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The Great Barrier Reef: Science & Management

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"America Salutes Australia's Bicentennial"

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AMERICAN-AUSTRALIAN BICENTENNIAL PROJECT

In 1988, Australians will celebrate 200 years of European settlement. They have invited the United States to join in their year-long celebration as Australians did in the U.S. Bicentennial in 1976.

For this purpose, the U.S. Department of State formally endorsed the creation of the American-Australian Bicentennial Foundation. Its task is to develop a series of commemorative projects worthy of America's close relationship with Australia. This issue of *Oceanus* is one of the first of these projects.

America's participation in Australia's Bicentennial depends on contributions from corporations doing business in Australia. Contributions to the Foundation are tax deductible: 1910 K Street, N.W., Suite 711, Washington, D.C. 20006. Tel. (202)467-6988.

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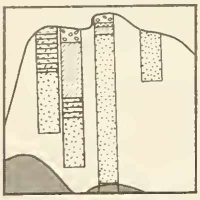

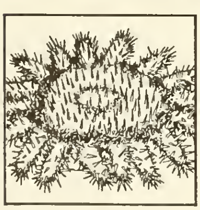

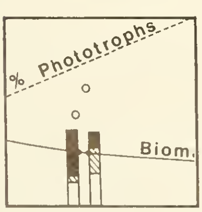

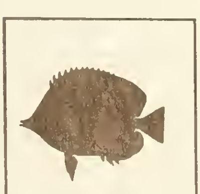

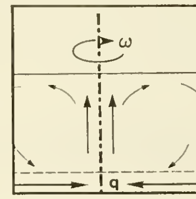

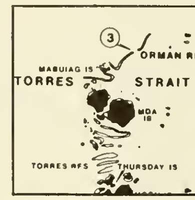

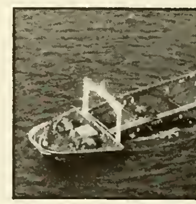

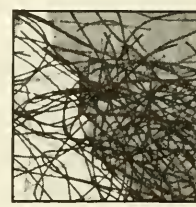

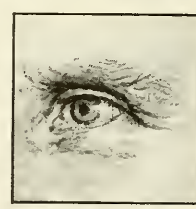

Cover: Red harlequin tusk fish found on the Great Barrier Reef. Photo courtesy of Ron and Valerie Taylor/Great Barrier Reef Marine Park Authority (GBRMPA).

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Introduction:

The Great Barrier Reef:

by Barry O. Jones

Australian Minister for Science

Although man has ventured to the moon and to outer space, developing sophisticated satellite systems for communications and remote sensing along the way, his understanding and exploration of oceanic space on Earth is relatively crude. The application of science and technology to land-based resources has resulted in highly innovative agricultural, manufacturing, and mining industries, whereas little attention has been given to the utilization of marine resources for aquaculture, mining, and entrepreneurial developments.

These marine inadequacies are highlighted at a time when the focus of world trade and development shifts more and more to nations in the Pacific and Southeast Asia. Much of this area is tropical: many of the shorelines of the numerous developing countries are fringed by corals and/or mangroves, and the marine living resources appear barely able to support existing population demands.

In this complex environment, Australia's increased commitment to marine scientific and technological research during the last 10 years has produced results that are directly relevant to a better understanding of its own tropical resources. It also has provided a basis for interactive development of marine resources with other countries in these tropical seas. Particular areas of collaboration include studies of coral reefs, coastal zone management, mangroves, oceanography, cyclones (typhoons/hurricanes), and satellite imagery.

The Great Barrier Reef, which stretches some 2,000 kilometers along the Australian Pacific coast, has been a focal point for international interest and tourism, as well as for marine scientific and technological research. Its unique status has been formally recognized by its inclusion on the World Heritage List. Publication of this special issue of *Oceanus* recognizes this level of international interest and of Australia's particular responsibility to preserve for posterity this complex ecological system with its wonderful diversity of species and endless variety of color and form.

The Australian Marine Science and Technology Advisory Committee (AMSTAC) advises me on priorities for marine research in general and has been instrumental in making me increasingly aware of the need for a greater research investment in the Reef region. The Marine Research Allocations Advisory Committee (MRAAC) administers the Marine Sciences and Technologies (MST) Grants Scheme and, in the initial years of the Scheme, the greatest proportion of available funds has been allocated to barrier reef research. Evidence of the wide distribution of research involvement on Great Barrier Reef topics can be seen from the contents of this special issue, where many of the major articles represent joint authorship from people at two or more Australian institutions.

There is a heavy concentration of research effort at Townsville with interactive programs undertaken at the Australian Institute of Marine Science (AIMS), James Cook University of North Queensland (JCUNQ), and the Great Barrier Reef Marine Park Authority

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(GBRMPA). Major studies involving all three institutions include the Crown of Thorns starfish research program, a collaborative tripartite development of a three-dimensional numerical modelling program to understand the hydrodynamics of the water movements in the reef region, and a proposal to develop a satellite receiver station with image processing facilities to analyze data from Landsat, and the geostationary meteorological satellites.

Other research programs involve collaboration with the Commonwealth Scientific and Industrial Research Organization (CSIRO), and the Bureau of Mineral Resources, Geology and Geophysics (BMR). These studies take advantage of a number of research vessels: *Lady Basten* (28 meters, AIMS), *Harry Messel* (21 meters, AIMS), *James Kirby* (17 meters, JCUNQ), and a large number of smaller craft available along the coast, and the oceanographic research vessel *Franklin* (55 meters, CSIRO), and the geologically equipped research vessel *Rig Seismic* (72 meters, BMR). These vessels conduct research programs throughout Australian waters. The Inaugural Great Barrier Reef Conference, held in Townsville in 1983, provided evidence of the extent of coral reef research. Significant research discoveries were reported involving coral spawning, weather records in corals, ultra-violet-blocking agents in corals, mariculture of prawns and clams, cyclone impacts, coral regeneration, marine stingers, the Crown of Thorns starfish, and oceanography in the reef region. These discoveries have provided for sound management practices by the Great Barrier Reef Marine Park Authority.

The mosaic of research presented in this issue provides an exciting picture of Australia's determination to unlock the scientific marvels of this natural wonder, and also to preserve it for posterity. This issue of *Oceanus* gives added incentive to these aims.

Scientists and technologists from other countries are always welcome to share in these research programs. In 1988, the Sixth International Coral Reef Congress will be held in Townsville as part of that year's bicentennial celebrations marking European settlement of the continent. In addition, the Great Barrier Reef Wonderland aquarium, designed to represent a microcosm of the actual reef, will be opened as a bicentennial project, also in Townsville. This issue of *Oceanus* is therefore most timely.

Acknowledgments

***Oceanus* magazine would like to thank the following organizations for their support of this issue: the American-Australian Bicentennial Foundation, Washington, D.C.; the Australian Marine Research Allocations Advisory Committee (MARAAC); the Great Barrier Reef Marine Park Authority (GBRMPA); the Australian Institute of Marine Science (AIMS); the Sir George Fisher Centre for Tropical Marine Studies; James Cook University of North Queensland; and Qantas Airlines.**

***Oceanus* also would like to thank Professor Michael Champ for his advice and help in producing this issue. Dr. Champ acted as co-editor. He is Senior Science Advisor at the Environmental Protection Agency in Washington, D.C., and was a Senior Queens Fellow in Australia in 1984/85.**

Windward margin, Redbill Reef, central Great Barrier Reef. (Photo courtesy of David Hopley)

The Pompey Reef Complex comprises some of the largest and most complex reefs in the whole of the Great Barrier Reef province. They are cut by narrow deep channels and contain numerous lagoons. (Photo courtesy of David Hopley)

The Evolution of the Great Barrier Reef

by David Hopley, and Peter J. Davies

The Great Barrier Reef is an immense, unique environment of global aesthetic and scientific significance comparable to any of the largest reef structures that have existed in the last 450 million years of the geological past. It is not a single reef, but a whole series of individual reefs and reef complexes occupying the Continental Shelf of northeastern Australia for a distance of 2,300 kilometers over 14 degrees of latitude. Reef waters exceed 230,000 square kilometers. Almost 9 percent of the area is occupied by reefs or submerged reef shoals.

Even within the area of the Great Barrier Reef Marine Park, which extends only to the tip of Cape York, there are 2,900 individual reefs, including 750 fringing reefs attached to the mainland or high continental islands (inclusion of the Torres Strait reefs would increase this figure by at least 30 percent). Quite clearly from size alone the Great Barrier Reef warrants the awe it has inspired since the first descriptions of the early explorers:

> *A Reef such as one I now speak of is a thing scarcely known in Europe or indeed anywhere but in these seas.*
>
> **—Joseph Banks on James Cook's voyage, 1770.**

However, the size and the morphological and biological diversity of the Great Barrier Reef is not matched by a lengthy geological history. Much of the reef is young—little more than 2 million years old. It has thus evolved during the Quaternary period when ice advances and retreats in higher latitudes caused major sea-level fluctuations, probably the most important single factor in the evolution of the Great Barrier Reef.

Morphological Diversity

Enormous regional diversity exists. Influence of varying geological structures beneath the shelf is probably paramount in producing macroscale regional patterns, but even the modern environment is sufficiently diverse to produce morphological contrasts. For example, the incidence and severity of tropical cyclones, the numbers of coral species, tidal range, and water temperatures vary from north to south. Equally important differences exist across the shelf in the form of freshwater runoff and sediments, and increasing influences of incursions of open ocean waters.

The northern region of the reef has developed on a narrow shelf, no more than 50 kilometers wide (Figure 1). Its most distinctive features are the linear or ribbon reefs running parallel to the edge of the Continental Shelf almost as far south as Cairns. The ribbons are up to 25 kilometers long and rarely more than 500 meters wide, are separated by narrow passes, and lie at the very edge of a steep Continental Shelf. Water depths exceed 1,000 meters within a few hundred meters of the outer reefs. Inside many of the ribbon reefs are large sand banks at depths of 20 to 40 meters. These have been built by the calcium carbonate secreting alga *Halimeda* (see pages 43, 45, and 49), which appears to have built structures equal in size to many of the coral reefs.

The middle shelf is occupied by large platform reefs with extensive reef flats, some up to 25 kilometers in length. Closer to the shore is a more open area of inner shelf, the main shipping channel where a number of small reefs capped by distinctive low, wooded (mangrove) islands are found.

In Torres Strait, the distinctive regional pattern breaks down. The middle section of the shelf is dominated by a mosaic of small reefs. Ribbon reefs become shorter, and eventually alter into complex splayed "deltaic" reefs with numerous passages, reflecting the influence of the strong area tides. A well defined line of larger reefs occurs northwards from Cape York, including the Warrior Reefs, with high seagrass-covered reef flats. Within Torres Strait, the reefs are aligned east-west in response to the high-velocity tidal currents.

As the Continental Shelf widens south of Cairns, the Great Barrier Reef occupies only the outer third of the shelf. Reefs are more widely spaced and generally have less well developed reef flats. Most reefs are irregular reef patches, or crescentic features aligned toward the dominant southeasterly tradewinds. Back reef areas and lagoons can be large, but are frequently dominated by sand. No ribbon reefs are found on the outer shelf, but recent research has defined a more or less continuous line of outer shoals rising from depths of about 70 meters. Only fringing reefs on the high continental islands are found on the inner shelf.

To the south, the Continental Shelf widens even further to about 300 kilometers. From about 20 degrees South, reefs increase in size, and, with an increase in tidal range (to more than 4 meters on even the outermost reefs in the Pompey Complex), narrow, well defined tidal channels up to 70 meters deep intersect the reefs. Even the innermost reefs are 100 kilometers from the mainland, but this is one of the most spectacular parts of the Great Barrier Reef. A series of submerged reefs occupies the shelf edge, but about 10 kilometers back is an area containing some of the largest and most intricate reefs up to 100 square kilometers in area. This is the Pompey Complex, stretching for 200 kilometers as a solid mass of reefs and lagoons 15 kilometers wide with narrow intricate channel systems. The southern extent of the Pompey Complex is a distinctive T-line junction of reefs to the south of which are the contrasting Swains Reefs, smaller flat topped reefs, closely spaced and with numerous sand cays. The tidal range on the adjacent mainland reaches 10 meters in Broad Sound, but declines rapidly seawards. The innermost reefs, however, still experience ranges of up to 6 meters, and this results in massive algal terraced rims that isolate internal lagoons nearly 3 meters above the level of the surrounding ocean at low tide.

South of the Capricorn Channel, the shelf narrows again to less than 100 kilometers. The Bunker-Capricorn Groups of reefs are the southernmost of the Great Barrier Reef, a series of 22 reefs and 11 shoals of only moderate size and with numerous vegetated cays. Corals do grow further south, but the southern extent of the reef is determined by the massive amounts of sand that cross the shelf south of Lady Elliott Island. This sand has moved northwards up the coast from southern Queensland and, as the coast and shelf change direction at about 25 degrees South, the sand crosses the shelf obliquely via Fraser Island and Breaksea Spit.

Origins of the Reef

In 1926, the first effective attempts to study the origin of the Great Barrier Reef were made by the Great Barrier Reef Committee when holes were drilled to 183 meters at Michaelmas Cay in the northern reef region. In 1934, holes were drilled on Heron Island in the south to 223 meters. At the time, these bores were considered disappointing as they did not achieve the intended objective of proving that Darwin's subsidence theory of coral reefs was applicable to the Great Barrier Reef. This objective clouded the interpretations of much crucial data in the cores.

Both holes bottomed in sands, but their significance was ignored as Darwin's theory demanded volcanics; reef was therefore thought to occur below the sands. The drill core from both holes indicated the presence of unconformities detectable on the basis of observation as well as geochemical data. The now accepted possibility of reef growth in superincumbent positions, many times producing what are now seen as unconformities related to sea-level changes, was not recognized.

However, the initiation of the Great Barrier Reef is related to the more recently developed ideas of continental drift and sea-floor spreading (see *Oceanus*, Vol. 22, No. 3). Until about 75 million years ago, Australia and Antarctica were joined. Most of Australia lay south of 40 degrees South, far from waters warm enough for coral growth. About 65 million years ago, Australia began to split from Antarctica and move northwards.

Subsequently, northeastern Australia was formed by rifting between the Australian and Pacific plates and, by the time a Continental Shelf had formed, northern Australia lay close to 30 degrees South latitude. Uplift, rifting, and volcanism produced a complex rift basin system that has controlled the location and form of the Continental Shelf.

As Australia continued to move north, the first development of ice in Antarctica caused worldwide falls in sea level. Recent seismic investigations have shown that shelf evolution was dominated by fluvial sediment yield (current annual sediment input from North Queensland rivers alone is estimated at 28 million tons). The relative height of sea level provided the principal control of development (Figure 2).

During periods of low sea level, alluvial processes affected the shelf. At the shelf edge fluvial and wave dominated deltaic progradation* took place into deeper water. During the high sea-level phases, sedimentation was generally restricted to coastal deltaic progradation into the shallow water of the inner shelf and onlap of the continental slope by submarine fans together with extensive upper slope erosion. This main phase of shelf construction from the late Oligocene to the Pleistocene (11 to 2 million years ago) produced about 10 kilometers of shelf outbuilding off Cairns and about 50 kilometers off Townsville, a sediment sequence 2.5 kilometers thick.

The seismic records, with the exception of the northernmost reef region, show a distinctive lack of reef growth. Initially, this can be attributed to Australia's latitudinal position and seawater temperatures too cool for coral growth, but subsequently high turbidity levels on the shelf during high sea-level periods may have produced conditions that were not conducive for reef building. Earliest reef development was restricted to the Gulf of Papua shelf area, which would have reached the warm waters of the tropics earliest. By early and middle Miocene times (12 million years ago), barrier reefs had developed at the edge of a carbonate shelf and platform reefs had developed on highs in front of the shelf. However, following uplift and erosion, they were rapidly buried by massive Pliocene to Recent tide-dominated deltaic progradation.

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* A seaward advance of the shelf resulting from the nearshore deposition of sediments brought to the sea by rivers.

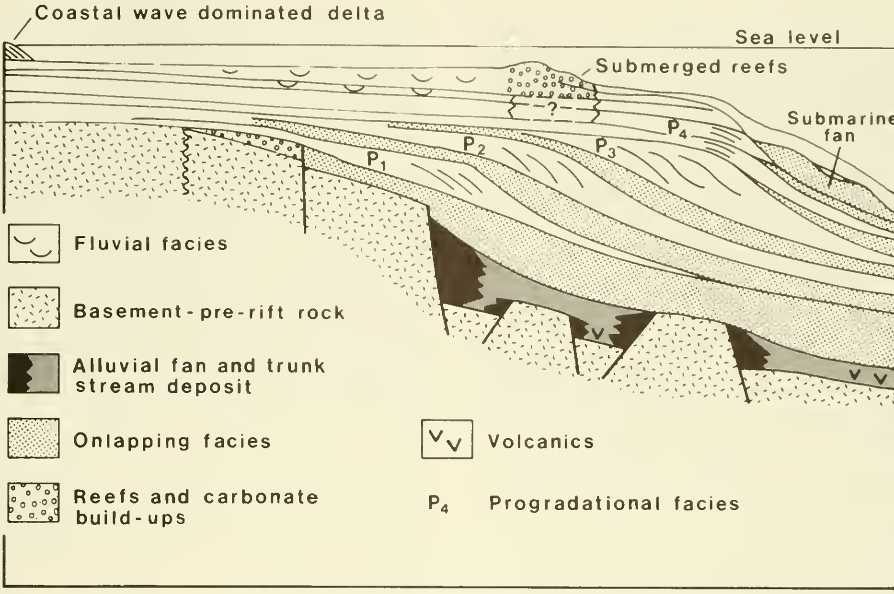


Figure 2. The types of depositional systems in the development of the shelf of the central Great Barrier Reef. (From Symonds and others, 1983)

To the south, the reef sequence is thin, less than 300 meters thick. It also is young, almost certainly less than 2 million years—that is, mainly Pleistocene in age and built during a period of rapidly fluctuating worldwide sea levels. Reef growth has occurred during short periods of high sea level. During the intervening periods of low sea level, the reefs were subaerially eroded. Continual recolonization of sites throughout their growth history has produced reefs that are composite features made up of a series of remnant reefs separated by unconformities.*

On a regional scale, there can be no doubt that basement structure has exerted a profound control on the development of major reef tracts. Mid-shelf reefs in the central and northern areas are coincident with a prominent mid-shelf fault line, although the reason is obscure. Further, the scattered reefs of the central Great Barrier Reef border the fault-controlled confluence of the Queensland and Townsville troughs. The ribbon reefs in the north occur at the shelf edge, the position of which is controlled by the western boundary faults of the Queensland trough. Further south, however, the seismic studies have shown that the drowned ribbon reefs did not develop along the paleoshelf break, but a few kilometers west of it. Shelf edge reefs in the vicinity today have formed their own shelf break feature through vertical growth. These also have modified upper slope deposition during periods of low sea level by funneling fluvio-deltaic sediments through gaps in the barrier reef, directly feeding upper slope canyons and depositing submarine fans on the middle and upper slopes.

* A surface of erosion or nondeposition, usually the former, that separates younger strata from older strata.

Sea-Level Changes and Reef Growth

Once established, the layer-cake structure of most reefs indicates that subsequent growth was usually on the older reef surface during high sea level phases. High sea levels approximating that of the present time have had a periodicity of about 120,000 years during the Pleistocene. Individual reef growth phases seem to have lasted from 4,000 to 14,000 years. Growth periods are clearly short compared to low sea level phases of subaerial destruction. Growth probably represents a maximum of 10 to 20 percent of time available. For the whole of the Quaternary, (1.8 million years) actual growth occurred for only 180,000 to 360,000 years.

The new reef veneer added at each high sea level was draped over the older reef, which would undoubtedly have undergone erosion while subaerially exposed. The original aragonite and high magnesium calcite deposits of the reef plants and animals are subjected to diagenesis* in the subaerial environment and revert to low magnesium calcite clearly detectable, for example, beneath the Holocene reefs at depths of between 4 meters and more than 30 meters below modern reef flat level. Soils and calcite stringers (horizontal layers of dense calcium carbonate produced by soil processes on limestone) also formed and also mark the position of each unconformity.

The reefs are limestone and their subaerial erosion has the potential to create karst landforms.** Up to 15 meters of reef may have been removed during the last low sea level period. Debate exists as to whether it is the karst erosional forms, such as

* The process involving physical and chemical changes in sediment after deposition that convert it to limestone.

** Marred by sinks, abrupt ridges, and channels.

enclosed solution depressions, that influence the morphology of the modern reef, or the shape of the earlier reef. In all probability both are important, and occasional "blue holes" up to 40 meters deep in the reefs attest to large scale karst collapse at least on a local scale.

Maximum lowering of sea level at the height of the last glaciation was about 150 meters. It is probable that, based on ice volumes in previous glaciations, this was close to the maximum glacio-eustatic lowering during the Pleistocene. Although the periods of absolute low sea level may have been even more restricted than the interglacial highs, they were important periods for reefs. World oceanic temperatures were reduced on average by about 2.3 degrees Celsius, enough to restrict coral growth only marginally. However, 150 meters of lowering of sea level places the majority of world coastlines on the slope of the Continental Shelf thus severely restricting the available area of shallow (less than 40 meters) water for reef growth.

Recent research submersible dives off the ribbon reefs near Cooktown have shown that from depths of 90 to 210 meters there exists an almost sheer wall on which no late Pleistocene reef growth could have taken place. Increased cave development in this wall between 130 and 150 meters depth may relate to the lowest sea levels. In another dive off Myrmidon Reef near Townsville, the slope at the critical 150 meters depth was 45 degrees and consisted largely of unconsolidated scree, or loose rock debris, which would provide too unstable a substrate for reef growth. Apart from very restricted local refuges, it has been hypothesized that the major larval replenishment areas for recolonization of the Great Barrier Reef during the post-glacial transgression may have been the banks of the Coral Sea plateaus. This could have played a part in the delay between submergence of the older reef foundations and initiation of Holocene growth.

Reef Growth During the Holocene

The rapid rise in sea level that accompanied the melting of northern hemisphere ice sheets resulted in the margins of the Great Barrier Reef shelf being inundated 12,000 years ago. Most older reef foundations were submerged 8 to 9,000 years ago, when sea level was rising at a rate of 7 to 10 meters per 1,000 years. Because of isostatic responses, details of sea level change are regional in pattern and modern sea level had been achieved on the Great Barrier Reef by about 6,500 years Before Present (BP), some 6,000 years earlier than for Caribbean counterparts.

The modern reefs have thus had time to grow up to present sea level. The thicknesses of Holocene growth varies from as little as 5 meters in the northern region reef to 8 meters on southern reefs, and generally greater than 20 meters on the central Great Barrier Reef. Considerable detail is available for this latest phase of reef growth from a data base collected by the authors during the last 10 years. The data base consists of more than 100 drill holes in 30 reefs and more than 300 radiocarbon dates.

Five major biologic-sedimentary associations comprise the Holocene reef: coralline facies, coral head facies, branching coral facies, rubble/sand facies, and terrigenous facies (Figure 3). Windward margins of reefs show regional variation. In the Cooktown region, both branching and coral head facies occur on inner and outer shelf reefs. In the central reef, coral head facies dominate particularly in midshelf and fringing reefs, although on outer shelf reefs both branching and head corals occur. In the southern region, branching corals dominate all windward margins except at One Tree Reef where a mixed branching-head assemblage occurs. Throughout the Great Barrier Reef the coralline facies occurs as a crust on framework facies, particularly in the upper 50 centimeters of reef.

Reef flat areas today are dominantly mixed branching-head assemblages and have developed as such throughout their history, although in some examples a lower branching facies is replaced upwards by a head facies. Leeward margins have been dominated by branching framework facies throughout their growth history.

The fabric of the midshelf reefs of the central Great Barrier Reef is quite different to that of reefs in higher energy areas. They are dominated by detrital facies of sands, coral gravel, stick shingle, rubble, and storm boulder beds. Some reefs are little more than detrital piles with coral caps. Terrigenous facies are limited to the fringing reefs and are normally minor components.

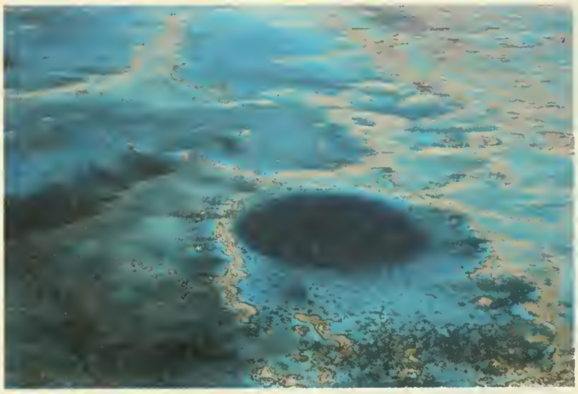
Vertical accretion rates vary with facies type, location of reef (inner, mid or outer shelf) and location on reef. The modal rate for framework accretion is 7 to 8 meters per 1,000 years, but higher rates, up to 16 meters per 1,000 years are associated with open branching coral framework and generally lower rates for head dominated facies. Lowest rates of about 2 meters per 1,000 years are associated with coralline algae. Depositional rates for detrital carbonate facies vary from 1 to 4 meters per 1,000 years for sand flat progradation to 13 to 18 meters per 1,000 years for deposits associated with high-energy, low-frequency events.

Despite the wide range of depths to the pre-Holocene reef substrate, initiation of growth ubiquitously appears to have been between 8,300 and 8,500 years BP, with earliest growth normally on the windward margins. This means that water depths of up to 20 meters existed over the reefs as they grew upwards, although the greater the depth the more optimal were the conditions for growth, as fastest accretion rates are recorded for such reefs. Thus, once sea level stabilized about 6,500 years ago, reefs quickly caught up with sea level and the majority were within 2 meters of modern sea level between 6,500 and 4,500 years BP. In the final approach to sea level, particularly where coralline or head facies become dominant, the rates of accretion slowed down significantly, possibly reflecting a decrease in calcification accompanying environmental change or a physical loss of calcium carbonate in the high energy surface environment.

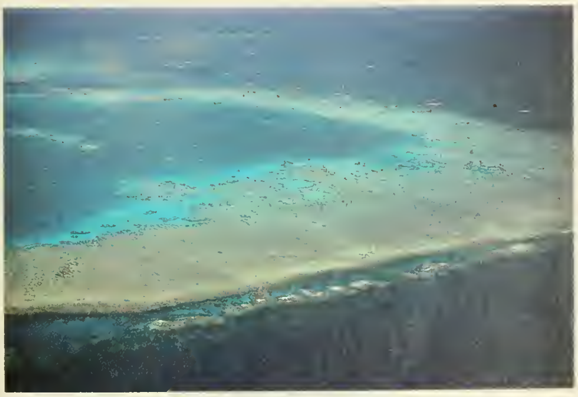
The outer edge of the northern Great Barrier Reef has an almost continuous line of linear ribbon reefs rising from oceanic depths of 1,000 meters or more. These are generally narrow and have been at sea level for at least 5,000 years. Sediment is swept from the reef top towards the lee side where a significant sand slope can be seen. (All photos this page courtesy of David Hopley)

The southern end of the Pompey Complex, showing the deltaic-like pattern of channels that cut through these massive reefs.

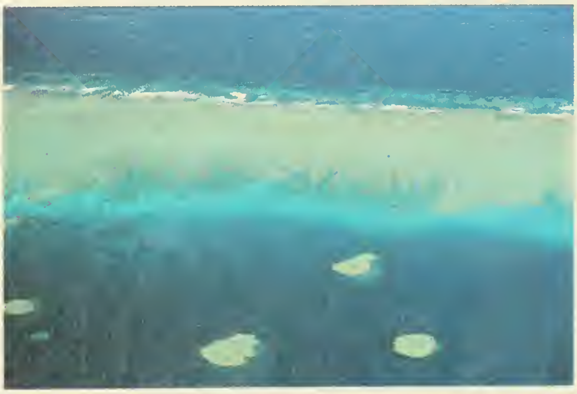
In the northern region, the reefs closest to shore are often capped by low wooded islands. These consist of shingle ridges around the windward margins that give protection for the growth of reef flat mangroves. Small sand cays are frequently found to the lee side. This example is Low Isles near Cairns.



An almost circular blue hole on Molar Reef in the Pompey Complex formed by the collapse of a subsurface cavern developed by karst solution processes during Pleistocene low sea levels.



A further example of the open, crescentic type reefs of the central Great Barrier Reef. This example, Centipede Reef near Townsville, has a secondary reef front and a deep lagoon with a sand slope on the leeward side of the windward edge.



As the reef develops at sea level and grows horizontally, it commences to develop a zonation in response to the refracted wave fronts. In particular, sediments are swept from the productive windward margins toward the lee of the reef.

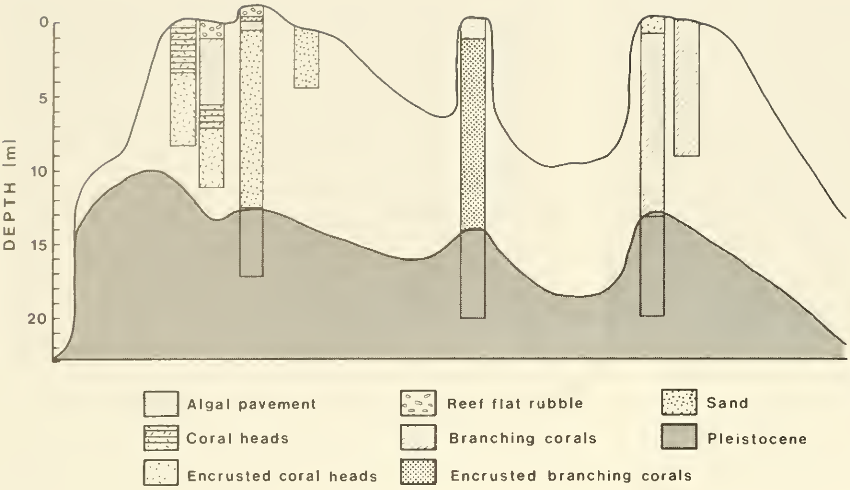


Figure 3. The distribution of One Tree Reef facies. (from Marshall and Davies, 1982)

The Final Details

For most of the Great Barrier Reef, sea level has not varied significantly for the last 6,500 years. Only on the fringing reefs of the inner shelf is there evidence of a slightly higher (+ 1 meter) sea level. The reefs that grew up to sea level 6,500 to 4,500 years ago thus have had time to develop significant horizontal growth expressed in the extension of reef flats.

Surface zonation* is a reflection of growth at sea level. The coralline rim in windward margins is usually only 50 centimeters thick and is a response to high physical energy. The mixed coral assemblages of the coral flat are likewise responses to energy conditions, with the alignment of the corals into "windrows" in this zone a response of growth to the direction of energy dissipation.

A major effect of growth at sea level is reef destruction, resulting in production of sediment and its deposition as shingle banks, cays, prograding sand flats, lagoon infills and leeside tails. These accumulations result from erosional transport and depositional processes associated not only with the ambient southeasterly conditions, but also with tropical cyclones. The end result of growth at sea level is modification of the original zonation through sedimentary infill, secondary coral growth as microatolls in moated reef flat locations, and ultimate loss of zonation. Finally, significant growth may be confined only to the reef margins.

Conclusions

Although comparatively young, geologically, the Great Barrier Reef contains such a diverse range of environments that it may provide the model for development, maintenance and management of continental shelf reef systems on a global scale. Until approximately 10 years ago the relatively small amount of information available on reef development came largely from locations outside the Great Barrier Reef province. Work in the last 10 years has drastically changed this situation and although many questions remain unanswered, an understanding of the reef as a complex geological system is closer. Recognition that the reef is dynamic, not just during periods of rapid environmental fluctuation such as sea-level changes, but during for example the last 6,500 years of relative sea-level and climatic stability, is important for a more complete understanding of ecology, and as the basis for management.

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Selected Readings

Davies, P. J. 1983. Reef growth. In Barnes, D. J. (ed.) *Perspectives on Coral Reefs*. Aust. Inst. Mar. Sci., 69–106.

Davies, P. J. and D. Hopley. 1983. Growth facies and growth rates of Holocene reefs in the Great Barrier Reef. *B.M.R. J. Austr. Geol. and Geophys.*, 8, 237–251.

Davies, P. J., J. F. Marshall, and D. Hopley. 1985. Relationship between reef growth and sea level in the Great Barrier Reef. *Proc. 5th Inter. Coral Reef Symp.*, 3, 95–103.

Hopley, D. 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. Wiley-Interscience N.Y., 453 pp.

Marshall, J. F. and P. J. Davies. 1982. Internal structure and Holocene evolution of One Tree Reef, southern Great Barrier Reef. *Coral Reefs*, 1, 21–28.

Symonds, P. A., P. J. Davies, and A. Parisi. 1983. Structure and stratigraphy of the Great Barrier Reef. *B.M.R. J. Austr. Geol. and Geophys.*, 8, 277–291.

* The condition of being arranged or distributed in bands or zones, generally more or less parallel to the bedding.

Figure 1. Map of Great Barrier Reef.

The four research stations referred to on page 116 are highlighted in red.
(Courtesy of David Hopley and Great Barrier Reef Marine Park Authority)

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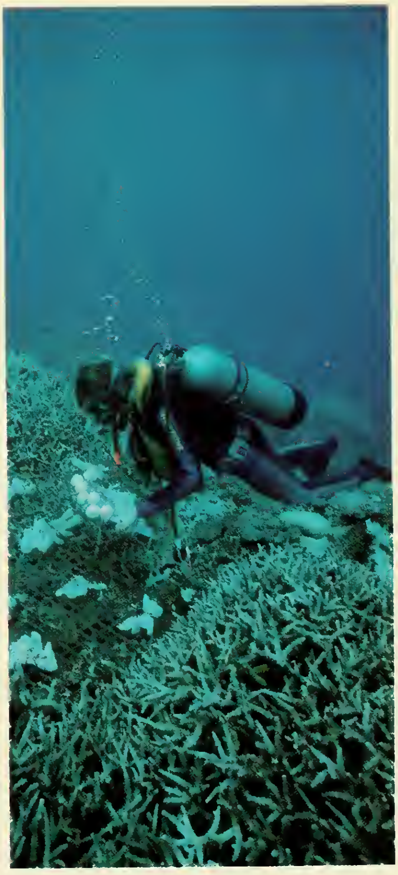


TORRES STRAIT
GULF OF
CARPENTARIA
Warrior Rf
Darnley Is
PAPUA
NEW GUINEA
C York
Murray Is
145° 00' E
10° 41' S
FAR NORTHERN SECTION
Cockburn Rf
C Grenville
Sir Charles Hardy Is
Temple Bay
Gallon Rf
Forbes Is
North Eel Rf
Quoin Is
C Weymouth
C Direction
BLIGH ENTRANCE
N
0
100
200 km
Magpie Rf
Hedoe Rf
Corbett Rf
13° 00' S
LOCALITY MAP
Princess
Charlotte
Bay
Flinders Group
Pipon Rf
C Melville
Osprey Rf
Lizard Is
Three Isles
Ribbon Rf
C Bedford
146° 00' E
15° 00' S
COOKTOWN
GREAT
MOSSMAN
Bougainville Rf
CAIRNS
Green Is
CAIRNS SECTION
CORAL SEA
Holmes Rf
147° 00' E
17° 30' S
Hinchinbrook Is
Barnett
Patches
Willis Group
Herald Cays
Orpheus Is
GREAT
BARRIER
Flinders Rf
South West Is
TOWNSVILLE
Davies Rf
BARRIER
CENTRAL SECTION
10°
145°
10°
15°
150°
15°
145°
20°

CENTRAL SECTION
Lihou Reef and Cays
BARRIER REEF MARINE PARK BOUNDARY
REEF
BOWEN
Hardy Rf
Hook Rf
Whitsunday Islands
C Conway
Cumberland Group
MACKAY
Redbill Is
Northumberland Group
Marion Rf
CAPRICORN SECTION
POMPEY COMPLEX
Broad Sound
Shoal Water Bay
152° 55' E
21° 00' S
20°
Frederick Rf
Saumarez Rf
155°
ROCKHAMPTON
SWAIN REEFS
CAPRICORN CHANNEL
Heron Is
One Tree Is
Hoskyns Rf
GLADSTONE
Wistari Rf
25°
CURTIS CHANNEL
CAPRICORNIA SECTION
BUNKER CAPRICORN GROUP
Lady Elliott Is
150°
BUNDABERG
Fraser Is
Tropic of Capricorn
154° 00' E
24° 30' S
25°
155°

Managing The Great Barrier Reef

by Graeme Kelleher

How complex and unexpected are the checks and relations between organic beings, which have to struggle together in the same country.
—Charles Darwin, 1882.

Australia has a federal system of government. The complex relations between the federal and state governments and their agencies are determined in accordance with the provisions of a written constitution, which was adopted when the six independent colonies became Australia on federation in 1901.

This constitution specifies the functions and powers of the federal and state governments and provides, as does the U.S. Constitution, that residual powers and responsibilities—those which are not expressly provided for in the constitution—lie with the states.

Before federation, the Great Barrier Reef was administered by the colony of Queensland. After federation, this arrangement continued largely unchanged, except that the federal government was given the responsibility for fisheries beyond the 3-mile Territorial Sea and for navigation.

Serious conflict on and about the reef and its management first arose in the 1960s when the people of Australia became aware of, and objected to, proposals to drill for oil and to mine limestone. The ensuing controversy disclosed that the reef was treasured by many Australians for its uniqueness, biological diversity, beauty, and grandeur. The successful management of the reef depends primarily on maintaining and encouraging these values in the hearts and minds of Australians.

The Great Barrier Reef

The Great Barrier Reef is the largest system of corals and associated life forms anywhere in the world. It is encompassed in a Marine Park within the Great Barrier Reef region, covering an area of about 350,000 square kilometers on the Australian continental shelf—larger than the land mass of the United Kingdom. The reef stretches for more than 2,000 kilometers along the northeastern coast of Queensland in a complex maze of approximately 2,600 individual reefs, ranging in area from less than 1 hectare (2.5 acres) to more than 100 square kilometers. In the north, the reef is narrow and its eastern edge is marked by a series of narrow "ribbon" reefs, but in southern areas it broadens out and presents a vast wilderness of "patch" reefs, many in the shape of a boomerang.

The reef is diverse not only in the form and size of its individual reefs and islands, but in its inhabitants. Six species of turtle occur in the region and it is believed that there are more than 1,500 species of fishes. The reef may be the last place on earth in which dugong (*Dugong dugon*—an endangered species) are still common and not in jeopardy.

About 350 species of hard coral have been identified on the reef and the islands are inhabited or visited by more than 240 species of birds.

Human Use of the Reef

Commercial fishing and tourism, recreational pursuits—including fishing, diving, and camping—aboriginal fishing, scientific research, and shipping all occur within the reef region.

Tourism is the largest commercial activity in economic terms. In 1983-84, there were an estimated 140,000 visitor trips to the 24 island resorts in the region, resulting in 660,000 visitor nights spent at the resorts, along with some A$60 million. Resort guests make extensive use of reefs and waters for recreational activities, including fishing, diving, and snorkeling, water sports, sightseeing, reef-walking, and some shell collecting.

The popularity of the reef and adjacent coast region as a tourist destination increased 40-fold during the period from the 1940s to 1980 and is continuing to increase. Recently, interest has been expressed in building hotels directly on reefs. The last five years have seen the introduction of several large, stable, high-speed catamarans that provide day trips to islands and outer reefs.

There is conflict between the various users of the reef and those who wish to see it maintained in its pristine state forever. Some uses of parts of the reef have already reached levels that appear to exploit fully the productive capacity of the system—bottom trawling for prawns, for example. Run-off from islands and the mainland contains suspended solids, herbicides, pesticides, nutrients, and other materials. They must have effects on the reef, but the magnitude of the effects is not yet known.

This description also applies to other reef systems throughout the world's tropical seas. The difficulties of managing uses of an ecosystem "forever" are common to other reef systems. Perhaps the system of management that has been developed on the Great Barrier Reef could be applied elsewhere, although the acceptability of any management system is likely to be diminished where there are very high levels of usage and economic dependence on reef areas—for example, in many parts of Asia.

Legislation and Administration

In 1973, Australia's federal Parliament passed the *Seas and Submerged Lands Act*, which established federal jurisdiction over, and title to, the seabed below low-water mark outside state internal waters. This act was challenged by some of the states, but its constitutional validity was upheld by the High Court in 1975.

Also in 1975, the federal Parliament passed, with the support of all political parties, the *Great Barrier Reef Marine Park Act*. This act provides the legal basis for management of the reef. It has some novel and critically important provisions in relation to the establishment, control, care, and development of a marine park in the region. They include:

- *Establishment of the Great Barrier Reef Marine Park Authority, consisting of three members, one nominated by the Queensland government and two by the federal government. The Authority has a staff of about 70, most of whom are headquartered in Townsville.*
- *Establishment of a Consultative Committee—at least a third of its members nominated by Queensland, two-thirds by the federal government, with one Authority representative.*
- *Specification of the Authority's functions—recommending areas to be included in the Marine Park, carrying out or arranging for research, preparing zoning plans, the establishment of education and management programs, and anything incidental to these functions.*
- *Giving the Authority power to perform its functions in co-operation with Queensland or its agencies.*
- *Prohibiting drilling or mining in the Marine Park, except for approved research purposes.*
- *Providing that the Act, and zoning plans and regulations made under it, prevail over conflicting provisions of all state legislation and all federal legislation, except in relation to the navigation of ships and aircraft.*

The Authority was established, and continues to operate, in a situation of controversy regarding federal and state powers and rights in the Territorial Sea, within which lies a large part of the Great Barrier Reef.

No other state of Australia is bordered by reefs approaching the size, diversity, and splendour of the Great Barrier Reef. The reef is regarded by most as a national asset and by many as an international asset. Many Australians, including scientists, demand that the federal government retain a dominant role in the management of the reef. Others, not all in Queensland, maintain that management of the reef, including the islands, should be carried out by the state government. Constitutionally, the Queensland government has responsibility for all the islands within the outer boundaries of the reef region above low-water mark, except for those few that are owned by the federal government. The latter, and all the waters, reefs, and shoals below low-water mark are the responsibility of the federal government.

Australia has a democratic system of government, and action by the government is frequently in response to public pressure. Much that has been done so far to protect and manage the reef has resulted from this process. Because many of the pressures have been conflicting, as in all controversial public areas, government action has involved compromise.

The essence of the compromise has been for the federal government to maintain over-riding power in the region, while involving Queensland co-operatively in all aspects of the establishment and management of the Marine Park. The Queensland National Parks and Wildlife Service carries out day-to-day management of the Marine Park for the Authority. The service also is responsible for management of most of the islands in the reef region. The two governments have agreed to manage adjacent areas on a complementary basis.

This arrangement recognizes that the islands, reefs, and waters of the reef are a continuum, and should be managed accordingly. The compromise has been reflected in the creation and composition of a Ministerial Council, which coordinates the policies of Queensland and the federal government on the reef, the Authority itself, and the Consultative Committee.

The Authority

The Great Barrier Reef Marine Park Authority (GBRMPA) has derived a primary goal and a set of aims from the provisions of the Act and recognition of the political, legal, economic, sociological, and ecological environment in which it operates.

The Authority believes that any use of the reef or associated areas should not threaten its essential ecological characteristics and processes. Activities depending on the reef's renewable resources should generally be held at or below maximum sustainable intensities indefinitely. This

People collecting on the rocky edge of Hardy Reef. (Photo courtesy of GBRMPA)

The Lizard Island resort, one of the fashionable tourist areas on the Great Barrier Reef. (Photo courtesy of GBRMPA) belief has led the authority to adopt the following primary goal:

> *To provide for the protection, wise use, appreciation, and enjoyment of the Great Barrier Reef in perpetuity through the development and care of the Great Barrier Reef Marine Park.*

If the reef is to be protected, more than the physical aspects of the reef need to be considered. Administrative arrangements also must be durable. In Australia, the major determinant of administrative survivability of organizations like the Authority is public support. In the long run, government support flows from it. Recognizing that the Authority and the Marine Park concept already have a degree of public support, the Authority must act in ways that sustain or increase that support. What are those ways? It seems clear that the ground work has been well established in the Act through the formal requirements for public participation, the provisions for a Consultative Committee, the composition of the Authority itself and its functions, as well as the ability to perform those functions in association with Queensland or its agents.

Generally speaking, the public is likely to continue to support the Marine Park and the Authority if the primary goal is perceived as being achieved efficiently. For this to occur, the public will have to be aware of what the Authority and its day-to-day management agencies are doing and the way they are doing it, the effectiveness and costs of their programs and the reasons for them, and, to the extent practicable, to be involved in the establishment and management of the Marine Park.

The Park and the Zoning System

The Great Barrier Reef Marine Park is a multiple-use protected natural area, fitting the definition of Category VIII of the classification system used by the International Union for the Conservation of Nature and Natural Resources (IUCN). It also meets the criteria for selection and management as a Biosphere Reserve (Category IX), although it has not been formally proposed or established as one. The reef has been inscribed on the World Heritage List as a natural site (Category X).

The concept of zoning was introduced as the best solution to resolving the dual goals of preservation and multiple use by possibly conflicting activities. Through the use of zoning, conflicting activities are separated, areas are provided that are suitable for particular activities, and some areas are protected from use. Levels of protection within the park vary from almost complete absence of restriction on activity in some zones, to zones within which almost no human activities are permitted. The only activities that are prohibited throughout the park are oil exploration, mining (other than for approved research purposes), littering, spearfishing with SCUBA, and the taking of large specimens of certain species of fish.

In the zoning plans that have been developed so far, there are three major categories. They are:

- ***Preservation zones*** *and* ***scientific research zones*** *(equivalent to IUCN Category I, Scientific Reserve/Strict Nature Reserve). The only human activity permitted is strictly controlled scientific research.*
- *Three marine* ***national park zones*** *(equivalent to IUCN Category II, National Park). The major uses permitted are scientific, educational, and recreational.*
- *Two* ***general use zones*** *(equivalent to IUCN Categories IV, Managed Nature Reserve, and VI, Resource Reserves). Uses are held at levels that do not jeopardize the ecosystem or its major elements. Commercial and recreational fishing are generally permitted, although bottom trawling is prohibited in one of these two zones.*

The zoning plans for the Cairns and Cormorant Pass sections of the Great Barrier Reef Marine Park cover an area of 35,000 square kilometers. The zones are fixed during the life of a zoning plan (generally five years). They are complemented by generally smaller areas that give special protection from time to time to animal breeding or nesting sites, to sites in general use and other zones that are required to be protected to allow appreciation of nature — free from fishing or collecting, and to sites suitable for scientific research.

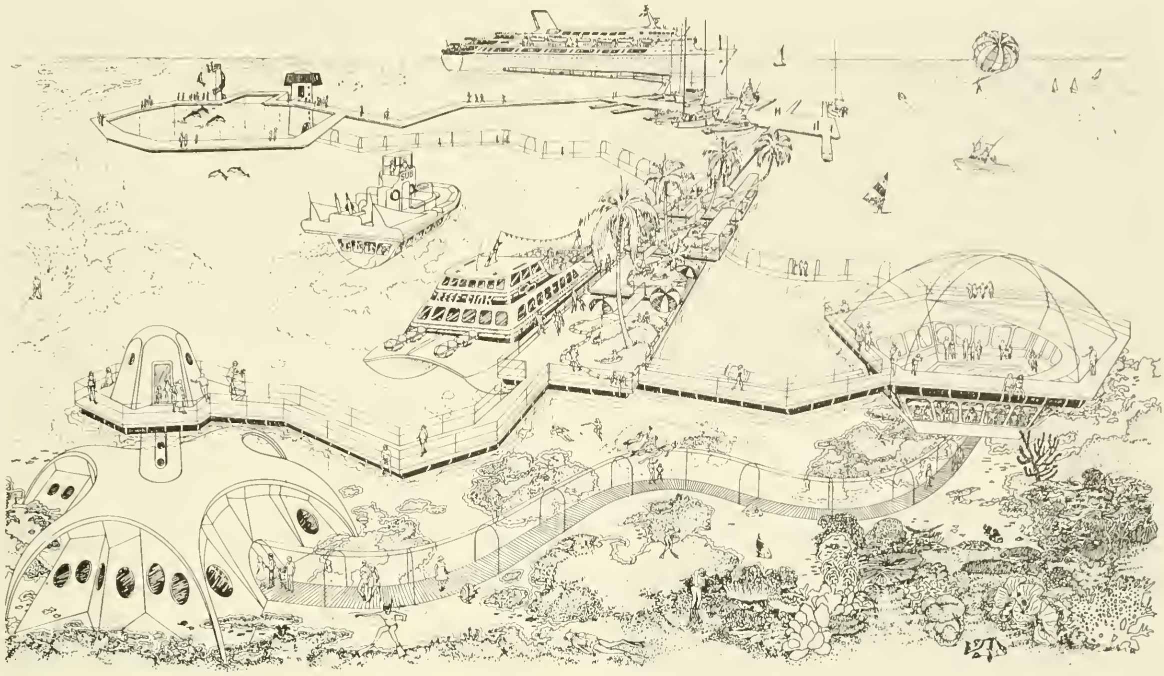
The authority is progressively developing zoning plans for sections of the Marine Park. We expect the whole area to be zoned by Australia's Bicentenary in 1988. Intensive and extensive consultation with the general public and interest groups will continue to be a feature of the process.

Zoning and Managing the Park

There are two principal categories of information that are critical to making a zoning plan and managing the park. These are:

- *Resource Analysis—measuring and gaining an understanding of the systems that make up the Great Barrier Reef region, and, particularly the area under consideration. The aims are to compile an inventory of the physical, chemical, biological, human, and human-built resources; to identify processes; and to develop theoretical models that will enable the processes occurring within the area to be described, and will allow the authority to make intelligent zoning and management decisions.*
- *Analysis of Use—defining the uses of the area: their physical, chemical, and biological effects, their value and economic importance; and measuring their intensity and distribution. The aim also is to predict future levels of use and their potential effects.*

In preparing to make a zoning plan, both categories of information are compiled on transparent overlays. The base is an accurate map of the section of park being zoned. The map shows the location and shape of all reef and non-reef



Public participation and recreation is central to management goals. Several components in this conception of a recreational facility already exist (sub, Reef Link, boardwalk) on John Brewer Reef.

structures to international cartographic standards of accuracy.

The ability to produce such accurate maps over such a large area is something of a technological triumph. Collaboration between the Authority and the Water and Land Resources Division of the Commonwealth Scientific and Industrial Research Organization (CSIRO) has resulted in the ability to produce such maps from Landsat data, with very little ground control (see page 90). Cost savings over conventional survey methods are estimated to be A$21 million for the Authority.

The resource information included on overlays comprises: distribution of fish and benthic reef communities; dugong feeding grounds; turtle nesting sites; significant land and water bird breeding colonies; mangrove and seagrass communities; and historic shipwrecks.

The usage information included on overlays comprises: distribution of potential and actual trawling areas for prawns, scallops, crayfish and crabs; location and extent of areas for pelagic (open water) fisheries; location and extent of areas for demersal (bottom living) fisheries, both commercial and recreational; areas where gill, drift and bait netting occurs; areas where collecting of coral, shell, and aquarium fish occurs; spearfishing areas; diving areas where scientific research is conducted; tourist resorts, camping areas and possible offshore developments; charter vessel and aircraft operating and landing areas; navigation, shipping and defense areas; and adjacent land use (national parks, aboriginal reserves, agricultural areas, industrial or urban development).

The aim of zoning and management is to provide for reasonable use of the Marine Park consistent with conservation of the reef's natural qualities. Reasonable use is taken to mean a usage level that can be sustained forever.

Experience has shown that in many cases it is not difficult to decide on the most appropriate zoning for individual reef and inter-reef areas. The combination of their natural qualities, location, and present and predicted usage patterns often makes the choice obvious.

An initial draft zoning plan is drawn up on this basis and goes through many modifications and adjustments before it is approved by the Authority for release to the public for review.

The final zoning plan takes account of public comments on the draft, as well as reactions from government departments and agencies. Of course, it would be naive to expect universal acclaim of a plan — such as the completed zoning plan for the Cairns Section — by all users, but it has been in effect for two years and has received a high degree of public acceptance.

The authority takes great care to avoid inadvertently over-riding the provisions of other legislation, whether state or federal, in making a plan. It is equally careful not to interfere with people's freedom unnecessarily or excessively. The justification for any restriction must be clearly specified in terms of the objectives of a zoning plan and the authority's guidelines, goals, and aims.

Research and Monitoring

Adequate knowledge of the baseline (or reference)

Fishing fleet in port. (Photo courtesy of GBRMPA)

ecological characteristics of the reef is essential to monitor the changes wrought by man's activities. It also is necessary to be able to roughly predict the type and scale of effect likely to be produced by individual activities and combinations of them, so that the intensity and distribution of usages can be controlled—but not overcontrolled—in a manner compatible with the conservation of the reef's natural qualities.

The authority carries out, or funds, a comprehensive research program in order to manage the reef on the basis of knowledge. There are three general areas of research (Table 1)—two of them, resource analysis and analysis of use, are necessary for supporting zoning and management decisions. The third—information management—is concerned with research leading to the development of information systems that will allow data to be stored and managed efficiently so that it can be used in decision-making and in research and education.

Oceanography

The basis of understanding the reef's processes can fairly be attributed to studies in physical oceanography. Knowledge of year-round water quality characteristics throughout the region, and of the small- to large-scale water movements that transport chemicals, nutrients, and living organisms is necessary if we are to understand, and manage the reef. The Authority is cooperating with other research institutions in a physical oceanographic research program that is aimed at developing a computer-based predictive model of the hydrodynamics of the reef region. Such information is critical to zoning.

