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CHEMICAL ECOLOGY OF MARINE ORGANISMS: AN OVERVIEW

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Abstract—An overview of marine chemical ecology is presented. Emphasis is placed on antipredation, invertebrate-toxic host relationships, antifouling, competition for space, species dominance, and the chemistry of ecological interactions.

Key Words—Chemical ecology, ecological chemistry, defense, predation, antipredation, symbiosis, biological associations, fouling, biofouling, antifouling, communities, succession, dominance, competition, marine chemistry, medicine, toxin, noxin, venom, poison, marine natural products chemistry, natural products chemistry.

INTRODUCTION

The chemical ecology of marine organisms is described by a vast assemblage of papers and books, representing a wide variety of subdisciplines within biology and chemistry. Much of the recent interest in marine chemical ecology has developed historically as offshoots from natural products chemistry (i.e., novel compounds, Manes et al., 1985) and drug and health-related studies. Among some of the most interesting applied topics, in which considerable basic research has been and is being done, are health problems such as worldwide human marine poisonings, numbering over 20,000 cases and 150 deaths annually (Russell, 1984). Paralytic shellfish poisoning or PSP, including saxitoxin, annually numbers about 2000 cases and 33 deaths (Hashimoto, 1979;

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Russell, 1984; Steidinger and Baden, 1984). Ciguatera or fish poisoning causes deaths in the Indo-Pacific region in particular (Randall, 1980). Poisonings from eating other dangerous seafoods (e.g., snails and crabs) number about 530 cases and 37 deaths annually; (Garth and Alcala, 1977; Yasumoto et al., 1983a,b; Russell, 1984).

Swimmer's itch from the blue-green *Lyngbya majuscula* (now *Microcoleus lyngbyaceus*), is caused by the inflammatory agent debromoaplysiatoxin, one of the most potent skin irritants known (Russell, 1984). Some 1.5×10^6 humans are stung every year as a result of contact with marine organisms (Kohn, 1958; Plessis, 1975; Russell, 1984). Dermatitis from haptens in bryozoans is also common (Russell, 1984). In addition to the above poisons and irritants, a variety of antibiotic (i.e., antibacterial, antifungal, antiviral) agents, antitumoral compounds such as didemnins or depsipeptides (Burkholder, 1973; Mynderse et al., 1977; Weinheimer et al., 1978; Rinehart et al., 1981a,b; Jacobs et al., 1985; Thompson et al., 1985), prostaglandins (Weinheimer and Spraggins, 1969; Ruggieri and Thoroughgood, 1985), and antiinflammatory agents such as potassium fluorosilicate are known to occur in marine species (Gregson et al., 1979).

Other topics of interest in chemical ecology include mutualism (Muscatine and Porter, 1977; Wilkinson and Vacelet, 1979; Glynn, 1983), chemical communication (Reiswig, 1970; Barbier, 1981; Liley, 1982), chemoreception (e.g., in larval settling, Hadfield, 1977; Hadfield and Ciereszko, 1978; Crisp, 1984; Morse and Morse, 1984; food recognition and detection of predators, Noakes and Ward, 1981; Croll, 1983), bioluminescence (Ruby and Morin, 1978; Morin, 1981), immunological responses such as the death of subordinate corals and graft acceptance in sponges (Hildemann et al., 1981; Jokiel et al., 1982; Neigel and Avise, 1983; Kaye and Reiswig, 1985), growth controls (Sullivan et al., 1983; Rinkevich and Loya, 1985), the use of marine pesticides (Padan or nereistoxin; Ruggieri, 1976), the weakening of calcareous structures by boring organisms (Goreau and Hartman, 1963; Anderson and Stonard, 1979; Young and Nelson, 1985), the use of marine bioactive substances in neurophysiology (McClure and Martin, 1983; Koenig et al., 1984), natural shark repellents (pardaxin, see discussion below; Bakus, 1983a; Bakus et al., 1983; Tachibana et al., 1985), natural antifouling agents (Riegle, 1982; Targett et al., 1983; Bakus and Kawaguchi, 1984), the stunning of fishes (Plessis, 1975), and chemotaxonomy (Bergquist and Wells, 1983; Gerhart, 1983; Bergquist et al., 1984; Lee and Gilchrist, 1985; Tymiak et al., 1985).

In addition, there are fascinating cases of symbiosis. For example, the clownfish, *Amphiprion clarkii*, that forms a mutualistic association with the sea anemone *Stechodactyla haddoni*, has a mucus layer of relatively inert glycoprotein that is three to four times thicker than that of many other reef fishes (Lubbock, 1980; Brooks and Mariscal, 1984). This mucus layer protects the fish from stings by nematocysts of the sea anemone. Another example is the juvenile damselfish, *Abudefduf leucogaster*, that lives among the soft coral *Litophyton viridis* in the tropical Pacific. These fish are protected from potential predators by chemicals released by the soft coral which are noxious to most fish but to which the damselfish have developed a tolerance (Tursch, 1982).

An exhaustive review of marine chemical ecology is not possible at this time. Instead, we will provide an overview, concentrating on the following aspects of chemical ecology that represent our different principal interests, that is, antipredation, invertebrate–toxic host relationships, antifouling, competition for space, species dominance, and the chemistry of ecological interactions. The reader is referred to other recently published reviews for additional information (e.g., Herring, 1979; Fenical, 1982; Norris and Fenical, 1982; Faulkner and Ghiselin, 1983; Faulkner, 1983; 1984; Wright, 1984; Scheuer, 1985; Coll et al., 1985).

ANTIPREDATION

Predators (in the broad sense) are widespread in the marine environment. This is reflected in numerous types of offensive and defensive mechanisms among their prey. Protective and defensive mechanisms evolved by the biota against vertebrates and invertebrates include rapid growth and growth in wave-washed and cryptic areas by benthic algae, unpredictable occurrences in time and space, burrowing, boring, large size, structural defense, evasive movement, cryptic coloration and form, nocturnal activity, symbiotic associations, parental protection, and chemical defenses (Bakus, 1964, 1969, 1983b; Menge and Lubchenco, 1981, Norris and Fenical, 1982). Many interactions of attack, defense, and behavioral response involve not physical force but chemical agents. A great many of these chemical agents can be assigned two or three adaptive roles (Whittaker and Feeny, 1971; Janzen, 1979). For example, secretion of mucus may serve to clear a hard coral of sediment but may also provide a mechanism for concentration of allelochemicals, preventing excessive dilution by currents (Jackson and Buss, 1975; Sullivan et al., 1983). This may also be the case in Maldivian soft corals (e.g., *Dendronephthya* and *Sarcophyton*, Bakus, personal observation). The retention of pigments is a passive chemical defense mechanism, effective in cryptic coloration, warning coloration, and countershading. For example, juveniles of the burrfish *Chilomycterus antennatus* reportedly are Batesian mimics in shape and coloration of the sea slug *Aplysia dactylomela* (Norris and Fenical, 1982).

