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HALIMEDA

Edward Drew
Townsville, Queensland, Australia

Synonyms

Siphonales (in older literature); *Siphonous* algae

Definition

Halimeda is a genus of warm temperate to tropical macroalgae classified into

Phylum: *Chlorophyta*
Class: Bryopsidophyceae
Order: *Bryopsidales*
Family: *Halimedaceae*
Genus: *Halimeda*

Phytochemistry

Photosynthetic pigments

Halimeda chloroplasts contain the characteristic photosynthetic pigments of the Chlorophyta, plus ***siphonoxanthin*** and ***siphonein***, which are specific to the Bryopsidales.

Cell wall

Halimeda and most other Bryopsidales have cell walls composed of a **xylose**-based ***β-1–3 linked xylan***, not the glucose-based cellulose found in all other Chlorophyta.

General

Author's *Halimeda* Web site:

http://members.iinet.net.au/~edrew1/halimeda/halimeda.htm

Appearance

Halimeda thalli are composed of branching chains of calcified green segments joined together by flexible, uncalcified nodes. The thalli may be erect, pendant, or sprawling. They may grow up to 25 cm high or cover over 1 m if sprawling. They are anchored by holdfasts, which may be

(i) A small basal mass about a cm long, consisting of matted rhizoidal filaments adhering to rocks.
(ii) Or a large, dense bulbous mass, 1–13 cm long, buried in the sediment. It consists of fine rhizoids with adhering sediment particles and can be up to 40% of the plant's total weight.
(iii) Or several diffuse, inconspicuous patches of rhizoids arising at intervals from segments or nodes of the algae sprawling on rocks or unstable surfaces.

Segment size and shape vary considerably between species. They may be flat, keeled, or even cylindrical in some. Their outline varies from ovate to cuneate and may be distinctly lobed. The width varies from 2 to 55 mm.

Taxonomy

Halimeda tuna, from the Mediterranean Sea, is the holotype of the genus. It was first described, but named *Sertolara,* by Imperato (1599). During the next century, it was given several different generic names and was considered to be a coralline animal. In 1812, it was finally recognized as a plant and given its currently recognized binomial name, Halimeda Tuna (Ellis and Solander, 1786; Lamouroux, 1816). At that time, exploration of tropical regions had just begun, and the number of described *Halimeda* species reached 26 by 1887, most species being described solely on the basis of their segment morphology.

Currently, 44 species are recognized, distinguished using the morphological and anatomical characters

David Hopley (ed.), *Encyclopedia of Modern Coral Reefs*, DOI 10.1007/978-90-481-2639-2,

introduced by Barton (1901) and expanded by Hillis (1959); Hillis-Colinvaux (1980) also defined five distinct taxonomic Sections within the genus, based on anatomical details of the uncalcified nodes (see also "Internal structure" below).

Molecular systematics, first applied to the genus by Hillis et al. (1998) and expanded by Kooistra et al. (2002), yielded (i) a well-resolved phylogeny, (ii) confirmation of the five lineages, but requiring some re-organization, and (iii) demonstration of high cryptic species diversity, most tropical *Halimeda* species found consisting of two distantly related, genetic entities, which are indistinguishable by current methods of morpho-taxonomy. Verbruggen (2005) provides a detailed account of recent taxonomic progress within the genus.

Distribution

Halimeda is a warm water alga well represented in the tropics, mainly on coral reefs. There is one species, *H. cuneata*, which is strictly subtropical, while a genetically distinct form of the tropical species *H. tuna* is the only species found in the temperate Mediterranean Sea.

Of the 30 species then recognized by Hillis Colinvaux in 1980, 77% occurred in the Indo-Pacific Region and 46% in the Western Atlantic Region (Caribbean). Of the 13 species in the Caribbean, seven also occurred in the Indo-Pacific. The remaining six endemic species are presumed to have evolved after the rise of the Isthmus of Panama closed the Central American Seaway, separating the Western Atlantic from the Pacific in the Miocene (circa 3.5 Ma ago).

On coral reefs, *Halimeda* can occur from protected lagoons to the shallowest reef flat environments, exposed seaward reef fronts and as deep as 140 m on fore reef slopes (Hillis-Colinvaux, 1985; Littler et al., 1986) (see also "Contribution to carbonate sediments" below).

While *Halimeda* is the only genus in the family *Halimeda*ceae, it is closely related to the larger family Udoteaceae, which contains several other calcified, green macro algae, such as *Udotea*, *Penicillus*, and *Rhipocephalus*. These are often conspicuous in *Halimeda* habitats, as are several species of the closely related, but uncalcified, genus *Caulerpa* (family Caulerpaceae).

Internal structure

Halimeda segments consist of a central medulla of intertwining, branched, and sometimes anastomosing siphons (medullary filaments) running the length of the segment. These segments, with their large vacuoles, are continuous throughout the plant with a central few forming the uncalcified nodal region, a flexible joint between the segments. Within the nodes, the walls of the filaments may become thickened, fuse for part of their length, and even develop connecting pores, but there are no cross walls anywhere in the plant. The entire thallus is thus one multinucleate cell and is described as a **coenocyte**.

Near the segment surface, the medullary filaments branch vertically to form a cortex consisting of up to four layers of variously inflated utricles. The top layer (the primary utricles) is closely packed and appears polygonal in surface view. The size, shape, and branching patterns of these utricles are important taxonomic characters (Hillis-Colinvaux, 1980).

Growth

Individual *Halimeda* thalli grow by producing new segments. These develop from small tufts of medullary filaments, which grow out from the distal perimeter of a segment at or near the tip of a branch. This process begins in the afternoon and the tuft of filaments becomes organized into a new soft, uncalcified segment overnight. This new segment is initially white, but by dawn it is bright green. A few hours after dawn it is whitish green, having already begun to calcify (see also "Diurnal color change (ii)" below). Fast growing branch tips can produce a new segment every few days.

Calcification

The calcium carbonate endoskeleton is laid down in the internal spaces between the medullary filaments forming the segments. This is a light-driven process, requiring only that the superficial utricles contain functional chloroplasts and are closely adpressed, effectively isolating the interfilamental spaces from the external seawater. This happens within 36 h of initiation of the new segment.

Thereafter, whenever photosynthesis occurs, the resulting removal of CO_2 from the water in the interfilamental spaces raises its pH and causes deposition of calcium carbonate as aragonite crystals (Borowitzka and Larkum, 1976).

The overall degree of calcification varies (i) between species; (ii) within the algal thallus, with the lower, older segments more calcified than those at the growing tip; and (iii) with water depth and levels of irradiance.

Diurnal color change

Halimeda thalli become almost white after dark and then green again by next morning. This is due to mass relocation of chloroplasts, and probably other organelles, from the peripheral utricles into the medullary filaments. There they remain, hidden beneath the calcium carbonate endoskeleton, until re-emergence begins a few hours before dawn. This mass relocation of organelles, which can only occur because of the coenocytic structure of the thalli, involves an extensive cytoskeleton of microtules and actin fibers and will consume a considerable amount of energy every day (Drew and Abel, 1990; 1992). This energy-intensive endogenous rhythm may, however, give *Halimeda* crucial advantages in the dynamic coral reef environment, including

(i) **Daily** – minimization of grazing damage because chloroplasts and other organelles are protected within the calcium carbonate endoskeleton when surface-scraping grazers are most likely to be active.

Rapid paling of the green segments also occurs in response to damage during the day.

(ii) **Every few days** – relocation of chloroplasts beyond their parent segment allows the new segments, which develop overnight, to be populated with functional chloroplasts before dawn, via the nodal filaments. This allows calcification to start in the new segments at first light, rather than awaiting subsequent activation of its proto-chloroplasts by light-dependent *de novo* synthesis of chlorophyll.

(iii) **Only once – immediately before death** – facilitation of rapid overnight redistribution of the entire contents of the medullary filaments into the superficial gametangia in preparation for holocarpic sexual reproduction (see also ***Reproduction*** below).

Grazing

Halimeda is often found in abundance in areas on coral reefs where herbivorous fish exert high grazing pressure, but it is among the least preferred food items there. This is probably because of the high levels of calcification, a major physical defense against predation. In addition, the new segments, which are very vulnerable until calcified, are always produced at night when grazing pressure is low (Hay et al., 1988).

Halimeda also has chemical defenses against grazing. It synthesizes two secondary natural products, the diterpenoids halimedatetracetate and halimedatrial, which have considerable grazing deterrence properties, but are also potentially toxic to *Halimeda* itself. However, although both are present at high concentrations in the young, uncalcified segments, only reduced concentrations of the less toxic halimedatetracetate occur in the older segments, which are now heavily calcified, and so less vulnerable (Paul and Alstyne, 1988a).

Although these mechanisms can help to minimize grazing on *Halimeda*, it can still be heavily grazed, especially on seaward reef fronts where the lower parts of thalli, which have been severely cropped by herbivorous fishes are often found in inaccessible crevices. Once parts of a *Halimeda* thallus have been damaged, its coenocytic structure makes it vulnerable to catastrophic loss of cell contents. However, constrictions at branching points in the medullary filaments, and between the layers of cortical utricles, can quickly become plugged by organelles flowing toward the leak. This will retain the cell contents while the rapid wound repair processes temporarily seal the damaged area within a minute and construct a new wall within an hour (Menzel, 1988).

A very specific and widespread grazer on *Halimeda* is *Elysia halimedea*, a small Saccoglossan Ophistobranch mollusc. It is a surface scraper completely undeterred by the diterpenoids, which help keep other grazers away. Instead, it actually modifies and accumulates the deterrent chemicals up to 7% of its body weight and then, when irritated, it secretes a defensive mucilage containing them (Paul and Alstyne, 1988b).

Elysia halimedea is about 20 mm long and extremely cryptic as it is exactly the same color as the plants it feeds on. This is because it uses modified radula teeth to harvest intact chloroplasts from the outer utricles of *Halimeda* and stores them in specialized "digestive cells" within its body. This process is called ***kleptoplasty***). The chloroplasts are unable to divide within the animal but can continue to photosynthesize and supply it with nutrition for weeks or even months (Trench, 1973; Evertsten et al., 2007). A number of other saccoglossan molluscs also use chloroplasts from other bryosidalean algae such as *Caulerpa* and *Codium*.

Another small animal closely associated with *Halimeda* is the crab *Huenia* heraldica, which grazes on the filamentous epiphytes growing on the segments. It is about 25 mm long, green in color, and has a wide, segment-like carapace. It does graze on *Halimeda* itself to a limited extent, removing segments, and holding them in small specialized claws on its upper body to complete its camouflage.

Reproduction

Halimeda plants bearing gametangia were first reported by Derbes and Solier (1856) and Schmitz (1880). Both also reported the release of biflagellate zooids, although these were not demonstrated to be gametes until Nasr (1947) reported sexual fusion. However, collection of fertile plants has been so infrequent that Hillis Colinvaux (1980) still considered sexual reproduction to be of minor significance in the production of new *Halimeda* plants compared with asexual cloning involving rhizoidal runners and also the continued growth of dispersed plant fragments.

The paucity of field observations of sexual reproduction in *Halimeda*, even after the advent of scuba diving, is probably because it is completed in only 36 h. Healthy green plants transfer their entire protoplasm overnight into large numbers of newly formed, stalked bunches of gametangia that developed on the edges and surface of the segments the day before. The segments themselves are empty and white by dawn. These conspicuous green gametangia mature during that first day and explosively release their contents as gametes soon after dawn on the following day. This can produce a spectacular green soup of gametes in an aquarium tank, leaving a white thallus that is dead and soon disintegrates into a pile of calcified segments.

This process, whereby the plant dies after the whole thallus has taken part in simultaneous conversion of the entire cell contents to gametes, is called **holocarpy**.

Sexual reproduction in *Halimeda* is anisogamous and dioecious, two types of gametes being produced, each on different individuals. The larger "female" macro- gametes are bright green and contain a distinct red eyespot while the smaller 'male' microgametes are golden green and have no eyespot (Hillis-Colinvaux, 1980). Gametangia-bearing material is now known for most *Halimeda* species and gamete release and fusion have been reported upon in several, but development of zygotes has only been studied in the laboratory in one species, *H.tuna* from the

Mediterranean (Meinesz, 1980). Development was reportedly very slow and had not progressed beyond a small, uncalcified filamentous plant after 13 months. The characteristic *Halimeda* plant is presumed to be a haploid gametophyte, but it is not known when meiosis occurs, leading to speculation that a second, spore-producing, phase may be involved.

Some species of *Halimeda* may reproduce sexually at species-specific times of the year, while synchrony between field and laboratory populations, and also over considerable areas of *Halimeda* meadows, has been observed on the Great Barrier Reef (Drew and Abel, 1988b).

Recent observations show conclusively that sexual reproduction in seven species of *Halimeda* as well as 15 other Bryopsidalean algae from four genera, is an organized and pervasive phenomenon of coral reefs (Clifton and Clifton, 1999). It is comparable in synchrony and precision with the mass spawning of the corals themselves. Mass spawning of these green algae is also equally spectacular, releasing so many gametes that visibility on shallow reefs can be greatly reduced. Unlike the corals, however, in which entire populations spawn simultaneously on a single day, and live to spawn again next year, only a small part of the algal populations spawn each day, so that spawning can continue for several months, but the participating plants die and the population is progressively reduced. The lifespan of *Halimeda* thalli may be only months, to a maximum of a year, depending on species.

Contribution to carbonate sediments

Halimeda segments may be shed intermittently by living plants or *in toto* after holocarpic sexual reproduction. They contribute much to the structure of coral reefs and atolls as they accumulate between the branching framework produced by the corals themselves. In some reefs, they also cascade down steep fore-reef slopes to form thick sediment deposits on the seabed (Freile et al., 1995).

In the outer lagoon of the Great Barrier Reef, *Halimeda* can also form extensive "meadows" between reefs, growing atop mounds of *Halimeda*-rich gravels, which have been deposited in situ by the meadows themselves (Drew and Abel, 1988a). The substratum, of loose dead segments, is stable enough to support *Halimeda* vegetation dominated by the same lithophytic species found on nearby coral reefs, rather than species with holdfasts better adapted to soft substrata. The individual mounds are typically 200–300 m in diameter, coalescing laterally to form 30 m thick banks several kilometers wide. These banks are easily identified by their sinusoidally undulating surface and characteristic seismic signature. They are usually associated with up-welling of cooler, nutrient-rich water from below the thermocline in adjacent oceanic waters (Wolanski et al., 1988), and have accumulated since the underlying carbonate rock was exposed during the last low sea-level event 10,000 years ago. They have actually grown faster than the nearby coral reefs. Pinnacles of the underlying Pleistocene-age bedrock frequently occur in the hollows between the mounds of *Halimeda*-rich gravels (Phipps et al., 1985). Similar *Halimeda* banks have been found in Indonesian waters (Phipps and Roberts, 1988).

The banks closely resemble geological structures known as "bioherms" – dome-shaped structures composed mainly of the remains of one type of animal or plant (Marshall and Davies, 1988). Fossilized *Halimeda* bioherms are known from India, the Caribbean, and Spain. The latter form part of aerially exposed reefs and are described as "segment reefs."

Fossil Halimeda

The unlithified banks of *Halimeda*-rich gravels described above are potential precursors of the carbonate wackestones, rocks composed mainly of fossilized *Halimeda* segments, which occurred in fossil reefs as far back as the early Jurassic, circa 190 Ma ago. The carbonate structure is often very well defined and the rocks are relatively porous, due to voids between the loosely packed segments deposited in situ. There are also micro-voids within the segments reflecting the internal anatomy of the algae themselves.

These deposits are very similar to much earlier calcareous fossil algae (collectively known as Phylloid algae), which are widespread in ancient reefs in many parts of the world. Here, their considerable porosity has often allowed the accumulation of hydrocarbons (Wray, 1977).

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Cross-references

Algae-Macro
Binding Organisms
Reefal Sediments
Sediment Dynamics
Sediments, Properties
Tidal Jets
Wackestone

HALIMEDA BIOHERMS

Peter J. Davies
University of Sydney, Sydney, NSW, Australia

Introduction

Halimeda Bioherms – two words with separate biological and geological connotations – have been used cojoined since 1985 by Davies and Marshall (1985) and Orme (1985) to describe Holocene mounds (bioherms) of dominantly *Halimeda* derived carbonates in water depths generally deeper than 30 m (sometimes 20 m) and forming undulating banks. Some confusion does exist within the literature, not because colleagues do not understand the use of the above authors but because of other discipline-related terms coined and used both before and since 1985. The geological understanding of Bioherm, therefore, needs to be clarified, as does its relations to a term coined at the same time – Biostrome – and their likely (possible?) relation to the more recently coined biological term, Meadows. For these reasons, it is proposed to very briefly clarify as follows:

First, *Halimeda* are green calcareous precipitating algae from the phylum Chlorophyta in the order Bryopsidales and in two families – Halimedaceae and Udoteaceae. The taxonomy is described by Hillis-Colinvaux (1980) and in the Great Barrier Reef in various papers by Drew and Abel (see references in Drew and Abel, 1988a, b). There is no confusion over the term *Halimeda*, only sometimes over the identification of species.

