CHAPTER 14

THE ECOLOGY OF CORAL REEFS

14. 1. INTRODUCTION: ECOLOGICAL PROCESSES ON REEFS

14. 1. 1. Introduction

In our last chapter, we introduced the coral reef, the organisms that build reefs, and some of the processes involved in reef building.

In this chapter we will continue our study of the reef. This time we will focus on how the living reef and its inhabitants are a complex system--an ecosystem.

Imagine the coral reef as a ***superorganism***: a system that is made up of many parts interacting in many different ways, yet acting together, as a single entity.

14. 1. 2. Two Puzzles

We will consider two important questions that have intrigued scientists for many years. The solutions of these puzzles are related to a singular characteristic of reef organisms:

The complicated community structure of the coral reef is based on tightly linked interactions between the reef's organisms.

Coral reefs are incredibly crowded places. Competition is keen, especially for space; yet the reef is a virtual zoological and botanical garden, with an immensely diverse array of plants and animals. These facts lead us to our first question:

How can so many species of plants and animals live together in one place?

Coral reefs are often considered oases in the midst of a nutrient poor oceanic "desert." It seems impossible that rich communities like coral reefs could flourish under such poor conditions. This raises our second question:

How can such a productive community exist where there is not a visible source of nutrients--in tropical oceans?

A coral reef can be considered a superorganism.

14. 2. SYMBIOSIS: “LIVING TOGETHER”

14. 2.1. Introduction

In this chapter, we will review examples of symbiosis on coral reefs. These examples represent survival strategies that have worked for coral reef organisms. They also characterize the high proportion of organisms on coral reefs that are specialized in this and other ways.

Coral reefs are extremely complex communities.

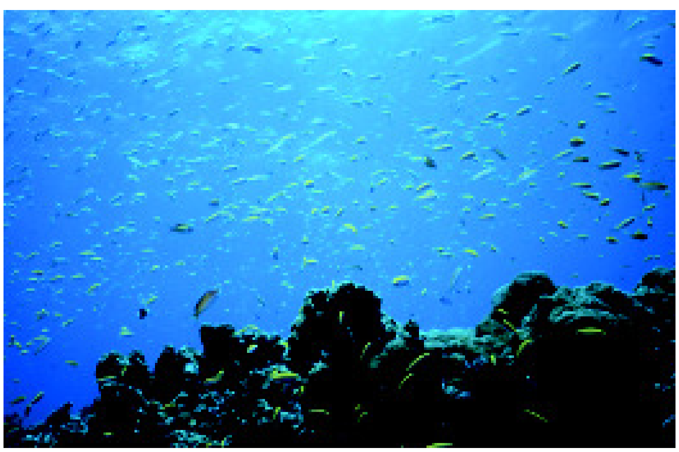
Coral reefs are extremely complex communities. They have many species of plants and animals living together in a complex network of relationships. Coral reefs have more species than almost any other community on earth, except for tropical rain forests.

These plants and animals are associated with each other in distinct networks of relationships. The relationships include food specialization and others that we will consider in this section.

Compared with most other terrestrial environments, photosynthesis takes place at a much higher rate on coral reefs. In spite of limited supplies of nutrients in surrounding open ocean waters, it is this photosynthesis that supports the reef. When reefs were first studied, scientists found their **productivity** amongst the highest on earth. This was a puzzle to the scientists until the discovery of the enormous number of symbiotic relationships on the reef.

Symbiosis, meaning literally “living together”, refers to a number of specialized relationships between two or more species. Each partner gets some benefit from the relationship. Symbiosis helps explain how so many species of organisms can coexist on the reef.

Symbiosis also explains how coral reefs can be so productive in the open ocean with its lack of nutrients. The diversity of organisms and the rich productivity of coral reefs can be best understood through symbiosis.



Coral reefs are highly productive.

The food webs of reefs are complicated networks with many examples of specialization. Habitats of coral reefs also involve specific types of prey. Coral reefs are highly productive, but the surrounding oceans are nutrient poor. (Recall our Open Ocean chapter, Ch. 12).

The key to the success of coral reefs is its tight coupling of nutrients. An important aspect of this coupling involves close interactions between diverse reef organisms.

Many of those nutrient-coupling interactions are mutualistic symbioses. Organisms of different species both benefit from the association. Remember that symbiosis means “living together” and mutualism demonstrates a cooperative association.

Coral reefs harbor a remarkable number of symbiotic relationships. In some of these associations, organisms get food through their partnerships. In others, shelter, transportation, or defense may be obtained from an association. We will discuss a few of these associations. In all cases, each of the partners has improved chances to survive and reproduce as a result of the relationship.

One or both partners *requires* its partner in order to survive in **obligate symbioses**. The relationship is *optional*, however, in **facultative symbioses**.