Consumer pressure is severe in tropical rocky intertidal communities, where most organisms are located in holes and crevices for protection from predators (Menge and Lubchenco, 1981). The ultimate in consumer pressure occurs on coral atolls (Bakus, 1967, 1969). However, chemical defenses are not limited to species occurring in low latitudes. The kelp *Alaria marginata* produces antiherbivore phenolic compounds (Steinberg, 1984) as does the Caribbean brown alga *Stypopodium zonale*. The holothurian *Psolus chitinoides* in the San Juan Islands, Washington, is highly unpalatable to fish and has the highest saponin content of the four species of sea cucumbers examined (Bingham and Braithwaite, 1985). Many species of the green algae *Caulerpa* and *Halimeda* are ichthyotoxic (Gerwick and Fenical, 1981; Norris and Fenical, 1982; Russell, 1984). Genera within the Udoteaceae and Caulerpaceae are highly resistant to fish grazing (Lewis, 1985). In particular, certain *Halimeda* species contain halimedatriol, a diterpenoid trialdehyde, which shows antibiotic activity, inhibits cell division and sperm motility, and is ichthyotoxic (Paul and Fenical, 1984). Some *Halimeda* and *Caulerpa* species also produce diacetoxybutadiene-containing terpenes which deter fish feeding even when coated onto their preferred food, the seagrass *Thalassia testudinum* (Targett et al., 1986). However, the reef flat blue-green *Schizothrix calcicola* contains a major toxic metabolite (debromoaplysiatoxin) yet is consumed in large quantities by surgeonfishes at Enewetak Atoll (Bakus, 1967; Mynderse et al., 1977). This tends to support Lewis' (1985) conclusion that the susceptibility of tropical algal species to fish grazing is not clearly correlated with morphological (e.g., calcification) or chemical (e.g., allomones) characteristics that have been previously suggested as plant defenses against herbivory.

Similarly, toxic sponges and probably soft corals are consumed by certain fishes (Randall and Hartman, 1968; Anderson et al., 1981; Tursch and Tursch, 1982). The sponges *Neofibularia* spp. contain some of the most painful undescribed marine chemicals known to man (Hartman, 1967). Several flatworms including *Thysanozoon* spp. and even certain brittlestars secrete an acid, as do some opisthobranchs (Marbach and Tsurnamal, 1973; Cimino et al., 1983; Faulkner and Ghiselin, 1983; Russell, 1984). Opisthobranchs also release terpenes and a variety of other compounds which are thought to function in defense (Lewin, 1970; Faulkner, 1983; Mebs, 1985). Faulkner and Ghiselin (1983) believe that the loss of the shell in dorid nudibranchs and other opisthobranchs is correlated with defense chemicals, the chemical defenses being elaborated gradually as the shell was being lost.

Coelenterates employ nematocysts offensively and defensively. The most toxic are cubomedusae such as the sea wasp, *Chironex fleckeri*, which has been known to cause human death in less than five minutes (Russell, 1984; Halstead, 1985). Nematocysts in hydroids (*Lytocarpus* spp. and *Millepora* spp.) and some hard corals (*Acropora palmata*) are known to sting divers (Halstead, 1985). Zoanthids containing palytoxins are reportedly among the most toxic marine organisms known (Moore and Scheuer, 1971; Moore and Bartolini, 1981; Russell, 1984; Uemura et al., 1985). The sea anemone (*Stoichactis* spp.) contains polypeptides that are proteinase inhibitory, toxic, and hemolytic (Mebs and Gebauer, 1980). Many sea anemones have cytolytic toxins, principally proteins and peptides (Russell, 1984). However, not all cnidarian defenses are contained within the nematocysts. For example, gorgonians (*Lophogorgia* spp., *Plexaura* spp.) have terpene and prostaglandin defense toxins (Fenical et al., 1981; Gerhart, 1984).

The polychaete *Eurythoe* has hollow, sometimes fluid-filled stinging chaetae; the sea hare *Aplysia brasiliana* produces antishark chemicals (Kinnel et al., 1979); and the blue-ringed octopus in Australia (*Hapalochaena maculosa*, which contains the venom maculotoxin, identical to the chemical poison tetrodotoxin) has caused human fatalities (Russell, 1984). Even the eggs and/or larvae of some seastars (*Asterias rubens*, *Acanthaster planci*) are protected by saponins or glycosides (Lucas et al., 1979). In fact, it is likely that the larvae of many asteroids may contain saponins that act against predators such as polychaete worms and fishes. Palytoxin also occurs in the eggs of the zoanthid *Palythoa tuberculosa* (Endean and Cameron, 1983).

Russell (1984) has questioned whether offensive sponge odors and taste play a defensive role. Green (1977) found that the sponge *Iotrochota birotulata* has a colored, strong-smelling exudate that, when released in water, is avoided by fishes. Green and Bakus (personal observation), in 1973 found that several species of foul-smelling gorgonians from the region of Veracruz, Mexico, were ichthyotoxic.

Aposematism is poorly studied in marine invertebrates. Some zooanthids are aposematically colored (Lewis, 1982), but sponges seem to display a large variety of colors whether toxic or not (Bakus and Thun, 1979). Some fishes have what appears to be warning coloration and erectile caudal spines as defensive mechanisms (surgeonfishes or Acanthuridae). Others secrete a mucus that prevents predaceous fishes from eating them (Kerstitch, 1984). Perhaps the most incredible case of antipredation occurs in the Moses sole found in the Red Sea. This diminutive flatfish secretes a milky toxin that in some instances paralyzes the jaws of a biting shark (Clark, 1983; Dr. Eugenie Clark, personal communication).

Many marine toxins appear to be feeding deterrents also. Echinoderm noxins and toxins appear to be the same chemically, that is, triterpenoid and steroidal saponins (Burnell and ApSimon, 1983; Dr. G. G. Habermehl, personal communication). Terpenoids in sponges may be unpalatable to predators (Manes et al., 1984, 1985; Russell, 1984; Bescansa et al., 1985). More than half of nontoxic soft corals are noxious to fishes, their chemicals causing 48–88% feeding deterrency in fish (La Barre et al., 1986b). Feeding deterrency is as common among nontoxic fish corals as among toxic soft corals. The herbivorous fish *Sparisoma radians* avoided the milky exudate released from injured tips of the green alga *Halimeda incrassata* (Targett et al., 1986).

A variety of marine organisms are venomous, including octopuses (via their salivary glands), snails (especially *Conus geographus* and *C. textile*), sea urchins (*Toxopneustes*), sea stars (*Acanthaster planci*), fishes (scorpaenids or rockfishes such as the turkeyfish, stingrays; Roche and Halstead, 1972), and of course, all of the 51 species of sea snakes (Family Hydrophiidae, Voris, 1972). There are about 700 species of toxic (i.e., venomous and poisonous) fishes known. Rather few of the fishes (3%) on the Great Barrier Reef are venomous (Cameron, 1976). Many species are poisonous, either with toxic skin (about 50 species, e.g., crinotoxic soapfish, boxfish, puffers, and stonefish) or nocturnal mucus cocoons (wrasses and parrotfishes). There are even cases of fishes with toxic models (*Canthigaster*) and edible mimics (*Paraluteres*, Cameron, 1976). Recent summaries of information on venomous and poisonous marine organisms are found in Habermehl (1981), Sutherland (1983), Russell (1984), Russell et al. (1984), and Halstead (1985).

Defensive toxicity is prevalent in warm waters (Table 1). This high incidence in the tropics probably is an evolutionary response to a sessile or slow-moving habit, exposure coupled with high-diversity and high-intensity predation (especially by fishes), and rapid turnover rates (Bakus, 1969, 1983b; Cameron, 1976; Miller, 1982; Hay, 1984a,b). Recent findings indicate that the toxicity of sponges to fishes is relatively high in northern France and even the Antarctic (Hugsecom and van de Vyer, 1985; James B. McClintock, personal communication). This toxicity may represent adaptive responses to invertebrate predators, the broad spectrum toxins also affecting fishes.