Secondly, Bioherm is a geological term coined by Cummings (1932) to describe both bedded and nonbedded lens-like or mound-like accumulations, comprised of the often in situ accumulation of invertebrate organisms. The original definition had reefs in mind, invoking topographic relief above the sea floor, an in situ framework and rapid accumulation. In a modern sense, the bioherms described in this entry are not reefal, yet they are mound-like, often with significant relief above the surrounding sea floor and with internal characters, which are bedded or nonbedded and composed of in situ and derived biologic accumulations that have accreted rapidly. In a geological sense, mound-like structures sometimes show substantial mud and few framework organisms (many Carboniferous mounds) and are still legitimately termed bioherms. In the original definition, Cummings (op cit) distinguished bioherms from related structures termed Biostromes (see review by Kershaw, 1994), defined as nonreefal flat bedded structures often but not necessarily comprised of organic accumulations. It is noted here because Orme (1985) and Orme et al. (1978) rightly pointed out that in the northern Great Barrier Reef, large areas of the mid shelf behind the Ribbon Reefs (termed "back-reef" by Orme op cit) appear to be comprised of crudely bedded laterally extensive nonmounded "biostromal sediments" and are associated with *Halimeda* Bioherms (called "banks" by Orme et al., 1978). Later, Drew and Abel (1988a) described the surface characters of such areas as "Meadows" and Hillis-Colinvaux (1988), in a reef lagoonal environment, postulated that Meadows might evolve into Bioherms.

In the present contribution, *Halimeda* Bioherms are used to denote mounds showing relief above the surrounding sea floor and built by the in situ accumulation of *Halimeda* together with other infauna. They are sometimes called Banks (Orme and Salama, 1988) although Banks should rightly be reserved for much larger structures, for example, Bahama Banks. In the Great Barrier Reef and elsewhere, *Halimeda* Bioherms are associated with often larger areas having an extensive sheet-like form and called Biostromal areas (Orme and Salama, 1988, p. 136), the surface of such areas are called *Halimeda* Meadows by Drew and Abel (1988b). Thus, the origin of biostromes (a 3-D geologic term) might be elucidated by studying their surface "Meadows" (a 2-D biological term). Further, the origin of the Bioherms might be determined through studies of the spatially related Meadows/Biostromes. This entry follows this treatment. First however, the biology of *Halimeda* Bioherms and their related meadows are briefly reviewed.

Halimeda Bioherms, Table 1 The species diversity of *Halimeda* meadows compared to adjacent reefs in the Great Barrier Reef region

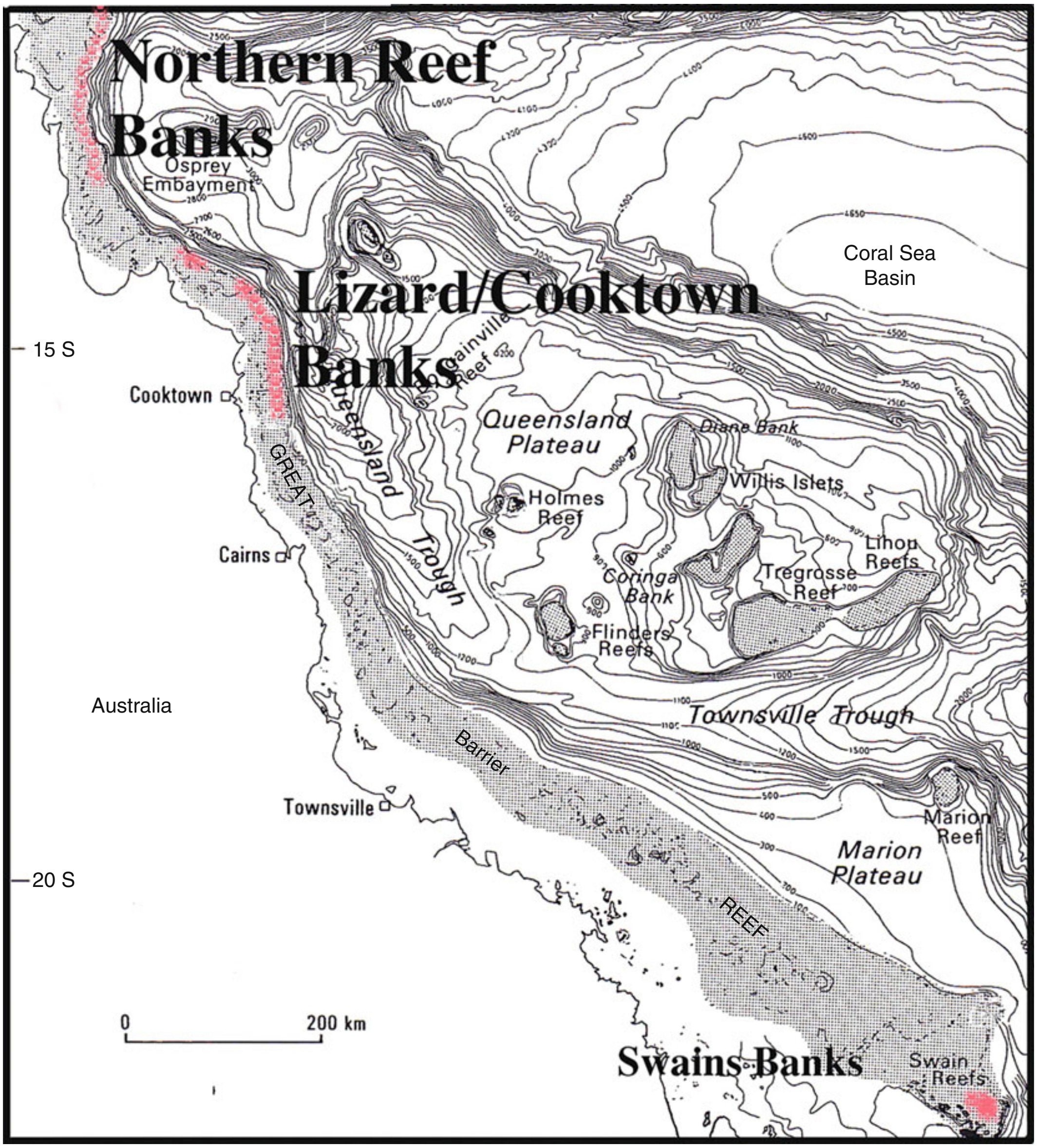
Species	Meadows	Reefs	Conclude
H. opuntia	0.6%	40.2%	Reef dominant
H. hederacea	48.4%	38.3%	Both reefs and meadows
H. copiosa	26%	2.5%	Meadows
H. minima	Absent	0.2%	In reefs at low level
H. micronesica	0.6%	10.%	Reefs
H. distorta	4.4%	Absent	Meadows
M. melanesica	Absent	3.8%	Reefs
H. lucanalis	0.5%	1.0%	Both at low levels
H. macrophysa	Absent	2.1%	Reefs
H. fragilis	5.6%	Trace	Meadows
H. tuna	2.0%	1.0%	Both at low levels
H. discoidea	1.1%	1.7%	Both at low levels
H. gigas	Absent	0.5%	Reefs at low levels
H. taenicola	0.3%	Absent	Meadows at low levels
H. gracilis	2.9%	Absent	Meadows
H. incrassata	7.2%	Absent	Meadows
H. cylindracea	0.1%	present	Meadows in trace amount
H. macroloba	trace	present	Meadows and reefs at very low levels

The biology of *Halimeda* bioherms and adjacent meadows (biostromes)

Halimeda are a green alga that belongs to the phyllum Chlorophyta in the order Bryopsidales. *Halimeda* are described by Hillis-Colinvaux (1980, 1988) as being either Rhipsalian and possessing a holdfast or non-Rhipsalian and possessing none or a limited holdfast. In the modern environment, *Halimeda* occur as an accessory component of reefs, or as principal components of bioherms and meadows.

Halimeda Bioherms generally occur above a base line of 50 m water depth while meadows generally occur below this depth. The most extensive publications on their biology are those of Drew and Abel (1988a, b). The species composition of bioherms and meadows in the Great Barrier Reef is shown in Table 1.

Species diversity is high. A total of 12 *Halimeda* species, 2 *Udotea* and 1 *Penicillus* occur in water depths above 50 m dominated by the non-rhipsalian *H. opuntia* and *H. hederacea* while in water depths greater than 50 m, only *H. copiosa* and *H. hederacea* occur. Growth occurs via multiple obscure holdfasts restricted to the surface of the sediments. In other areas of the Pacific and Indian Oceans where *Halimeda* bioherms and meadows have been described, the same species predominate. Accumulations of *Halimeda* as meadows have also been reported from the lagoon of Enewetak atoll



Halimeda Bioherms, Figure 1 Distribution of *Halimeda* bioherms in the Great Barrier Reef. They occur in three areas, Northern reef region, Lizard Island to Cooktown, and in the Swains reefs region.

(Hillis-Colinvaux, 1988) where the dominant species are the rhipsalian *H. incrussata* and *H. cylindrica*.

The global distribution of *Halimeda* bioherms

The Great Barrier Reef

Halimeda Bioherms have been described in two areas: (1) two parts of the northern GBR and (2) in the Swains region of the southern GBR (Figure 1).

In the northern Region, *Halimeda* Bioherms have been described by two separate groups in the Lizard Island – Cape Flattery region and in the Ribbon 2–Ribbon 7 region.

The Lizard Island – Cape Flattery region (Figure 1) has been described by Orme and coworkers (Orme et al., 1978; Orme, 1985; Orme and Salama, 1988). They report that 26% of the total shelf area (effectively the outer shelf area behind the shelf edge reefs) between latitudes 14.27S and 15.02S is occupied by *Halimeda* litho-facies (Bioherms and Biostromal meadows). *Halimeda* bioherms are up to 19 m thick and sit on a prominent seismic reflector assumed to be the transgressed pre-Holocene/Pleistocene unconformity. The bioherms (= banks in Orme and Salama, 1988) that rise to within 25 m of current sea level are best developed in the eastern part of the region and their surface is mounded and “cloaked by *Halimeda* meadows – and a limited veneer of reef coral – especially in troughs." Little sedimentologic data on the *Halimeda* sediments and no dating have been published.

The bathymetry, seismic structure, submersible examination and photography, sedimentology, and biology of *Halimeda* banks in the region east of Cooktown (Figure 1) have been described by Davies and coworkers (Davies and Marshall, 1985; Phipps, Davies and Hopley, 1985; Marshall and Davies, 1988). They report that between 15.10S and 15.35S in the lee of Ribbons 2–7, the "reefless" tract supports a luxurious growth of *Halimeda* that during the Holocene have developed *Halimeda* bioherms in water depths between 30 and 50 m.

In the southern Great Barrier Reef region, *Halimeda* bioherms have been reported from the Swains reefs region, west of Frigate Shoals in water depths of 20–32 m (Figure 1) (Searle and Flood, 1988).

The Sahul shelf

On the Sahul Shoals, *Halimeda* are integral components of large "banks" such as Big Bank, Snow White, Happy, Grumpy and Udang (Rees et al., 2007). The banks are generally flat topped with few bioherms in the sense of those described from the Great Barrier Reef.

The Java Sea bioherms

In the Java Sea, Phipps and Roberts (1988) describe *Halimeda* bioherms on K Bank in the eastern part of the Makassar Straits (Figure 3). They are similar to those described from the Great Barrier Reef, if not a little larger.

The Miskita bank/channel bioherms

Several generations of *Halimeda* bioherms occur on the shelf northeast of Nicaragua (Figure 4), as seen mainly on multichannel seismic sections.

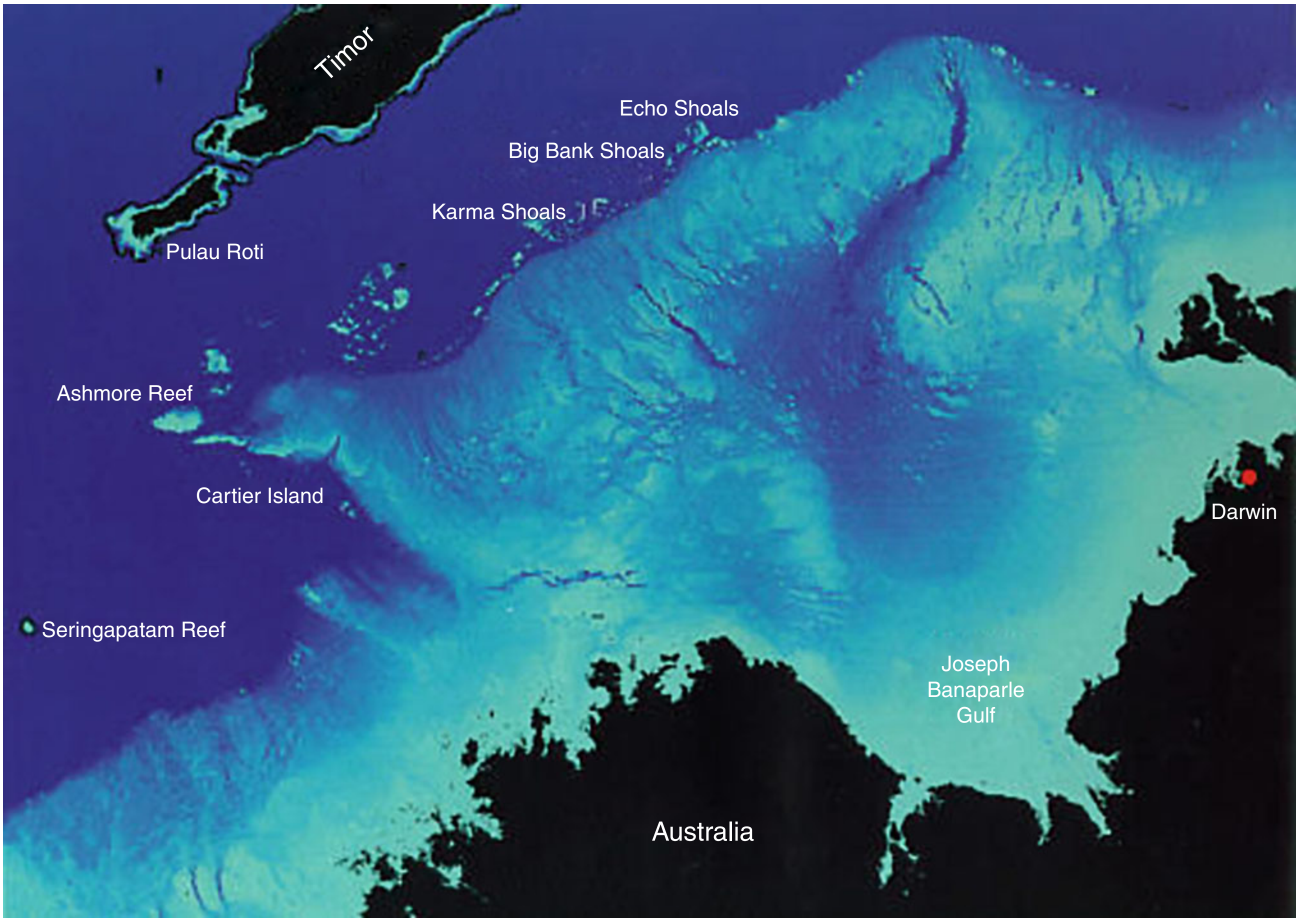
Descriptive features of *Halimeda* bioherms

In the Great Barrier Reef, *Halimeda* bioherms occur over large areas behind the outer reefs, as "fields" or "complexes" of inter-fingering or inter-merging individual elongate bioherms, 150 m long (N–S) and 100 m wide (W–E), slightly flat topped and sloping away in all directions at 5–15° (Figure 5a). The most striking surface feature is a forest of soft green algae, sometimes 50 cm thick on the tops and thinning down the sides of each bioherm. This forest is dominated by various species of *Caulerpa* and *Halimeda*. Structurally, it is similar to rain forest in that there is a thick undergrowth on a sandy/gravely surface, a middle layer of less dense cover and a top canopy. This forest is an ephemeral feature, appearing and disappearing within months. Mollusks, foraminifera, and bryozoans form integral and important parts of the epifauna with *Halimeda*. These collectively mantle the surface of the top and sides of the bioherms but stop suddenly 3–5 m above the troughs between adjacent bioherms.

Seismic data shows in the Great Barrier Reef and the Java Sea, the bioherms are up to 15 m thick in the GBR (Figure 5a, b + c) but are substantially thicker (+20 m) in the Makassar examples (Figure 5d). In the northern Great Barrier Reef, the bioherms sit on a prominent seismic reflector (Figure 5a + c) which dips from around 33 m immediately west of the reefs to around 65 m some 5–10 km west of the reefs. The bioherms themselves also decrease in size and increase in depth in the same direction. The reflector in Figure 5a + c, is a leached skeletal, limestone whose vugs are partially filled with soil. The geometry of the bioherm complexes bear no relation to the geometry of the prominent reflector. A similar seismic reflector also underpins the bioherms in the Makassar Straits (Figure 5d).

Bedding is the commonest internal structural feature (Figure 5a–d); internally bioherms are sometimes bedded, sometimes transparent and often multigenerational. Individual bioherm complexes show bedding suggestive of several generations of growth. Tops are frequently seismically transparent. Sometimes, there are two seismic facies – a lower indistinctly bedded unit that merges laterally with a biostromal sheet facies and an upper bedded facies forming the upper two thirds of the banks.

Sedimentologically, as seen in cores (Figure 6), the bioherms are comprised of *Halimeda* sands and gravels in an olive green matrix. Large foraminifera, *Marginopora vertebralis* and *Alveoinella quoyi* are subordinate but important parts of the gravel fraction, as are mollusks and bryozoans. The *Halimeda* are dominantly *H. opuntia, v. hederacea, and H. copiosa* with subordinate amounts of *H. fragilis, H. discoidea*, and *H. gracilis*. Texturally the bioherms are gravelly, sandy muds throughout but with slight textural variations down the core. At the surface, the gravel fraction (largely *Halimeda*) comprises 50%, this dropping to 20–30% within 1 m of the top. Deeper in the core the gravel fraction either remains at 20–30% or drops even further to less than 10%. The sand fraction in most cores stands at 20–30% and is comprised dominantly of broken *Halimeda* leaves with contributions also from foraminifera, bryozoans, and mollusks. Mud in the cores measures around 10% in the top half meter of the cores and then increases substantially to between 30 and 50% throughout the rest of the core. Approximately half of this mud fraction is carbonate and half non-carbonate or terrigenous (quartz, kaolinite, and smectite). However, in the Swains Reefs bioherms, the mud matrix is totally carbonate and devoid of terrigenous material, reflecting the distance of these bioherms from the Australian mainland. In the Java Sea, Phipps and Roberts (1988) describe the bioherms as disarticulated *Halimeda* plates with a fine grained matrix of foram-rich carbonate mud (usually less than 40%), only a small percentage of which is non-carbonate (volcanic shards and siliceous spicules). In some cores, *Halimeda* plates form a disorientated open-textured accumulation. Locally, within cores, sediments



Halimeda Bioherms, Figure 2 *Halimeda* bioherms in the region of the Sahul Shoals, Timor Sea.

are composed of coarse *Halimeda* plates, some of which are still unbroken. Occasionally, layers 5–10 mm thick are comprised of *Halimeda* plates orientated parallel to the bioherm surface.

