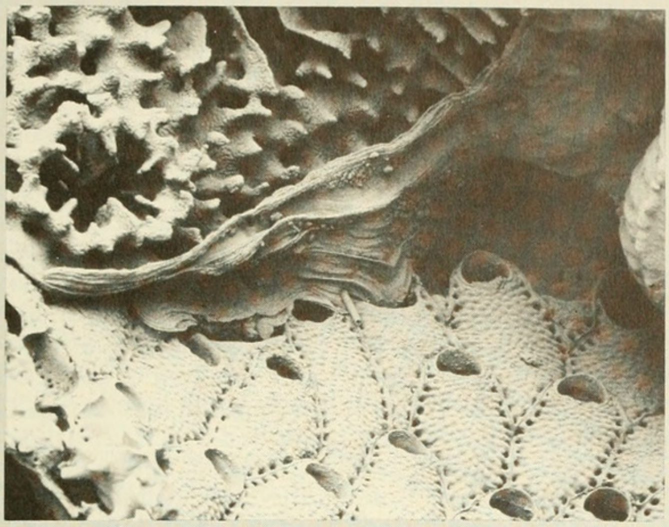
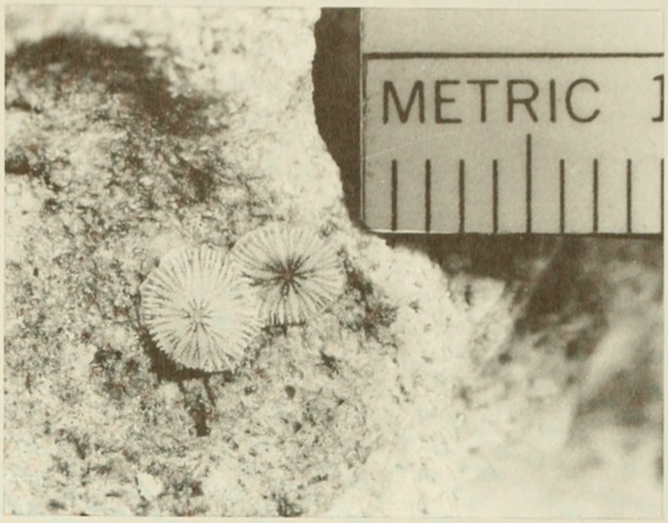
Dispersal, and Survival



Since space is a limiting factor for survival, competitive interactions involving coral spat can be highly complex. Here, an oyster is overgrowing an *Acropora*, which in turn is overgrowing an encrusting foraminiferan, which in turn is being overgrown by a coralline algae.



Coral planulae often aggregate upon settlement. If two or more spat abut in their initial growth phase, and if they are histocompatible, fusion occurs. This can enhance survival of both colonies by allowing them to grow into a size refuge more rapidly—where they can better survive predation, disturbance, or competition for space. (Photo courtesy *J. Exp. Mar. Biol. Ecol.*, 1982)

Larval Dispersal and Settling

Coral settlement and survival has been examined by our laboratory in the recent Helix Experiment. Successful dispersal and settlement appears tied to both species and regional differences.

Although the larvae of some organisms have high dispersal capabilities, the average distances that they actually traverse can be surprisingly short. For example, at times, pollen seems almost ubiquitious in the lower atmosphere. Yet most of the wind-dispersed pollen of pine trees falls within a few meters of the parent plant. Coral larvae exhibit a similar pattern. Most settle directly on the reef, or within 600 meters of it—a fraction of the distance they are capable of traversing. On a finer scale, the pattern is genus-specific, and also tied to reproductive mode, as described previously. Planulae and fertilized eggs are certainly capable of travelling much further, and many do, as others have suggested. These individuals are important for the spread of coral populations, and the question of actual dispersal distances of larvae remains open at this time. It is an active area of research.

Settlement geography also is important, and cross-shelf differences are clear. Species that successfully settled on an inshore reef were different from those on mid- and outer-shelf reefs. Mortality rates were higher inshore, suggesting that high sedimentation and salinity variation created a harsher environment, and in shallow water on the outer shelf, where wave action inhibits settlement. The optimal conditions for settlement and survival of the coral appeared to be on the mid-shelf.

Survival

After settlement, juvenile corals must survive the rigors of not only their physical but also their biological environment. Grazing by predators and competition for space are the principal factors. While these same factors continue to operate and act on adult corals, mortality levels are greatly reduced due to their refuge in size. Adult colonies may be composed of thousands of polyps, each capable of regeneration and regrowth, whereas juveniles will have only a few. Thus, mortality to several polyps would usually be fatal to the juvenile, but insignificant to the adult—leaving the adult to survive, reproduce, and begin the life cycle anew.