What we do not know is often more interesting than what is known. Although exposed coral reef holothurians are toxic to fishes, and cryptic sea cucumbers in the same area are not, some cryptic sponges are toxic to fishes (Green, 1977; Bakus, 1981). Is this an accidental metabolic byproduct resulting from transposons, a feature selected in the past that has not yet been eliminated from the gene pool, or does this represent a species that occurs cryptically in some regions and exposed in others? Green (1977) found that most nontoxic sponges were unexposed in the tropics but exposed in cold temperate waters. As a general rule, opisthobranchs are both distasteful and cryptic (Faulkner and Ghiselin, 1983), the latter especially common in the tropics (Bakus, personal observation). Only seldom has it been demonstrated that even suspected toxins vary seasonally (e.g., saponins in the seastar *Asterias amurensis*, Yasumoto et al., 1966). How widespread is this phenomenon? Is it simply a Q_{10} response or could it be an adaptation to a seasonal increase in predation pressure, or both?

Bakus (1969) illustrated how the holothurian *Holothuria atra* secretes a toxin when disturbed. Parrish (1972) reported that the holothurian *Actinopyga agassizi* releases a noxious substance from the body surface when attacked by the snail *Charonia variegata*. Advanced hunger and periods of exposure in close proximity to the holothurian appear to give *C. variegata* sufficient resistance to the noxin to permit successful predation. Green (1977) suggested that sponge toxins may be released continuously into the surrounding water and serve as a warning deterrent to predators. Lucas et al. (1979) stated that saponins diffuse from starfish and are detected by their prey. They also serve as defense chemicals in asteroids and holothurians. The first chemically demonstrated release of an allelochemical from a marine organism was from an Australian soft coral (Coll et al., 1982a). Toxins are secreted more or less continuously in several species of soft corals (Sammarco et al., 1982; Coll and Sammarco, 1983) and in at least two species of sponges from California (*Spongia idia* and *Aplysina fistularis*, Walker et al., 1980; Thompson, 1985). We know nothing about this phenomenon in hundreds of other species of toxic sponges, gorgonians, and holothurians. The intensity of fish grazing on the benthos certainly appears to be greater in the tropics in general than that of higher latitudes (e.g., note the high-standing crops of algae in the latter, Bakus, 1969; Choat, 1982). However, is the encounter rate between predators and prey also greater in the tropics? This has never been investigated. How does a fish learn that a species is toxic? Presumably by trial and error feeding and/or by chemoreception (Bakus, 1981). This interaction needs considerably more study in the field.

Some marine toxicity studies have examined whole organisms from diverse geographical areas and pooled results. Questions regarding variations in toxicity with geography, age, sex, body part, depth, and so forth, need to be addressed in more detail. Based on analogies with terrestrial systems, one would expect to find variations in quality and quantity of allelochemics over the range of some species in response to changes in the environment or shifting selection pressures (Whittaker and Feeney, 1971). Dr. Valerie Paul (personal communication) is currently studying these subjects in marine algae, but we know virtually nothing about this in marine benthic invertebrates. There do not appear to be significant changes in the toxicity of soft corals with latitude along the Great Barrier Reef of Australia (Coll and Sammarco, 1983). This suggests that there is no significant change in the intensity of predation as long as coral reef communities persist. Toxicity in holothurians is weaker in cold waters than in the tropics (Bakus, 1974). Sponges that are toxic in colder waters were moderately to highly toxic whereas those in the tropics ranged from slightly to highly toxic (Green, 1977). Certain species of sponges and holothurians apparently are toxic in some localities and nontoxic in others (Green, 1977; Bakus, 1981). A sample of two species of blue-greens collected from the seaward side of Enewetak Island was much more toxic than a specimen collected on the lagoon side of the island (Mynderse et al., 1977), perhaps an adaptive response to high intensity grazing on the outer reef flat (Bakus, 1967). Two antimicrobial metabolites occur in the intertidal sponge *Aplysina fistularis* but not in the same species at depths of 5–15 m (Thompson et al., 1983; Thompson, 1985).

Several different toxic saponins can be found within an individual holothurian (Dr. G. G. Habermehl, personal communication), yet we know almost nothing about the adaptive advantage of having several compounds. One suggestion is that saponins are important in reproduction, antipredation, and antifouling. Prostaglandin A_2 in the gorgonian *Plexaura homomalla* (representing about 10% of the dry weight) is one million times more concentrated than in most other marine invertebrates. It has emetic properties in a very wide range

Table 1. Toxicity of Shallow-Water Marine Organisms at Various Latitudes[a]

Locality	Latitude	Taxonomic group	No. of Species		Species (%)	Source
			Tested	Toxic		
Canada	48°N to 78°N	freshwater and marine fish	? (770)[b]	12	1.6	McAllister, 1968
San Juan Islands, Washington	48°N	sponges	34	3	9	Bakus and Green, 1974; Green, 1977
		holothurians	12	3	25	Bakus, 1974; Bakus and Green, 1974
Nontropics	less than 20°N & S	marine organisms	937	262[b]	28	Various authors, in Bakus, 1969
Onagawa, Japan	38°N	holothurians	5	4	80	Yamanouchi, 1955
Seto, Japan	35°N	holothurians	9	7	78	Yamanouchi, 1955
Santa Catalina Island, California	33°N	sponges	44	9	21	Bakus and Green, 1974; Green, 1977
		holothurians	2	1	50	Bakus, 1974; Bakus and Green, 1974
Guaymas, Mexico	28°N	holothurians	6	5	83	Bakus, 1974; Bakus and Green, 1974

Zihuatenejo Bay, Guerrero, Mexico	17°N	sponges	11	7	64	Bakus and Green 1974; Green, 1977
La Blanquilla Reef, Veracruz, Mexico	19°N	sponges	36	37	75	Bakus and Green 1974; Green, 1977
Tropics	Approx. 20°N to 20°S	marine organisms	937	675[b]	72	Various authors, in Bakus, 1969
Cozumel, Mexico, to Belize, Belize	20°N to 17°N	sponges	54	31	57	Bakus and Thun, 1979
Eniwetok, Marshall Islands	12°N	holothurians	4	4	100	Bakus, 1968
Palau Islands, Pacific Ocean	7°N	holothurians	11	11	100	Yamanouchi, 1955
Cocos Island, eastern Pacific	6°N	holothurians	7	6	86	Bakus, 1974
Lizard Island, north Great Barrier Reef, Australia	14°S	sponges, soft corals, gorgonians, asteroids, criniods, holothurians, ascidians	42	25	60[c]	Bakus, 1981

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[a] Organisms toxic to fish unless otherwise indicated.
[b] Organism toxic to humans.
[c] 73% of exposed benthic species.

of organisms, causes learned feeding aversion in fish, and is ichthyotoxic (Gerhart, 1984). Many other gorgonians are ichthyotoxic (see above and Bakus, 1981). Toxins in soft corals, principally terpenes, constitute about 1% of their dry weight (Dr. John Coll, personal communication). About half of soft coral species are ichthyotoxic (Coll et al., 1982b; La Barre et al., 1986b). Siphonodictidine, a sponge chemical that kills coral polyps around the sponge *Siphonodictyon* spp., represents about 1% of the dry weight of the sponge. A congeneric sponge contains the chemical siphonodictyal, a very different metabolite that also kills nearby coral polyps (Sullivan et al., 1983). To what extent do inquilines occur in toxic animals such as sponges? The mildly toxic (to fish) Caribbean sponge *Spheciospongia vesperium* is teeming with inquilines (Pearse, 1932, 1950; Bakus and Thun, 1979), but the more toxic sponge *Ircinia campana* seems to have far fewer (Bakus, personal observation).