14. 2. 2. Struggles for Space and Nutrients

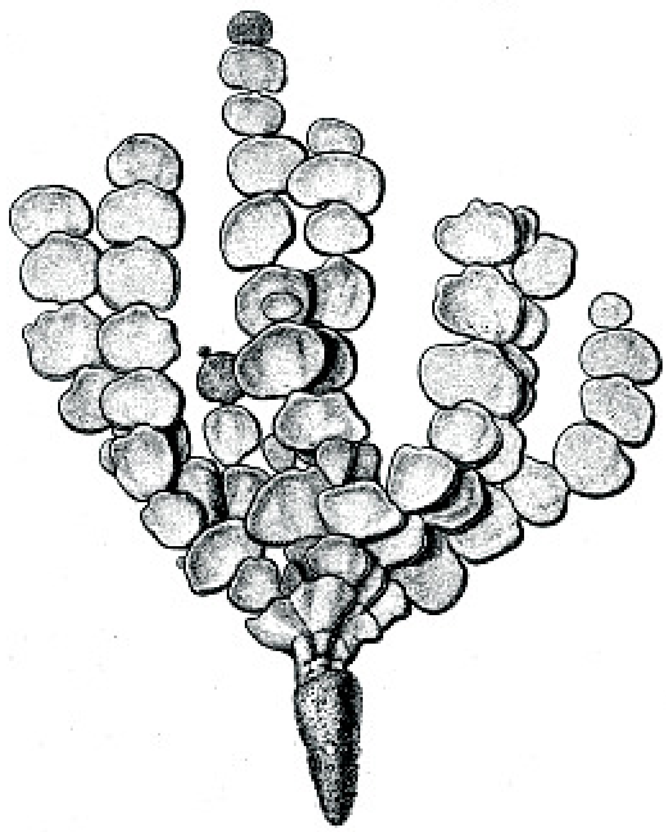
Several things argue against success for any organism trying to live on the coral reef.

All organisms on the reef are locked in an endless and unforgiving competition for survival. Recall that competition is an interaction over limited resources, such as food, mates, space, or shelter.

Recall also that nutrients are in limited supply in the open ocean environment that bathes the oceanic reef.

Space too is limited for **sessile** plants and animals like corals, sponges, soft corals, and coralline algae. Plants and corals must compete for sunlight. **Macroalgae** (large fleshy algae) find few free nutrients on the reef.

As a consequence, many fishes are territorial. Interestingly, the bluebanded surgeonfish, *Acanthurus lineatus*, is social on reefs that have abundant food, however it is territorial on reefs with less available food.

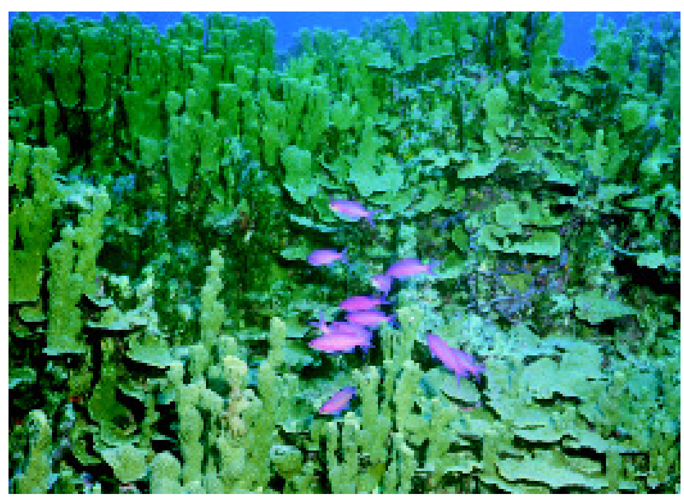


Macroalgae such as this Halimeda macroloba, find few free nutrients on the reef.

14. 2. 3. Plant-Animal Symbioses

The complex interactions between species on the reef and the relationships between animals and several kinds of microscopic plants are the hallmark of coral reefs. These relationships are present in other marine environments. On coral reefs, however, they have developed a dominant role.

Remember from Chapter 13 that certain dinoflagellates are microscopic plant-like protists called *zooxanthellae*. They live within many reef animals. They live in partnerships that give advantages to both the animals and the dinoflagellates.



The complex interactions between species is a hallmark of coral reefs.

These are not parasitic relations. Both partners benefit greatly and in important ways. The contribution of the zooxanthellae helps the coral to produce calcium carbonate ($CaCO_3$) limestone. This makes it possible for corals to produce coral reefs.

Zooxanthellae and other plants are linked with coral reef invertebrates. These include sponges, giant clams and other bivalves. Nudibranch molluscs, sea anemones, jellyfishes, and flatworms also form such associations on coral reefs.