—Paul W. Sammarco, AIMS

Southern Hemisphere—including Australia, India, Africa, and South America—were well south of their present positions, leaving a tropical/subtropical circum-global seaway linking all of the world's great oceans. This seaway, the ancient Tethys Sea, allowed many groups of tropical marine organisms, including corals, to range from the Atlantic to the central Pacific. Today many groups of marine organisms have this so-called "tethyian" distribution, established before the closure of the Tethys Sea more than 10 million years ago.

End of story for corals? Far from it. The mid-Pliocene heralded the commencement of the Ice Ages, the consequences of which, for coral reefs, can hardly be overstated. The build-up of the polar ice caps did not create a lethal temperature decrease in most tropical regions. Rather, damaging effects of the ice cap build-ups came from the lowering of sea level that accompanied them. A drop in sea level of 1 meter would mean death for most reef flat corals, and a drop of 100 meters would mean death to an entire reef region. This is what happened, repeatedly, during the Ice Ages. Vast areas of reef, including the entire Great Barrier Reef, were alternately left high-and-dry, then flooded, in a continuing series of catastrophic cycles. This process affects both the geomorphology of reefs and the evolution of corals.

While the effects of the Ice Ages on the evolution of corals are still being debated, the effects on the distribution of corals are clearer. Lowered sea level exposed and consequently killed most coral communities, and created new barriers to distribution. Many genera now restricted to the Indo-Pacific were common in the Caribbean before the final closure of the Panama Isthmus some 5 million years ago. This area was severely affected by glaciation as well as by sea-level change: all eastern Pacific corals were probably entirely destroyed at this time, with the present Caribbean fauna thus coming from refuges along the east coast of South America. Consequently, there are only a few species of coral in the eastern Pacific, and all these have their affinities with, or are the same species as, corals in the western Pacific. Only a single species has survived in both the Indo-Pacific and the Atlantic and no hermatypic species has survived in the Mediterranean.

Environmental and Ecological Controls

The combined effects of continental drift and sea-level changes still leave a lot to explain about coral distribution, reef distribution, and related subjects like coral community composition. Why, for example, does diversity decrease eastward and southward from the Great Barrier Reef? Why does the composition of coral communities vary from one reef, or region, to the next?

Here we must consider the spatial scales involved. The patterns of community types found on a *single reef* primarily reflect patterns in the physical environment, especially depth, wave action, light, and sediment load. Within a whole *region*, such as the entire east Australian coast, corals are distributed primarily according to ocean currents and temperatures, the availability of suitable sites for colonization, and the capacity of larvae to get to those sites. Within the *entire Indo-Pacific*, corals are distributed according to a mosaic of regional patterns, each with its own characteristics, superimposed on a historical background of continental drift and sea-level changes.

The effects of surface circulation patterns on coral distributions are seen very clearly in the western Pacific. Here, most tropical currents flow toward the west, allowing rapid transport of larvae toward the Indo-West Pacific center of high diversity, not eastward away from it (Figure 2). Thus, there is a "catch-all" effect in the west. Southward from the Great Barrier Reef, the East Australia Current flows unceasingly southward, and planktonic larvae can only travel south on nonreturn journeys. Thus, some coral species that are abundant on eastern Australia's southernmost reefs are rare or absent on the Great Barrier Reef: they have become trapped in the south and will remain so as long as the East Australia Current prevails. A very similar situation also applies to the Northern Hemisphere where the northward flowing Kuroshio Current flows northward past Japan's Ryukyu Islands, bringing planktonic larvae from tropical waters. It is not surprising, therefore, that Japan and Australia have so many coral species in common: both faunas have dispersed from the same general (western Pacific) region.

Temperature long has been considered the primary factor limiting corals to tropical and subtropical localities, and it has been generally considered that it does so by affecting the reproductive cycle. If this is so, it has yet to be demonstrated. Alternatively, the effects of low temperature may be indirect: it may slow the rate at which corals can calcify, thus making light availability (hence depth) more limiting. At high latitudes,