The extent to which activities that can take place at one area within one zone can be regarded as isolated from other zones must be determined. The linkages within marine environments tend to be much more significant than those in terrestrial environments. Largely through tidal and wind driven currents, the water mass is constantly moving in three dimensions. The water mass brings nutrients and recruits to the fauna and flora of the reefs. These are essential inputs. In developing a concept of zoning, the critical issue may thus be the extent to which reefs can be regarded as interconnected.

Of course, physical oceanographic knowledge is useful only if it is complemented by appropriate ecological knowledge. There has been significant government expenditure in reef research in the last two decades and this is continuing. A large part of current research is ecological or biological in nature.

The authority has developed a complex web of arrangements with marine research agencies to ensure that necessary studies are carried out by the most appropriate agency and that the authority and other institutions are aware of all relevant research information, including research in progress.

Table 1. Research programs of the Great Barrier Reef Marine Park Authority.

CATEGORY	PROGRAM
Resource Analysis	1. Bathymetry and Survey 2. Oceanography 3. Marine Geology 4. Marine Chemistry 5. Marine Ecology
Analysis of Use	6. Inventory of Uses 7. Impact of Uses 8. Management Strategies 9. Environmental Design
Information Management	10. Great Barrier Reef Data Bases 11. Mechanics of Information Transfer

Policies of the Authority

The Great Barrier Reef Marine Park Authority and its programs are acceptable to most sectors of the community because they are seen to be reasonable and to avoid unnecessarily restricting the use and enjoyment of the Great Barrier Reef. Without public acceptance, the Authority and its programs would be in jeopardy. But there is another factor contributing to the success of the Marine Park system. The Authority has a set of policies which, in my view, greatly contribute to the system.

Decisions about zoning and management are taken, and will always have to be taken, in the absence of complete knowledge. Nevertheless, our policy is to base decisions as far as possible on scientifically-derived information. To this end, we play a major role in the identification, coordination, establishment, and use of scientific studies directed toward answering management questions. Our experience has been that much can be accomplished without great expenditure of money.

The Authority does not make decisions lightly that adversely affect existing commercial or amateur activities. If those activities are already consistent with conservation of the reef, then the authority is likely to take decisions that support them and which prevent them from becoming destructive. As an example, we assist tourist operators in the development of activity programs that are conservationally and educationally focused for visitors.

The Authority is a small agency, and wishes to remain so. To the maximum extent practicable, we work through other agencies and with their officers. There are several reasons for this. We believe that the flexibility and efficiency of an organization tends to diminish with increasing size. We do not expect the public to be impressed by an agency which grows endlessly, absorbing vast sums of public monies.

The public is not interested in bureaucratic power struggles or in squabbles about precise boundaries of jurisdiction. It is interested in using and enjoying the Great Barrier Reef Marine Park, free from conflicts with other users and government officers. The Authority's policies are designed to achieve that situation, consistent with the primary aim of conservation.

Conclusion

The Great Barrier Reef is unique, and the commitment of the Australian people to its conservation is great. This commitment has led to the establishment of legislation and a management system in which *conservation* is the dominant theme, with reasonable use of the reef's resources being encouraged. The public participates in decision-making, and is to a degree self-regulating. The Authority acts as the trustee of the Great Barrier Reef, on behalf of the people of Australia.

How applicable is the system to the management of marine (or terrestrial) resources in other places? Probably much of the methodology could be applied with success in many parts of the world. However, it should be recognized that limitations on economic activities and on the actions and powers of influential private and government interests are essential if application of the system is to achieve conservation. Therefore, a strong public and government commitment to sustainable use of a natural resource would appear to be a necessary prerequisite to successful application of the system anywhere.

Graeme Kelleher is Chairman and Chief Executive of the Great Barrier Reef Marine Park Authority, a post he has held since 1979. He holds a degree in civil engineering from the University of Sydney and was awarded a Churchill Fellowship in 1971 to study environmental engineering and management in Canada and the United States. He has had wide experience in formulating and implementing the environmental policies of the Australian government.

Selected References

Darwin, Charles. 1882. *The Illustrated Origin of Species*. 1979. Melbourne, Australia: Oxford University Press.

Nomination of the Great Barrier Reef by the Commonwealth of Australia for inclusion in The World Heritage List. 1981. Prepared by the Great Barrier Reef Marine Park Authority.

Bertram, G. C. L. 1979. Dugong numbers in retrospect and prospect. In The Dugong, proceedings of a seminar workshop held at James Cook University 8–13 May, ed. by H. Marsh. Townsville: James Cook University.

International Union for the Conservation of Nature and Natural Resources Areas. 1982. *Categories, Objectives, and Criteria for Protected Areas*.

Harding, G., and J. Baden, eds. 1977. *Managing the Commons*. San Francisco: W. H. Freeman.

Recreational fishing is one use of the Great Barrier Reef Marine Park. (Photo courtesy of GBRMPA)

Commercial trawling for fish in the reef waters. (Photo courtesy of GBRMPA)

Green turtles mating. (Photo courtesy of GBRMPA)

Reef Metabolism

by David J. Barnes, Bruce E. Chalker, and Donald W. Kinsey

Coral reefs are structures that encompass many habitats, sheltering a huge diversity of organisms. The reef structure is created by a relatively few, simple organisms, which leave a skeleton of calcium carbonate, commonly known as limestone. Only in warm, essentially tropical, seas are these organisms able to calcify faster than the physical, chemical, and biological forces working to disperse the limestone the organisms create.

The organisms that calcify fast enough to create coral reef structures are either plants, or animals that have developed a symbiotic relationship with single-cell algae. The symbionts in reef-building animals are dinoflagellate algae, often referred to by the name of zooxanthellae. In all of the rapid calcifiers of coral reefs, photosynthesis by the plant leads to significantly increased rates of calcification. Thus, the development and maintenance of reef structure depends on photosynthesis—which in turn depends on light. Consequently, reef development is limited to relatively shallow water (essentially down to 200 feet) in tropical seas.

Shallow, tropical seas are relatively low in organic nutrients, and photosynthesis within reef boundaries appears to provide the bulk of the organic carbon required to sustain the organisms living on and within reef structures. Coral reefs have one of the highest rates of primary production of any natural ecosystem. Still, the daytime primary production is only just sufficient to sustain the requirements of the huge numbers and varieties of coral reef organisms over a whole day.

Measurements

Despite the complexity of reef structures, communities, and ecology, it is possible to make relatively simple measurements that explain how these elements are maintained and sustained. Such measurements are often referred to as measurements of reef or community metabolism. Although, in a strict sense, a reef or community does not have a metabolism, it is possible to determine the rates at which materials are imported, used, turned over, and exported. Coral reefs have proved very amenable ecosystems in which to make such measurements. There are several reasons for this. First, they have such sharp boundaries that it is easily possible to define input and output. Second, inputs and outputs must be through the overlying seawater, and they are so large that, in shallower areas, they measurably alter that seawater. Third, the shape of many reefs is a response to the prevailing weather conditions, the consequence is often that seawater approaches, crosses, and leaves them in a relatively simple, mostly single direction fashion. It is then possible to measure alterations in the chemistry or content of seawater flowing across a coral reef.

Sampling of seawater upstream and downstream as it crosses a shallow coral reef area is often known as flow respirometry. The name derives from work in rivers and streams where upstream and downstream sampling was first used. Indo-Pacific coral reefs are most amenable to flow respirometry-based measurements of community metabolism. This is because, compared to Atlantic coral reefs, they have wide areas of shallow reef flat that face into the prevailing weather. It is not surprising that most measurements of community metabolism come from Pacific coral reefs. These reefs also have proved the most suitable for whole system measurements, providing estimates of rates of gain or loss by whole reef systems. Such whole system measurements are only possible when reef physiography assists, as when all or most of the water entering a reef system exits through a few restricted passages or routes. Such measurements have shown that reasonable approximations for whole system gains and losses can be obtained by appropriate integration of results from zonal studies.

Flow respirometry was first used, in conjunction with measurements of oxygen concentration, to determine the primary production and respiration (day and night measurements) of shallow reef areas. The oxygen content of water was measured at an upstream point of a single directional flow across a shallow area of coral reef. The difference in oxygen concentration between this point and some downstream point was then ascribed to metabolism of benthic organisms in the area between the two sampling points. The difference in oxygen concentration was then adjusted for the volume of water flowing per unit of time between the sampling points and the area of benthos between the points. The results could then be expressed as the change in oxygen concentration per unit volume of seawater multiplied by the volume of seawater flowing over the area between the sampling points per unit time ($\Delta O_2/m^3 \times m^3/h/m^2 = \Delta O_2/m^2/h$). Such estimates are possible if the average depth and water velocity between the sampling points are determined. Alternatively, a sample can be taken and the patch of water marked with dye. After the dye patch has moved a significant distance across the reef (or resided for a significant time), a second sample can be taken close to the patch.

(a)

Figure 1. A floating instrument package capable of providing sophisticated, high-resolution measurements of reef flat productivity and calcification. (a) The instrument package is deployed from a small, inflatable boat moored in shallow water on a reef flat. (b) The package floats across the reef flat with the current and records changes in seawater pH, oxygen content, and temperature, as well as the incident light intensity. (Photo courtesy of the authors)

(b)

Oxygen-based Measurements

As already mentioned, early work on the productivity and respiration of coral reefs was based on changes in oxygen concentration. However, these estimates had two major drawbacks. First, oxygen readily exchanges between the water column and the atmosphere, and allowance must be made for oxygen exchange in measurements on coral reefs. Initially, techniques were devised for estimating the amount of exchange, but all of these were based on risky assumptions. More recently, sufficient understanding of exchange processes together with sufficient measurements of exchange in coral reefs have provided generalized data for exchange rates over shallow reefs. It is now possible to make reasonably accurate allowance for oxygen exchange. The second drawback is that changes in oxygen concentration do not directly measure the amount of carbon dioxide fixed by photosynthesis or released by respiration. Carbon, of course, is the basic unit in which primary production and respiration must be expressed. The majority of studies based on oxygen concentration have assumed a one-to-one relationship between oxygen change and carbon dioxide change. Here again, sufficient data has now accumulated to make generalizations less risky than when studies of coral reef productivity began.

Carbon Dioxide Measurements

In the early 1970s, Donald W. Kinsey and Steven V. Smith independently introduced what has since become known as the alkalinity anomaly technique. This is a CO_2-based technique. It is not normally subject to problems of air/sea exchange and it does not require an estimate or measurement of metabolic quotients. It has the additional major advantage that it allows measurement of community calcification (or dissolution). The technique requires measurement of changes in seawater pH and total alkalinity between upstream and downstream sampling sites. Total alkalinity, essentially, is the ability of the seawater to neutralize acid. Most of the change in total alkalinity of seawater above coral

Light and Corals

When solar light penetrates the ocean, it decreases in quantity and changes in spectral quality. At any given wavelength, the amount of light decreases exponentially with depth. There also is a shift in quality toward the blue end of the visible spectrum as red and ultraviolet light are preferentially absorbed. These changes in light quality and quantity profoundly influence coral physiology.

Reef-building corals contain within their cells large populations of the single cell brown alga Symbiodinium microadriaticum. *The presence of these algae (zooxanthellae) confers two major benefits to the coral. First, 95 to 98 percent of all the photosynthetically fixed carbon produced by the algae is transported to the host, where it is used as a major food source. Second, the act of photosynthesis by the algae causes the coral to grow its calcium carbonate skeleton two to three times faster in the light than in the dark.*

This light-enhanced calcification permits modern coral reefs to grow faster than they are eroded by physical and biological agents. Since light directly influences both nutrition and structural growth, it is the most important physical factor influencing the metabolism and ecology of coral reefs.

Hard coral *Turbinaria peltata*. (Photo courtesy of GBRMPA)

Hard coral *Acropora* sp. (Photo courtesy of GBRMPA)

Corals are common on reefs from the surface down to about the 1 percent light level. Successful growth over such a wide range of irradiances occurs because corals have evolved a variety of photoadaptive mechanisms. When growing at increasingly low light intensities many corals become progressively flattened. This presumably increases the fraction of the colony that is directly exposed to ambient light. Corals also decrease the number of polyps per unit surface area, which reduces coral respiration and conserves the available resources.

The symbiotic algae within corals adapt to decreasing light intensity by synthesizing increasing amounts of chlorophyll-a and other photosynthetic pigments. This increases the efficiency of light-absorption at lower light levels. In fact, at intermediate depths photoadaptation has often occurred to a greater extent than the available light has decreased. Thus, coral photosynthesis may be higher at 10 to 20 meters than at either shallower or deeper depths. For relatively autotrophic coral species, the lower limits of depth distribution will be reached when photoadaptation is no longer sufficient to compensate for decreasing irradiance. The precise depth at which compensation occurs depends on the availability and use of other food sources and the clarity of the reef waters. In very clear water

reefs is the result of removal of calcium ions from solution and their precipitation as calcium carbonate. Changes in seawater pH essentially reflect changes in the CO_2 concentration of the seawater. Thus, in essence,

$$\text{photosynthesis and respiration} = \Delta\text{pH} - \Delta\text{total alkalinity}$$

This equation is satisfied after pH and total alkalinity change have been converted to equivalent units of carbon. Present understanding of coral reef productivity and respiration is largely based on results obtained with this technique and present understanding of coral reef calcification is almost entirely due to the technique.

Combined Oxygen and CO_2 Measurements

The alkalinity anomaly and oxygen-based techniques recently have been combined by David J. Barnes to *on the edge of the continental shelf, reef coral community zonations are wide, and abundant corals are found down to a depth of at least 85 meters. The zones become increasingly narrow and more shallow as water turbidity increases on reefs progressively toward the coast.*

Ultraviolet Light

Until recent years it was a common misconception that ultraviolet (UV) light was attenuated within the first few centimeters of the ocean surface and thus had little significance in marine environments. On the contrary, ultraviolet light is now recognized as an important attribute of the shallow water environment of tropical coral reefs. This is due to both higher levels of UV light occurring at the ocean surface, resulting from the thinness of the earth's ozone layer near the equator, and to the general transparency of tropical ocean waters.

UV light is frequently divided into three bands: UV-C (200–280 nanometers), UV-B (280–320 nm) and UV-A (320–400 nm). High energy, ultraviolet light below 286 nm does not penetrate the earth's atmosphere and thus is not environmentally important. In contrast, solar UV-B and the shorter wavelengths of UV-A light can be physiologically and photosynthetically damaging to many forms of reef life.

Only a limited variety of organisms survive in the shallow waters of an Indo-Pacific reef flat. These include some species of hard and soft corals, sea mats (zooanthidians), sea anemones, giant clams, and some algae. Most other marine life, which may be abundant in deeper water or in shade protected crevices on the reef flat, die within a day when relocated to the intense shallow-water sunlight of the reef flat. Death to these organisms can often be prevented if they are placed under a sheet of clear plastic that filters ultraviolet, but not visible light. Thus, ultraviolet light can be demonstrated as a significant physical factor regulating the light (depth) distribution of organisms on a coral reef.

Most of the organisms abundant on shallow water reef flats are algae or are invertebrates that contain within their cells large populations of symbiotic algae. The tissues of these animals are all relatively transparent to facilitate transmission of photosynthetic sunlight to their algae. This creates a difficult evolutionary question. How can relatively transparent organisms surviving in shallow waters protect themselves from the damaging or lethal effects of high-intensity ultraviolet light?

In each case, the solution appears to be the synthesis of highly efficient, UV-absorbing compounds found within both the algal cells and that of the host animal tissue. At present, limited information is available about the structure and chemical distribution of these compounds in reef organisms; however, hard corals have received most attention. Extracts of coral tissue contain chemical compounds absorbing strongly at a wavelength of approximately 320 nanometers. In studies at the Australian Institute of Marine Science, we have separated and identified three major compounds from the Pacific staghorn coral, Acropora formosa, *each of which has a UV-absorption maximum in the region, 310 to 340 nanometers. In combination, these compounds form a broad-band filter, intercepting potentially damaging ultraviolet radiation without absorbing photosynthetic visible light.*

These compounds are produced in high concentrations by corals growing on the reef flat and concentrations decline in corals growing at progressively deeper depths; minimal concentrations occur at depths of 20 meters or less. This observed photobiological adaptation verifies the long dormant conclusion of the pioneering optical oceanographer, N. G. Jerlov (1950):

> This high transparency of the (tropical) oceans to the biologically important ultra-violet radiation would mean that the active region, where photochemical processes can be carried out, extends as far down as 20 meters.

Consideration should now be given to the combined ecological significance of UV light, photobiological mechanisms of chemical protection, and propagation. Do the eggs and larvae of reef invertebrates contain significant concentrations of UV-absorbing materials? Do environmental levels of ultraviolet light influence the dispersal and survival of young coral reef organisms? These questions and many others will undoubtedly be answered as more researchers become interested in UV-light and coral reefs.

—Bruce E. Chalker (AIMS), Walter C. Dunlap (AIMS), and Paul L. Jokiel (NMFS, Honolulu)

allow more or less continuous monitoring of changes in the chemistry of a patch of seawater as it moves across a shallow area of coral reef. The problem with the alkalinity anomaly technique is that it cannot easily be adapted to monitor changes in seawater chemistry as they occur. This is because the technique requires very precise laboratory work that is not easily automated for remote use. However, by combining pH measurements with oxygen measurements it becomes possible to develop an instrument package that will float across a reef with a patch of water and monitor the chemical changes induced in that patch of water by the reef benthos (Figures 1a and 1b). The alkalinity anomaly equation given earlier is rearranged to give:

$$\text{calcification and solution} = \Delta pH - (\Delta O_2 \times Q),$$

where Q is the metabolic (photosynthetic or respiratory) quotient. In fact, Q is more or less constant for a particular community and is best obtained by occasionally measuring changes in total alkalinity, concurrently with changes in oxygen concentration and pH. The beauty of a floating instrument package is that it can measure changes in seawater chemistry as the water moves as little as 1 meter across the reef benthos. Techniques based on taking seawater samples usually require the water to have moved over at least 100 meters of benthos. Moreover, the technique allows monitoring the response of relatively small areas of benthos with respect to changes in light intensity. This means that it permits investigation of the important relationships between community metabolism and light intensity, as well as allowing measurements at very fine spatial and temporal scales.

The important parameters estimated in studies of primary production, respiration, and calcification on coral reefs are as follows:

- *Gross productivity (P), that is, the gross photosynthetic fixation of carbon. This is usually expressed as gCarbon per m^2 per day.*
- *Respiration (R); the respiratory utilization of fixed carbon. This also is usually expressed as gCarbon per m^2 per day. Respiration of coral reef communities must be measured at night (that is, in the dark when photosynthesis is not taking place), and the nighttime rate is assumed to apply throughout the day.*
- *Gross production to respiration ratio (P/R).*
- *The "net" gain in calcium carbonate (G). This is the amount of calcium carbonate precipitated less losses due to dissolution. It is usually expressed as kg$CaCO_3$ per m^2 per year. The "net" gain is a practical measurement since changes in seawater chemistry actually estimate precipitation less solution.*

Problems exist in comparing data from different workers for different reefs, often because work was carried out where the geometry of a particular reef made it most convenient. Thus, the areas of reef reported in numerous studies of community metabolism are not directly comparable on any simple basis. Moreover, some workers have provided results for community metabolism that are, in essence, rates averaged over a whole year; other workers have provided results that are applicable only for the time of year and conditions under which measurements were made.

Some workers have made attempts to allow for daily changes in light intensity and, sometimes, for changes in day length through the year. Other workers have simply extended average rates measured during the day (for example, for productivity and calcification) over 12 hours and nighttime rates (for example, for respiration and, perhaps, solution of reef rock) have been extended over 24 hours. Some recent results are based on measurements of the light response curves for community productivity and calcification (Figures 2 and 3). There have been several recent attempts to pull together the varied and various results. Such attempts make it likely that future workers will be aware of the considerable problems that exist in comparing data, and will attempt to make their work fit with, and compare with, what has gone before.

Estimates of gross carbonate production on coral reefs (that is, total precipitation) are in the range 1–35 kilograms $CaCO_3$ per m^2 per year, with an average around 10 kilograms per m^2 per year and a most likely mean in the range 3–6 kilograms per m^2 per year. Thus, coral reefs are biologically adding 12 to 24 tons of calcium carbonate an acre per year. "Net" calcification measured from changes in seawater chemistry fits well with these "growth rate"-based estimates. Results suggest that fast growing, but limited, areas of reef may achieve deposition rates around 10 kilograms $CaCO_3$ per m^2 per year; that reef flats may produce 4–5 kilograms per m^2 per year, and that lagoonal and sand-covered areas produce 0.5–1.0 kilograms per m^2 per year. Estimates for whole reef systems suggest that 1 to 2 percent of the reef area achieves the higher rate; that the intermediate rate covers 4 to 8 percent of the reef area and the low rate is applicable to 90 to 95 percent of the reef area. Considering that living reefs cover about 15 percent of the shallow seabed and about 0.2 percent of the world's ocean area, these rates for precipitation demonstrate that coral reefs serve as an important buffer in the Earth's carbon dioxide cycle. In general, the calcification rates transform to upward growth rates for coral reefs of 1 millimeter per year in areas with slow calcification, 3 millimeters per year for intermediate areas and 7 millimeters per year in rapidly calcifying areas. These values translate directly into 1, 3, and 7 meters per 1,000 years. This means that, as major geological features on the earth's surface, coral reefs have extraordinary growth rates and growth potential.

The mechanisms of calcification in reef organisms—and, indeed, calcification and ossification in general—are little understood. This is perhaps surprising since such processes fall not far behind photosynthesis and respiration in their importance to the living world.

Perhaps the most important point to come out of recent reviews of nearly four decades of work on coral reef community metabolism is that regardless of where measurements have been made, particular coral reef environments appear to have very similar rates of community metabolism.

Figures 2 and 3 show light response curves for community metabolism across 300 meters of reef flat. Productivity is highest toward the reef crest and shows only a slight trend toward saturation with increasing light intensity. This suggests overlapping layers of primary producers and, since solution of reef rock is at its highest in this region, it is likely that a significant proportion of the primary production is due to endolithic* as well as epilithic** algae. It seems likely that high production by filamentous algae is maintained in this region because of continued disturbance of the substrate by waves.

The continual movement and turnover of the substrate prevents colonization of the region by longer-lived organisms, such as corals, or fragile organisms, such as some of the calcareous algae. With increasing distance across the reef flat, the

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* Living within rocks or other stony substances, such as mollusk shells or coral.

** Growing upon stones or stonelike material (in contrast to the above).

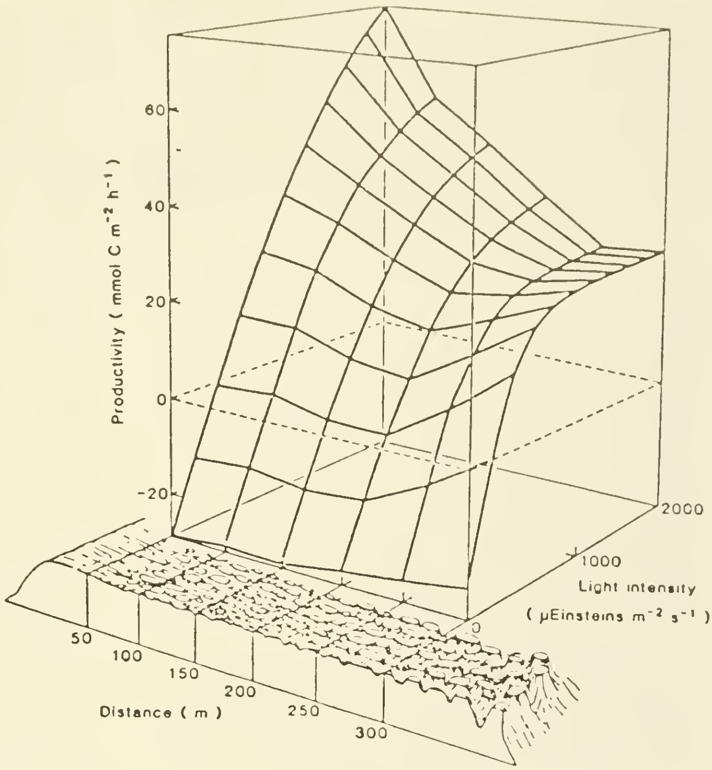


Figure 2. Light response curves for reef flat community primary production with distance across the reef flat. The shape of the curves change from front to back of the reef flat. At the front of the reef flat, the essentially linear response to light intensity reflects overlapping layers of filamentous algae on hard substrate. Toward the rear of the reef flat productivity is saturated at about half maximum light intensity. This reflects the presence of coral-dominated patches of hard substrate toward the rear of the reef flat. (Adapted from Barnes and Devereux, 1984. Barnes and Chalker, in press, Elsevier)

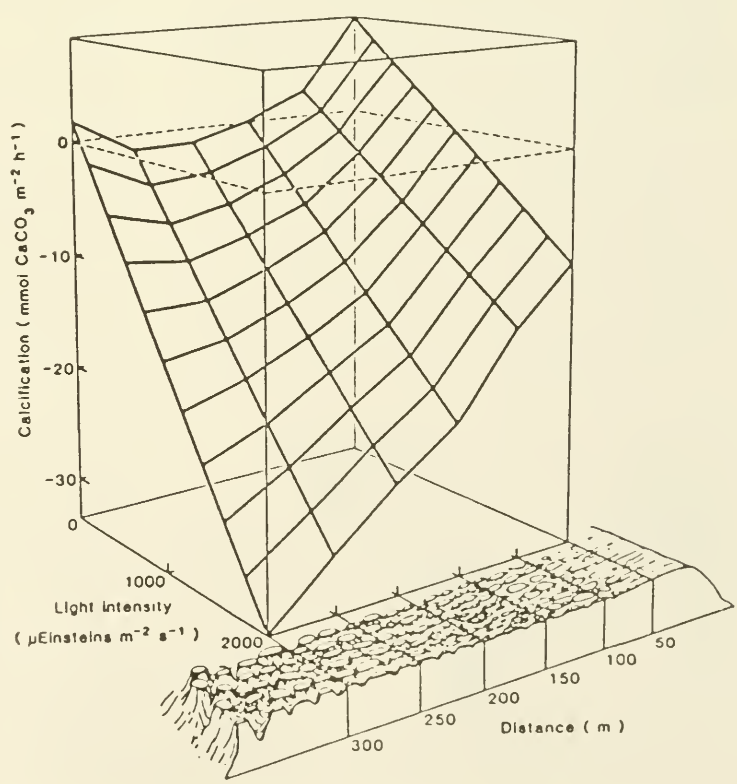


Figure 3. Community light response curves for net calcification (precipitation less dissolution) with distance across the reef flat. More negative values indicate higher rates of calcification. Linear responses are shown as this is the most appropriate way to treat the "noisy" data for community calcification. The response curves probably tend toward saturation at high light intensities. There is an increase in calcification rate and its dependence upon light intensity with distance across the reef flat. This shift in performance reflects a shift toward coral-dominated communities with distance across the reef flat. (Adapted from Barnes and Devereux, 1984. Barnes and Chalker, in press, Elsevier)

substrate becomes more stable and less subject to disturbance. This allows establishment and continued growth of calcareous algae, hard and soft corals, sponges, and encrusting plants and animals. As a consequence, community metabolic performance tends toward that exhibited by these organisms; productivity tends to saturate with increasing light intensity and calcification increases and becomes more light dependent.

Present understanding is limited for seasonality in coral reef primary production and calcification. Only seven studies have addressed these topics and, unfortunately, most of these studies have been on coral reefs growing in areas approaching the latitudinal limits of reef development (that is, where seasonal changes in conditions are so marked that they have to be taken into account). There appears to be a two-fold summer to winter decrease in productivity and respiration, with the greatest seasonal differences occurring, surprisingly, at lower latitudes. Calcification, on the other hand, shows little seasonality at lower latitudes but considerable seasonality as latitude approaches the limits for coral reef development.

Studies of community metabolism on coral reefs are fundamental to any understanding of how such systems develop, grow, and are maintained. The importance of calcification to reef development is obvious. Metabolic studies are providing information about the spatial variations in calcification rate and on the environmental factors that significantly affect reef growth. While the inorganic gain in most reef systems is high, the organic gain is around zero and may be slightly positive or negative over periods of months to years. The precise elucidation of the status of this delicate balance is proving to be critical to our understanding of the status of whole reef systems.

Reef flats, the areas most studied in terms of community metabolism, appear to have a slight excess of organic production. However, it is becoming clear that such excess is probably due to the short lived, filamentous algal communities. Anything that alters the productivity of such communities will greatly affect a whole range of organisms: those that can quickly respond to greater productivity, or those that will be quickly affected by a lowered productivity.

The organisms that are most obvious on coral reefs are those that have the metabolic reserves to carry through weeks to months of lowered productivity. However, the same drop in productivity probably has catastrophic consequences for the less obvious (but not necessarily less important) reef communities, such as those of bacteria and interstitial fauna. However, it is already apparent that normal coral reef communities are limited by the productivity of plants within the communities, and that an unusual or excessive input of organic nutrients seriously perturbs the communities.

Perhaps the most important practical aspect of metabolism studies is their potential to provide vital information about the operation of reef systems for people charged with managing such systems. The literature on reef form and reef community structure largely emphasizes the differences between reefs. Even adjacent reefs can be very different in form and community structure. Studies of reef metabolism have emphasized that such apparently different reefs and reef communities are likely to have very similar metabolic performances. Reef systems that perform outside "standards" of the sort already provided by metabolic studies must be examined carefully to determine whether the unusual performance reflects perturbation by some outside agency. At present, community metabolism studies on coral reefs are defining the "normal" range of performance. Recent studies are reaching a level of sophistication where second order variations in community metabolism, previously attributed to noise, are becoming understood as important facets of system operation (Figures 2 and 3).

Kaneohe Bay Studies

At present, there is only limited understanding of the causes (that is, the meaning) of excursions outside of "normal" metabolic performance. By far the best studied metabolic responses to external perturbation resulted from discharge of sewage and increased terrigenous sedimentation in Kaneohe Bay, Hawaii. Measurements were taken before and after sewage was diverted from the bay in 1977 and early 1978. Very clear temporal and spatial patterns emerged for reef metabolic performance following the onset of the perturbation. Generally speaking, the reefs became less self-sufficient in organic production and calcification decreased greatly. The perturbations essentially shifted community structure away from the sorts of organisms that characterize and maintain coral reefs.

The Kaneohe Bay studies established that marked shifts in community metabolism are associated with equally marked and visually obvious shifts in community structure and sedimentary character. The real question is whether metabolism studies can provide early warnings of impending or potential catastrophic changes, and thus provide time to take action before major, perhaps irreversible, changes occur in community structure.

David J. Barnes and Bruce E. Chalker are biologists at the Australian Institute of Marine Science. Donald W. Kinsey is Executive Officer of the Great Barrier Reef Marine Park Authority.

References

Barnes, D. J., and M. J. Devereux. 1984. Productivity and calcification on a coral reef: a survey using pH and oxygen electrode techniques. *J. Exp. Mar. Biol. Ecol.* 79:213–231.

Kinsey, D. W. 1983. Standards of performance in coral reef primary production and carbon turnover. *In:* Perspectives on Coral Reefs. Australian Institute of Marine Science. pp. 209–218.

Kinsey, D. W. 1985. Metabolism, calcification and carbon production: I. System level studies. *Proc. Fifth International Coral Reef Congress, Tahiti.* Seminar B.

Smith, S. V. 1978. Coral reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature* 273:225–226.

Smith, S. V. 1983. Coral reef calcification. *In:* Perspectives on Coral Reefs. Australian Institute of Marine Science. pp. 240–247.

Stoddart, D. R., and R. E. Johannes, eds. 1978. *Coral Reefs: Research Methods.* UNESCO, Monographs on Oceanographic Methodology. Paris. No. 5. 581 pp.

Distribution of Reef-Building Corals

by J. E. N. Veron

Just as the living reef forms a veneer on the foundation structure below, so do recent studies seek to layer new information onto the existing foundation of coral reef studies begun by Charles Darwin in 1842.

While Darwin's work remains a research paradigm, recent findings in related fields have contributed greatly. When Darwin wrote, he did not enjoy the perspective gained from knowledge of 1) plate tectonics, and 2) sea-level changes. Both have played a major role in addressing a basic topic in coral reef biology: the distribution of reef corals in space and time.

Is the present distribution of corals correlated with the present distribution of reefs? Are corals found where they originally evolved, or have they traveled (using their planktonic larvae) away from their place of origin? Are present distribution patterns mostly a matter of geological history, or are physical environmental factors (like ocean currents and temperatures), or biological factors (like species interactions) more important? In short, why and how do corals exist as they do?

Most of these questions and others like them have no simple answers, for each involves an intriguing mixture of geological history, environmental and geological constraints, evolutionary processes, and reproductive biology.

Coral Distribution Patterns

There are only about 500 species (88 genera) of reef-building (or hermatypic) corals in the Indo-Pacific. On the broad scale, hermatypic corals are characterized by a low number of species, wide species ranges, and a lack of endemics (species native to a particular locality). As shown in Figure 1, the numbers of genera of Indo-Pacific corals are fairly evenly distributed across the tropical reefs of the Indian Ocean, from the Red Sea to western Australia and Indonesia. Further to the east, a north-south belt of relatively high diversity (the Indo-West Pacific Center) extends from the Philippines south to the Great Barrier Reef. Further eastward across the island archipelagoes of the South Pacific, diversity gradually decreases, with only a few genera reaching the west coast of the Americas.

Curiously, some species of coral span almost the entire Indo-Pacific, while others are found only in isolated areas.

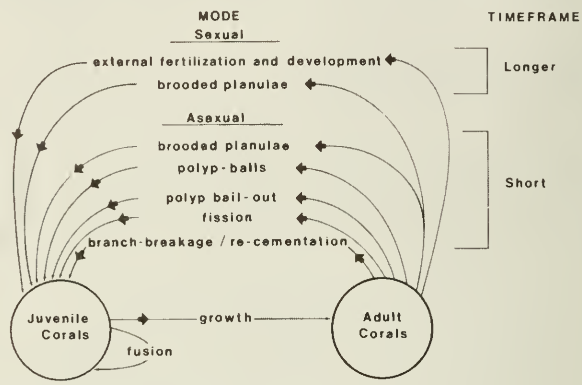
The Great Barrier Reef is home to 350 named species, hence most of these have wide distribution ranges. For example, 89 percent of the species recorded from Japan's Ryukyu Islands, and 94 percent of the species recorded from western Australia, also occur on the Great Barrier Reef. Over these great distances, however, a species' abundance, color, and range of growth forms may change, sometimes making identification difficult or doubtful.

Within the Great Barrier Reef, the distribution and abundance of species is more uniform. Some are more common in muddy waters near the coastline, others are more common in the clear waters of outer reefs. Only the southern-most (Capricorn and Bunker) groups of reefs show a significant reduction in the number of species compared with the rest of the Great Barrier Reef. South of the Great Barrier Reef, coral reefs are widely spaced and the number of species decreases rapidly. What then has determined the abundance and distribution of corals on the Great Barrier Reef?

Figure 1. The diversity of reef-building coral. The index is compiled by adding the known distribution ranges of the individual genera. The highest diversity occurs in the Indo-West Pacific, from the Great Barrier Reef to the Philippines.

Coral Reproduction,

Corals utilize a diverse set of reproductive options, both sexual and asexual. The propagules* associated with each have different dispersal capabilities. When the propagules settle, and growth begins, the physical and biological forces of natural selection influence their survival. While the average person envisions the coral reef as waving fronds or massive structures, most of the individuals in a coral community are small (less than 500 microns), and not readily visible to the naked eye. These members range from a few days to a few years in age. Mortality rates at this stage of development can be high.



Reproductive modes of coral.

Asexual Reproduction

At present, there are five known modes of asexual reproduction, and each results in propagules genetically identical to the parent colony. Most have short dispersal capabilities, and remain near the parent. The asexual modes are:

- Branch-breakage. Common in branching and plating corals, such as *Acropora* spp. When disturbed, either physically (storm) or biologically (predatory fish), pieces may break off and re-cement themselves to the reef surface.

- Fission. A number of corals, among them the motile fungiids or mushroom corals, may split into two or more colonies during early development.

- Polyp Bail-Out. In special cases, some brown corals (for example *Seriatopa hystrix, Pocillopora damicornis*) dissociate individual polyps within a colony from each other and the colony skeleton. These polyps then drift to a new area of settlement. This process has been observed under conditions of environmental stress.

- Polyp-Balls. In *Goniopora* spp., for example, a dissociation from the main colony occurs in which a structure containing coral tissue with a separate, primordial skeleton sets adrift, falls to the reef surface near the parent, and initates a new colony.

- Asexual Brooded Planulae. As described by James Stoddart (see page 41), the planulae, or ciliated larvae, are now known to be produced by a type of budding mechanism, as well as sexually.

Sexual Reproduction

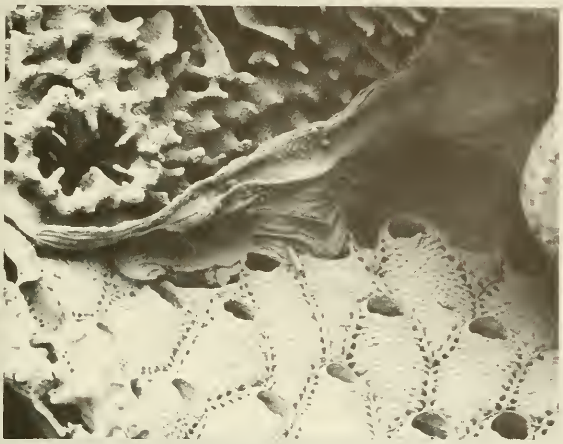
Sexual reproduction occurs in two forms: fertilization and brooding of the larvae within the polyp, and external fertilization and development. Research reported by Carden Wallace and others (see page 38) suggests that the sexual brooded planulae may play a smaller role than previously believed. The major mode of sexual reproduction on the reef may be the spawning of eggs and sperm into the water column, with fertilization and embryonic development of the planulae occurring while adrift in the plankton. The additional time afforded the propagule for development likely yields greater dispersal capabilities.

* The parts of an organism capable of growing into a new one; in plant life, for example, a spore, seed, or cutting.

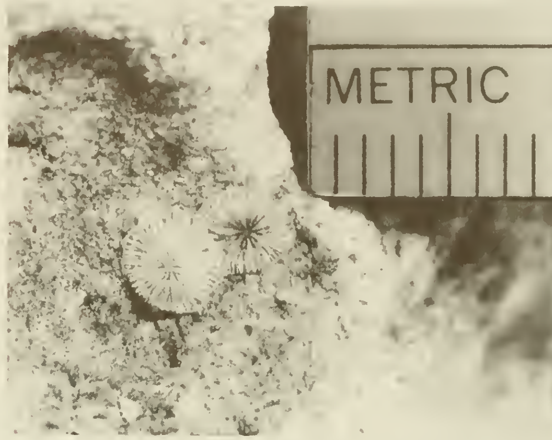
Geological History

The discovery of continental drift has now shattered most of the old Darwinian concept that species had "centers of origin" and that old species were displaced, or replaced, by more successful ones evolving at the center. During the time period of the evolution of most coral genera (the Tertiary Period—70 million years before present), and probably that of many of today's species, the continents of the

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.

J. E. N. Veron is a researcher at the Australian Institute of Marine Science, Townsville, Australia.

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

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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.

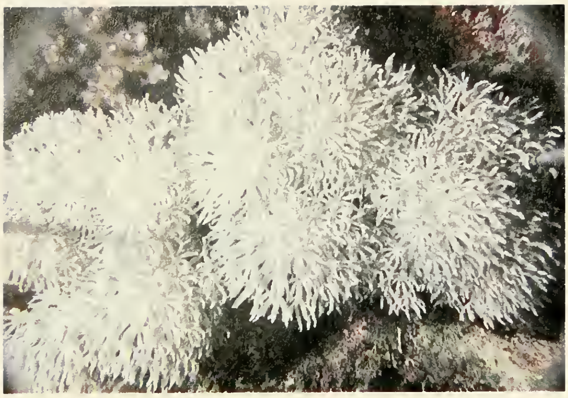


Figure 1. The Xenia *species is soft, like firm gelatin, with non-retractile, fully exposed polyps. (All photos courtesy of John Coll unless otherwise indicated.)*

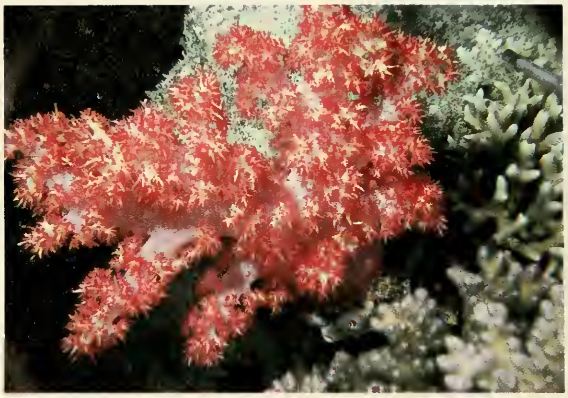


Figure 2. The colorful Dendronephthya *species' polyps are protected by small spicules composed of needle-like pieces of calcium carbonate.*

Predation

As mentioned previously, soft corals vary in structure and form (morphology), particularly regarding characteristics that protect either the polyps or the colony as a whole from predation. Another type of protection—toxicity—varies widely in both its occurrence within species and its intensity. A positive relationship has now been found between the lack of physical defense characteristics and toxicity to fish. Soft corals that bear physical defenses against predators seem to be less likely to be toxic to fish.

Soft corals, such as *Sarcophyton* can retract their polyps completely inside the surface layer of the colony (Figure 6), while the polyps of others, such as *Xenia* and *Cespitularia*, are constantly exposed (Figure 7). Another type of polyp and colony defense involves small sharp calcium carbonate spicules. These long, needle-like parts often surround and protect the polyp-head in a canopy-like fashion (Figure 8). In other colonies, such as *Sinularia dura*, the spicules are tightly packed throughout the body of the colony, and the polyps can retract completely into a protected area. Other species exhibit a combination of these characteristics: *Sinularia flexibilis* possesses a heavily spiculated base, devoid of polyps, but with soft flexible branches into which polyps can completely withdraw.

Neither these physical mechanisms nor toxicity guarantees safety against predators. Some specialized predators feed on highly toxic species of soft corals. Examples of this type of coevolution may also be found in the terrestrial environment. A *Chrysalina* sp. beetle—immune to the effects of the secondary compound hypericin—feeds largely on the toxic fruit and leaves of *Hypericum* sp. This opens up a food source to the species generally unavailable to other predators. Mollusks are the major group in the marine environment from which several such predators have evolved. On the Great Barrier Reef, the egg cowrie *Ovula ovum* feeds almost exclusively on soft corals of the genus *Sarcophyton* (Figure 9). This gastropod is capable of transforming the highly toxic sarcophytoxide into a less toxic compound without ill effects. A similar example of predators modifying the toxins of their prey may be found in other nudibranchs,* such as *Aplysia californica*, which prey on algae.

Some predators even exploit the toxins of their prey. Immune to the toxic molecules, they store them in specialized glands in the outer surface of their body. The aeolid nudibranch *Phyllodesmium longicirra* selectively stores toxins from *Sarcophyton trocheliophorum* in its cerata** but not in other parts of its body. If predatory fish attack, the cerata may be autotomized (voluntarily detached). In this way, the predator is provided with an unpalatable if not toxic sample of food. Similar examples may be found in other nudibranchs, particularly *Phyllidia*.

Competition for Space

The use of chemicals is not limited to fending off predators. They also are employed in competing for living space with other species as well as with other soft corals. Many sessile, colonial organisms on coral reefs possess specialized mechanisms that allow them to maintain and expand their living space, a resource that can be limiting in a crowded community. Hard corals possess elaborate mechanisms, such as nematocysts or stinging cells on their tentacles, to kill neighboring sessile organisms; these long, specialized sweeper tentacles can extend up to 15 centimeters—many times the length of the polyp. Mesenterial filaments, digestive filaments that extrude from the gut, are capable of extracoelenteric digestion. Soft corals, on the other hand, possess none of these apparatus and depend on other adaptations, such as their chemical composition, to maintain living space.

We hypothesized that the toxins present in soft corals may help them compete for space, a hypothesis supported by observations of retarded growth and dead tissue in hard corals adjacent to

* Any mollusks of the order Nudibranchia.

** Long tubular projections on the backs of aeolid nudibranchs.

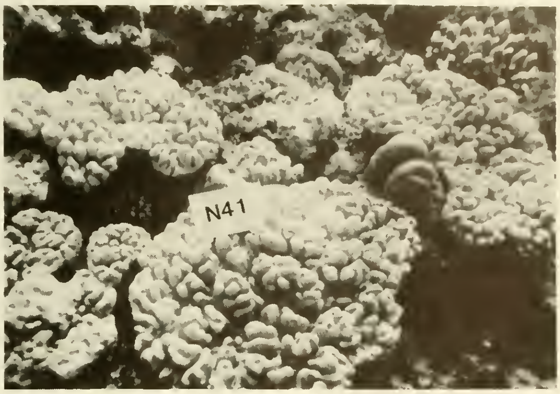


Figure 3. Sinularia *is an encrusting soft coral with hard tissue. Common on the reef crest where wave action is intense, this soft coral exhibits low relief profile.*

Figure 4. Sinularia flexibilis *is one of the most common soft corals found throughout the Indo-Pacific region especially in areas with high currents.*

toxic soft corals (Figure 10). Selecting several common species of both soft and hard corals, we performed manipulative relocation experiments, demonstrating that this effect was indeed significant and reproducible in the field. It first appeared that soft corals were immune to the harmful effects of hard corals, such as *Porites andrewsi* and *Pavona cactus*. A subsequent experiment, however, showed that some soft corals do in fact suffer local mortality from hard corals. Our most striking find was the incidence of local mortality, tissue necrosis,* and growth retardation in hard corals occurring without contact. This is an example of allelopathy in the marine environment—the influence of one living organism on another due to secretion of toxic substances.

To illustrate that the observed effect was indeed caused by chemicals transmitted through the water column from soft corals, a submersible water sampling device was developed. It was selective for organic molecules suspended or dissolved in seawater. Compounds found in the water surrounding one of the most toxic and most effective allelopathic soft corals were identical to those within the organism. To confirm that these toxins were indeed the active allelopathic agents, pure crystalline samples of chemicals from the soft corals were dissolved in seawater and then tested in the laboratory for potency. The pure compound killed both *Porites andrewsi* and *Acropora formosa* at concentrations of less than or equal to 10 parts per million.

Soft corals have other mechanisms that protect them from the harmful effects of scleractinian or hard corals. For example, some can secrete a protective polysaccharide layer in areas close to or in contact with the hard coral's tentacles (Figure 11). This layer then allows soft corals to overgrow living scleractinian tissue by providing a base for colony attachment and expansion. Once attachment is complete, movement across a living scleractinian coral can occur through directional growth. A good example of this is *Nephthea brassica* moving across the plating scleractinian coral *Acropora hyacinthus*.

Competition between soft corals also occurs

* The pathologic death of living tissue in a plant or animal.

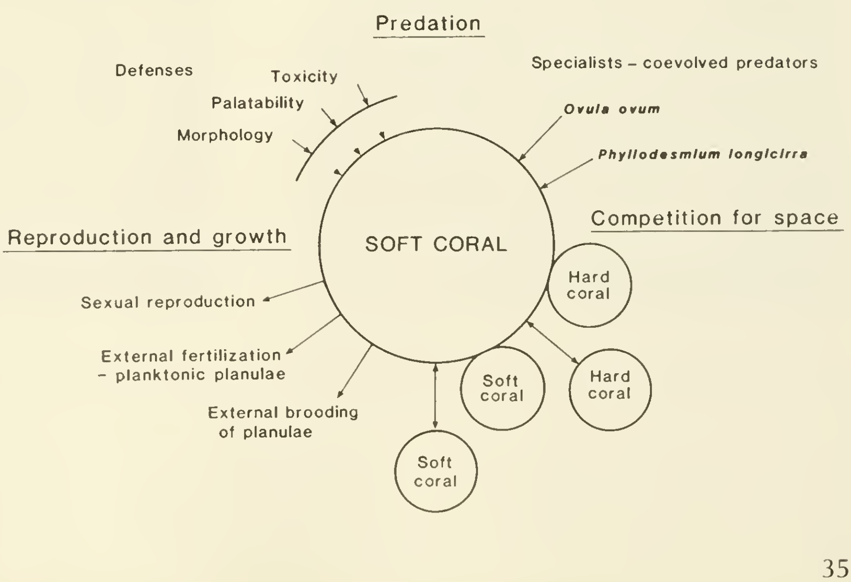


Figure 5. Summary of ecological interactions in soft corals that are chemically mediated by secondary compounds such as terpenes.

for space. The same effects of local mortality and tissue necrosis may be observed in the field, but at a much lower frequency. Manipulative experiments have confirmed that these effects are similarly chemically mediated and are experimentally reproducible in the field. Our experiments also explained the apparent low frequency of observations of these interactions in the field at any one time. Upon contact with soft corals, localized tissue necrosis occurs very rapidly, but within several days an avoidance response occurs as the two colonies bend away from each other. This is followed by a somewhat slower but longer term reaction whereby each colony moves away from the other in a manner analogous to that in *Nephthea brassica*. Soft corals can move and space themselves in their environment, which helps them to decrease the probability of contact with potential competitors.

Chemicals and Reproduction

Chemical ecology not only helps soft corals defend themselves and their living space from others, but also may play a role in reproduction. Although little is known about the reproductive biology of the Alcyonacea (soft corals), a number of interesting facts have recently emerged. Soft corals are now known to reproduce three ways: 1) externally fertilized eggs are brooded on the surface of the soft coral, 2) externally fertilized eggs develop planktonically in the water column, and 3) asexual reproduction occurs via colony growth and fragmentation. The last of these includes production of stolons* and runners.

The concentration of major secondary compounds in certain soft corals varies markedly throughout their reproductive cycles. A recent study covering the period immediately preceding and subsequent to ovulation showed that certain toxic metabolites increase markedly during the month prior to ovulation. These same compounds also were found in high concentrations in the eggs released from the same colonies (*Sinularia spp.*) and were virtually absent several months later after the peak reproductive season.

Further insights into the complexity of the terpenes' role in soft coral reproduction were derived from the chemical composition of two species of *Lobophytum*. In the case of *L. compactum*, the story parallels that of *Sinularia* above, with one compound found exclusively within the eggs of the soft coral. In the other species, *L. crassum*, the major terpene present in the soft coral was completely absent in the eggs. Thus, the chemicals may possess ecological functions that vary even between related species.

* Stem-like structures from which new individuals within a colony develop by budding.

Studies Under Way

Studies are presently under way to investigate three possible roles these chemicals may play: 1) toxicity or feeding deterrence in potential predators; 2) chemotaxis—for these chemicals may play a role in attracting sperm to the egg, and 3) accumulation of the chemicals, acting as a stimulus, indicator, or trigger for release of gametes.* At present, the chemical ecology of soft corals is not fully understood. Since 50 percent of the species possess chemicals—in particular terpenes—that may be the basis of important interactions both among themselves and within the larger ecology of the Great Barrier Reef, secondary compounds may be a major contributing factor to the evolutionary success and abundance of soft corals on the Great Barrier Reef.

John C. Coll is a professor in the Department of Chemistry and Biochemistry at James Cook University in Townsville, Australia. Paul W. Sammarco is a research scientist at the Australian Institute of Marine Science, also in Townsville.

* A mature egg or sperm capable of participating in fertilization.

Selected Readings

Bowden, B., J. C. Coll, D. Tapiolas, and R. Willis. 1985. Some chemical aspects of spawing in alcyonacean corals. *In: Proc. 5th International Coral Reef Congress*, Vol. 4, C. Gabrie and B. Salvat, eds., Antenne Museum-Epha, Moorea, French Polynesia, pp. 325–329.

Brawley, S. H., and W. H. Adey. 1982. *Coralliophila abbreviata*: A significant corallivore. *Bull. Mar. Sci.*, 32(2): 595–599.

Coll, J. C. 1981. Soft coral research at James Cook University of North Queensland. *Proc. 4th Asian Symp. Medicinal Plants and Spices*, Bangkok. *UNESCO Spec. Publ.*, pp. 197–204.

Coll, J. C., B. F. Bowden, D. M. Tapiolas, R. H. Willis, P. Djura, M. Streamer, and L. Trott. 1985. Studies of Australian soft corals—XXXV. The terpenoid chemistry of soft corals and its implications. *Tetrahedron*, 41(6): 1085–1092.

Coll, J. C., and P. W. Sammarco. 1983. Terpenoid toxins of soft corals (Cnidaria: Octocorallia): Their nature, toxicity, and ecological significance. *Toxicon*, Suppl. 3: 69–72.

Dinesen, Z. D. 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. *Coral Reefs*, 1: 229–236.

Jackson, J. B. C. 1977. Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am. Nat.*, 111(980): 743–767.

La Barre, S., and J. C. Coll. 1986. Movement in soft corals: An interaction between *Nephthea brassica* (Coelenterata: Octocorallia) and *Acropora hyacinthus* (Coelenterata: Scleractinia). *Mar. Biol.* (Berlin), 72: 119–124.