The question comes up, "*How do the young animals get their symbionts?*"

In some species of invertebrates, the mother passes zooxanthellae to her offspring. This type of donation of zooxanthellae is a "closed system." In fire corals, *Millepora sp.*, the egg already has zooxanthellae when the mother releases it. Six species of scleractinian corals are also known to use closed systems of zooxanthellae transmission.

Zooxanthellae live inside organisms as non-motile cells. However, they also live in open water and may assume a flagellated form. These are called **swarmers**.

Swarmers may be, in turn, captured from the environment by the host invertebrates. This type of acquisition of symbionts is called an “open system”.

Most scleractinian corals, the upside-down jellyfish, *Cassiopeia spp.*, some sea anemones, some alcyonarians, and the giant tridacnid clams also capture them as they mature.

In fire corals, Millepora sp., the egg already has zooxanthellae when the mother releases it.

It is believed that swarmers can locate hosts by **chemotrophic behavior**. The swarmers sense the host chemically. They change their behavior so that they move toward the source of the chemical stimulation. In this way, after corals have “bleached” from environmental stress, they often re-acquire their zooxanthellae.

Corals and Zooxanthellae

Coral reefs are the most massive biologically-produced structures on earth. Many coral reefs are like mountains, a mile or more thick. We have already referred to what is probably the strangest of all symbioses: the partnership between reef corals and zooxanthellae.

A common zooxanthella in corals is *Symbiodinium microadriaticum. Prochloron spp.* is another dinoflagellate. It has partnerships with some sponges. [Note: sponges are classified as animals.] *Prochloron spp.* also has some other symbiotic relationships with other animals on the reef.

Both plants and animals benefit from such partnerships. The relationship is important to the health and prosperity of both partners.

The zooxanthella is a photosynthesizing organism. It produces food containing carbon (**C**). Like all plants, it requires nutrients. It especially needs nitrogen (**N**) and phosphorus (**P**). It receives nitrogen from the animal, which donates its waste nitrogen directly to the plant cell. Since zooxanthellae live right in the tissues of the animal, it is very easy to obtain the animal’s wastes.

Meanwhile the zooxanthellae are busily photosynthesizing, making their own food. They also make food for the coral. The most important aspect of the exchange between these partners is the nutrients and shelter which corals exchange for food in the form of sugar and other carbon compounds.

Zooxanthellae Assist the Calcification Process

By now we can understand the two-way exchange between coral and zooxanthellae. One important part of this relationship remains. The zooxanthellae play an important role in making limestone.

We have said that non-reef building (**ahermatypic**) corals do not produce a strong skeleton like reef building (**hermatypic**) corals.

All hermatypic corals have zooxanthellae. None of the ahermatypic corals have them. Hermatypic corals are sometimes called “zooxanthellate corals.”

Assisting in limestone production is also crucial to the pairing of zooxanthellae with a number of other animals. An excellent example is the giant clam, *Tridacna*. The shell of the largest of these clams, *Tridacna gigas*, can grow to a length of at least four feet, by far the most massive of all shelled molluscs. Yet, without the help of their microscopic zooxanthella symbionts, it is unlikely that the giant clams would be giant at all.

Hermatypic corals have zooxanthellae...

The specific role of zooxanthellae in the production of limestone, or **calcification** is not yet fully understood. It is known that the rate of stone production is much higher in sunlight. Some relationship with photosynthesis is apparent, since carbon dioxide, CO_2 is the basis for limestone, $CaCO_3$.

Recently, scientists discovered that corals possess more than one species of zooxanthellae. Each one is adapted for different light conditions. A single species of coral may have one species of zooxanthellae in well-lit waters. It has another species in less well-lit environments, on the side of a reef wall, for example. It may have a third species in deeper water, where light is even dimmer. A single colony may have three different species of zooxanthellae in different parts of the colony if light levels differ.

Other Reef Invertebrates with Plant Symbionts

A large number of other reef animals have zooxanthellae and other microscopic plants living in their tissues. The animals and the plants both benefit from the partnership in all of these associations.

Giant Clams

Giant clams, bivalve molluscs of *Family Tridacnidae*, are structurally adapted for the zooxanthellae they harbor. There are special eye-like structures on the exposed mantles on these clams. They are not present in other bivalves.

These "eyes" focus light deep into the tissues of the clams. They let light into special blood-sinuses where zooxanthellae live. Unlike the zooxanthellae that live in the cells of corals, the zooxanthellae of these clams live free inside the clam. The clams can digest zooxanthellae if their numbers increase to higher levels than the clam can support.

while ahermatypic corals do not.

As mentioned, these clams can reach a size of four feet. They are the only clams that produce such massive shells. The shells are made of calcium carbonate stone, like coral skeletons. Like the corals, the zooxanthellae assist Tridacnids in the stone production process. This is the reason these clams can produce these massive structures.