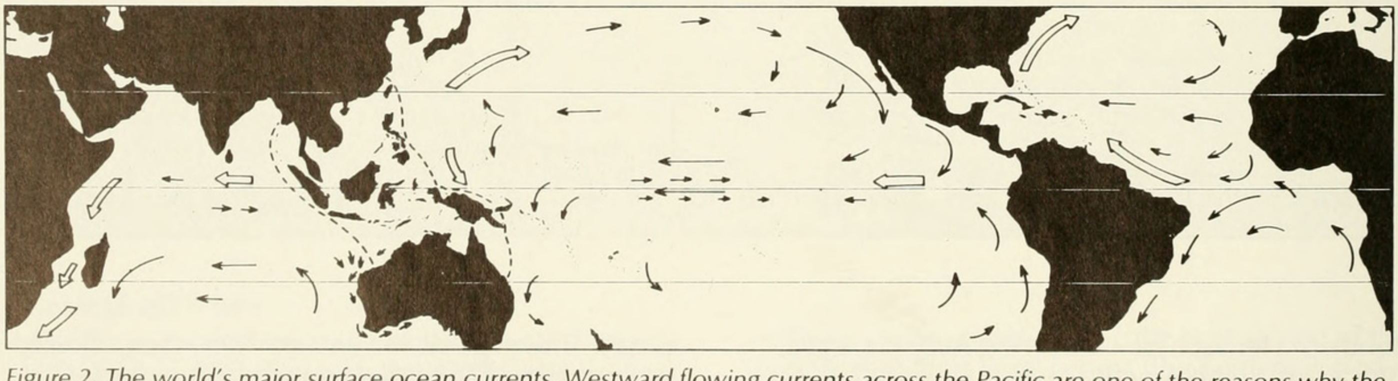


Figure 2. The world's major surface ocean currents. Westward flowing currents across the Pacific are one of the reasons why the Indo-West Pacific has a high coral diversity. The dashed lines enclose about 75 percent of the world's coral reefs, another reason why this region is so diverse.

therefore, the rate at which corals can construct reefs may not be sufficient to outstrip the forces of erosion.

There are several other environmental constraints affecting hermatypic corals that may be important in any particular region. Of course, most of the world's oceans are too deep for reef growth. Some regions are greatly affected by major rivers, which decrease salinity to levels lethal to corals. Others have substrates of soft terrigenous mud, unsuitable for coral growth. Biological controls also limit reef development. Important among these is competition between corals and macro-algae (for example, kelp and *Sargassum*), which are easily able to out-grow corals. On coral reefs, algal growth is held in check by herbivorous fish. However, where reef development is poor, especially in the higher latitudes, this is often not the case, and corals are forced to compete directly with algae.

Dispersal and Speciation

Like most marine fauna, corals disperse by means of tiny planktonic larvae, the fate of which depends on prevailing ocean currents and the ability of the larvae to settle and grow should they be able to find suitable conditions. That corals are capable of long-distance journeys has been disputed for some time, and, for most species, still needs to be experimentally demonstrated. However, taxonomic evidence that most species do indeed make long journeys is overwhelming. Most species are very widespread, and few are endemic to any particular region.

What, then, can be said of the origin of species? Where in time and space did they originate? Some claim that the sea-level changes earlier described have created barriers to dispersal (barriers to gene flow) which, as in the case of Darwin's finches, have been a major cause of speciation. The rise and fall of sea levels would have created and removed all manner of barriers, especially land bridges, causing separate species to form, then allowing them to intermix. Others claim that sea-level changes have acted to retard speciation. The high frequency of sea-level fluctuations, combined with the great longevity of corals and their capacity for dispersal, has kept the gene pool mixed and the number of species low.

The latter of the above two models now appears to be the more likely for most hermatypic corals that are indeed characterized by a low number of species. Perhaps the very wide range of growth forms displayed by most species also reflects a lack of speciation. To find the origins of most species, we should look back to an earlier time of long-term climatic stability, perhaps late Tethyian times, when tropical conditions prevailed over most of the earth's surface and ocean currents did not provide the communication between reefs that they now do and would have done during the Ice Ages.

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Coral Rings Give Clues to Past Climate

Coral skeletons contain annual rings analogous to tree rings. The rings are revealed as alternating light and dark bands when coral skeletons are X-rayed. A pair of these bands represents one year's growth. The bands are best seen in large rounded coral colonies that grow 0.5–1.5 centimeters in a year. On the Great Barrier Reef, 600-year-old colonies are frequent, and occasional colonies are older than 1,000 years. Systematic changes in these rates of coral growth have been found across the width of the Great Barrier Reef from turbid coastal waters to the clear waters of the Coral Sea.

Research in progress at the Australian Institute of Marine Science in Townsville indicates that growth patterns in coral skeletons are a potentially important record of weather and climate trends in the recent past.

The fundamental record in massive corals is a marked annual variation in skeletal density. This was first described in 1972, and is now recognized as a characteristic of many species of coral. The underlying causes of the annual density variation have not been firmly established. The seasonal timing of high and low density growth appears to vary from one part of the world to another.