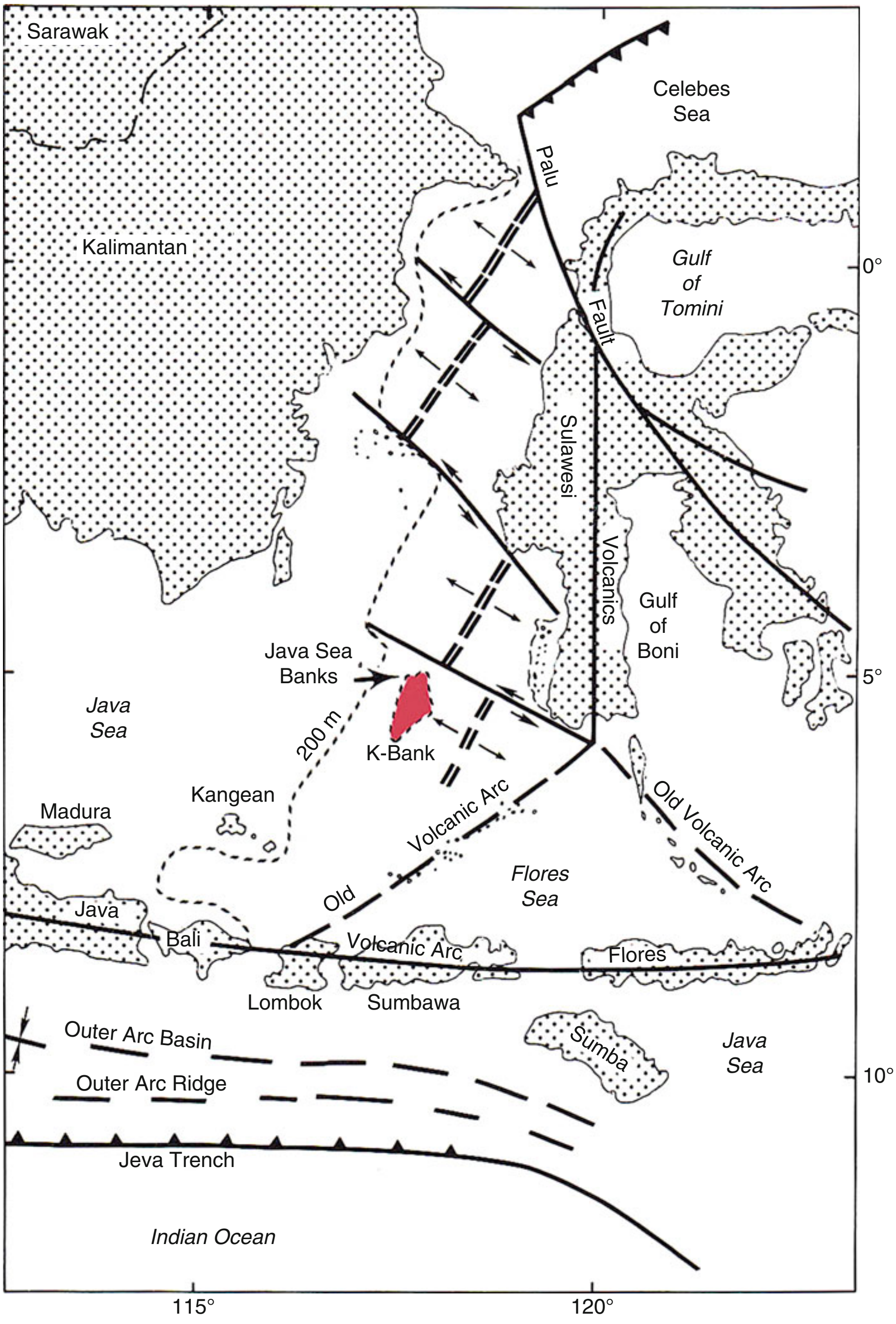
Rates of growth of *Halimeda* bioherms

Biologic studies report a wide range of growth rates for *Halimeda*, varying from 420 g $CaCO_3$ m^2 $year^{-1}$ in the Florida Straits to 2,234–3,000 g m^2 $year^{-1}$ in the Great Barrier Reef (Drew, 1986). The high rates in the GBR are attained by the plant doubling the biomass of the colony every 15 days. This represents an enormous production of carbonate sediments indicating that *Halimeda* are a major contributor to tropical marine environments. The bioherms described in this entry are testimony to that conclusion. Radiocarbon dating (Table 2) provides some indication of the vertical accumulation rates of the bioherms in the Great Barrier Reef and Makassar Straits.

Table 2 indicates clearly that accumulation rates have been similar in both the Great Barrier Reef and in the Makassar Straits. Depending on porosity, accumulation rates of close to 3 m/1,000 years are very close to Drew's estimates and confirm that not only are *Halimeda* significant contributors to reef ecosystems, but that they are capable of producing geologically significant ecosystems in their own right.

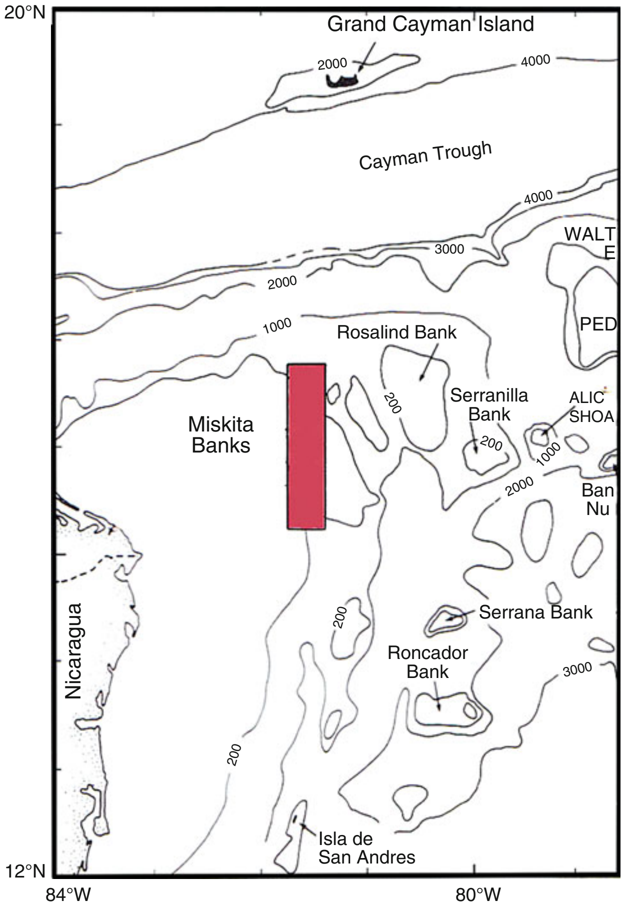
Relations between bioherms (banks) and meadows (biostromes) and the lagoonal meadows at Enewetak

In the Great Barrier Reef, Bioherms are intimately associated with widespread crudely bedded areas which are not mounded and which have been described by Drew and Abel (1988a) as Meadows. Such areas occupy a range of water depths but often deeper than 50 m and extending down to 96 m in places. Similar deposits are reported to occur extensively over K bank east of Makassar Straits. The growth of such features and their relations to the truly biohermal deposits is, therefore, pertinent to the current discussion. Clues as to growth were defined at Enewetak by Hillis-Colinvaux (1988) where various ages of thalli (successional development) were observed to spread



Halimeda Bioherms, Figure 3 *Halimeda* bioherms in the Java Sea, in the region of the Macassar Strait (After Phipps and Roberts, 1988).

across unconsolidated sediment producing a raised terrace above neighboring barren sands. First, an extensive holdfast system developed together with buried thalli; secondly, *Halimeda* plates were shed and they and associated sediments were stabilized by cyanobacterial algal mats; thirdly, elevation of thalli above the sediment surface anchored by the holdfast system with further in situ accumulation of plates and platelets and further stabilization by mats; fourthly, the development of an associated flora and fauna, particularly sponges and fifthly,



Halimeda Bioherms, Figure 4 *Halimeda* bioherms on the Nicaraguan shelf in the region of the Miskita Channel (After Hine et al., 1988).

a thickness was achieved by continuous shedding from perennial growth and algal mat development. This may define a mechanism of growth applicable to the early stages of meadow development of the transgressed Pleistocene surface. However, Drew and Abel (1988a) showed that shallow meadows in the Great Barrier Reef are comprised of non-Rhipsalian algae without strong holdfasts. Further work is required to determine whether such meadows grow out of meadows like those at Enewetak.

Growth of *Halimeda* bioherms

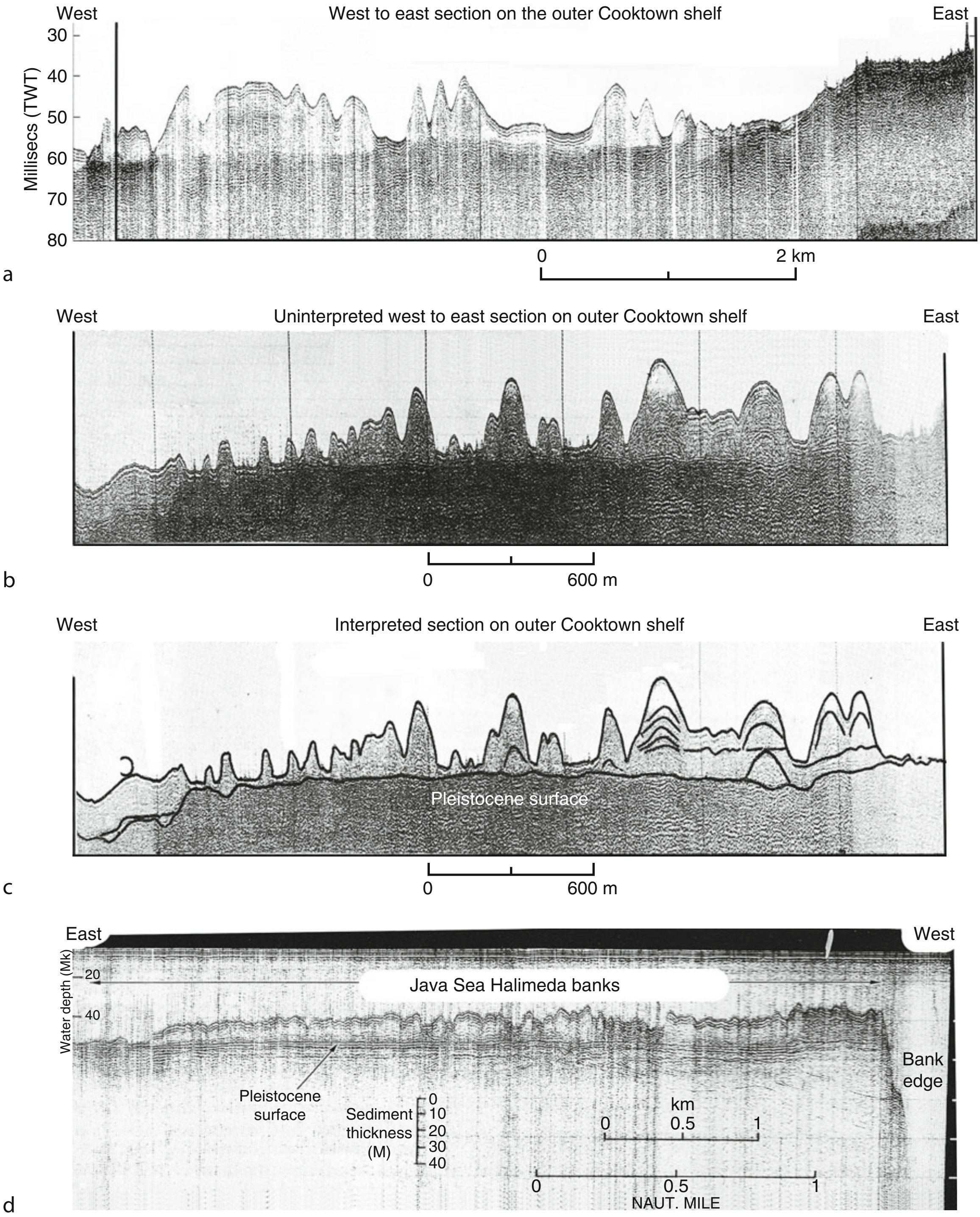
A number of features are pertinent to growth and origin:

1. They grow from a prominent surface defined in the Great Barrier Reef as the transgressed Pleistocene surface. A similar reflector also occurs below the Makassar Strait bioherms and is also interpreted as the Pleistocene transgressed surface. The shape of biohermal mounds bears no relation to any minor relief features on this transgressed surface. There is little antecedence effect.
2. They occur intimately associated with sheet-like bedded biostromal deposits (Meadows).
3. In the Great Barrier Reef they occur in the lee-shelter of the Holocene outer barrier.
4. At least in the Cooktown region, they are largest close to the outer barrier, becoming smaller to the west.
5. They are comprised of in situ and derived accumulations of *Halimeda* leaves and an associated fauna of foraminifers, bryozoans, and mollusks, which form a series of multigenerational mounds, sometimes bedded, sometimes transparent.
6. In the Great Barrier Reef and in the Makassar Strait, their presence on the same Pleistocene surface that underlies the modern reefs, places their age as post Pleistocene, growing at the same time as the Reefs. Radiocarbon dating corroborates this conclusion.

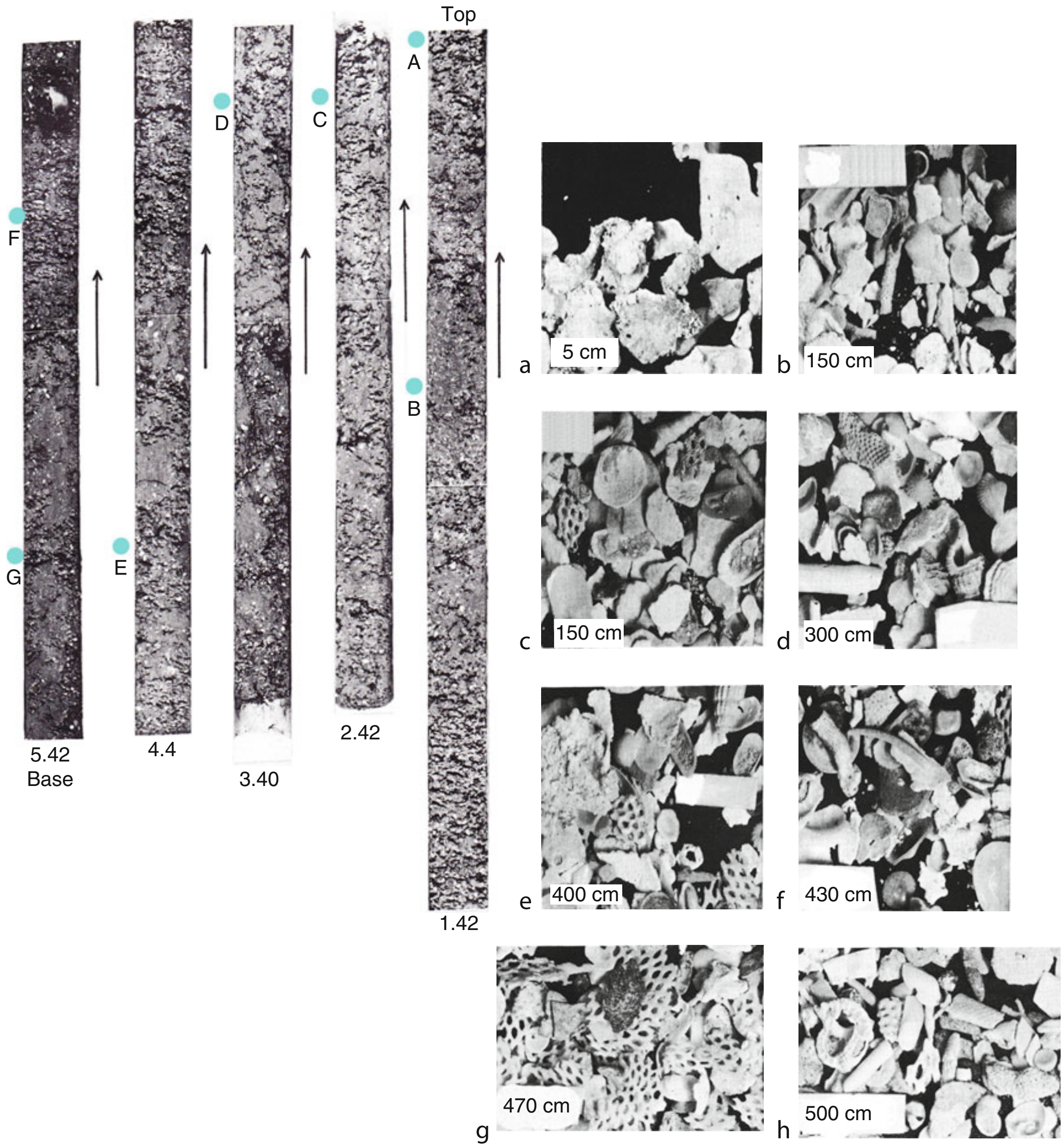
The relations (if any) of Bioherms to the Biostromal meadows has intrigued many. Orme et al. (1985, 1988) and Davies and co-workers (1985, 1988) have drawn attention to the co-occurrence of bioherms and biostromes (meadows) and Davies and coworkers in particular cite a variety of evidence (seismic, bathymetric, and visual observations from submersible) to indicate that meadows grade into biohermal areas. In the Great Barrier Reef, a case can be made, therefore, to suggest that meadows (biostromes) first occupied the transgressed Pleistocene surface and evolved into bioherms in places favorable to vertical growth. However, the development of a vertical growth potential demands special conditions and Davies et al. (op cit) and Drew and Abel (1988b) point to the likely importance of enhanced nutrients as an essential requirement. Thompson and Wolanski (1984) proposed that strong tidal currents operating in the inter-reef channels produce a Bernoulli Effect, lifting off-reef water onto the shelf through passes deeper than 50 m. Further Wolanski et al. (1988) propose that off the Cooktown region, upwelling and development of a tidal jet is occurring and carrying nutrient rich water from a reef passage to the Halimeda meadows. Such upwelling is limited to channels shallower than 45 m. These mechanisms add substantial weight to the timing and modes of origin defined by Davies and Marshall (1985) and summarized in Figure 7.

