CHEMICAL SIGNALS IN CORAL REEFS

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Contents

Summary

Chemical signaling is an important communication mechanism within and between species in the marine environment. Chemical cues are of particular importance in aquatic systems since visibility can be greatly impaired by sediment load and the attenuation of light at greater depths. The physical and chemical properties in the marine environment influence the way chemical signals are produced, transported and detected, and also determine the nature and success of ecological interactions. Marine animals have very well developed chemical senses and chemical signals can help animals to identify conspecifics and regulate social behavior. Reproductive processes such as mate recognition and synchronization in gamete, or larval release, may be highly influenced by chemical signals especially in plants and invertebrates where hormonal signaling is not complex. The establishment and maintenance of symbiotic associations as well as homing behavior may require of chemical signaling although these processes are less understood. Chemical signals are also important in food recognition and ingestion by grazers, carnivores and scavengers, predator detection and avoidance, alarm responses and deterrence of feeding behavior. Chemical signals are recognized as having great importance in ecological interactions, but little is known by which mechanisms chemical stimuli contribute to processes that structure communities. Most studies

involving chemical signaling in coral reefs have been focused in defensive interactions. There is ample evidence that secondary metabolites produced as chemical defenses against consumers, competitors or pathogens may have important effects that can affect marine biodiversity at the genetic, species and ecosystem levels. In this chapter some relevant examples of chemical communication and chemical signaling among coral reef organisms will be discussed.

1. Introduction

Many interactions within and between species involve chemical agents that mediate behavioral responses and/or mechanisms of attack and defense. Traditionally, these chemical agents have been classified depending on their role in mediating these interactions. Chemical signals that mediate communication between conspecifics such as reproductive behavior, social regulation and recognition, alarm and defense signals, territory and trail marking and food location are known as pheromones. The importance of pheromones has long been recognized in mate recognition and communication in insects. In the marine environment however, there are some well-documented examples of pheromones that have a crucial role in reproductive processes in nereid polychaetes and brown algae. Chemical agents also mediate interactions between different species. Some chemical agents produced by one species can affect the growth, health, behavior and / or population biology of another species. These chemicals are known as allelochemicals and may be involved in processes such as predation, parasitism, habitat and food selection, competition, dispersal and defense.

Chemical signaling is an important communication mechanism within and between species both in terrestrial and marine environments. However, the physical and chemical properties between these environments influence the way chemical signals are produced, transported and detected and also determine the nature and success of ecological interactions. In the aquatic environment, solubility rather than volatility, determines the capacity of specific compounds as chemical signals due to the characteristics of water of being a slower carrier medium than air in terms of diffusion and current. Non-water soluble compounds can also be effective chemical signals when suspended and transported by fluid flow in the water column. Dispersal of metabolites and chemical cues depends on patterns of circulation, flow speed and water motion. Processes such as diffusion, advection, turbulence in the boundary layer or habitat characteristics such as bottom structure, habitat characteristics, tidal currents and waves, help disperse these signals. Therefore, aquatic organisms face a series of chemically stimulating patches rather than continuous odor plumes or gradients.

Marine animals have very well developed chemical senses and chemical signals can help animals to identify conspecifics and regulate social behavior. Reproductive processes such as mate recognition and synchronization in gamete or larval release, may be highly influenced by chemical signals especially in plants and invertebrates were hormonal signaling is not complex. The establishment and maintenance of symbiotic associations as well as homing behavior may require of chemical signaling although these processes are less understood. Chemical signals are also important in food recognition and ingestion by grazers, carnivores and scavengers, predator detection and avoidance, alarm responses and deterrence of feeding behavior.

Peptides have been recognized as important signal molecules in aqueous environments. Nanomolar concentrations of peptides can elicit attraction to new shells, attraction to living prey, release of larvae and induction of larval settlement. Exogenous factors such as animal, plant or bacterial uptake, adsorption to sediments, biofilms or suspended clays can have an influence in the concentration of peptide signal molecules in the environment. Therefore, amino acid sequences of peptide molecule signals may be crucial in reducing their bacterial uptake. Basic carboxy terminal residues may be removed at significantly lower rates thus being of advantage in selecting them as chemical cues.