La Barre, S., J. C. Coll, and P. W. Sammarco. 1986. Competitive strategies of soft corals (Coelenterata: Octocorallia): III. Spacing and aggressive interactions between alcyonaceans. *Mar. Ecol. Prog. Ser.*

Muller, C. H. 1966. The role of chemical inhibition (allelopathy) in vegetational composition. *Bull. Torrey Bot. Club.*, 93: 332–351.

Sammarco, P. W., J. C. Coll, and S. C. La Barre. 1985. Competitive strategies of soft corals (Coelenterata: Octocorallia): II. Variable defensive response and susceptibility to scleractinian corals. *J. Exp. Mar. Biol. Ecol.*, 91: 199–215.

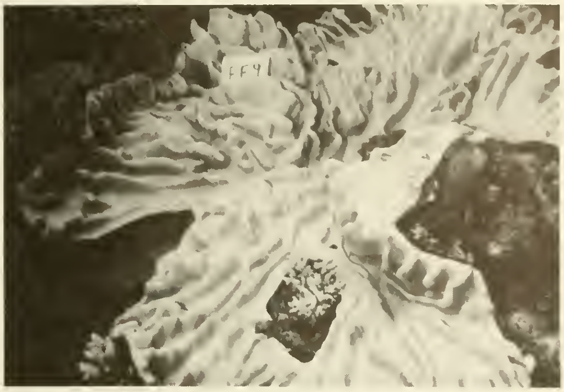


Figure 6. The Lobophytum *species is commonly found on reef crests and exhibits a colony form with low relief.*

Figure 7. A species of Cespitularia *exhibiting a soft flexible body with polyps permanently exposed to potential predators.*

Figure 8. The tree-like Nephthea *species has polyps that are grouped at the ends of its branches; each polyp is protected by micro-spicules.*

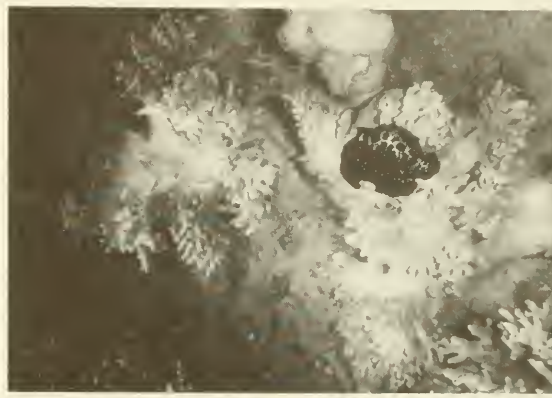


Figure 9. The egg cowrie Ovula ovum *can ingest and assimilate some highly toxic soft corals without ill effects. The shell is white, but when feeding, the mantle of the mollusk covers the shell giving it a black appearance.*

Figure 10. A large colony of Sinularia flexibilis *releasing chemicals into the surrounding water that can kill or inhibit growth in the nearby hard coral* Pavona cactus. *(Photo courtesy of Bette Willis.)*

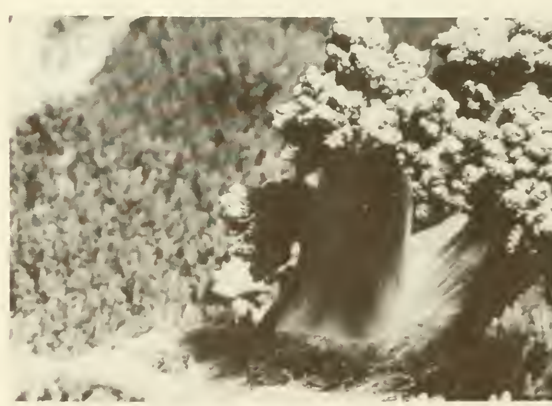


Figure 11. A colony of Nephthea brassica *growing on live* Acropora hyacinthus. *Note the dark brown cuticle secreted by the soft coral. (Photo courtesy of Stephane LaBarre)*

Sex on the Reef:

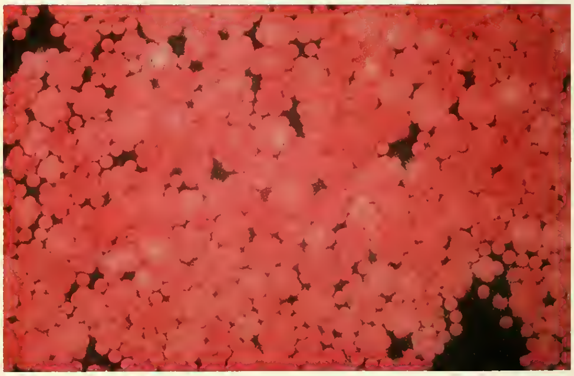
by Carden C. Wallace,
Russell C. Babcock,
Peter L. Harrison,
James K. Oliver,
and Bette L. Willis

Many spawning events in the sea are linked to the lunar cycle. Why then are recent discoveries on coral spawning so remarkable? It's the scale—one that is apparently unparalleled in the animal kingdom.

At least one third of the 350 species of hard corals occurring throughout the entire expanse of the Great Barrier Reef concentrate their reproductive activities for a year into the same few nights in late spring or early summer. Eggs and sperm are released *en masse* into the waters above the reefs, and the next day slicks of eggs and developing embryos can be seen on the sea surface.

It is a spectacle that can be observed by divers, and its timing can be predicted from phases of the moon. Its combination of brevity and participation by so many species seems to be unparalleled. Biologists are fascinated by an occurrence that seems to defy ecological common sense, for although it is advantageous for all the individuals of one species in one place to spawn together, thus ensuring that a large number of eggs will be fertilized, spawning at the same time as many other species would seemingly reduce the chances of encountering the correct mate.

During spawning night, the sea surface becomes filled with egg-sperm bundles. These soon break up, allowing fertilization to occur.



A blizzard of egg-sperm bundles is created by the spawning of Acropora tenuis *just at dusk.*

Textbook View

Many aspects of the massed spawning phenomenon contradict previously-held notions of coral biology. Until recently, all corals were thought to reproduce throughout the year, and to release fully developed larvae rather than eggs and sperm. This textbook view of the way corals reproduce was based on a few common coral species that could be observed to spawn at any time of the year. Even for these, the evidence was incomplete, but it seemed to indicate that eggs were somehow fertilized while still inside the parent polyp, and developed into larvae that were brooded before being released. Such larvae would not spend much time in the water before settling to begin new coral colonies.

Some researchers, however, began to point out that evidence for reproduction was lacking for most corals. This resulted in the suggestion that many corals rarely used sexual reproduction to produce offspring—*asexual* reproduction being the usual mode. Coral colonies develop by a process of *replication*: a basic unit, the polyp, carries all the features necessary for animal existence, and a colony is formed by polyps dividing again and again while maintaining tissue connections. This process is regarded as growth. Coral colonies, however, can sometimes be subdivided by breakage. The resulting pieces can survive and exist independently. Thus, a kind of reproduction without sex results in new coral colonies. It was suggested that corals might typically devote their energy resources to this type of reproduction, sexual reproduction occurring only as a rare event. The nagging fact remained, however,

Mass Spawning of Corals

Red egg-sperm bundles lie beneath the tentacles of the hermaphroditic brain coral Platygyra sinensis, *minutes before they will be released. (All photos courtesy of authors).*

that the natural history of corals had not really been studied well enough to resolve this question.

Hints and Hypotheses

There were always hints of a major spawning event for reef corals. Pink slicks appearing in the sea in late spring or early summer were well known to fishermen and coastal dwellers. Whenever such slicks were investigated, they were found to be composed of the alga *Trichodesmium*. Scientists dismissed the possibility that they could ever be composed of coral eggs. In Japan, however, certain communities of coastal dwellers have observed for many generations slicks of red eggs and larvae in the sea during the days following spawning time. To these folk it had a mythological significance as the *punitsu* or "menstrual waters of the princess of the dragon palace in the sea." Sadly, as Japan's coastal reefs have diminished with encroaching development, the *punitsu* has not appeared for some years.

In the early 1970s, some reef ecologists proposed that some modes of sexual reproduction other than brooding of larvae must exist for corals, and that spawning might be a regular, but brief, event. Only by studying the natural history of individual coral species could such a hypothesis be tested. The challenge was quickly taken up by workers at Heron Island, in the southern Great Barrier Reef region. By combining field and laboratory studies with great vigilance on the reef, they were able to show that some corals do indeed have an annual reproductive cycle and shed eggs and sperm for external fertilization.

A Group Effort

Several post-graduate students at James Cook University in Townsville independently began research on the biology and ecology of various coral species in 1979. Part of this research involved studies of spawning in the corals. During 1979 and 1980, evidence accumulated that most of the species had annual reproductive cycles with ripe gonads disappearing from the entire population in the Austral spring. These initial results were tantalizing, but despite intensive efforts, only one species was observed to spawn, so we still knew nothing of the degree of synchrony in spawning that existed for these corals. In 1981, we decided to pool our time and resources. We established a field camp at Magnetic Island off Townsville so that we could monitor the corals daily, both on the reef and in aquaria.

The group effort was rewarded that year when 14 species were recorded to spawn, after dark, a few days after the full moon. Many of the species spawned together on the same night. All released eggs and sperm (gametes) into the water for external fertilization, rather than expelling fully developed larvae. This added further substantial evidence for the recent suggestions of the Heron Island workers, that the majority of coral species might not brood larvae. One month later, we observed a second spawning episode, at the same interval past full moon, and after this no corals on the reef could be found to contain ripe gametes.

We realized that we had happened on an occurrence of great significance, and from that year onwards our research efforts have concentrated on exploring the events occurring in this narrow window of time in late spring. We now believe that this reproductive mechanism is used by the majority of the corals on the Great Barrier Reef.

The Sexual Organs

Corals exist as colonies, not in the sense of communities of individuals living together, but as interconnected units (the polyps), each containing the same organs. There is a mouth surrounded by tentacles for food capture and defense, and a cylindrical gut cavity divided by fleshy partitions called mesenteries, which function as organs of digestion. During part of the year this is the mesenteries only role, but for some months they contain the developing sexual organs (gonads). The structure of the gonads and the type of sexuality of the polyps varies with species. Many corals are *hermaphroditic*, both female and male cells developing in each polyp of the colony. Some species have separate sexes (the *gonochoric* condition). In this case, colonies have either all female or all male polyps. Female gonads develop as strings of eggs in the mesenteries, males as carrot-shaped or rounded bundles in which sperm are produced. In some hermaphroditic corals, eggs and sperm develop in a single organ, but more commonly testes and ovaries are separate, developing in different mesenteries, or different parts of the same mesenteries.

Development of eggs and sperm is called *gametogenesis*, and for corals participating in the massed spawning event this begins some time early in the year. By early spring, large white eggs and developing testes can be seen in the polyps. As the waters around the reef become warmer, the eggs become colored: usually pink or red, but sometimes orange, purple, or green.

Onset of Spawning

We believe that spawning occurs in response to a series of cues which operate on increasingly fine time scales. Once the seawater temperatures have climbed from winter low levels and gametes are mature, the corals will spawn after the next full moon. Sometimes when full moon occurs early with respect to rising sea temperatures, some corals will not be ready for spawning, and a "split spawning," such as that we saw in 1981, will occur. We know that temperature is important, because corals occurring inshore, where the sea water warms earlier, spawn one month before those offshore.

Spawning "events" are spread over the third to sixth nights after full moon. Lunar/tidal cycles determine the date of spawning, which occurs during the period of least difference between successive high and low tides. This is a period of very low water exchange over the reef and probably is important to the spawning corals as a time during which the high concentration of eggs and sperm necessary for good fertilization rates is maintained for the longest time possible. A period of darkness must pass before the corals will release. We know this because corals kept under artificial lighting delay their spawning until an equivalent time after the lights are switched off. Each species seems to have a characteristic time during the evening when it spawns, although many of these times overlap. Nocturnal spawning is extremely important for corals since the eggs and larvae are readily eaten by the clouds of planktivorous fish which inhabit the reef during the day.

What Does It Look Like?

Many people have now observed the mass spawning event, and its features are becoming well known. Shortly before releasing their reproductive products, the polyps in the corals can be seen "setting." The area around the polyp-mouth becomes distended by the presence of eggs and sperm, which have been gathered within the polyp, most often into a compact ball. Since coral tissues are semi-transparent, the brightly colored gamete ball can be seen within the swelling. The coral can remain in this setting state for about an hour. Then, suddenly in some cases, rapidly in others, the bundle is pushed through the polyp-mouth and released. Gamete bundles begin to stream upward from the colony, to join those released from other colonies nearby. In corals with separate sexes, clouds of eggs or sperm are released.

Development in the Sea

Shortly after reaching the surface of the sea, the egg-sperm bundles break up. Sperm stream away from the bundle and toward other eggs, which they may penetrate and fertilize. Following fertilization, the egg begins to develop until a free-swimming larva (the *planula*) is formed. This drifts without feeding until it is mature enough to settle, usually about 4 to 10 days after the spawning night. Then it descends toward the hard reef surface, where it settles and begins to take on the appearance of a coral polyp. As the polyp is developing a mouth, tentacles, gut, and mesenteries, it also is secreting a skeleton, in which it sits. Then through a process of budding new

Coral Genetics: New Directions

*The planula larva has been traditionally accepted as the result of sexual reproduction in corals. Settlement by planulae has been considered a diversifying force within populations that balanced diversity-reducing, asexual modes of reproduction, such as skeletal fragmentation and tissue dissociation (**see page 28**). It also has been considered to be a cohesive force providing gene flow between geographically separate populations.*

Coral populations once were viewed as heterogeneous, outbred aggregations recruited from a diverse larval stock representing the output of many reefs. Ecological and evolutionary models of corals have been constructed using this assumption. Recently, important exceptions to this view have emerged, and the assumptions on how planulae are produced are being tested.

Early studies of coral reproduction focused on species that brooded their young. Brooded planulae are pervasive reproductive features because of their size, and the regularity and frequency of their appearance. The temporal coincidence of sperm, eggs, and planulae in the tissues of individual corals convinced workers that the planulae were produced sexually. However, embryogenesis was never documented, and studies examining mechanisms by which parental genes were passed to offspring were deferred.

When research turned to genetic studies—using electrophoretic techniques to examine the enzymatic proteins, and thereby assign a genetic basis—the results were surprising. When the analysis was first applied to parent-offspring sets from the common Indo-Pacific brown coral, Pocillopora damicornis*, the genetic modelling showed that the probability that a meiotic process had occurred was about 1 to 20 billion. These planulae were produced asexually! Other populations of* P. damicornis *showed the same pattern. Similar results have been demonstrated for* Tubastrea coccinea *and* T. diaphana*, two "daisy corals." (In the species of coral that retain the ability to produce brooded planulae sexually, the genetic analyses conform with expectations of meiosis).*

The genetic structure within populations of P. damicornis *suggests that, while most recruitment originates from locally-produced asexual propagules, a complementary production of sexually-produced planulae also occurs. On the broad scale, the species conforms to the evolutionary theories that predict asexual propagules will settle close to their parent, maximizing their chances of occupying an environment in which their genotype has already proven successful, and that the sexual propagules will be more widely dispersed—encountering novel environments.*

The asexual production of planulae allows each coral head to produce thousands of clonal propagules. Localized propagation by fragmentation, on the other hand, restricts each head to a few effective propagules, and also implies a significant chance of mortality to the parent. The ability to produce these larger numbers of propagules of a locally successful genotype confers an advantage to corals subject to severe periodic mortalities caused either by physical or biotic agents.

Techniques that examine in detail the genetic structure of coral populations have wide application. For example, studies will further our understanding of the role reproductive tactics play in shaping the complex evolutionary patterns of corals. Coupling these tactics to the peculiar evolutionary patterns of these modular organisms is central to interpreting the ecological significance of coral life history data. Future research must seek evolutionary paradigms more appropriate to corals, rather than those drawn from theories developed for organisms with population structures in which individuals may be clearly defined.

—James A. Stoddart, AIMS

polyps, the change from single polyp to coral colony is made.

As a consequence of mass spawning, most new corals are recruited into reef communities at about the same time every year. They grow very slowly in the first year of life, being just visible to the naked eye at about 8 months old. Between 3 and 6 years old, most are ready to begin the process of sexual reproduction again. Coral colonies may live for many decades, even centuries, and continue to reproduce once a year.

Significance of Mass Spawning

Scientists and those concerned with preserving and managing the Great Barrier Reef puzzle over the degree to which reefs might be interdependent. The prevailing view in the past was that the reefs of the Great Barrier Reef were mainly self-seeded. In this view, occasional larvae might be dispersed more widely to colonize other reefs, but most new corals on each reef are the offspring of local corals. Such a situation might prevail if all or most corals brooded larvae, which were ready to settle soon after release. Now that we know most corals release buoyant gametes and that development of larvae takes several days, we favor the opposite view, that coral larvae are most likely to be dispersed away from the parent reef, and new corals on a reef must come mainly from other reefs. Thus, each reef is dependent on other reefs and on inter-reef waters for its continued supply of new coral generations. This has significant implications for the management of the Great Barrier Reef Marine Park, since it suggests that all reefs are functionally interconnected, and individual reefs cannot be managed in isolation.*

Why Multispecific Spawning?

Synchronized spawning by one species accrues advantages in maximizing chances of fertilization and avoiding wastage of gametes. There also are some disadvantages, such as the possibility of complete reproductive failure because of events on the chosen night—for example, a rainstorm can kill the eggs. When multispecific spawning occurs, many eggs and sperm of different species, even of very close relatives, are present in the water at the same time. This might be expected to have a number of accompanying problems, such as wastage of gametes, the risk of hybridization, and competition for settling sites when larvae settle a few days later. Some powerful advantage must override these difficulties.

What are the advantages of synchronized multispecific spawning? In truth—we don't yet know. We have, however, suggested two alternative hypotheses. The first is that by spawning at the same time as other corals, each species will reduce the chances of its offspring being lost to predators. Second, there may be a unique combination of ecological and physiological factors that all the participating corals require, and which occurs only once a year. We are presently exploring both of these avenues.

Geographic Extent of Mass Spawning

Corals in some areas, such as the Red Sea, the Caribbean, and possibly Hawaii, do not seem to exhibit mass spawning. There is evidence, however, that areas other than the Great Barrier Reef do. We have mentioned Japan; mass spawning also has recently been observed in western Australia, Fiji, and Vanuatu. By comparing time of the year, lunar phases, prevailing temperatures, and tides during spawning at other locations with those on the Great Barrier Reef, we should get further clues about the factors that are important for the timing of the event.

By looking at differences between places with and without mass spawning, we might gain insight into how the phenomenon came to be. Many other reef organisms may be mass spawners, and indeed some other animals, such as soft corals and certain polychaete worms, spawn at the same time as corals. It seems the extent and significance of this event will keep us and other biologists interested for many years to come.

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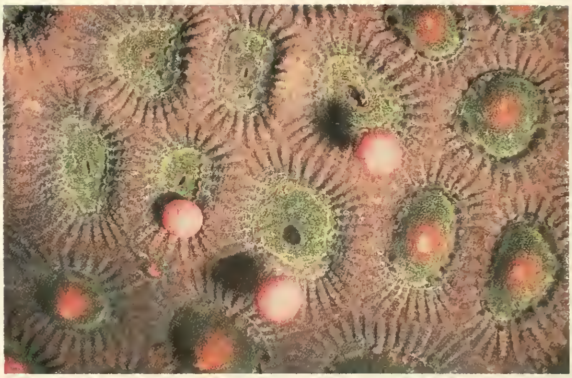
* The question of the degree of interconnectedness of reef coral populations is not yet answered, however, as results of settlement experiments by P. W. Sammarco can be interpreted as suggesting the opposite view, and indicating only a limited dispersal away from reefs. Both research groups plan to resolve this important problem.



Some polyps are "setting," some have released bundles, and some are in the process of releasing in this colony of Montastrea *sp.*

The staghorn coral, Acropora formosa, *is festooned with red egg-sperm bundles just before they are released. This species may have red, white, or pink eggs.*

Letter Writers

The editor welcomes letters that comment on articles in this issue or that discuss other matters of importance to the marine community.

Early responses to articles have the best chance of being published. Please be concise and have your letter double-spaced for easier reading and editing.

Historical Perspectives on Algae and Reefs:

Have Reefs Been Misnamed?

by Llewellya Hillis-Colinvaux

Rain forests and coral reefs—the two most productive, most species rich ecosystems of our planet—are striking features of tropical latitudes. Although vegetation is unmistakably the dominant feature of the forest, plants seem almost absent from the visual panorama of the reef. The stony and horny edifices produced by the corals, and the many colorful fish, blind the eye to traditional plant forms, while other photosynthetic organisms are hidden in the reef structure. The image of plantlessness, or else of limited vegetation is induced, too, by the name: coral reef. So the casual visitor and the armchair reader, with good reason, are encouraged to regard the reef as animal-based, and animal-created. Yet, plants and photosynthesis are as much the basis of the coral reef system as of the forest. Tropical reefs could not exist were it not for a very large photosynthetic component.

The Coral Reef Paradox

The coral structure characterizing tropical reef systems is the skeletal frame of invertebrate animals called cnidarians (the phylum containing jellyfish, sea anemones, and corals). Naturalists, such as John Ray, classified them as plants because of their vegetative appearance. In the 18th century, Jean A. Peyssonnel and John Ellis, the latter using a microscope he had modified for aquatic work, discovered that animal

Above, an algal ridge. The framework in this region of strong wave action is predominantly calcareous red algae. (Photo from Enewetak Atoll) polyps were part of many calcareous reef organisms, and concluded they were animals. These tiny tube-shaped animals, attached so as to produce massive carbonate structures of many different shapes, confirm their animal nature by filtering planktonic food, using their crown of tentacles. The reef, as viewed from a ship, distant shore, or by wading in the shallows—essentially the only methods for reef study in the 18th and 19th centuries apart from dredging—would provide the same vast expanse of life that a tropical forest does from the air. However, from their vantage point, the "dominant" component of a tropical reef was an animal! Consideration of the reef as an ecosystem, and questions about the energy support of the coral mass in a system where plant numbers seemed low—the paradox of the reef—had to await development of the field of ecology and the research tools of the mid-20th century.

Discoveries at Funafuti

In the 19th century, with the foundation laid of basic knowledge about coral reefs, and ships of exploration to traverse oceans, Charles Darwin was able to take up one of the grand basic questions of science: the origin of coral reefs. He also envisioned a grand experiment to test his hypothesis of their origin—a long core extending through the carbonate of the reef, to its base.

It was close to the end of the century, however, before the first long cores were obtained from a reef in a project involving the British Royal Society and the Australian province of New South Wales. The site was Funafuti Atoll in the Ellice Islands (1,800 nautical miles northeast of the Great Barrier Reef) of the South Pacific. Although the first hole had to be abandoned after about 25 meters of drilling, two long cores were taken, the longest penetrating 339 meters into the reef. It was a spectacular achievement even though the base of the reef was not reached. Nor was this goal attained until the coring of Enewetak Atoll in the Marshall Islands in the 1950s (2,000 nautical miles north-northeast of the Great Barrier Reef).

The results from the analysis of the Funafuti cores are an important benchmark in the study of tropical reefs for they demonstrated that reefs are built of organisms other than cnidarians. When the Funafuti team ranked the reef organisms according to their contribution of bulk during reef development, they assigned corals to fourth place, and foraminifera to third. Plants, represented by calcareous red and green algae with *Halimeda* the principal representative of the latter, were tied for first place. They had, for example, discovered in the core taken through the lagoon that 80 to 90 percent of the material in the first 18 meters below the lagoon floor was *Halimeda* debris. In the final ranking, however, calcareous red algae, also known as corallines, were listed first, because their greater visibility to earth-bound scientists was equated with greater importance.

Calcareous Algae

About 100 genera, or somewhat less than 10 percent of the algal species calcify. Most calcareous algae belong to the phyla Rhodophyta (red algae, ~15 percent) and Chlorophyta (green algae, ~10 percent). Among the Phaeophyta (brown algae) only the genus *Padina* calcifies. Although now unequivocably considered plants, for more than a century the plant nature of a number of these genera was controversial. Ellis, in his classic study of calcareous organisms called "Corallines," then defined as calcareous and horny sea organisms (1755), included calcareous algae along with corals. He made brilliant microscopical studies of the internal anatomy of some of the algae and observed what he considered might prove to be "orifices for polype-like suckers" when "magnifying glasses have been improved." He also demonstrated by a public chemical experiment that burning corallines smelled not "like burnt vegetables," but had the "offensive smell like that of burnt bones, or hair," so much so that the door of the room "was obliged to be opened, to dissipate the disagreeable scent and let in fresh air." These investigations, outstanding for the time, led him to conclude that organisms such as *Halimeda* were animals, just as were the cnidarians for which he had demonstrated an animal nature by discovering polyps.

Such problems, however, were history by the end of the 19th century. Perhaps the finest general tropical algal collections of the first half of this century were made during the Siboga Expedition. The results, recorded in outstanding monographs, have had an important influence on subsequent reef botany, including studies of calcareous algae. The "*Lithothamnion* ridge," a framework of predominantly calcareous red algal construction, was a prominent feature of reefs visited by the *Siboga*, and undoubtedly contributed to the ready and continuing acceptance of calcareous red algae as major contributors to reef structure.

Prominent *Lithothamnion* ridge algae include *Neogoniolithon, Porolithon*, and *Lithophyllum*, but not the genus *Lithothamnion*. Hence the name of this reef feature has been changed in recent years to "algal ridge" to reflect more accurately its nature. But whatever the taxonomy, the presence of these algae at this very critical site, where the intense force of the ocean regularly charges against the reef, serve in the buttressing of the land, or in other words, the providing of "reef." The ridge is most extensive in reefs where the wave force is intense; there the calcareous red algae, but not the corals, grow successfully, and, in so doing, they secure the reef environment for other reef organisms, including corals.

In contrast, the discovery of the importance of calcareous green algae in the tropical reef system of Funafuti generally has been overlooked, especially by biologists. The apparent fragility and inconspicuousness of these algae when compared to the massive and exposed algal ridge forms, undoubtedly has contributed to this oversight. However, with underwater exploration made possible by skin and scuba diving techniques, and especially submersibles, we have become increasingly aware of extensive populations of green algae, such as the *Halimeda* meadows of the Great

Barrier Reef and the wall populations of the deep fore-reef of Enewetak Atoll.

Three genera—*Halimeda, Penicillus,* and *Tydemania*—are of special interest in modern reef structure, but *Halimeda*, a genus resembling a cactus, is the only one of global importance. *Penicillus*, the merman's shaving brush, is an important sand former in the Caribbean; *Tydemania*, which most commonly appears like a long string of spherical brushes, may have a similar role in Indo-Pacific reefs. All the calcareous green algae, with one exception, are tropical or subtropical, but some calcareous red algae also form massive calcareous banks in subpolar waters.

New Perspectives on *Halimeda*

Halimeda has generally been characterized as a plant of sand substrata, growing most prolifically in fairly shallow lagoonal environments. Some species do indeed grow in sand, where they are fixed by a large holdfast, usually of one to several centimeters in length. *Halimeda incrassata* is the classic example. However, three quarters of the taxa have very different habitats and growth forms. Several species, attached by a single, small holdfast, usually 1 centimeter long or less, grow or hang from rock surfaces that themselves may be buried under sand. A third group of species sprawl across rock, sand, or coarse algal and coral debris. Attachment is by thread-like filaments produced at intervals along the plant. Since most other algae are restricted to one of these substrata, the ability of *Halimeda* to grow on a very wide range is notable. This capability undoubtedly contributes to the considerable success of the alga in tropical reefs.

These different substrata are not restricted to lagoons or back reefs. Just as they occur across the entire reef system, so *Halimeda* appears able to colonize successfully most zones of the reef, including the region of spurs and grooves. Notable exceptions are the very high energy algal ridges where calcareous red algae flourish, and the region of breaking waves.

There are three general regions, however, where *Halimeda* populations may be exceptionally large: the sands and pinnacles of the back reef or lagoon, the *H. opuntia* zone behind the algal ridge, and the fore-reef. In the first region, extensive meadows of *Halimeda* grow over some of the flatter areas while dense hangings or draperies are associated with the more vertical surfaces of bommies (large heads of coral), pinnacles, or patch reefs. Shallow flat tops also may have sizeable populations of the genus. All three categories of species can occur, and members of the "rock" growing group sometimes seem surprisingly common on what would be casually classified as a sandy environment. When extracted carefully, however, they generally are found to be attached to a small piece of rock.

The *H. opuntia* zone occurs where strong currents flow over very shallow rock surfaces behind the algal ridge, or the breaker zone if the ridge is not present. Compact cushions, generally of *H. opuntia*, frequently develop a three-dimensional cover so dense that most other large organisms are excluded. The morphologically distinct, tightly branched form of the plants appears to be the parallel of the compacted form of calcareous red algae growing in highly turbulent waters.

The third region, the fore-reef, has traditionally not been considered a habitat where substantial populations of *Halimeda* would grow. Recently, however, investigators using small submersibles have discovered sizeable populations on the fore-reefs of Pacific and Atlantic reefs. The Enewetak Atoll project is the only one in which some of the transects concentrated on this particular genus. *Halimeda* populations were found to cover 10 to 50 percent or more of the atoll slope down to greater than 110 meters, with at least a third of the

Halimeda—The Sand Producing Alga

Geological studies in coral reef regions usually mention Halimeda *flakes, often as an important component of the sediments. These flakes are in fact the individual segments of a relatively small and often cryptic green alga. Their preservation is due to the large amounts of calcium carbonate deposited internally as dense masses of interlocking needle-like crystals of aragonite. When the organic tissues decompose, the calcium carbonate retains the shape of the segments, often in sufficient detail to permit identification of the fragments to species.*

To contribute significantly to coral reef sediments, Halimeda *also must be productive. It grows by producing discrete new segments at branch tips and a complete but uncalcified segment can be produced in a single night. This initially consists of a flattened, white mass of filaments, but as soon as chlorophyll has been formed the next morning, and an outer layer of swollen filament tips, the primary utricles, has sealed the surface, calcium carbonate deposition within the segment begins.*

On reefs, only about 1 percent of the branches grow actively, but as they may produce a new segment every three to four days, production of organic matter and accompanying calcification is substantial. In the central Great Barrier Reef (GBR), biomass of Halimeda *vegetation can double in 15 days with, on average, 7 grams dry weight being produced per day per square meter of solid substratum.*

In the main species involved on these reefs, 10 percent or less of this will be organic matter, the rest calcium carbonate. It can be calculated that a reef lagoon could accumulate 13 centimeters of Halimeda *flakes over 1,000 years.*

—Edward A. Drew (AIMS)

A sprawling species of Halimeda. *Each unit, or segment, follows another, as if strung on a thread. (Photo courtesy of D.L. Meyer)*

A sand-growing species of Halimeda. *Whitish, dead, segments about to be shed can be seen on the large tagged plant in the center foreground. The fallen* Halimeda *segments make up a large portion of the substratum. Since* Halimeda *also provides a habitat, parts of the plants are overgrown by other reef organisms. (The diameter of the reference tag is about 2.5 centimeters) (Photo from Enewetak Atoll)*

species growing to more than 90 meters. Sizeable populations of *Halimeda* as well as calcareous red algae also grew considerably deeper than hermatypic corals, which at 90 meters were estimated as covering less than 1 percent of the region.

These data also have been important in changing our concept of the vertical range over which *Halimeda* can develop substantial populations. Although the genus does not grow as deeply as some calcareous red algae that extend to 268 meters, *Halimeda* was observed to 140 meters at Enewetak, and to 150 meters in the Bahamas. For the clear fore-reef waters of Enewetak Atoll, photon flux densities at 140 and 150 meters were calculated as 0.08 percent and 0.05 percent surface irradiance. Growth therefore continues considerably deeper than the 1 percent light level, or lower limit, of the euphotic zone.

Impact of Calcareous Algae

The 1980s picture of calcareous algal distribution in tropical reef systems provides a range for *Halimeda* that is considerably more extensive, both horizontally and vertically, than that of hermatypic (reef-building) corals. Populations of at least two other calcareous green algae also may be substantial in some geographical regions. The genus *Penicillus* produces extensive meadows in the Caribbean, and may have a greater distribution in the Great Barrier Reef than presently known. *Tydemania* also may prove to be more widely dispersed in the Indo-Pacific. This alga, once considered a rare "deep-growing" plant was found growing abundantly in the shallows of Indonesian reefs in the 1960s. It later was discovered to be relatively common at 8 meters and deeper in the lagoon of Enewetak Atoll.

The area of world reef occupied by sizeable populations of calcareous green algae of the lagoon and fore-reef, and calcareous red algae of the algal ridge and fore-reef, can be very large. To understand the reef building process and the functioning of the reef ecosystem it is necessary to consider the contributions of algae, especially calcareous species, to the carbonate and organic carbon budgets of tropical reefs.

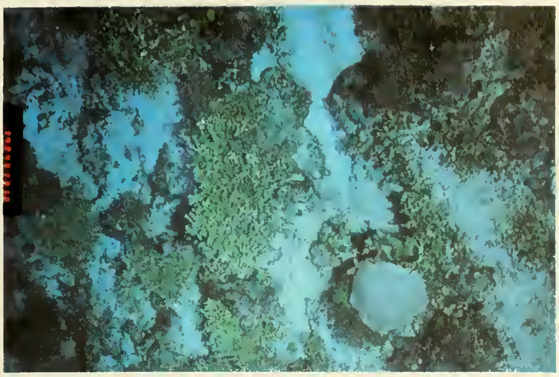
Primary Productivity

Primary productivity of the ocean historically has been associated with phytoplankton. Although the importance of these small organisms to open ocean production of organic carbon is indisputable, in tropical reef systems fleshy and calcareous macroalgae, seagrasses, and zooxanthellae—the dinoflagellate symbionts of corals and foraminifera—are key participants in organic carbon production. Since primary production is, in effect, the engine that drives the entire reef system, awareness of the potential of the macroalgal contribution is a prologue to understanding reef ecosystems.

Primary productivity data for specific taxa are very limited and often cannot meaningfully be compared because of the different methods used, or because there is too little information about the quantity of biomass involved. Baseline net productivity values for calcareous red algae on Hawaiian reefs of 0.6–5.7 grams of carbon per square meter per day, and for sand-growing *Halimeda* of 2.3 grams of carbon per square meter per day (conservative) indicate that contributions to the organic carbon pool of the reef system by sizeable populations of at least some species of calcareous algae are far from negligible. A perspective on this contribution is obtained by comparing these net productivity values with those for Nova Scotian kelps and tropical seagrass beds which are of the order of 4.8 and 3.8 to 5.8 grams of carbon per square meter per day, respectively. Values for some of the least productive regions of the oceans are of the order of 0.01 to 0.05 grams of carbon per square meter per day.

Carbonate Productivity

The major contribution of calcareous algae, however, is to the physical system of the reef itself,



Colonies of a sprawling species of Halimeda *growing on the fore-reef wall at a depth of about 100 meters. Size of the colony in the center is about 0.6 by 1 meter. (Photo is from Enewetak Atoll)*

A Halimeda *meadow with mounds of sand created by* Callianassa *shrimp, at a depth of 20 meters.*

by the deposition of calcium carbonate. Red algae provide framework and sand, and by their growth promote the consolidation and cementing of algal and coral frameworks. Segments, or growth units, of *Halimeda*, discarded as part of the life history strategy of this alga, add fill to lagoons and reef framework, and produce extensive *Halimeda* banks or bioherms. Finer materials from *Halimeda* and other calcareous green algae produce sands and muds.

Other researchers have underscored the importance of loose carbonate sediments in reef building, estimating that 4 to 5 times more loose sediment is produced than is incorporated as reef framework. The Funafuti borings implicated *Halimeda*. The recent discoveries of large populations of this alga in the lagoon and the deep fore-reef, together with cores taken from lagoons where the *Halimeda* contribution is likely to be large, further implicate *Halimeda* as a major sediment producer.

The extent of the contribution cannot be assessed, however, without knowledge of the rate at which sediments are produced. For this, we need to know the rate of growth of the alga, and the size of the contributing population. The first indication of the rate of growth of *Halimeda* was an opportunistic observation at Funafuti. A branch of *Halimeda* was observed growing through a hole in a submerged board of wood on the reefs. It was more than 60 years later before the next observations were made by transplanting sand-growing species from Caribbean reefs to aquaria, and the production and loss of segments recorded regularly. Growth involves the development of new segments (the primal sediment material) as well as the loss of old segments from the living plant, shed somewhat like leaves from deciduous trees. Segments also are contributed by the death of the plant itself. From such laboratory work, as well as from field studies of growth and population density, and the analysis of core samples, baseline data on rates of vertical accretion have been calculated. Most of the values lie between the conservative figure of 0.5 centimeters per 1,000 years for a dense cover, by sand growing species, to 14 centimeters per 1,000 years for the very dense covers provided by sprawling species in certain regions of the Great Barrier Reef.

Two segments of a Halimeda *with the calcium carbonate removed, showing the filamentous construction of the segments. Crystals of calcium carbonate develop in the spaces between the filaments. Note the central medullary filament, from which the others branch. The width of the lower segment is about 0.5 centimeter. (Photo by Tom Goreau)*

The extent to which *Halimeda* actually covers reef surfaces with dead calcareous segments is especially sensitive to the density of the population and certain environmental conditions, such as nutrient enrichment. A very few species generally appear to provide the bulk of the sediments. The accretion rates clearly demonstrate that *Halimeda* produces significant quantities of sediments annually in the Great Barrier Reef and in many other reef systems. The Great Barrier Reef represents a sizeable proportion of the world tropical reef area, however, and so contributions of *Halimeda* to this one reef system alone are a significant statement of this alga's importance in the entire tropical reef system.

The role of calcareous green algae perhaps can be best appreciated by considering the reef ecosystem to be composed of two subsystems, the reef ridges and the lagoonal or non-rigid framework regions. Accordingly, the ultimate origin of the reef mass depends on the relative rates of accretion by the calcifiers of the two compartments. Where lagoonal regions are large, as in some atolls and the Great Barrier Reef, they may contribute most to the mass of the reef. The lagoonal area has only to be four to five times that of the reef ridges for its total contribution to be the larger. Skeletal materials from the calcareous algal populations of the fore reef would mostly be contributed to the ridge system where they are growing, as sand or framework, unless moved into deeper water or carried away from the reef system.

The evidence from the boring of the Funafuti lagoon—that *Halimeda* and calcareous red algae are major contributors to reef structure—has been amplified in the past three decades by a series of studies in the Great Barrier Reef, Enewetak, and the Caribbean. Although the contribution by hermatypic corals to the reef is important, as well as very obvious, it is now possible to see the process of reef building as more than the construction of coral framework. The combined contribution of calcareous green and red algae may account for more than half the accretion of carbonates in some of the world's reef systems. The recent discovery of extensive *Halimeda* bioherms in the northern part of the Great Barrier Reef emphasizes the need for renewed attention to the nonframework portions of tropical reefs.

"Coral" Reefs Reconsidered

Now well into the 1980s, we have accumulated and refined our knowledge about coral reefs for more than two centuries. What once appeared to be predominantly an animal system and so was appropriately named "coral" reef, is now understood, by the solving of the paradox of the coral reef, to be a system in which plant biomass predominates just as in the similarly productive and species-rich tropical rain forests.

Coral reefs are plant systems, and algae are essential to the survival of the reef system in ways beyond the accepted photosynthetic role. Not only does the dinoflagellate symbiont of corals promote calcification of its cnidarian host and consequently make coral framework possible, but calcareous plants are important contributors of reef framework and sand.

The name "coral" reef, used to describe a certain association of animals before there was an understanding of communities or ecosystems, has been outgrown. Just as the name "*Lithothamnion* ridge" has been changed successfully in recent years, it is perhaps time to exchange the epithet "coral" for a more suitable one. Names such as "tropical" and "biotic" have been introduced into the literature but have a restricted following. Neither is as misleading to scientist and nonscientist alike as the present one, and yet neither indicates the reef's basic nature. A more appropriate name is "algal" reef.

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Selected References

Hillis-Colinvaux, Llewellya. 1980. Ecology and taxonomy of *Halimeda*: primary producer of coral reefs. *Advances in Marine Biology* 17: 1–327.

Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Enewetak Atoll. Ecological Monographs 25: 291–320.

Proceedings of the Fifth International Coral Reef Congress, Tahiti, 1985.

Reef Algae

by Michael A. Borowitzka, and Anthony W. D. Larkum

Algae may not be the most obvious members of coral reef ecosystems, but they are a vital component. They not only provide nearly all the organic material for the other reef organisms, but their calcification activities are essential to the formation of the reefs. Figure 1 shows the general distribution of algal species across part of One Tree Reef. Each reef habitat has its distinct algal flora, as well as its distinct fauna. In this article, we refer to the algae of One Tree Reef, but the species and habitats are common to most other offshore reefs in the Great Barrier Reef region.

Distribution

The upper reef slope is dominated by encrusting coralline algae, such as *Paragoniolithon conicum* on the exposed (windward) side of reefs, and *Porolithon onkodes* on the more sheltered reefs. The deeper reef slopes are usually coral dominated with many cryptic fleshy algae as well as turf algae. In deeper waters, larger fleshy algae also may be found.

The reef crest of One Tree Island consists of an extensive layer of the crustose coralline alga *Porolithon onkodes*, which may be overgrown by mat-forming algae, such as *Laurencia* sp. and *Caulerpa racemosa*. Unlike most central Pacific and Caribbean reefs, the reefs of the Great Barrier Reef (GBR) do not have a raised algal ridge of *P. onkodes* (sometimes called a *Lithothamnion* ridge). This absence of a distinct raised ridge is presumed to be the result of the high tidal range and the periodic absence of ocean swells in the GBR region, which leave the reef crest exposed for long periods.

Inshore of the *Porolithon* zone is a region consisting usually of extensive rubble deposits that are fully exposed at low tide. Except for shallow pools where algae, such as *Yamadaella coenomyce* and *Caulerpa* sp. grow, there is little algal growth other than various blue-green algae that grow within the limestone rubble giving it a characteristic black-green color.

Behind this rubble crest is the outer reef flat, which is largely exposed at lagoon low water and consists of small, 5 to 50-centimeter high, coral lumps interspersed by sand patches. This zone progrades into the deeper inner reef flat with larger coral bommies.* The algal flora in this region is very diverse and consists of many "turf" algae (Figure 1) as well as the very conspicuous *Chlorodesmis*, and fleshier algae, such as *Caulerpa* spp., *Padina*, *Dictyota*, *Halimeda* and *Laurencia*. Underneath these macrophytes smaller algae, such as *Valonia* and *Dictyosphaeria* may be found. During spring, this zone may be dominated by large brown algae, such as *Turbinaria*, *Sargassum*, *Hydroclathrus*, and *Chnoospora*. The latter often form a thick matt which eventually sloughs away in clumps of up to 0.1 square meters and up to 1 kilogram fresh weight. The clumps are swept by currents into the lagoon, where for a short time they "litter" the floor before they are rapidly degraded by bacteria and eaten by detrivores. At the lagoon rim and near the upper edges of the coral bommies, branched unarticulated coralline algae, such as *Lithophyllum kotchyanum* and *L. molluccense*, are also very common.

One Tree Reef has a 3 to 6 meter deep central lagoon with extensive coral bommies reaching from the sandy lagoon floor to the low water mark. A definite zonation of algae can be observed on the vertical sides of these bommies (Figure 2). The shallow pools within these bommies have a flora similar to that of the outer reef flat. The sand floor of the lagoon also has a distinct algal flora of filamentous blue-green algae, such as *Hormidium* and *Oscillatoria*, which grow over and through the sand, forming distinct purplish patches. Loosely attached algae, such as *Hydroclathrus clathratus* and stoloniferous algae, such as *Caulerpa serrulata* and *Halimeda cylindricea*, are also locally abundant.

Near the shore of the island, especially in the area where beach rock occurs, three definite algal zones usually can be distinguished. This is more obvious on sand cays, such as Heron Island. At the intertidal fringe there is a band of the small rhodophyte *Gelidiella bornetii* obscured by a layer of loose sediment. In winter, this band may appear greenish because of the seasonal development of *Enteromorpha* spp. Above this band in the lower eulittoral, there is a pale pink to white band of various blue-green algae firmly entrapping fine sediment, and above this, near the high tide mark, is a black to brown band of the blue-green *Entophysalis deusta*.

Inter-Reef Areas

Interestingly, the reefs themselves are largely free

* Large coral masses rising from the lagoon floor up to 20 meters high.

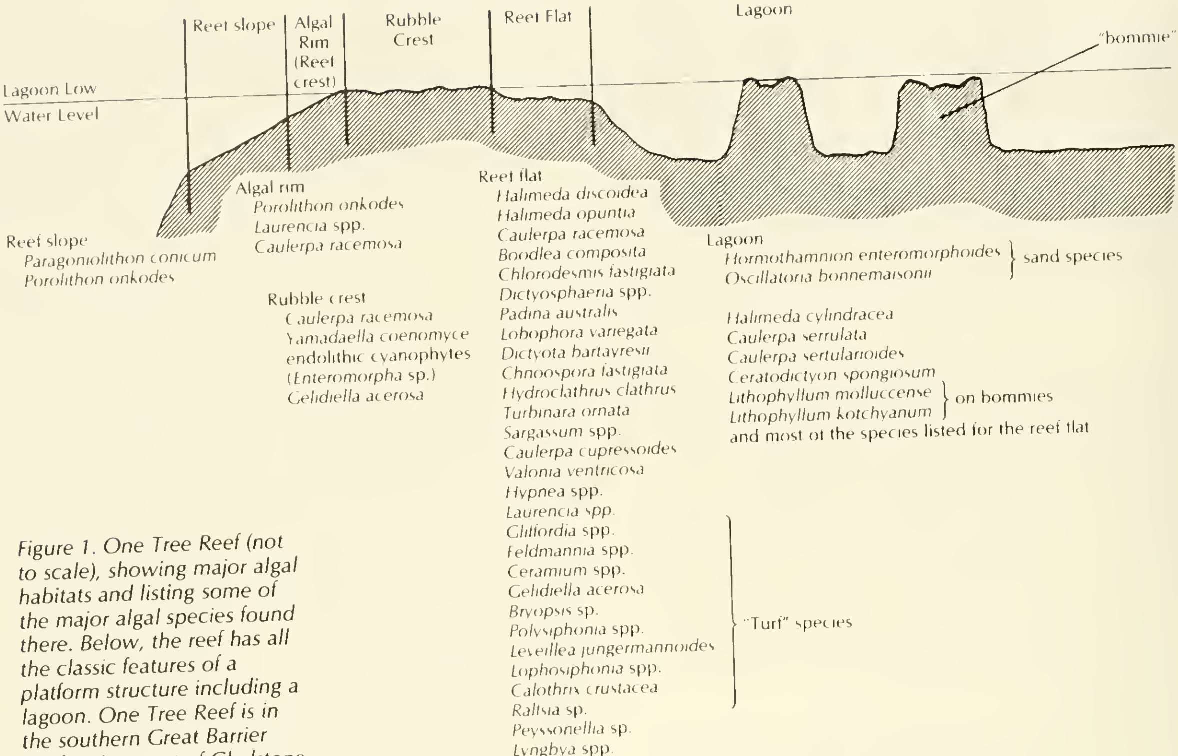
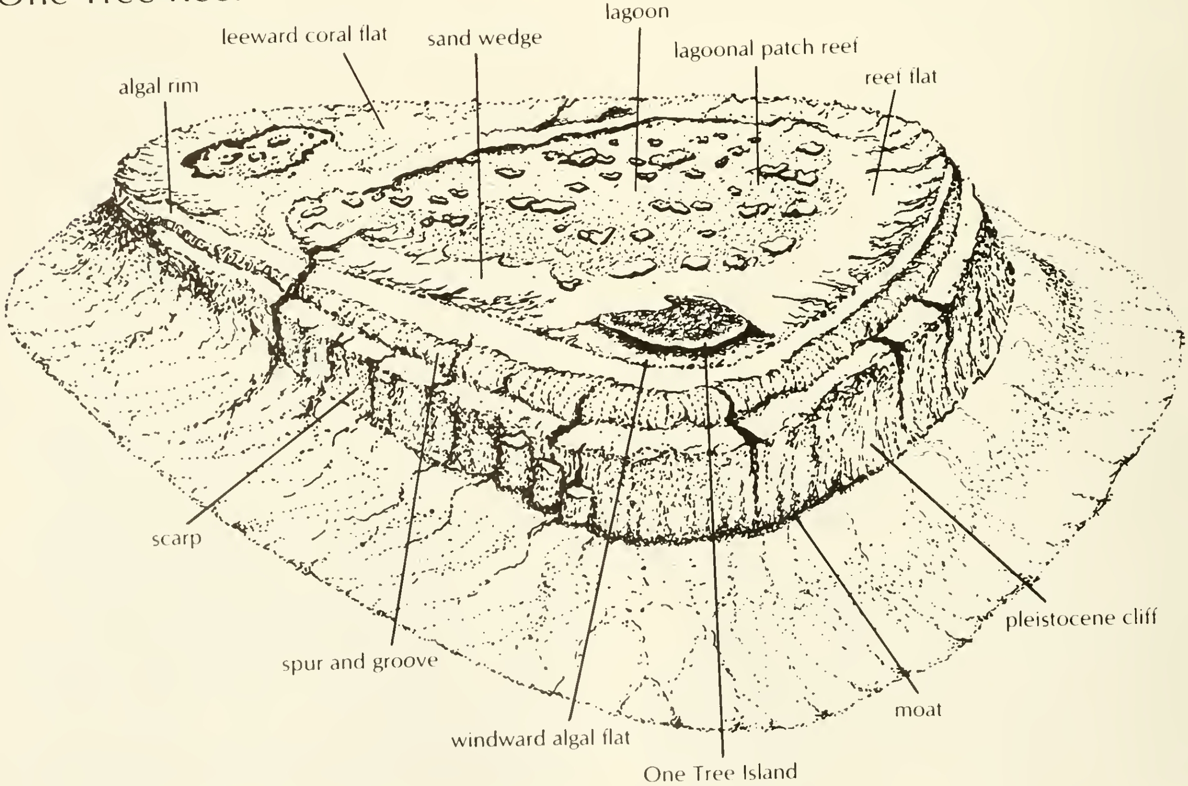


Figure 1. One Tree Reef (not to scale), showing major algal habitats and listing some of the major algal species found there. Below, the reef has all the classic features of a platform structure including a lagoon. One Tree Reef is in the southern Great Barrier Reef region, east of Gladstone.

One Tree Reef



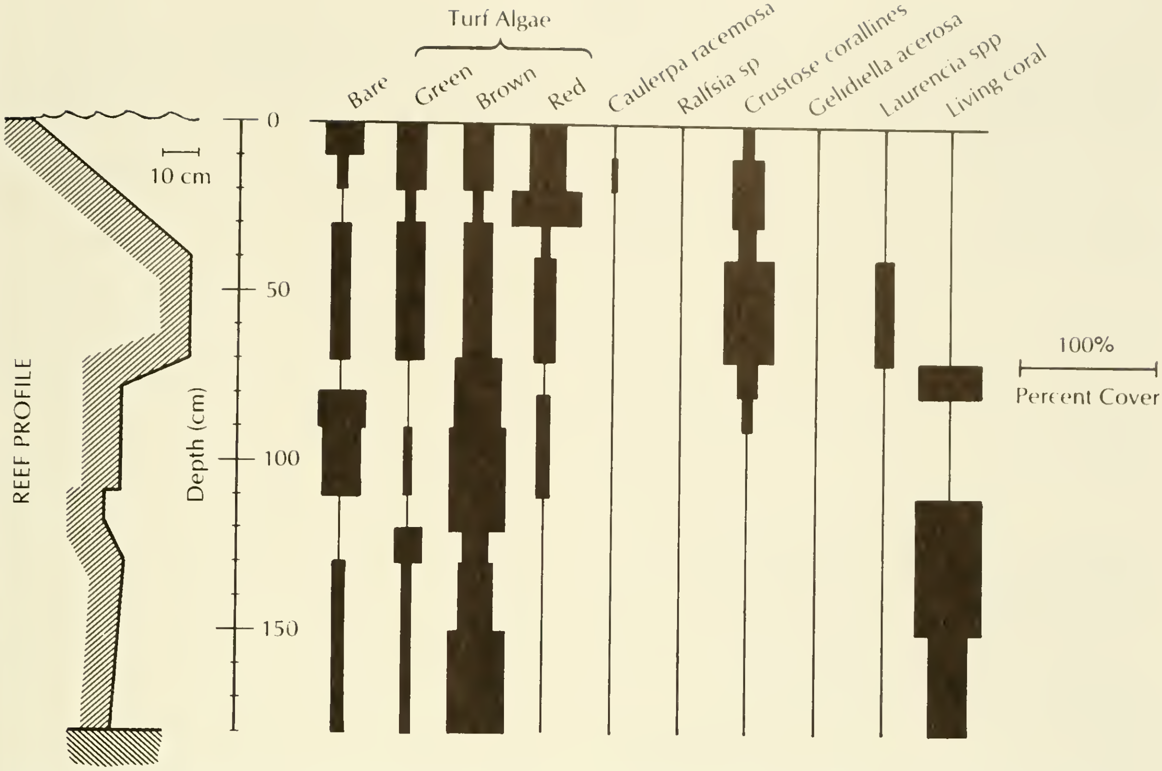


Figure 2. The vertical face of a "bommie" in One Tree Lagoon, showing the relative abundance of the benthic algae and coral (Redrawn from Borowitzka, 1981).

of large fleshy algae, and seagrasses are rare. However, in the deeper waters of the inter-reef areas, extensive beds of larger algae may be found. These may consist of algae, such as *Halimeda* spp., or may be mixed with seagrass. A new species of *Halophila* (*H. tricostata*) was discovered by dredging in the northern section of the Great Barrier Reef as recently as 1980. To date, little is known of these plant communities or why they occur there.