Significance of *Halimeda* bioherms

Originally the term “bioherm” was coined and used by petroleum geologists, particularly in an exploration sense, to describe features that did or could contain petroleum. Thereafter, it became synonymous with “reef-like” structures and important targets in petroleum exploration. Davies et al. (1988) described *Halimeda* bioherms as potential exploration targets in the Australian region. More recently, however, Davies and Marshall (1985) pointed out a different and perhaps more significant



Halimeda Bioherms, Figure 5 (**a**) West to east seismic section across the outer Cooktown shelf showing bedded nature of the *Halimeda* banks in 30 m of water. (**b** + **c**) Uninterpreted and interpreted seismic section across the banks on the outer Cooktown shelf. The multigenerational nature of the banks together with their planal Pleistocene growth surface clearly visible. (**d**) Seismic section of thick *Halimeda* banks in the Makassar Strait, Java Sea. The banks are clearly sitting on a planar surface interpreted as the Pleistocene.



Halimeda Bioherms, Figure 6 Cores from the *Halimeda* banks on the Cooktown shelf. The positions of detailed photographs are shown on the cores.

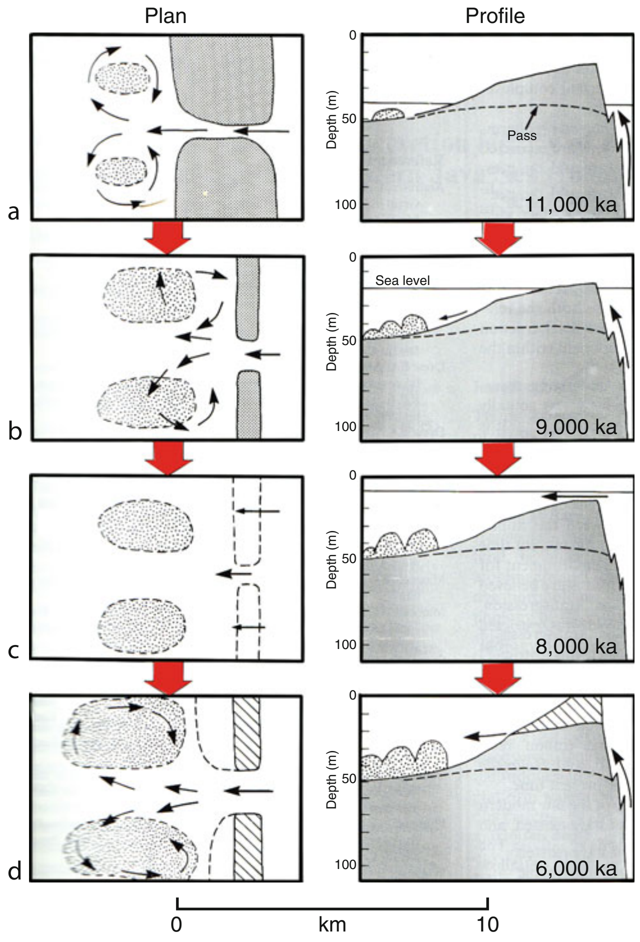
feature of *Halimeda* bioherms in the Great Barrier Reef at least, that is, they produce 3 kg $CaCO_3$ m^2 $year^{-1}$ compared to 3–4 kg for the reefs; however, the bioherms occupy a larger area. They may, therefore, lock up a greater proportion of $CaCO_3$ than do the reefs. Since the correlation between carbon dioxide (CO_2) levels and global temperatures was established in the ice core records, this conclusion assumes an even greater significance because it indicates not only the relevance of calcareous algae as important additional CO_2 sinks but when estimated on a global basis it also doubles the contribution of shallow water carbonate sediments (in conjunction with reefs) as CO_2 reservoirs (Rees et al., 2007).

Summary

Halimeda bioherms have been described from three parts of the Great Barrier Reef: from the Sahul Shelf, from the Makassar Straits, and from the Nicaraguan Bank. They form mounds that are up to 20 m height and are comprised of the skeletal remains of various species of *Halimeda*

Halimeda Bioherms, Table 2 Vertical accumulation rates of bioherms in the Great Barrier Reef and Makassar Straits

Region	Location	Exact position	Ages (years BP)	Sed rate
GBR	North bank	0–5 m	270–2,760	2 m/1,000 years
GBR	Big bank	0.4–2.8 m	270–1,300	2.33 m/1,000 years
GBR	Big bank	2.8–5.4 m	1,300–4,750	0.75 m/1,000 years
Java Sea	PC 12	0–100 cm	0–1,000	1 m/1,000 years
Java Sea	PC12	100–250 cm	1,000–1,250	0.6 m/1,000 years
Java Sea	VC 4	0–250 cm	0–1,250	0.2 m/1,000 years
Java Sea	VC 4	250–450 cm	1,250–2,000	2.7 m/1,000 year



Halimeda Bioherms, Figure 7 Origin of *Halimeda* bioherms as proposed by Davies and Marshall (1985). The key to growth are strong nutrient eddies produced by jets of upwelled oceanic waters flooding through the inter-reef passes before the modern reefs began in the time frame 11–9,000 ka (**a** + **b**). *Halimeda* banks grew well in this time frame. However, when the Pleistocene substrate was topped by the rising sea level (**c**) nutrient concentrations were not delivered specifically to the banks but, generally, to the leeward environments. Bank growth may have slowed down at this point. However, when the Holocene reefs reached sea level, flow into the back reef was again forced through the passes, leading to more nutrient availability and a spurt in the growth of more banks (**d**). Thus multigenerational growth relates to nutrient flux.

(*H. opuntia, v. hederacea*, and *H. copiosa* with subordinate amounts of *H. fragilis, H. discoidea*, and *H. gracilis*) together with large benthic foraminifera, mollusks, and bryozoans. The bioherms are bedded, sometimes transparent and often multigenerational, and sit astride the late Pleistocene transgressed surface. They have grown at the same time as the adjacent reef ecosystem and at rates almost equivalent to the reef systems. This suggests not only a critical relevance of calcareous algae as important additional CO_2 sinks but when estimated on a global basis it also doubles the contribution of shallow water sediments (in conjunction with reefs) as CO_2 reservoirs.

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Cross-references

Bioherms and Biostromes
Great Barrier Reef: Origin, Evolution, and Modern Development
Halimeda
Solution Unconformities

HAWAIIAN EMPEROR VOLCANIC CHAIN AND CORAL REEF HISTORY

Richard W. Grigg
University of Hawaii, Honolulu, HI, USA

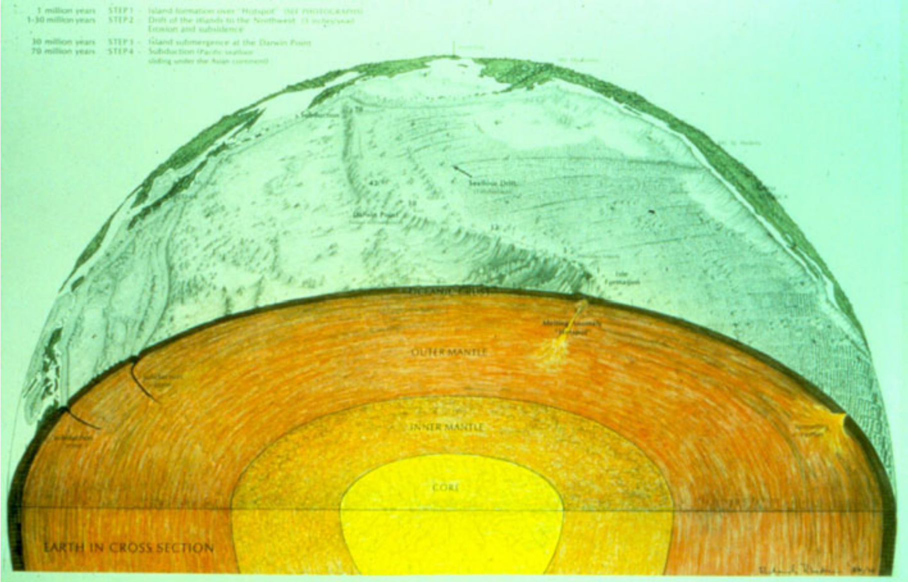
Definition

The palaeoceanography of the Hawaiian Emperor volcanic chain of islands and seamounts and the presence of coral reefs share an incomplete history. The first known Hawaiian Island to emerge from the Hawaiian hotspot was Meiji Guyot approximately 70+ Ma ago. Today, movement of the Pacific Plate has transported Meiji Guyot from its original location at approximately 19° north latitude and 157 west longitude almost 6,000 km to the northwest to about 54° north latitude, to a location near the edge of the juncture of the Kuril and Aleutian trenches, virtually on the edge of subduction below the Asian Plate (Figure 1). Unlike all of the islands in the Hawaiian Archipelago today, Meiji Guyot was never surrounded by a coral reef. Present theory, if correct, holds that the first half of the Hawaiian Emperor history was devoid of coral reefs (Grigg, 1988). Several explanations have been advanced to explain their apparent absence during this early period of Hawaiian history.

However, before discussing the palaeoceanographic evidence for the early absence of coral reefs in Hawaii, it is first important to reiterate the chronological, geographic, and geochemical evidence that shows that all of the Emperor Seamounts and Hawaiian Islands in the chain originated from the same hotspot in the North Pacific (Wilson, 1963; Morgan, 1972). Perhaps the best evidence for a common origin of the volcanoes over the Hawaiian hotspot is the continuous age progression (K-Ar radiometric dates) of the volcanic edifices with distance from Kilauea (location of the present hotspot) (Jackson et al., 1980, Figure 4). Relatively continuous motion of the Pacific Plate at about 8 cm/yr over the Hawaiian hotspot during the last 70+ Ma resulted in the formation of an almost linear geographic chain of volcanic islands. A bend in the chain at approximately 43–50 Ma is explained by a shift in the direction of plate propagation from north to northwest. The geo-chemical evidence for Hawaiian volcanoes and the Emperor Seamounts also supports the common origin hypothesis. All the lavas exhibit a similar sequence of eruption (tholeiitic followed by alkalic basalts) as well as similarities in chemical composition of all the basalts (Fletcher et al., 2008; Rooney et al., 2008).

The claim that coral reefs were absent in the Hawaiian chain during the first half of the Tertiary rests on the fossil record of shallow marine organisms in the Hawaiian Emperor (H-E) Chain today. The oldest reef corals that have been recovered from dredged limestones and deep-sea drilling cores in the Emperor Seamounts and guyots, range between 21 and 34 Ma. The oldest samples (33 and 34 Ma) are specimens of *Porites* and *Astreopora* from Kanmu and Yuryaku Seamounts (Grigg, 1988). The biostratigraphy based on cores from the older and more northern Emperor Seamounts (Ojin, Nintoku, Suiko, and Meiji) consists primarily of a tropical biofacies of shallow warm water coralline algae, bryozoa, benthic foraminifera, ostracods, spirorbids, echinoid spines, bivalves, and brachiopods, but no reef building corals (Jackson et al., 1980). Possible causal factors for their absence could be sampling error, a more northerly position of the palaeo-Hawaiian hotspot, cooler sea-surface temperatures in the Paleogene, rarity of corals worldwide in the early Tertiary, or insufficient transport of coral larvae from the Indo-West-Pacific (IWP). While a combination of these factors could also explain the early absence of coral reefs in the history of the H-E chain, the theory that is best supported by the palaeoceanographic history of the Pacific Ocean, is isolation of the Hawaiian Archipelago from the IWP (Grigg, 1988). All of the fossil corals and all of the reef corals that exist in the H-E chain today are IWP in origin, although some endemism (~25%) has evolved over time.

During the middle Tertiary, a series of gradual palaeoceanographic changes, including closure of the Tethys Sea, development of thermohaline circulation, isolation of Antarctica, and intensification of latitudinal temperature gradients are believed to have combined to intensify gyral circulation in the North Pacific Ocean (Kennett, 1982). As a result, the Kuroshio Current in the Western Pacific and the Subtropical Counter Current would have



Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 1 Cutaway of the earth showing the location of the Hawaiian hotspot and the Hawaiian-Emperor chain of islands and seamounts from Hawaii in the southeast to Meiji Guyot at the juncture of the Kuril and Kamchatka trench subduction zone.

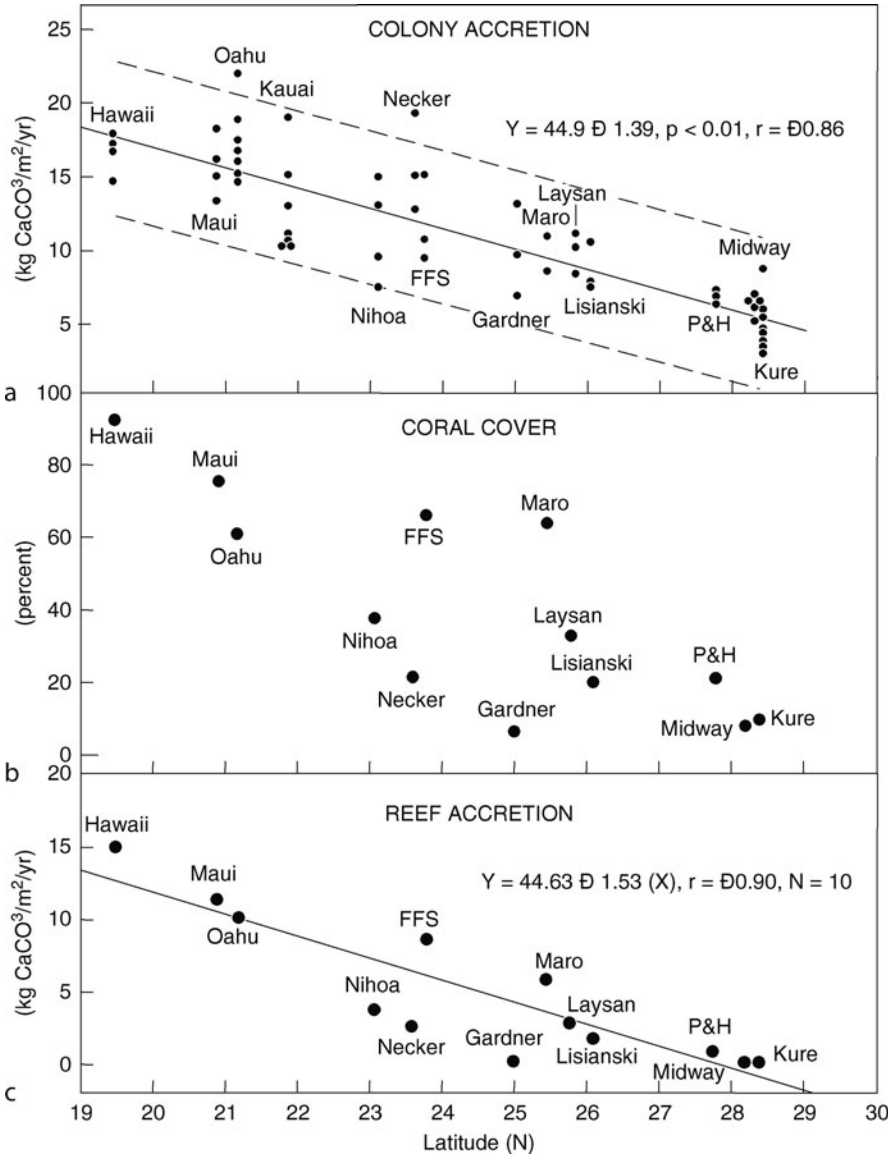
strengthened and both are sources of transport of IWP coral larvae into the northern Pacific Ocean. Hence, the sudden appearance of reef corals in the Hawaiian Archipelago and their continual presence throughout the Neogene to the present day might best be attributed to ocean circulation. Even today, the coral fauna of Hawaii is highly attenuated and consists of less than 10% of the coral species now present in the IWP.

Although the fossil record shows that reef corals have been in the Hawaiian Archipelago since Mid-Oligocene time, a moderate degree of taxonomic turnover has occurred. Extinction and re-colonization events are particularly evident in the Midway core from the present all the way back to early Miocene time (Wells, 1982). This is not surprising, nor unexpected, given the northerly position of the Hawaiian Islands near the latitudinal limits of reef building corals as well as their relative isolation from island stepping stones to the south and west.