There is a dearth of information on whether the compounds toxic to fishes also serve other adaptive roles, such as antifouling agents or species spacing allomones. Sammarco et al. (1982) suggest that toxic compounds from soft corals serve both an antipredator function and a role in competition for space. However, it is not known whether chemically identical terpenes are involved in multiple roles. Coral reef sponges, soft corals, and ascidians that lack allelochemicals have a hardened body or secrete copious amounts of mucus (Bakus, 1969, 1981; Green, 1977; Bakus and Thun, 1979; Dr. John Coll, personal communication). The behavior of fishes exposed to benthic invertebrate toxins suggests that the chemicals are interfering with oxygen transport across gill membranes and/or that a strong chemoreceptive response is occurring. Mackie et al. (1975) reported that the toxic effects of saponins are similar to those of synthetic surfactants. They damage the gill epithelium, reducing gas exchange across the gill surface. Pardaxin, a polypeptide of the size of about 3800 daltons in the Moses sole, is hemolytic and ichthyotoxic (Primor and Zlotkin, 1976; Dr. Samuel Gruber, personal communication). It is a potent gill ATPase inhibitor and clearly causes structural damage to gill tissues (Primor et al., 1980). It also acts as a surfactant (Primor et al., 1983; Gruber and Tachibana, 1986). These appear to be the only instances where the physiological effects of antipredatory toxins are known.

INVERTEBRATE-TOXIC HOST RELATIONSHIPS

Benthic marine organisms containing bioactive compounds, such as some sponges, cnidarians, mollusks, holothurians, and asteroids, are probably never completely devoid of either predators or symbionts. Because of this, it is necessary to examine how predators and symbionts (i.e., associated species) handle the toxic or noxious compounds that their hosts produce. A toxic compound is thought to provide general protection to the host; therefore, any associate would be expected to be specialized in their adaptations to the host. As an example of this, Coll et al. (1983) briefly describe the relationship of the prosobranch mollusk *Ovula ovum*, an egg cowry, to the highly allelotoxic soft coral *Sarcophyton* spp. The prosobranch grazes on the corals' tissue without apparent harm. By way of a reduction-elimination reaction believed to be enzyme-mediated, the egg cowry transforms sarcophytoxide, the most abundant terpene in the soft coral, into a much less toxic, 7,8 deoxysarcophytoxide. This process probably occurs in the digestive diverticula/stomach region. Similarly, in a review article, Faulkner and Ghiselin (1983) discuss numerous cases in which nudibranchs selectively incorporate sponge toxins that are capable of acting as feeding inhibitors, the only exception being the *de novo* synthesis of polygodial in *Dendrodoris limbata* (Cimino et al., 1983). The secondary metabolites of the nudibranch *Cadlina luteomarginata* are found only in the dorsum and act as antifeedant chemicals to fish (Thompson et al., 1982). Additionally, herbivorous marine mollusks (e.g., *Aplysia*, saccoglossans) contain protective compounds dietarily derived from their algal food sources (Norris and Fenical, 1982; Faulkner, 1984).

In many other cases, however, the means by which an associate handles the toxins of its host are not well understood. Sponge-zoanthid associations appear to be of two distinct types in the central Caribbean. One group consists of dull-colored zoanthids, lacking toxicity, thus offering no protection to their sponge host. Brightly pigmented zoanthids, toxic in nature, comprise the second group, possibly representing a mutualistic association in which the toxic zoanthid reduces predation on host sponges (Lewis, 1982). It seems likely that sponge hosts are never exposed to zoanthid toxins. This may also be the case in zooxanthellae-coelenterate relationships. Many toxic alcyonaceans and gorgonians contain algal symbionts which contribute to the nutrition of the host (Muscatine, 1980). Kokke et al. (1984) present strong evidence that the zooxanthellae do not synthesize these bioactive compounds nor do they provide an immediate precursor to toxin (terpene) synthesis (e.g., a mevalonic precursor). Since these terpenes are probably stored in membranous vacuole-type structures similar to those proposed in sponges (Simpson, 1984), any toxin-resistance hypothesized from the mere existence of the algal-toxic host relationship might simply be explained by stating that the zooxanthellae are never exposed to these bioactive compounds (Dr. William Fenical, personal communication).

Other toxic host-associate interactions simply have not been examined in detail. A variety of animals (worms, sea urchins, crustaceans, and fishes) feed on the seastar *Acanthaster* in spite of its toxic saponins (Glynn, 1984). The prosobranch gastropods *Cyphoma* and *Neosimnia* feed on gorgonians containing bioactive compounds without deleterious effects (Dr. Eric Jordan, personal communication). Sundial shells (*Heliacus* spp.) eat some of the polyps of the zoanthid *Palythoa* (Endean and Cameron, 1983). The seastar *Evasterias troschelii* has a commensal polychaete, *Arctonoe fragilis*, that is immune to the hosts' saponin, whereas the noncommensal polychaete *Arctonoe pulchra* is not

(Patterson et al., 1978). Some tropical fishes feed on toxic sponges with no visible negative reactions (Randall and Hartman, 1968). These are only a few examples of the wide variety of interactions between an associate and its toxic host yet to be explored and understood.

In summary, a species that closely associates with (i.e., lives within in some manner or feeds on) a toxic host species may handle bioactive compounds by one of the following means: (1) excrete or secrete the toxins unchanged (e.g., some opisthobranchs), (2) incorporate the toxins or a derivative thereof, possibly for their own defensive benefit (e.g., many sponge-feeding nudibranchs; *Ovula ovum*), (3) be immune to any toxic effects yet forced to handle bioactive compounds in some manner, and (4) avoid contact with its host's toxins (e.g., possibly zooxanthellae).

ANTIFOULING AND SUCCESSION

The initial stages of marine community development involve several steps: (1) adsorption of biopolymers in water to a surface (Mitchell, 1977; Baier, 1984; Lewin, 1984), (2) chemical attraction of bacteria, (3) reversible adsorption of bacterial populations, the bacteria adhering within minutes after settling onto a surface (Colwell, 1984), (4) irreversible adsorption of bacteria involving macromolecular fibrils, the attachment occurring by flagella and other cellular structures (a typical adhesion polymer on a bacterial surface might be making at least 10,000 contacts with a surface; Robb, in Lewin, 1984), (5) agglomeration and colony formation, and (6) growth of a secondary bacterial population, pennate diatoms, protozoans, and adhesion of particulate matter (Cuba and Blake, 1983; Mitchell and Kirchman, 1984). Whether microfouling is a general prerequisite to subsequent settling has not been resolved (Little, 1984).

Larval settling behavior is dependent on substratum type, substratum rugosity, light intensity, existing surface films, host inductance, larval chemoreception and other factors (Meadows and Campbell, 1972; Birkeland, 1977; Chia and Rice, 1978; Costlow and Tipper, 1984; Crisp, 1984; Morse and Morse, 1984). Three ecological models have been developed to explain the causes of succession or the replacement of species over time. They include: (1) "facilitation" or alteration of conditions by early species that allow later species to replace them, (2) "inhibition," that is, early colonists inhibit the invasion of later species, and (3) "tolerance," that is, early colonists do not affect the recruitment and growth of later species. There is ample evidence to support both facilitation (Gallagher et al., 1983; Turner, 1983; Harris et al., 1984) and inhibition (Sutherland and Karlson, 1977; Sousa, 1979; Standing et al., 1982; Rittschof et al., 1985). Breitburg (1985) recently concluded that examples of all three models appear to occur in marine community development. She and Dean and Hurd (1980) showed that more than one mechanism may be present in the same community. Inhibition seems to be more prevalent than facilitation, and tolerance appears to be relatively rare (Bergen, 1985).