Inshore Reefs

There also is a marked difference between the algal communities of the offshore reefs and the inshore fringing reefs along the mainland, or those bordering large continental islands, such as Magnetic Island near Townsville. Large algae are much more common in the more turbid waters of these inshore reefs than on the outer reefs where the terrigenous influence is absent. In spring, a very diverse and extremely abundant algal flora may develop on the inshore reefs with larger algae, such as *Sargassum* spp., *Lobophora variegata*, *Galaxaura* spp., *Taonia* sp., *Botryocladia* sp., and many others, growing there. These algae achieve a quite large biomass, but they usually die back in late summer and are almost completely absent in winter.

Algal Roles

As indicated already, algae are an essential component of coral reefs and they play a crucial role in coral reef ecosystems. The various functions of algae in reef systems are illustrated in Figure 3.

Primary Producers

Algae, like all plants, capture light energy and use this to convert CO_2 into organic carbon in photosynthesis. Thus they are the primary producers in coral reefs. This organic carbon enters the reef food chain by a number of paths. Many of the algae are consumed by herbivorous zooplankton, crabs, fish, or echinoderms, while the symbiotic algae of corals and sponges release some of their photosynthetically fixed carbon directly to their animal partner. The organic carbon released by the algae into the water also is consumed by heterotrophic bacteria, which in turn may be consumed by a wide range of filter feeders. The algae are thus the primary source of energy for all other reef organisms.

Estimates of primary production on One Tree Reef have shown that three algal communities make the major contribution to the primary production of this reef. These are 1) the "turf algae" (that is, the small filamentous and fleshy algae growing over most of the dead coral and rubble on the reef), 2) the "sand algae" growing on the surface of the sand, and 3) the "symbiotic algae," such as the symbiotic dinoflagellates found in corals and clams, or the blue-green symbionts of sponges.

The rich animal life of coral reefs means that much of the algal biomass is consumed by various herbivores almost as fast as it grows, so that large accumulations of algae are rarely seen except in shallow waters where grazing pressure is reduced,

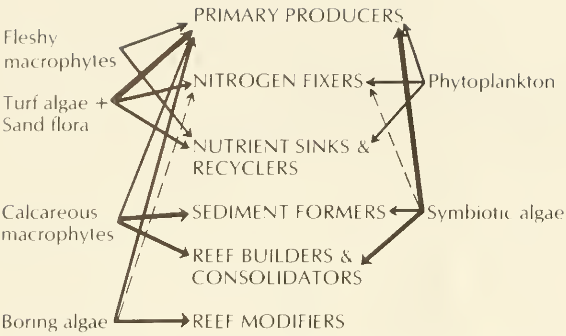


Figure 3. The main algal groups and their roles in the coral reef ecosystem. The thickness of the lines is an indication of the relative importance of that algal group to a particular process. Dashed lines indicate a possible role for that algal group.

or in spring, when algal growth can outstrip consumption by herbivores. The importance of grazing in structuring reef algal communities can be seen in experiments, such as when algae are protected from fish grazing by cages.

If patches of reef are caged, thick growths of algae soon develop. Similarly, algal growth is always more extensive in the territories of Pomacentrid fish, which actively defend their territories against other fish, thereby reducing the grazing pressure on the algae. The extent of fish grazing also can be seen in transplantation experiments. In one experiment, plants of *Sargassum* were transplanted from the reef flat, where grazing pressure is lower as a result of the lack of water at low tide, to the reef slope, where fish have access to the algae throughout the day. Transplanted *Sargassum* plants that were unprotected from grazing were all eaten within 24 hours, whereas *Sargassum* plants protected by cages remained intact.

The high grazing pressure in coral reefs maintains the algal community, especially the turf algal community, in a state of high productivity. Repeated grazing selects for fast-growing plants and prevents the build-up of dead plants that would shade actively growing plants and thus reduce their growth. Regular grazing also means that nutrients are not tied up in nonproductive biomass, but are made available to the growing plants via the excretory products of the herbivores.

Nitrogen Fixers

Primary production by algae not only involves the fixation of carbon but also the incorporation of inorganic nitrogen from dissolved nitrates and ammonium. While carbon dioxide forms a plentiful supply of carbon, there is no such ready supply of nitrogen.

The tropical ocean waters in which coral reefs occur are characteristically low in organic nitrogen sources. This has led to the well known anomaly first commented on by Charles Darwin of extremely rich and diverse coral reef ecosystems existing side-by-side with ocean ecosystems that are the marine equivalent of deserts.

During the last decade, the activity of nitrogen-fixing blue-green algae (*Calothrix crustacea*) on coral reefs has been widely studied. These microscopic members of the "turf" algae had previously been largely overlooked but in fact they fix considerable quantities of atmospheric nitrogen into ammonia, which is then used by the blue-green algae themselves to build organic matter. Because of the rapid turnover of these algae and the intense grazing on coral reefs, the organic nitrogen derived from nitrogen fixation is quickly distributed throughout the reef ecosystem.

At One Tree Reef, the mean nitrogen fixation activity is high by any standards: being not far short of that occurring in paddy fields or in fields of leguminous crops (Table 1). Is this, then, the answer to Darwin's anomaly? The answer is probably "*only in part*." The algae of One Tree Reef have carbon to nitrogen ratios of between 10:1 and 20:1. From this and the data on primary production, the annual budget for nitrogen can be computed: it turns out that nitrogen fixation accounts for only 20 to 40 percent of the overall annual need for nitrogen. The role of algae as nutrient sinks and recyclers is therefore important to further understanding of this apparent shortfall.

Nutrient Sinks and Recyclers

As shown previously, nitrogen fixation alone cannot account for the nitrogen needs of reef algae. Studies elsewhere have shown that algae are very adept at taking up available nutrients, such as phosphate and nitrogen, and converting this into algal biomass, or storing it in times of excess for later use when the nutrient supply is limited. If algae do this efficiently on reefs, then the nitrogen excreted by animals or released from dead remains of plants and animals would be recycled and not lost by tidal currents to the surrounding oceans. Thus, nitrogen fixation by blue-green algae would merely "top up" the system as some inevitable losses occurred to the ocean.

Alternatively, the surrounding ocean itself may be a source of nitrogen. Recent evidence suggests that the rich life of coral reefs may be partly dependent on periodic upwellings of nutrient-rich deep water. The algae would be the likely traps for these nutrients, releasing them later to the other reef organisms either by grazing or

Table 1. Rates of nitrogen fixation by various biological systems. The rates quoted are for maximum rates under ideal conditions, with the exception of the estimate for One Tree Reef, which is based on seasonal changes and includes areas of poor nitrogen fixation, such as the lagoon floor.

	Kg $N \cdot ha^{-1} \cdot yr^{-1}$
Azolla **associations**	**80–600**
Red clover	**80–300**
Other leguminous crops	**20–100**
Polar/subpolar soil cyanophytes	**20–100**
Rice paddies, soil cyanophytes	**10–80**
Trichodesmium **phytoplankton blooms**	**5–30**
Coral reef cyanophyte communities	**1–330**
Annual mean, One Tree Reef	**8–12**

remineralization following death. The algae thus act as nutrient "sinks" and recyclers.

The various symbiotic algae in coral reefs also conserve the nitrogen reserves of their animal partners by taking up waste nitrogen products, such as urea and ammonia, and eventually re-releasing it to the animal partner in the form of amino acids and other N-containing compounds.

Reef Formers

The algae are an essential component of that group of organisms that actually forms the physical limestone structure of these biotic reefs. The reef formers can be separated into three functional groups: the cementers, the structural element formers, and the sediment formers.

The cementers are crustose red coralline algae, such as *Porolithon onkodes, Hydrolithon megacystum*, and *Paragoniolithon* spp., which have cell walls that are heavily impregnated with the calcite crystal isomorph of $CaCO_3$. These algae grow over the reef structure and cement it, forming a hard skin over the softer limestone. They are most developed in areas of high wave energy, such as the upper reef slopes and reef crest, where they form a solid barrier resisting the erosive action of the ocean swells. Cores through the reef crest of a number of reefs have shown that the coralline algal layer may be many meters thick. Without the solid limestone barrier formed by these algae, the structure of the reef would soon be worn away by the pounding of the ocean swells.

The structural element formers are the dinoflagellate symbionts (zooxanthellae) found in almost all corals. Together with their animal partner, these algae form complex skeletons of aragonite, another crystal form of $CaCO_3$. Although not as hard as the calcite produced by the coralline algae, the branching aragonite skeletons of corals form the basic three-dimensional structure of coral reefs and provide the necessary habitats for many other plants and animals.

The spaces between the coral skeletons are filled with the smaller skeletal remains of many other calcareous organisms, such as foraminifera, echinoderm spicules, mollusk shells, and so on. A large component of this sand is made up of the fine needle-like aragonite deposits of calcareous green algae, such as *Halimeda* and *Udotea*, and red algae, such as *Galaxaura* and *Nemalion*. Up to 80 percent of the sand fraction of portions of reefs, such as Heron Reef, may consist of the skeletal remains of algae.

Reef Modifiers

The algae not only participate in the formation of new reef limestone, but some of the algae also contribute to the breakdown processes of the reef limestone. These are the boring algae, which penetrate into the dead skeletons of corals and other limestone forming organisms, and slowly break these down into smaller fragments. These smaller fragments become part of the sand fraction and fill the interstitial spaces between coral skeletons thus modifying and consolidating the reef structure.

Symbiotic Algae

Symbiotic algae are ubiquitous on coral reefs. Associations occur with all kinds of animals and the list appears to be by no means complete since discoveries of new associations are being made every year. Reef-forming corals are functionally dependent on dinoflagellate algae (zooxanthellae), which provide organic carbon from photosynthesis and aid in nitrogen conservation. Zooxanthellae also are found in the mantles of the giant clam *Tridacna*, and a wide variety of other reef animals. Blue-green, green and red algae, diatoms, and cryptomonads have all been found in symbiotic associations and the list of algal groups involved continues to grow.

Recent work in this area has even brought to light an alga which could not be placed in any known algal group. For this reason, Ralph Lewin of the Scripps Institution of Oceanography in California created a new division, the Prochlorophyta, to accommodate the find. The alga is *Prochloron* sp., a large, single cell prokaryote, differing from blue-green algae in having no phycobiliprotein pigments but possessing chlorophyll *b*, in addition to chlorophyll *a*. It is found in a number of didemnid ascidians, which are common on reef crests and outer reef slopes.

Phytoplankton

Phytoplankton are generally not very abundant in coral reef ecosystems with the exception of the blue-green *Trichodesmium* spp., which forms large brownish windrows of many kilometers in length floating at the surface of the ocean. *Trichodesmium* remains an enigma in that it is abundant in all tropical areas of the world yet little is known of its biology. The algae grows from small filaments that appear to develop deep in the water column and which only aggregate and float to the surface as they age. The floating accumulations observed consist largely of senescent colonies. *Trichodesmium* has been reported to fix nitrogen, despite the fact that it does not contain heterocysts; however little is known of its role in coral reef systems.

Other common phytoplankters are dinoflagellates and diatoms, many of which also harbor symbiotic blue-green algae.

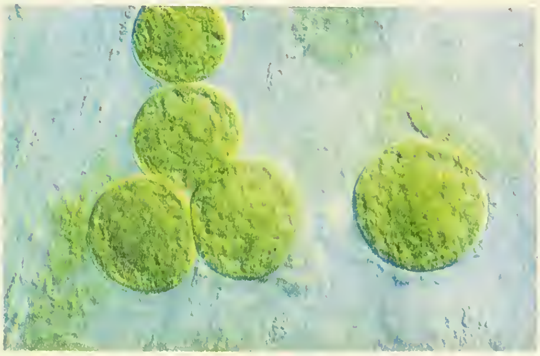
Algae and Man

Aside from the importance of algae in the formation and maintenance of coral reef ecosystems and thus to man, the algae also affect man in other ways.

The food-poisoning called ciguatera, which is contracted by eating affected fish, has its origins in a small benthic, single celled dinoflagellate *Gambierodiscus*, which produces a potent toxin, ciguatoxin, that fish accumulate. Similarly, a fatal poisoning called paralytic shellfish poisoning, is caused by the accumulation of cells of the toxic dinoflagellate *Gonyaulax* by shellfish. When these shellfish are consumed, poisoning, which is often lethal, occurs. At this time, no cases of paralytic shellfish poisoning have been reported in

Chlorodesmis fastigiata, *growing on the side of a bommie in One Tree Lagoon. (Photo courtesy of A. W. D. Larkum)*

The ascidean Didemnum molle, *growing on dead* Acropora *among the turf algae covering the coral skeleton. (Photo courtesy of R. Lethbridge)*



Australian waters, although cases have been reported in New Guinea and elsewhere.

The algae also are a potentially important source of new chemicals and drugs. Many of the algae produce a unique range of biologically active molecules that have been found to act as antibiotics, pharmacologically active substances and possible anti-cancer compounds. Therefore, there is extensive study of the chemistry of tropical algae in various parts of the world to isolate these compounds and to test their efficiency in human and animal medicine. Tropical reef algae seem to be particularly good sources of such substances.

The possible reason for this is the high grazing pressure. Algae can reduce grazing pressure by either growing in habitats inaccessible to many grazers, or by producing grazing-deterring substances. Many of the biologically active molecules seem to belong to the latter category. For example, the conspicuous green alga *Chlorodesmis fastigiata* produces an acyclic diterpene that causes avoidance behavior in herbivorous fishes and which also is quite toxic. Similar substances have been isolated from some of the larger reef algae, such as *Udotea, Halimeda, Caulerpa*, and *Laurencia*. The algal symbionts of sponges, such as the *Oscillatoria symbiotica* found in the common sponge *Dysidea herbacea* have been implicated in the synthesis of the toxic halogenated metabolites produced by sponges.

Conclusions

Algae are an integral component of "coral" reefs. A better term for these reefs, therefore, might be "biotic" reefs. In a basic sense, reefs such as those of the Great Barrier Reef can be considered to be driven by the photosynthetic activity of the algae. Corals should be considered to be just as much plants as they are animals. Although reef algae are not normally as spectacular as the animals on coral reefs, nor as large as their temperate counterparts, they are an important and major part of reefs.

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Selected References

Borowitzka, M. A. 1981. Algae and grazing in coral reef ecosystems. *Endeavour*, N. S., 5: 99–106.

Borowitzka, M. A. 1983. Calcium carbonate deposition by reef algae; morphological and physiological aspects. *In*: Perspectives on Coral Reefs, D. J. Barnes, ed. pp. 16–28. Australian Institute of Marine Science: Townsville.

Hatcher, B. G., and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.* 69: 61–84.

Hillis-Colinvaux, L. 1980. Ecology and taxonomy of *Halimeda*: primary producer of coral reefs. *Adv. Mar. Biol.* 17: 1–327.

At left, Prochloron didemnii, *the unique prokaryotic symbiont of the ascidean* Didemnum molle. *(Photo courtesy of A. W. D. Larkum)*

The Crown of Thorns Starfish

by John Lucas

The author, gingerly holding a Crown of Thorns starfish.

The Crown of Thorns starfish is *the* major scientific and management issue of the reef. Because of recent publicity, one could be forgiven for thinking that the Crown of Thorns starfish is a very recent species, and that it suddenly appeared a few decades ago as a coral predator causing widespread consternation and fear for the future of coral reefs, including the Great Barrier Reef. In fact, however, this is far from the truth. The Crown of Thorns starfish (*Acanthaster planci*) has been known to scientists since the 17th century. Long before this, it was undoubtedly known to the people of the tropical Indo-Pacific region, some of whom have special names for the starfish. For instance, the Japanese call it "One-hito-de" (devil starfish), obviously referring to its poisonous spines, and their painful effect on anyone unfortunate enough to get pierced by them.

The Crown of Thorns starfish is a normal member of the coral reef communities of the Great Barrier Reef and throughout the tropical and subtropical regions of the Indian and Pacific Oceans. It also is found in the Red Sea and in the Gulf of California (Sea of Cortez). It does not occur in the Atlantic Ocean; the Caribbean coral reefs are free of this predator. Thus, there was recent concern that proposed enlargement of the Panama Canal could allow the starfish's planktonic larvae to be carried through to the Caribbean, where it probably would become established.

An Extraordinary Starfish

Although a typical member of reef communities, the Crown of Thorns starfish is not an ordinary starfish: it has some extraordinary features. First, its size: adult starfish are typically 30 to 40 centimeters in diameter, but some very large specimens are seen occasionally on the Great Barrier Reef. There have been accounts of specimens five feet (160 centimeters) in diameter, but the largest specimens officially reported are about 70 centimeters in diameter. Second, the Crown of Thorns starfish has numerous arms—usually about 15—but ranging from 7 to 23 arms. Other starfish typically have 5 arms, with body organs, guts, gonads, nerves, and so on, repeated in each arm—a body pattern known as pentamerous symmetry. The Crown of Thorns briefly passes through a phase of being a tiny 5-armed starfish, but as it develops, it adds arms and reaches its adult arm number at about 6 months of age. Third, there are long poisonous spines covering its upper surface. Other starfish have spines, but they are usually short and blunt, while those of the Crown of Thorns are long, sharp, and spear-like.

There are other unusual features of this starfish that are not as obvious as the previous three. These include its very high fecundity (reproductive output of eggs) and the presence of strong wax-digesting enzymes in its stomach. The high fecundity is partly a function of its large size; for example, female starfish of 35 and 40 centimeters diameter release more than 20 and 50 million eggs, respectively, each breeding season. These are enormous outputs of eggs for starfish. The presence of strong wax-digesting enzymes relates to the Crown of Thorns' diet of corals, which store waxes (for example, cetyl palmitate) as a major energy reserve.

Morphology

Other external features of the Crown of Thorns starfish are a large central mouth, rows of tube feet

The underside of an arm showing the tube-feet used in locomotion. (Photos by the author unless otherwise indicated)

with suckers down a groove on each arm, and rows of blunt spines along each arm on the undersurface. On the upper surface are a number of structures that can only be seen by careful examination. Among these are an anus, situated near the middle of the central body region (the disk), a number of madreporites (small stony bodies occurring around the outer portion of the disk) and numerous pedicellaria (pairs of tiny pincer-like spines that are used to clean the surface). Papulae are small finger-like sacs that project through the surface and are used for respiration. Then, at the tip of the arms, there are small, pink, light-sensitive structures surrounded by specialized tube feet, the sensory tentacles that wave about and detect chemical stimuli. The color of the Crown of Thorns starfish varies from subdued green-red combinations to grey-green.

As a group, starfish are noted for their regenerative powers after damage. Crown of Thorns starfish, however, have limited powers of regeneration. Its internal skeleton is not as strong as is that of many other starfish. Therefore, when badly damaged, they are inclined to fall apart and become diseased. Damaged individuals with regenerating arms are common, and two halves may survive when an individual is bisected, but fragments and detached arms will not regenerate to whole Crown of Thorns starfish.

Behavior

Because the Crown of Thorns starfish is radially symmetrical (its structures are repeated around a central vertical axis), it has no front or back and moves with any of its arms leading. The hundreds of tube feet under its arms moves the animal slowly, at a rate of centimeters per minute. Each tube foot reaches forward and attaches to the substrate by its sucker. The tube foot contracts, pulling the starfish forward, then it detaches and reaches forward again. How the literally brainless starfish coordinates these movements of hundreds of tube feet working at various angles to the arms is a puzzle.

The starfish feeds by forcing its convoluted stomach out through its mouth. The starfish locates itself on some suitable coral, everts its stomach, and then spreads it out over the coral to cover an area almost equal its own diameter. It secretes digestive enzymes onto the coral tissue and then absorbs the digested tissue as it withdraws its stomach. As the process takes hours, the Crown of Thorns feeds just once or twice a day even when coral is plentiful. Since reef-building corals consist of a thin veneer of tissue on a calcareous skeleton, the feeding process removes the veneer of tissue and leaves an area of white skeleton. White feeding scars are often the first evidence observed of the presence of Crown of Thorns starfish in an area of coral.

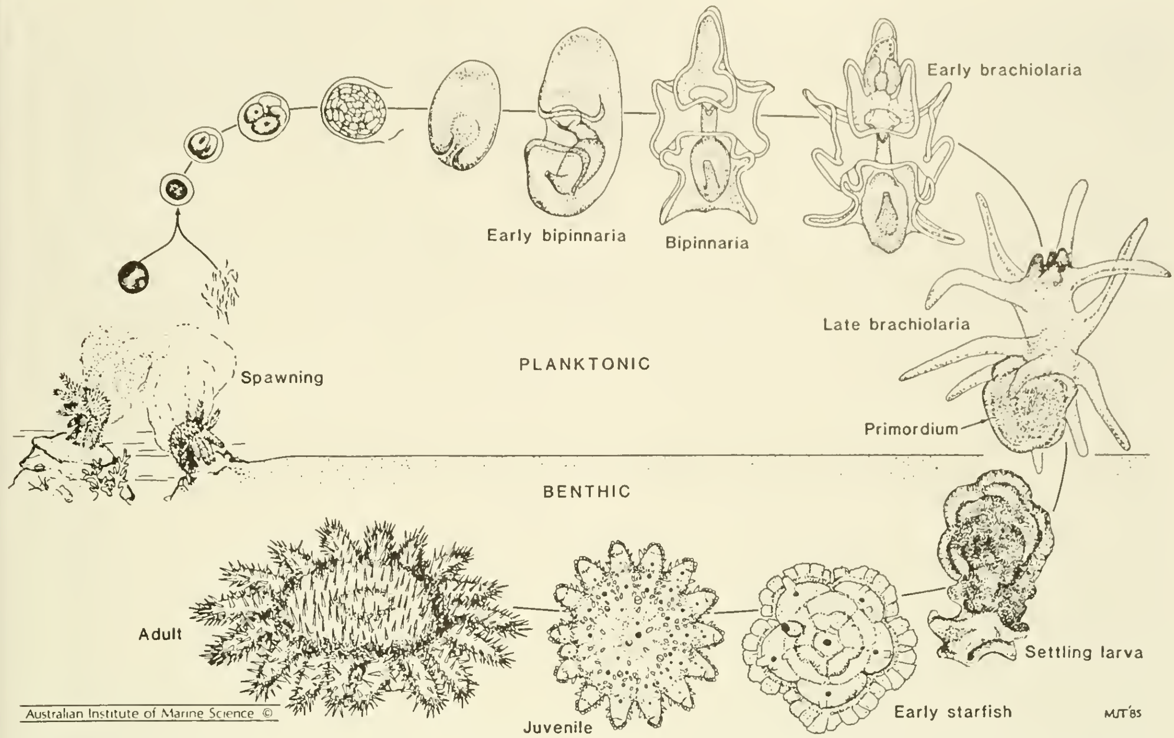
Most likely, the Crown of Thorns starfish perceives its environment mainly through chemicals in the water. Although there are light receptor organs (optic cushions) at the tip of each arm and probably light sensitive cells over its body surface, none of these are capable of producing visual images. These light receptors indicate light intensity, enabling the starfish to detect daylight.

The starfish detects its food, perhaps the presence of other starfish, and certainly the presence of spawn from other starfish, by chemoreception. Chemoreceptors are concentrated in the sensory tentacles at the tips of the arms and these wave actively on the leading arms as the starfish moves. They can pick up the presence of a feeding starfish several meters or more away.

Typically, the starfish remains hidden beneath coral during the day and is active at night. This behavior changes when the starfish are numerous and competition for coral food forces them to seek food day and night. At times the starfish aggregate, perhaps because they are attracted to other feeding starfish by the chemicals released from coral during feeding or, perhaps they release chemical attractants for other starfish.

Chemical Defenses

All the soft tissues of the Crown of Thorns starfish contain saponins, surface-active or detergent-like substances. In fact, saponins are present throughout the life-cycle in the eggs, larvae, and juvenile starfish, serving as a chemical defense. Saponins are toxic at low concentrations in solution, but their presence in the starfish is not to poison predators, but rather to discourage them. Saponins impart a bad taste and irritate wounds caused by the starfish's spines. Human injuries from punctures by the Crown of Thorns spines are more painful than would be expected from the puncture alone because the spines are coated with saponin-containing tissue. In



The life-cycle of the Crown of Thorns starfish. (©1985 Australian Institute of Marine Science; used with permission)

addition, the brittle spines often break off in the wound if they penetrate deeply.

Coral Predation

The Crown of Thorns starfish is not the only species that eats corals. The coral predators include a variety of fishes (belonging to at least 12 families), crabs, nudibranch, and gastropod mollusks, an encrusting sponge (*Terpios* sp.), worms, and at least one other starfish, the pincushion starfish (*Culcita novaeguineae*). What distinguishes the Crown of Thorns from these other coral predators is the extent of coral deaths that it causes during phases of high population densities. None of the other coral predators has been reported to cause significant levels of coral damage in the Great Barrier Reef region. Only two of them, the gastropod *Drupella* and the starfish *Culcita*, have been observed to kill even small coral colonies.

This is a little surprising when one considers that corals represent a major food resource. It is not unreasonable to think of "meadows" of corals on the surfaces of coral reefs. It would seem then that more animals should be engaged in harvesting these "meadows." The reason they are not may be because the coral tissue is a thin veneer on the surface of and within a massive calcareous skeleton. A starfish is well-suited to feeding on a surface veneer of tissue by virtue of its mode of feeding: everting the stomach over the surface and digesting the tissue *in situ*. The problems of this mode of feeding in a coral reef environment are that it is a slow process and that, while engaged in feeding, the starfish exposes itself to a range of predators, especially bottom-feeding predatory fishes. A variety of starfishes inhabit coral reefs, but only three of them—*Culcita*, *Linckia*, and the Crown of Thorns—live conspicuously. Each of these has particular adaptations to deal with potential predators, those of the Crown of Thorns being its battery of long, sharp spines and saponins.

Reproduction

There are about equal numbers of males and females in Crown of Thorns populations. Males and females are identical in external appearance. Their gonads develop from late winter (August) as water temperature rises and they breed in mid-summer (January) in Great Barrier Reef waters. Spawning has been observed only infrequently. The starfish climbs up onto high points, such as the upper branches of corals, where they shed their eggs or sperm into the water through pores on the upper surfaces of their arms. Many starfish in a group will spawn simultaneously as they are stimulated by the presence of spawn from other animals.

Tens of millions of the tiny eggs (1.2 millimeters in diameter) are released by large females. Sperm swim to locate eggs. As each egg is penetrated by a sperm, its membrane swells away from the yolk to prevent further sperm from entering. The eggs float in the water and are carried away from the breeding site by water currents. The eggs and the larvae that soon develop from them are temporary members of the plankton of the Great Barrier Reef waters. Thus, they are carried away by water currents; sometimes traveling over the surfaces

The Significance of the

Corals are to a coral reef what trees, shrubs, herbs, rocks, and local topography are to a forest. Much more than vegetation, which simply covers a landscape, corals are both the clothing of the reef and the architects of its complex form—the very foundation of its teeming abundance and diversity of life.

Or are they? These same corals that are so fundamental to the reef ecosystems of the Great Barrier Reef are presently being eaten in vast numbers by the large, coral-feeding Acanthaster planci, *the Crown of Thorns starfish. What becomes of the coral community, the reef structures, and the dependent biotic communities? And how should we view the Crown of Thorns starfish? As a demolition team that tears down the national heritage, or as renovators which strip off a veneer before it gets too shabby? To address these questions, it is necessary to consider the impact of the starfish in the context of both the reef-building process and the types of disturbances that occur in the absence of feeding outbreaks.*

Coral Dynamics

The contribution of corals to growth of reef features is not a simple additive process, where successive generations of corals merely grow on the dead skeletons of their predecessors. This simple picture is true in few situations. Rather, coral communities exhibit all the short- and long-term changes of recruitment, growth, interaction, and death typical of any natural community. More often than not, an individual or piece of coral is not incorporated into the framework of the reef, evidence that the forces of destruction are always present on reefs. Some corals are broken off by storm waves, especially when a multitude of different boring organisms have weakened their limestone skeletons. Others (slower-growing corals) are overgrown or overtopped by faster-growing species, which may cause death through either interference or shading. A whole catalogue of other causes of death could be given.

Whether or not the dead skeleton is dislodged from its place of growth, it is seldom long before the area becomes reoccupied by a succession of algae, other sessile organisms, and then, perhaps, by various species of coral. These coral may derive from planulae that settle in the area, from adjacent corals, or from attached or unattached fragments of colonies that regenerate in the area. The "rules" of succession and the role of chance in such situations vary, depending on the size of the disturbed area, the intensity of the disturbance, the location on the reef, and the coral species involved.

Against this background of chronic patchy disturbance and localized secondary succession, there is a component of coral communities that, in human time scales, seems to transcend such fluxes. This component consists of large corals of a hemispherical or other massive form that can live for centuries. The larger they grow, the less vulnerable they seem to become to natural mortality. Such corals sometimes are numerically dominant, and if they are of great size, contribute more than any other living or non-living component to local topographic relief. Elsewhere, they are scattered sparsely, or perhaps in small local aggregations, throughout communities consisting primarily of more ephemeral corals with life expectancies measured in years to decades. In these situations, they constitute striking exceptions to the usual cycle of short-term localized disturbance and secondary succession.

Crown of Thorns

Twice in recent years, the Crown of Thorns population explosions have inflicted enormous levels of coral mortality over large areas of reefs in the Great Barrier Reef. The ecological significance of the phenomenon is not clear, and is the subject of both investigation and dispute among reef scientists. Crown of Thorns starfish moving through coral communities at densities of thousands per hectare can reduce the quantity of living coral tissue to only a few percent of the normal—90

of coral reefs, other times being in open ocean far from reefs.

Life Cycle

Within a day, the fertilized egg hatches and a gastrula larva emerges. This is an extremely simple sack-like larva with the beginnings of a gut and cilia, beating hair-like structures, by which it swims. The gastrula develops into a bipinnaria larva that in turn develops into a brachiolaria larvae, both characteristic larval stages of starfish. The larvae are about 1 millimeter long; they are transparent and they swim with their long axis vertical, rotating slowly about the axis. They swim and feed using cilia, which are organized into bands, and their food is microscopic algal cells (phytoplankton). In the latter part of development, an opaque structure develops at the posterior of the brachiolaria larva. This is the developing starfish or starfish primordium.

After several weeks in the plankton, if

Crown of Thorns Starfish

percent devastation is not uncommon. In Japan, bounties have been paid to divers to protect reefs. In some areas of the GBR, copper sulfate injections have been used to kill the starfish.

This widespread, intense, and synchronous disturbance contrasts markedly with the patchy, chronic, and localized disturbances previously described and changes the essential ecological character of the affected areas. Where reef-building corals formerly prevailed, a swift shift to algal dominance follows. Scientists have seen in the 15-year interval between the two recent outbreaks (the late 1960s and the early 1980s) that high coral cover can be re-established in that time. What is not known, however, makes a far longer list:

- Are outbreaks a normal part of the population dynamics of *A. planci*, and if so, is the recently observed 15-year interval also normal?
- Do outbreaks affect the diversity of hard corals present? (Both an increase and a decrease in diversity may be argued on theoretical grounds.)
- Are reef-building activities of corals affected by outbreaks? Again, both a suppression and an acceleration of localized reef growth may be argued.
- Can the massive corals sustain the levels of damage observed in recent outbreaks, given that the replacement time for individual corals may be as high as several centuries?
- Are there secondary effects on other reef biota, such as favoring of other benthic groups that are free to settle and grow without interference from a high cover of corals, or disappearance of fish that previously depended on live coral to provide microhabitats and/or food?

The damage caused by A. planci *may be compared to the destruction caused by a forest fire. Most observers would assess the severity of a forest fire by the level of damage to the trees, giving a lesser value to an undergrowth that can regenerate itself relatively quickly from dormant seeds, rootstock, and the like. Like the forest undergrowth, the more ephemeral coral species regain their dominance, in this case from growth of new individuals derived from planktonic larvae, and from regeneration of an abundance of surviving remnants. And, as with the forest fire, scientists attribute a greater significance to the death or damage of the very old, large, and slow-growing corals, some so huge that they must have already been giants when Captain Cook first explored these waters more than 200 years ago. Although they seem to be among the least preferred foods of* A. planci, *the populations of these corals do bear the scars of the outbreaks, with some large colonies killed and many injured.*

Assessing the ecological significance of the impact on coral communities is complex. Many characteristics of species involved need to be taken into account: an apparently sporadic success in colony establishment despite an enormous and regular reproductive output; an impressive ability of some species to regenerate entire colonies from small remnants of living tissue; the protection which the size of large species seems to confer against starfish predation; the interactions with competitors, predators, and symbionts; and, very likely, the intervention of further disturbances. Ecological theory and recent coral research on the Great Barrier Reef have provided an unsurpassed foundation for the important and exciting ecological research that is now underway.

The Crown of Thorns starfish is usually cast in the role of the villain. Maybe the benefit of hindsight will confirm this view, when we are left with a reef that is but a poor caricature of what once was. Or maybe time will decide that what we really saw was a passing renovator, making a terrible mess in the short-term, on the way to home improvements in the longer term. For it is the long-term persistence of the system with all its richness and complexity that really matters.

—by T. J. Done, AIMS

development has been successful, the larva has a large starfish primordium on its posterior. At this stage, the larva must be carried over the surface of a coral reef, where it will attach to algae-coated surfaces, such as coralline algae. There follows a most dramatic metamorphosis over several days, when all the larval structures are absorbed into the tiny starfish.

The initial starfish is cream-colored, has five arms, and is about 0.7 millimeters in diameter. It is far too tiny to feed on coral. In fact, coral polyps would feed on it, or damage it with their nematocysts. Instead, the starfish feeds on algae, especially the abundant coralline algae. It feeds by extruding its stomach over the algae in the same manner as the adult starfish feeds on coral.

The juvenile starfish feeds on algae for about six months while growing to about 10 millimeters in

Giant Clams

One of the most spectacular and enthralling sights when diving on the Great Barrier Reef is a giant clam, its brilliantly-colored mantle fully exposed over the convoluted edges of the massive shell. These clams are the largest bivalve mollusks in the world, some growing over a meter long and weighing more than 300 kilograms.

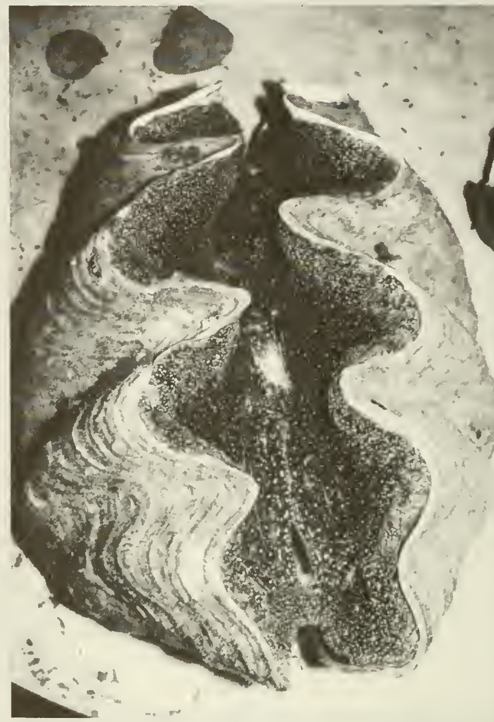
Seven species of giant clams (family Tridacnidae) inhabit the tropical Indo-Pacific region, and six of these are found on the Great Barrier Reef. All species need clear, warm, shallow waters that have a high salinity content. Typically, they live among the corals or on sand and coral rubble. The largest giant clam, Tridacna gigas, *can live in 20-meter-deep waters, but also can be exposed at low tide.* Tridacna derasa, *the second largest tridacnid, grows to more than 50 centimeters in length, and is common in oceanic environments, particularly in the 4 to 10 meter deep waters of the outer reef edges.*

The scaley or fluted clam, T. squamosa, *usually inhabits sheltered environments, such as back-reef lagoons, in depths to 15 meters.* T. maxima, *one of the most common species, is found on reeftops and slopes, often partially embedded in coral. The latter two species grow to a maximum of about 40 centimeters long. The boring clam,* T. crocea, *is the smallest of the giant clams. Fully embedded in coral boulders, just the top edge of its shell and its mantle are visible. The most abundant on the interior reef flat, it may reach 15 centimeters in length.* Hippopus hippopus, *the horse's hoof clam, resides on reef flats down to 6 meters deep and grows about 45 centimeters long.*

Life Cycle

All giant clams are hermaphrodites, releasing both eggs and sperm into the seawater, where fertilization takes place. Sperm are spawned first, followed by hundreds of millions of microscopic eggs. The release of gonadal products from one clam apparently triggers spawning by others nearby, thus ensuring cross-fertilization. Reproductive success, therefore, most likely depends on a critical minimum population density of breeding adults.

The early life histories of all clam species are similar. Fertilized eggs develop into planktonic trochophore larvae, which later become free-swimming veliger larvae. The larval life span is comparatively short; after 7 to 12 days,



An adult Tridacna gigas. *The largest of the giant clam species, it may grow to more than 1 meter in length.*

they settle onto the reef substrate, where they metamorphose into juvenile clams 0.2 millimeters in length. Initially, the juveniles are mobile, crawling by means of a well-developed foot until they find a suitable substrate for attachment by byssal threads. These threads gradually are lost in the largest three species, which then rely on their own weight to maintain position.

Food Sources

Giant clams have two sources of food. They filter-feed in phytoplankton from the surrounding seawater and also obtain nutrients from specialized algae, the Symbiodinium *species. These algae, commonly called zooxanthellae, live symbiotically within the exposed mantle tissue of the clam. They obtain both energy from the sun and nutrients from the seawater, and photosynthetically produce carbohydrates, which are released directly into the tissues of the clam. In turn, the zooxanthellae use the clam's waste products.*

Only larvae and newly-metamorphosed juveniles are entirely dependent on exogenous phytoplankton as a food source. During these early life-cycle stages, the zooxanthellae are ingested from the surrounding seawater and *move by unknown means to the enlarged mantle tissues. Once the symbiotic relationship has been established, giant clams obtain almost all of their nutritional requirements from the zooxanthellae. Therefore, they are capable of a high degree of autotrophy (self-feeding) and can thrive in the nutrient-deficient waters of the reef. This symbiotic relationship explains both the large size attained by the giant clam and its restriction to shallow, sunlit waters.*

Recent studies have shown that, contrary to previous beliefs, giant clams are relatively fast-growing. Growth rates of juveniles are rapid after they have established symbiosis; T. gigas *can reach more than 10 centimeters in length in the first year, with annual growth increments of 8 to 12 centimeters during the next few years. The clam may even attain a length of more than 60 centimeters in 10 years. Other species are slower-growing, such as* T. derasa, *which reaches 5 centimeters after the first year.*

Because the sedentary giant clam is conspicuous in shallow water, it is easily harvested, making it vulnerable to over-exploitation. Stocks of giant clams have been severely depleted throughout much of their range, becoming extinct in some areas. The two largest species, T. gigas *and* T. derasa, *are listed as threatened by the International Union for the Conservation of Nature.*

The principal causes of the population decrease are over-fishing by local peoples and poaching by foreigners. Clam meat, an important component of the diets of Indo-Pacific Islanders, has been harvested on a subsistence level for centuries. The adductor muscle, which comprises 10 percent of the flesh weight, is in high demand in Southeast Asia as a high-priced delicacy. In addition, the shell is coveted as a decoration.

In Australia, giant clams are protected by law, making population densities on the Great Barrier Reef much higher than those of other countries. Several reefs support more than 30 T. gigas *or* T. derasa *per hectare, with* T. crocea *densities regularly exceeding 100 animals per square meter. Even so, giant clams occasionally are taken in enormous quantities by Taiwanese fishermen.*

Commercial Cultivation

Research on giant clam biology in recent years has highlighted the mollusk's potential for commercial cultivation: it spawns prolifically, the larvae and juveniles are amenable to high density cultivation in artificial conditions, growth rates of the larger species are high, it does not require supplementary feeding after the first month, and well-established markets already exist.

Significant advances in mass culture techniques, particularly for T. derasa, *have been made at the Micronesian Mariculture Demonstration Center in Palau, where more than 100,000 juveniles were produced in 1984. On the Great Barrier Reef, research into giant clam mariculture techniques is underway at Orpheus Island, near Townsville, and is funded by the Australian Center for International Agricultural Research. A commercial hatchery also has been established on Fitzroy Island, off Cairns.*

Giant clam farming currently is receiving enormous interest, and, if it proves to be economically feasible, a new industry undoubtedly will arise in the Western Pacific region. Many depleted reefs possibly can be restocked with farm-reared juveniles, thus reversing the increasing trend toward extinction of this important component of coral reef communities. If this does not occur, then the Great Barrier Reef may well be the last bastion for the largest bivalves ever to exist.

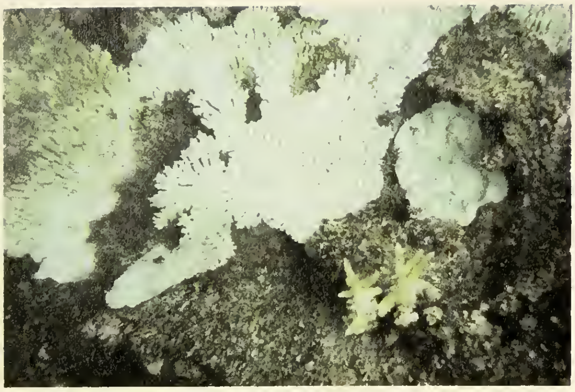
—Christine Crawford and Warwick Nash,
James Cook University, Townsville.

diameter and adding arms to reach its adult number. Then, it begins to feed on coral polyps.

Feeding on coral it grows rapidly, reaching about 5 centimeters at one year of age, 20 centimeters at two years of age, and 30 plus centimeters at three years of age. However, if it cannot find coral to feed on, it remains very stunted in size.

Crown of Thorns starfish reach sexual maturity at 2 to 3 years of age. Growth rate slows down after they reach sexual maturity because of the diversion of energy from body growth to production of gametes. In laboratory studies, the starfish ceased growing after 3 years of age, and finally went into a senescent phase after 5 years. In the senescent phase, they ceased gonad development and actually shrank somewhat in size. Most died before 8 years of age. It has not been possible yet to confirm these observations of cessation of growth and senescence in the field. A major problem for growth studies and population studies in the field is that no effective tagging method has been developed. The Crown of Thorns starfish is a master of getting rid of foreign objects from its body.

What are we to make of the occasional 70-centimeter starfish that occur on the Great Barrier Reef? Are they very old animals that kept growing or



White coral skeleton remaining after Crown of Thorns starfish have fed on the coral tissue.

Undersurface of Crown of Thorns starfish showing its stomach partly everted through its mouth.

Young juvenile Crown of Thorns feeding on coralline algae and leaving circular white feeding scars on the pink alga (Photo courtesy of L. Zann).

are they starfish that grew especially rapidly during the years of growth? The relationship between size and age is a loose one because of the strong influence of food on growth rate: thus bigger animals may not be older animals.

Mortality

One may ask: "What happens to the millions of eggs that are released by each female each summer?" The Crown of Thorns starfish is exceptional among starfish in its fecundity, but other marine invertebrates also release millions of eggs. The usual pattern of survival in these cases is for extremely heavy mortality of the eggs and early developmental stages, so that only a very small proportion survive even a few weeks of development. This is likely to be the case for the Crown of Thorns, but there are no field observations of larvae and early juvenile starfish to confirm this.

There are considerable problems connected with obtaining observations. The larvae are localized in time and space, and an extensive sampling program in Great Barrier Reef waters failed to locate more than a few, if any, larvae. The occurrence of juvenile starfish is also very localized, and looking for them in a coral reef community is like "looking for needles in a haystack," without being sure that the needles are there in the first place.

Eggs and Larvae

One of the first factors in mortality is whether the eggs are fertilized or not. Where starfish are aggregated it is likely that there will be high levels of fertilization as clouds of eggs and sperm are released in close proximity. However, where the starfish are at low densities, tens of meters and more apart, starfish may spawn without any other individual detecting gametes in the water. In this way, whole spawnings of eggs may suffer total or near total mortality.

The eggs are carried away from where they were spawned over the coral reef. Benthic predators, such as coral polyps and feather starfish, may feed on them. Also, the reef community contains small schools of plankton-eating fishes, which may prey on the eggs. Small fishes have been observed to eat the eggs, but, as described earlier, the eggs have chemical defenses that discourage predation.

The eggs will be carried off the reef into the open waters of the Great Barrier Reef region and subsequently develop into larvae. There are further potential predators in this open water plankton community—predatory copepods, medusae, arrow worms, larval fishes, and so on, but nothing is known of the severity of this predation.

Lowered salinity improves the survival of larvae which require particular levels of algal food (phytoplankton) for optimal development and survival. At low levels of phytoplankton, the larvae starve; at high levels, they literally choke on surfeits of algae because they cannot control their feeding rate. The larvae have very narrow temperature tolerances, in the range 26–30 degrees Celsius. This is the water temperature range in the Great Barrier Reef region where the starfish breed.

Juveniles

The small starfish have chemical defenses, but they lack the battery of spines of the larger starfish. Thus,

Giant Clams as Pollution Indicators

In addition to their commercial importance, the tridacnid clams appear to have applications in environmental research, specifically in monitoring heavy metal pollution. These bivalves accumulate metals such as zinc, copper, cadmium, lead, and mercury to levels which are dependent on, and therefore reflective of, concentrations available to them from their surroundings.

The bio-indicator capacity of the Tridacnidae is confined primarily to their kidneys. The large tridacnid kidney forms a single mass of brown pigmented tissue that represents up to 15 percent of the total wet flesh weight. Thus, the kidney is easily sampled and provides an abundance of tissue for analysis. Apart from their size, the Tridacnid kidneys appear similar in structure to those of other bivalve mollusks. It is the spongy internal structure of the kidney that is of greatest interest. Here, the tissues form a mass of fine irregular tubules. Each tubule opens to the renal lumen and is lined by secretory and ciliated columnar cells (nephrocytes). These cells have a basal nucleus and a highly vacuolated cytoplasm which may contain granular, laminate concretions, termed nephroliths. The nephroliths, which are excreted via the nephridiopore, are highly mineralized, spherical bodies composed primarily of calcium phosphate on a mucopolysaccharide matrix. They are the major sites of trace metal deposition in the kidney and are considered to play a prominent role in metal detoxification and excretion. Moreover, they are known to increase in quantity and in trace metal content in response to trace metal pollution and, therefore, are of central importance to the kidney's indicator capabilities.

Tridacnid clams from pristine or near pristine environments normally contain fairly low renal concentrations of cadmium and zinc, although rapid and substantial increases can occur in response to elevated ambient levels. For example, T. crocea, *held in Townsville Harbor for two months, accumulated zinc to 2000 micrograms per gram (dry weight) in their kidneys, where a range of 1 to 10 is normal. Clearly, clams are useful where episodic trace metal inputs are to be measured. Once bound within the clam's kidneys, most trace elements are lost very slowly. The biological half-lives (B1/2) for zinc, cobalt, and lead, in the kidneys of* T. crocea, *are in the order of 1 to 1.5, 2, and 4 years, respectively. Preliminary results indicate that the B1/2 for cadmium and mercury are of similar magnitude while copper, on the other hand, has a fairly rapid turnover (B1/2 = 60 days). With the exception of copper, the tridacnid kidney records and retains changes in the ambient availability of many elements over comparatively long periods. It is therefore particularly useful in multiple-year monitoring surveys, as it provides the investigator with information that would otherwise be lost using bio-indicators with shorter time-integrating capacities.*

Clearly, tridacnid clams show considerable promise as indicators of trace metal pollution in tropical waters. As phototrophic organisms, they are especially well suited for such purposes in the clear, relatively barren, waters of the Great Barrier Reef where other bivalve indicator species may fail to survive. The considerable scientific interest now centered on the culture of Tridacnia *can only add to our knowledge of the biology of these organisms, and facilitate a better understanding of their role in marine pollution studies.*

—G. R. W. Denton and L. Winsor,
James Cook University,
Townsville.

they are "fair game" for any predator that can locate them and stand their bad taste. A crab and at least one fish species are known to prey on juvenile Crown of Thorns starfish, but it is probable that many other predators attack them.

After six months of feeding on algae, the juvenile starfish is ready to transfer to coral feeding. This requires that suitable coral species be available in the near vicinity, which is not guaranteed because the settling of the juvenile starfish at this stage is limited by its small size (10 millimeters) and need to remain concealed. Thus, it may be months before the juvenile locates suitable coral, or it may never locate sufficient coral to enable it to get into the rapid growth phase that takes it out of its vulnerable small-size range.

Adults

Some fishes, such as toad fish and trigger fish, have been observed to feed on adult Crown of Thorns starfish. The fish avoid the spiny defenses of the starfish by turning it over and attacking its undersurface. The giant triton (*Charonia tritonis*) and the painted shrimp (*Hymenocera picta*) also are starfish predators. However, none of these predators has been observed to increase in numbers in response to outbreaks of Crown of Thorns starfish in the Great Barrier Reef region. In fact, it is probable that starfish populations increase and then decline on individual reefs at rates too rapid to allow for corresponding recruitment of predators. Even when these predators attack large Crown of Thorns starfish, they need not kill them. The predator may be satisfied with part of the starfish; the remaining portion then regenerates the lost tissue. Crown of Thorns with groups of regenerating arms are common in Great Barrier Reef populations. Thus, it seems that Crown of Thorns starfish reach a "size-refuge"—that is, by virtue of their large size in combination with their defenses they are relatively free of predation.

Disease

Another factor that may cause damage and mortality in Crown of Thorns populations is disease. I first observed a bacterial disease in an aquarium system that caused widespread rotting of the starfish and rapid mortality. Interestingly, the disease only affected Crown of Thorns among the various starfishes that were held in the aquarium. I controlled the disease by injecting the starfish with antibiotics.

Disease now has been observed in the field and is being studied by microbiologists and pathologists at James Cook University. Diseased individuals tend to occur in populations of "old" starfish or stressed starfish. It is not clear yet whether the bacteria are the cause or a consequence of the poor condition of the animals. The possibility exists that the high density populations of Crown of Thorns starfish are short-lived because at high density they are prone to epidemics of pathogenic bacteria.

Mathematics

The mathematics of fecundity and survival are interesting. If a female starfish reproduces for three of four successive breeding seasons, its total egg release will be in the order of 100 million. To replace itself and a male starfish, two individuals out of 100 million need to reach sexual maturity, a survival rate of 0.000002 percent. If, instead, the survival rate is 0.001 percent, still a very low rate of survival (one individual surviving from 100,000 eggs), there will be a population outbreak of 1,000 starfish where previously there were two. This gives an appreciation of the potential for starfish population fluctuations resulting from changes in the survival rates of the very abundant early stages of the life cycle.

It is not surprising that there should be marked fluctuations in the populations of Crown of Thorns starfish on various reefs of the Great Barrier Reef. However, this is not to say that the recently observed population outbreaks are "natural." Both "natural" and "unnatural" (human interference) factors may produce profound changes in starfish numbers through their effects on the survival of larvae and juvenile starfish.

Recruitment

Considering recruitment, as in the above example of 1,000 starfish instead of two: it is likely that juveniles recruit to reefs other than the reef from which the larvae were liberated. Over the period of several weeks of planktonic development the larvae will travel a considerable distance depending on the ocean currents. For example, in a prevailing current of 0.1 meters per second (approximately one quarter of a knot), the larvae will be transported more than 170 kilometers in 20 days of planktonic life. Thus, unless there are particular circumstances, such as gyral current systems or alternating current systems, it is likely that the larvae will be carried and recruited to reefs away from that of the parent population. In the two recent periods of Crown of Thorns starfish outbreaks in the central region of the Great Barrier Reef, in 1960/70 and 1970/80, the starfish were abundant on reefs off Cairns (17 degrees South), such as Green Island, several years before they were abundant off Townsville (19 degrees South). The prevailing currents are southerly in this region during the summer breeding season. It is thus reasonable to attribute the large populations off Townsville to southerly transport of larvae from the more northern populations near Cairns.

Conclusion

This article does not address the controversy surrounding the Crown of Thorns starfish—whether recent population outbreaks on the Great Barrier Reef and elsewhere are unique events caused by the unprecedented level of human interference in the marine environment or whether they are recurring natural events that simply have not been witnessed by marine biologists prior to the 1960s. There is no compelling evidence to support either viewpoint (see box page 58).

Contrary to the popular view which sees the Crown of Thorns starfish as an arch villain, I see it as a magnificent creature, beautifully adapted to its role as a coral predator. This is not to say that we can be complacent about the large populations of the Crown of Thorns starfish currently on reefs of the Great Barrier Reef. These populations are having a profound effect on the coral communities of many reefs. Undoubtedly, the Crown of Thorns starfish is the major scientific and management issue of the reef at this time. If the recent population outbreaks are not a unique event, and if they continue, then we face the prospect of long-term changes in the coral reef communities. The reef will not be "eaten away" as has been suggested. It will remain, but the coral communities and all the other reef organisms that depend on them will be changed. Obviously, the Crown of Thorns phenomenon needs to be treated very seriously, as the Australian government is doing, having recently allocated A$3 million for research on the starfish over the next few years.

John Lucas is a biologist and professor at James Cook University of North Queensland in Townsville, Australia.

Suggested Readings

Branham, J. M. 1985. The Crown of Thorns on coral reefs. *BioScience* 23(4): 219–226.

Lucas, J. S. 1984. Growth, maturation and effects of diet in *Acanthaster planci* (L.) (Asteroidea) and hybrids reared in the laboratory. *Journal of Experimental Marine Biology and Ecology* 79: 129–147.