Today, approximately 59 species of reef building corals have been recognized in the main Hawaiian Islands while 57 are reported in the Northwestern Hawaiian Islands (NWHI), (Maragos et al., 2004). These totals, while significant, are still relatively depauperate compared to the IWP where about 700 species are reported to exist (Veron, 2000). The low species diversity of modern Hawaiian reef building corals underlines the significance of the isolation of the Hawaiian Archipelago, as well as, its northerly latitude. The effect of latitude is particularly important when applied to the growth rate of individual corals.

Using *Porites lobata* as a proxy for all other common reef corals in the Hawaiian Archipelago, Grigg (1982, 1997, 2008) showed that growth rates at the southeastern end of the chain are typical of tropical coral growth rates in general, while moving northwest in the chain, they decline in a linear fashion almost as a direct function of latitude (Figures 2 and 3). At the very end of the Archipelago, at a latitude of ~29° north at Kure Atoll, the net growth rate was found to be virtually zero if losses due to bio-erosion, mechanical erosion, and the subsidence rate of the island were all taken into account. If this fact is considered over geological time in combination with the northwesterly movement of the Pacific Plate, then subsequent drift of the atoll to the northwest would cause it to gradually drown, setting the northern limit (threshold) of atoll formation (Grigg, 1982). In recognition of Darwin's original theory of atoll formation (Darwin, 1842), Grigg labeled this threshold "The Darwin Point".

Looking at coral reefs today in the Hawaiian Archipelago, they span about 10° of latitude stretching from optimal environments in the southeast to those in the northwest at the extreme limits of coral reef growth. Considering the natural constraints associated with this geography, most Hawaiian reefs today are exceptionally healthy. The most common natural disturbance events are large episodic waves that abrade and scour the reefs (Dollar, 1982). Within the major high Hawaiian Islands from Hawaii to Kauai, the most significant anthropogenic impacts include sedimentation events from land runoff,

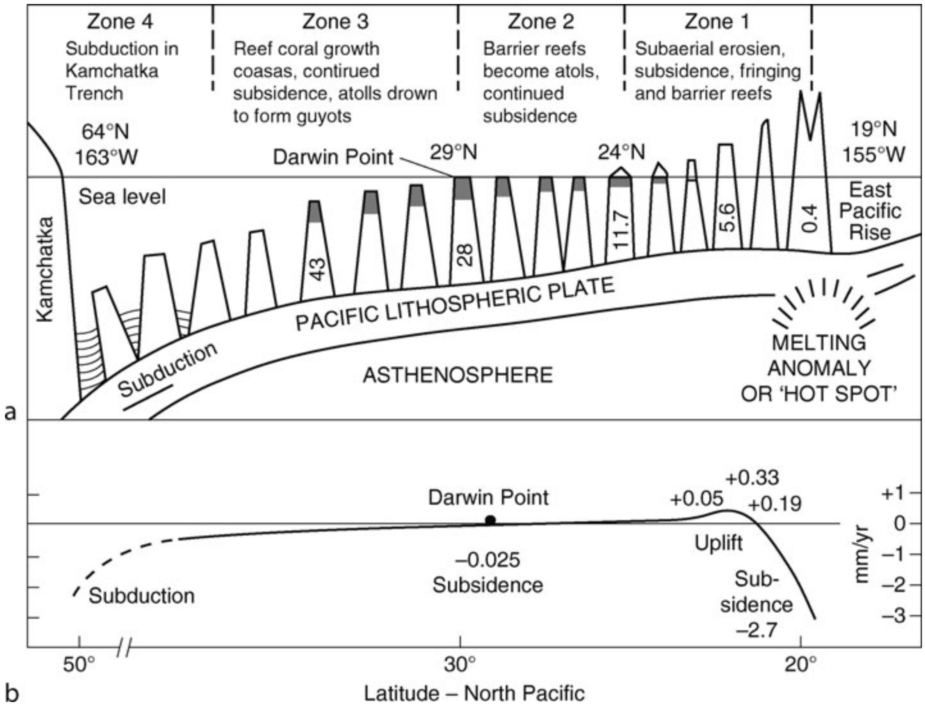


Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 2 Colony accretion of *Porites lobata*, coral cover, and reef accretion on seaward reefs off all major Hawaiian Islands. Note that coral reef accretion goes to zero near 29° north latitude.

eutrophication in areas of confined circulation, particularly in shallow water bays and on reef flats, and widespread over-fishing of reef fish on practically all offshore reefs. There is an urgent need to strengthen the enforcement of fish and game regulations by the State of Hawaii. The State should also actively increase the number of Marine Protected Areas (MPA's) in the main islands where today only about 1% of the coastline is protected. In contrast, the NWHI have been almost completely protected under a recent (2006) Executive Order that reclassified the entire area (except Midway Island) as a Marine Monument.

Outlook

Looking ahead toward the present century, particularly with regard to global climate change (GCC), coral reefs in the Hawaiian Archipelago may be relatively well situated. The four most important factors associated with GCC that may affect coral reefs are sea-level rise, increases in sea surface temperature, increases in ocean acidification, and increased storminess. Rising sea level may pose a flooding problem for the lowest isles in the northwest but it will also raise the "lid" providing more accommodation space for coral reef growth to take place on most island shelves throughout the chain. Given the northern latitude of



Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 3 Schematic figure of the Hawaiian-Emperor chain showing Zones 1–4 tracing the evolution, subsidence, drowning, and subduction of volcanic edifices and the location of the Darwin Point and northern limit of drowned guyots (From Scott and Rotondo, 1983).

the Archipelago, rising sea surface temperature may not be as great a problem as it could be for more tropical reefs. Although effects due to increasing ocean acidification are not well understood, large carbonate deposits that exist throughout the Archipelago may buffer the potential impacts of slightly lower pH. Increased storminess is also hard to predict depending on frequency, magnitude, and location, but if larger wave events are produced, then intermediate disturbance may become more limiting to coral development and abundance. Overall, while it may be premature to predict dire consequences for the health of coral reefs globally, the coming century clearly contains as many challenges as it does uncertainties.

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Cross-references

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Climate Change: Increasing Storm Activity
Darwin Point
Density and Porosity: Influence on Reef Accretion Rates
Midway Atoll (Hawaiian Archipelago)
Ocean Acidification, Effects on Calcification
Oceanic Hotspots
Pacific Coral Reefs: An Introduction
Submerged Reefs

HEAVY METAL ACCUMULATION IN SCLERACTINIAN CORALS

Sofia Shah, Edward Lovell
University of South Pacific, Suva, Fiji

Synonyms

Heavy metals are also referred to as trace metals or trace elements

Definition

Heavy metals are metals and metalloids, which have atomic weights between 63.5 and 200.6 g/mol and density > 4.5 g/cm^3 (Shah, 2008). Heavy metals are conservative in nature as they persist in the environment for longer periods. Heavy metals are both naturally occurring and anthropogenically introduced in the marine environment and are toxic to both aquatic biota and humans at low concentrations.

Heavy metals in the marine environment

Elevated concentrations of the heavy metals are the consequence of effluent discharge, urban stormwater, sewage pollution, harbor dredging, sedimentation, and agricultural and industrial runoff. According to Al-Rousan et al. (2007), these heavy metals occur in the coral skeletons as a result of structural incorporation of metals into the aragonite (Goreau, 1977), inclusion of particulate materials in skeletal cavities (reviewed by Howard and Brown, 1984), surface adsorption onto exposed skeleton (St. John, 1974; Brown et al., 1991), and chelation with the organic matrix of the skeleton (Mitterer, 1978). Once incorporated into the coral skeleton, the metals will remain embedded forever since the new growth covers the old carbonate surface (St. John, 1974).

This study

The metals of interest in this study were copper (Cu), zinc (Zn), lead (Pb), cadmium (Cd), and iron (Fe). Cu, Zn, and Fe were of particular interest as they are the essential elements required for growth of organisms as well as humans. On the other hand, Cd and Pb, being the nonessential elements, are harmful to the marine organisms due to their polluting effects and toxicity. The concentrations of these metals together with the partitioning of these metals in the skeleton, tissue, and zooxanthellae of three different coral families were looked into. Heavy metal accumulation rates were also studied in the three different families for a 5-day period. Coral samples were taken from three different sites, namely reefs encountering significant terrigenous inputs from rivers, fringing reefs (with a chain of hotels), and a pristine reef.

Scleractinian corals

Scleractinian corals are the architects of coral reefs and hence good indicators of environmental changes due to the fact that their skeletons assimilate records of the presence and concentrations of certain metals over centuries (Esslemont, 1999). Scleractinian corals incorporate the trace elements (or heavy metals) in their living parts and skeletons. *Acropora formosa*, *Pocillopora damicornis*, and *Porites spp*. were studied for heavy metal concentrations.

Outcomes

High metal concentrations were determined for the zooxanthellae, than the tissue and the skeleton, suggesting that the zooxanthellae are responsible for the metal uptake in corals. Reichelt-Brushett and McOrist (2003) suggest that symbiotic zooxanthellae play an important role in the accumulation and regulation of trace metals. The variation among the three different families of corals suggests that *Porites spp*. tend to accumulate lower concentrations of heavy metals than the other two species studied. Scleractinian corals in pristine environments recorded a lower metal concentration than those obtained from fringing reefs and reefs closer to significant terrigenous inputs.

Fe and Pd were found to be in higher concentrations than Cu, Zn, and Cd at all the study sites. The most probable reason that Fe reaches the marine environment is through suspended sediments and aeolian dust. Fringing reefs and reefs near terrigenous inputs have constant influences of suspended sediments and hence it is most likely that Fe enters the marine environment through this means. High concentrations of lead in the samples were mostly from sewer outfall, industrial discharge, and agricultural/storm water runoff and wastes discharged from hotels and piggery farms.

Dose-response curves from the bioassays showed that as the nominal concentrations increase, the heavy metal uptake in corals also increases. Zooxanthellae were lost to the aquaria water as a result of stress on the corals. High concentrations of Pb and Fe were accumulated in the corals for each dosage period.

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HISTORICAL ECOLOGY OF CORAL REEFS

John M. Pandolfi
The University of Queensland, Brisbane, QLD, Australia

Definition

Historical ecology: Using time-series data collected over single or multiple temporal scales to lend insight into the history of modern communities and ecosystems.

Introduction

The diversity, frequency, and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened globally (Wilkinson, 2008). The direct and indirect effects of overfishing and pollution from agriculture and land development have been the major drivers of massive and accelerating decreases in abundance of coral reef species (Moberg and Folke, 1999; Abram et al., 2001; Jackson et al., 2001; Gardner et al., 2003; Hughes et al., 2003; Pandolfi et al., 2003). These human impacts and the increased fragmentation of coral reef habitat are unprecedented and have the possibility to undermine reef resilience (Bellwood et al., 2004), raising the likelihood that modern coral reefs might be much more susceptible to current and future climate-change than is suggested by their geologic history (Hughes et al., 2003; Bellwood et al., 2004).

One of the most urgent questions in conservation science is: What was natural in the world before humans impacted it? Study of past ecosystem condition and the relationship between ecosystem health and human–ecological interactions provides a way to gain insight into what was natural in the sea. Historical ecology is the name generally given over to such study. It provides a basis for avoiding the "shifting baseline syndrome" (Pauly, 1995) which undermines current perspectives on what constitutes a pristine ecosystem.

The conceptual framework surrounding historical ecology finds its roots in Aldo Leopold who in 1941 called for study of wilderness areas, for "…a science of land health needs, first of all, a base-datum of normality, a picture of how healthy land maintains itself…" (p. 3). Several papers on terrestrial ecosystems in the early 1990s have set the tone of historical ecology (Morgan et al., 1994; Swetnam et al., 1999). In general, historical ecology links past ecosystem condition with the present state using time series data over a number of temporal scales, from decades to millennia, though shorter term studies conducted over discrete time intervals can also be used. Insights generally sought over the long temporal frames of historical ecology include changes in states of populations, species, and ecosystems (e.g., abundance, biomass, geographic ranges), changes in environmental parameters (e.g., sea surface temperature fluctuations), and changes in magnitudes and rates of both biological (e.g., mortality rates, trophic flows, disturbance regimes) and physical (e.g., El Nino-Southern Oscillation, climate change) processes.

The tools of marine historical ecology

Practitioners of marine historical ecology on coral reefs use a number of different kinds of data from multiple time periods to examine the recent past history and present condition of reef ecosystems to provide a natural baseline for community ecology and coral growth rates. Archaeological sites provide insight into the relationship between the development of civilization and its evolving impact on coastal marine resources. Historical records such as those found in ships logs, and publications of early naturalists and European colonialists provide a moving window of the natural history and inferred ecology of many coral reef inhabitants. Fisheries records and modern ecological surveys can be used in association with remote sensing data (going back the last 20 or 30 years) to provide a detailed picture of changing environments and biodiversity as human population and consumption, as well as economic globalization, have accelerated during the past several decades. Taken together, these databases provide a holistic view of changing environments and ecology on coral reefs that includes the onset of human disturbances and against which the acquisition of present day data can be evaluated.

Paleontological (Aronson and Precht, 1997; Wapnick et al., 2004; Pandolfi and Jackson, 2006), archaeological (Erlandson and Rick, 2008), historical (Starkey et al., 2000; Bolster, 2006; Lajus, 2008), ecological (Greenstein et al., 1998; McClenachan et al., 2006), genetic (Roman and Palumbi, 2003; Alter et al., 2007), and modeling studies are all contributing to a new awareness of the past bounty and diversity in the sea (Jackson, 2008; Pinnegar and Engelhard, 2008). Historical data sources include oral histories (Dulvy and Polunin, 2004), photographs (McClenachan, 2009), museum records (Robinson and Frid, 2008), early scientific studies (Lajus et al., 2007), fisheries information including logbook data (Klaer and Polacheck, 1997), landings, effort, and gear (Bager et al., 2007; Lotze, 2007; MacKenzie et al., 2007), and fishing charts (Claesson, 2008). Historical studies are limited to the periods of time and geographic areas for which data are available (MacKenzie et al., 2007). Some studies are limited to more recent history (McClenachan, 2009), while others date back to the sixteenth century (MacKenzie et al., 2007). Many fisheries records are only available for disjointed time periods (Gaumiga et al., 2007; MacKenzie et al., 2007), while others provide continuous time series lasting over a hundred years (Holm and Bager, 2001; Lajus et al., 2007). Some data sources provide only a snapshot of past conditions such as journal entries and photographs; however, when viewed together over a period of time such information can reveal substantial changes in marine environments (Jackson, 1997).

Historical ecology of coastal ecosystems

Recent papers on the historical ecology of coastal ecosystems have demonstrated the importance of time-series data to understanding the ecology and degradation over long temporal scales. For example, by employing a multidisciplinary approach involving ecologists, oceanographers, archaeologists, and social scientists, Jeremy Jackson and his colleagues (Jackson et al., 2001) investigated the ecological history of coastal ecosystems worldwide. The work documents in broad terms the history of human alterations in the sea, identifying overfishing as the first and farthest reaching cause of decline in coastal marine ecosystems. Historical marine ecology has since investigated a broad range of ecosystems and problems in the sea (for recent review see Lotze and Worm, 2009).

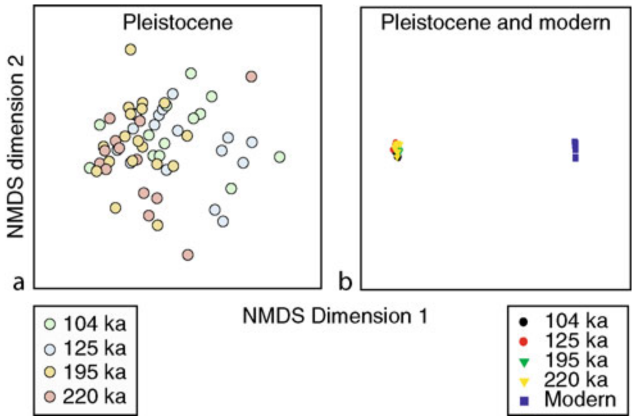
Key findings on coral reefs

Study of coral reef ecosystems has also been subject to the "shifting baseline syndrome" – coral reef systems have undergone systematic degradation prior to recent ecological studies in the last three or four decades. This strongly implies that no reef can be considered "pristine", and that no standard exists by which to compare the magnitude of these changes (Jackson et al., 2001). Through paleoecological reconstruction of coral reefs from the Caribbean region, recent studies have highlighted the collapse of coral communities at a regional level, which is unprecedented within the Holocene (12,000 years ago – present), (Greenstein et al., 1998; Aronson et al., 2002) and Pleistocene (1.8 million – 12,000 years ago), (Jackson, 1992; Greenstein et al., 1998; Pandolfi, 2001; Pandolfi and Jackson, 2006).

Very recent work has sought to understand human impacts by developing time-series data archives that can be used to evaluate trends in the global decline of coral reefs since the arrival of humans (Pandolfi et al., 2003; Daley et al., 2008). Study of the historical ecology of coral reefs, relying on the past history of corals and other components of the reef ecosystem showed that the history of ecosystem changes among 14 different tropical reef sites worldwide, with early and effective overfishing as the major culprit in reef decline (Pandolfi et al., 2003; Pandolfi et al., 2005). These findings point to the immense importance of understanding historical events when attempting to tease out factors that have influenced or may influence present coral reef biodiversity (Pandolfi et al., 2003). By considering these global "ecological trajectories" in the light of potential responses to projected global climate change, the history of human exploitation can be linked with global environmental parameters (Hughes et al., 2003). Knowledge of past ecosystem states provides at the minimum, an understanding of what was natural and may even aid in assessing the success of management toward particular conservation goals.