In this chapter I will explore on ecological interactions mediated by chemical signals in coral reef ecosystems. I will include some examples of chemical signals involved in feeding and deterrence, predator detection and alarm signals in reef organisms. I will also deal with other aspects of chemical signaling implicated in gamete recognition and spawning synchronization. Settlement of marine invertebrate larvae is greatly influenced by chemical signals. This aspect will be thoroughly explored in another chapter in this series so I will only include some relevant aspects in reef organisms. I will also include some examples of chemical signals involved in antifouling and allelopathic interactions and in the establishment and maintenance of symbiotic associations. Although most examples cited in this chapter come from reef organisms, in some cases I will also cite some examples from temperate water organisms.

2. Chemical signaling in coral reefs

The complex ecosystems of coral reefs are a result of the symbiosis between reef building (hermatypic) corals and dinoflagellate symbionts. Over centuries, algal productivity has been the major source of energy for the calcification process responsible for the formation and maintenance of reef structures. Coral reefs vary in size, shape, exposure to waves and currents, geological history and vertical depth contours. Niche partitioning and feeding specialization favored the evolution and diversification of coral reef organisms. In these highly diverse environments, the evolution of complex and diverse defensive strategies was necessary to guarantee the success and survival of reef dwellers. Many sessile reef organisms rely on structural defenses, but the evolution of chemical defenses has been crucial to the survival of many others. Other factors such as access to light have lead to the development of competitive interactions between coexisting species in coral reef ecosystems.

Chemical signals are recognized as having great importance in ecological interactions, but little is known by which mechanisms chemical stimuli contribute to processes that structure communities. Most studies involving chemical signaling in coral reefs have been focused in defensive interactions. There is ample evidence that secondary metabolites produced as chemical defenses against consumers, competitors or pathogens may have important effects that can affect marine biodiversity at the genetic, species and ecosystem levels.

The production and dispersal of chemical compounds in the sea may have favored the evolution of chemosensory capabilities in the marine environment. These chemicals, by-products of metabolic processes, may have been both cues for prey location and/or involved in initial phases of chemical protection. Later, chemosensory capabilities may have provided several functions in the evolution of multicellular animals as precursors of development signals, hormone function and communication signals.

2.1 Feeding Attractants

Chemical cues are of particular importance in aquatic systems since visibility can be greatly impaired by sediment load and the attenuation of light at greater depths. Detection and recognition of food sources from a distance should be more advantageous in aquatic environments. In these environments diffusion rates may be favored, carrying chemical odors over considerable distances and allowing organisms to detect food in large areas.

Most chemical ecology research has focused on feeding deterrents as defenses against predation, whereas few feeding stimulants and cues have been studied in an ecological context. Reports indicate that amino acids, sugars, glycerolipids and carbohydrates can act as feeding attractants and stimulants in marine gastropods. For most marine fish and crustaceans, major stimulants of feeding behavior are complex mixtures of low molecular weight metabolites including amino acids, quaternary ammonium compounds, nucleosides, nucleotides and organic acids. The fact that mixtures rather than individual compounds are responsible for the stimulatory capacity of natural extracts indicates that active compounds may interact additively or synergistically.

Chemical cues released from live prey may not be the same as those released from injured prey tissue. Olivid gastropods live buried in the sediment but readily detect fish carcasses and flesh upon which they feed. Carnivore gastropods of the families Naticidae and Terebridae also rely on chemical reception to locate their prey, which consists of polychaetes, bivalves and other gastropods. Chemoreception in nudibranchs and opisthobranchs is important in locating food sources and as phagostimulants. Rigorous field tests however, have shown that the foraging behavior of the mud snail *Ilyanassa obsoleta* is highly dependent on the release and physical transport of chemical stimuli, more than the molecular composition of specific amino acids in fluids leaking from injured prey.