Lucas, J. S., W. J. Nash, and M. Nishida. 1985. Aspects of the evolution of *Acanthaster planci* (L.) (Echinodermata, Asteroidea). *Proceedings of the Fifth International Coral Reef Congress*, Tahiti.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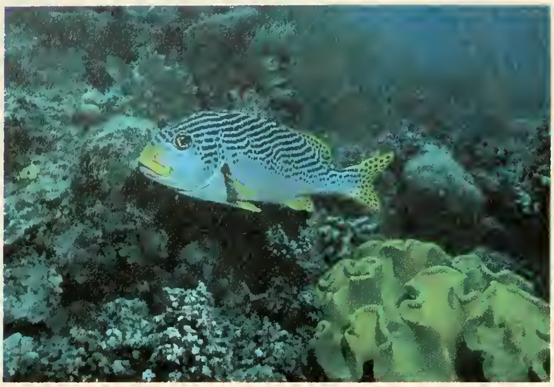
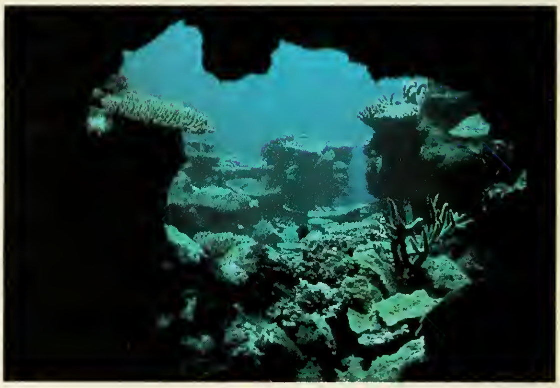


Goldman's sweetlip (GBRMPA)

Yellow-tailed Fusiliers

Giant clam (GBRMPA)



Cave on reef (GBRMPA)

Nudibranch, Flabellina sp.

White-tipped shark (GBRMPA)

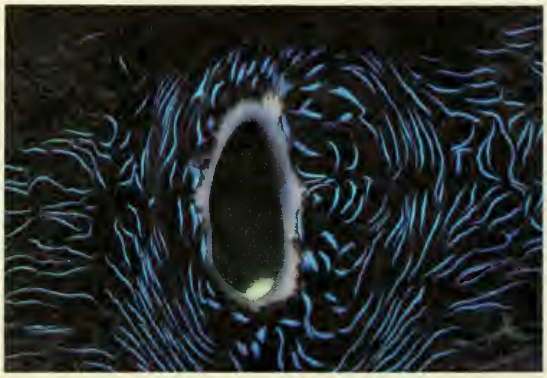
All photos unless otherwise indicated by James K. Oliver

Underwater Outback

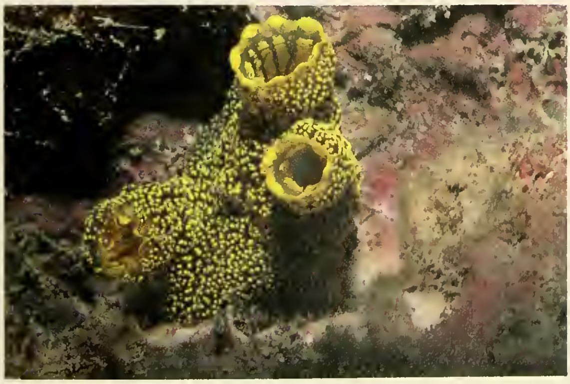
Potato cod being fed

Feather star, Himerometra robustipinni

Gorgonian, Subergorgia sp.



Coral clam siphon, Tridacna derasa



Gold-flecked ascidian, Phalusia julinea

Featherworm, Spirobranchus sp.

The Nutritional Spectrum of Coral Reef Benthos

or Sponging Off One Another for Dinner

by Clive R. Wilkinson

One feature that distinguishes coral reefs from all other ecosystems is that a significant portion of the primary production occurs within animals. Indeed, this production occurs, in conjunction with heterotrophic consumption, within animals which constitute the bulk of the animal biomass on coral reefs.

Nutrition in most ecosystems is derived from photosynthetic primary production, with the secondary production being consumed by organisms ranging from the smallest of bacteria to the largest of whales. In coral reef ecosystems, as in other systems, there are approximate balances between primary production and consumption. In coral reefs, though, the demarcation between the primary and the secondary producers is narrower, and a nutritional symbiosis* is characteristic.

Coral Reefs

The latitudinal range of coral reefs is relatively broad, roughly 25 degrees north and south of the equator. The reefs occur principally on the eastern coastlines of continents and around seamounts, in waters shallower than 30 to 40 meters. The reef ecosystems come under two different influences: the continental land mass, which contributes fresh water, nutrients, and sediments; and oceanic waters, which are clear and have low concentrations of nutrients. The only eastern continental shelf that does not feature coral reefs is that of South America, where the strong influences of the Amazon River preclude the growth of reef-forming corals.

Coral reefs occur along a spectrum from the relatively high terrestrial influences near the mangroves, to the oceanic environment at the outer edge of the continental shelf. Although all fit within the definition of coral reefs, the nature of the animal communities, their nutrition, and the nutritional balance of the reef itself may be quite different. Coral reefs nearer land masses are likely to be slightly heterotrophic, requiring additional nutrition from the surrounding environment, whereas reefs further offshore may be more autotrophic, generating all their own nutrition, and even exporting some organic matter.

Reef Studies

The area where the relationship between nutrition and the environment has been studied most intensively is a section of continental shelf extending from the coast near Townsville out to the Coral Sea (Figure 1a). This section is about 220 kilometers long, encompasses 2 degrees of longitude, and is at 18½ degrees south latitude. Within this section are contained considerable ranges in the critical environmental parameters (Figure 1b).

Populations of *Halimeda* algae, hard corals, soft corals, sponges, crinoids, and fishes have been examined on 11 reefs within this section. The fish studies are described by David Williams and co-authors on page 76. The description of benthic nutrition is based largely on work with sponges, done by our laboratory, and on the coral research of Terrence J. Done at the Australian Institute of Marine Science (AIMS).

These studies of nutrition and environment have sought to identify the factors that determine community development, and to build both explanatory and predictive models of coral reef ecosystems.

Nutrition of Benthic Animals

Sessile (permanently attached) animals are faced with a dilemma—to survive they depend on currents to provide sufficient dissolved or particulate food material. The problem confronting coral reef benthos is that the water around the reefs is usually clear, signaling that food matter is scarce. Unable to move and seek out other concentrations of food, the most prominent benthic animals have evolved an augmentative system of providing energy-rich carbon compounds. They "generate" food internally.

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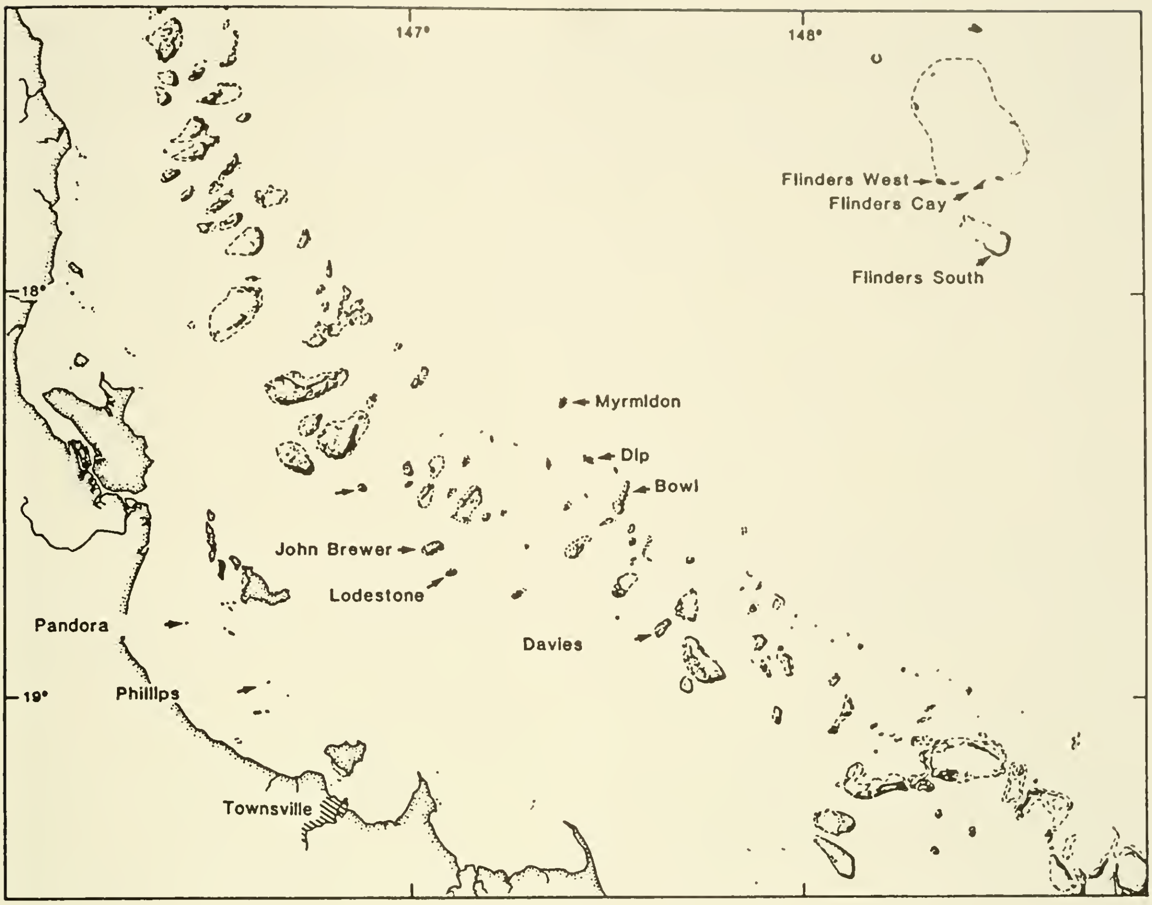
* Two dissimilar organisms living together in a stable association which sometimes is mutually beneficial to both.

(a)



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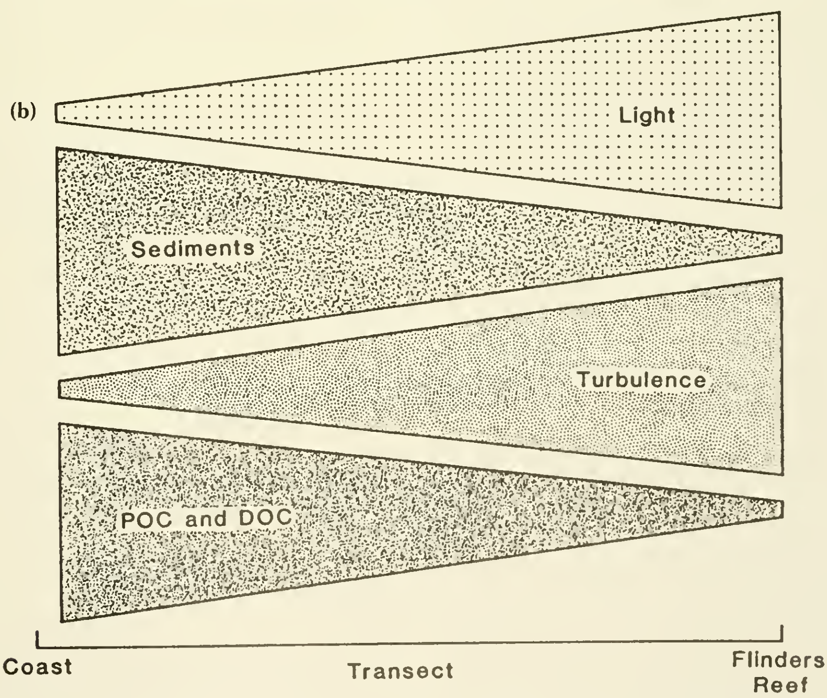

Figure 1(a). The transect used in studies of benthic nutrition, showing the location of reefs across the continental shelf of the central Great Barrier Reef region and out to the Coral Sea. (b) The major environmental parameters along the transect. POC = particulate organic carbon and DOC = dissolved organic carbon.

The photosynthetic symbionts in tridacnid clams, most scleractinian and alcyonacian corals, and many sponges and colonial ascidians (sea squirts) provide their animal hosts with an additional source of nutrient carbon not available to their relatives that lack symbionts. This combination of phototrophic and heterotrophic nutrition delineates coral reefs from other ecosystems—particularly as it relates to the system's major framework builders, the corals. Coral reefs and the animals associated with them owe their existence to this balance of nutrition.

Photosynthetic symbionts and their host animals have co-evolved over hundreds of millions of years, so that one partner or often both are totally dependent on the symbiosis for survival. Where light levels are adequate, the symbionts produce an excess of organic carbon photosynthate, some of which is translocated to the host. The success of phototrophic nutrition depends on the ability of the host to enhance the low levels of natural leakage from the symbiont. Corals induce a greater supply of photosynthate by causing the zooxanthellae* to become "leaky," and augment this by reducing the rate at which the symbionts grow and divide. Indeed, in some corals, as much as 95 percent of the carbon fixed by zooxanthellae is made available to the host. Similar levels of translocation are suggested for some sponges, tridacnid clams, and possibly some ascidians.

There are two groups of symbionts. In sponges and colonial ascidians, the photosynthetic symbionts are prokaryotic**—cyanobacteria and *Prochloron;* whereas in corals and tridacnid clams, the symbionts are eukaryotic*** brown algae—the zooxanthellae.

This phototrophic nutrition augments (or in another perspective—is augmented by) heterotrophic nutrition. Sponges, clams, and ascidians are filter feeders removing particulate matter from the ambient water. Sponges operate in the range of smaller particle size, being able to remove about 99 percent of bacteria less than 1 micron in diameter. The bacteria, however, are probably a minor constituent of the diet. In a detailed study of sponge nutrition on coral reefs, Henry M. Reiswig, writing in the *Biological Bulletin*, showed that the bulk of food intake was fine detritus of unknown origin, possibly algal fragments, animal feces, and the like. Particles in the larger size ranges, including algal cells and zooplankton, are apparently removed by clams and ascidians.

Some corals also may act as filter feeders by trapping detritus in waving tentacles, or on mucus mats produced by the coral and subsequently retrieved. Corals, however, are best known as predators of small prey animals, such as copepods, various larvae, and fish. Often, these prey are killed by toxin-bearing cells on the tentacles.

Recent studies have confirmed that many marine invertebrates are able to incorporate dissolved organic carbon (for example, sugars, amino acids, and short chain fatty acids) directly from seawater. The importance of this form of nutrition in the total energy balance of these invertebrates has yet to be determined. It is certain, however, that its role will vary among individuals and species.

A Nutritional Spectrum

The concept I wish to advance is that of a continuous nutritional spectrum involving corals, sponges, clams, and ascidians—a spectrum ranging from total dependence on heterotrophy for those animals without symbionts to almost total dependence on phototrophy. The "phototrophs" host large populations of photosynthetic symbionts, and have reduced capability for heterotrophic feeding. The opposite is true for the "heterotrophs." Between these extremes lie a broad band of organisms with various mixtures of feeding modes, and often with a high degree of "nutritional plasticity" (described later in this article). All of the afore-mentioned groups fit on this spectrum (Figure 2).

Distribution and Nutrition

In considering a cross-shelf situation, one would expect animal communities on coral reefs to vary across the shelf with respect to distinct environmental variations. In theory, the more heterotrophic animals will predominate on the turbid inner shelf, whereas animals nearer the phototrophic end of the spectrum will be more prevalent on the outer shelf. In recent research, using coral reef sponges, I sought to test this hypothesis—that distribution is related to position on the nutritional spectrum.

Like the other groups, the sponges span the nutritional spectrum. Some sponges on the Great Barrier Reef can obtain most of their nutrition from symbiotic cyanobacteria. In some cases, the production of fixed carbon in the whole animal may be 3 to 4 times respiration.

First, I divided sponge species into three nutritional categories: *heterotrophs* contain no photosynthetic symbionts, and obtain energy from the environment; *phototrophs*, which are generally flattened, obtain 50 percent or more of normal energy requirements from the symbionts; and a *mixed* category, where the principal mode of nutrition is heterotrophic feeding, with a small (less

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* Zooxanthellae are alga-like brownish or greenish-brown plant cells found in the tissues of marine animals of diverse groups. They use much of the nitrogenous wastes and carbon dioxide from the host before these substances enter the water. In turn, they liberate oxygen and food materials. Of vital importance to the host, there may be as many as 3 million zooxanthellae cells per square centimeter. In the spawning of some corals, when the planula larvae are discharged into the water, many already contain zooxanthellae.

** Prokaryotic cells have the genetic material in the form of simple filaments of DNA, and not separated from the cytoplasm by a nuclear membrane.

*** Eukaryotic cells are more complex in that the nucleus is separated from the cytoplasm by a nuclear membrane, and the genetic material is borne on chromosomes. This cell type is common to all organisms except bacteria and blue-green algae.

Bioerosion of Coral Reefs

The structure and form of ancient and modern coral reefs is the result of the interaction between growth and destruction. Considerable information on the mechanisms and rates of reef growth in a variety of reef environments is available. By contrast, information on destructive processes is scant, especially data on rates of destruction and the variation occurring between and within environments. Yet boulder tracts, eroded reef flats, islands, and lagoon sediments are visible reminders that destructive processes are continually operative, and are substantially affecting reefs.

Reef destructive processes include physical, chemical, and biological erosion of the hard skeletons of corals and other organisms on the reef. Studies have shown that biological erosion, termed bioerosion, may be the primary destructive process on modern day reefs and evidence from fossil reefs indicates bioerosion has been present in reef environments for millions of years.

Bioeroders can be conveniently divided into borers and grazers, and within each of these groups a wide variety of organisms are involved. Borers include micro-borers, such as algae, bacteria, and fungi; and macro-borers, such as polychaetes and sipunculan worms, bivalve mollusks, and sponges. Borers have a pelagic larval stage. They initially penetrate coral substrates as juveniles, and spend their adult lives in the coral skeleton. The majority of borers are restricted to dead coral substrates, as live corals are carnivorous and eat the juvenile boring organisms as they attempt to settle on the coral. The grazers are animals which rasp, scrape, or bite the surface of the reef feeding on algae. While removing the algae, grazers also remove a fine layer of hard substrate, which is expelled as detritus. Important grazers include a wide variety of fish, such as parrot fish with their beak-like jaws made for scraping, and sea urchins. Like the borers, most grazers attack dead substrates, however, some will graze live coral.

Studies from other areas pointed to the large destructive potential of boring and grazing organisms on coral reefs. In 1980, we undertook experiments to measure rates of bioerosion in a variety of reef environments on the Great Barrier Reef. Substrates, made from recently killed colonies of the coral Porites* were exposed in a variety of reef environments for varying lengths of time ranging from a few months to several years. These substrates imitate the natural process occurring on reefs where colonies of live coral are killed by such factors as predation, storms, or diseases.

Borers occurred at all sites studied on the Great Barrier Reef. Initially, micro-borers, such as algae, colonized the newly available substrate. Polychaetes also are important borers in the early stages of exposure. After about 12 months of exposure on the reef, sipunculans (peanut worms), sponges, and bivalve mollusks begin to appear. Although polychaetes are still common after 5 years, the dominant borers by this time are the sponges, sipunculans, and bivalves—due to their larger size.

Grazers begin to erode substrates soon after algal communities develop on their surfaces. Substrates exposed in reef slope environments experience large amounts of erosion because of grazing. In this environment, as well as in some lagoon habitats, grazers are the dominant bioeroders. In other environments, such as the reef flat, grazing is not as important, and borers are the main bioeroders. Environmental conditions that control the type and size of fish populations in various reef habitats are most likely responsible for these differences in grazing. Erosion by sea urchins, although significant in some parts of the world, is not as important on the Great Barrier Reef.

High rates of bioerosion in particular reef environments have important implications to the overall growth of reefs. On reef slopes, high rates of growth are matched by high rates of bioerosion that may limit the ability of this environment to build up. The skeletons of dead coral colonies are rapidly reduced to rubble and sand by bioeroders. Waves and currents redistribute this debris and deposit it on the reef flat, in the lagoon, or carry it away from the reef altogether. In this way, the process of erosion helps reefs to grow, through the accumulation of sediment bodies that subsequently provide a base for colonization by more reef-building organisms. The sediment and debris can also build up into the sand cays so characteristic of the reef environment. These cays are unstable initially, but if vegetated, can become permanent features.

The balance between growth and destruction processes in the reef community is a fundamental part of its development. Understanding the relationship between these processes is vital to the interpretation of many biological and geological features on reefs. In gaining this understanding, it also may be possible to predict the consequences of natural and unnatural disturbances to the coral reef ecosystem.

—Pat Hutchings, The Australian Museum, Sydney, and William E. Kiene, Australian National University, Canberra.

* Many coral genera have characteristic shapes that give rise to a common name, but the familiar and often dominant Porites have none—due to a variable color and shape (massive domes, encrusting plates, or lobed clumps).

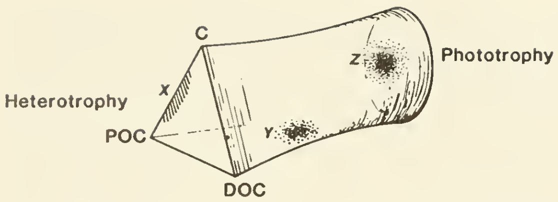


Figure 2. The Heterotrophy:Phototrophy Spectrum. The range of benthic animal nutrition from phototrophy to heterotrophy, with the three major sources of carbon acquisition in the latter—live particle capture (C), filter feeding of particulate organic carbon (POC), and direct incorporation of dissolved organic carbon (DOC). Animals without photosynthetic symbionts are totally heterotrophic, whereas those with symbionts will occupy a position or a span of the spectrum. The width of the span will depend on the plasticity of the animal's nutrition. Three examples are shown—X is a true heterotroph, such as a non-symbiotic coral that derives its nutrition from particle capture and DOC uptake; Y is a predominantly heterotrophic animal feeding on DOC and POC with a small phototrophic contribution; Z is predominantly phototrophic like a shallow water, symbiotic coral which obtains some nutrition from particle capture. It is unlikely that any animal has totally phototrophic nutrition.

than 50 percent) contribution from phototrophic nutrition. In general, sponge species in the mixed category are more heterotrophic, with the contribution from phototrophic nutrition estimated at less than 10 percent.* The three categories do not necessarily relate to taxonomy. For example, different species of the same family may be grouped into different nutritional categories.

When the distribution of sponges relative to these nutritional categories was summarized, it appeared that the initial hypothesis—distribution is related to position on the nutritional spectrum—was supported (Figure 3, next page). The largest sponge biomass occurred on the higher nutrient, and lower light, inner shelf reefs. All species were heterotrophs or mixed, indicating there was sufficient particulate and dissolved nutrient matter to sustain a population that averaged 500 grams wet weight per square meter. In contrast, a much lower biomass was found on the high light, and lower nutrient, reefs of the outer shelf and Coral Sea. Here, phototrophs were predominant. On the southeastern slope of the Coral Sea reefs, for example, the population consists of more than 85 percent phototrophs at depths down to 20 meters.

The link between light, nutrition, and distribution was further demonstrated in the vertical plane. Sponge populations were studied to a depth of 40 meters on nearby Davies Reef. Here, the sponge biomass peaked at a depth of 20 meters. At this depth, a large phototrophic component was present that was absent at 40 meters. Physiological experiments on specimens from 20 meters showed that these sponges were particularly efficient at using ambient light energy. At 40 meters, however, light levels were too low, and capable of supplying less than 10 percent of total energy requirements. As shown in Figure 4, overall biomass, as well as percentage of phototrophy decreases at these depths. Although light would appear not to be limiting in shallow water, another factor may be. Because sponges have soft tissues, sponge colonization in shallow water is likely limited by water turbulence.

Studies on coral distribution by Terrence J. Done at AIMS seem to corroborate the sponge data. The pattern of coral distribution, based on the nature of coral community structure, likewise shows a distinct cross-shelf gradient. The major factors causing this variation were considered to be light and degree of turbulence. Whether this distributional pattern is related to the nutritional spectrum of the corals is unknown, but, after

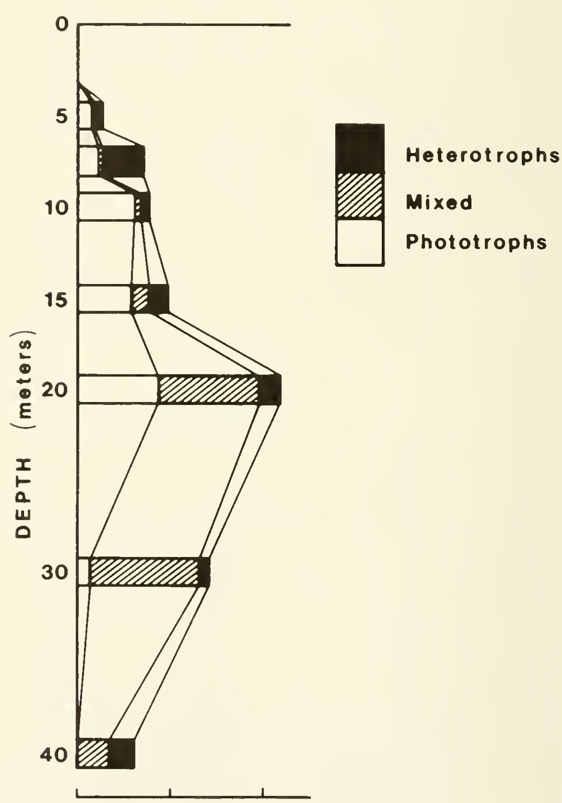


Figure 4. Sponge biomass with respect to depth on the southeast side of Davies Reef. Similar methods were employed as for the cross-shelf reefs. The peak in population between 15 and 30 meters also is paralleled by peaks in numbers of species and individual sponges. In this depth range, there is a corresponding decrease in the extent of live coral cover.

* Although this is true for adults, juvenile or freshly settled sponges in this category may have a larger nutrient contribution from the symbionts because of their larger surface area (relative to volume) for receiving light energy.

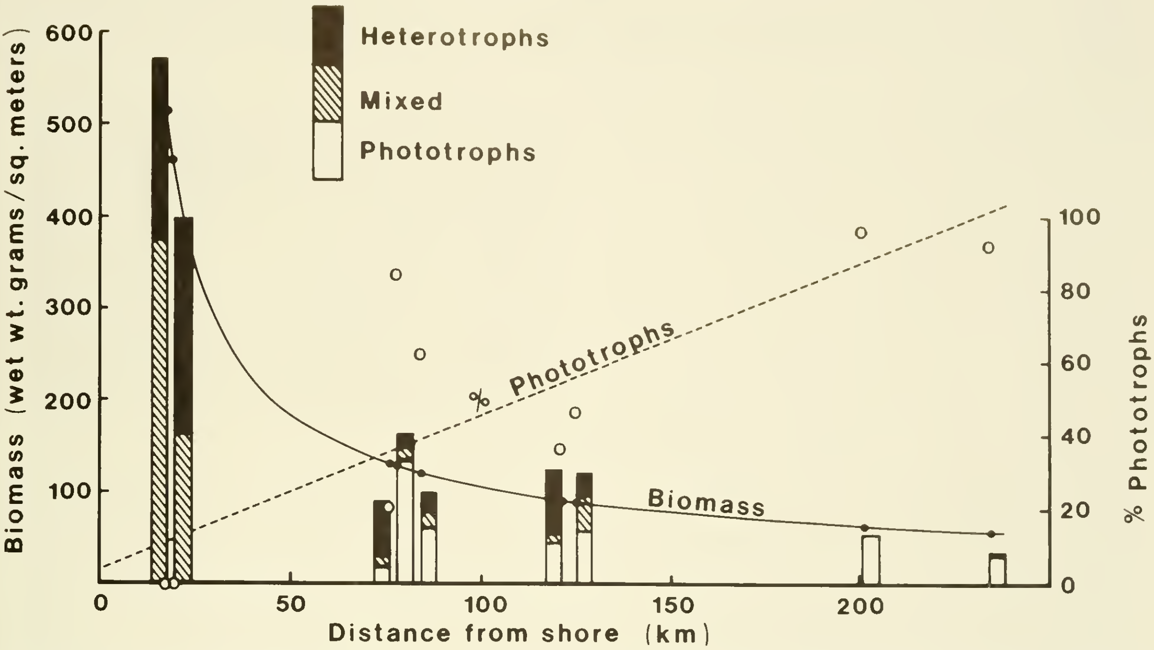


Figure 3. Biomass (wet weight) of sponges at 15 meter depth on the southeast sides of reefs along the cross-shelf transects. The histograms represent the mean biomass of triplicate 40-square-meter transects with sponges divided into nutritional categories on the reef. The distance from the shore is represented on the x axis. Superimposed on this is the proportion (as percentage) of phototrophic sponges within the total biomass at each reef (circles, R axis, dashed line). The regression lines are included to indicate that there are distinct trends in both biomass and proportion of phototrophy, however, they should not be taken literally or extrapolated as the shape of the curves will probably vary at different locations on the Great Barrier Reef.

consideration of the sponge data, I would not be surprised if inner-shelf corals are more heterotrophic, and those on the outer shelf more phototrophic.

Nutritional Plasticity

The coral reef is populated by animals that can be considered nutritionally "plastic." What does this mean, and why is it so?

Contrary to a popular concept, most of the coral reef animals are not specialists—either in nutrition or in choice of habitat. They are, in fact, generalists, or opportunists. This is true for the benthos, as well as many of the fishes.

By plastic, I mean animals that can obtain their nutrition from a wide variety of sources, subject to availability. These sources include dissolved organic carbon (DOC), particulate organic carbon (POC), predatory capture of small animals (all heterotrophy), and phototrophy. Such plastic nutrition is exploited by the most prominent animals on the reef, the same groups addressed throughout—corals, sponges, tridacnid clams, and colonial ascidians. This plasticity is less common at the extremes of the nutritional spectrum, and more common/important in the large central "mixed" area.

Plasticity as a concept may be applied to different species in a phylum, or to individual animals within a species. The breadth of the span also will vary on a qualitative scale: survival of an individual would presumably encompass a broader span of the spectrum than growth and reproductive success of the species.

If, for instance, water transparency is reduced through input of particulate nutrients during flood runoff or storms, some species will be able to compensate for the reduction in phototrophic nutrition by shifting in the direction of heterotrophy, and exploiting the particulate food. The opposite would occur when normally turbid environments experience periods of water clarity.

How does the concept of nutritional plasticity affect our concept of the nutritional spectrum? In this way: the placement of an organism within the spectrum is rarely fixed. Rather, shifts in feeding mode along the spectrum are common. In general, however, the assignment of species to one of three broad nutritional categories remains valid.

Integrating Environmental Factors

In seeking to understand the factors that determine the distribution of benthic populations on the reef, one must look not only at present conditions, (including perhaps previously unconsidered secondary factors), but also back to the historical. The major present environmental conditions alone may not adequately explain a distribution. For example, recent transplant experiments conducted by Janice E. Thompson, Stanford University, showed

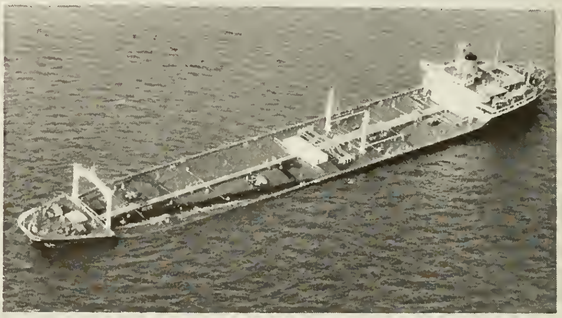
Pollution on the Reef

Will the waters of the Great Barrier Reef, because of their vast size, dilute any pollution to the point where it will simply disappear without effect or trace? This has been the thinking of some. Added to this is the notion that a sparse mainland population of some 300,000 people, distributed along 2,000 kilometers of coast, leads to relatively low runoff discharges. Some rethinking is now taking place, and perhaps a less sanguine view is in order.

One event that precipitated this revised thinking occurred in 1970. The near wreck of the oil tanker Oceanic Grandeur *in the Torres Strait raised the question of oil spills. In fact, at that time, this question was the subject of scientific debate, and a public controversy, since oil exploration had been proposed—with the potential for oil field development. To clarify the dangers to the reef, the Australian government initiated an inquiry which took the form of a Royal Commission (consisting of a presiding judge and two scientific commissioners). The commission took evidence from witnesses representing the oil industry, as well as scientific and environmental organizations from many countries. In 1974, a commission report suggested a variety of safeguards to protect the reef. In 1975, when the Great Barrier Reef Marine Park Act was passed, oil drilling was specifically forbidden in the park. Nevertheless, the risk of the spillage of oil from tankers and other craft in the area remains.*

Recent surveys of various types of petroleum hydrocarbons in the reef area have been carried out by the School of Australian Environmental Studies at Griffith University, and also by the University of Melbourne. As expected, only boat harbors were found to contain significant trace levels. But, very low concentrations also were found in various biota in the Capricorn Group at the southern extremity of the reef. This could have originated from industrial activities on the adjacent mainland such as alumina refining, aluminum smelting, coal exporting, and electricity generation. Alternatively, natural seeps could be a factor, since the area has some of the largest oil shale deposits in the world.

In intensive surveys of the reef, investigators from the Australian Institute for Marine Science near Townsville were able to detect trace amounts of lindane, and some other pesticides, in various reef organisms over extensive areas. They suggested these residues originated from pesticide useage in the sugar industry that operates along most of the reef coast. The levels were below those known to have any biological impact, but nevertheless, the vast dilution did not cause these residues to disappear.



The Oceanic Grandeur *awash in Torres Strait after striking an isolated reef in 1970. The oil released from the ruptured tanks was fortunately washed to open waters towards the Coral Sea. (Photo courtesy of the* Courier Mail, *Brisbane).*

Other work at La Trobe University in Melbourne has suggested that polyclorinated biphenols (PCBs) may also be present in reef organisms. This is another example of bioconcentration of trace amounts in the environment by organisms. The possible origin of these substances is unknown, since they are usually associated with large urban centers. However the nearest large urban center, Brisbane, lies around 400 kilometers to the south.

Entry routes to the reef have not been investigated. The contaminants mentioned above would be expected to be strongly adsorbed onto sediments. There is a movement of sediments from mainland estuaries—the focus of urban, industrial, and agricultural activities—out towards the reef. The establishment of equilibrium with seawater in the reef zone could release contaminants into water, which would then be bioconcentrated by organisms.

At present, pollution seems to present a low level threat to the reef. But, accidents with tankers carrying hazardous cargoes are possible, and spills in remote areas would pose a particularly difficult problem. Probably the low level pollution from activities on the mainland, which shows an incremental creep up in intensity with the passing years, is a more serious problem. The present low levels of contaminants represent a danger signal that contaminants do not disappear through dilution. Continued, careful monitoring of contaminants, and their possible effects, is essential, coupled with wastewater treatment and control of other contaminant sources. Preventative action is required at this stage. This course is preferred over an attack on a crisis situation in the future.

—Des Connell, Griffith University, Brisbane

that sponge species occurring on mid-shelf reefs would survive and grow on inner-shelf reefs where they do not appear to occur naturally. Their absence may be caused by larvae never reaching the inner-shelf reefs.

There also may be a caveat to considering historical factors. Rather than consider a continuum of stable or evolving environmental conditions, "spikes" also may play a role. Joseph H. Connell, University of California at Santa Barbara, has proposed that periodic catastrophic disturbances were a major factor in determining the species composition of natural populations. For example, cyclones or floods during prolonged monsoon periods may inundate the reefs with large volumes of low salinity, very muddy, water. These type of events may wipe out those species unable to tolerate the conditions.

As described by Peter Isdale (see p. 31), the environmental history of hard corals is locked up in the skeleton. Information on past rainfall and solar illumination is now available for hundreds of years. We likewise can use a knowledge of benthic community structure to hindcast the environmental conditions in the immediate past. What we require is additional information on the physiology of the animals, and how this varies with environmental parameters.

Management Questions

If we understand the present and the past, then our second type of modelling—predictive—can be used to look into the future. It is hoped that predictive models of coral reef communities may be an aid in reef management. With knowledge and understanding, we may be able to predict what will happen to coral reef communities if conditions vary.

The variations might relate to increased farming, land clearing, or large influxes of residents or tourists. This, in turn, could cause added sediment or sewage loads, leading to a shift from phototrophic-dominated communities to heterotrophic-dominated communities (provided suitable larval stocks existed in the vicinity). This would presumably be the case within the Great Barrier Reef region. However, if a supply of adaptable or specialized larvae is unavailable, the outcome might be different. A shift, therefore, in the environmental parameters of isolated atolls and islands could result in large-scale depletions of benthic communities.

Clive R. Wilkinson is a Senior Research Scientist, and Coral Reef Ecology Group leader at the Australian Institute of Marine Science (AIMS), Townsville.

Selected References

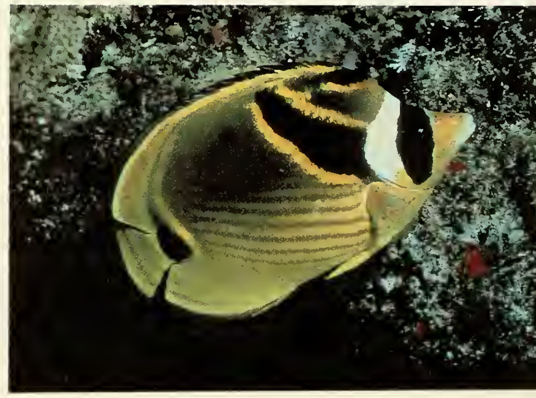
Done, T. J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95–107.

Isdale, P. 1984. Fluorescent bands in massive corals record centuries of coastal rainfall. *Nature* 310: 578–579.

Reiswig, H. M. 1971. Particle feeding in natural populations of three marine demosponges. *Biological Bulletin* (*Woods Hole*) 41: 568–591.

Wilkinson, C. R. 1983. Net primary productivity in coral reef sponges. *Science* 219: 410–412.

Reef Fish:



Raccoon butterflyfish, Chaetodon lunula. *(GBRMPA)*

by David McB. Williams, Garry Russ, and Peter J. Doherty

The approximately 1,500 species of fish on the Great Barrier Reef are spread among an immense array of more than 2,400 individual coral reefs. These reefs, usually thousands of meters in length, range from nearshore reefs fringing the Australian mainland to those perched on the outer edge of the continental shelf.

The species composition of reef fish communities varies significantly from reef to reef, and also from one time period to the next. Some of this variation can be attributed to chance replenishment of benthic populations by pelagic larvae, but this factor cannot explain all, or even most, of the variation observed among coral reefs. Recent surveys have shown that at certain scales of space and time there are consistent patterns in fish communities which reflect deterministic factors, such as cross-shelf (longitudinal) gradients in the physico-chemical and biological environment. The research also has provided some insight into feeding habits and trophic relationships.

Cross-Shelf Distributions

Intensive studies of fish communities on nearshore, mid-shelf, and outer-shelf reefs (see Figure 1 for station locations) using quantitative (explosive) collections have disclosed fundamental differences in the structure of fish communities on the outer slopes of these reefs. In addition to species composition, the major differences include the density of species per reef (mid-shelf highest, outer-shelf next, and nearshore least) and the trophic structure of the communities. The most striking variation in trophic structure is in the abundance of the herbivorous grazers and the planktivores.

Visual censuses by SCUBA divers of more than 100 species of fish covering a wide range of ecological types have demonstrated significant differences in fish abundances on adjacent reefs, but far greater differences among reefs at different cross-shelf locations: nearshore, mid-shelf, and outer-shelf (Figure 2). This trend has been confirmed in eight different cross-shelf transects spanning more than 10 degrees of latitude. These surveys also revealed a significant north-south variation in both species abundances and community structure. The amount of this variation, however, is small relative to the changes across the shelf. The abundance of some species on any given reef also varies considerably with time (over years), but again this temporal variation is small relative to the cross-shelf variation.

The physical environment of the central reef region ranges from the highly turbid and sheltered waters typical of the nearshore zone, to the clear, exposed waters typical of the outer-shelf. Not only the distributions of fishes, but also those of algae, plankton, corals, and other organisms on which fish are dependent, vary greatly across the shelf (see article by Clive R. Wilkinson, page 68). This physical and biological heterogeneity provides an ideal environment in which to generate and test hypotheses concerning factors determining the large-scale distribution of fishes and to assist in establishing the significance of this variation for other reef organisms, and for the dynamics of the reef communities as a whole.

Fish and Algae: Lawnmowers

One of the most characteristic features of coral reefs is their high-standing crops of herbivorous fishes and their generally low-standing crops of algae. It is not uncommon to see great numbers of herbivorous fishes feeding in areas that appear almost devoid of algae. Closer examination reveals that these fishes are exploiting a very light cover of small filamentous and microscopic turf algae that grows on almost all illuminated surfaces not covered by living corals. How does such a small amount of algae support such a large amount of fish flesh? The answer is that although the small filamentous algal turfs have a low standing crop, they also have a very high rate of productivity and are possibly the largest trophic flux on coral reefs.

Large-Scale Distribution and Recruitment

The saddled butterflyfish. (GBRMPA)

Visual censuses and quantitative (explosive) collections made in the central region of the Great Barrier Reef have shown that there are significantly more herbivorous grazing fishes on the coral reefs of the mid- and outer-shelf than on reefs nearshore. These patterns of distribution and abundance can be viewed from an additional perspective. How do the fish affect the benthos, and how does the benthos affect the fish?

To answer the first question, it is necessary to quantify the amount of algae eaten by the herbivores. This has been done by comparing the standing crops of algae (as grams per square meter per day of carbon produced) on dead coral surfaces, some of which were caged to exclude the common herbivorous fishes for short periods of time. Results show that the rate of trophic exchange between algal turfs and grazers is 6 to 7 times higher on mid- and outer-shelf reefs compared to those nearshore, and that this is correlated with standing crops (average fish wet weights per 150 square meters of reef) of herbivorous fishes that are three to five times higher on mid- and outer-shelf reefs compared with those nearshore (Figure 3).

This significant difference in intensity of grazing between the nearshore reefs and those reefs further from the coast appears to have some important implications. First, some algae grow faster when they are cropped, so that increased grazing pressure can actually enhance rates of production of algal tissue. Thus, the different grazing regimes across the shelf may enhance or retard production of the algal turfs.

Second, increased grazing of the algal community allows certain species, notably blue-green algae, to increase in relative abundance. This could be important, since the blue-greens are one of few groups of organisms capable of nitrogen fixation (the conversion of inorganic nitrogen to organic

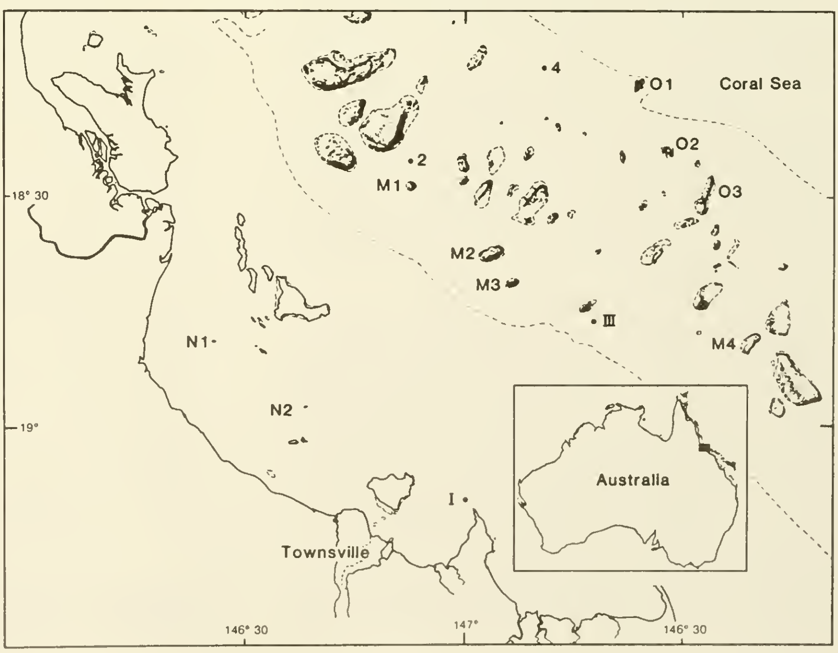


Figure 1. Location of nearshore (N1, N2), mid-shelf (M1–M4), and outer-shelf (01–03) reefs and zooplankton stations (I, III, 2 and 4) across the central region of Great Barrier Reef.

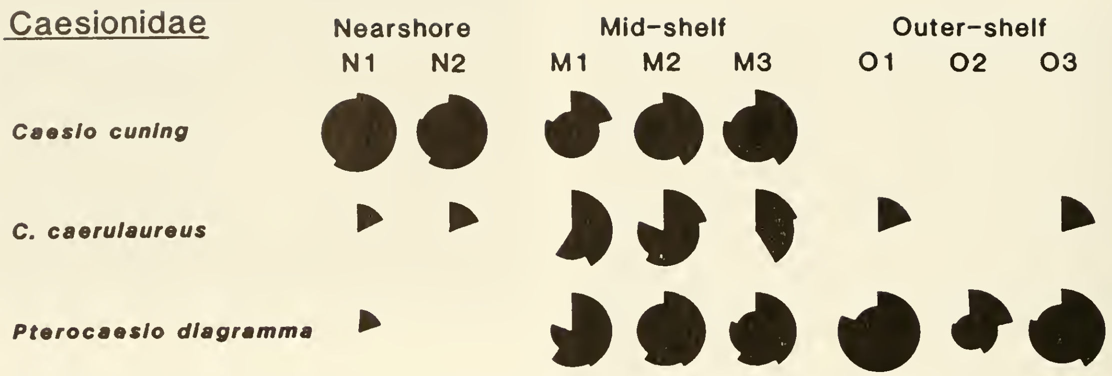


Figure 2. Distribution of the most abundant species of fusilier (Caesionidae) across the central transect. Reef codes as in Figure 1. Five sectors in each circle represent five non-overlapping censuses on each reef. The radius of each sector is proportional to the log-abundance category of the given species in a particular census. Each of the three species has a characteristic and distinct distribution relative to the three shelf regions.

nitrogen—required by plants and animals for growth). Differential grazing intensity may help to explain why rates of nitrogen fixation have been observed (by Wilkinson and others at AIMS) to be higher on mid- and outer-shelf reefs than on reefs closer to the coast.

Third, increased grazing may reduce the survivorship of young corals by removing coral spat (recently settled young coral larvae) along with the algae, thereby enhancing the survival of corals and spat by reducing the likelihood of overgrowth of corals by algae. In other words, the effect of grazers may result in differential survivorship of juvenile corals at different locations across the shelf.

Finally, grazing is a major form of bioerosion. Consequently, cross-shelf differences in the abundance of grazing fishes may be responsible for different levels of bioerosion across the continental shelf.

The greater productivity of algal turfs on offshore reefs means that more food is available to grazers on mid- and outer-shelf reefs, relative to nearshore ones. Thus, there is a positive correlation between food availability and standing crop of herbivorous fishes along the cross-shelf transect, but it is not yet clear to what extent fish are determining algal productivity or vice versa.

Fish and Plankton: A Wall of Mouths

The clouds of planktivorous fishes found on the outer reef slope during the day form a major link between the reef communities and the surrounding waters. These fishes, acting as a wall of mouths or a giant plankton net, filter plankton from the waters impinging on the reef and convert this external source of energy into feces, which are deposited within the benthic system. Although the relatively small proportion of inter-reef plankton production lost to reef fishes is not likely to have a major influence on the plankton communities, it is of considerable significance to the reef communities, and particularly to the fishes.

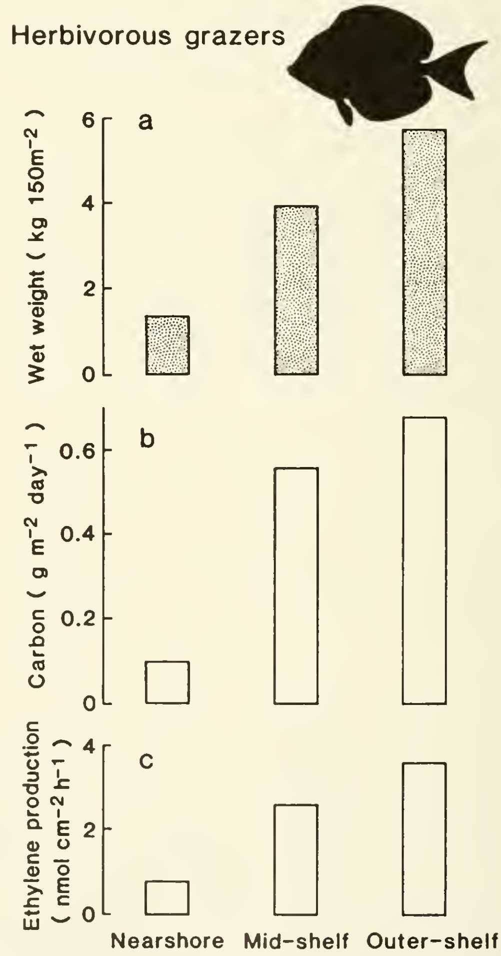


Figure 3. Cross-shelf distribution of a) standing crop of algal-grazing fishes, b) rates of trophic exchange from algae to grazers, c) rates of nitrogen fixation by algae. The herbivorous grazers are most abundant on the outer-shelf reefs.

Recent studies have demonstrated that the average summer biomass of plankton is significantly higher in mid- than in outer-shelf waters (Figure 4); a difference that is at least partly explained by phytoplankton blooms following intrusions into the reef area of cold, nutrient-rich water from the deep waters of the Coral Sea (through upwelling). Planktivores also are significantly more abundant on mid-shelf reefs than elsewhere (Figure 4), and hence fish are likely to import a greater amount of external energy to the mid-shelf reefs than to other reefs.

The high biomass of plankton feeding fish on the mid-shelf relative to the outer-shelf may well be the result of a greater availability of planktonic food on the mid-shelf. The lower biomass of planktivores nearshore relative to the mid shelf is clearly not because of a lower availability of food nearshore, however, since there is more plankton in the coastal waters. The decrease in planktivores nearshore may relate to the difficulties of feeding on plankton in very turbid waters, or, may be a response to an entirely different factor such as larval survival.

Corals and Fish: a Natural Experiment

Reef fishes use corals directly for both food and shelter, and indirectly, because many of their prey also are dependent (to some degree) on corals for food and shelter. The structure (species composition and growth forms) of coral communities varies from nearshore waters to the outer-shelf as much as fish communities. On the central reef transect, it is quite possible for an experienced observer to accurately predict the fish community in a particular area given only knowledge of the coral community, and vice-versa. This, however, does not demonstrate an invariable, or even a causal, relationship between these two taxa.

Comparisons of fish and coral communities on other transects with those of the central reef region suggest that the overall correspondence between fish and coral communities is not necessarily close, and that different factors are likely to be affecting the large-scale distributions of both. For example, the coral communities on the inner reefs of the Pompeys complex in the southern GBR are similar to those of the central mid-shelf and outer-shelf, but the fish communities are more similar to those on nearshore reefs in the central region.

A large-scale natural experiment testing the significance of corals for fish communities occurred recently in the central region when Crown of Thorns starfish, *Acanthaster planci,* caused extensive destruction of the hard-coral cover on several mid-shelf reefs (see article by John Lucas on page 55). The starfish digest away the thin veneer of living coral tissue and leave behind the carbonate skeleton which is overgrown rapidly by filamentous algae. Large infestations of these starfish are able to remove up to 90 percent or more of the live coral on the outer slopes of average-sized reefs within six months.

Of four reefs where fish communities had been examined previously three suffered extensive mortality of coral and the fourth did not (Figure 5).

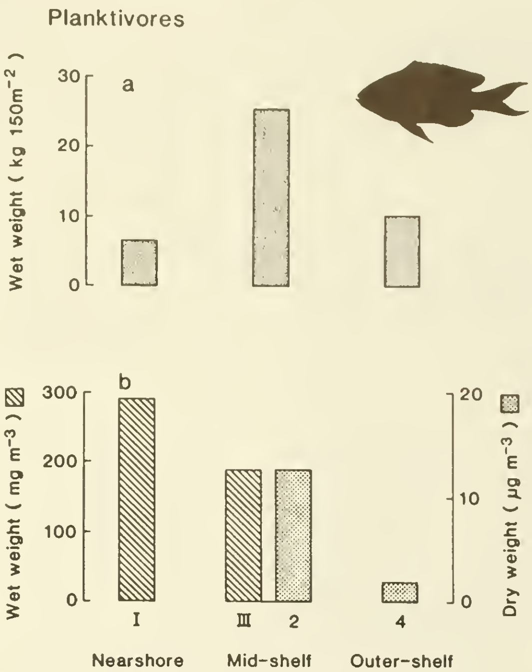


Figure 4. Cross-shelf distribution of a) standing crop of planktivorous fishes, b) mean summer biomass of plankton (from Williams and P. Dixon, unpublished data). The plankton-eating reef fish have their greatest biomass in the mid-shelf region.

By comparing the composition of fish communities before and after *Acanthaster* infestation on affected reefs and unaffected reefs, a relatively direct test was made of the significance of living coral communities for fishes. Within 12 to 18 months of the major decrease in live coral cover, species of previously abundant coral-feeding butterflyfish (*Chaetodon* spp.) had decreased in abundance by an order of magnitude. During the same time period, no other species, including algal grazers and planktivores, showed any obvious effects. Ongoing studies suggest that death of the coral may have a long-term more than several years) effect on the fish communities by modifying recruitment patterns of different species, in addition to the relatively short-term effect on coral-feeding species.