Numerous other smaller scale studies have been undertaken on individual reefs and reef areas around the world, including Hawaii (Herman, 1979), the Great Barrier Reef, (Daley et al., 2008), Florida (McClenachan, 2009), Bahamas (Blick, 2007), Solomon Islands (Aswani and Hamilton, 2004), Indonesia (Palomares et al., 2007) and the Caribbean (Jackson, 1997; McClenachan et al., 2006). The demise of many coral reef fisheries has been traced to their historical beginnings including Florida sponges (McClenachan, 2008), Caribbean turtles (McClenachan et al., 2006) and monk seals (McClenachan and Cooper, 2008), sea turtles in Oceania (Allen, 2007), and Hong Kong fisheries (Cheung and Sadovy, 2004). Through these studies, there is now general recognition throughout the coral reef scientific and management communities of the importance of considering changes in ecosystem state over appropriate time scales (Dulvy and Polunin, 2004; Knowlton and Jackson, 2008; Pinnegar and Engelhard, 2008). Importantly, there is far greater appreciation of the historical development, timing, and ecosystem responses to the ultimate drivers of coral reef ecosystem decline, namely overfishing (Roberts, 2007), climate change (Hughes et al., 2003), and coastal development and pollution (Ramade and Roche, 2006).

An understanding of the history of reef coral communities can aid conservation initiatives by supplying information on natural baselines in the sea that are immune to the "shifting baseline syndrome". For example, in Barbados coral community composition was very similar during four separate reef-building episodes between 220 ka and



Historical Ecology of Coral Reefs, Figure 1 Non-metric multi-dimensional scaling (NMDS) ordination of the relative abundance of the common coral taxa in Pleistocene and modern assemblages from Barbados, West Indies. (**a**) Coral assemblages aged 104, 125, 195, and 220 ka from the Pleistocene leeward reef crest of Barbados. (**b**) Combined analysis of Pleistocene and modern coral assemblages surveyed in the 1980s by Tomascik and Sander (1987) (from Pandolfi and Jackson, 2006).

104 ka (thousand years ago) (Pandolfi and Jackson, 2006), and community structure is now very different in modern degraded habitats (Lewis, 1960, 1984; Tomascik and Sander, 1987) (Figure 1). The same six most common coral species comprise >97% of the total coral density in the fossil assemblages: *Acropora palmata*, *A. cervicornis*, organ-pipe *Montastraea*, *M. annularis* s.s., *Diploria strigosa*, and *M. faveolata*. *Acropora palmata* was overwhelmingly the most abundant species at all four time periods. In marked contrast to the Pleistocene coral assemblages, those from the living reef on Barbados are dominated by species that were rare in the Pleistocene communities. The most abundant coral is *Porites astreoides*, followed by *P. porites*, *Siderastrea radians*, and *Agaricia agaricites*. Living communities contained very little *A. palmata* and no *A. cervicornis*. Similar contrasts between ancient and modern assemblages have also been derived from reef framework cores taken from the nearshore Great Barrier Reef (Perry et al., 2008; Pandolfi et al., 2009).

Management implications

The descriptive side of marine historical ecology has been vigorously pursued, especially after the publication of Jackson et al. (2001). This has been confined mainly to admonitions about how resources "then" were unimaginably greater than they are "now" (summarized in Lotze and Worm, 2009). But marine historical ecology has lagged behind its terrestrial counterpart (Swetnam et al., 1999; Froyd and Willis, 2008) in harnessing the enormous scope and information potential of direct import to the understanding and management of marine environments. This has resulted in several disadvantages to coral reefs and our understanding of them: (1) management without a temporal context; (2) a diminished ability to differentiate between chronic and cumulative impacts; (3) uncertainty in attributing ecological changes to human or natural agency; (4) encouraged equilibrium views of ecosystem dynamics; and (5) difficulty in setting management goals and assessing the effectiveness of management actions.

The challenge for natural resource managers is in understanding where the ecosystem they are managing stands in relation to its natural state. Historical knowledge of ecosystems is critical for understanding natural variability and temporal dynamics and provides an essential bridge between science and management goals and outcomes. More positive outcomes are possible when managers possess clear goals for ecosystem restoration derived from knowing how different today's oceans are from their pristine condition.

Summary

Seascapes, nearly anywhere you care to investigate, have undergone undeniable transitions from "nature-dominated" to "human-dominated" regimes (Figure 1). Knowing the nature and timing of these transitions cannot be attempted outside of a historical context. How do humans interact with seascapes? How long ago was this interaction first detectable? Lengthening the temporal scale of ecological studies affords the opportunity to debate the characteristics of the transition from nature to human-dominated seascapes along slowly changing gradients. It is also of critical importance to reef management for (1) identifying drivers of ecosystem change, (2) providing meaningful goals for successful management and a means for measuring success of management actions, and (3) adopting a dynamic view of ecosystems.

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Cross-references

Conservation and Marine Protection Areas
Heavy Metal Accumulation in Scleractinian Corals
Paleoclimate from Corals
Reef Restoration
Sediment Durability

HOLOCENE HIGH ENERGY WINDOW

Chris Perry
Manchester Metropolitan University, Manchester, UK

Definition

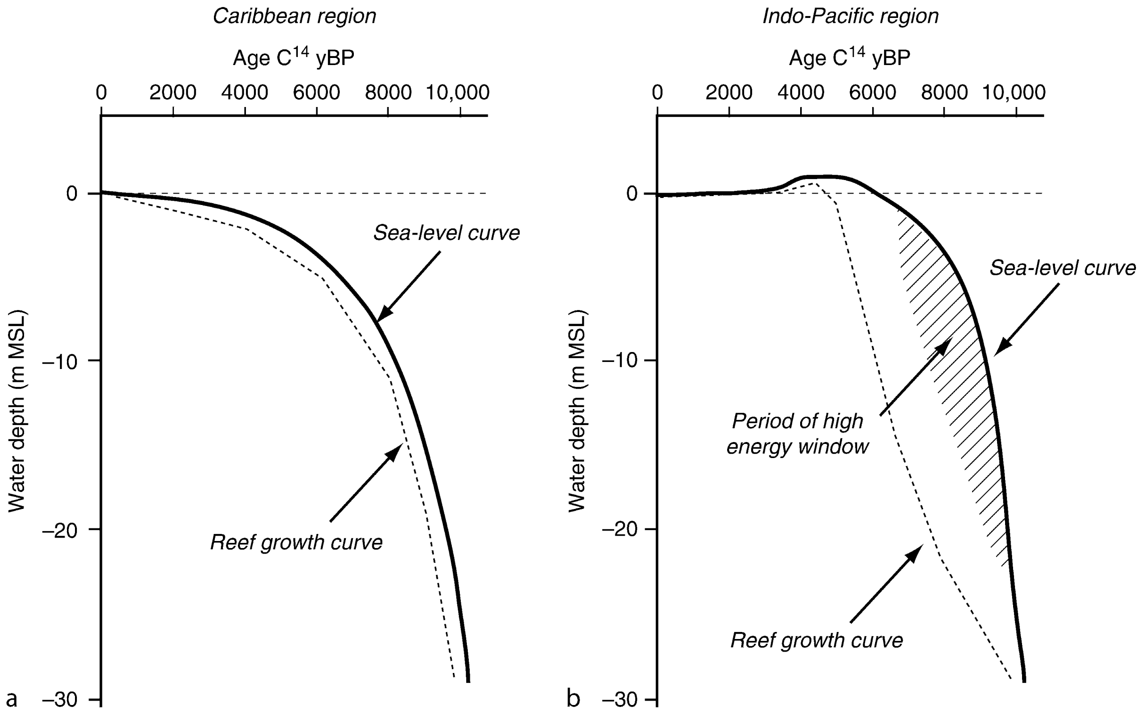
Holocene high energy window: A period of higher wave energy conditions across submerged reef or continental shelf environments that was caused by reef growth lagging behind rising sea levels during the Holocene transgression.

Introduction

The concept of a Holocene "high energy interval" or "window" was first introduced by Neumann (1972) as a mechanism to explain the emplacement of relict sedimentary deposits that appeared to have formed under higher energy conditions than those prevalent in the present. Specifically, it was suggested that these deposits might have formed during periods when coastlines were less protected than at present. This concept was subsequently developed by Hopley (1984) as a potential control on the nature and character of shelf sedimentary environments, using Australia's Great Barrier Reef (GBR) shelf as an example. Such temporal changes in energy conditions are believed to have occurred in settings where the outer shelf or barrier reefs failed to keep pace with rising sea levels during the Holocene transgression. Rather they adopted "catch-up" (*sensu* Neumann and Macintyre, 1985) growth trajectories, with the lag interval providing a depth window through which waves could propagate across both developing reef surfaces and wider shelf sedimentary systems. The legacy of this is seen today as the occurrence of high energy sedimentary deposits that could not have formed under present energy regimes. As reef growth reached present sea-levels the "window" was progressively shut resulting in reduced wave energy conditions to leeward of reef crests or across open shelf environments and a consequent transition in styles of reef growth and sediment accumulation.

Global and regional scale perspectives

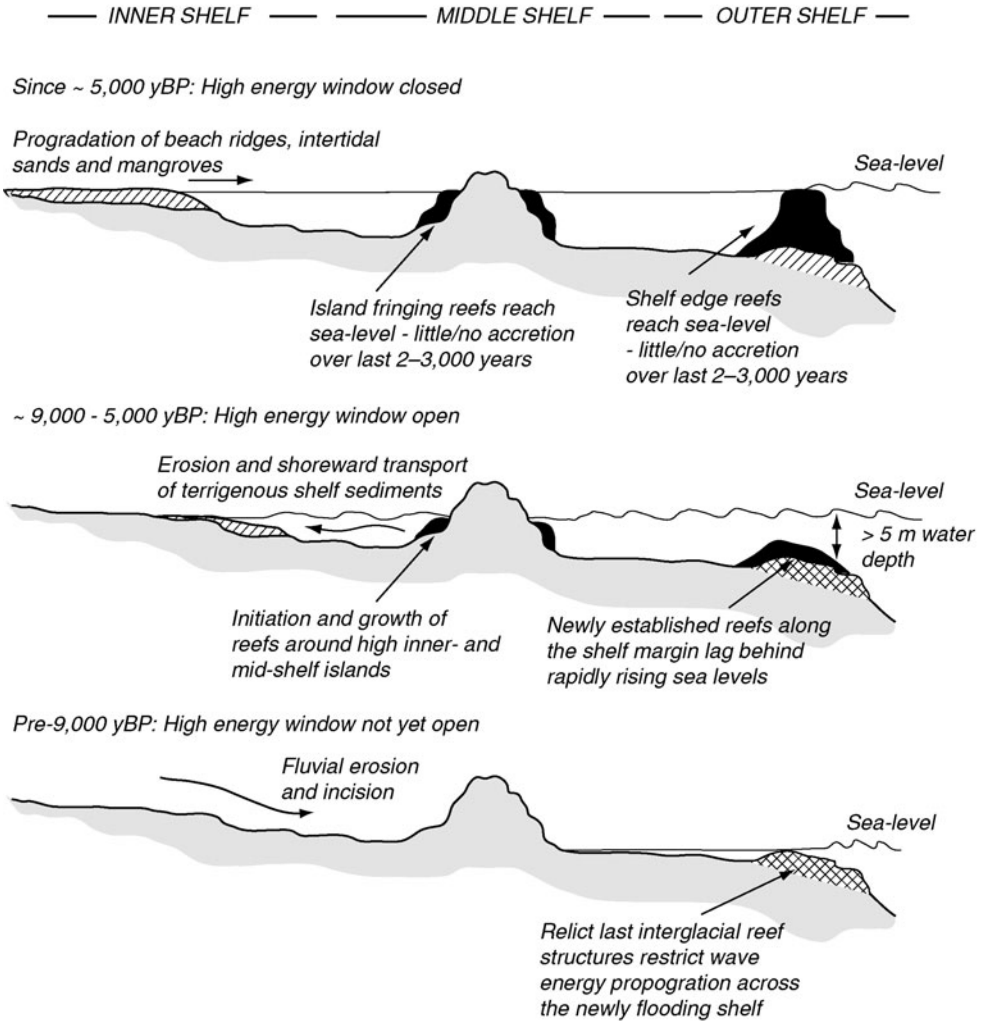
The potential for the occurrence of a high energy window during the Holocene transgression was entirely controlled by the interactions that occurred between the rate of coral reef growth and the rate of sea-level rise. These interactions must, inevitably, have differed between reef sites and on a regional basis, and thus the potential for the occurrence, and longevity of any higher energy periods must have been spatially very variable. For example, in the Caribbean region, reconstructed Holocene sea-level curves show that rates of sea-level rise have steadily fallen since ~10,000 years BP (when sea level was at ~–24 m below present) through to the present day. Rates of rise averaged ~5.2 mm year^{-1} up until ~8,000 years BP, ~1.5 mm year^{-1} from about 8,000 to 4,000 years BP, and 0.93 mm year^{-1} from 4,000 years BP to present (Toscano and Macintyre, 2003). Taking a modal long-term rate of reef accretion of ~6–7 mm year^{-1} (e.g., Montaggioni, 2005) most reefs would have had the potential to track rising sea-levels ("keep-up" growth mode: *sensu* Neumann and Macintyre, 1985), thus minimizing the potential for the development of a high energy window (Figure 1a). In contrast, rates of sea-level rise during the early phases of the Holocene transgression were much faster in much of the Indo-Pacific basin (Camoin et al., 2004).



Holocene High Energy Window, Figure 1 Regional variations in the potential for the existence of a Holocene high energy window for (**a**) the Caribbean, and (**b**) the Indo-Pacific regions (based on sea-level curves from the central Great Barrier Reef Shelf, Australia). Note that under scenario (**b**) reef growth lags a rapidly rising sea level, providing a window for high wave energy propogation across the shelf.

In eastern Australia, for example, where Hopley (1984) discussed the potential for the development of periods of high energy conditions during shelf flooding, sea-levels during the early-mid Holocene are estimated to have been rising at ~10 mm year^{-1} from about 9,000 to 7,500 years BP, and then at ~2–2.5 mm year^{-1} through to ~6,000 years BP when sea levels slightly exceeded their present day position. Since this, highstand sea-level has fallen to its present level. This faster rate of sea-level rise during the early-mid-Holocene period is believed to have resulted in reef growth lagging behind sea-level, thus temporarily allowing higher wave energy regimes to propagate across reefs and the inundating shelf environments (Figure 1b). However, as plots of sea-level position against reconstructed reef growth trajectory plots demonstrate, the potential for the development of a high energy window appears very variable even at an intra-regional scale (Camoin et al., 2004).

The existence of such a high energy window has been most widely discussed in relation to the GBR shelf of Australia (Hopley, 1984; Hopley et al., 2007), although the timing and existence of such a window probably varied at different points along the shelf. This has been viewed, in large part, as a function of variations in the depth from which Holocene reef growth was re-establishing - those areas with deeper Pleistocene foundations having greater potential to adopt catch-up growth modes as they lagged behind sea-level (Hopley et al., 2007). For example, along the northern and southern sections of the GBR reef establishment occurred above foundations at depths of ~15–20 m and the high energy window is inferred to have been open only for a relatively short period of time between ~8.0 and 6.0 ka. In contrast, the greater depth (~20–25 m) of the Pleistocene foundations in central areas of the GBR means that the window may have been open for longer. In this area of the shelf, the occurrence of relict Pleistocene reefal substrates along the shelf margins is believed to have protected the newly submerging shelf from high wave energy conditions prior to ~9,000 years BP (Figure 2). However, from about 8,500 years BP these relict reef structures were progressively over-topped as newly established outer-shelf reef growth lagged behind rapidly rising sea levels. The result was a marked increase in energy levels across the newly submerged shelf, with important impacts on mainland coast and shelf sediment dynamics. Significant onshore transport of coarser-grained sediments is believed to have occurred during this period, and has been citied as a causal factor in the deposition of high energy features such as boulder beaches and spits around some of the inner-shelf high islands (illustrated in Hopley et al., 2007, fig 7.4). Also during this time significant onshore migration of reworked terrigenous shelf sediments is believed to have occurred, producing the presently well-defined inshore terrigenous sediment prism (Larcombe and Woolfe,



Holocene High Energy Window, Figure 2 Schematic diagram showing the influence of a Holocene high energy window on the development of shelf environments based on the central Great Barrier Reef region of Australia (stage concepts developed from Hopley, 1984; Hopley et al., 2007).

1999). During the final stages of the transgression, when present sea-levels were reached (or exceeded), reefs along the outer-shelf margin caught up with sea-level, leading to closure of the high energy window. Numerous headlands were incorporated into the coast during the final stage of the transgression resulting in the development of a much more indented coastline. This facilitated the trapping of longshore-driven sediments and the development and progradation of extensive coastal beach ridge sequences.

Impacts of a high energy "window" at the reef and reef island scale

Whilst the concept of a Holocene high energy window is perhaps best known from discussions regarding its influence on the GBR shelf, the concept has also been considered in relation to different phases of reef and reef island development. This is evident, for example, along reef-fronted coastlines and narrow shelves where reef growth appears to have lagged behind sea-level. Subsequent accumulation of barrier-type reefs up to sea-level resulted in a closure of these more localized high energy windows, leading to a transition in the nature and character of reef-building to leeward of the main reef structures. Examples include those reefs described from the Ryukyu Islands (Kan et al., 1997), Palau (Kayanne et al., 2002), and Madagascar (Camoin et al., 2004). The concept of high energy phases has also been discussed as an important potential control on reef island building. Kench et al. (2005), for example, have invoked periods of higher wave energy and associated sediment transport to nodal sites of accumulation, as an important control on the development of reef islands in the Maldives. Similar views have also been discussed in relation to a range of reef islands in the Pacific (Nunn, 1997) and on the GBR (Hopley, 1984).