Replacement of species during succession has been reported as orderly (Anger, 1978; Murray and Littler, 1978; Sousa, 1980; Sutherland, 1981) and disorderly (Fager, 1971; Osman, 1977; Sutherland and Karlson, 1977). Species composition in succession is affected by prior residents, grazing, temporal variability in recruitment and growth, small-scale differences in settlement, growth and/or survival of colonists, and the physical regime (i.e., disturbance ranging from mild to severe) under which they occur (Bergen, 1985; Breitburg, 1985). However, if successional studies are examined in detail, the actual mechanisms by which species growth is enhanced or inhibited are poorly known. To predict changes in species composition, interactions between the various pairs of early and late colonizers must be taken into account (Breitburg, 1985).

Woodin and Jackson (1979) suggested that different species of the same functional group (i.e., guild) may help each other in competition with species in different functional groups. This may be related in part to the fact that there is more evidence for competition between distantly related taxa than between closely related forms. Thompson (1984) proposed that communities develop by certain species secreting allomones in concert, preventing other species from settling. Thompson (1985) demonstrated that exudates from the sponge *Aplysina fistularis* inhibited metamorphosis of gastropod veliger larvae, reduced settlement of larvae, and caused behavioral modifications in five species of adult invertebrates, but were not toxic to dorid nudibranchs. They also reduced tissue damage from browsing animals by repelling them.

Walker et al. (1985) reported that the sponge *Aplysina fistularis* responded to a simulated injury by exuding 10–100 times more antimicrobial metabolites within about the first 5 min than normally. They found that marine sponges with clean surfaces exhibited greater antimicrobial activity than those with biofouled surfaces. This phenomenon was also reported from Australia (McCaffrey and Endean, 1985). Nakatsu et al. (1983) suggest that sterol sulfates may be responsible in part for the lack of fouling organisms on the sponge *Toxadocia zumi*. Crinoids contain polyketide sulfates which may serve not only as a defensive mechanism against fish (Rideout et al., 1979), but as antifouling agents. Even asteroids may discharge saponins into water in part to prevent fouling (Russell, 1984). Certainly one of the most unusual cases of antifouling occurs in the stonefish (*Synanceja horribilis*) which moves so seldom that it must shed its biofouled skin periodically (Cameron, 1976).

In addition to the above, evidence is beginning to accumulate which suggests that chemistry may play an important role in succession. Kirchman et al. (1983) proposed a lectin model system (i.e., proteins or glycoproteins with carbohydrate-binding specificity) to explain biochemical processes in the settling of fouling organisms (see also Lewin, 1984; Mitchell and Kirchman, 1984). Stoecker (1980a, b) showed that acidity and high vanadium contents are defenses against fouling in some ascidian species. Targett et al. (1983) found that the growth of the diatom *Navicula salinicola* is inhibited by the substance homarine from gorgonians, a simple 2-carboxy *n*-methyl pyridine. A furanogermacrene isolated from the gorgonian *Pseudopterogorgia americana* inhibits both *N. salinicola* and *Nitzchia* spp. at naturally occurring concentrations in *in situ* experiments (Targett, 1985). Experiments conducted by Bakus et al. (1983) indicate that extracts from tropical gorgonians and sponges can inhibit, enhance, or not affect the settling of dominant marine fouling organisms. Preliminary evidence supports the suggestion that tropical marine organisms may show greater potential as antifoulers than do temperate latitude species (Bakus and Kawaguchi, 1984). Moreover, antibiosis in sponges near Cancun, Mexico, appears to be seasonal (Green et al., 1986; Batus et al., 1986).

The occurrence of clean-surfaced animals that lack appendages, such as sponges, ascidians, soft corals, gorgonians, and holothurians, suggests that antifouling allomones may be present. This is especially true of species on coral reefs, animals potentially exposed to a great variety of algal spores and especially invertebrate larvae. We are beginning to test this hypothesis, working on the assumption that tidy tropical species remain clean by preventing the initial irreversible adsorption of bacteria on their surfaces. Thus, experiments with antibiotics in the laboratory coupled with antifouling experiments in the field may answer some important questions in this regard.

We know very little about the interaction between species pairs during marine succession, especially on the chemical level. Laboratory experiments are needed to demonstrate chemical interactions, corroborated by field experiments. We need to determine how certain species maintain clean body surfaces. If chemicals are secreted, where are they produced and where are they stored; what controls their production and release?

COMPETITION FOR SPACE

Marine organisms, in competing for space, may crowd, undercut, crush, overshadow, overgrow, digest, or poison their neighbors (Quinn, 1982; Branch, 1984). Soft corals may leave trails by moving over hard corals and killing them, offering space susceptible to secondary colonization (Benayahu and Loya, 1981; La Barre and Coll, 1982). Kittredge et al. (1974) brought to attention the role of allelochemics in the sea. Recently, Bak and Borsboom (1984) demonstrated an allelopathic interaction between the giant sea anemone *Condylactis gigantea* and benthic algae. They emphasized that the widely differing results between their laboratory and field experiments were due to the considerable dilution of toxin released by the anemone into the sea. Sheppard (1979) suggested that a toxic secretion may be responsible for the gap between certain hard corals competing for space. Benayahu and Loya (1981) reported that although massive soft corals (e.g., *Lobophytum, Sacrophyton, Sinularia*) inhibit hard coral growth, some hard corals can inhibit the growth of smaller soft corals. There is rapidly growing interest in the biological role of terpenes in hard corals.

The role that toxins might play in competition for space among cryptic coral reef species was suggested by Jackson and Buss (1975). They proposed competitive networks or a feedback loop in an otherwise hierarchical sequence of interference competitive abilities. For example, species 1 is dominant over species 2, species 2 over species 3, species 3 over species 4, yet species 3 dominates over species 1 (feedback loop). Later they suggested that where competitive networks exist, competition for space may increase diversity (Buss and Jackson, 1979), in comparison with the generally accepted theory of competitive hierarchies disturbance. Quinn (1982) found that the competitive organization of low intertidal rock faces in Washington was essentially hierarchical. Reversals in the outcome between pairs of competing species may occur seasonally or in response to changing physical conditions or even composition of the plankton. Russ (1982), in a long-term study, demonstrated that major groups or taxa are hierarchical (e.g., ascidians and sponges overgrow everything else), that species networks did not exist, that there was no single competitively dominant species, and that larger colonies often would win in competition for space between pairs of species. He also indicated that except in one case, Jackson and Buss had not demonstrated competitive networks. Other criticisms of Jackson and Buss were reported by Quinn (1982); Russ (1982); and Walker et al. (1985). Huston (1985) suggested that an alteration of competitive hierarchies by changing environmental conditions is an alternative mechanism that could produce a nonhierarchical competitive networks on the underside of coral shelves.

Porter and Targett (1985) have quantitative evidence that the proximity of the sponge *Plakortis zygomorpha* to the scleractinian coral *Agaricia lamarki* stressed the coral to the point where in situ P/R (productivity/respiration) ratios were less than 1. Sammarco et al. (1982) demonstrated that soft corals could retard the growth of hard corals, effectively competing with them for space. They considered the secreted compounds important in both antipredation and competition for space. These discoveries have clarified some perplexing problems concerning competition for space between these two major coral taxa (Sheppard, 1979; Benayahu and Loya, 1981) and showed that contact was not essential for inhibition. Birkeland et al. (1981) found that the coral *Mycetophylla aliciae,* strongly competitive for space among Caribbean hard corals, is apparently defenseless against overgrowth by ascidians. The movement of larger didemnids is a frequent source of small-scale (about 100 cm^2) disturbance of occupation of space by hard corals, yet sponges were overgrown but not damaged. Bakus (personal observation) found that ascidians were the only organisms growing over the living basal tissues of the Maldivian soft coral *Dendronephthya* spp. Space for recruitment may not be a limiting factor for the giant sea anemone *Condylactis gigantea* in a supposedly space-limited environment, due to the toxins it secretes (Bak and Borsboom, 1984).