Recruitment Patterns: The Larval Connection

Recent studies of coral reef fishes have drawn attention to the fact that while they are relatively sedentary as adults (most do not move between reefs and some may not move more than a few meters during juvenile and adult life), the vast majority of species have a pelagic larval phase during which there is a potential for extensive dispersal, and during which there is enormous mortality. After a period of pelagic life lasting from a week to 3 months, competent larvae settle to the reef surface, gain pigmentation, and recruit to the community of reef residents. There is evidence that fewer than one recruit is returned for every 100 thousand to 1 million eggs cast into the sea.

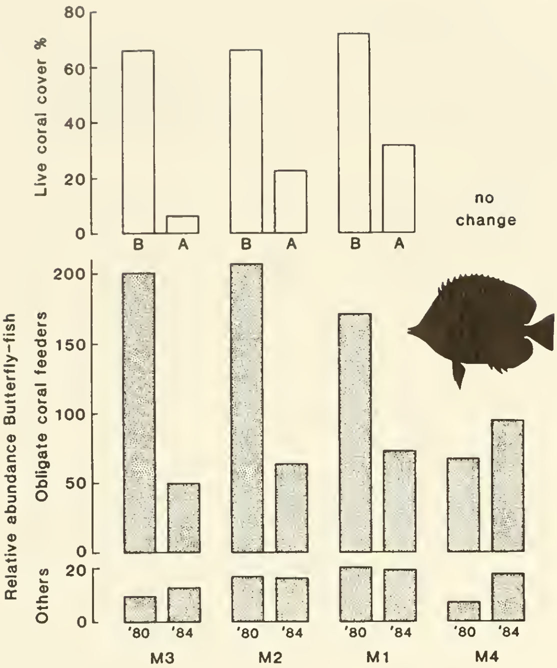


Figure 5. Changes in live coral cover on four mid-shelf reefs, 3 of them affected by Crown of Thorns starfish (M1–M3) and relative abundances of obligate coral-feeding butterflyfishes (Chaetodontidae), and other butterflyfishes. B = estimated coral cover before starfish infestation, A = coral cover after infestation. Fish abundances shown are in 1980 (prior to infestation), and in 1984 (18 months after infestation). Both live coral and fish abundance decreased dramatically following the starfish infestation.

Patterns of distribution could be determined at any one, or more, of three stages in the life-cycle of a fish: a) prior to settlement (larval stage), b) at the time of settlement, or c) post-settlement. To determine which of these stages is most important, patterns of recruitment across the central transect were examined. For 16 out of 18 species, there was a close relationship between the distributions of recruits and adults. Despite variation in recruitment on any given reef from year to year and differences in recruitment to different reefs at the same shelf location during the same year, species which occurred nearshore as adults tended to recruit only to nearshore reefs. The same was true for species characteristic of mid- and outer-shelf habitats (see Figure 6, which presents the number of individuals per 750 square meters of reef for 3 species of fish). It appears that (for those species studied) cross-shelf distributions of adults are determined largely at, or by, the time of settlement into the reef environments. Therefore, hypothesis c (post-settlement) can be eliminated as a determining factor.

Additionally, two sets of observations suggest the distributions may be determined before (during the larval phase of the life cycle), rather than at, settlement. First, patterns of recruitment of fishes to identical coral heads placed across the shelf, and from which all fishes were removed frequently, appear as clearly defined as those to the natural substratum of reef slopes. Second, sampling of mature larvae attracted to lights suspended from a boat at night yielded primarily larvae of nearshore species in nearshore waters, and mid-shelf species in mid-shelf waters.

If cross-shelf distributions of adults are determined by larval distributions, what determines larval distributions at this scale? Our hypotheses are becoming more and more speculative as our line of questioning gets further from the available data, but it would appear that passive dispersal of larvae from the adult habitat is not an adequate explanation for, say, larvae produced on the outer-shelf recruiting only to the outer-shelf. There are many physical

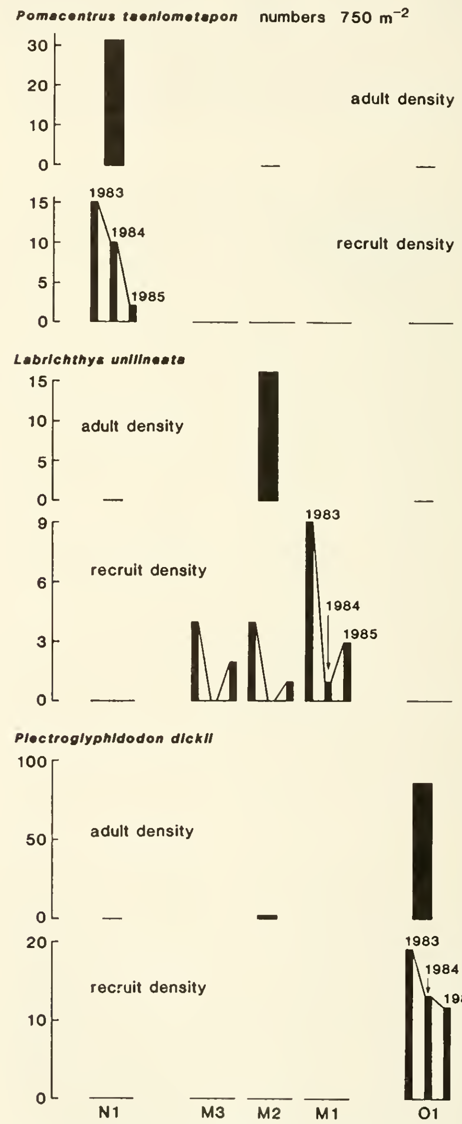


Figure 6. Densities (average number of individuals per 750 square meters of reef) of three reef fish species (both adults and recruits) for three successive years on one nearshore (N1), three mid-shelf (M1–M3) and one outer-shelf (O1) reef of the central transect.

Reef Fisheries

The Great Barrier Reef region supports a number of significant recreational and commercial fisheries. These fisheries, which extend along the 2,000 kilometer length of the Great Barrier Reef off Queensland, include otter trawling for prawns, shovel-nosed lobsters (known as "bugs"), and scallops; trolling, gill, and drift netting for mackerel and other pelagic species; handlining for reef fish; gill netting for coastal pelagic fishes such as trevally (mackerel), queenfish, and threadfin salmon; mudcrabbing; collection of aquarium fishes, coral, beche-de-mer (edible sea cucumber), and trochus (mother-of-pearl); and trolling for big and small game species, such as marlin, sailfish, and tuna. The commercial catch in the region in 1979–80, the most recent year for which data are available, was estimated at about 8,000 tons, worth an estimated A$27 million, about half the Queensland fisheries production. This can be compared with the total Australian catch of 150,000 tons (live weight), valued at A$360 million in 1980–81. In 1980, commercial fishing in Queensland was estimated to be less important to the Queensland economy than sugar, beef, grains, wool, and dairying, but ahead of tobacco, cotton, barley, eggs, and other primary industries.

Recreational fishing in 1980/81 was more important than commercial fishing—both in monies invested, and in percentage of catch. The recreational fishing population in the Great Barrier Reef region in 1980 consisted of about 15,000 motorboats (about 5 meters in length), making about 197,000 fishing trips, and averaging 2.6 fishermen per boat. Recreational fishermen also used charter and party boats (carrying 5 to 25 anglers), or fished from the beach. In 1980, these fishermen took about 70 to 80 percent of the finfish caught in the Great Barrier Reef region. As always seems to be the case, the majority of the non-commercial reef fish catch was taken by a small percentage of the fisherman. About 10 percent of the fishermen took about 40 percent of the catch; the least successful 50 percent of the anglers took 10 to 20 percent of the catch. The reef fishing may have had some effects on the stocks. The average size of reef fish landed from charterboats in the Townsville area has declined from 2.5 kilograms in 1957 to 1.4 kilograms. There also have been reports of increases in catch with increasing distance from shore — attributable in part perhaps to nearshore fishing pressure.

*Game fish, large and small, also occur in the region—and form the basis for a substantial recreational fishery. Starting initially off Cairns in 1966, for black marlin (*Makaira indica*), the big game fishery, from about Cairns to just north of Lizard Island, now involves about 40 vessels. Most marlin are tagged and released, although an angler's first fish, potential record fish, and fish over 1,000 pounds may be weighed in (usually about 5 percent of the season's catches). It has been suggested that the marlin grounds off the outer reef off Lizard Island may be a spawning area for black marlin, as the large marlin caught are gravid females. Light game recreational fishing for small marlin, tunas, queenfish, and others also is a rapidly expanding fishery along the Queensland coast. Game fishing clubs in most major coastal centers conduct annual tournaments.*

Black Marlin being weighed in. (GBRMPA)

Minor recreational fisheries also exist for the collection of aquarium fishes and shells. The extent of the recreational aquarium fishery is unknown, although it is believed to be more intensive in areas where the reef is close to the coast. Recreational shell collectors operate throughout the Great Barrier Reef, with active shell clubs in Yeppoon, the Whitsunday area, Townsville, Innisfail, and Cairns.

—Wendy Craik, GBRMPA, Townsville.

processes (wind, tides, currents) operating in the sea that ought to promote the widespread dispersal of planktonic larvae. The mixing potential of these processes is such that larvae should be far more mixed in their cross-shelf distribution than is suggested by the patterns of recruitment. Thus it would appear necessary to invoke either some habitat selection by larvae at the cross-shelf scale, or a differential survivorship of larvae in coastal and oceanic waters. At this time, we have no reason to prefer either of these hypotheses ahead of the other.

Summary

Large scale variations in the structure of fish communities on the Great Barrier Reef and trophic interactions related to this variation are extraordinarily complex. Nevertheless, considerable pattern does occur, and a number of plausible hypotheses have been forwarded to account for this pattern. Variations in the biomass of trophic groups in some, but not all, cases is correlated with the availability of resources in the reef environment, although causal relationships have yet to be established. Species distributions, on the other hand, may be determined largely by factors influencing egg and larval fish distribution, and survival.

David McB. Williams and Garry Russ are researchers at the Australian Institute of Marine Science, Townsville. Peter J. Doherty is at the School of Australian Environmental Studies, Griffith University, in Nathan. Both institutions are in Queensland, Australia.

Selected References

Done, T. J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95–107.
Russ, G. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* 20: 23–34.
Wilkinson, C. R., D. McB. Williams, P. W. Sammarco, R. W. Hogg, and L. A. Trott. 1984. Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. *Mar. Biol.* 80: 255–262.
Williams, D. Mc.B. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 33–43.
Williams, D. Mc.B., and A. I. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf, and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 10: 239–250.

Currents and Coral Reefs

by Eric Wolanski, David L. B. Jupp, and George L. Pickard

The Great Barrier Reef incorporates several thousand coral reefs spread over the continental shelf of northeast Australia for more than 2,000 kilometers in a longshore direction, from roughly 23 degrees South to 9 degrees South. In the north, long "ribbon" reefs are spread over the length of the shelf break, separated by reef passages typically 1 kilometer wide. In addition, there are a large number of reefs scattered, often very densely, over the width of the shelf. The inner shelf, or what is known as the lagoon, is thus restricted to the shallow, turbid, coastal zone. Near Barrow Point (Figure 1), the shelf width is about 30 kilometers (its narrowest point) and the reef-free lagoon is only 8 kilometers wide, offering a tortuous and shallow (less than 20 meters deep) passage.

In the central region, roughly between 15.5 degrees and 20 degrees South, the reef consists of a loose matrix of individual reefs widely scattered on the mid- to outer shelf, and the inner shelf forms a reef-free lagoon (Figure 2). Further south, the lagoon is much wider (up to 100 kilometers) and the outer shelf is a dense matrix of reefs up to 50 kilometers wide and separated by passages typically 10 kilometers in width.

The water circulation over the Great Barrier Reef is primarily directed by wind conditions, tides, and oceanic currents, and other events in the adjacent Coral Sea. The water circulation over the shelf responds to these force factors, but the response is strongly dependent on the blocking effect of the reefs. Hence, reef density within the matrix is an all-important parameter in the analysis of water circulation patterns. In this manner, one can distinguish between features of water circulation that are typical of reef-free continental shelves elsewhere in the world, and features unique to a reef-studded continental shelf.

Classical Continental Shelf Circulation

In the central and the southern regions of the Great Barrier Reef, the lagoon is essentially reef-free. The large-scale, wind-driven circulation in the lagoon is typical of that of a classical continental shelf. There exists a southward current (the East Australian Current [EAC]) which runs typically 30 to 50 centimeters per second over the continental shelf slope. This current is a near-surface phenomenon, as there is a return flow in deeper water. The surface current thickness is largest (about 250 meters) in the ocean, and smallest (100 meters or so) on the upper continental slope. Hence, the zone of return flow creeps up on the upper slope, as is typical of other shelves, for example in California. Thus, the current is a 100-meter-thick feature near the shelf break.

Because the East Australian Current is accompanied by a longshore pressure gradient, a southward drift also is felt on the continental shelf of the Great Barrier Reef, but, because of bottom friction, the strength of this southward drift decreases with increasing distance from the shelf break. The lateral shear of this current can be very large near the shelf break. As a result, hydrodynamic instabilities can develop and generate eddies such as those observed, for example, in the Gulf Stream. Such eddies have indeed been observed to exist on the shelf slope of the Great Barrier Reef, either directly from satellite images (Figure 3), or indirectly from moored current meter data.

These eddies presumably have the thickness of the East Australian Current, that is, 100 to 200 meters, so that they are deep enough to touch the seafloor of the upper continental slope and the outer shelf, should they drift there. In that case, they generate considerable suction near the bottom, resulting in major upwelling events.

Another classical upwelling event that can occur is caused by wind-forced long waves that cause density changes on the continental slope. The longshore wind-stress τ with frequency ω drives a bottom friction-limited longshore current over the vertically quite well-mixed Great Barrier Reef shelf of typical depth on the order of 40 to 60 meters. This current rarely exceeds 50 centimeters per second, and results in mean sea-level fluctuations of up to 35 centimeters peak to trough. Near the shelf break, these sea-level fluctuations are much smaller (on the order of a few centimeters) and the cross-shelf currents are small enough (on the order of a few centimeters per second), that, over the long periods of a normal wind event (typically 5 to 20 days), the shelf waters remain hydrodynamically coupled to the ocean waters.

The coupling implies that both the sea-level and the cross-shelf water fluxes are the same on both sides of the shelf break. The effect of the blockage of the flow through the Great Barrier Reef

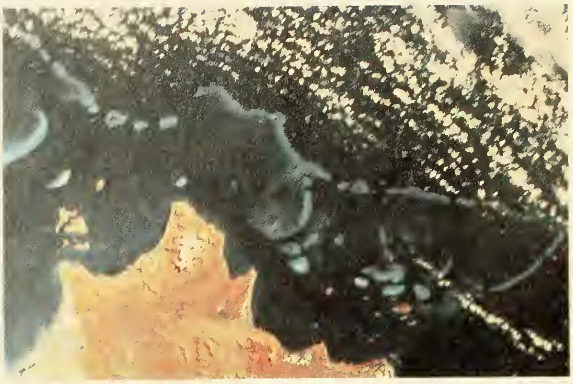


Figure 1. False color LANDSAT view of the area around Barrow Point.

matrix near the shelf break is to slow down the coupling somewhat, but, at the long periods of the wind (typically one to a few weeks), the density of reefs is unable to prevent the ocean-shelf coupling. As a result of this coupling, the thermocline* separating the mixed layer (typically 80 meters thick in winter) from the nutrient-rich deeper waters is

* A vertical temperature gradient, negative with respect to depth and appreciably greater than the gradients above and below it.

raised or lowered by a given amount. It appears that these vertical oscillations, confined to the vicinity of the shelf break, may be sufficient at times for nutrient-rich water from below the thermocline to spill onto the continental shelf.

In the central region and northern regions, the Great Barrier Reef matrix is sufficiently porous so that at least the dominant daily tides are able to propagate through the reef matrix with only small or moderate changes in phase and amplitude. In those cases, classical continental shelf oceanographic processes roughly prevail, and the topography of the shelf (that is, the longshore-dependent shelf width and bottom slope) largely controls the distortion of the tidal wave and the generation of longshore currents over the shelf.

Reef-Controlled Shelf Circulation

In the southern region, extremely large tides of up to 10 meters amplitude of vertical oscillation are experienced at the coast near 22 degrees South at Broad Sound. Yet the tidal range near the shelf break is only a third as large with small longshore gradients in phase and amplitude.* Two effects combine to generate this tidal enhancement. First, the shelf width is the largest in that area. About 200 kilometers to the north, the shelf width is about half

* The vertical distance from low water level to tide crest. Phase is the time of the wave crest at a given point.

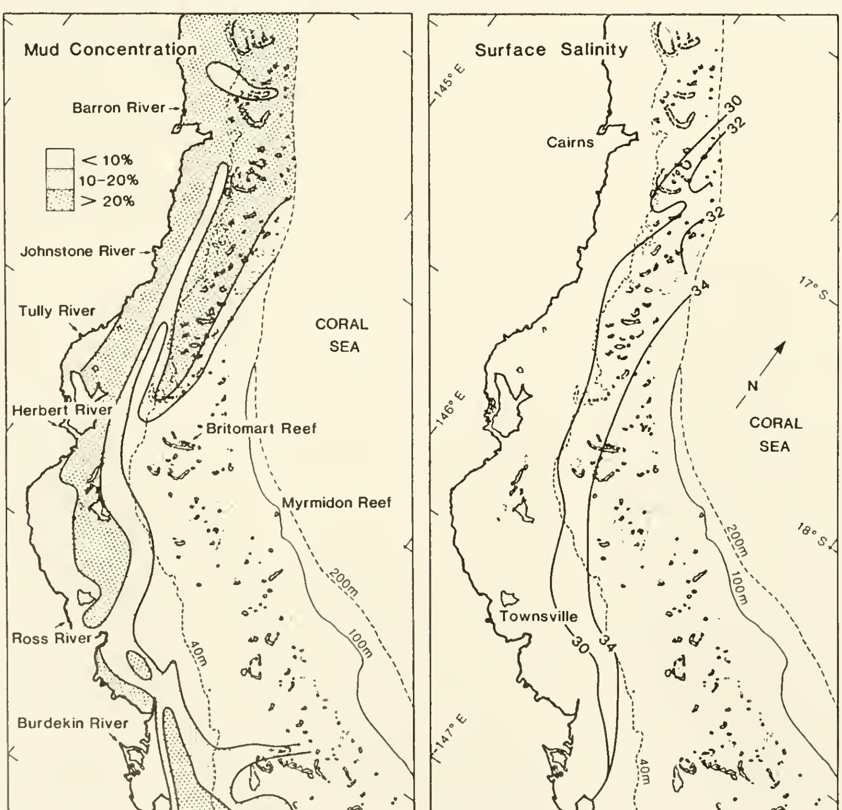


Figure 2. Simplified distribution, on the left, of the concentration of terrigenous mud on the seafloor in the central region of the Great Barrier Reef, and, on the right, of the minimal surface salinity measured during the January, 1981, flood event.

as large, and, about 200 kilometers to the south, the shelf width decreases abruptly and the reef-free isobaths* run nearly perpendicular to the coastline. It may thus be "easier," in terms of bottom friction effects, for the tidal wave to converge toward Broad Sound from both north and south.

The second effect compounds the first one, in that the density of reefs offshore from Broad Sound is much greater than that both further north and south. In fact, the reef density is so large that, at the twice-daily frequencies, the tide is measurably blocked by the reef matrix. This blocking is illustrated in Figure 3, which is a Coastal Zone Color Scanner (CZCS) satellite image of the reef matrix. This figure shows tidal jets in front of reef entrances. Such current features significantly enhance the overall friction of the prevailing currents by dissipating a large fraction of the kinetic energy of the incoming flow in the eddies. This energy loss is most prevalent for strong prevailing currents, such as exist at tidal frequencies. In this way, the southern Great Barrier Reef matrix helps decouple the shelf from ocean tides.

The large tides in Broad Sound can then be explained as the result of the convergence of two tidal waves propagating toward the Broad Sound area from both north and south. This property results also from numerical and analytical models of the tidal circulation in the southern reef region. In such models, the complex water circulation introduced near reef passages is neglected, but the overall obstruction of the currents by the Great Barrier Reef is still included by modelling the reefs as weir-type structures.

Another example of reefs blocking the water circulation occurs near Barrow Point (Figure 1), where the reefs are so densely packed across the shelf width that only a narrow and shallow lagoon remains. As a result, there is so little water transport through this passage that for all practical purposes the northern and the central regions of the Great Barrier Reef are hydraulically disconnected. A similar situation occurs in the shelf region of the Torres Strait, north of Cape York, making this region a backwater of the Gulf of Papua. In this case, the bulk friction coefficient at low frequencies is enhanced further by the very strong tidal currents through the Strait.

The increased friction resulting from the interaction of currents and reefs is the result of at least two hydraulic phenomena, namely the island wake effect (when there is only one obstacle), and the tidal jet effect (when there are two obstacles in close proximity).

The Island Wake Effect

One of the most dramatic effects of the circulation around islands and coral reefs is the generation of recirculating flows downstream. LANDSAT views (computer-enhanced for depth of penetration using the techniques discussed by D. A. Kuchler page 90) and aerial observations show that such recirculating flows are visible when sufficiently strong currents are present, and whenever there exists in the water a natural "dye" (such as mud on the seafloor, or particulates released from a reef). Topographically-shed eddies are visible near the coast, in relatively shallow (15 to 30 meter depth) waters around coral reefs and islands, and around coral reefs in deeper waters (60 meters depth) see Figure 4.

An intensive field experiment was carried out to measure the recirculating flow around Rattray Island at 20 degrees South. The shape of the wake resembled that obtained in two-dimensional laboratory investigations at low values (of the order 10 to 30) of the Reynolds number (a parameter expressing the ratio of inertia to viscous forces). However, the field data disclosed that there is no valid analogy between the island wakes in two-dimensional laboratory experiments and those observed in nature. Indeed, the eddy in the laboratory is composed of a mass of water that is nearly stagnant, while at Rattray Island the waters in the eddy are under very rapid rotation. Further, the Reynolds number of Rattray Island, based on the turbulent eddy viscosity, is a thousand times larger than in the laboratory.

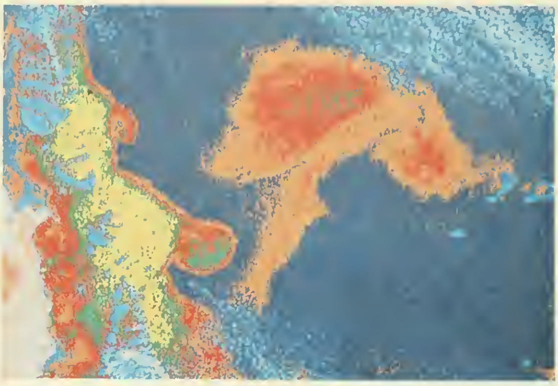


Figure 3. CZCS view, enhanced to emphasize chlorophyll, of the central reef region. Note the two eddies at the shelf break in the north and a complex jet-vortex system in the south.

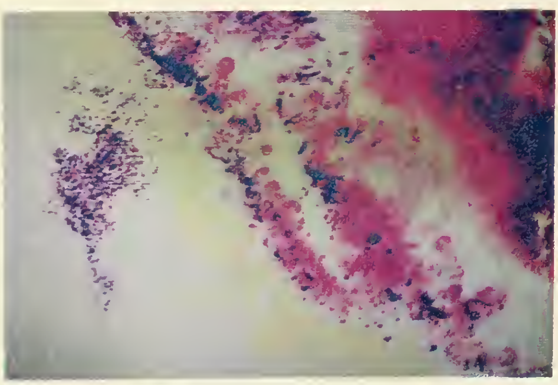


Figure 4. Aerial view of the eddies shed by coral reefs in 60-meter-deep waters.

* Contours of equal depth.

The Reef, Tides, and

In 1802, one of Australia's foremost maritime explorers, Captain Matthew Flinders was charged with the first circumnavigation and charting of the Australian coastline in the ship H.M.S. Investigator. *During this expedition, he noted the unusual nature of the tides in the southern region of the Great Barrier Reef.*

Commenting on his observations in the vicinity of Broad Sound, Flinders stated in his journal, published in 1814: "On the west side of the sound, . . . the rise at spring tides is not less than 30, and perhaps reaches to 35 feet." He remarked on currents associated with "a tide which ran at the strongest between 4 and 5 knots and that the flood came in, 6 or 8 inches perpendicular with a roaring noise," presumably a reference to the tidal bore that is known to exist in the sound. Flinders also noted the unusual phase of the tides, stating that "the time of high water is nearly 11 hours after the noon's passage over and under the meridian."

Flinders' observations have been confirmed by direct measurement in recent times. What is more remarkable is the perspicacity that Flinders displayed in deducing a convincing physical explanation for tides that are both very much higher and later than those in neighboring reef waters to both the south and north, and which peak in Broad Sound itself.

Flinders went on to write of a "super-adding cause . . . a vast mass of reefs which lie from 20 to 30 leagues [100 to 150 kilometers] from the coast. These reefs, being mostly dry at low water will impede the free access of the tide; and the greater proportion will come in between Break-sea Spit [to the south] and the reefs, and be late in reaching the remoter parts; and if we suppose the reefs to terminate to the north, or northwest of the Sound, or that a large opening in them there exists, another flood tide will come from the northward, and meet the former; and the accumulation of water from this meeting will cause an extraordinary rise in Broad Sound and the neighboring bays. . . . I am disposed to think that it is at the entrance of Broad Sound where the two floods meet each other."

The map after page 8 gives some idea of the density of these reefs (between 19 degrees and 22 degrees South), in both the longshore and cross-shelf directions. After considerable difficulties (during a period of more than two weeks), Flinders eventually found a passage, subsequently named after him, out into the Coral Sea. It must have been most unnerving to explore for possible passages among reefs that are more often than not invisible, especially given the presence of such strong currents, in a small and unwieldy sailing vessel—the Investigator *was*

To reconcile these observational differences, it is believed, as is shown in Figure 5, that there exists a mass of water in solid body rotation separated by a dividing streamline from the surrounding waters. Rotation in the eddy is maintained by the large vorticity flux at the separation point at the tip of the island. By analogy with the circulation in a tea cup, the combined effects of bottom friction and of rotation in the eddy, generate a self-driven bottom benthic boundary layer. As a result, water is sucked downwards from the eddy to the bottom layer and upwelled near the center. The upwelling process near the eddy center, which brings fine particulates to the surface, makes the eddy often readily visible from the air. The downwelling controls the time and length scales of the eddy.

The secondary circulation in the island wake also is reflected in the sediment size distribution on the seafloor, with less mud and more sand near the eddy center than elsewhere.

The island wake parameter (P) determines the wake shape; satellite and aerial views indicate that, for increasing values of P, the downstream flow becomes perturbed by meanders even very far downstream. For higher values of the island wake parameter, these meanders can become unstable and form small eddies at their troughs and crests. For very high values of P, the wake is fully turbulent with no organized recirculating flow structure.

The "standard" depth-averaged numerical models, developed for open waters, are generally unable to yield a wake effect and predict a quasi-potential flow pattern. A numerical scheme that accounts for flow separation effects has been developed recently. The resulting predicted currents agree closely with the currents measured with current meters moored at 26 sites.

It is now feasible to reliably model eddies and their fate, when the eddies detach themselves from their natal reefs. Two important properties of these topographically-shed eddies are that they generate patchiness and hence control the rates of diffusion and dispersion through the reef matrix, they also dissipate much of the kinetic energy of the incoming flow facing the island, so that they greatly enhance the bulk friction coefficient of the prevailing current.

If the water column is vertically stratified in

Flinders' Perspicacity

condemned the following year as unseaworthy! Only in the last year has the charting and marking of a navigational channel (Hydrographer's Passage) for large cargo vessels from the port of Mackay been accomplished. From personal observation, tidal currents near individual large reefs (for example, White Tip Reef at the seaward entrance of this passage) can be as high as 8 knots!

Present-day marine scientists may find it sobering to read these extracts from Flinders' account. They are a tribute, not only to his navigational and cartographic skills (many of his maps still form the basis of today's charts), but also to his ability to conceptualize this large-scale and unusual tidal flow pattern, along with the active involvement of the reef itself, from only a few key observations—all of this from a man of only 26, recently given command of his first ship.

Essentially, Flinders' hypothesis was that the tides are inhibited in their cross-shelf passage by the high density of coral reefs in this vicinity. As a consequence, the major streams flow through the very large passages that exist to the north and south (Flinders' Passage and the Capricorn Channel, respectively), to converge near Broad Sound. The position and geometry of the sound results in further local amplification of the tides. The considerable heads of water that are induced by this inhibition result in very large currents in the gaps between reefs, although the actual proportion of water that crosses the reef matrix is relatively small.

Interestingly, Flinders' hypothesis came to light only recently, after a number of investigators, using both analytical and numerical models, had come to similar conclusions (roughly 160 years later). Of course, the Broad Sound area is just one portion of the reef; Flinders' description does not apply universally. How then do reef structures elsewhere affect tidal as well as other flows, given the contrasting geometric reef patterns that exist? North of the dense reef pattern, the reefs of the central reef region, centered on Townsville, are relatively sparse. They have little effect on the large-scale tidal pattern. Farther north, the "ribbon" reefs exist, with often 90 percent linear coverage along the edge of the continental shelf, over large distances. There, in contrast with the Mackay/Broad Sound area, reefs are effectively transparent to the tides, although the almost unbroken reef chain does appear to act as a semi-permeable barrier, modifying both the amplitude and phase of the tidal wave passing "through" it.

—Lance Bode,
James Cook University

density, the flow separation at the tip of the island or headland will still generate an eddy downstream. However, and such is the case in the deep waters near the shelf break, the strong current may be only a near-surface phenomenon, and the eddy may be confined to the well-mixed layer. The interfacial stresses between the well-mixed layer and the deeper water are small, so that the eddy in the well-mixed layer does not have a tendency to be spun down rapidly by suction. Hence, flow disturbances are introduced and felt very far downstream. The thermocline can take the shape of a dome in such near-surface eddies. If the thermal dome of an eddy comes in contact with the seafloor, considerable suction and upwelling result.

The Tidal Jet Effect

In the northern and southern regions, strong tidal currents can exist in the reef passages between long ribbon-shaped reefs spread along the shelf break. When the currents are small, the density (thermal) stratification results in selective withdrawal, as in a stratified water reservoir, and, at rising tide (Figure 6), only nutrient-poor water from the mixed layer is flowing in the passage, the water from below the thermocline being at rest. However, when the tidal currents are very strong (say on the order of 100 centimeters per second), nutrient-rich deep water can be entrained vertically up to 100 meters into the reef passage (Figure 7). This water mass, and the nutrients it contains, is then entrained by the tidal jet effect into the shelf.

In calculating the bulk properties of such jet flows, we determined that these eddies are basically vortices which are self-propelled, that is, they tend to move together away from the reef passage. These eddies are not sucked back into the reef entrance at the following falling tide. The mass of jet-injected water will spin down by friction, but does not return to the ocean and indeed stays roughly in the same area for a very long time, giving plenty of time for nutrient uptake at tidal frequencies nearly every day of the year.

This phenomenon is believed to account for the profuse meadows of the calcareous green alga, *Halimeda* (see page 45), in the areas where the tidal jet-vortex pair system appears to penetrate on the shelf. These meadows are most prevalent near reef

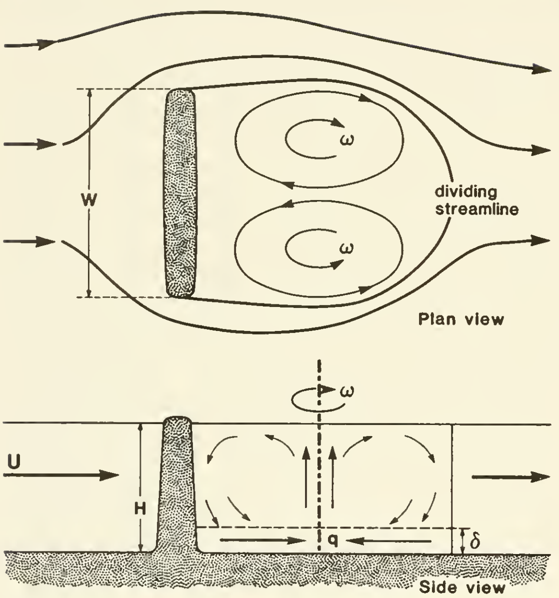


Figure 5. The three-dimensional circulation in an island wake.

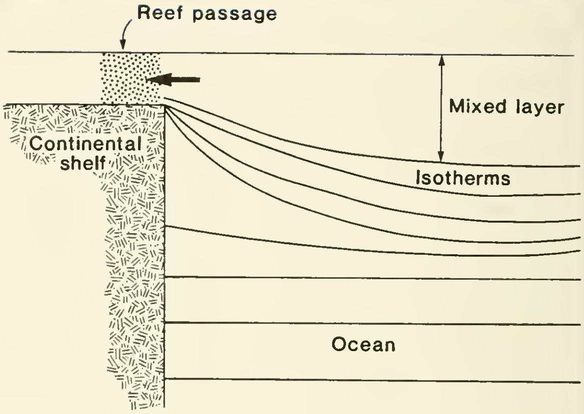


Figure 6. The upwelling by tidal jet pumping at a reef passage.

passages forming a small canyon, hence where upwelling is facilitated, and appear not to exist in areas where the shelf elevation is too high for nutient-rich deep water to be upwelled by tidal jets. The vortices dissipate much of the kinetic energy of the incoming flow, and this may explain the blocking effect by ribbon reefs on tidal propagation.

Surface Gravity Waves

Every sailor who takes shelter from the wind behind a coral reef knows that reefs also measurably affect surface gravity waves. Reefs provide a platform for wave-breaking, diffraction and refraction. These processes also control the formation and migration of sand cays by establishing a zone of wave convergence in the weather lee of platform reefs. Wave breaking also raises sea level. This combination can drive a net unidirectional current over long thin reefs, such as the "ribbon" reefs. On the other hand, a strong, two-dimensional flow prevails over platform reefs near the shelf break with areas of higher elevation where waves break preferentially, and areas of slightly lower elevation where the return flow occurs after wave breaking. In more sheltered reefs, one commonly finds a submerged coral seawall, with occasional gaps, running parallel to the reef it protects, and separated from the reef by a drainage channel that accommodates the return flow of the breaking wave.

Wave data from a site offshore of the Great Barrier Reef show the presence of a classical oceanic saturated wave spectrum under strong winds, with the 10-second period wave (swell) dominating the energy spectrum. On the other hand, inshore wave data show that the swell is much smaller, and local wind-sea, 4-second waves predominate. Thus, the Great Barrier Reef matrix does indeed shelter the lagoon.

In the lagoon, the 4-second wave introduces pressure and current fluctuations near the bottom that are too small to move the sediment except in the nearshore zone. As a result, terrigenous sediments may accumulate in the lagoon. This hypothesis also is suggested from a comparison of the distribution in the central region of the reef of terrigenous mud on the seafloor, with that of the minimal surface salinity during major river floods (Figure 2). The shape of the salinity and mud distributions is quite similar, except for a tongue of mud through the reef matrix off the Burdekin River mouth. That tongue is believed to be a relic one, attributed to the old mouth of the river as the sea level started to rise 10,000 years ago. The Burdekin river plume, by buoyancy and effects of the Earth's rotation, moves northward along the coastline and against the prevailing weak southward currents. The width of the river plume increases with distance from the mouth of the Burdekin river, as a result of both lateral mixing and of the additional freshwater input from the Ross, Herbert, Tully, and Johnstone Rivers. The Burdekin River, however, has by far the largest freshwater discharge. Along the way, terrigenous mud falls from suspension and accumulates at the bottom. This mud may be quite stable on the seafloor, since the swell is unable to penetrate the lagoon, and because tidal and wind-driven currents are quite small.

Conclusions

The large-scale water circulation on the continental shelf of the Great Barrier Reef is complex, driven mostly by currents, tides, and the wind. A full understanding of this circulation still eludes us. On a small scale, the presence of coral reefs and islands serves to substantially modify the general water circulation by increasing the overall friction, as well as the wave climate of the Great Barrier Reef. The existence of tidal jets and large eddies downstream of a reef has profound effects on 1) the formation of fronts, 2) the trapping of water and particulates, 3) the mixing rates in inter-reef shelf seas (by creating patchiness), 4) the overall water circulation (by increasing the overall friction coefficient), and 5) the sedimentology (by forming tidal banks and shoals and possibly helping shape the reefs during geological time).

The topographically directed flows around reefs are believed to influence the aggregation of plankton, fish eggs and larvae, benthic invertebrates, and, possibly, the location of fisheries. These complex flows are probably the dominant physical process producing patchiness (advection and diffusion in the inter-reef shelf seas of reef-born suspended particulates once they drift away, as a patch, from their natal reef). Hence, they help to determine the level of biological exchange between reefs. Collecting statistics on this exchange may be the most useful information that physical oceanographers can provide to the users and the managers of the Great Barrier Reef. The tool for understanding such information may be a recently developed numerical model that can, with very reasonable assumptions, reproduce such complex flows.

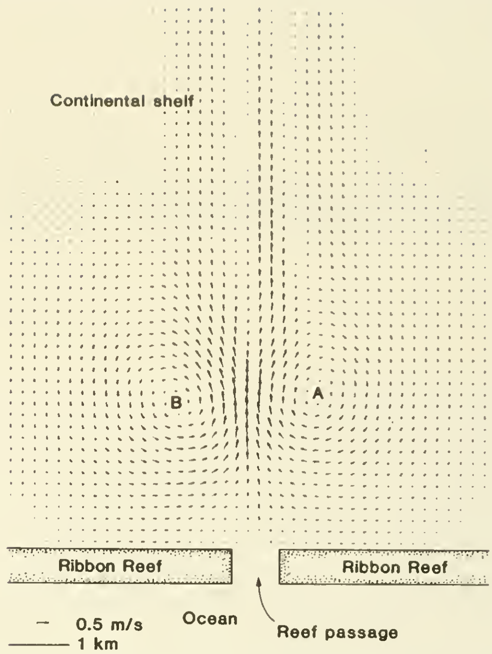


Figure 7. Predicted depth-averaged velocity field over the continental shelf in front of a reef passage at slack high tide. The tidal current through the passage has a peak velocity of 100 centimeters per second. The shelf is assumed to be flat; water depth = 37 meters.

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Selected Readings

Wolanski, E., G. L. Pickard, and D. L. B. Jupp. 1984. River plumes, coral reefs and mixing in the Gulf of Papua and the Northern Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 18, 291–314.

Wolanski, E., J. Imberger, and M. L. Heron. 1984. Island wakes in shallow coastal waters. *Journal of Geophysical Research* 89 (C6), 10553–10569.

Falconer, R. A., E. Wolanski, and L. Mardapitta-Hadjipandeli. 1986. Modelling tidal circulation in an island's wake. *Journal of Waterway, Port, Coastal and Ocean Engineering*, Amer. Soc. Civil Engineers 112 (2), 234–254.

Onishi. 1984. Study of Vortex Structure in water surface jets by means of remote sensing. In: *Remote sensing of Shelf Sea Hydrodynamics*, J. C. J. Nihoul, ed. Elsevier Publ., Amsterdam, pp. 107–132.

Remote Sensing: What Can It

by D. A. Kuchler

Sunlight reflected from shallow seas and submerged features is providing a wealth of information on coral reef ecosystems. Until recently, recording and interpreting this data on a routine basis was not economically feasible. The advent of the space age, however, ushered in the development of advanced sensor systems and the platforms that support them. These technological gains now have made remote sensing a viable method of collecting data for coral management and research. For the Great Barrier Reef, remote sensing has saved researchers and management both time and money by providing information that is otherwise unavailable.

Remote sensing's main advantage is that it can collect some coral reef information faster and less expensively than ground-based techniques. In addition, it can measure uniformly the abundance and distribution of phenomena in time and space. Land- or ship-based measurements are only capable of patchy sampling. While methods for deriving chemical information from remotely-sensed coral reef and oceanic data are still being designed, research into the nature of remotely-sensed physical and biological data is comparatively well advanced. Among information gathered from the latter group are data on reef geography, form, cover, and vegetation.

Reef Geography

The geography of reefs is of extreme importance to mariners, researchers, and administrators who assess coral reef resources, plan shipping routes, and locate potential fishing grounds. Until the processing of 24 Landsat Multispectral Scanner (MSS) images in 1985, however, maps giving such information were not available. Rectified satellite images, taken from the Landsat satellite now provide such maps at scales of 1:250,000 and 1:100,000.

Once image distortions have been removed, the map is accurate to within 200 to 500 meters. While sufficient for many applications, this level of accuracy is not precise enough for navigation, cartographic, or environmental monitoring purposes. By registering the images with a cartographic base, higher map accuracies (± 64 meters) that meet the National Map Accuracy Standard have been achieved.

In addition to maps of a relatively small area, satellites can produce much larger views as well. Just two Coastal Zone Color images taken aboard the Nimbus 7 satellite provide a total perspective of the 1,900-kilometer extent of the Great Barrier Reef, while a regional perspective is available from images taken aboard the space shuttle.

Reef Form

The form of a reef and its surroundings contains an abundance of information that is key to innumerable scientific and administrative concerns. Because reef topography is virtually unseen from a land-based perspective and at best obscure when viewed on a raw Landsat image, a reef exposure image has been devised to enhance images of topographic features. It uses a technique of relief shading to clarify reef features.

Through this relief shading, the exposure images provide information on reef form that can be used to:

- *plan geophysical field programs on individual reefs;*
- *update site morphology;*
- *give clues to structural or stratigraphic features; and,*
- *show relationships between structure and site, important in determining areas for research.*

The exposure image also gives increased edge enhancement for both the detection and mapping of paleochannels and for an indication of a reef's exposure to weather.

A further understanding of reef form is gained from submergence and turbidity levels. These can be estimated using remotely-sensed data of reflected light from the sea, since depth of light penetration tells us approximate water depths and turbidity levels. The Landsat satellite has recorded water depths varying from just below the sea surface down to 20 meters. Factors affecting the satellite's ability to get such information include the conditions of both

Offer Coral Reef Studies?

the sky and the water, and the absorption of light by the water at the wavelength received by the satellite.

Reef Cover

A basic goal of research is to both understand and explain the abundance and distribution of reef cover types over time and space. With the availability of Landsat data in 1972 (originally called ERTS-1 data), the speed and sophistication of taking an inventory of reef covers have increased significantly. Methods of analysis range from visually interpreted maps to advanced computer interpretations.

Variations in light reflected from a submerged reef surface can be interpreted and utilized for a number of different mapping purposes. This is possible because a computer statistically classifies digital image data into a number of classes. One study determined the extent to which Landsat mapped classes cross-compare with reef cover classes on the ground. At most, classes showed 85 percent cross-comparison with reef zones, 82 percent with reef features, and 64 percent with reef feature components. The results illustrate that Landsat data can be used as a surrogate source of ground information and that mapping precision increases with smaller mapping scales (large area, small detail).

Overseas, two successful projects are using large scale (small area, large detail) remotely-sensed data to map reef covers. For coral reefs in the Red Sea, digitized aerial photographic data are being used to make periodical surveys of seasonal change. In New Caledonia, simulated SPOT satellite* images are mapping possible trochus shell (*Trochus niloticus*) habitats on offshore coral reefs.

The higher spatial resolution of a SPOT image can be seen by comparing it with an aerial photograph. Such resolution could be used to map the devastating effects of Crown of Thorns starfish (*Acanthaster planci*) on some corals of the Great Barrier Reef (see page 58).

Vegetation & Micro-studies

Studies often are conducted to provide reef vegetation cover maps either for management inventories, research projects, or environmental impact assessments. Conventional field mapping takes weeks to produce such maps, but processing remotely-sensed data with computers can take only a few hours.

Maps showing the dispersion of vegetated coral cays and algal vegetation on shallow reef flats can be produced from Landsat data. Digitized aerial photographic data or SPOT satellite data can map vegetation diversity and human or natural interferences with vegetation cover.

Coral calcification and accretion studies also can rely on remote sensing technology. Coral cross-sections are digitized, and growth bands within the resulting images are classified, contoured, and measured using image processing techniques.

Remote sensing is providing another broader view of the recently discovered coral spawning phenomena. After the spectral reflectance characteristics of coral spawn are determined, the dynamics of coral spawn dispersal and settlement are examined using a multistage remote-sensing approach involving sensors aboard boats, aircrafts, and satellites.

A Broader Look

Since coral reefs are a small subsystem of a much larger oceanic system, they are often studied in this context. Scientists have used remotely-sensed data to study the oceans for many years. Typically, the studies are at synoptic scales because oceanic processes interact over wide ranges of space and time.

Ocean color studies on the Great Barrier Reef have concentrated on utilizing back-scattered radiation in the visible part of the spectrum. Nimbus 7 Coastal Zone Color Scanner data have been used to conduct synoptic surveys of phytoplankton concentrations, to study mesoscale circulation structures, and to map eddies and wakes. Other researchers investigating ocean color have used Landsat data to view sediment plumes and to monitor high concentrations of material, such as *Trichodesmium* blooms. Remotely-sensed information on such blooms has been plentiful: recordings have been made from the Landsat satellite, from a NOAA satellite, and from the space shuttle.

Not An Automatic Process

Interpreting remotely-sensed coral reef data is by no

* The SPOT satellite is a high resolution (10 and 20 meters) data collection system from which data will be available in mid-1986.

means an automatic process. Rather, it involves unravelling the spectral and spatial relationships within the data, requiring much more basic research. Consequently, researchers are focusing their efforts on the collection and analysis of reflected surface radiation from reef cover types.

Such emissions will provide the trained interpreter with a vast amount of information about the spectral composition of a coral reef. This knowledge, coupled with the new generation of sensors optimized for oceanographic applications, will mean that coral reef and oceanic studies will adopt newer, more precise, and more extensive applications of remote sensing technology.

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Aerial photograph of Tetembia Reef, New Caledonia.

Acknowledgments

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References and Selected Readings

Bina, R. T., K. Carpenter, W. Zacher, R. Jara, and J. B. Lim. 1978. Coral reef mapping using Landsat data: follow-up studies. *Proceedings Twelfth International Symposium Remote Sensing Environment*. Ann Arbor, Michigan. 2051–2070.

Bour, W., L. Loubersac, and P. Rual. 1985. Thematic mapping of reefs by processing of simulated SPOT satellite data—application to the *Trochus niloticus* biotope on Tetembia reef, New Caledonia. *Marine Ecology*.

Jupp, D. L. B. 1985. Report on the application and potential of remote sensing in the Great Barrier Reef region. *GBRMPA Research Publication*.

Jupp, D. L. B., P. Guerin, and W. Lamond. 1982. Rectification of Landsat imagery to cartographic bases with application to the Great Barrier Reef. *Proceedings URPIS 10*, Sydney, NSW, Dec., ed. K. R. Nash. 131–147.

Jupp, D. L. B., K. K. Mayo, D. A. Kuchler, S. J. Heggen, and S. W. Kendall. 1981. Remote sensing by Landsat as support for management of the Great Barrier Reef. *"Landsat 81," Proceedings 2nd Australasian Remote Sensing Conference*, Canberra, 9.5.1–9.5.6.

Jupp, D. L. B., K. K. Mayo, D. A. Kuchler, S. J. Heggen, S. W. Kendall, B. M. Radke, and T. Ayling. 1985. Landsat based interpretation of the Cairns section of the Great Barrier Reef Marine Park. CSIRO Division of Water and Land Resources, Natural Resource Series No. 4, 51 p.

Jupp, D. L. B., K. K. Mayo, D. A. Kuchler, D. V. R. Classen, R. A. Kenchington, and P. R. Guerin. 1985. The application and potential of remote sensing to planning and managing the Great Barrier Reef of Australia. *Photogrammetria*, 40. 21–42.

Kuchler, D. A. 1985. Geomorphological separability Landsat MSS and aerial photographic data: Heron Island Reef, Great Barrier Reef, Australia. Ph.D. Thesis, Department of Geography, James Cook University of North Queensland, Australia.

Maniere, R., and J. Jaubert. 1984. Coral reef mapping in the Gulf of Aqaba (Red Sea) using computer image processing techniques. *Proceedings Symposium on Coral Reef Environment of Red Sea*. Jeddah, Saudi Arabia.

Landsat satellite image of Heron Island and Wistari Reefs on the Great Barrier Reef. Red is the spectral response to vegetation, white is the beach around the cays. (Image courtesy of D.A. Kuchler)

Islands and Birds

by Harold Heatwole, and Peter Saenger

A view of the Swain Reefs showing two small sand cays, Bacchi Cay in foreground, Thomas Cay in background. (Photo courtesy of Menna Jones)

The islands of the Great Barrier Reef range from tiny sand patches so small you can barely stand on them to mountainous islands more than 150 square miles long with rocky peaks rising 3,650 feet above sea level. Some are remote and visited only by an occasional, lone scientist or beachcomber; others are built-up tourist resorts with helicopters constantly flying people in and out. The islands are also a haven for birds.

Islands and birds go together. Birds deposit guano on islands, which not only forms phosphate rock (or cay rock), but also fertilizes the soil and thus stimulates plant colonization. Birds also bring seeds to islands. In turn, the islands provide birds with a place to breed and/or nest without the disturbance of humans or mainland predators, such as rats, foxes, snakes, monitor lizards, and raptorial birds.

Although there are many species of birds on the islands, there are only two kinds of islands on the Great Barrier Reef: continental islands and cays.* Continental islands are located on continental shelves that were once part of the mainland geological formation, but became isolated as either the land sank, the sea level rose, or a combination of the two occurred. Cays are formed *in situ* as the sea and wind act on local sediments. While cays may lie on continental shelves or on remote reefs, they were never part of the mainland.

Along the Great Barrier Reef, the prevalence of these two types of island changes. The northern and southern parts of the reef contain numerous cays, whereas the central region has few. Throughout there are more than 240 cays. By contrast, the continental islands are located primarily in the central section of the reef. All in all, more than 2,100 individual reefs make up the main barrier, with 540 continental islands closer inshore supporting fringing reefs.

Cays

On the Great Barrier Reef, sand cays are composed primarily of the remains of marine organisms, such as coral, mollusk shell, calcareous algae, and foraminiferans. These organisms may be ground into small particles to form sand; water currents then deposit them on the top of the reef. A cay evolves as enough sand accumulates to be exposed at low tide and winds add more sand on top. Since cays are formed at the surface, they can date only from the time the coral reached present sea level; those on the Great Barrier Reef are only about 4,000 years old.

In addition to currents and winds, storms also are a potent force in cay development. Hurricanes can tear pieces of coral from the reef front and hurl them onto the reef. These large pieces of shingle may accumulate and form a shingle cay. On some islands, successive storms have left their mark in concentric ridges of shingle, the most recent storm composing the outer ridge and earlier ones forming the inner ridges.

Once formed, cays often change their shape. One way this occurs is through the formation of beach rock. Beach rock develops below the sand surface at the periphery of a cay. How it forms is still not completely understood, but it seems to involve the precipitation of calcium salts among the sand grains, consolidating them into rock. This can occur very rapidly. When the beach subsequently erodes, the exposed beach rock is left as an outcrop.

Cays are not only unstable, but because of the various ways they are formed, they are quite diverse: they can be all sand, all shingle, combinations of both, or have large outcrops of beach rock or cay rock.

Occurring only on the northern Great Barrier Reef, low-wooded islands form from a combination of a sand cay on the leeward side of a reef platform and a shingle cay on the windward side. The

* Keys is the American spelling. Cays is used elsewhere in the English speaking world.

A colony of Crested Terns nesting on Bell Cay, Swain Reef. (Photo courtesy of H. Heatwole)

depression between the two is then colonized by mangrove trees which, in turn, result in deposition of organic materials and the build-up of sediment. Thus, low-wooded islands often are composed of sand, shingle, and organic sediment.

Colonization of Islands

Amazing though it is, even tiny, remote islands support plants and animals. Continental islands have a head start in this regard since some of their species may have been stranded when the island formed, and have simply persisted there ever since. For coral cays, the situation is quite different. When cays emerge from the sea, they contain no terrestrial life: all their plants and animals must reach them across a seawater barrier.

The ways that life arrives are varied. Many insular plants have seeds or fruits that can float for weeks or even months and remain viable in seawater for long periods of time. Such plants are dispersed long distances by sea currents. Others have hooks or sticky secretions on their fruits, or seeds that adhere to feathers; these plants are widely dispersed by birds as they fly from island to island. Still other plants reach the islands inside birds' digestive systems.

On One Tree Island, 48 percent of the plant species were sea dispersed and 22 percent bird dispersed. The rest were distributed either by the wind, humans, or unknown means. Curiously, few species of plants seem to reach the islands by wind. In general, the pioneer plants on small and/or new islands are sea dispersed while plants in the center are bird dispersed.

Along with plants come insects, many of which reach the islands through offshore winds. When the winds are right, many insects reach tiny, remote Willis Island, 280 miles from Australia; some are even blown from as far away as New Guinea, a distance of more than 370 miles. Although nearly 97 species of insects were carried to this island in a single season, most did not become established. Even small, weakly flying insects can be passively wafted by winds. Such strong flyers as butterflies and dragonflies, however, can cover long distances under their own power.

Another way that small, terrestrial invertebrates—insects, spiders, centipedes, and mites—reach islands is by flotsam. Logs or other debris cast adrift from beaches or flooded rivers carry on or within them a surprising variety of such animals, and help colonize distant islands.