Summary

The concept of a Holocene high energy window has been evoked to explain the presence of sedimentary deposits that appear to have formed under higher wave energy conditions to those operating in the present. Such periods of higher energy can occur where vertically accreting reefs lag behind rapidly rising sea levels – thus opening up the potential for wave energy to propagate across both reef structures and adjacent shelf environments. Such periods of higher wave energy have been invoked in a number of areas where rapid rates of sea-level rise occurred in the early-mid Holocene, and discussed in relation both to large shelf systems, and the development of reefs and reef islands. However, spatial variations in the rate and timing of the post-glacial marine transgression, and variations in the depth of the substrates over which flooding occurred, means that the extent and longevity of any such window was probably highly variable between regions. Of interest in the context of near-future environmental change is the idea that such high energy windows may once again open up across reefs where the combined effects of environmental and anthropogenic disturbance interact to suppress reef growth potential (or even to drive reef erosion). Under such scenarios reefs may not be able to respond to even modest rises in sea level, thus allowing greater wave energy transfer across reef flats (see Sheppard et al., 2005). Where this occurs there will be obvious implications for lagoon and island sediment dynamics and shoreline stability.

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Cross-references

Accommodation Space
Antecedent Platforms
Boulder Beaches
Boulder Zone/Ramparts
Climate Change: Increasing Storm Activity
Postglacial Trangression
Sea Level Change and Its Effect on Reef Growth

HOLOCENE REEFS: THICKNESS AND CHARACTERISTICS

Eberhard Gischler
Institut fuer Geowissenschaften, Frankfurt am Main, Germany

Continuous coral reef growth since the last glacial lowstand of sea level some 18 kyrs BP has been documented by drilling around the islands of Barbados (Fairbanks, 1989) and Tahiti (Bard et al., 1990). In the majority of cases investigated though, shelf reefs started to accrete not earlier than the Holocene (< 10 kyrs BP). Holocene reef thickness and accretion-rates exhibit large variation and can be as high as > 40 m and > 20 m/kyr, respectively (Dullo, 2005; Montaggioni, 2005). Scoffin (1992) has summarized how the synchronously operating processes of framework growth, bioerosion and breakage (reef destruction), encrustation, loose sediment accumulation, and cementation have resulted in late Quaternary reef accretion. A number of external factors such as antecedent topography, water temperature, nutrient concentrations, and exposure to waves and currents influence Holocene reef growth; however, sea level appears to exert major control. Neumann and Macintyre (1985) have elegantly categorized reef response to postglacial sea-level rise into keep-up, catch-up, and give-up reef anatomies. The keep-up type is characterized by branched acroporids and the catch-up type by branched and/or massive corals and shallowing upward facies. The give-up type shows a deepening upward facies and the reef top is located in deeper water, in contrast to the keep-up and catch-up types where the reef top is more or less at sea level. Recently, Gischler (2008) and Hubbard (2009) have shown for the western Atlantic that Holocene reefs dominated by acroporids do not accrete faster as compared to massive coral reefs, even though acroporid corals exhibit growth-rates one magnitude higher as compared to massive corals. Also, reef accretion-rates did not correlate negatively with increase in paleo-water depth over an investigated range of 25 m. An explanation for these unexpected results might be that the effects of destructive processes in reefs decrease with depth. First, massive corals are more resistant and accrete with little disturbance in deeper water whereas shallow water acroporids are repeatedly leveled by cyclones. Second, current knowledge indicates that rates of bioerosion apparently decrease with increasing water depths. These findings also contribute to the question as to how much of a reef is represented by *in situ* framework and what percentage comprises transported detritus, a question that has been discussed for over a century by reef workers (e.g., Hubbard, 2009). It seems that in Holocene reefs – and possibly the same holds true for their fossil counterparts – detritus clearly exceeds autochthonous framework, and destructive processes are an integral component of reef accretion.

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Cross-references

Barbados
Bioerosion
Eastern Caribbean Coral Reefs; Eastern Tropical Pacific Coral Reefs
Indian Ocean Reefs
Pacific Coral Reefs: An Introduction
Reef Structure
Sea Level Change and Its Effect on Reef Growth
Sediments, Properties
Submarine Lithification
Tahiti/Society Islands
Taphonomy
Western Atlantic/Caribbean, Coral Reefs; Eastern Caribbean Coral Reefs

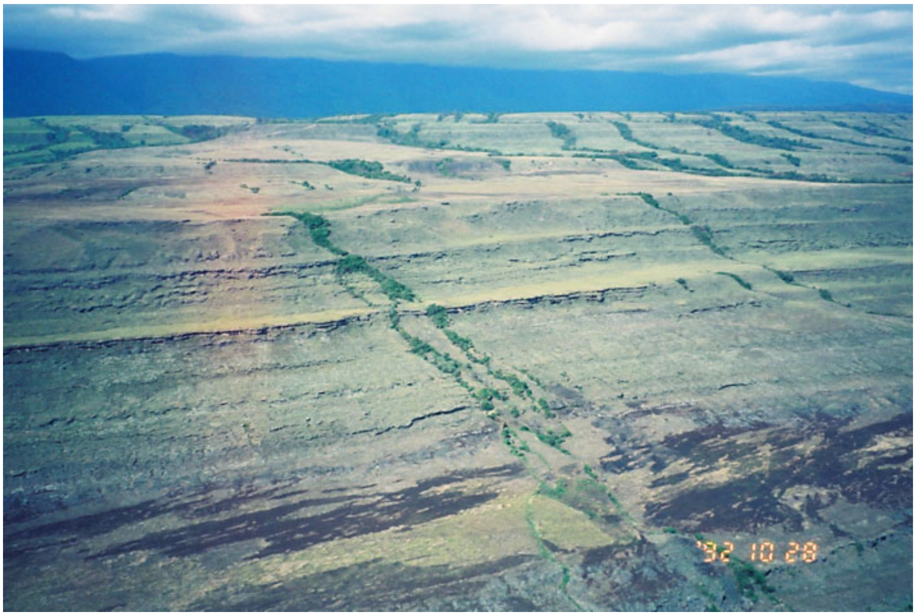
HUON PENINSULA, P.N.G.

Yoko Ota
Yokohama National University (Professor Emeritus),
Otaku, Tokyo, Japan

Huon Peninsula on the northeastern coast of Papua New Guinea is located at the overriding South Bismarck plate on the Australian plate and at 6°S. This tectonic and latitudinal setting allows the formation of spectacular uplifted coral terraces, which are regarded as one of the standards for eustatic sea level changes superposed on tectonic uplift (Chappell, 1974; Chappell and Shackleton, 1986). Terraced area ranges from ca. 2 to 15 km in width, separated by NW–SE trending Kalasa Fault from the Cromwell Range. However, Kalasa Fault partly truncates older terrace (Terrace XIV or XV), and branches into two on the southeastern end, cutting younger terraces.

The major coral terraces, I–XV in ascending order, record the high sea level of interglacial period and are constructional terraces underlain by coral limestone with transgressive facies, correlated with MIS 1 to 14 (Figure 1). Correlation of each transgressive terrace with MIS is supported by many U-series dates for Terrace VII and younger terraces (Chappell et al., 1996; Yokoyama et al., 2001; Cutler et al., 2003); however, older terraces are not well dated. Terrace VII (MIS 5e, ca. 124 ka) is especially continuous, and its height shows northwestward down tilting from ca. 400 to 50 m over ca. 70 km long coastline with the maximum uplift rate of 3.3 m/1,000 years. Preservation of original terrace surfaces is closely related to the amount of uplift and age of terraces. Holocene terrace of MIS 1, dated by radiocarbon method at many sites, also tilts from 25 to 5 m. Maximum height of preserved terrace XV is ca. 1,500 m. Formation of multiple terraces, including those for the relatively low sea level (MIS 5c, 5a, and 3), is resulted from such a high uplift, which has continued throughout the middle Quaternary.

The rapid uplift of the peninsula is associated with the repeated coseismic uplift, which is expressed by a series of small terraces cutting into the major terraces (Ota et al., 1993). Coseismic uplift has an order of 2–5 m in magnitude and ka order of repeat time, judging from the terrace height and ages. Coseismic uplift is recorded not only in the Holocene terrace but also in late Quaternary terraces (Ota and Chappell, 1996). This is very unique phenomenon caused by the good preservation of coral limestone resistant to physical weathering.



Huon Peninsula, P.N.G., Figure 1 View of coral terraces at the Huon Peninsula. (Photo by Ota.)

Morphology of major terraces is characterized by the prominent barrier, lagoon, and barrier following streams. Presence of dense short gullies also characterizes the morphology of terrace risers. Doline is often seen on very extensive Terrace X and XI. Landslides and related debris flows, destructing or overlying the coral terraces, also provide characteristics features, many of which can be regarded by paleoearthquake (Ota et al., 1997).

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Cross-references

Emerged Reefs
Pacific Coral Reefs: An Introduction
Uranium Series Dating

HYDRODYNAMICS OF CORAL REEF SYSTEMS

Clifford J. Hearn
Working Science Consultancies, St Petersburg, FL, USA

Synonyms

Coral reef hydrodynamics; Currents on reefs; Water flow over coral reefs

Definition

Hydrodynamics. The science of water flow and the forces that cause flow.

Hydrodynamics of coral reef systems

Water flow in coral reef systems

Coral reef systems are spatially inhomogeneous and consist of an amalgam of sub-systems, which have different benthos and widely varying geomorphology. These include the reef, or reefs, one or more lagoons, and regions of the neighboring ocean that are affected by the reefs. All of these sub-systems are connected hydrodynamically by processes on the reef and these processes are the focus of the present article. Much of what happens on the reef, in terms of hydrodynamics, is controlled by the topographic complexity of the reef and is also affected by the surrounding environment of the reef system. Our attention is primarily directed towards shallow reefs and these may be either sub-tidal, or inter-tidal. Reefs may have varying types of benthos (coral, algae and sand) and are zonated in a way that affects bottom friction and many other aspects of their hydrodynamics. A recent survey of coral reef hydrodynamics is given by Monismith (2007).

Coral reef hydrodynamics differs in many important respects from the hydrodynamics of other coastal systems and these differences will be discussed here. The science of water flow over reefs is the cornerstone of much of our understanding of the ecology and biogeochemical dynamics of reefs. Its effects are multifarious and occur at many space and time scales. Coral reefs efficiently dissipate wave energy and constitute some of the best submerged breakwaters in the natural world (von Arx, 1948). This creates low-energy lagoons, which are fed with water from the reef (Hench et al., 2008) and also have their own patterns of water circulation ("entry lagoons"; "entry lagoon circulation"). Reef hydrodynamics can be greatly affected by conditions in the lagoons, and the outside ocean, and there are processes of continual recirculation of water that are augmented by astronomical tides.

Coral reefs have high biological productivity that is the marine equivalent of tropical rain forests (Hatcher, 1998). There are many similarities between the two systems: the structural complexity of reefs seems to have an important analog in tropical rain forests with the same degree of ecological complexity and biodiversity (Brown et al., 2002). At the heart of the processes which control such productivity are the dynamics, transport and recycling of nutrients and their dependence on the hydrodynamic processes at a variety of space and time scales (Hatcher, 1997). This includes all of the complex small scale vortices, and wave motions found on reefs, which are part of the turbulence field. Unlike most coasts systems, the spectrum of significant topographic complexity in reefs appears almost continuous from scales of hundreds of meters down to millimeters. There is a possible distinct change in the nature of this complexity at the scale of individual coral colonies and this is a physical scale that can be utilized in conceptual (and numerical) models of reef hydrodynamics.

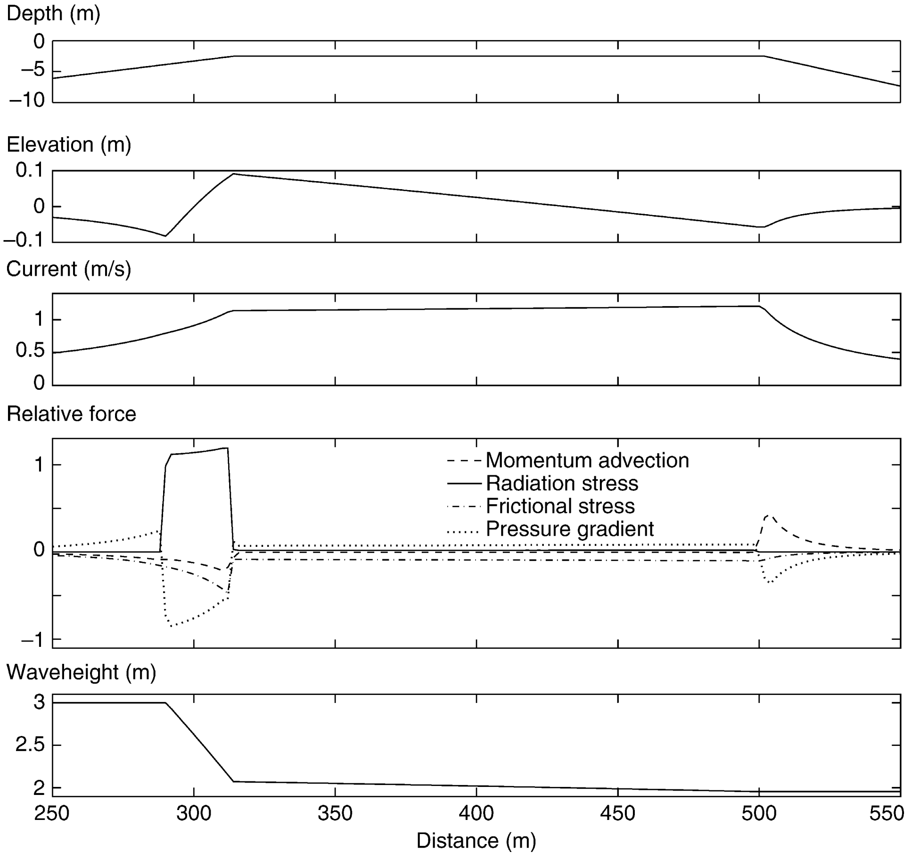
Reef currents are produced by many types of environmental forcing of which the most important are breaking surface waves ("entry Waves and wave driven currents"), astronomical tides, and wind stress (Munk and Sargent, 1954; Kench, 1998). Other influences may also be present on some reefs such as the thermohaline processes (Monismith et al., 2006) and long period ocean oscillations; for the Great Barrier Reef see the excellent volume by Hopley et al. (2007). Of all these forcing processes, the most important is wave breaking and the quintessential, and fundamental, problem of water flow in coral reefs involves waves breaking on a well-defined fore-reef ("entry Fore reef/reef front") and flowing across the adjoining reef flat into a lagoon. The waves are usually ocean swell but can be wind waves (Kraines et al., 1998). This topography fits many reef systems and has been studied through conceptual and numerical models by Tait (1972); Symonds et al. (1995); and Hearn (1999) and recently reviewed by Monismith (2007). This "classical reef flow" problem is illustrated in Figure 1 and we shall discuss this prototype of all reef models in some detail.

There are two basic conceptual models of the physical structure of a coral reef. The first is the "solid reef model," in which the reef is represented as a solid body (without reentrant surfaces in the vertical plane) to which are added "roughness elements." This can alternatively be described as a "bathymetry model" since it can be totally described by a conventional bathymetry dataset with depth as a function of horizontal position. It is discussed in the following sections. The other type of model is the "porous reef model" mentioned later in this article. These conceptual models, which are used for analytical and numerical simulations, have been accompanied by so-called "physical models" built in many laboratories and also, at larger scale, as the coral reef mesocosm at the Biosphere 2 facility in Arizona (Atkinson et al., 2001). Such physical models provide much important hydrodynamic, chemical and biological data although there is limited guidance as to the correct physical, and ecological scaling parameters to be used in this model building.

In the solid reef model, the reef can, in principle, be treated by conventional coastal models (Peterson et al., 2006; Hearn, 2008). However, there are many aspects of flow over a reef that make it distinct from conventional coastal flow and these will be explored in this article.

Friction on reefs

Part of the hydrodynamic uniqueness of coral reefs is that they are submerged natural structures that have the same efficacy as do solid barriers in dissipating ocean waves and creating calm lagoons. Their dissipation of waves is due to a resistance to water flow that can be treated as friction although it cannot be purely "skin friction" as in most coastal models. Instead, the friction comes primarily from "form drag" created by the irregularity and complexity of the structure. In solid reef models, the friction offered by reefs is created by the "roughness elements." The simplest representation of such friction is a frictional drag coefficient. Approximate coefficients for bottom friction on reef flats were originally derived from field data relating incoming wave height and reef current (Hearn, 2008). A coefficient of friction for coral can also be obtained by measuring the current produced by a known head of water in a flume filled with living coral cut from a reef (Atkinson and Bilger, 1992). It is also possible to estimate friction coefficients from acoustic measurements of current either using profiles of current against height or by determining



Hydrodynamics of Coral Reef Systems, Figure 1 The classical reef problem showing a typical reef with water elevation, current, relative dynamical forces and wave height.

the Reynolds stress. A review of some of this work, is given by Monismith (2007). These methods give values of quadratic friction coefficient of the order 0.01–0.1 compared with a typical value of 0.0025 for the skin friction from sand particles in coastal waters.

The use of a drag coefficient is rather limited for several reasons. Firstly, it follows from the theory of the logarithmic layer, that the coefficient will always increase as water depth decreases and so a comparison between values in the scientific literature necessarily requires a knowledge of that depth. Secondly, as discussed later in this article, the presence of waves causes the quadratic dependence of frictional stress to fail at low currents. Finally, the height of the "roughness elements" on reefs is necessarily an appreciable fraction of the height of the water column so that the simple models that lead to quadratic friction in coastal models are not completely applicable.

The part of the bottom of the water column around the roughness elements is called the "roughness layer" and fluid flow in this region is complex and dominated by inertia forces. We are only now starting to understand how to model water flow within the roughness layer and there are some similarities here with flow through canopies formed by submerged aquatic vegetation (Cornelisen and Thomas, 2009). Experiments have been performed within flumes although the experimental reef structures built in the laboratory can lack important aspects of the real structural complexity found in nature.