Lang (1973) concluded that a strict hierarchy of aggression (i.e., one species destroying another species by exocoelenteric digestion with extended mesenteric filaments) occurs in Caribbean corals. Sheppard (1979, 1981), however, found that such a rigid hierarchy was not characteristic of scleractinian corals in the Indian Ocean. Coral aggression was not related to general morphology, taxonomic position, or corallum shape. Wellington (1980) demonstrated that the previously reported hierarchy for some Pacific corals, based on extension of mesenterial filaments, was a short-term response. Aggression by corals also occurs by catch or sweeper tentacles (Sebens, 1984; Hidaka, 1985). However, Bradbury and Young (1981) and Cope (1981) maintain that physical factors (i.e., temperature, wave action, light) rather than competition or predation, explain the distributions of scleratinian corals. Many ecologists would agree that physical–chemical factors are most important because they determine which species have the physiological ability to survive in a new habitat.

Scleractinian corals are not alone regarding agonistic behaviors. Intraspecific agonistic behavior has been reported in the large temperate sea anemone *Anthopleura xanthogrammica* (Sebens, 1984). Nonneighbor anemones exhibit an acrorhagial response, producing vesicular extensions at the column margin over a period of up to about 10 min, damaging other anemones. The chemistry of this interaction is apparently unknown; it presumably involves the secretion of digestive enzymes. All anemones with acrorhagi reportedly use them agonistically, intra- or interspecifically, except for genetically identical clonemates (Sebens, 1984). Webb and Coll (1983) showed that hard corals die within 24 hr of exposure to soft coral terpenes at a concentration of $\geqq 10$ ppm. Finally, Theodor (1966, 1971, 1975) showed that tissue necrosis resulted from contact between gorgonians, and La Barre et al. (1986a) demonstrated that soft corals move apart to avoid tissue degradation resulting from tissue contact.

It is now known that community structure can be controlled by chemical interactions from direct contact, from the release of chemicals into surrounding waters, by overgrowth (nearly a kilometer of reef at Gaum was covered by the sponge *Terpios* sp., Bryan, 1973; Plucer-Rosario, 1983), by agonistic behavior, and by "sessile" species moving apart from one another (La Barre et al., 1986a, b). We do not know what the total pattern of these interactions is for any single community nor how these patterns vary with latitude.

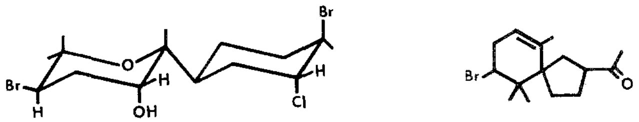
COMMUNITY DOMINANCE AND BIOACTIVE SUBSTANCES

It has been accepted dogma that dominance is a distinguishing trait of species-poor ecosystems. However, Birch (1981) showed that dominance increases as marine benthic communities become more species-rich. Highly aggressive Caribbean corals reportedly are relatively minor components in all reef habitats (why should this be?), whereas many of the most aggressive corals in the Indian Ocean are extremely dominant in certain zones (Stoddart and Yonge, 1971; Lang, 1973; Sheppard, 1979). Many ecologists have proposed that allelochemics may play an important role in contributing to the maintenance of high species diversity (e.g., Sammarco et al., 1982), but some of these chemicals may also be responsible for creating dominance in toxic tropical species (Birch, 1981). Endean and Cameron (1983) claimed that many coral reef animals that are well protected by toxins are normally rare but live long. However, Bakus maintains that many tropical species with defenses are dominant by biomass and/or number (e.g., the corals *Acropora* spp. and *Porites* spp., the surgeonfishes *Acanthurus* spp., the two-species scleractinian coral reefs of Cocos Island, off Pacific Central America, Bakus, 1967, 1975; Sheppard, 1979; Potts et al., 1985). Other species that are dominant and toxic include the algae *Halimeda* spp., *Caulerpa* spp., and *Laurencia* spp.; the sponges *Ircinia* spp. and *Terpios* spp.; the soft corals *Sarcophyton* spp. and *Dendronephthya* spp.; the stinging corals *Millepora* spp.; the sea cucumbers *Holothuria* spp.; and the diadematid sea urchins; to name but a few (Bakus, 1968; 1973; Bryan, 1973). Although these species may not reflect overall dominance, they dominate in patches. Patchy dominance, a phenomenon of scale, may be an ecologically significant factor in the tropics.

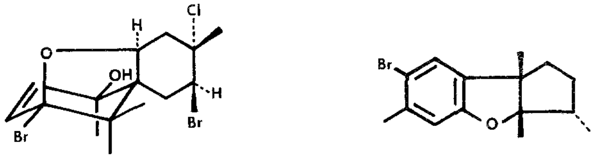
CHEMISTRY

Marine organisms often possess characteristic and/or unique chemical features. These components have served as the starting point for many chemical-ecological studies, although it has been shown that marine chemical-biological interactions are by no means restricted to uniquely marine compounds. The general classes of interest to marine chemical ecologists are outlined below.

Terpenes. Terpenoid compounds have been isolated from algae, sponges, coelenterates, mollusks, and echinoderms. From algae alone more than 60 sesquiterpenes have been identified. These can be divided into 18 skeletal types, at least two thirds of which are new to science (Martin and Darias, 1978). More than 90 diterpenes have also been isolated from marine organisms. Of these, about 25% represent new skeletal classes (Fenical, 1978). Carbon-halogen bonds are characteristic of many marine terpenoids, particularly those isolated from algae. Bromine is the halogen most frequently incorporated into these marine secondary metabolites. Most typically, halogen-containing terpenes are found in algae in the genus *Laurencia* where they are thought to function in part as herbivore feeding deterrents (Figure 1) (e.g., Fenical, 1975; Erikson, 1983). The sea hare *Aplysia* spp. is one of the few herbivores adapted to grazing on *Laurencia* spp. Halogenated metabolites from the plant are concentrated in the sea hare and are thought to provide it with a means of defense against its own predators (Fenical, 1975). Other marine animals are capable of elaborating



Isocaespitol **Spirolaurenone**



Pacifenol **Aplysin**

FIG. 1. Some terpenoid skeletal types typical of marine organisms include: the bisabolane, isocaespitol, from the red alga *Laurencia caespitosa* (Gonzalez et al., 1973; 1975); the chamigrane, spirolaurenone, from the red alga *Laurencia glandulifera* (Suzuki et al., 1970); pacifenol, a trihalogenated chamigrane from the red alga *Laurencia pacifica* (Sims et al., 1971); and the bromocuparane, aplysin, known from the opistobranch mollusk *Aplysia* and its algal diet, *Laurencia* (Yamamura and Hirata, 1963; Irie et al., 1969).

terpenoid metabolites de novo for use in chemical defense (Cimino et al., 1983). In sponges, terpenes represent the most abundant nonsteroidal metabolites; over 100 have been identified (Figure 2) (Minale, 1978). Sponge terpenes typically contain a multiplicity of prenyl units and furan rings (e.g., Cimino et al., 1971, 1975a,c). The naturally rare isonitrile function is also known from several sponge terpenoid compounds (e.g., Fattorusso et al., 1974, 1975). Sesterterpenes are also relatively abundant in sponges (Cimino et al., 1972; Fattorusso et al., 1972). In coelenterates, terpenes are known only from the Order Alcyonaria. These include sesquiterpenes and diterpenes. Most characteristic is the cembranolide skeleton (Figure 3) (Tursch et al., 1978). In general, terpenoid compounds are thought to function in antipredation, competition for space, and possible antifouling.