A few other clam species, like *Fragum fragum*, also have zooxanthellae. No other species produces such massive skeletons as Tridacnid clams, however.

14. 2. 4. Symbioses Involving Bacteria

Interestingly, bacteria are also linked with many organisms in various ways. Bacteria unite with a number of sponges. Bacteria also help organisms to digest plant material by living in their guts. Even we humans have mutualistic symbiotic bacteria living in our guts.

14. 2. 5. The Sea Anemone and the Clownfish

Clownfish seek protection among the tentacles of the sea anemone.

Clownfishes, *Amphiprion spp.*, cannot freely range around on the reef. These fishes have cultivated a dangerous friendship.

They seek protection among the tentacles of the sea anemone. Other fishes are killed by these sea anemones. The clownfish--also called the anemonefish--has become adapted to its host. Fascinated by this relationship, many scientists have investigated the adaptation of the fish and anemone.

The anemone can probably live without the fish. However, the fish takes special care of the anemone. It sometimes brings food to the anemone. Rather than being lost in the currents, the wastes of the fish may provide fertilizer to the zooxanthellae of the anemone.

Unlike its other Damselfish cousins of the *Family Pomacentridae*, the anemonefish cannot live out in the open on the reef. It depends completely on its anemone for protection.

The anemonefish is one of the few fishes which has found a safe place to establish a nest. It lays eggs underneath or next to the anemone. As soon as the larva hatch, apparently on a high tide in early evening, they leave the many dangers of the reef.

They follow the currents of the open ocean for a few weeks. Later, after growing up a bit, the few lucky individuals that once again find reefs will also have to find anemones. In many anemones, we see a pair of adults with one small fish, an apprentice.

14. 2. 6. Cleaning Symbioses

The conspicuous coloration of the cleaner wrasse advertises its presence to larger reef fishes.

Several examples of **cleaning symbioses** are also fascinating. Several reef species are well known as cleaners. The cleaner wrasse, *Labroides dimidiatus*, is the best known example. Several other fishes and cleaner shrimps on the reef are also known.

Cleaning symbioses are understood to play a grooming role. They help the host fishes get rid of skin parasites. An unusual example of a probable cleaning symbiosis has been observed on drifting logs in the open ocean. Fishery scientists have observed trigger fishes cleaning dolphinfishes (Mahimahi).

The Cleaner Wrasse

The cleaner wrasse is a few inches long, with a conspicuous coloration. This coloration advertises its presence to larger reef fishes. Large fish seek cleaning services from the much smaller cleaner wrasse. The wrasse maintain “cleaning stations”. There are often lines of larger fishes waiting to be cleaned.

The social life of *Labroides dimidiatus* has been intensely studied. Male wrasses may keep harems of several females. The cleaning stations of several such females are found within a single territory, along with juveniles. This social system has been found to be quite complex.

Once a fish has reached the head of the waiting line, the cleaner performs a dance consisting of a series of darting motions. Other fishes recognize this dance. It certifies the cleaner's identity.

Once the customer has been convinced of the cleaner wrasse's intentions, it adopts a submissive posture. These large fishes open up their mouths and gill covers, to allow the cleaner to enter. The wrasse dutifully cleans parasites from the gills and internal surfaces of the mouth. It also cleans external parasites and other foreign matter.

Parasites can be a significant problem. Just like lice or ticks on humans, parasites on a fish's skin are robbing their hosts of energy. It is obviously helpful to a fish, which has no hands, to be groomed by a cleaner. Can you think of the benefit to the cleaner wrasse?

Both partners benefit from this relationship. Such an association is called **mutualism**. The host benefits by being groomed. The cleaner obtains food--the parasites it cleans off its host.

Some researchers have studied the extent of this service. They have observed different reefs over a long period after removing all the cleaners from the reef.

In at least one case, fishes began to leave the reef after beginning to show obvious increases in the number of skin parasites. In other research, no such observation nor exodus occurred.

A Clever Thief--The Cleaner Mimic

The above relationship is very unusual, but very beneficial to the cleaner. Another reef dweller has noticed the benefits. The blenny *Aspidontus taeniatus*, is called the **cleaner mimic**. The cleaner mimic closely resembles the cleaner wrasse in behavior and appearance.