The crown-of-thorns starfish *Acanthaster plancii* is attracted by chemical cues released from viscerae of the urchin *Toxopneustes pilosus*. The feeding attractants in the urchins' viscerae were identified as arachidonic acid and α-linoleic acid. Arachidonic acid was also detected in corals of the genus *Montipora*. Since feeding in injured corals is greater than in unharmed ones, these findings suggest that enzymes liberated by the starfish may release arachidonic acid from glycerophospholipids in the coral tissue, attracting more predatory starfish.

2.2 Feeding Deterrents

Corals, sessile invertebrates such as sponges and octocorals, and algae dominate the primary space in reef communities. The abundance of many sessile organisms is often determined by the activities of mobile invertebrate and vertebrate predator and grazers.

Some invertebrate predators can have negative impacts in reef communities by localized feeding. However, fishes are considered the greatest threat to reef dwelling invertebrates due to their high mobile capability, feeding rates, size and abundance. Some of the adaptations to overcome predation and grazing are the development of physical or structural defenses, low nutritional value, spatial refuges, temporal escapes, fast growth and chemical defenses. In some sessile benthic marine invertebrates there is a strong correlation between the lack of apparent physical defenses and the occurrence of unusual secondary metabolites in their tissues. Additionally, these organisms also seem to have few known generalist predators. On the basis of these observations, antipredatory defensive roles have been attributed to secondary metabolites from many sessile invertebrates.

A common method of testing feeding deterrent properties of secondary metabolites consists in incorporating crude extracts, partially purified chromatography fractions, purified metabolites or mixtures (at natural concentrations) into a palatable diet. This is achieved either by coating the substance(s) unto a palatable seaweed or by mixing it (them) into gel based foods that are nutritionally similar to the prey. Comparisons of feeding rates on treated foods versus appropriate controls allow for determination of the deterrent effects of compound(s) or extract(s). Reef fishes inhabit clear waters and rely heavily upon vision. Some fishes can learn to associate chemical deterrence with certain physical characteristics such as color. In most cases, fish-deterrent effects of secondary metabolites appear to be based primarily on the taste of treated food, rather than olfaction. Other fishes however, may show strong avoidance of identically looking treated seaweeds relative to controls. This suggests that besides vision, there may be other mechanisms that allow fish to assess quality of food. Chemically mediated foraging in marine fishes has been difficult to test since changes in behavior upon addition of stimuli may or may not indicate the ability of a predator to use those stimuli to detect and track prey.

Feeding deterrence is not an inherent feature of any particular metabolite but rather results from the interaction between a consumer and the compound itself. Secondary metabolites considerably differ in effectiveness as feeding deterrents, and different organisms may vary in their sensitivity to these metabolites. The compound cymopol (1) (Figure 1) produced by the green alga *Cymopolia barbata*, is highly deterrent against grazing fish but acts as a feeding stimulant in the long spined urchin *Diadema antillarum*. Secondary metabolites and nutritional value can influence a predator's choice of the type and amount of food consumed. Some predators readily detect and avoid chemically defended prey whereas others have evolved mechanisms to overcome harmful effects. These include alteration of gut pH, detoxification, rapid excretion, target site insensitivity, modification of mouthparts, changes in foraging strategy and/or sequestration of metabolites.

I will not include other examples of feeding deterrents since these can be found elsewhere in the extensive literature that has been published in the topic. A list of useful reviews on the subject is cited at the end of this chapter.

2.3 Predator detection and alarm substances

Prey organisms may rely on chemical cues as warning signals indicating the proximity of predators or that conspecifics are being attacked and injured. These cues include substances actively released by conspecifics that function as alarm signals or cues passively released once tissue is damaged by predators. Chemicals released upon attack can serve to mark a location as dangerous to conspecifics. A classic example of alarm reactions elicited by chemical signals occurs in the intertidal Western Pacific anemone *Anthopleura elegantissima.* Anthopleurine (2) (Figure 1) is a pheromone released by injured anemones and elicits an alarm response at concentrations as low as 35 x 10^{-10}M. Anthopleurine has ionic character. The positive ion of anthopleurine interacts with the receptor molecule of the recipient anemones eliciting a contracting response.