The density variations probably reflect complex seasonal phenomena, such as cloud cover and nutrition, rather than simple factors, such as temperature. Nonetheless, the annual density bands provide a reliable and accurate temporal record of skeletal deposition. Research shows that a resolution of about 14 days is possible from this density record. The presence of an accurate temporal record makes possible the deciphering of a range of other environmental records that the coral incorporates during growth.

Supra-annual peaks in skeletal density have been found to coincide with El Niño years. Records of the last 30 years can be easily obtained from coral colonies collected from reefs. Longer records can be obtained only by drilling a core sample along the growth axis of larger colonies. We have thus far obtained about 30 such cores from very large colonies. These cores represent growth over the last 200 to 600 years (shortest to longest cores).

Only one core has been analyzed in detail. The core came from Pandora Reef and provided information back to 1862. Pandora Reef lies inside the Palm Islands, close to the mainland. Annual density variations along this core showed a 60 percent correlation with atmospheric pressure at Darwin from 1882 to the present (the extent of the pressure record).

Whereas currently available models are based on only several decades of conventionally recorded weather and hydrological data, new models resulting from our research will derive from weather analogues in the form of bands in coral cores that go back about 1,000 years. The goal is to produce seasonal and other long-range forecasts.

—Peter J. Isdale, AIMS

Soft Corals: Chemistry and Ecology

by John C. Coll, and Paul W. Sammarco

Soft corals (Coelenterata: Alcyonacea) are one of the most important groups of animals on the Great Barrier Reef. They are abundant over the 2,000 kilometers of this reef complex and are a most diverse group, possessing hundreds of different species. They occur as attached colonial organisms, with each colony made up of thousands of interconnected individual and identical polyps. They vary widely in form from the soft and fleshy members of the Xeniidae family to the very beautiful but prickly members of the genus *Dendronephthya*, and from the hard, leatherlike forms of the genus *Sinularia* (*S. dura*) to other erect, tree-like forms of the same genus (*S. flexibilis*) (Figures 1–4).

Soft corals produce natural compounds that play important roles in their ecology—particularly in their defense against predators, in competition for space, and in reproduction. These secondary compounds are novel in structure. The majority of them belong to the chemical class called terpenes*, and are responsible for the odors and distastefulness of common plants and trees such as pines, eucalyptus, sagebrush, and so on. These compounds (and hence the organisms which produce them) interest natural-products chemists because of their potential application as pharmaceutical agents (for example, antibiotics, antifungal agents, and antitumoral agents).

These compounds appear to offer a distinct adaptive advantage to the organisms that possess them, helping them to survive in their natural environment. In any community, particularly where organisms are sessile (permanently attached to the bottom), interactions between individuals can become intense (Figure 5).

Toxicity As Protection Against Predation

In general, coral reefs possess many would-be predators—fish, crustaceans, echinoderms, and so on. Most common soft corals are fleshy in texture and thus appear defenseless against predators. Chemical analysis suggests that they are rich in nutritionally important substances (such as protein, fats, and carbohydrates) and could serve as a valuable food source to predators. Yet, recent surveys show that the incidence of predation on this group is low.

In contrast, hard corals constitute a major food source for some common groups of reef fish: parrotfish, starfish (crown-of-thorns), mollusks, and crabs. Soft corals thus appear to possess defenses not immediately obvious to the observer. Chemical analyses have revealed high concentrations of certain terpenoid compounds in many soft corals that may serve as a defense mechanism.

Laboratory tests have been performed on the mosquito-fish (*Gambusia affinis*) using aqueous extracts of numerous soft corals collected over the full range of the Great Barrier Reef. These tests show that about 50 percent of the extracts are toxic. In addition, the level of toxicity across families and between species varies greatly, ranging from lethal to harmless. Because toxicity does not seem to account entirely for the very low levels of predation observed in the field, other defenses are suspected.

Feeding Deterrence

Tests also were performed to determine whether soft coral extracts possessed characteristics which rendered them distasteful to fish. We impregnated standard tropical fish food with soft coral extracts of various concentrations and then tested them for feeding deterrence in test fish. Almost 90 percent of the samples possessing the highest amounts of extract were found to deter from feeding. Even at the lowest concentration, 55 percent of the samples still elicited the same response—suggesting that feeding deterrence is a common characteristic of soft corals.

However, no easily definable link or positive relationship was found between the incidence of toxicity and that of feeding deterrence. Some very unpalatable soft corals were shown to be harmless while apparently palatable soft corals were lethal. Thus, these characteristics, toxicity and feeding deterrence, 1) probably evolved independently, 2) may involve different sets of chemical compounds, or 3) may represent adaptations that simply perform different rather than dual functions in the organism.

* Any of certain types of organic compounds present in essential oils of plants.