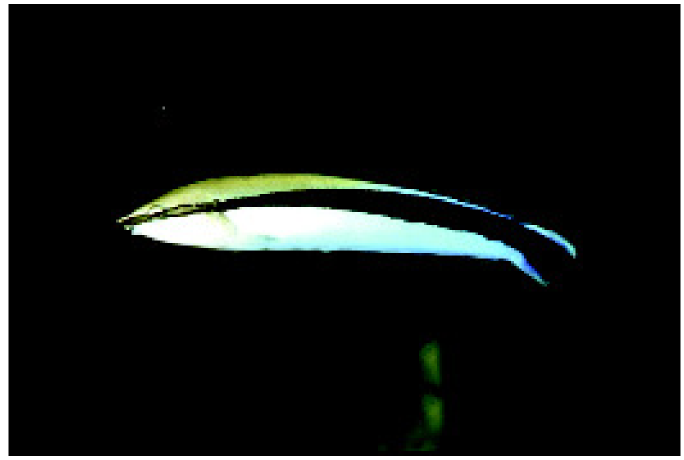
The cleaner mimic can approach even large fish. It even performs a dance similar to the cleaner wrasses' (though imperfectly) to gain the confidence of the unwary fish.

Once it does so, the mimic does not clean the "customer", but, instead takes *a bite*. Larger fishes may eventually learn to become wary of the cleaner mimic. The mimic even has the boldness of visiting the cleaner wrasse to be cleaned!

Other Examples of Cleaning Symbioses

Other reef organisms have adopted cleaning behavior as a strategy for survival.

Another organism is the Barber Pole, Candy Cane, or Peterson's Shrimp, *Stenopus hispidus*. These conspicuously colored cleaners are common on Micronesian reefs. People also like to keep them in aquariums.



The cleaner mimic closely resembles the cleaner wrasse in behavior and appearance.

The conspicuously colored barber pole shrimp are common on Micronesian reefs.

Trapezia punctata protects it's host coral from the crown-of-thorns starfish.

Cleaning symbioses are not well understood. The cleaner fish obtains free food for its part; the fishes are cleaned of parasites. Thus, it appears that both members of the partnership obtain a benefit from the cleaning association.

14. 2. 7. A Small Crab Protects Corals from a Predator

Special unions between reef species often have unexpected results. Several small crabs live on corals. They often have symbiotic relations with corals. The small and colorful crab *Trapezia punctata* lives with the corals of the genus *Pocillopora*.

We suspect that such crabs might somehow groom the coral. They may somehow trim off diseased tissues. If this were so, there would be some minor benefit to the coral. The crab would gladly provide this service in exchange for shelter and food.

However, it may come as a surprise that the crab provides a much more important kind of assistance to the coral. This crab protects these coral species from the crown-of-thorns starfish, *Acanthaster planci*.

How can a small crab, less than an inch across possibly protect a coral from a hungry, spiny and "mean" starfish like the crown-of-thorns, which can span a foot or more in diameter?

In order to defend its *Pocillopora* home, this tiny crab will harass any hungry starfish that tries to dine on its coral home. It pinches the tube feet of the starfish repeatedly, until the hungry starfish gives up and flees. The starfish then goes on to find other corals upon which to feed--corals, hopefully which are not so well protected.

On reefs that have been infested by the crown-of-thorns, this tiny *Trapezia* crab has made a difference. In many cases, *Pocillopora spp.* are found to be the predominant species.

On reefs that have been infested by the crown-of-thorns, the tiny Trapezia crab has made a difference.

Other species were weeded out by the starfish. It has even happened that favorite food species of *Acanthaster planci* were left alone when they were surrounded by *Pocillopora spp.*

Several other crustaceans are also involved in symbiotic associations with corals. Obligate symbionts of corals include the xanthid crabs *Tetralia spp.*, associates of the *Acropora spp.*

As mentioned, the crab *Trapezia punctata* lives mainly with *Pocillopora spp.* An alpheid shrimp also occurs on *Pocillopora spp.* These crustaceans cannot survive without their coral hosts, which provide shelter and food.

The corals can live without these crustaceans. However, in the case of at least *Trapezia* species, an extremely important service is rendered to the coral in times of need--when *Acanthaster planci* is attacking.

14. 2. 8. Medusafish

A small fish can sometimes be seen swimming with medusae. This fish is protected by the stinging tentacles of the medusae, like the anemonefish. It is uncertain what benefit the medusa receives. Perhaps this is a **commensal relationship**.

14. 2. 9. The Alpheid Shrimp and the Goby

The alpheid shrimps are small shrimps with one claw larger than the other. They are somewhat common on coral reefs. Some of them are called "snapping shrimps".

Come of these small shrimps have formed partnerships with small fishes called gobies. We can find many of these on the reef flats in very shallow water. The fish and shrimp stay together in a hole constructed by the shrimp.