Steroids. The biosynthesis of steroids is intimately related to that of the higher terpenes, particularly the triterpenes. Marine organisms contain a far more diverse array of sterols than do terrestrial organisms. Marine organisms produce sterols with a remarkable variety of side chains, unconventional nuclear structures, and assorted hydroxylation patterns (Figure 4) (Schmitz, 1978). Sponges yield the most varied and biogenetically unprecedented array of sterols found among the invertebrate phyla (Goad, 1978). Dinoflagellate sterols are characterized by more heavily alkylated side chains and the presence of a 4-

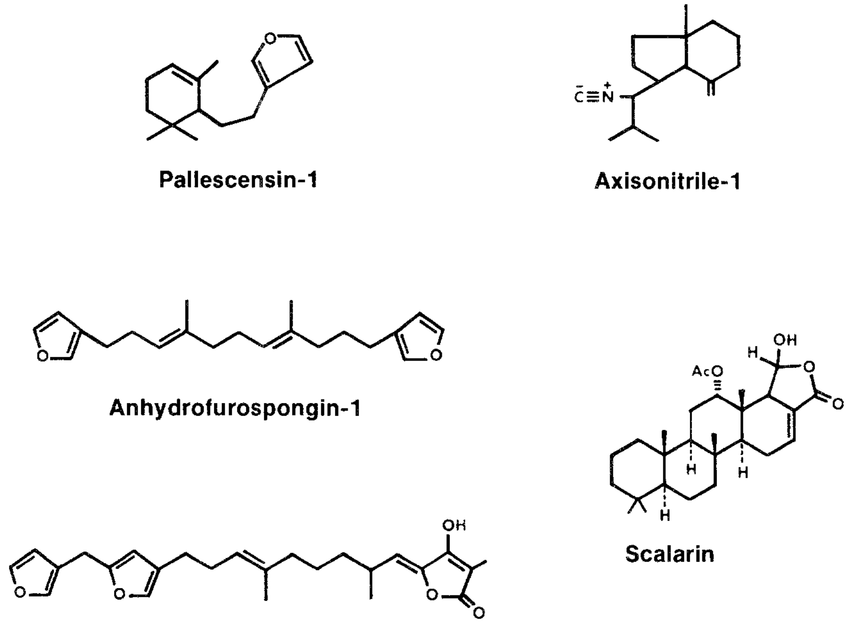


FIG. 2. Terpenoids typical of marine sponges include sesquiterpenes with furan rings (pallescensin-1, Cimino et al., 1975a–c) which are often joined with linear prenyl groups (anhydrofurospongin-1, Cimino et al., 1971), sesquiterpenes with the rare isonitrile functional group (axisonitrile-1, Cafieri et al., 1973), and linear and cyclic sesterterpenes (ircinin-1, Cimino et al. 1972; scalarin, Fattorusso et al., 1972).

alpha methyl group (Withers, 1983). The gorganians are characterized by their content of gorgosterol and related sterols (Goad, 1978; Withers, 1983), which contain a cyclopropane group in the side chain. Sterols are of interest principally because of their role in the production of steroidal hormones such as ecdysones with which regulate molting in Crustacea (Goad, 1976). They also are known to play a role in the defense of certain species (Burnell and ApSimon, 1983).

Carotenoids. Carotenoids are encountered in bacteria, algae, fungi, inver-

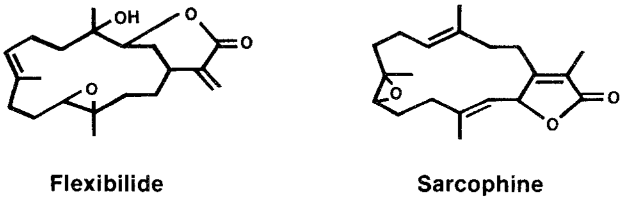


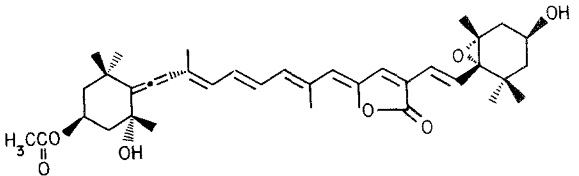
FIG. 3. Flexibilide and sarcophine, two biologically active cembranolide diterpenes from the soft corals *Sinularia flexibilis* and *Sarcophyton crassocaule* (Webb and Coll, 1983).

A-norstanol skeleton **19-norstanol skeleton**

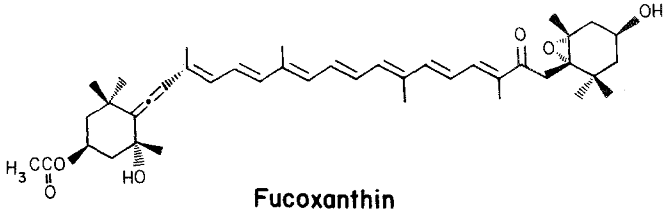
Dinosterol **Gorgosterol**

FIG. 4. Steroid types typical of marine organisms include: the A-norstanol and 19-norstanol skeletal modifications (Minale and Sodano, 1974a,b); dinosterol with the 4α-methyl group and additional side chain aklylation that is characteristic of many dinoflagellate sterols (Shimizu et al., 1976); and gorgosterol which shows the side chain with the cyclopropyl bridge typical of gorgonians and their dinoflagellate symbionts (Ciereszko et al., 1968).

tebrates, and vertebrates. More than 100 carotenoids have been isolated from marine sources and of these, about 40% are exlusively marine (Liaaen-Jensen, 1978). The most abundant are two carotenoids found in phlytoplankton, peridinin and fucoxanthin (Figure 5) (Strain et al., 1976). In general, marine carotenoids have more complex structures and more structural variation than do



Peridinin



Fucoxanthin

FIG. 5. Two exclusively marine carotenoids. Peridinin has a unique C_{37} skeletal structure bearing lactone, allenic, epoxy, acetoxy, and alcohol functions (Rapoport, 1971; Strain, 1976; Kjoesan et al., 1976).

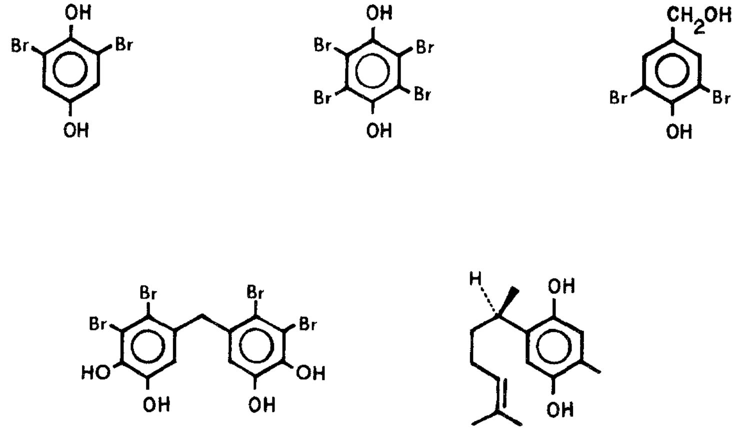
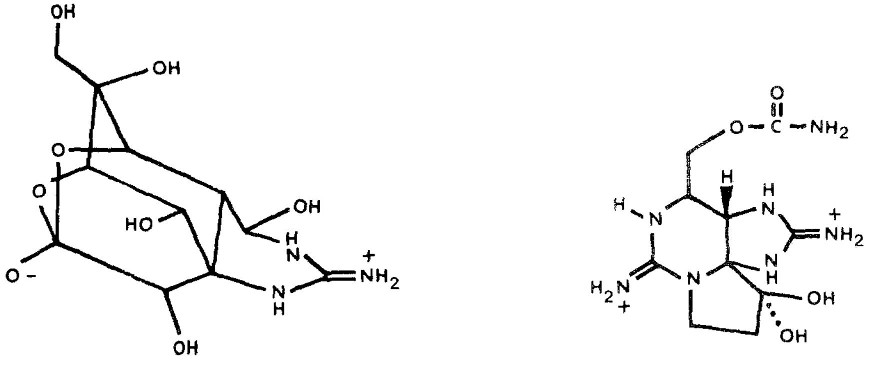


