulkner and Giselin, 1983). Such organisms include holothurians (Bakus, 1981), sponges (Randall and Hartman, 1968; Green, 1977). crinoids (Rideout *et al.*, 1979), ascidians (Stoecker, 1980; Bakus, 1981), and the larvae of *Acanthaster planci* (crown-of-thorns starfish) (Lucas *et al.*, 1979). Saccoglossan nudibranchs are also known to exude a defensive secretion upon disturbance (Edmunds, 1966). This toxicity, although common, does not occur in the high frequency previously assumed for organisms lacking mechanisms of escape or physical defense (Bakus, 1981), such as in many of the Alcyonacea.

With respect to feeding deterrence, the soft corals examined exhibited a wide range and generally clear ranking as determined by the criteria used in this experiment. Almost 90% of all soft corals examined elicited some level of feeding deterrence in test fish. Many alcyonaceans (about 50%) on the Great Barrier Reef also exhibited ichthyotoxic characteristics. Our tests of association, however, were unable to reveal any significant relationship between these two characters. That is, the two attributes (as measured here) appear to co-occur within soft corals at random. The compounds which are responsible for the ichthyotoxic characters may well be different from those responsible for feeding deterrence. The majority of pure compounds derived from

TABLE I

Ichthyotoxicity and feeding deterrence data derived from laboratory experiments exposing Gambusia affinis *to crude soft coral extracts and food impregnated with extracts*

Species name	Specimen number	Toxicity time (Min) 22	45	90	180	360	720	Toxicity rank	Acceptance: Proportion of trails 1 ml/100 mg	2 ml/100 mg	4 ml/100 mg	Feeding deterrence rank
Category 1: 100% lethal												
Lemnalia sp. c	RIB 15	6	6	6	6	6	6	1	0.5	0.0†	0.0†	2
Sinularia capillosa	JUL 35	3	6	6	6	6	6	2	0.8	0.2	0.0	3.5
Sarcophyton glaucum	BRI 5	2	5	6	6	6	6	3	0.7	0.4	0.1	12
Sarcophyton sp. c	RIB 13	0	3	5	6	6	6	4	0.5	0.3	0.0	5
Sinularia sp. e	RIB 23	0	0	5	6	6	6	5	1.0	0.9	0.8	32
Sinularia flexibilis	BRI 1	0	0	0	2	6	6	6	0.8	0.2	0.0	3.5
Sarcophyton sp. b	JUL 4	0	0	1	2	4	6	7	1.0	0.6	0.5	22
Cladiella sp. a	RIB 12	0	0	0	0	0	6	8	1.0	0.7	0.4	9
Category 2: Toxic												
Sinularia polydactyla	JUL 1	0	0	1	1	2	4	9	1.0	1.0	0.7	30.5
Sinularia sp. c	RIB 5	0	0	0	0	2	4	10	1.0	1.0	1.0	37.5
Sinularia peculiaris	RIB 21	0	0	0	0	0	4	11	1.0	1.0	0.7	30.5
Efflatounaria sp. b	RIB 16	0	0	0	2	2	3	12	1.0	0.2	0.2†	15
Paralemnalia sp. c	RIB 9	0	0	0	0	1	3	13	1.0	1.0	0.4	20
Lemnalia sp. a	RIB 20	0	0	0	1	2	2	14	0.4	0.1†	0.1†	10
Lemnalia sp. b	RIB 8	0	0	0	1	1	2	15	0.9	0.6	0.0	8
Paralemnalia sp. b	RIB 4	0	0	0	0	1	2	16	1.0	0.9	0.4†	24
Paralemnalia sp. d	RIB 17	0	0	0	0	0	2	17	0.9	0.6	0.7	26
Lemnalia sp. d	RIB 19	0	0	0	0	0	1	18	0.9	0.3	0.5	21