Robert Myers, in his book *Micronesian Reef Fishes*, discusses this relationship:

> "The prawn builds a burrow in sand or muck and is blind, or nearly so, and unable to see approaching danger. The goby uses the burrow as a refuge, and ... acts as a sentinel for the prawn. The gobies, usually singly or in pairs, spend most of their time at the entrance of the burrow and feed on small sand-dwelling invertebrates, many of which are exposed by prawn's excavations. When shoveling sand around the entrance, [the prawn] usually maintains contact with the goby by touching the goby's tail with one of its antennae. When alarmed the goby flicks its tail, signaling the prawn to retreat. If the danger persists, the goby dashes headfirst into the burrow. "

Alpheid shrimps build holes in which they live with small fishes called gobies.

Both partners benefit from the association. This relationship may be obligatory. Each of the several Micronesian reef-dwelling goby species associates with specific species of prawns.

We encourage our readers to obtain and read Myers' excellent *Micronesian Reef Fishes* book. Robert took great pains to take beautiful underwater photographs and to research and discuss fish histories and fish ecological interactions. The above is just a brief example of his fine work.

14. 2. 10. The Hermit Crab and the Anemone

Maybe you have seen the rather bizarre sight of a hermit crab wandering around on the reef platform with one or more sea anemones attached to its shell.

Certain species of hermit crabs enjoy the protection of anemones which live on their host's aquired shell.

Did you ever wonder why? Well, let's look a bit closer--the story may be even stranger than it seems. In the end, though, we can find a good explanation.

Why Does the Hermit Crab Welcome the Anemone?
Octopi prefer hermit crabs as food. A hermit crab that is placed in an aquarium with an octopus is quickly eaten.

However, if a sea anemone were on its shell-home, the octopus not only refuses the hermit crab but moves as far away as it can to hide from the hermit crab. Clearly, the toxin in the anemone's nematocysts is painful to the octopus.

Thus, the association of hermit crabs with anemones is beneficial to the hermit crab. The anemone gets a free ride, and possibly dines on scraps of food; there is definitely a benefit to each partner.

A Whole Society?
Two species of anemone live with this hermit crab. The larger one lives on top of the crab's shell. A smaller one lives under the lip of the shell opening, beneath the crab.

If one of these hermit crabs is picked up and temporarily placed in a plastic bag, a small amphipod crustacean will be seen swimming around the anemones picking up left over food.

Pearlfishes live within the body of echinoderms.

14. 2. 11. Mitten Crab and Sea Anemones

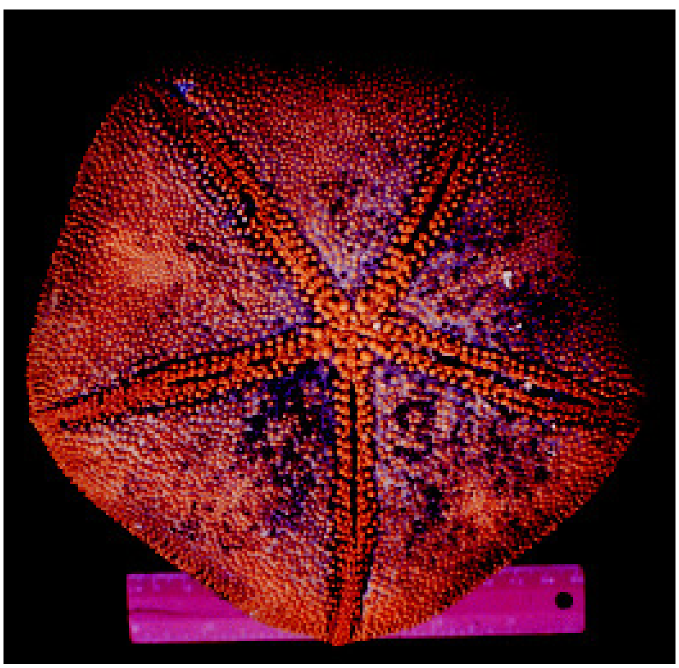
The mitten crab *Lybia sp.* carries two sea anemones around like mittens, or perhaps more like boxing gloves, in its pincers. These may benefit this crab the same way the anemones are beneficial to the hermit crab mentioned above.

14. 2. 12. Pearlfishes and Sea Cucumbers

Pearlfishes, of the *Family Carapidae*, live on coral reefs. Pearlfishes are entirely whitish to clear in color, hence their name. They have an association with large sea cucumbers and with the pincushion starfish, *Culcita novaeguineae.*

Pearlfishes live within the body of these echinoderms. They are only rarely observed outside their hosts. These fishes are shaped somewhat like eels. They have a long, sharply tapering "tail" that is used as a tool to enter the sea cucumbers.

This is not likely to be a mutualistic symbiosis, but biologists are trying to determine any benefits that the host might receive. The pearlfish benefits from shelter, and it may eat certain parts of the insides of the sea cucumber. These, however, rapidly grow back.



The cushion starfish plays host for both pearlfishes and pyramidellid snails.