FIG. 6. Phenols arising from a variety of biosynthetic pathways are characteristic of many marine plants and invertebrates (Craigie and Gruenig, 1967; Kurata and Amiya, 1977; McEnroe and Fenical, 1978; Higa et al., 1980).

their terrestrial counterparts (Liaaen-Jensen, 1978). Marine carotenoids have a photoprotective role in photosynthetic bacteria and algae and play an important role in cryptic coloration and form (Burnett, 1976). The presence of oxygenated carotenoids is correlated with the tolerance of certain marine mollusks to environmental pollution, suggesting that they provide an intracellular reserve of oxygen (Karnaukhov et al., 1977). Carotenoids and carotenoproteins may also have a functional role in the reproduction of brown algae, crustaceans, and sea urchins (Lee, 1977; Hallenstvet et al., 1978). They are also useful in chemotaxonomy (Lee and Gilchrist, 1985).

Phenolics. Phenolic compounds occur in bacteria, algae, seagrasses, sponges, coelenterates, annelids, echinoderms, hemichordates, and protochordates. They are best known in brown and red algae, sponges, and echinoderms (Higa, 1981). More than 220 phenolics have been described from marine organisms (Figure 6). They arise via a variety of biosynthetic pathways. Their most obvious characteristic is the presence and abundance of halogenated substituents. Bromine is the halogen most frequently incorporated. Halogenated and nonhalogenated phenolics have been shown to have a multiplicity of potential ecological roles. For example, they are known to function as feeding deterrents in certain marine macrophytes (Valiela et al., 1979; Geiselman, 1980; Phillips and Towers, 1982a,b; Steinberg, 1984, 1985) thought to be responsible for defense or recognition in several species of enteropneusts (Higa, 1981).

Nitrogeneous Compounds. A wide variety of nitrogeneous compounds have been isolated from marine organisms, ranging from simple compounds such as tetramine to complex ones such as tetrodotoxin and saxitoxin (Figure 7). The latter are powerful neutrotoxins which inhibit sodium passage through axonal

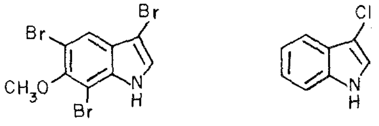


Tetrodotoxin **Saxitoxin**

FIG. 7. Tetrodotoxin and saxitoxin are the two most widely known marine guanidino compounds (Woodward, 1964; Shimizu, 1978). Both have the high ratio of heteroatoms to carbon that is typical of many marine toxins.

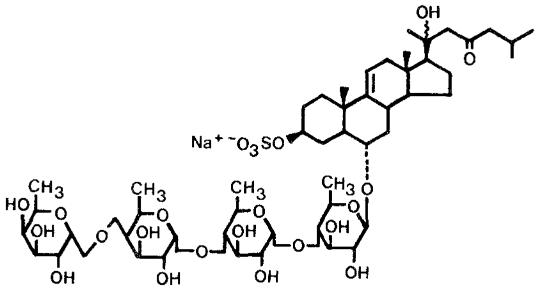
membranes (Chevolot, 1981). Other simpler nitrogenous compounds play important roles in marine biological interactions. For example, gamma-aminobutyric acid (GABA), produced by encrusting algae (*Lithothamnium* and *Lithophyllum*), induces settlement and metamorphosis in abalone larvae (Morse et al., 1979; Morse and Morse, 1984). Alkaloids unique to the marine environment are being isolated and identified in growing numbers. They are often characterized by a bromine substituent. Haloindoles isolated from marine acorn worms (*Ptychodera flava* and *Glossobalanus* spp.) are responsible for the characteristic odor of these species and are thought to function as a chemical defense against micro- and macroorganisms (Figure 8) (Higa et al., 1980; Christopherson, 1983).

Compounds of Mixed Biogenesis and Miscellaneous Compounds. Many compounds are derived from the condensation of products arising from different biogenetic pathways (Figure 9). For example, asterosaponin A is an oligosaccharide with a steroidal aglycone. It is responsible for the pronounced avoidance behavior of numerous marine species when they are placed in the vicinity of a



Haloindoles

FIG. 8. Examples of halogenated indoles, these are found in marine acorn worms in the genera *Ptychodera* and *Glossobalanus* (Higa and Scheuer, 1977; Higa et al., 1980).

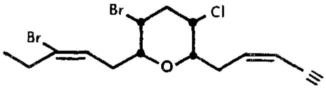


Asterosaponin A

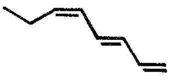
FIG. 9. A biologically active compound of mixed biogenesis, asterosaponin A is an oligosaccharide β-linked to a steroidal aglycone (Ikegami et al., 1972a–c).

$CHBr_3$, $CHBr_2I$, $CHBr_2Cl$
Haloforms

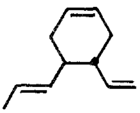
Cyclic polysulfides



Dactylyne



Fucoserratene



Aucantene

FIG. 10. Examples of miscellaneous compounds from marine organisms: Haloforms from the red alga *Asparagopsis* (Burreson et al., 1975, 1976); cyclic polysulfides from the red alga *Chondria californica* (Wratten and Faulkner, 1976); dactylyne, an enyne containing compound from the digestive gland of the sea hare *Aplysia dactylomela* (McDonald et al., 1975); and fucoserratene and aucantene, hydrocarbon pheromones from the brown algae *Fucus serratus* and *Cutlaria multifida*, respectively (Jaenicke et al., 1974).

starfish (Burnell and ApSimon, 1983). Miscellaneous compounds include compounds such as haloforms, acetylenes, sulfur compounds prostaglandins, and unusual lipids (Figure 10). To these compounds have been attributed a variety of roles, including chemical defense and species recognition (Jaenicke et al., 1974; Mueller, 1979; Gerhart, 1984).

Despite the considerable work on natural products chemicals since the early 1960s, many questions concerning the chemical nature of biological interactions remain unanswered. We need information on the origin of the compounds (de novo synthesis, diet, or symbiosis, e.g., Barrow, 1983; Catalan et al., 1985), whether the compounds are continuously produced or induced in response to an external stimulus, whether they are sequestered or free within their hosts, whether they are directly released into the sea, the nature of the released form compared with the stored form, and what the modes of action are. In an applied sense, we need to know more about the potential for these compounds as prototypes for antifoulants, pharmaceuticals, and agrichemicals (Colwell, 1983; Colwell et al., 1984).

CONCLUSIONS

For chemical ecologists, natural products chemistry has little meaning without a framework based on ecological and evolutionary theory. Similarly, understanding the fundamental mechanisms of many ecological interactions can be achieved only with an investigation of the chemistry involved. We are beginning to realize that current ecological theory may be too general or insensitive (e.g., in marine succession), that generalizations about populations will be made at a lower level of generality with much more detail and more restrictive conditions than previously anticipated (Krebs, 1985). It is also apparent that interdisciplinary studies between ecologists and chemists are rewarding because they seek the fundamental mechanisms behind ecological phenomena. Marine chemical ecology, an emerging discipline, seeks to create an interdisciplinary understanding of chemical-biological interactions occurring in the sea.

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