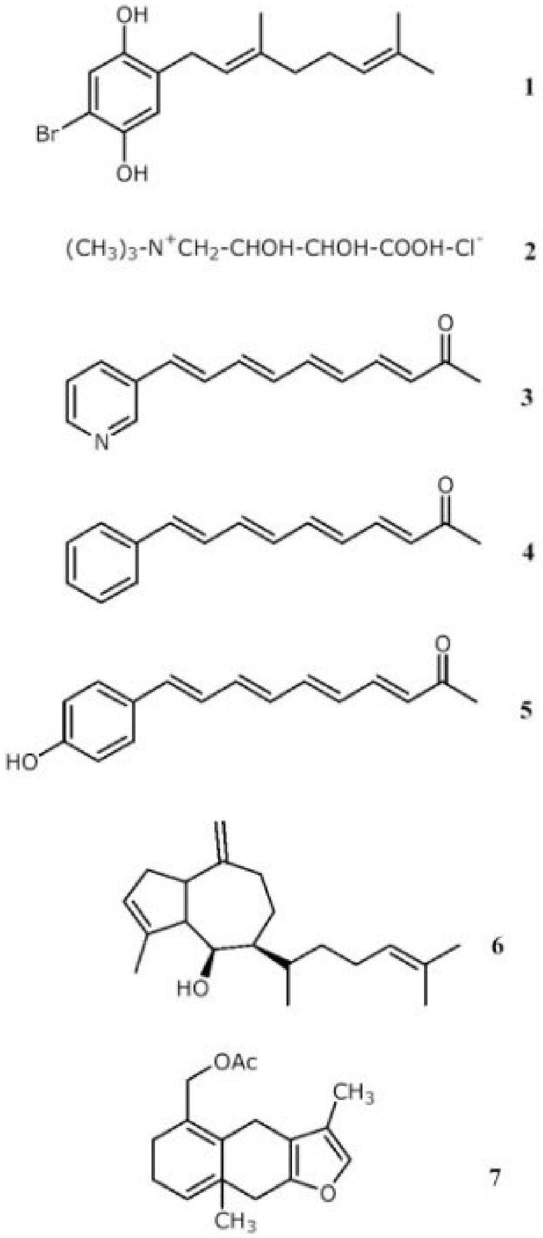

Figure1. Feeding stimulants, feeding deterrents, and alarm substances from algae, nudibranchs and cnidarians

The Caribbean urchin *Diadema antillarum* moves away from areas where a conspecific has been crushed. Alarm reactions are very fast and evident in urchins down current but not in urchins next to the injured one. *Diadema* does not exhibit such a dramatic response to body fluids of other crushed echinoderms.

Slime trails in nudibranchs and opisthobranchs are rich sources of chemical signals important in locating prey and avoiding predators. The Californian nudibranch *Navanax inermis* is a highly voracious, cannibalistic species that follow slime trails of other *Navanax* to find potential preys or mates. However, upon attack these animals exude a bright yellow material that acts as a clear chemical warning. Other *Navanax* following a slime trail and finding this substance will abruptly change course. Navenones A-C (3-5) (Figure 1) are responsible for the avoidance behavior and elicit this response at concentrations as low 10^{-5}M. Navenones act as warning signals and also disrupt other chemical signals in the original slime trail.

2.4 Induced Defenses

Morphological changes triggered by chemical cues released from predators and/or competitors have been reported in various marine organisms. The cold-water bryozoan *Membranipora membranacea* produces large, permanent spines as a defensive mechanism within two days of detecting chemical cues from its predator, the mollusc *Doridella steinbergae*. Although no specific chemical cues were isolated, the responses obtained by exposing *M. membranacea* to *Doridella* slurries were clear. Physical defenses are induced upon predation risk, even if this means some metabolic cost for the producing organism, usually reduced growth or diminished reproductive output. Octocorals can develop modified tentacles laden with nematocysts upon activation by proximity of a competitor. Juvenile barnacles exposed to predatory gastropods develop asymmetrically, causing great difficulty to predatory gastropods trying to open the opercular plates. Some fresh water cladocerans and rotifers can produce progeny with spines induced by biotic cues from their consumers.