14. 2. 13. Other Symbionts; Crabs and Snails

A small black and white crab lives on outer surfaces of some sea cucumbers. If this crab is disturbed, it crawls into the sea cucumber's mouth or anus.

Tiny pyramidellid snails also live on the surface of sea cucumbers. They may be considered a parasite. This depends on whether they eat some part of the sea cucumber, or if they eat other material on the surface of the sea cucumber. This is unknown at present.

Pyramidellid snails also live on starfishes. Other snails are also associated in various ways with different kinds of reef organisms. Certain snails feed only on coral polyps. Some snails live as prisoners of soft corals.

14. 3. CORAL REEFS ARE SPECIAL ECOSYSTEMS

Coral reefs are special environments. They are well known for their numerous examples of symbioses. Recall that an ecosystem is a biological community together with its physical environment. In the next section, we will consider how symbiosis is essential to the life of the coral reef.

14. 3. 1. Recycling and Symbiosis: The Role of Associations on the Coral Reef

Have you ever marveled at the large number of species on a coral reef? Coral reefs are very special in this way, with a multitude of species.

Are you beginning to notice the many kinds of associations by which these organisms are linked together into a community? These associations are like a glue for the community. They make it possible for this assemblage to stay and live together as they do.

Coral reefs live best in the tropical open ocean. Tropical oceans are lacking in nutrients near the surface, so that growth of primary producers (plants and plant-like protists) is limited by lack of nitrogen and phosphorus.

Yet, scientists have been quick to point out that the coral reefs in the midst of the open ocean are highly productive. This has long been a puzzle to scientists. Associations are the key to this puzzle.

Associations between plants and animals enable the plants to scavenge nutrients directly from the animals before they can be eliminated into the water column.

The coral reef is a dangerous place to live. Animals and plants vie in an eternal struggle for resources. They mainly compete for food and nutrients, and mates.

The key to survival of so many species together on the reef appears to be their associations and interdependencies. Symbioses are a hallmark of life on the reef.

Great white sharks are top predators which are sometimes found hunting near Australia's barrier reef.

14. 4. ENERGY: THE UNUSUAL CORAL REEF FOOD WEB

The coral reef community is incredibly complicated. It is impossible to simplify the coral reef food web to a few food chains.

The chief problem lies in the special association between corals and zooxanthellae. These are the primary producers at the base of the food chain, living within cells of the consumer--the coral.

The coral gets much of its energy from the zooxanthellae through their partnership. However, the situation is more complicated than that. Corals also consume zooplankton, which in turn depend on phytoplankton.

The interaction between the coral and the zooxanthella involves more than an exchange of food for nutrients. Corals protect the zooxanthellae and control their growth. We cannot reduce this food web to a food chain. Moreover, the zooxanthellae upon which the coral depends is, in return, dependent upon the coral. It depends on the coral for shelter and nutrients.

More than any other community on earth, coral reef communities feature specialized interactions. Besides the symbiosis between coral and zooxanthellae, many coral reef predators specialize in specific types of prey.

It is impossible to simplify the coral reef food web to a few food chains.

Other symbiotic relationships are exchanges for food, shelter, defense, and transportation. No other type of community supports so many symbiotic relationships. The tendency in coral reef communities towards specialization leads to complicated food webs. There are networks of interdependency unmatched in other ecosystems on our planet.

Butterflyfishes that are corallivores (coral feeders) live in pairs and defend territories.

Beside symbiotic associations and their influence, the food web of the reef is unique in other ways. Other groups of primary producers are also important on the reef. Beside zooxanthellae, there are surface films of algae and **endolithic** (inside of rock) algae. There are small macroalgae which are small fleshy algae and filamentous algae. There are also large macroalgae.

Films of algae grow on exposed surfaces. Filamentous endolithic algae live within the reef rock. They contribute an important source of food to scrapers and grazers such as sea urchins and parrotfishes.

Small filamentous surface algae and small fleshy algae are continually being grazed by herbivorous fishes and invertebrates. They constitute the main pathway from primary producers to humans. Large algae are obvious on the reef, but small fleshy algae are more important in food webs.

Territoriality

Many reef fishes hold and defend territories. As mentioned, Fishery scientists think that the blue-lined surgeonfish, *Acanthurus lineatus*, holds territories on reefs where food supplies are marginal. Yet, on reefs where there is abundant food, this fish maintains schools.

Territoriality is a way to defend a less-than-ample food supply. Territorial fishes like *A. lineatus* may tolerate or exclude other fishes. Interactions between it and different species are not yet fully understood.

Damselfishes will aggressively defend their territory, often attacking species much larger than themselves.