Even after these invertebrates and plants reach the islands, they still must survive the hot, salty, waterless, and nutrient-poor conditions of newly formed sand cays. Thus, only the hardiest species persist on newer islands. As cays grow large enough to retain freshwater, and the interiors are further removed from the effects of salt spray, conditions become more benign, and more immigrant species become established. Plants help both stabilize the substrate and enrich the soil with organic matter as they die and decay. These improved conditions allow additional species of plants to colonize. The variety of plants increases from four or five species to as many as 40 species on older cays. These insects and plants change the

Beach near lighthouse bordered by shrubs (Octopus Bush, Argusia argentea*) on North Reef Cay, Capricornia Reefs. (Photo courtesy of H. Heatwole)*

The forested interior of a cay in the Capricorn Islands, Masthead Island. (Photo courtesy of H. Heatwole)

environment. For example, plants cast shade and lower the ground temperature, form leaf litter which serves as cover for invertebrates, and add organic matter to the soil.

On very small or newly formed cays, the food basis for the terrestrial community is not the plants that colonize, but the marine community. The first truly terrestrial organisms that become established on new islands are scavengers feeding on dead fish, other marine organisms that wash up onshore, and on guano and the carcasses of dead seabirds. These include earwigs, beetles, and flies. Next to settle on the cays are predators such as spiders, centipedes, and other invertebrates that feed on scavengers. Proof of this is the number of sand cays, completely devoid of vegetation, that have been found to have scavenger-based communities, complete with predators, of up to 11 species of terrestrial invertebrates. The final colonization phase involves the establishment of green plants, and the subsequent herbivores and additional species of predators. As the islands grow and contain increasing numbers of plant species, the local plants become the principal food base for the community, which thus depends progressively less on the marine community.

Insular Instability

Continental islands are more stable than cays because of their rocky substrate, high topography, and relatively large size; cays, in contrast, are usually small, flat, and sandy. While some cays remain in the same place for a long time, others have only a stable center and the edges, particularly the ends, shift back and forth with temporal changes in currents. Varying currents and storms can build and erode cays. Some cays tend to move in a continuous direction, eroding from wave action on the windward side, and redepositing sand on the leeward side. Cays can creep progressively across the reef seemingly destined to disappear over the reef edge into deep water.

Instability is related partly to cay size. The smaller, lower cays are generally less stable than the larger ones. Successive aerial photographs can map the changes of an island such as Bylund Cay in the Swain Reefs section of the Great Barrier Reef. In 20 years, this cay moved across its reef so much that only about a fourth of it overlapped in photographs taken in 1964 and again in 1984.

Insular Vegetation

As an island changes, so does its vegetation. Cay vegetation relates to an island's size, age, and stability. Generally, the larger the island, the greater the number of species of plants. Large cays are less susceptible to washover by the sea, except on the edges, and the intensity of salt spray diminishes toward the interior. Many islands have a ring of shrubs, especially *Argusia argentea* and *Scaevola sericea*, around the edge. A comparison of the levels of salt spray on the seaward and interior sides of the shrubs demonstrates that they form an effective barrier against air borne salt and thus ameliorate conditions inside the shrub ring. This permits plants that could not otherwise survive to grow, increasing the number of species that can eventually culminate in a forest.

In these ways, the cay and its vegetation develop together in five stages. In the first Pioneer Stage, only low, hardy plants cover the entire island sparsely. Next the Herb Flat Stage contains two vegetation zones: 1) the pioneer vegetation around the edge where conditions are harsh and unstable; and 2) a denser, lusher cover with more species in the milder interior conditions. The third stage is the Shrub-Ring Stage which differs from the second one by the presence of shrubs separating the beach and interior zones. In the fourth Parkland Stage, shrubs and trees occur in the interior herb flat forming an open woodland. Finally, the Forested Stage features a series of concentric vegetation zones: the pioneer vegetation on the edge followed by a ring of shrubs with a forest replacing herb flat and parkland in the center.

Although many islands on the Great Barrier Reef conform to these stages, many do not, but instead are affected by local conditions. Shrub rings

*Mangroves (*Rhizohora stylosa*) with their graceful stilt roots form part of the vegetation of low wooded isles. (Photo courtesy of Peter Saenger)*

A pair of Brown Boobies and their chick on Bylund Cay, Swain Reefs. (Photo courtesy of H. Heatwole)

may be incomplete or the interior may have parkland in some places and forest in others. Low areas with brackish water seepages may have a mat of succulents, and mangroves may produce different conditions.

Composite islands with mangroves are a special case. The vegetation of sand and shingle sections often resembles that of sand cays and shingle cays, respectively. However, the parts of islands with mangroves are unique and consist of many species of mangrove trees. In the leeward sites, the mangroves are divided into two communities. In one, mature woodlands of up to six species of trees occur on the higher, more protected sediments. The second community, peripheral to woodland on the leeward reef margin, is a mangrove forest, primarily of the stilt-rooted *Rhizophora stylosa*, but occasionally containing other species. This mangrove forest extends out to the edge of the sediment zone where live corals begin. The more exposed windward sites support dwarfed mangrove shrubs in small, outlying patches.

Mangrove or otherwise, the development of islands is often reversed by a degradational process of deterioration. Since cays usually erode only on one side, a lopsided vegetational pattern occurs: while the sea eats away the beaches and encroaches directly on the later-stage vegetation on one side, the Pioneer zone is still intact between the sea and the mature vegetation on the other side. In other words, when erosion and sand deposition occur on opposite sides, the central type of vegetation is left as a remnant near the eroding edge, and the newer part of the island is covered with pioneer vegetation.

Seabirds and Vegetation

Island vegetation and seabirds are intimately associated. Not only do birds carry seeds to the islands and fertilize the soil, but they also affect plants by trampling on them. Heavy birds such as gannets can break off parts of plants and compact soil. Where bird densities are high, this effect causes some cays to appear bare when, in fact, live roots are in the soil.

For example, Gannet Cay was once heavily vegetated with Tah-vine (*Boerhavia diffusa*). Now the large fleshy roots send up shoots, but they seldom get more than a half inch tall with a few small leaves before birds destroy them. Eventually, if this situation continues, the roots use up their stored energy reserves and die. In this extreme case, birds virtually strip a cay. Wire-mesh cages that exclude seabirds have been built around several small plots on Gannet Cay, and the vegetation growing inside shows the effect of the absence of birds.

Another way seabirds adversely affect plants is by producing excessive guano. Although guano is beneficial as fertilizer, too much can burn plants. Although some species of plants on coral cays can tolerate levels of guano that would kill other plants, even these plants can succumb to both the trampling and excess guano prevalent immediately around nests.

Sometimes, however, another cycle occurs: birds nesting on bare sand improve the soil and permit plants to grow. This provides suitable nesting sites for additional species of birds that, in turn, kill the plants, opening up bare patches. When these birds leave and the vegetation recovers, this cycle continues as birds return to nest on the sand.

Birds on the Islands

Continental islands have a wide variety of land birds living in habitats similar to those they occupy on the mainland. Cays, in contrast, have fewer such habitats and thus more seabirds than land birds.

Seabirds are mainly associated with coral cays where they breed. The Great Barrier Reef, with its abundance of cays and coral reefs is one of the richest areas in the world for tropical and subtropical seabirds. Twenty-nine species of seabirds from seven different families, including gulls, terns, gannets, shearwaters, herons, and frigatebirds are distributed throughout this region. Of these, 19 species breed there with colonies occurring on at least 78 different islands.

Sea Turtles

The Great Barrier Reef is one of the few places in the world where several species of sea turtles still abound. Although vast numbers of immature and adult green turtles, Chelonia mydas, *live year round within the Great Barrier Reef, most that breed there actually live in the waters of neighboring countries. Green turtles, for example, inhabiting the Coral Sea/Arafura Sea region, usually migrate to breed on a few coral cays such as Raine Island and Pandora Cay in the north and the Capricornia Islands in the south.*

The Hawksbill turtles, Eretmochelys imbricata, *live sparsely on every coral and rocky reef, and also migrate to specific nesting beaches–small sand cays on the inner shelf in the far northern section and in Torres Strait. Some, however, migrate internationally to breed as far afield as the Solomon Islands. Most loggerhead turtles,* Caretta caretta, *living in the Coral Sea/Arafura Sea region breed on the small sand cays of the Capricornia Section and the surf beaches of the adjacent mainland in the south. Loggerheads live principally in the sandy lagoons of the reefs and in the inshore bays.*

While green and loggerhead turtles migrate across deep oceanic waters, the flatback, Natator depressa, *never leaves the shallow waters of the continental shelf. Within the Great Barrier Reef, flatbacks migrate to the southern end to nest on continental islands such as Peak and Wild Duck Islands. Small numbers of olive ridley turtles,* Lepidochelys olivacea, *also live in the inshore turbid waters along the reef, but it is not known where they breed, only that they have not been found breeding within the Great Barrier Reef.*

Each turtle has a home feeding ground, probably encompassing 100,000 square meters, where it can be found for many years. At breeding time, the adults migrate to their own specific breeding areas. The peak breeding season lasts from October to February, but may occur less frequently at other times of the year. Courtship occurs in the sea; each female mates with a series of different males for a few days. In this way, she acquires enough sperm to fertilize the hundreds of eggs she lays in the following weeks. The males return home after a month of courtship while the females move to their inter-nesting habitat, usually quiet, shallow areas near the nesting beaches.

During one nesting season, each female will lay three to five clutches of approximately 120 eggs (with flatbacks averaging 50 eggs to the clutch) in two weekly intervals. According to estimates of growth rates, the turtles appear to be about 50 years old when they mature for first breeding. After a breeding season, female turtles return immediately to their home feeding ground where they remain for many years before migrating again, usually to breed at the same beach.

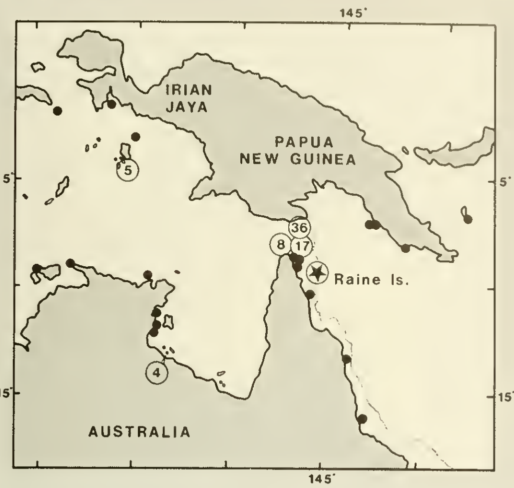
Many green turtles, *Chelonia mydas*, nest on Raine Island, one of the few remaining green turtle rookeries in the world and the only one in the southern Pacific Ocean. (Photo courtesy of Colin Limpus)

When sea turtles nest, they dig a large pit in the sand in which they lay their eggs. In so doing, they break vegetation and tear up whole plants by the roots. On small islands, the nesting area may cover the entire island, and be heavily pitted throughout. Only the pioneer plants, especially the vines and those that send out runners, survive; thus, sea turtles tend to keep the parts of the islands where they nest in the pioneer stage.

Sea turtles require specific nest temperatures. Temperature at nest depth determines the location of major turtle rookeries. Turtle eggs will not hatch if the nest sand is cooler than 24 degrees Celsius or warmer than 34 degrees Celsius. The beaches of the Great Barrier Reef are a suitable temperature for successful year round breeding in the north, but are suitable only for summer breeding in the south.

The nest temperature during the middle 50 percent of incubation determines the sex of the hatchlings. Each species has a temperature that determines sex and uses nesting beaches that provide the range of temperatures necessary to ensure hatchlings of both sexes. However, the number of turtles that survive from hatchlings to breeding adults is extremely low, perhaps as low as a few hatchlings per 10,000.

Sea turtles and their eggs long have been the traditional food of coastal and island peoples. Unfortunately, turtle and egg harvests have



Feeding ground recaptures of female turtles, *Chelonia mydas*, tagged while nesting at Raine Island and adjacent Pandora Cay. Circles designate a single recapture; circled numbers denote multiple recaptures.

escalated in the 20th century with the use of more efficient catching techniques and improved transport facilities. This, along with the degradation of many turtle habitats, now threatens sea turtles. Positive conservation management by both Australia and her neighbors is required to ensure the survival of turtles, which by their intrinsic biology, cannot adapt to long-term intensive harvests or rapid alteration of their environment.

—Colin Limpus, Australian National Parks and Wildlife Service

Some of the colonies are large: 20,000 Sooty Terns (*Sterna fuscata*) nest on Michaelmas Cay and 10,000 on Raine Island (along with 12 other species); 70,000 Black Noddies (*Anous minutus*) nest on Heron Island and 160,000 on North West Island. In addition, 8,000 Common Noddies (*Anous stolidus*) nest on Michaelmas Cay and 6,000 on North Reef Cay on Frederick Reef; 750,000 Wedge-tailed Shearwaters (*Puffinus pacificus*) nest on North West Island. The amounts and types of seabirds that breed on any particular island usually depend on the accessibility to their hunting grounds and the presence of suitable habitats for nesting.

Some islands are more important breeding sites than others. The 10 most important ones in descending order are: Raine, Bramble, Michaelmas, Swain Reefs (a number of small cays), Masthead, North West, One Tree, Wilson, Pipon, and Fairfax. Many more are collectively important nesting areas such as the Capricorn group of islands. Including both breeding and non-breeding birds that use the cays for roosting, there are an estimated 1.5 million Wedge-tailed Shearwaters, half a million Black Noddies, more than 3,000 each of Crested Terns and Bridled Terns, and 2,000 each of Black-naped Terns and Roseate Terns in the Capricorn area.

Along with the seabirds, many shorebirds and waders, such as sandpipers, plovers, curlews, whimbrels, and tattlers inhabit the beaches of cays. These birds are closely linked with the sea, but are not usually considered true seabirds. Some remain only seasonally or during pauses in their migratory flights. The reefs and beaches of some of the Great Barrier Reef islands have become important habitats for their feeding and roosting since estuaries and continental shores have either been destroyed or populated by humans.

Land birds are a less conspicuous part of the avifauna of cays, although a few species such as the Silvereye (*Zosterops lateralis*), Buff-breasted Rail (*Rallus philippensis*) and Bar-shouldered Dove (*Geopelia humeralis*) breed on the more heavily vegetated cays. Many land birds that are lost, blown offshore by storms, or merely stop during migration are non-breeding transients on cays. For example, 18 transient species of land birds have been sighted on One Tree Island.

As long as there are islands, birds probably will inhabit them. Continental islands and cays attract different species of birds because of their varying resources. As cays and their vegetation change, so does the bird fauna. Some of the islands and cays are already national parks, a situation that will protect the birds and encourage them to continue nesting there.

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Suggested Readings

Bennett, I. 1971. *The Great Barrier Reef.* Lansdowne: Dee Why West.

Farrow, R. A. 1984. Detection of transoceanic migration of insects to a remote island in the Coral Sea, Willis Island. *Australian Journal of Ecology*, 9: 253–272.

Fosberg, F. R. 1976. Coral island vegetation. In *Biology and Geology of Coral Reefs*, eds. O. A. Jones and R. Endean, Vol. 3, Chapter 8, pp. 255–277. New York: Academic Press.

Heatwole, H. 1976. The ecology and biogeography of coral cays. In *The Biology and Geology of Coral Reefs*, eds. O. A. Jones and R. Endean, Vol. 3, Chapter 11, pp. 369–387. New York: Academic Press.

Heatwole, H. 1981. *A Coral Island.* Sydney: Collins

Heatwole, H., T. Done, and E. Cameron. 1981. *Community Ecology of a Coral Cay.* The Hague: Dr. W. Junk.

Heatwole, H. 1984. Island and plant and animal life: biological microcosms. *Reader's Digest Book of the Great Barrier Reef*, ed. F. Talbot, pp. 324–353. Sydney: Mead & Beckett.

Hopley, D. 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs.* New York: John Wiley & Sons.

Kikkawa, J. 1976. The birds of the Great Barrier Reef. In *Biology and Geology of Corals Reefs*, eds. O. A. Jones and R. Endean, Vol. 3, Chapter 9, pp. 279–341. New York: Academic Press.

Maxwell, W. G. H. 1968. *Atlas of the Great Barrier Reef.* Amsterdam: Elsevier.

Dugongs and People

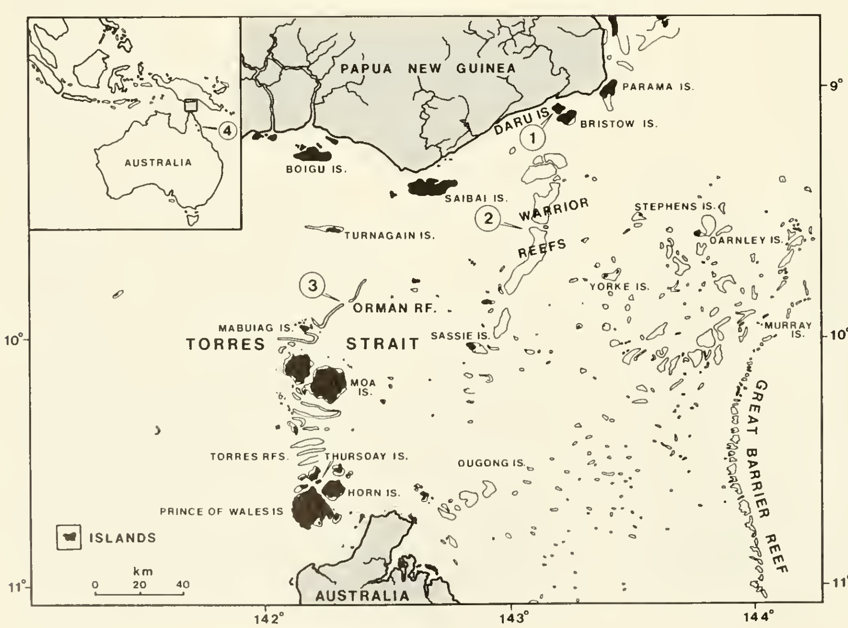
by Brydget E. T. Hudson

Dugongs. (Photo courtesy David Parer)

Sealore has it that the appearance of one or more of the species of sea cows, or Sirenians, gave rise to mariners' tales of mermaids. One species within this taxonomic order is now extinct (the Stellar sea cow), and most others are threatened. In the Indo-Pacific, the dugong has likewise come under increased hunting and environmental pressures. In the Great Barrier Reef region, steps are being taken to ensure its survival.

The dugong fishery has followed a path paralleled by other of the world's fisheries. A current Northern Hemisphere example is the bowhead whale fishery of western Alaska (see *Oceanus*, Vol. 29, No. 1, pp. 81–84). In these and other cases, the pattern is similar: a traditional fishery exists on a small scale, largely in balance with the resource, and is self-regulating. Due to economic factors and technological improvements, the fishery changes in nature and scope. As the resource is depleted, concerns surface (often belatedly), and management plans are called for. These plans are difficult to design, implement, and enforce (for reasons described later). When modern management plans are successful, it is often found that many of their components resemble elements of the self-regulating system contained within the former traditional fishery.

The difficulties in effective management stem from the duality of purpose. That is, while it is clear that a species needs protection, and that commercial hunting should be restricted or banned, it is not that easy. There also is a compelling argument in favor of



Location of traditional communities, hunting reefs, and major dugong habitats. Circled highlight numbers indicate (1) Daru, capital of the Western province of PNG. A site of hunting, research, and management; (2) Warrior Reefs hunting area; (3) Orman Reefs hunting area; and (4) Lockhart River and Hopevale Aboriginal communities.

traditional hunting by indigenous peoples, and a maintenance of their culture and traditions. With these dual goals, conflicts are inherent, and an agreeable compromise is often difficult to attain.

The dugong fishery in and around the Torres Strait region is illustrative of the pattern, the issues, and the attempts at resolution. Its management is a complex biological and sociological undertaking, with both economic and political implications. The principal peoples involved are the Kiwai of the Western Province of Papua New Guinea (PNG), to the north of the Torres Strait; the Torres Strait Islanders; and the Aboriginal people of eastern Australia.

Modern Management Regimes

As the dugong were depleted, management plans were set into place. At present, there are several levels: international, national, and local (for example, specific to the Great Barrier Reef). Although the general goals are similar, there are incongruities in the mechanisms, and in the definition of terms.

In Papua New Guinea, the Fauna Protection and Control Act of 1968 enables protection of species declared as "National Animals." Such species may not be commercially exploited, but may be taken by indigenous people if they use "traditional" techniques, and hunt for "traditional" purposes. The act also enables creation of "Wildlife Management Areas," where a community may designate an area for local management.

Across the straits in Queensland, fisheries legislation prohibits the taking of dugongs except by indigenous people living on reserves. There is no restriction on hunting techniques.

On the international level, a treaty between Australia and Papua New Guinea, commonly called the "Torres Strait Agreement," was ratified at the beginning of 1985. It defines traditional fishing liberally—in light of prevailing custom. It institutes an "International Conservation Area" and establishes reciprocal rights for traditional fishing and use within the defined area.

Lastly, the Great Barrier Reef Marine Park Authority (GBRMPA), under its legislation and through consultation with the public, includes in its management two groups of indigenous people living on reserves within the park: the Hopevale and Lockhart River Aboriginal communities. At present, the people of the Hopevale Community, in the Cairns Section of the park, are required to apply for a restricted number of permits to hunt dugongs within their traditional hunting area. Presumably, this system will be extended to the Lockhart community, in the Far Northern Section, at a later date.

Traditional Hunting

Before 1920, the people of the Torres Strait used two methods for hunting dugong. The first and perhaps oldest method was the use of a platform set over the seagrass beds where dugongs came to feed at night. In the second, dugongs were hunted from single-outrigger canoes using harpoons. The Kiwai have an intimate knowledge of the movements of the dugong relative to the moon-phase and tidal state—a knowledge vital to the positioning of the platforms and the canoes. Hunting was only possible in the season at the end of the year when the northeasterly winds were light, the seas calm, and the dugongs fat and near calving.

A dugong herd in Moreton Bay, near Brisbane. (Photo courtesy of George Heinsohn)

The number of hunters was limited by access to the knowledge of the best hunting locations, the useable reef areas, access to the magic stones and other charms needed, and the technical skill and courage needed for such hunting.

Prowess as a dugong hunter earned the hunters great prestige within the community. Each village had only a few skilled "dugong-men". The rights to hunt on certain reefs were jealously guarded, and the "home reefs" close to each village were sacrosanct. Dugong hunting had a role in training young men for adulthood, in maintaining the social position of women, and in the social organization of the villages.

The human population was small and kept in check by limited resources, disease, and infanticide. While the hunting technology was effective, the numbers taken were limited by the difficulties of transporting such a large animal back to the village for the ritual butchering that appears to have been a feature of all these societies. Dugong meat was typically used only for special occasions such as traditional feasts. However, these occurred infrequently, and although several dugongs could be eaten at each feast, excessive hunting beyond the needs of the community was unthinkable.

This general pattern was repeated by

'Dugong Is Number One Tucker'

If you ask a coastal Aborigine or Islander from the Great Barrier Reef region to nominate his favorite food, he will probably tell you that "dugong is number one tucker" (outback word for food). Dugong meat is delicious tasting—rather like beef or veal, and is typically reserved for special, often religious, occasions—much like turkey at Thanksgiving in the United States. Dugong oil is also valued for its medicinal properties.

The dugong is one of only four surviving species of sirenians, or sea cows. The other existing sirenians are the three species of manatee that occur in the Caribbean region and the southeastern United States, the Amazon River Basin, and West Africa, respectively.

Although the dugong looks like a rotund dolphin, it is an herbivore feeding on seagrasses. Its nearest non-sirenian relative is thought to be the elephant. Dugongs grow to about 3 meters and weigh from 250 to 400 kilograms. (Photo courtesy of Tony Preen)

Manatees tend to be riverine or estuarine, and are believed to be physiologically dependent on fresh water. In contrast, the dugong is the only herbivorous mammal that is strictly marine. It is usually seen in shallow, sheltered bays that support extensive beds of the seagrasses on which it feeds. Within the Great Barrier Reef lagoon, dugongs have been sighted up to 55 kilometers from land. Often, the dugongs form herds, consisting sometimes of up to several hundred animals. The Aborigines believe that these herds are controlled by animals known as "whistlers." Unlike dolphins, dugongs are not known to echolocate. The only sounds recorded to date are bird-like chirps.

Historically, the dugong's range extended throughout the tropical and sub-tropical coastal and island waters of the Indo-West Pacific from East Africa to Vanuatu (an independent nation of some 70 islands, 1,200 miles east of the Great Barrier Reef). It is now considered rare over much of this range.

On the other hand, aerial surveys conducted in northern Australia since the mid-1970s have shown that substantial numbers of dugongs still occur in this area. It may be that a major portion of the world's remaining dugong stock is located in these waters. On a still more localized level, up to 600 dugongs have been seen from survey aircraft near the mouth of the Starcke River, in the Cairns Section of the Great Barrier Reef Marine Park, making this the most important dugong habitat yet identified.

Recent studies of dugong life history have been based on more than 600 dugongs caught by Aborigines or Islanders, or killed accidentally in the shark nets set for bather protection. The results show that the dugong life span may be greater than 70 years, and that females do not bear their first calf until they are at least 10. A single calf is produced at intervals of from 3 to 7 years. Most calves are born between September and January—just before the seagrasses are at their most nutritious. Calves remain with their mothers for at least two years, and suckle for at least 18 months. The cow-calf bond appears to be extremely well-developed.

Because dugongs are such slow breeders, they are vulnerable to over-exploitation. Population models indicate that, even with the most optimistic combination of life history parameters and a low level of natural mortality, a dugong population is unlikely to increase by more than 5 percent per year. This means that at least 200 dugongs are needed to be able to harvest five females per year without causing the population to decline. Plummeting catches suggest that the level of harvest in the Torres Strait Region in the late 1970s far exceeded this level.

—Helene Marsh
James Cook University, Townsville.

aboriginal people throughout the region—as far south as Botany Bay, near Sidney.

A Changing Technology

The changes that have taken place in the technology relating to dugong hunting underline the complexity of management in such situations.

In the 1920s, the use of the hunting platforms ceased, and a new form of double-outrigger canoe was developed by the Kiwai. Where previously their

Kiwai hunter with harpoon on the bow of a double-outrigger canoe. (Photo courtesy of Elizabeth Parer-Cook)

single-outrigger canoes could only be used as nearshore craft, the new canoes—up to 30 feet in length, and requiring 9 to 11 men to sail them—made longer visits to the reef possible, and thus extended their hunting range. The number of dugongs that could be carried in these boats also was increased to four or more.

In recent times, the canoes have been replaced by dinghies powered by outboard motors. Some trawlers and other commerical fishing boats also have appeared. A few indigenous trawler owners have used their boats as "mother-ships" when hunting dugongs on the reefs in quasi-traditional fashion.

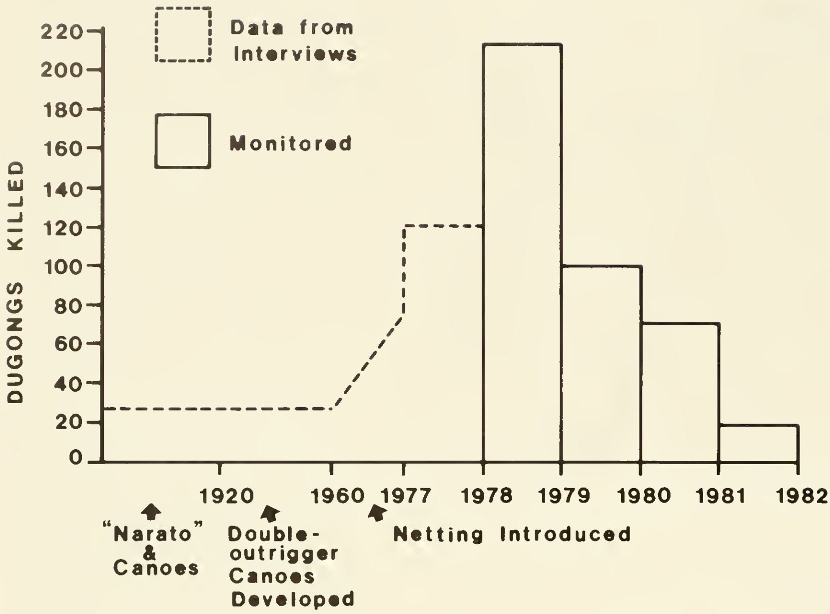
There also was a change in the outlet for dugong meat. In 1957, a market was established at Daru (provincial capital, Western Province, PNG). The Kiwai requested permission to hunt dugongs and turtles to provide meat for the expanding population. This commercial outlet for dugong meat increased their annual kill from about 25 to 75 dugongs per year.

The take of dugong next became linked to other developing fisheries. In the 1970s, efforts were made to develop economically the Western Province of PNG. Two high-value marine resources, the barramundi (perch-like fish) along the coast, and crayfish (or lobsters) on the reefs, became the basis of fishing industries. The Kiwai soon discovered that the nets introduced for barramundi fishing also caught dugongs very efficiently. They considered this particularly beneficial in the southwest wind season, when other forms of hunting and fishing were impossible because of the rough sea conditions. During this time, the dugongs came close to Daru Island and residents, often people with other forms of income, constructed bigger nets. The dugong kill increased dramatically.

Likewise, because of the cray fishing, longer periods of time were spent at the reef, where the focus of hunting could easily switch from craying to dugong hunting. As more money was injected into the community, more people bought outboard motors and dinghies. The hunting became easier and more efficient.

In a very short period, many traditional restrictions on hunting were altered. The new boats and motors meant that hunting could be undertaken at almost any time. There was a large demand for

A dead dugong on a canoe. (Photo courtesy of Brydget Hudson)



The effect of changing technology and commercialization of dugong hunting by the Kiwai.

dugong meat among the nearly 8,000 residents of Daru, and for the money this highly profitable hunting could provide. Detailed knowledge and magic were no longer required, as the reefs could be patrolled until a dugong was sighted. Butchering on the reef also meant that more than one animal could be brought to the market at once. A few facets of traditional practice remained: traditional reef usage was maintained, as was the dipping of the harpoon in the water to bring luck.

The rapidity of these changes was phenomenal. It precluded management by education (concerning the need for conservation). At the same time, the regulation of hunting by legislation was politically untenable, and would have been unenforceable if enacted.

Management Initiatives

In 1978, the Kiwai formed the Maza Wildlife Management Area. Rules were enacted to reduce the kill by limiting the gear to canoes and harpoons (banning nets and dinghies). Animals had to be brought whole to the market—in keeping with custom—to 1) restrict the kill per trip, and 2) enable the collection of biological data which in turn would aid further management. The capture of juveniles and mothers with calves also was banned. Lastly, an education program emphasizing dialogue with the hunters was established.

Modern Threats

Despite early efforts, financial pressures and the demand for meat caused the local stocks of dugong to be precipitously depleted. From 1978 through 1982, hunting was directed further and further down the Warrior Reefs. In 1982, a ban on the sale of dugong meat was instituted.

Turtles now appear to be the major target for hunting, and their decline as the result of commercial fishing pressures exerted by people of the Torres Strait and Indonesia may occur in the not too distant future. Since the dugong and turtle harpoons are usually carried on any fishing expedition, a classical multispecies fishery situation is now occurring. The focus of hunting can change between commercial and traditional, with the danger of depleting all stocks below economic and sustainable levels.

In addition to directed hunting, incidental kills do occur. Trawlers occasionally catch dugongs, and the barramundi nets are responsible for a presently unquantified dugong kill. Nets set to protect swimmers from sharks have killed significant numbers of dugongs off Townsville. Lastly, mining is a possible threat because of the increased silt burden in certain areas.

Can Traditional Practices Help Management?

Active participation involving all members of the community was a feature of traditional management. An understanding of the environment and duty toward its management also were a part of the traditional education system. The people considered themselves stewards of their environment for perpetuity. These facets are required in management today as in the past.

The conservation of human societies as well as marine species should likewise be an aim of management. Many human societies, too, are endangered. Our world would be poorer without their contribution, as it would without the dugong.

Other members of modern society also need to use the resources of the Great Barrier Reef. Commercial fisherman need to make their living economically, efficiently, and in an ecologically sound manner. The aims of the manager and the fisherman should coincide. The goals of all—commercial fisherman, traditional hunter, and

Human Exploitation of Shellfish

Numerous shell-midden deposits along the northeastern coast of Australia testify to the frequent consumption of shellfish by Aboriginal groups in the Great Barrier Reef region. Shellfish constitute a dependable source of protein, important during periods when other animal food sources are scarce.

Recent studies by archaeologists and anthropologists in northern Australia and Papua New Guinea have demonstrated that a wide range of gastropod and bivalve species have been harvested by traditional gatherers (usually women and children) from the extensive intertidal back-reef areas in the region. A particular locality frequently yielded from 20 to 50 shellfish species from more than 10 families. The shellfish could be gathered from a variety of habitats, including reef flat and coral platform areas, sand or mud flats, seagrass beds, mangroves, and rocks.

Many of the preferred species are found mainly in soft-sediment areas, either buried or on the surface. Unfortunately, there has been little documentation of traditional Aboriginal knowledge of shellfish or their harvesting methods, possibly because coastal researchers have focused mainly on the hunting of turtle, dugong, and fish by men. Furthermore, shell-gathering has rapidly declined in groups that have adopted a more Westernized lifestyle, so that a large amount of traditional knowledge of reef shellfish—poorly known by white Australians, including scientists—will soon have disappeared.

Despite the wide range of species gathered, a few species from particular families often make up a large proportion of the catch. In clear water reef areas, there is often a predominance of conchs, Strombus, *and spider shells,* Lambis, *and members of the giant clam family (Tridacnidae). In more estuarine areas, mudwhelks (family Potamididae) and large bivalves, family Corbiculidae, are more common. Various members of the bivalve families Arcidae (particularly* Anadara *spp.), Veneridae (particularly* Tapes *spp.), and Ostreidae (oysters) may be common in either type of area, as may periwinkles of the family Neritidae.*

Most contemporary white Australians eat very few shellfish other than scallops and cultured oysters, even though there are major commercial Anadara *and giant clam fisheries in the Asia/Pacific region.* Pinctada *(pearlshell) and* Trochus *(topshell) species are commercially exploited in restricted sections of the Great Barrier Reef and Torres Strait for mother-of-pearl.*

The present shellfish communities may be different from those existing several hundred years ago in the times of heaviest Aboriginal exploitation. The exploited communities may have been more heavily dominated by species whose life-histories enabled populations to persist in the face of gathering, perhaps attributable to a propensity to bury in the substrate, a highly mobile adult stage, a well developed swimming larva, or the existence of subtidal populations. Certain species, such as some Strombus, Anadara, *and* Tapes, *are exceptionally common in some midden deposits, and the little available information on the biology of these species shows that they share many of these characteristics, making them resilient to gathering.*

Contemporary shell-gathering and harvesting practices may have different effects on shellfish populations and communities. For example, many Strombus gigas *(queen conch) populations in the Caribbean have recently been overfished following the use of SCUBA equipment and outboard motors by collectors, together with the introduction of export markets. Since the biology of shellfish on the Great Barrier Reef has been largely overlooked by scientists, it will be difficult to assess the effects of similar impacts. This will have to change if sound conclusions about the effects of past, present, and future exploitation are to be drawn.*

—Carla P. Catterall,
Griffith University,
Brisbane

manager—should be in maintaining a sustainable environment. Each has much to give the other. The fisherman and hunter work continuously in coastal waters and can provide information needed for management. The professional manager, in turn, can aid in advising on gear selection and hunting areas that will minimize accidental catch of non-target species.

The recreational users of the reef are fascinated by its unique creatures—such as the dugong. They too need information about how they can assist in conservation and management; as user involvement programs demonstrate, they are eager to participate in the reef's management.

The Great Barrier Reef Marine Park Authority is active in these areas—through its funding and support of management research, liason with all users, and through its excellent educational programs. Thus, a convergence between traditional and modern management has occurred. But, even

A double-outrigger canoe under sail. When these larger canoes were developed in the 1920s, they extended the range and time on the reef of the Kiwai hunters. (Photo courtesy of John Mason)

so, complacency with regard to the management of the dugong would be unfounded. The precipitous decline of a dugong population has been recorded, and what might be regarded as minor changes in technology and the environment require careful monitoring to ensure that our already reduced herds are not threatened further.

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A meeting of the Maza Wildlife Management Area Committee. Here rules were enacted to reduce the dugong kill. (Photo courtesy of Elizabeth Parer-Cook)

Selected References

Baldwin, C. 1985. *Management of dugong: An endangered species of traditional significance.* Technical Report GBRMPA-TR-1, Great Barrier Reef Marine Park Authority.

Chase, A. 1981. Dugongs and indigenous cultural systems: some introductory remarks. In *The Dugong*, pp. 112–123, James Cook University.

Fisher, M. 1985. *Aboriginal customary law: The recognition of traditional hunting, fishing, and gathering rights.* The Recognition of Traditional Fishing Proposals for Change. Sydney: The Law Reform Commission.

Laade, W. 1971. *Oral Traditions and Written Documents on the History and Ethnography of the Northern Torres Strait Islands, Saibai-Dauan-Boigu.* Weisbaden: Franz Steiner Verlag.

Risk Analysis: Cyclones, and Shipping Accidents

by M. K. James, and K. P. Stark

The Great Barrier Reef stands as a bulwark along the Queensland coast and in some places is impenetrable to ships. Between the reef and the coast, the waters provide protected shipping routes and ideal sites for developing tourism facilities, offshore structures, and port and harbor facilities. Sea conditions within this area are dominated by prevailing winds so that the worst conditions usually anticipated are 30 knot winds and 3 meter waves; however, three or four times a year, tropical cyclones—called hurricanes or typhoons elsewhere—cross the reef from the Coral Sea and approach the coast. Along with the risk of cyclones, the reef area also is vulnerable to shipping accidents, both rare, but potential threats.

However rare, both nature and man must develop mechanisms to cope with disastrous events. Many corals, such as foliaceous *Leptoseris cucullata*, have adapted to this environment by developing high mobility and rapid growth. Man, on the other hand, has developed risk analysis techniques so that rare events, possibly those for which no local experience exists, can be simulated to provide an appreciation of how best to adapt and cope. Risk analysis for cyclonic effects and for shipping accidents help us predict the probability and consequences of disasters.

Figure 1. Tropical cyclone tracks in the Great Barrier Reef region (1910–1969).

Risk Analysis of Cyclones

Cyclone paths have no simple pattern, as shown in Figure 1. Many cyclones affect the areas they traverse very little because their central pressure ranges from 980 to 1,000 millibars. However, under particular circumstances, the cyclone can intensify and create widespread, disastrous consequences.

Cyclones with a central pressure below 950 millibars are classified under the Saffir-Simpson scale as severe; if the central pressure is below 915 millibars, the classification becomes very severe. A very severe cyclone in the Great Barrier Reef region would have the following characteristics: 1) a maximum wind gust of 270 to 300 kilometers per hour or 145 to 160 knots; 2) a coastal storm surge greater than 6 meters; and 3) a wave height in open ocean greater than 8 meters. Such conditions damage coral reefs, create extreme shipping hazards, and impose excessive loads on both natural and man-made structures. Fortunately, the probability of a very severe cyclone passing over any selected point in the oceans is quite low.

Using the meterological details associated with the tracks in Figure 1, a statistical extreme value analysis can be used to provide a stochastic simulation of anticipated cyclonic strengths over time. From the air-sea interaction produced in each cyclone, the complex wind field generates wind-waves that can be deduced.

Simultaneously, the wind will create hydrodynamically an oceanic tidal surge that, when superimposed on the predicted tide level, produces abnormal water levels. If the cyclone landfalls at high tide, then the combined tide and storm surge can penetrate inland with disastrous consequences. Buildings in the path of such storm surges would require evacuation.

There are two mitigating circumstances on the reef. First, away from the coastline, storm surge development is restricted to the inverted barometer effect, and abnormal water levels for the very severe cyclone should not exceed 1.0 to 1.5 meters. Second, if both man-made and natural structures are within a lagoon protected by coral at mean sea level, then wave heights will be weakened as they break over the coral; thus, maximum waves within the lagoon are unlikely to exceed 3 meters. Of course, since maximum winds will persist within the lagoon, 160 knot or 300 kilometers per hour winds must be considered in designing reef structures to survive such extreme events. Detailed computer simulations can now be done before any offshore structures—whether floating hotel, drilling rig, navigation beacon, or artificial reef—are built.

Risk Analysis for Navigation

The increasing use of Great Barrier Reef waters for navigating large vessels raises concerns over the risks and repercussions of shipping accidents. The higher traffic densities have already resulted in many close encounters and the sinking of at least one trawler. The potential clearly exists for more serious accidents that could possibly lead to major oil spills.

Risk analysis is concerned with estimating the probabilities of shipping accidents—collisions and groundings—and the distribution of that risk over a region, that is, the likelihood of accidents at different locations. These accident statistics are then used to determine the geographical distribution of spills and to provide input to various areas: navigation management in the area, spill trajectory models to determine impact zones, and logistic analyses to plan the location and movement of materials, equipment, and personnel for dealing with spills.

Since no statistical data exist to estimate probabilities of these events and statistical estimation techniques cannot be applied, an approach based on computer simulation of the navigation process is used. A computer program models the passage of vessels through the restricted waters of the region as well as close-quarters situations where ships must maneuver to avoid collision or grounding. The risk analysis model allows important causal factors to be considered, such as environmental conditions (poor visibility), mechanical conditions (steering failure), and human error (positioning errors). The outcome of an encounter between two ships depends on the interaction of these factors.

Accident scenarios are represented by fault-trees (Figure 2) used extensively to assess safety. The accident appears as the top event and is linked to more basic fault events by various logic gates. An accident occurs when one or more basic failures occur, enabling a causal path that leads to the accident. Some methods from fuzzy set theory are also employed to model mariners' decision processes and their compliance with the Collision Regulations.

Many years of shipping experience can be simulated this way, and many potential accident situations analyzed to give statistical estimates of accident probabilities. These results are expressed on risk distribution maps that highlight the areas most likely to receive pollution from dangerous chemical spills. The analysis thus contributes to the knowledge of human influences on the environment in the Great Barrier Reef Marine Park.

Risk analyses of navigation and cyclones demonstrate the dynamic processes influencing the Great Barrier Reef. The more that is known about the potential risks to the area, the more likely they can be either avoided or monitored safely.

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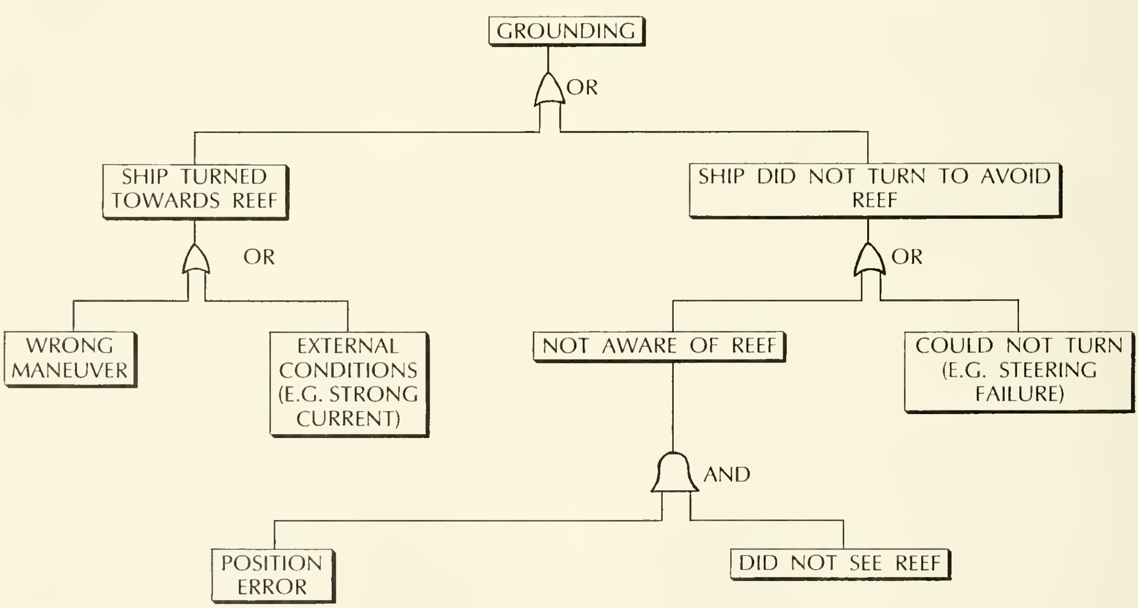


Figure 2. Example of fault tree.

Toxins and Beneficial Products from Reef Organisms

by J. T. Baker, and J. A. Williamson

The diversity of a tropical reef's fauna and flora has attracted significant attention from those interested in characterizing the active compounds of the often complex venoms transmitted by several marine species. In addition to the obviously venomous marine animals, many other species of tropical fauna and flora offer potential for scientific investigation. Ninety percent of all species of living organisms live in the ocean in totally different biosynthetic conditions than terrestrial fauna and flora. Thus, it is highly probable that the oceans will yield as yet unknown chemical substances with novel structures and a wide range of biological activities.

Since the mid-1960s, scientific literature has reviewed many new substances available from marine organisms, but to this day, only a few biologically active compounds have attracted the interest of major pharmaceutical companies as potentially marketable drugs. Future advances in the medical aspects of marine venoms require research into effective methods of immediate pain relief and prevention of scarring, such as with jellyfish stings, and the immunological characterization of marine toxins.

Marine animals with toxic compounds are often put into three broad categories based on their potential threat to human life or health: 1) marine animals that have caused documented death in northeastern Australian seas by envenomation or poisoning; 2) marine animals that produce either common or serious envenomations, but currently have not caused documented death; and 3) marine animals that have caused allergic reactions.

The Box-Jellyfish

The two closely related box-jellyfish species, *Chironex fleckeri* and *Chiropsalmus quadrigatus*,* are distinguished morphologically by experts, but from the practical medical viewpoint, their distinction is unnecessary. However, the latter may be slightly less dangerous. These box-jellyfish occur in the summer months only in northern Australia, dwell and breed on the coast, and are often found in tidal streams or near-shore waters (Figure 1).

Figure 1. An adult box-jellyfish (Chironex fleckeri). *Its sting can be fatal. (Photo courtesy of J. A. Williamson)*

Although the box-jellyfish is not encountered on the reef, it is responsible for at least 64 documented Australian deaths since 1884, and many other undocumented deaths due to the remoteness of the northern Australian coast. Thirty-four of these deaths happened in the coastal regions adjacent to, but not on, the Great Barrier Reef.

An intensive marine biological and medical research program has existed in North Queensland since the animal's identification in 1956. Details of serious envenomations, progress with management and prevention, research into the envenomation process and into the life-cycle have been published elsewhere.

The venom of *Chironex fleckeri* is a mixture of high molecular weight proteins, containing

* Recent field work has thrown doubt on the accuracy of this naming for the Australian version.

cardiotoxic and haemolytic components to small experimental animals, and capable of killing human skin. The precise pharmacology of its lethal action in humans is still uncertain, but direct, central neurological toxicity is suspected. The venom probably disrupts cell membrane stability by inhibiting calcium ion re-uptake of the sarcoplasmic reticulum. Further characterization of this venom, together with other Australian and world jellyfish venoms of clinical significance, using immunological techniques, is already under way, and therapeutic advances are expected.

The venom produces immediate, savage pain, and skin destruction (Figure 2) that may result in scarring if untreated. A specific anti-venom, concentrated immunoglobulins from hyperimmunized sheep, has been available since 1970, and is dramatically effective in life threatening situations, for pain relief, and probably also prevention of scars. Any clothing, including pantyhose and the Townsville stinger suit, can prevent jellyfish tentacle stings.

Ciguateric Fish

Ciguatera poisoning is caused when ciguatoxin, a complex toxin whose structure has been extensively studied, contaminates the flesh of fish. One of the most potent toxins known, it remains active even after the fish is cooked. Its detection in fish is presently impossible, although researchers in Hawaii claim to have developed a stick test for field detection of toxin. The toxin does not affect the fish's health or appearance, but causes 1,200 annual cases of disease, and death in the Pacific region where fish is a staple diet.

Ciguatoxin, thought to be transmitted via the marine food chain, affects pelagic reef fish, appearing and disappearing unpredictably in a wide range of edible species. However, certain species are believed to be more commonly affected than others, such as chinaman, *Symphorus nematophorus*, red bass, *Lutjanus bohar*, moray eels, and the larger predatory reef fish, such as Spanish or grey mackerel.

The toxin predominantly induces gastro-intestinal symptoms, but more seriously affected persons demonstrate peripheral neurological features. Potentially fatal cases show central neurological depression with coma, convulsions, and respiratory failure. Without resuscitation and medical assistance, death may occur from hypoxia.*

Blue-ringed Octopus and Cone Shells

The toxin of the blue-ringed octopus is tetrodotoxin, one of the few marine toxins whose structure and action are known. With a molecular weight of 319, it is non-antigenic and causes selective inhibition of sodium ion transport across cell membranes. Thus it has proved useful as a neurophysiological research tool. It is distributed naturally, notably in the puffer fish—the "fugu" of Japan. Cone shell venoms, by contrast, produce post-synaptic neuromuscular

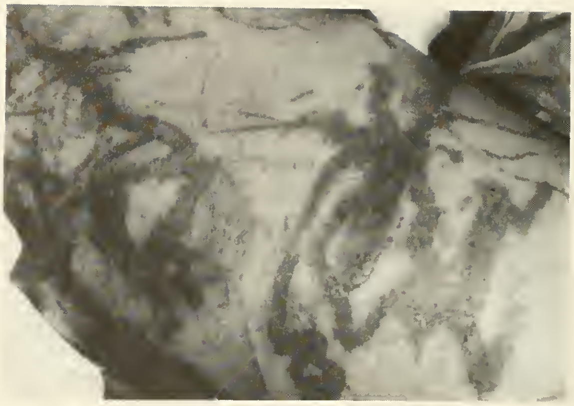


Figure 2. A large Chironex fleckeri *sting after 24 hours showing skin death. (Photo courtesy of J. A. Williamson)*

inhibition, have a higher molecular weight, and offer the promise of anti-venom production (*Conus geographus* venom).

These cone shell toxins act peripherally at the human somatic neuromuscular junction (Figure 3), and death results from respiratory failure and consequent hypoxis; assisted ventilation, such as expired air resuscitation (E.A.R.) is life saving. First-aid for blue-ringed octopus or cone shell venom is of life-saving importance in seriously affected persons, and is identical to that used now for Australian snake bites. Full recovery of muscle power can be expected in 6 to 10 hours in severely poisoned patients who are protected from hypoxia.

Sea Snakes

Australia possesses the world's most formidable array of venomous sea snakes; at least 12 species of sea snakes, most of them venomous, are found in tropical Queensland waters alone. They have an efficient fang mechanism with very toxic venoms. The beaked sea snake, *Enhydrina schistosa*, is considered one of the most dangerous to man, and the Commonwealth Serum Laboratories sea snake anti-venom is based on this venom, along with that of the Australian terrestrial tiger snake, *Notechis scutatus*. Since the anti-venom works with all Australian sea snakes, precise identification of the offending species is unnecessary.

Sea snake venoms act neurologically, affecting both the peripheral and central nervous systems. They consist of extremely complex protein mixtures that can produce haemolysis, muscle cell breakdown, and blood coagulation, possibly resulting in attendant renal and electrolyte complications in seriously affected patients. Near fatalities from sea snake bites have occurred increasingly in Australian waters.

Non-fatal Jellyfish

Nowhere is the present ignorance of marine envenomation better illustrated than by the fragmentary knowledge of tropical stinging jellyfish species and their toxins. As well as genera common to many other parts of the world (*Physalia, Pelagia, Cyanea, Catostylus*), the Great Barrier Reef houses an extraordinary group of Cubozoan jellyfish

* Deficiency in the amount of oxygen reaching bodily tissues.

Sea Snakes

The Australian sea snakes (family Hydrophiidae) share several morphological characteristics with the venomous terrestrial family Elapidae, from which they have probably evolved.

At least 32 species of sea snakes inhabit Australian waters, 16 of which are found on the Great Barrier Reef. One species, Aipysurus laevis, *the olive sea snake, has been the subject of a 5-year study conducted by researchers from the University of New England in New South Wales. The study has centered on the Swain Reefs area at the southern end of the Great Barrier Reef. Researchers have conducted an ongoing mark and recapture program, using a population of* A. laevis *found at Mystery Reef within the Swain Reefs complex.*

At Mystery Reef, it has been estimated that between 2,000 and 3,000 adult olive sea snakes reside in the 1 square kilometer that comprises the reef's lagoon. This figure is typical of most of the reefs in the Swains complex that support A. laevis *populations. Although neighboring reefs seem ecologically similar, only 22 reefs of the 40 examined to date support resident populations. This patchy distribution is consistent yearly and has not been accounted for in terms of either physical or biological factors. Neither water temperature, salinity, distribution of prey, nor numbers of predators has been shown to affect the distribution of* Aipysurus laevis *along Australia's Great Barrier Reef.*

Sonic tracking equipment has been used to monitor movements of individual snakes for periods of up to 7 days. This technique has provided information on foraging behavior and range size. Males have exhibited a slightly smaller mean range size (1,500 square meters) than have females (1,800 square meters). Movement is generally centered on a section of reef edge less than 150 meters in length. Neighboring ranges may overlap by as much as 85 percent, with snakes occupying the same range for three consecutive years.

Sea Snakes courting.