2.5 Mate and kin recognition

Even in dense populations specific chemical signals may be necessary to find receptive mates. Male brachyuran crustaceans may recognize the premolt female by the release of a female sex pheromone. Once the premolt female is located, the male carries her until ecdysis, when copulation is possible. In the crab *Portunus sanguinolentus*, a male attractant pheromone is released with urine by conspecific females. Mature males commenced active search and exhibited behavioral displays when they were exposed to premolt female crabs, water that had flowed past these females or urine from premolt female crabs. Males that were exposed to water from a female with capped excretory pores did not display any search behavior. When urine production was resumed, the males gave positive responses indicating that the pheromone was indeed released in the female urine. Once the pair is formed, females may be able to inhibit the release of pheromone by controlling the release of urine and possibly releasing a masking factor therefore eliminating chemical cues for other males in the vicinity.

Stomatopod shrimp seem to rely on chemical signals to recognize individual conspecifics. If individual pairs of *Gonodactylus festai* are allowed to fight in order to establish dominance, loosing shrimp will only enter cavities scented by previously unencountered shrimp, but will avoid water scented by dominant shrimp.

2.6 Associational chemical defenses

Small sedentary consumers can deter or escape predation by associating with chemically defended hosts. On Caribbean reefs, the amphipod *Pseudoamphitoides incurvaria* lives and feeds on the chemically defended alga *Dictyota bartayresii*. The alga is chemically defended by the diterpene alcohol pachydyctiol A (6) (Figure 1) and it is avoided as food by fishes. By making small folded domiciles of the alga, the amphipods gain protection from predation. Pachydyctiol A also cues domicile building by *P. incurvaria*. Amphipods living in domiciles made from *D. bartayresii* are promptly consumed if removed from them or if they build domiciles from palatable algae such as *Ulva* sp.

The Caribbean nudibranch *Tritonia hamnerorum*, a specialist on the sea fan *Gorgonia ventalina* can occasionally reach very high densities on individual sea fan colonies. *Tritonia hamnerorum* sequesters from its host the terpene juliannafuran (7) (Figure 1). This compound makes the nudibranchs highly unpalatable to fishes.

The chemically defended Caribbean alga *Stypopodium zonale* provides refuge and increases survivorship to several species of macroalgae that live in close association with it. Living in the vicinity of chemically defended plants such as *S. zonale* may cause herbivorous fishes to fail to locate normally palatable prey. Other palatable algae may also gain protection from grazing by associating with the chemically defended sea fan *Gorgonia ventalina* or the hydrozoan *Millepora alcicornis*.

The chemically defended alga *Chlorodesmis fastigiata* from the Great Barrier Reef provides refuge to a species of amphipod, a crab and three species of ascoglossan molluscs that when removed from the alga are readily consumed by fish. This alga also harbors a dorid nudibranch that appears to feed exclusively on the ascoglossans. Additionally, on heavily grazed reefs, several species of algae were found in the vicinity of *Chlorodesmis* and not elsewhere in the reefs.

Carnivorous nudibranchs and opisthobranch molluscs sequester cnidocytes from cnidarian prey or secondary metabolites from sponges, soft-corals and ascidians. Diet-derived chemicals provide means of chemical defenses. They protect egg masses and adults from predation and act as cues for settlement and metamorphosis. Some sacoglossans that feed on algal sources also rely on diet-derived secondary metabolites for their own defense.

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Member Third World Organization for Women in Science.

Seminars and congresses:

17th Annual Meeting of the International Society for Chemical Ecology. Poços de Caldas, Brazil. August 15-19, 2000. One talk. Student Travel awardee.

29th Benthic Ecology Meeting. Wilmington, North Carolina. USA. March 9-12, 2000. One talk.

28th Benthic Ecology Meeting. Baton Rouge, Louisiana. USA. March 25-28, 1999. Two talks.

9th International Symposium on Marine Natural Products. Townsville, Australia. July 5-10, 1998. One Poster.

5th International Sponge Symposium. Brisbane, Australia. June 29-July 3, 1998. Participant.

14th Annual Meeting of the International Society for Chemical Ecology. Vancouver, Canada. July 12-16, 1997. Participant.