Category 3: Non-toxic												
Efflatounaria sp. a	RIB 10	0	0	0	0	0	0	29.5	0.1	0.0	0.0	1
Sinularia sp. d	RIB 7	0	0	0	0	0	0	29.5	0.8	0.3	0.0	6
Sinularia sp. a	RIB 1	0	0	0	0	0	0	29.5	0.7	0.0†	0.1†	11
Sinularia mollis	BRI 6	0	0	0	0	0	0	29.5	0.8	0.6	0.0	7
Litophyton sp.	JUL 3	0	0	0	0	0	0	29.5	0.9	0.2	0.1	13
Lemnalia sp. b	RIB 6	0	0	0	0	0	0	29.5	0.7	0.1	0.3	14
Sinularia sp. g	BRI 2	0	0	0	0	0	0	29.5	0.9	0.8	0.0	9
Paralemnalia sp. a	RIB 3	0	0	0	0	0	0	29.5	0.8	0.6	0.7	16
Capnella sp. c	RIB 11	0	0	0	0	0	0	29.5	1.0	0.8	0.3	18
Dendronephthya sp.	MYR 3	0	0	0	0	0	0	29.5	1.0	0.8	0.3†	17
Sinularia sp. b	RIB 18	0	0	0	0	0	0	29.5	1.0	0.8	0.5	23
Capnella sp. d	BRI 4	0	0	0	0	0	0	29.5	1.0	1.0	0.5†	25
Sinularia variabilis	RIB 25	0	0	0	0	0	0	29.5	1.0	0.6	0.7	27
Sinularia sp. f	RIB 2	0	0	0	0	0	0	29.5	1.0	0.9	0.7	28
Sinularia dura	MYR 2	0	0	0	0	0	0	29.5	1.0	1.0	0.7†	29
Capnella sp. b	RIB 14	0	0	0	0	0	0	29.5	1.0	1.0	1.0	37.5
Capnella sp. a	RIB 24	0	0	0	0	0	0	29.5	1.0	1.0	1.0	37.5
Capnella sp. a	RIB 26	0	0	0	0	0	0	29.5	1.0	1.0	1.0	37.5
*Control one	C1	0	0	0	0	0	0	29.5	1.0	1.0	0.97	33.5
*Control two	C2	0	0	0	0	0	0	29.5	1.0	1.0	0.97	33.5
*Control three	C3	0	0	0	0	0	0	29.5	1.0	1.0	1.0	37.5
*Control four	C4	0	0	0	0	0	0	29.5	1.0	1.0	1.0	37.5

n = 10
* n = 30

Data represent number of fish (out of a total of 6) killed within time period specified (in min). Toxicity ranking also shown. Toxicity category determined by all (1), some (2), or none (3) of the fish dying. Palatability data also shown for each soft coral as indicated by acceptance by test fish of food impregnated with extract. Data represent proportion of trials (out of 10) with unequivocal acceptance at various concentrations for each extract (see text for details). † represents occurrence of avoidance response at the 10% level, except in the cases of RIB 1 and RIB 15, where the response levels were 20% and 30–40%, respectively. Feeding deterrence rank also shown. No significant association between ichthyotoxicity and feeding deterrence ($P > 0.05$, Kendall's Coefficient of Rank Correlation).

these soft corals which have been demonstrated to have ichthyotoxic properties have been terpenoids, belonging predominantly to the di- and sesquiterpene classes (Ne'eman *et al.*, 1974; Tursch *et al.*, 1978; Coll *et al.*, 1983).

Some pure sesquiterpenes have been shown to possess properties of feeding deterrence in reef fish (Tursch *et al.*, 1978), and this class of compounds is commonly found in alcyonaceans. Polyhydroxysterols also commonly occur within this group (Schmitz, 1978). These are known to be highly biologically active in certain terrestrial systems (Nakanishi, 1974), but their levels of activity, with respect to both ichthyotoxicity and feeding deterrence, specifically within the Alcyonacea, are as yet undetermined. We have shown that these classes of compounds (sterols and terpenes) are present in the aqueous extracts of soft corals (Coll *et al.*, 1982b), although they would generally be regarded as non-water-soluble compounds. The only set of toxins not assessed in our studies would be membrane-bound molecules (*i.e.*, peptide toxins) not present in the supernatant after centrifugation. Therefore, we are unable to comment on the efficacy of this latter group of compounds in the chemical defense of soft corals.

Extracts of several species of *Sinularia*, including *Sinularia* sp. a (RIB-1), *S. flexibilis* (BRI-1), *S. capillosa*, and *S. mollis* (BRI-6), were frequently rejected by the fish at low concentrations, indicating the presence of efficient feeding deterrents in the soft coral tissues. In addition, in almost all trials, *Efflatounaria* (RIB-10) was found to be clearly unpalatable. Specimens of this genus, including this one, are generally known to have little or no ichthyotoxic properties, as determined by this and previous studies. However, they are rich in terpenoid compounds (Bowden *et al.*, 1983). These compounds may be responsible for the low palatability of the tissue extracts, for such compounds are known to be unpalatable in terrestrial systems (Schwartz *et al.*, 1980).

Chemical warning signals are used by a variety of marine organisms as a defense against predation (*e.g.*, Glynn, 1980). The substances responsible for these signals are often secondary metabolites which may be toxic and can sometimes be released by the prey into its immediate surroundings. The physical basis of feeding deterrence, particularly olfaction, is generally attributed to the action of volatile substances (Kittredge *et al.*, 1974; Little, 1983). Terpenoids, although often cytotoxic, may or may not possess odorous properties. For example, the diterpene sinularin has been shown to be cytotoxic (Weinheimer *et al.*, 1977) but is certainly not volatile (pers. obs., J.C.C.). By contrast, sesquiterpenes derived from *Lemnalia* (*e.g.*, *Lemnalia* sp. c, RIB-15) are known to be ichthyotoxic (La Barre, 1984) and yet are highly volatile and pungent in odor (J.C.C. and co-workers, pers. obs.). Thus, a given compound may be an effective toxin but a poor chemical signal, as is the case in the monarch butterfly *Danaus plexippus* and its toxicity to the blue-jay *Cyanocitta cristata* (Brower, 1969). Volatility or solubility of individual terpenes within a given soft coral may be an important factor in determining the presence and intensity of their feeding deterrent capabilities.