Butterfly fishes that are **corallivores** (coral feeders) live in pairs and defend territories. The size of the territory shows the abundance of corals in their home range. Where there are many corals, smaller territories provide enough food for one pair. Fish pairs must patrol larger territories to provide the same amount of food where there are fewer corals.

14. 5. CHEMICAL ECOLOGY OF CORAL REEFS

14. 5. 1. Introduction

As stated earlier, ecologists sometimes call the reef a war zone. It is just too crowded. The self interests of too many species are in conflict. Among the strategies for survival on the reef, we have mentioned specialization and symbiosis. These are two hallmarks by which we know the coral reef.

Another feature of coral reefs, just as fascinating, makes the reef a deadly place--not only for humans, but especially for reef animals and plants. Reef organisms are specialists in chemical warfare.

This feature of coral reefs has attracted much scientific and commercial interest. Reef organisms are valuable not only as food; some toxic organisms are potentially valuable as well. Even the earliest Micronesians arrived with a "bag of tricks" based on their familiarity with reefs and reef organisms. Reefs and beaches were abundant in our ancestor's original homes, in both the Philippines and Indonesia.

Over the centuries, the people of Micronesia continued learning to accommodate to, and to utilize, the inhabitants of our reefs. The toolkits of indigenous knowledge included knowledge of the venoms and toxins of the reef. Our ancestors knew which plants and animals were good to eat, and which were poisonous.

14. 5. 2. Venoms and Toxins

Compared with a temperate coastal marine environment, a coral reef has a large number of toxic and venomous plants and animals. In the fierce struggle for existence on the reef, the battle amongst the fittest led to a large number of chemical innovations.

14. 5. 3. Antiherbivore Compounds

Certain species of algae and some invertebrates have discovered a secret to long life. Fishes don't eat you if you taste bad. Distasteful substances, as well as poisons, are found in algae, which use them to discourage fishes from eating them.

Nocturnal fishes, such as this lionfish, become active at night.

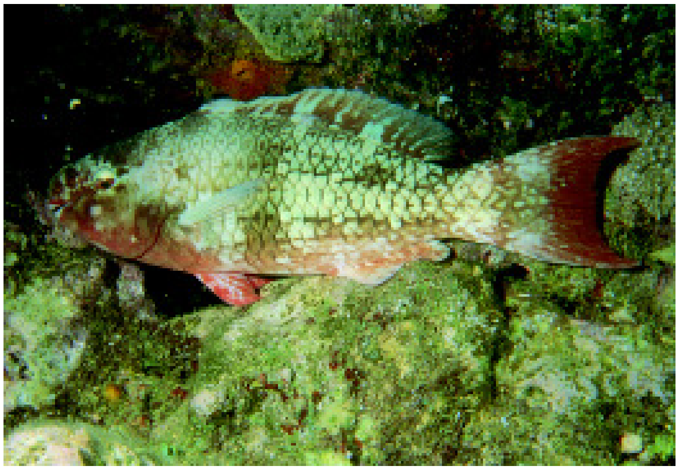
14. 6. DAYTIME REEF... NIGHTTIME REEF... TWILIGHT REEF

As mentioned the reef is a crowded place. It is a veritable circus of many colorful species interacting and avoiding one another. What most of us see, however, is only ½ the picture.

At sunset, **diurnal fishes**, the colorful fishes of daytime, disappear. They hide in the nooks and crannies of the reef. Shortly afterwards, the **nocturnal fishes**, nighttime fishes, then appear.

Then, at sunrise, the changing of the guard happens again, only this time in reverse. At first light, the nighttime fishes disappear and daytime fish reappear.

In some cases, a relatively long range daily migration may be involved. Fishes may have feeding ranges far removed from the places where they sleep.



Diurnal fishes, such as this parrotfish sleep in crannies in the reef at night.

Motile invertebrates, like crabs, snails, and octopi, are more common at night. During the day they hide in crevices and under stones. Many species of plankton are associated with the reef, and many of these species hide on the reef during the day, emerging only at dusk. These are called **emergent zooplankton**.


NUOUA, et ACCURATA CARTA dell'ISOLE FILIPPINE, LADRONES, e MOLUCCOS, o ISOLE delle SPEZIARIE come anco CELEBES &c. data in luce da ISAAC TIRION in AMSTERDAM
Miglia Inglesi
Miglia Francesi, o ore di Camino
MANILA
FILIPPINE
ANDAYA o SAMAR
NVOUE ISOLE FILIPPINE
MINDANAO
ISOLE LADRONES
Guam
MARE DEL ZUID o sia MARE PACIFICO
Linea Equinoziale
MOLUCCOS o ISOLE delle SPEZIARIE
CERAM
NVOUA GUINEA abitata dalli Papuas
Terra alta
Li Scogli di St. Bortolamio di Dudley
TIMOR
Terra Alta
Timorland