Additional studies have found that males and females have synchronous, seasonal reproductive cycles. Courtship and mating occur during winter, after which the female stores sperm in the uterus until ovulation occurs in the spring. Following a 6-month gestation, the young are born at the end of summer. Mature female A. laevis *in the southern areas of the Great Barrier Reef reproduce biennially, producing two or three young per clutch. There is evidence of geographical variation in the reproductive cycle.*

Several species of Australian sea snakes possess attractively patterned skin that is coveted for shoes, belts, handbags, and a variety of other clothing accessories. Potential overseas markets include Japan, the United States, and Italy. Sea snakes are not protected in Queensland waters. However, the Australian government has refused to grant export permits until the effects of large-scale harvesting (30,000 skins or more) on natural sea snake populations have been assessed.

—Glen W. Burns,
University of New England,
New South Wales.

collectively known as the family *Carybdeidae*. The three identified species of this family are very venomous. Many other as yet unidentified species exist, but nothing is known about the structure or pharmacology of their toxins.

Two species of these simple, four-tentacled jellyfish with which painful encounters have occurred in Queensland and other Australian waters are "Irukandji," *Carukia barnesi*, and "Morbakka," *Tamoya* spp. Irukandji is a tiny jellyfish, invisible under natural conditions, whose initially painful sting subsides in about 30 minutes, only to be replaced by prostrating muscular pain, nausea, vomiting, and incapacitating headache. Hospitalization and intravenous analgesia provide relief from these symptoms which last 12 to 24 hours.

The existing confusion concerning the precise identification of different *Tamoya* species is such that the nickname Morbakka has been suggested and is pending world wide clarification of this group's taxonomy. *Tamoya* is a larger, four-tentacled, open-water jellyfish (Figure 4) aptly nicknamed "fire jelly" for its painful sting that can cause generalized effects. Unconfirmed fatalities in the western Pacific exist, but Australian cases of exhaustion and mental confusion have occurred.

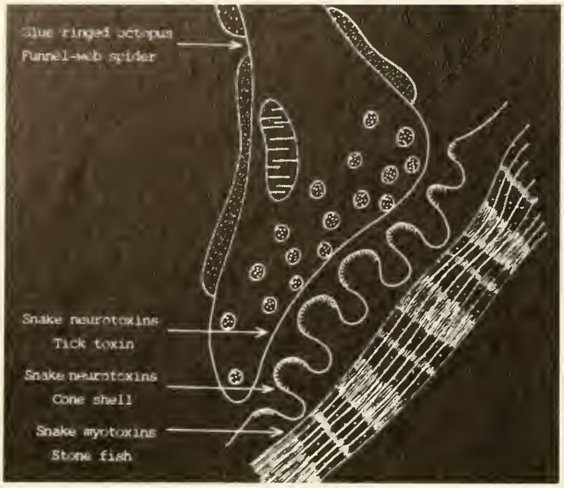


Figure 3. A somatic neuromuscular junction, showing sites of action of various zoo-toxins. (Courtesy of V. Callanan)

Stonefish

The venomous stonefish is not rare in northeastern Australia. Since the painful encounter invariably results from the fish's superb camouflage, most wounds occur on the sole of the foot, or occasionally, on the palm of the hand. At least one of the 13 erectile dorsal spines, each with its own venom sac, penetrates deeply, depositing venom in the wound. The venom is a high molecular weight, heat-labile protein for which a specific anti-venom, horse anti-serum, exists.

Immediate pain is followed quickly by a bluish discoloration of tissues near the venom deposit. Pain can be reduced by immersing the poisoned part in hot water. Despite repeated, contrary statements, no documented death from a stonefish exists in Australia to date, although more than 80 cases have reportedly received hospital treatment. Medical attention for a stonefish sting is always necessary to relieve pain and prevent local complications.

Figure 4. A large Morbakka jellyfish of the Tamoya *species. Note the four solitary tentacles, and the papules of nematocysts on the bell. (Photo courtesy of Ben Cropp, Port Douglas)*

Stinging Corals, Starfish, and Sea Urchins

These less dramatic, but troublesome stingers are more frequently encountered because of the popularity of snorkeling and SCUBA diving. The stings are nematocyst-mediated, as with all stinging Coelenterates, and treatment is symptomatic, but effective. Little is known about their toxins.

The Crown of Thorns starfish is of special interest as it is present from time to time in plague densities on parts of the Great Barrier Reef. The starfish's venom is contained in the lining of the spines, and the calcified core of the spine tip commonly breaks off in the wound. The nature of the toxin is presently unknown. Localized allergic reactions to this venom occur in susceptible individuals, and treatment is largely symptomatic, but helpful.

Injuries from sea urchins are similar to those from the Crown of Thorns. The sea urchins are widely dispersed over the reef and nothing is known about the toxin which at least one species, *Toxopneustes*, possesses.

Stingrays

Although lurid stories relate the threat of these animals, injuries are relatively uncommon, and are invariably the result of man disturbing the animal, either accidentally or intentionally. Stingrays are seen commonly in northeastern Australian water, and are speedy swimmers. Injuries are sustained from the one or two barbed spines located halfway along the dorsum of the muscular tail. The spines are used in defense and can penetrate powerfully. Most injuries occur on the lower limb and are severely painful. Two-thirds of Australian species inject a protein venom via their spine that can kill local tissue and may require surgical excision. No anti-venom exists, but there have been no confirmed Australian fatalities to date.

Allergic Reactions

Although clinicians have long observed puzzling or unusual reactions to marine envenomations, it is only recently that it has become understood that many of these could be allergic reactions to the foreign venom material. These reactions include localized inflammation, either immediate or delayed for up to two weeks, or a hypersensitive systemic reaction, anaphylaxis. Such reactions have detectable sero-immunological markers.

Delayed allergic reactions, still serologically unproven, have been connected to envenomations or contacts with *Chironex fleckeri*, *Acanthaster planci*, and a toxic marine sponge. The swelling, itching, blister formation, weeping skin, and burning pain that can characterize delayed reactions occur in patients with a personal history of allergies, even without further contact with the offending marine animal or its venom. Such reactions are effectively controlled by systemic steroids. Medical attention of the fortunately rare, but life-threatening anaphylactic reactions is crucial to the survival of the patient.

Promising Therapeutic Substances

Scientific work on marine toxins has concentrated on organisms that are visible and obtainable in high biomass. Scientists have ignored the enormous variety of novel bacteria, microalgae, and fungi in marine waters; dedicated research in this area could yield an even more spectacular array of novel metabolites than have thus far been obtained from the marine macroorganisms. In addition, marine microorganisms lend themselves more readily to genetic engineering and manipulation than more complex macroorganisms.

In our limited work, we have been impressed by the wide variety of metabolites obtainable from marine bacteria and the interesting pharmacological properties of substances and extracts. An interesting biological effect has been noted in the macroalgae species, *Chlorodesmis fastigata*, which produces a metabolite containing enol acetate grouping. In the north, one acquires a different metabolite than from the south, but both compounds appear to act as fish repellants. Brown algae, which have been isolated often, contain phenolic compounds, initially indicating strong antibiotic activity; but, so far, no commercially viable substances have been isolated.

By far the widest range of organisms studied in the Great Barrier Reef are the sponges. One of the most interesting single species is *Dysidea herbacea* which, depending on where it is collected and whether it is associated with symbiotic blue-green algae, may yield metabolites with a predominance of chlorinated substances, or in another instance, there may be no chlorinated compounds, but brominated metabolites, or metabolites containing neither chlorine nor bromine. This series of metabolites, although including in one case a very active topical antiseptic, has not produced a single, commercially therapeutic substance.

The Great Barrier Reef sponge *Aplysinopsis reticulata* yielded a metabolite, methylaplysinopsin, that was very active in reversing ptosis caused in mice by preadministration of tetrabenazine—a test which preliminarily indicates that an active substance may show human antidepressant activity. Tests on this compound were conducted for seven years, reaching the penultimate stage prior to human administration, before adverse side-effects caused the end of the study. This factor alone indicates the cost and necessary commitment for therapeutically marketable substances to be available from marine organisms.

In tests conducted at the Suntory Institute for Biomedical Research, crude extracts were applied to screens for antimicrobial assay, cytotoxicity assay, coronary vasodilation assay, cardiotonic assay, antiulcer assay, angiotensin converting enzyme inhibition assay, and platelet aggregation inhibition assay. Many of the crude extracts showed strong pharmacological activities and then were purified further. Table 1 indicates the summary results where a check indicates that activity was detected. The actual results provided a more detailed analysis of the significance of the activities obtained.

The Future

The development of any pharmaceutical product is risky. An initial activity may result in many years of work before a final decision can be made to proceed to commercial development or to end work. Additional problems exist with marine organisms and many of these relate to the fact that the metabolites obtained will be different from those traditionally available to the microbiologist and pharmacologist whose results are so important in interpreting an activity, and determining whether further tests should be done. The metabolites often have halogen substitution with a high probability that marine-derived metabolites will act differently than those of existing drugs. The traditional screens of the pharmaceutical industry may not be adequate to detect novel substances with novel mechanisms of action.

The move by many innovative drug evaluators to test the molecular mechanism of action is probably the greatest chance of success for marine-derived metabolites. Studies of receptor binding, displacement, and tissue culture may provide more reliable evaluations of potential therapeutic application than conventional screens. In addition, before a new product can enter the market in all developed countries, it must show a significant therapeutic advantage over those already available.

Table 1. Activities noted with marine species.

	antimicrobial*								cytotoxicity	coronary vasodilation	cardiotonic	antiulcer	ACE inhibition	platelet aggregation inhibition
	S.a.	B.s.	M.l.	M.s.	E.c.	P.a.	A.f.	C.a.						
sponges	√	√	√	√	—	—	√	√	√	√	√	√	√	√
algae	√	√	√	√	—	—	—	—	√	√	√	—	√	√
corals	√	√	√	√	—	—	—	—	√	√	√	√	√	√
sea cucumbers	—	—	—	—	—	—	√	√	√	√	√	√	√	—
higher plants	—	—	—	—	—	—	—	—	—	√	√	—	√	—
gastropod mollusks	—	—	—	—	—	—	—	—	√	√	√	—	—	√
sea urchins	—	—	—	—	—	—	—	—	√	√	√	—	—	—
tunicates	—	—	—	—	—	—	—	—	√	√	√	—	√	—
sea anemones	—	√	—	—	—	—	—	—	√	√	√	—	√	—
others	√	√	—	—	—	—	√	√	√	√	√	—	√	√

*** Abbreviations of microorganisms:**
B.s. = ***Bacillus subtilis*** **P.a.** = *Pseudomonas aeruginosa* **S.a.** = *Staphylococcus aureus* **E.c.** = *Escherichia coli*
M.s. = ***Mycobacterium smegmatis*** **C.a.** = *Candida albicans* **M.l.** = *Micrococcus luteus* **A.f.** = *Aspergillus flavus*

Nevertheless, the sea's potential to produce novel biological compounds, coupled with human perception of interaction between species, should lead to new therapeutically valuable substances to apply to health, agriculture, veterinary science, and the production of fine chemicals. The road to success could be underwater.

J. T. Baker is Director of the Australian Institute of Marine Science at Cape Ferguson outside Townsville. J. A. Williamson is a Consultant in Diving Medicine in Townsville.

Selected Readings

Baker, J. R., B. Brooks, A. Hinder, R. Pollard, K. P. Stark, J. A. Williamson, B. Zerner. 1984. Task Force Report, *Chironex fleckeri* (Southcott). Government of Queensland.

Barss, P. 1984. Wound necrosis caused by the venom of stingrays. *Med. J. Aust.* 141: 854–855.

Endean, R., C. Duchemin, D. McColm, E. H. Fraser. 1969. A study of the biological activity of toxic material derived from nematocysts of the cubomedusan *Chironex fleckeri. Toxicon* 6: 179–204.

Endo, M., M. Nakagawa, Y. Hamamoto, M. Ishihama. 1985. Pharmacologically active subtsances from southern Pacific marine invertebrates. Paper presented at the IUPAC Symposium on Marine Natural Products, Paris.

Fenner, P. J., P. F. Fitzpatrick, R. F. Hartwick, R. Skinner. 1985. "Morbakka": another cubomedusan. *Med. J. Aust.* (In press)

Hartwick, R., V. Callanan, J. Williamson. 1980. Disarming the box-jellyfish: nematocyst inhibition in *Chironex fleckeri. Med. J. Aust.* 1: 15–20.

Olson, C. E., M. G. Heard, G. J. Calton, J. W. Burnett. 1985. Interrelationships between toxins: studies on the crossreactivity between bacterial or animal toxins and monoclonal antibodies to two jellyfish venoms. *Toxicon* 23: 307–316.

Southcott, R. V. 1956. Studies in Australian cubomedusae, including a new genus and species apparently harmful to man. *Aust. J. Marine Freshw. Res.* 7: 254–263.

Sutherland, S. K. 1983. *Australian animal toxins: the creatures, their toxins, and care of the poisoned patients*, 359–373. Melbourne: Oxford University Press

Togias, A. G., J. W. Burnett, A. Kagey-Sobotka, M. Lichtenstein. 1985. Anaphylaxis after contact with a jellyfish. *J. Allergy Clin. Immunol.* 75: 672–675.

Williamson, J. A. 1984. The blue-ringed octopus. *Med. J. Aust.* 140: 308–309.

Williamson, J. A., V. I. Callanan, M. L. Unwin, R. F. Hartwick. 1984. Box-jellyfish venom and humans. *Med. J. Aust.* 140: 444–445.

Williamson, J. A. 1985. *The Marine Stinger Book*. Brisbane, Qld. State Centre, Surf Life Saving Association of Australia.

Williamson, J. A., L. LeRay, M. Wolfhart, P. Fenner. 1984. Acute management of serious envenomation by box-jellyfish (*Chironex fleckeri*). *Med. J. Aust.* 141: 851–853.

Great Barrier Reef Echinoderms

This drawing is from the first scientific study of the reef, detailed in the book The Great Barrier Reef *by E. Saville-Kent, 1893.*

Research Stations on the

Lizard Island

The Lizard Island Research Station, situated at the center of one of the richest coral reef regions known, is a facility of the Australian Museum. The laboratory provides access to a wide range of tropical habitats including sand and mud flats, mangrove swamps along the mainland coast, sea grass beds, fringing reefs, platform reefs, continental islands, raised limestone islands, vegetated and bare coral cays, outer barrier or ribbon reefs, and oceanic habitats outside the reefs with depths to 5,000 meters only 10 miles away. True atolls in the Coral Sea (such as Osprey Reef) are also within easy access. Lizard Island itself is a high (370 meters), granitic, continental island, covering 7 square kilometers with permanent fresh water and a variety of terrestrial habitats. The island is fringed by a coral reef which also encompasses two nearby islands (Palfry and South), and encloses a 10-meter-deep lagoon.

*The objectives of the Lizard Island Research Station are to provide optimal logistic support for a maximum of 14 visiting researchers. Facilities include four, fully self-contained bungalows, diving equipment, sea-water aquaria, laboratory space, equipment, and services. The laboratory also operates 10 small, aluminum, outboard-powered boats which can be used by visitors around the island, in the lagoon, or further afield, depending on experience. For extended voyages, the research station operates a 14 meter motor-sailing catamaran research vessel—*R.V. SUNBIRD*, powered by twin diesel engines and sail, and accommodating two crew and up to 5 researchers.*

Researchers from anywhere in the world are welcome to come and pursue their research at the Lizard Island Research Station. An all-inclusive bench fee is charged. This fee covers accommodation and use of all laboratory facilities. Post-graduate students are invited to enquire about the Doctoral Fellowships which are awarded each year to support field studies at Lizard Island.

For more information, a more detailed brochure on the station's facilities, current bench fee rates, and booking forms, please write to:

The Secretary
Lizard Island Research Station
P.M.B. 37
Cairns, Queensland
Australia 4870

—Barry Goldman,
Lizard Island Research Station

One Tree Island

One Tree Island is a four-hectare (10-acre) cay situated on the Tropic of Capricorn at the seaward (southeast) end of a biologically rich reef 5.5 × 3.5 kilometers in size. It lies in the center of the Capricorn Group about 20 kilometers east of Heron Island and about 100 kilometers off the Queensland coast. The nearest mainland port is Gladstone.

The Australian Museum began research at One Tree Reef in 1965. Three primitive buildings were completed by 1972. Ownership and operation of the station was transferred to the University of Sydney at the end of 1974. In the 11 years since, there have been substantial improvements to the quality of the station, including a fourth building, but the station has been kept small and dedicated to field as opposed to laboratory research. The University has sole occupancy of the island under a lease from the Queensland Department of Lands and operates the station under a permit from the Great Barrier Reef Marine Park Authority (GBRMPA).

The station provides basic accommodation for up to 8 scientists, and excellent facilities for field research. The whole of One Tree Reef and surrounding waters to a distance of 1 kilometer from the reef edge is a Scientific Zone within the Capricornia Section of the Great Barrier Reef Marine Park. This zone is off-limits to all parties except scientists with research permits.

The station, although owned by the University of Sydney, is accessible to scientists from all institutions, and provides immediate access to a biologically rich lagoon which provides ideal sheltered waters for many kinds of research. The station is equipped with boats and diving gear. There is limited laboratory space and some instrumentation.

Scientists interested in working at the station should write to:

The Executive Officer,
One Tree Island Field Station,
School of Biological Sciences,
University of Sydney,
Sydney, N.S.W., Australia 2006.

Access to the station is via the port of Gladstone and thence Heron Island. Transport from Heron Island to One Tree Island is included in the standard fee for accommodation and use of the station's facilities, which is presently A$40 per day.

—Peter F. Sale,
University of Sydney

Great Barrier Reef

Orpheus Island

The Orpheus Island Research Station is located at Pioneer Bay on the western side of Orpheus Island, a 170-meter-high continental island in the Palm Islands Group, 30 kilometers north of Townsville. The Bay faces northwest, providing excellent shelter from the prevailing southeasterly winds.

The island is mainly granite, with some volcanic material. Vegetation is mainly dry sclerophyll (scrub) forest, with some vine thickets and palms in the gullies, and grassland on the eastern side. Strand vegetation is evident, and there are several areas of mangrove on the western side of the island with Rhizophora especially well represented. Aboriginal middens and ceremonial sites remain from pre-European times at various sites around the island.

Sandy shores are found at several locations along the western side, while the many promontories provide a variety of rocky shore habitats. Orpheus Island is surrounded by an excellent fringing reef with extensive reef flats developed in both north and south Pioneer Bay, Hazard Bay, and on the northeast and southeast ends of the island. Reef flats are walkable at low tide. The combination of coastal proximity and shelter from strong wave action provides opportunity for great diversity of marine and benthic plants and animals.

The facilities at the station include a four-bedroom house for use by visiting scientists (capacity 20). Also available is a laboratory equipped with seawater aquaria and laboratory equipment, which includes balances, microscopes, freeze drier, ovens, and other laboratory equipment. The laboratory is divided into wet and dry sections, and is partially air-conditioned. Power (240 v) is provided on a 24 hour basis, as is filtered seawater. Diving facilities include compressor and dive tanks, and there are four small boats available. All food and provisions must be brought to the Island.

All inquiries and bookings relating to the Marine Research Station at Orpheus Island should be directed to:

The Director,
Sir George Fisher Centre for Tropical Marine Studies,
James Cook University
Townsville, Queensland
Australia 4811

Heron Island

The Heron Island Research Station was established in 1951 by the Great Barrier Reef Committee. It was the first permanent, land-based center for coral reef studies on the Great Barrier Reef and has grown steadily since that time to become the largest coral island research facility in Australia.

In 1980, the ownership of the station was transferred to the University of Queensland. It is now a fully integrated research and teaching center of that university.

The station's facilities are available to scientists and students throughout the world to pursue independent studies in any discipline, and on any subject pertaining to coral reefs. The major attractions of the station for researchers and educational groups are:

- Its unique location on a coral sand cay, surrounded by a large (9.5-kilometer long, 3.5-kilometer wide) and flourishing lagoon platform reef.
- The space and the staff to support several research projects simultaneously. Educational groups are provided with completely separate laboratory facilities.
- The close proximity of Heron Island to other reef systems in the Capricorn and Bunker Groups for comparative and inter-reef studies.
- The proximity of the southern capital cities of Australia, which serves to reduce traveling time and costs. It is possible to stand on the reef at Heron Island within 2½ hours of leaving Brisbane, using scheduled air services to the island.

The site of 2 hectares (5 acres) contains 29 buildings occupying a floor area in excess of 2,000 square meters, approximately 900 square meters of which consists of space for research and teaching. A total of 21 buildings is related to accommodation and the others are used for research, teaching, administration, and technical services.

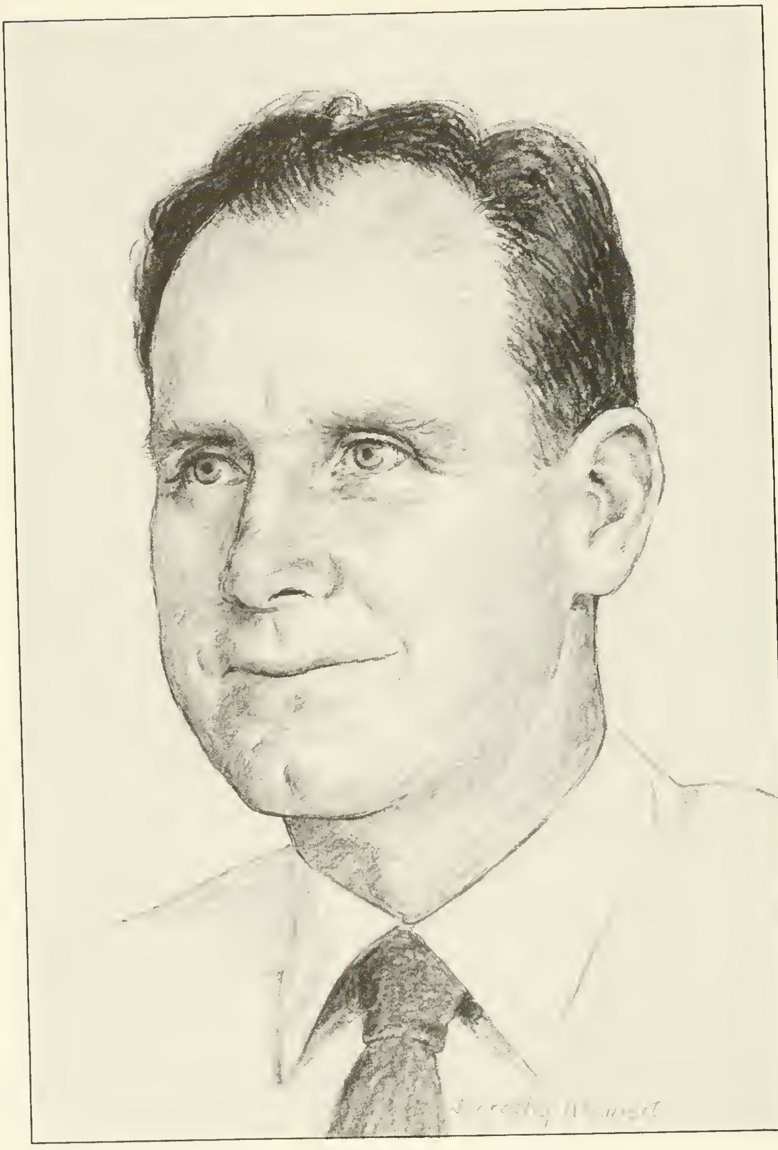
Scientists interested in working at the station should write:

Director
Heron Island Research Station
University of Queensland
Gladstone, Queensland
Australia 4680

—I. D. Lawn,
University of Queensland

profile

Joseph T. Baker



Portrait by Dorothy Meinert

Early Man (3 a.m.)

by Barbara E. Kinsey

It is not uncommon when seeking an appointment with Joseph Thomas Baker, the Director of the Australian Institute of Marine Science (AIMS), for him to suggest 3 a.m. "You must be kidding," might be a natural reaction. He would not be.

Joe (he is widely known by his Christian name) thrives on a busy schedule, which he packs into a 20-hour working day. I know because I worked for Joe on a number of projects when he was head of the Sir George Fisher Centre for Tropical Marine Studies at James Cook University in Townsville. I found him to be exceptionally pleasant—with a rare capacity for bringing scientists, policy- and decision-makers together to exchange viewpoints. I also know him as a dedicated family man—proud of his wife, Val, and four children (two sons and two daughters). However, I knew very little about his "off duty" life. Thus it was a challenge to write this profile and to discover the "other Joe Baker."

A Struggle Early On

Joe Baker was born in Warwick, in the south of Queensland, in 1932. He attended the local primary and high schools in that town. His father was a railway worker. During the war years, his father was transferred north to Townsville, which was at that time a large base for U.S. military forces in northern Australia. Young Joe continued his schooling at South Townsville and Railway Estate schools. This was to be a very valuable introduction for him in later years.

The family could not afford to support Joe as a full-time student at university, and at that time there were only a few scholarships available. He started out in 1950 as a laboratory cadet with the Commonwealth Scientific and Industrial Research Organization (CSIRO), working full time during the day as a histologist cum dishwasher, and attending classes five nights a week. The situation improved in later years, as the course requirements dropped to three or four nights a week, but doing it this way meant that it took him 6 years to complete his basic degree. This is, of course, standard for part-time students, in contrast to 3 years for full-time students.

Joe's father had played Rugby League for Queensland, in the state team. Joe grew up close to football, playing Rugby Union for his school in Warwick and on Sundays playing Rugby League in the local competition. He first played A grade in the Warwick Representative Team at the very young age of 16, as a fullback.

Turning up for Rugby Union training, when he started at university, he was asked by the coach if he was in either the School of Medicine or Law (Rugby Union being the "gentlemen's game" in distinction to Rugby League, which was professional). On learning that Joe was a Science student, the coach asked him at which college (Hall of Residence) he was living. "None, I am an evening student." Having filled none of the social requirements, he was told by the coach that there was no point in him turning up for training for the university team.

Joe then decided that he would play Rugby League for Easts, one of the major Brisbane teams. He captained the Brisbane team, and in the year he was working as a Senior Demonstrator at the university, was selected for the State Team of Queensland. At this point, the registrar called him in to explain why he, a member of staff, was not playing Rugby Union for the university. Joe had much delight in telling him. He advanced the case for Rugby League, and after two years it was reintroduced to the university as a team sport.

Of course, being Joe Baker, these were hardly conventional fishing trips.

His habit of a long working day developed in these first two years, when he never returned home from university before 11 at night. As he was then too tired to start studying, he would go to bed, getting up at 3 a.m. to continue his studies. Finding that practice to be perfectly satisfactory for him, he has maintained it ever since. He considers that while such a work practice was forced on him initially, that he is not a workaholic. Others do tend to view him in that light.

Joe's entry into marine science was indirect. Australia is a large continent, with most of its major population centers lying on the coastal fringes. So most Australian children grow up with memories of seaside vacations, surf and sand, exploring rockpools, and fishing. Every year a large number of our student intake to the universities is spurred on by the hope that they will be able to work in the field of marine science. The selection process is quite intense, because entry to university is highly competitive. There are comparatively few openings for such students, and when they do obtain tertiary qualifications, very few positions are available.

After doing honors in organic, inorganic, and physical chemistry, because Joe was not sure in which aspect of Chemistry he wished to specialize, he did his Master's degree on the essential oils of Australian eucalypts. Then, fate intervened; he met his future wife, Val, a dedicated angler. He maintains that the only way he could get near her was to become interested in fishing himself. He also involved his supervisor, Maurice Sutherland, in some of his fishing expeditions.

The Dye Is Cast

Of course, being Joe Baker, these were hardly conventional fishing trips. They would set out from Brisbane at 2 a.m. and head for Currumbin, 60 to 65 miles away, fish for tailor (American bluefish, *Pomatomus saltatrix*), then return to the University of Brisbane by 9 a.m. at the latest.

One particular morning, having exhausted their regular bait on a very substantial run of tailor, and not wanting to leave when the fish were in such plentiful supply, they decided to try some nearby gastropods as bait. Joe broke them out of their shells and handed them to Maurice Sutherland to try. This was an extremely successful ploy. They went home with the best catch of fish they had ever had.

On the return trip, however, they began to feel uncomfortable. A foul smell pervaded the car. Each was reticent to comment until they noticed their hands developing a decided greenish cast, and then an indelible purple coloration, and that their hands were the source of the odor.

A literature search provided the clue to what had happened. The dye was Tyrian purple, the royal purple of antiquity. Nobody had ever characterized the colorless precursor, and this search became Joe Baker's doctoral topic. He comments on his felicitous choice of organism *Dicathais orbita* Gmelin: "I was very lucky because the Australian species has only one precursor to the purple dye, unlike Mediterranean gastropods, which may have as many as three." With the technology and instrumentation available in the late 1950s, a more complex pathway could not have been as readily elucidated.

In 1961, before he had completed his doctorate, he was offered the lectureship in chemistry at the new University College at Townsville. University Colleges were set up from parent universities in the state capital cities in a few large country towns throughout Australia; they became autonomous later, as in the case of James Cook University in 1970). His versatility was an asset here because, where there could only be one lecturer in chemistry in the new college, it was an advantage to have someone who had a reasonable breadth in all three major sections of chemistry. Recognizing the problems of isolation in a town so far from the academic centers of the south, he enlisted the aid of the professor of chemistry at Brisbane University in starting a visiting lecturer system to broaden the student's exposure to a variety of topics. This practice is still maintained.

The new college to which he reported consisted of some pegs laid out on the ground. Eight weeks before lectures were to commence, there was no building, and the first term's lectures were conducted in Pimlico High School, just across the road. Having very little time for research, but a lot of time for collecting, he developed the practice of collecting during the academic year. During his summer vacation, his family and he would go south and while his family vacationed at the Gold Coast, he would work intensively on his research. Because of the photosensitivity of the material and his minor need for sleep, much of the work was done at night.

In the first year, Joe Baker was the Chemistry Department. Not entirely comfortable with physical chemistry as a discipline, he took the recommended text and worked out every problem, so that he would be able to understand any difficulties his students might have. Determined to have the new school produce quality graduates, he ran tutorials for those finding difficulties with the subject. Friends remember with awe that not only were some of those tutorials held in the small hours of the morning, but that the students actually attended them!

As if his commitments to teaching and research were not enough to more than fill the day, there was football. His love for the game stood him in good stead in Townsville. It was a bridge between the townspeople and the new University College, at a time when each was wary of the other. His big straw hat, which he wore every Sunday when he went as coach with the fledgling university team, was his trademark. He is particularly proud of the fact that his hat, raffled to assist in defraying the medical costs of an injured player, earned $208 and sat for many years in the bar of one of the local pubs. To this day, friends are awed when people everywhere know him, especially cabbies and airport staff. Many of the senior politicians in the Queensland Government are either friends from his football days or former players, students, or supporters of clubs for whom he played and this has often been helpful in establishing a dialogue. The University team reached A grade status in 1970. The North Queensland team he coached in 1971–1972 won the State Championships in 1971.

In one night, he can probably do more work than a conventional staff can do in a week.

Each year, an additional member of staff was added to the new School of Chemistry, and an additional year of course work instituted, so there was no hiatus in graduating for that first intake of students. In 1962, he was appointed Senior Lecturer (Associate Professor in the U.S. system), and in 1970 Associate Professor (Full Professor in the U.S. system). He was involved with the architectural planning of the Chemistry School and is credited with much of the planning of a comprehensive curriculum for it.

In the late 1960s and early 1970s Joe's work on Tyrian Purple became recognized. He went overseas, on a sabbatical to the United States and to Italy, where he worked on those Mediterranean mollusks which are sources of the dye. Developing an international reputation, he was retained as a consultant to the Roche Institute in Switzerland in the early 1970s.

His consultancy with Hoffman-La Roche, Switzerland, led to him being asked in 1974 to set up the Roche Research Institute of Marine Pharmacology (RRIMP) in Sydney. As a now well-recognized marine scientist, appointments to a variety of committees followed. He became a member of the Heron Island Research Station Board in 1974 and a member of the Great Barrier Reef Marine Park Authority in 1976, a position he has held ever since, and of which he is very proud. The Authority is basically a triumvirate, each member representing different concerns. The Chairman, Graeme Kelleher, represents the Commonwealth Government, Sir Sydney Schubert is the nominee of the Queensland Government, and Joe Baker represents the independent viewpoint.

Stands Up for Staff

The period at RRIMP established Joe Baker as a marine scientist. As distinct from a marine chemist, he had to develop a broad base of knowledge on all aspects of marine science, physiology, and pharmacology. It was an active, productive institute in 1981, when the parent company decided that their research efforts should lie in other directions and that RRIMP would close its doors. On the staff of 80 was one of Joe's original students and he recounted the stand that Joe made, on behalf of his staff, so that they did not suffer from the closure to the extent that was initially considered likely. Joe maintained that he would, if they could not find alternative employment, look for appropriate openings for them himself. And he did.

Joe Baker returned to Townsville in 1981 to set up the Sir George Fisher Center for Tropical Marine Studies at James Cook University. This is a multidisciplinary, marine oriented center charged with the responsibility of developing research programs within the center, maintaining contact with other research organizations locally and overseas, coordinating the use of the university's research vessel, the *James Kirby*, and administering the Orpheus Island Research Station. The center houses the RRIMP Collection of marine microorganisms, and has an active microbiological research program with cross disciplinary ties to other university departments.

The involvement with advisory committees built up to an even greater commitment in the late 1970s, often to the point that one meeting would conflict with another. Joe became a latter day "flying doctor." He developed the habit of making the airplane his office. This is rather hard on his secretary, because he is quite capable of dictating more in one night's flight than she can transcribe in a day (and he has had some extremely competent secretaries). In fact, in a single night, he can probably suggest more work than the laboratory staff can add into their busy week's schedule. Because his time scale is so radically different to that of most people, he sometimes fails to comprehend the reasons for the hiatus between his suggestion and another person's implementation of it.

Joe Baker accepts all commitments, declining none, but he has not yet solved the problem of how to be in two different places at the same time. A colleague recalls that a meeting of the Marine Research Allocation Advisory Council had been scheduled in Darwin, and was to be followed by a further meeting of the Council on the following day at an aboriginal reserve situated in one of the most remote areas of Australia, the Cobourg Peninsula, well to the North. While the council was in Darwin, Joe received a telephone call from the Minister for Arts, Heritage, and the Environment asking him to go to Canberra. His presence was also expected at the Cobourg Peninsula meeting. He solved the problem that time by going to Canberra. However, as no direct flights were available at that time his route was via Perth and Melbourne, thousands of extra miles and a very long flight time (because of the limited number of flights). And how to occupy oneself on such a flight? No problem. En route to Canberra flying over the middle of nowhere, a message for the Advisory Council was sent via the airline radio. Joe had sent his comments on all the papers on the agenda for the meeting. The transmission was equivalent to six handwritten pages.

Joe is also a Member of the Great Barrier Reef Marine Park Authority, the Chairman of the Committee of Directors of Island Research Stations, the immediate past President of the Australian Marine Science Association, the Vice-Chairman of the World Wildlife Fund (Australia), the past President of the Australian Museum Trust, and a member of the Advisory Committee to the Federal Minister for Science and Technology on Grants for Marine Science. He also is the immediate past Chairman of both the Australian Special Programme Committee for the World Heritage Convention and of the Australian Committee for the World Heritage Commission, a position he had to relinquish on taking up the appointment as Director of AIMS last fall. AIMS, located near Townsville, is one of the largest and best institutions dedicated to tropical marine science today. Joe was awarded the OBE (Officer of the Order of the British Empire) in 1982 for services to marine science. It is the first to be given to an Australian in this category. He is very pleased to have been part of the Australian delegation that carried the nomination of the Great Barrier Reef to the World Heritage Committee for listing in 1981.

Joe had ties to AIMS long before he was appointed to the directorship. In 1972–73, he was a member of the Scientific Advisory Committee to the interim AIMS Council and Ken Back, the Vice Chancellor of James Cook University, was on that council. Sites had been examined for the new laboratory complex, but the decision had not been made. The Cape Ferguson site, 30 miles from Townsville, had been inspected from the air, but not at ground level. The day for the council meeting dawned, and the Vice Chancellor suggested that, before the meeting, they should take a four-wheel drive vehicle out and have a look at the area from the land approach. The roads were poor to nonexistent, and the jeep became bogged. Forgetting he had on his best shirt in preparation for the meeting, Joe leaped out in the mud and lifted the rear of the vehicle at the same time that Ken put his foot on the accelerator. Joe was covered from head to toe with mud — his first physical contact with the site.

And how does he see the future for AIMS? Basically, rather similar to the tried and true approach which has worked so well for it, but with some additional input and output. He would like to see the institute with a more informative role, exposing it to greater public scrutiny. He favors an open door approach, with visiting scientists and students filling some of the gaps in the staff's areas of research. He would like to see aspects of mariculture examined, complementary to that of other institutions, and aimed toward solving some of the problems inherent to high-density stocking.

He hopes to be able to bring in some staff who are skilled in finding practical uses for pure research, so that there will be an applied component without losing that very special advantage of free ranging thought that is the hallmark of pure science. At its present level of staffing and support, Joe believes that the Australian Institute of Marine Science must concentrate the majority of its research in a few specialized fields in which it can establish world leadership.

book reviews

***The Art of Captain Cook's Voyages* by Rüdiger Joppien and Bernard Smith. 1985. Two volumes. Volume One, *The Voyage of the Endeavour*, 1768–1771. Volume Two, *The Voyage of the Resolution & Adventure*, 1772–1775. Published for the Paul Mellon Centre for Studies in British Art by Yale University Press, New Haven and London. Volumes $50.00 each.**

The Art of Captain Cook's Voyages provides an opportunity to observe Europeans in the initial process of discovering, interpreting, and mastering "a new world in the Pacific." Captain James Cook's three voyages to the Pacific, 1768–1780, were the first of the great European voyages of discovery to carry professional artists. These two handsome volumes (with a third forthcoming) are published in support of the high value Cook and his famous colleague Sir Joseph Banks placed on visual description to supplement the verbal records of the journals. Each volume is devoted to a separate voyage; together they describe in detail and illustrate all the known drawings and paintings that relate to the peoples of the Pacific, the lands and islands they inhabited, and the artifacts they used in daily life.

The first section of each volume includes a critical and analytical account of the professional artists associated with the relevant voyage: Parkinson (first voyage), Hodges (second voyage), Webber (third voyage). The work of important amateur artists, such as Herman Spöring and William Ellis, is also discussed in detail.

The second section of each volume provides a full descriptive catalogue of the drawings and paintings associated with the voyage. It is arranged chronologically. Within this framework, items of similar subject matter are brought together so that the progress from a field sketch to a developed painting or published engraving can be observed.

The first objective of the *Endeavour's* voyage was to observe the 1769 transit of Venus across the face of the sun at Tahiti, and then to seek the great then unknown southern continent of Australia. Any relationships established with the peoples encountered in the Pacific area were secondary to these goals.

The tradition of drawing for informational purposes that Banks brought to the *Endeavour's* varied undertakings consisted of three main divisions: that which served the purposes of navigation, that which served the purposes of natural history, and drawings of places visited, people encountered, and artifacts noted. It is the last division that is the focus of the first volume.

Portrait of an Australian Aborigine by Charles Praval, 1770.

The second volume of *The Art of Captain Cook's Voyages* depicts visits by the *Resolution* and *Adventure* to New Zealand, the Society Islands, the New Hebrides, New Caledonia, Antarctica, Eastern Island, and elsewhere. It also details the circumstances in which William Hodges took over from Banks as chief artist on the voyages, an interesting tale in and of itself.

These volumes will be of interest to historians, geographers, and anthropologists. They also will be of importance to anyone interested in the study of the Pacific region in its widest context, or in the study of European art, ideas, and attitudes in the latter 18th century. The scholarship is exceptional.

Paul R. Ryan,
Editor, *Oceanus*

Books Received

Aquaculture

Mussel Aquaculture in Puget Sound by Douglas Skidmore and Kenneth K. Chew. 1985. Washington Sea Grant Program, Seattle, WA. 57 pp. + viii. $5.00

Recent Advances in Aquaculture: Volume 2, James F. Muir and Ronald J. Roberts, eds. 1985. Westview Press, Boulder, CO. 282 pp. $42.00.

Biology

Basic Marine Biology by A. A. Fincham. 1984. Cambridge University Press, New York, NY. 157 pp. $37.50.

The Behavior of Teleost Fishes, Tony J. Pitcher, ed. 1986. The Johns Hopkins University Press, Baltimore, MD. 553 pp. $57.50

Biotechnology of Marine Polysaccharides, Rita R. Colwell, E. R. Pariser, and Anthony J. Sinskey, eds. 1985. Hemisphere Publishing Corp., New York, NY. 559 pp. + xi. $79.95.

Proceedings of the Nineteenth European Marine Biology Symposium, P. E. Gibbs, ed. 1984. Cambridge University Press, New York, NY. 541 pp. + viii. $99.00.

Chemistry

Geochemistry of Marine Humic Compounds by M. A. Rashid. 1985. Springer-Verlag, New York, NY. 300 pp. + xii. $68.00

Diving

Living and Working in the Sea by James W. Miller and Ian G. Kablick. 1984. Jones and Bartlett, Boston, MA. 433 pp. + xiv. $32.50.

The Professional Diver's Handbook, David Sisman, ed. 1985. Gulf Publishing Company, Houston, TX. 304 pp. $48.00.

Engineering

Introduction to Naval Engineering by David A. Blank, Arthur E. Bock, and David J. Richardson. 1985. Naval Institute Press, Annapolis, MD. 545 pp. + x. $17.95.

Environment/Ecology

California's Battered Coast by Jim McGrath. 1985. California Coastal Commission, San Diego, CA. 403 pp. + v. $6.00.

Coastal Wetlands, Harold H. Prince and Frank M. D'Itri, eds. 1985. Lewis Publishers, Inc., Chelsea, MI. 286 pp. + xvii. $39.95.

Dwellers in the Land: The Bioregional Vision by Kirkpatrick Sale. 1985. Sierra Club Books, San Francisco, CA. 217 pp. + x. $14.95.

Early Life Histories of Fishes: New Development, Ecological and Evolutionary Perspectives, Eugene K. Balon, ed. 1985. Kluwer Academic Publishers Group, Boston, MA. 280 pp. $75.00

The Ecology of Rocky Coasts, P. G. Moore and R. Seed, eds. 1986. Columbia University Press, New York, NY. 467 pp. + xi. $45.00.

El Niño North: El Niño Effects in the Eastern Subarctic Pacific Ocean, Warren S. Wooster and David L. Fluharty, eds. 1985. Washington Sea Grant Program, Washington, D.C. 312 pp. + v. $10.00.

Key Environments: Western Mediterranean, Ramon Margalef, ed. 1985. Pergamon Press Ltd., Elmsford, NY. 363 pp. + ix. $23.95.

Lake Stechlin: A Temperate Oligotrophic Lake, S. Jost Casper, ed. 1985. Dr W. Junk Publishers, The Netherlands. 553 pp. + xiii. $95.00.

Marine and Estuarine Geochemistry, A. C. Sigleo and A. Hattori, eds. 1985. Lewis Publishers, Inc., Chelsea, MI. 331 pp. $39.50.

Marine Mammals & Fisheries, J. R. Beddington, R. J .H. Beverton, and D. M. Lavigne, eds. 1985. Allen & Unwin, Inc., Winchester, MA. 354 pp. + xxi. $55.00.

The Oregon Oceanbook by Tish Parmenter and Robert Bailey. 1985. Oregon Department of Land Conservation and Development, Salem, OR. 85 pp. $6.00 (+ $1.25 shipping & handling).

Practical Estuarine Chemistry, P. C. Head, ed. 1985. Cambridge University Press, New York, NY. 337 pp. + x. $54.50.

Reefs and Banks of the Northwestern Gulf of Mexico: Their Geological, Biological, and Physical Dynamics by Richard Rezak, Thomas J. Bright, and David W. McGrail. 1985. John Wiley & Sons Inc., New York, NY. 259 pp. + xvii. $48.95.

Sea Fog by Wang Binhua. 1985. Springer-Verlag. New York, NY. 330 pp. + iv. $79.00.

Field Guide

Alaska's Saltwater Fishes and Other Sea Life by Doyne W. Kessler. 1985. Alaska Northwest Publishing Co., Anchorage, AK. 358 pp. + xxvi. $19.95.

The Bunker Climate Atlas of the North Atlantic Ocean-Volume 1: Observations by Hans-Jorg Isemer and Lutz Hasse. 1985. Springer-Verlag, New York, NY. 218 pp. + vii. no listed price.

Dangerous Marine Animals of the Pacific Coast by Christina Parsons.

1986. Sea Challengers, Monterey, CA. 96 pp. $4.95.

Marine Fauna and Flora of Bermuda: A Systematic Guide to the Identification of Marine Organisms, Wolfgang Sterrer, ed. 1986. John Wiley & Sons, New York, NY. 742 pp. + xxx. $99.95.

The Marine Mammals of Virginia with Notes on Identification and Natural History by Robert A. Blaylock. 1985. Virginia Sea Grant College Program, Gloucester Point, VA. 34 pp. + iii. $1.00.

Plant Lore of an Alaskan Island by Frances Kelso Graham and The Ouzinkie Botanical Society. 1985. Alaska Northwest Publishing Co., Anchorage, AK. 194 pp. + xvi. $9.95.

Fisheries

Fish Catching Methods of the World by Andres von Brandt. 1984. Avon Litho Ltd., Warwickshire, England. Distributed in U.S.A. by Unipub, New York, NY. 418 pp. + xiv. $66.00.

General Reading

The Antarctic Circumpolar Ocean by George Deacon. 1984. Cambridge University Press, New York, NY. 180 pp. + viii. $24.95.

Dame by H. Greeley Thornhill. 1985. Coolidge Press. Chattanooga, TN. 270 pp. $15.95.

Pacific Explorer: The Life of Jean-François de La Perouse 1741–1788 by John Dunmore. 1985. The Naval Institute Press, Annapolis, MD. 318 pp. $19.95.

The Sea Peoples: Warriors of the Ancient Mediterranean by N. K. Sandars. 1985. Thames and Hudson, New York, NY. 224 pp. $10.95.

Seven Clues to the Origin of Life by A. G. Cairns-Smith. 1985. Cambridge University Press, New York, NY. 131 pp. + xii. $17.95.

Trails of an Alaska Game Warden by Ray Tremblay. 1985. Alaska Northwest Publishing Co., Anchorage, AK. 176 pp. + xv. $9.95.

Underwater Acoustics: A Linear Systems Theory Approach by Lawrence J. Ziomek. 1985. Academic Press, Inc., New York, NY. 290 pp. + xi. $45.00.

Geology

General Bathymetric Chart of the Oceans. 1984. Canadian Government Publishing Center, Ottawa, Canada. $100 (Canada), $120.00 (Other Countries).

The Ocean Basins and Margins: Volume 7A The Pacific Ocean, Alan E. M. Nairn, Francis G. Stehli, and Seiya Uyeda, eds. 1985. Plenum Press, New York, NY. 733 pp. + xiv. $95.00.

Great Barrier Reef

A Coral Island: The Story of One Tree Reef By Harold Heatwole. 1981. William Collins Pty Ltd., Sydney, Australia. 200 pp. A$10.00. Available through H. Heatwole, The University of New England, Armidale, N. S. W. 2351, Australia.

A Coral Reef Handbook, Patricia Mather and Isobel Bennett eds. 1984. The Australian Coral Reef Society, Brisbane, Australia. 144 pp. A$11.00.

The Great Barrier Reef: The World's Wild Places/Time-Life Books by Craig McGregor and the editors of Time-Life Books. 1974. Time-Life Books, Amsterdam. 184 pp. A$22.95.

The Mysterious Undersea World by Jan Leslie Cook 1980. National Geographic Society, Washington DC. 104 pp.

Perspectives on Coral Reefs, D. J. Barnes, ed. 1983. The Australian Institute of Marine Science, Manuka, Australia. 277 pp. +ix.

Proceedings of the Great Barrier Reef Conference, J. T. Baker, R. M. Carter, P. W. Sammarco, K. P. Stark, eds. 1983. James Cook University of North Queensland, Queensland, Australia. 545 pp. + xviii.

History

Secrets of the Bible Seas: An Underwater Archaeologist in the Bible Seas by Alexander Flinder. 1985. Severn House Publishers Ltd., London, England. 174 pp. £10.95.

South Atlantic Paleoceanography, K. J. Hsu and J. J. Weissert, eds. 1985. Cambridge University Press, New York, NY. 350 pp. + vi. $69.50

Marine Policy

Marine Mining: A New Beginning, Peter B. Humphrey, ed. 1985. Department of Planning and Economic Development, Honolulu, Hawaii. 319 pp. $10.00.

Ocean Yearbook 5, Elisabeth Mann Borgese and Norton Ginsburg, eds. 1985. The University of Chicago Press, Chicago, IL. 544 pp. + xvi. $49.00.

Wastes in the Ocean Volume 5: Deep-Sea Waste Disposal, Dana R. Kester, Wayne V. Burt, Judith M. Capuzzo, P. Kilho Park, Bostwick H. Ketchum, and Iver W. Duedall, eds. 1985. John Wiley & Sons, Inc., New York, NY. 346 pp. + xvii. $79.95.

Wastes in the Ocean Volume 6: Nearshore Waste Disposal, Bostwick H. Ketchum, Judith M. Capuzzo, Wayne V. Burt, Iver W. Duedall, P. Kilho Park, and Dana R. Kester, eds. 1985. John Wiley & Sons, Inc., New York, NY. 534 pp. + xx. $95.00.

Physical Science

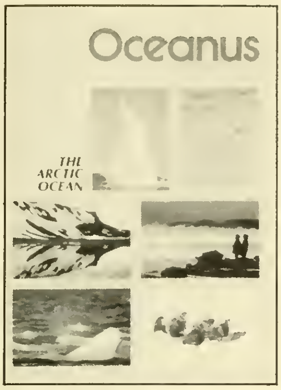
Intrinsic Geodesy by Antonio Marussi. 1985. Springer-Verlag, New York, NY. 219 pp. + xvii. $56.00.

Storm Surges—Meteorological Ocean Tides by T. S. Murty. 1984. Friesen Printers Ltd., Manitoba, Canada. 897 pp. + ix. $34.95 (Canada), $41.95 (Other Countries).

Ships and Sailing

Ships of the Panama Canal by James L. Shaw. 1985. Naval Institute Press, Annapolis, MD. 269 pp. + x. $29.95.

Oceanus back issues



The Arctic Ocean

Vol. 29:1, Spring 1986—It's frozen. It's remote. But scientists, the military, lawyers, corporations, governments, and investors are paying particular attention to the Arctic. Some call it a stampede. Find out who, why, and what it means. Topics include exploration, U.S. and Soviet security, sea ice, climate, shipping, pollution, and policy.

The Titanic: Lost and Found

Vol. 28:4, Winter 1985/86—The most comprehensive account available of the *Titanic*'s loss in 1912 and recent discovery. Includes a detailed account of how the ship was found, a profile of discoverer Robert Ballard, details of the *Argo* system used to find the ship, as well as articles containing many new historical details of the wreck.

Beaches, Bioluminescence, Pollution, and Reefs

Vol. 28:3, Fall 1985—Articles deal with topics of great current interest, such as latest scientific perspectives on oil pollution, threats to the beaches of the U.S. East Coast, the strangely lit world of the deep ocean, and the unique ecosystems of Australia's Great Barrier Reef.

The Oceans and National Security

Vol. 28:2, Summer 1985—The U.S. Navy's effectiveness relies on proper use of strategy, technology, and marine science. This issue looks at all these areas: from details of specific weapons systems, to the proper role of the U.S. Navy, to the importance of marine science research. Additional articles examine the Soviet Navy and the U.S. Coast Guard.

other available issues...

- **Marine Archaeology,**
  Vol. 28:1, Spring 1985—History and science beneath the waves
- **The Exclusive Economic Zone,**
  Vol. 27:4, Winter 1984/85—Options for the U.S. EEZ
- **Deep-Sea Hot Springs and Cold Seeps,**
  Vol. 27:3, Fall 1984—A full report on vent science.
- **El Niño,**
  Vol. 27:2, Summer 1984—An atmospheric phenomenon analyzed
- **Industry and the Oceans,**
  Vol. 27:1, Spring 1984
- **Oceanography in China,**
  Vol. 26:4, Winter 1983/84
- **Offshore Oil and Gas,**
  Vol. 26:3, Fall 1983
- **Summer Issue,**
  1983, Vol. 26:2—CO_2, mussel watch, warm-core rings, MIZEX, the U.S. EEZ
- **Summer Issue,**
  1982, Vol. 25:2—Coastal resource management, acoustic tomography, aquaculture, radioactive waste.
- **Summer Issue,**
  1981, Vol. 24:2—Aquatic plants, seabirds, oil and gas
- **The Oceans as Waste Space,**
  Vol. 24:1, Spring 1981
- **Senses of the Sea,**
  Vol. 23:3, Fall 1980
- **Summer Issue,**
  1980, Vol. 23:2—Plankton, El Niño and African fisheries, hot springs, Georges Bank, and more
- **A Decade of Big Ocean Science,**
  Vol. 23:1, Spring 1980
- **Ocean Energy,**
  Vol. 22:4, Winter 1979/80
- **Ocean/Continent Boundaries,**
  Vol. 22:3, Fall 1979.
- **The Deep Sea,**
  Vol. 21:1, Winter 1978
- **Summer Issue,**
  1977, Vol. 20:3—The 200-mile limit, the Galápagos rift discovery, nitrogen fixation, shark senses.

Issues not listed here, including those published prior to 1977, are out of print. They are available on microfilm through University Microfilm International, 300 North Zeeb Road, Ann Arbor, MI 48106.

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