In our study, only 22% of the soft coral extracts elicited avoidance responses, and even these were mostly at the 10% level. This indicates that olfaction was probably not a major factors in feeding deterrence. In addition, those cases where avoidance was elicited were not necessarily associated with extracts exhibiting high rejection levels. Thus, feeding deterrence via olfaction is not necessarily linked with the degree of palatability of the tissue in question. The major exception to this was the case of extracts derived from *Lemnalia* sp. c (RIB-15), where it is possible that olfaction may be at least as important in feeding deterrence as taste. This set of particularly odorous and toxic extracts deterred hungry fish from even touching the food particle on several occasions.

Common reef alcyonaceans are typically sessile, non-cryptic, and possess drab coloration. There would be a distinct adaptive advantage for such organisms to release olfactory warning substances or feeding deterrents into the water column. Since this would appear to be independent of their degree of toxicity, a type of diffuse Batesian mimicry may be occurring. Remarkably high concentrations of secondary metabolites are indeed found in some soft coral tissues, but certainly not all (Coll *et al.*, 1981; Coll and Sammarco, 1983). This is not to say that coevolution of specialized predators has not occurred. It is known that *Ovula ovum* is adapted to prey specifically on *Sarcorphyton glaucum* and detoxify the most toxic metabolite (Coll, 1983). Fish such as *Chaetodon ocellicaudus* readily feed upon such alcyonaceans as *Litophyton viridis, Sarcophyton glaucum, Clavularia inflata, Nephthea* sp., etc. (Tursch and Tursch, 1982). Other *Chaetodon* spp. are also known to feed on soft corals.

Direct extrapolation of results from laboratory data on standard test fish to field situations involving coral reef fish should be made with caution. Field observations suggest, however, that feeding deterrents are indeed effective against predation. We have observed very low levels of natural predation on these organisms in the field consistently over the past 5–6 years (pers. obs.; PWS, unpub. data).

The secondary metabolites of soft corals from the Great Barrier Reef may possess three distinct ecological functions: (1) ichthyotoxicity (Coll *et al.*, 1982b; Coll and Sammarco, 1983; this study) which may well be indicative of an anti-predatory role (Gerhart, 1984); (2) a feeding deterrent role (this study); and (3) an anti-competitor role, causing mortality in scleractinian and alcyonacean corals, demonstrated experimentally both in the laboratory and the field (Sammarco *et al.*, 1982, 1983, 1985; Coll and Sammarco, 1983; Coll *et al.*, 1982a; La Barre *et al.*, 1986). Each of these characteristics varies from species to species, both at the intergeneric and interspecific levels. The characters do not appear to be linked. Thus, feeding deterrence does not necessarily indicate toxicity, toxicity does not imply allelopathy, allelopathy does not imply feeding deterrence, and so forth. Indeed, different classes of compounds (*e.g.*, terpenes *vs.* sterols) may be responsible for these different characters in some species.

It seems highly likely that those biologically active compounds occurring within the Alcyonacea of the Great Barrier Reef, irrespective of their chemical class, serve different ecological functions, depending upon the evolutionary history of the species in question (also see Stoecker, 1980). These might include anti-predatory, anti-competitor, anti-fouling, etc. adaptations, which can occur individually or in any random combination within a species. In addition, each character can function at different levels of effectiveness in different species. Survival of individual soft corals may well be influenced by chemically mediated processes which vary in type, intensity, and co-occurrence between species. These characters have most likely played an important role in contributing to the evolutionary success of soft corals in the Indo-Pacific region.

The major findings of this study may be summarized as follows: (1) approximately 50% of the soft corals surveyed in this study from the central region of the Great Barrier Reef were found to be ichthyotoxic. These results are consistent with earlier results from other parts of the Great Barrier Reef, including the northern, central and southern regions. (2) Extracts derived from almost 90% of these same soft corals had detectable deterrent effects on the feeding activities of test fish at the highest concentrations utilized here. (3) Despite the existence of these traits, no significant association could be found between ichthyotoxicity and feeding deterrence in the soft coral species tested. That is, their co-occurrence appeared to be random. (4) It is hypothesized (a) that different chemical compounds may be responsible for the different responses in test organisms, and/or (b) that the biologically active compounds in the various species of Alcyonacea may be adapted for different functions (anti-predation, competition for space, anti-fouling, etc.) which may have evolved independently.

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