Solid reef models, can accommodate some part of the processes within the roughness layer by a phenomenological modification of the Prandtl formulation of a vertical "mixing length." For a roughness layer that is thin (compared to water depth), this mixing length method reproduces the familiar logarithmic layer profile of current against height within the water column. In such cases, measurement of this profile is a valuable method of finding the roughness lengths (Lacy et al., 2005). The value of the mixing length concept is that for a thick roughness layer, it can be modified so that, within the roughness layer, it has a polynomial dependence on height (Hearn, 2008).

Spatial variability of roughness

Rough reef flat

The original solutions of the classic reef problem, illustrated in Figure 1, simply assumed that the drag coefficient, or roughness length, for the reef flat was the same as that on the fore-reef. This creates a balance of forces on the fore-reef which is mainly between radiation stress and pressure gradient. The radiation stress is a representation of the force from breaking waves and the pressure gradient is due to a build up of water in the direction of those breaking waves called the “wave set up” (“entry Wave set up”). This results in the water level at the reef crest being higher than the outside ocean by as much as tens of centimeters. A similar effect can be seen on a seawall as waves break against it. This wave set up then causes water to flow across the reef flat, i.e., there is a pressure gradient across the reef flat which is balanced by the friction created by the current. Although smaller waves propagate across the reef flat, wave breaking there is very limited.

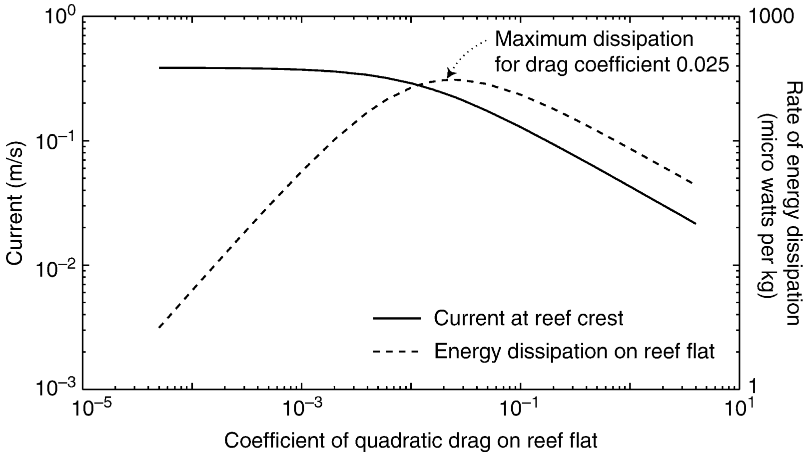
The zone of breaking waves is called the “surf zone” and is the most easily recognized region of a coral reef with its line of white breakers. The width of the surf zone is controlled by the height of incoming waves (usually swell) and the slope of the fore reef. The width varies greatly amongst the coral reefs of the world. Fore reefs with steep slope have narrow surf zones while gently sloping fore reefs have much wider surf zones. The current that is forced across the reef flat by the breaking waves originates in the region beyond the surf zone. It must then pass through the surf zone, onto the reef flat, and out to the lagoon where it returns back to the surrounding ocean. This essentially creates a large circulation cell, or a series of cells, the sizes of which are mainly controlled by the morphology of the lagoon. Circulation in the cells becomes very dispersive in the deeper ocean outside of the reef system. Water may also form closed gyres, or eddies, on the reef itself because the wave set up can vary laterally along the line of the reef crest. Water also flows laterally along the fore reef. The extent of this lateral flow is controlled by the lateral bathymetry and friction (which may be highly anisotropic).

The dynamical force which moves water onto the fore reef is a pressure gradient and this requires a “wave set down” to be there, just in front of the surf zone which causes water to flow inward towards the surf zone where it must then ascend to the raised water level above the reef crest (Figure 1). It does this by using its own momentum or inertia. The region in front of the surf zone is therefore called the “acceleration zone.” Friction opposes this acceleration and so tends to increase the wave set down. This is illustrated in Figure 1. A major difference between the wave set up, produced by wave breaking, and the wave set down, due to friction, is that the latter increases with current. The wave set down therefore acts as a form of resistance which lowers the net water elevation at the crest when the current over the reef flat would otherwise become too high.

The model used in Figure 1 assumes that the lagoon is sufficiently deep to produce negligible surface elevation immediately behind the reef flat. In practice, most reefs have a “back reef” which is also shallow so that narrow lagoons behind fringing reefs such as Ningaloo (Hearn and Parker, 1988) may experience significant wave set up against the coast behind the lagoon.

Smooth reef flat

Many reef flats can be quite smooth and this alters the reef hydrodynamics. If we reduce the roughness of the reef flat, we would expect the wave-driven current flow to increase since we would anticipate that the water level at the reef crest remains unchanged. This does occur provided that we do not decrease the roughness of the reef flat too much. As we further lower the roughness of the reef flat, the current increases sufficiently for the wave set down on the fore reef to effectively reduce the elevation at the crest so as to eventually limit the current. At sufficiently low roughness, the current across the reef flat tends towards a constant value and eventually becomes independent of that roughness. Figure 2 shows the current at the reef crest as a function of the coefficient of quadratic friction on the reef flat. This is derived from the simple one-dimensional



Hydrodynamics of Coral Reef Systems, Figure 2 Current and energy dissipation at the reef crest as a function of the coefficient of quadratic friction on the reef flat.

model of flow across the reef, shown in Figure 1, and based on a traditional quadratic friction law using a coefficient of friction on the fore reef of 0.1. This illustrates the importance of the spatial variability of roughness in a reef system across its many zones.

Currents around reefs

Currents flow around reefs, as well as over, and through, the actual structure of the reef. As they do so, they create a series of coastal boundary layers near the reef and form island wakes. The structure of these wakes is controlled by the frictional Reynolds number (Hearn, 2008). The high friction, and limited water depth, associated with reefs lowers this Reynolds number and so causes island wakes around these structures (Tomczak, 1988). There are a series of studies of these wakes and the role of friction; for a good review see Wolanski (1994). Local artisan fisheries use their knowledge of these wakes, and whirlpools, around reefs, and their variation with the state of the moon, to navigate these waters and optimize catches (Johannes, 1981).

Waves on reefs

Wave processes

The hydrodynamics of reef systems is closely connected with the processes of wave propagation and breaking on reefs. Waves are present on reef flats whenever there are incoming waves on the fore reef, and in the presence of breaking on the fore reef, the waves on the reef flat are just below the height at which they would break (for example, waves of height 0.8 m on a reef flat of depth 1 m). There are very considerable areas of research devoted to wave breaking and its dependence on the depth and shoaling of the reef and to the effect of the strong wave-current interaction on wave propagation, refraction and diffraction over reefs ("entry Wave refraction"). These processes have many interesting, and distinct, forms on reefs due to their unique structural and hydrodynamic properties.

Wave boundary layer

After breaking on the fore-reef, smaller waves (just below breaking height) continue to propagate over the reef flat and these effectively increase friction on the reef flat. In the solid reef model, this wave-current interaction occurs through the "wave boundary layer." The usual situation of waves propagating in the ocean is that their associated currents are not affected significantly by bottom friction. The reason is that the bottom stress is oscillatory and therefore has only the very limited time of half a wave-period to propagate up through the water column. Consequently, until waves enter very shallow water they do not feel significant influences of bottom friction; the vertical current is zero at the bottom of the water column (it is this constraint that changes the speed of propagation of waves in shallow water and produces refraction).

The limited time for propagation of the bottom stress into the water column restricts its influence to a bottom layer (called the "wave boundary layer"). This layer is very thin in most coastal situations and so it just has the simple effect of increasing the coefficient of quadratic friction through the "wave-current" interaction. This situation is changed on reefs because the greater friction produces considerable turbulence from waves with much greater penetration into the water column. Consequently, the wave boundary layer on reefs can have a thickness comparable to the height of the water column and this effectively increases the roughness of the reef. The usual quadratic friction which we find in most coastal situations is a consequence of the current being responsible for both the generation of turbulence and bottom stress. Within the wave boundary layer, that turbulence is created by the waves. A consequence is that at low currents the bottom frictional stress on the reef can be linearly related to the current. This affects some of the basic hydrodynamics such at the relationship between incoming wave height and current (Hearn, 2008). The current-wave interaction always increases friction; it acts by preventing bottom stress decreasing quadratically at low currents. Parts of the wave boundary layer lie inside the troughs, or cavities, of the roughness elements. These are regions with only marginal penetration by the residual currents from the main part of the water column, and so (depending on their size) some of the cavities may be dominated by wave currents (Lowe et al., 2005a, b).

Wave breaking can produce currents in the order of 1 meter per sec on the reef flat although this is very dependent on the width of the reef flat and its friction. Currents in narrow lagoons behind wave-forced reefs can also be high and especially if there is a deeper trench, or "gully," running through the lagoon. Nearshore reefs parallel to shore ("entry Fringing reef circulation") have breaks in the reef line for water to exit the lagoon ("entry Boat channel"), and during heavy-swell conditions, currents can become extremely high and dangerous to swimmers and novice boaters. Currents on reefs advect and disperse suspended material, and particulate and our knowledge of currents and circulation is vital to an understanding of sediment dynamics and all mass transport ("entry sediment-dynamics").

Tidal influences

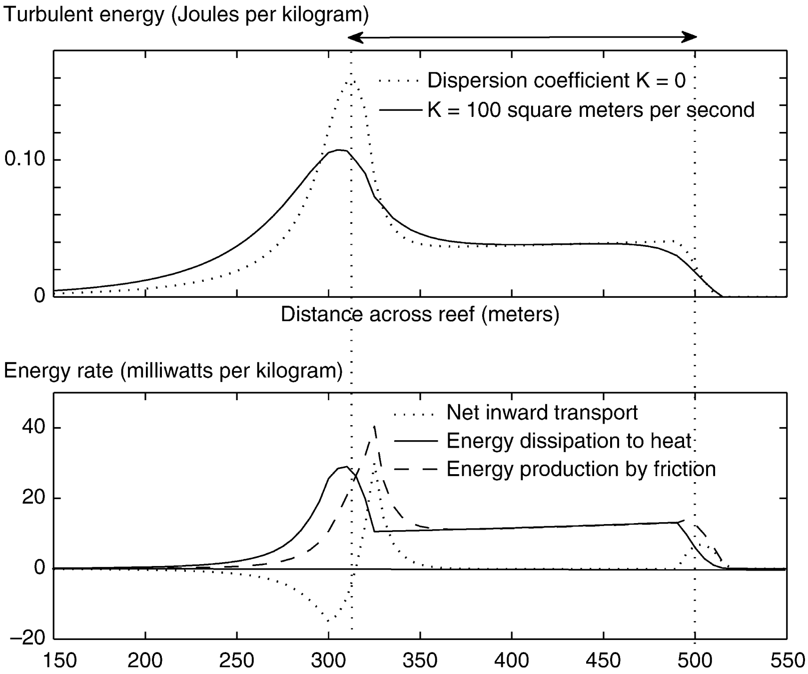
Astronomical tides modulate all of the hydrodynamic processes in a reef system ("entry Tidal effects on coral reefs"). Within the solid reef model, shallow reefs may be completely dry at spring low tides so that the wave set up is confined to the face of the fore reef. In a porous reef model, water continues to have limited flow at these low tides. The overall effect of astronomical tides is to create a net inflow, or outflow (considering all boundaries of the reef system) that is controlled by the tidally varying water level in the reef system. Without the tide, this net flow will be essentially zero. These net tidal currents do depend on the size of the reef system but for small systems the net current is 90 degrees out of phase with the water elevation. This is based on the water level inside the coral system remaining very close to that in the outside ocean and requires that the size of the system be much less than the distance traveled by a gravity wave in one tidal cycle (this is satisfied by most systems of size a few tens of kilometers).

In addition to these "out of phase" tidal currents, time series of water elevation and currents in a reef system, show currents that are "in phase" with the elevation (Kraines et al., 1998). If these are comparable in magnitude to the measured wave driven currents over the reef, it is likely that they are due to the modulation of those currents caused by the changing water level. If the periodic in-phase currents are positively directed over the reef on the rising tide, this means that increasing the water level increases the wave driven current. That may be due to the dilution of the effects of friction with increased height of the water column. Conversely, a decrease in current might be due to reduced wave breaking. This was studied in detail by Hearn (1999) and modeled by Hearn and Atkinson (2000) and is confirmed by measurements at Ningaloo Reef by Hearn and Parker (1988) ("entry Sea level changes and effects on reef growth").

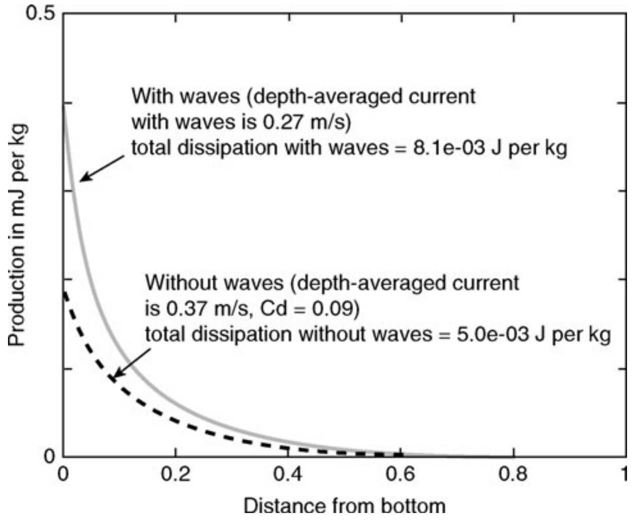
Turbulent energy

Friction in reef systems produces turbulent kinetic energy in the water column. The rate of production depends on both friction and current. The simplest physical picture of the turbulence is a set of vortices, or eddies, with continuous variation of size. It is believed that after kinetic energy enters the turbulence spectrum it cascades down through the vortices, with decreasing spatial scales, until it is dissipated at small scales by molecular viscosity (as heat). Production rates of turbulent energy vary spatially across the reef and are controlled by current strength and roughness (which includes the wave-current interaction). Some part of that energy production is transported to other parts of the reef, where it may dissipate, or leave the reef system, and the remainder is dissipated locally. This balance of turbulence generation by friction, transport of turbulence (by advection and diffusion) and its dissipation, is important to organisms for which biogeochemical and other processes are controlled by some aspect of turbulence. Many organisms, such as coral, have a major role in the development of the roughness elements which promote friction.

Figure 3 shows turbulent energy on the reef which was featured in Figure 1, for the case of a rough reef flat. The upper panel shows the turbulent energy distribution with, and without, the diffusion of turbulence. It shows that diffusion tends to broaden the peak in turbulence at the reef crest. The lower panel shows the rates of production of turbulence, dissipation and net transport which demonstrates that production and dissipation are balanced on spatial scales of meters, over most of the reef, although there is net transport away from the reef crest. A caveat is necessary here regarding the turbulence closure scheme of the model (Hearn, 2008), which is based on conventional coastal models and not yet verified for very rough surfaces. The measurement of production and dissipation in the field are technically



Hydrodynamics of Coral Reef Systems, Figure 3 Turbulent energy on the reef (featured in Figure 1), for the case of a rough reef flat. The *upper panel* shows the turbulent energy distribution in the absence of diffusion (*broken line*) and with a high diffusion coefficient of 100 m^2s^{-1} (*full line*). The lower panel shows the rates of production of turbulence, dissipation and net transport.



Hydrodynamics of Coral Reef Systems, Figure 4 Rate of turbulent energy production on reef flat (shown in Figure 1) without waves (*broken line*) and with maximum (just below breaking point) waves.

challenging tasks which were performed at Biosphere 2 in Arizona (Hearn, 2001b), Kaneohe in Hawaii and the Gulf of Aqaba in the Red Sea (Reidenbach et al., 2006). These measurements generally support the local balance of production and dissipation; the values for dissipation are based on the spectral use of the “inertial subrange” for turbulence (Hearn, 2010).

Turbulence production is increased by wave motion, especially at the bottom of the water column and Figure 4 illustrates the effects of maximum waves (just below breaking point) on turbulence production on the reef flat. The figure shows production with, and without, waves. In the absence of waves, the depth averaged current is 0.37 ms^{-1} (drag coefficient 0.09), giving a total production of 5.0 mJ kg^{-1}. With waves, the current drops to 0.27 ms^{-1} but production increases to 8.1 mJ kg^{-1}. We note that waves reduce the residual current but, through their effect on friction, increase turbulence production (and therefore dissipation).

Returning to Figure 2, the broken curve shows the rate of energy dissipation at the reef crest as a function of the coefficient of friction on the reef flat (with a fore reef of fixed roughness). Significantly, this shows there is an optimum value of the coefficient of friction on the reef flat that optimizes dissipation and therefore would provide maximum nutrient uptake rates within the dissipation-uptake law (Baird et al., 2004). Importantly, increasing roughness does not necessarily increase dissipation because the spatial variability of roughness is always an important control of hydrodynamic processes.

Flushing times of reef systems

Flushing times, or residence times, of reef systems are controlled by advection and dispersion (“entry Residence time”). Flushing processes resemble those in other coastal systems (Hearn, 2008) except that reefs have topographic complexity, high friction and turbulence, with strong wave induced advection (Kraines et al., 1998). Flushing times are defined for the whole reef system, or a sub-system (control volume). They are very dependent on the spatial scale of this subsystem. There are important issues as to the relative strengths of advection and diffusion (dispersion) which are dependent on spatial scale and have important consequences for the transport of many materials and the ecological dynamics of the reef.

Consider particles that are carried onto the reef from the surrounding ocean and have a volume concentration of C in the water column. If there is a sink for these particles on the reef, its strength can be represented by $-\gamma C$ where γ has the dimensions of speed. Suppose h is the depth of the reef and u a typical current strength. In the absence of dispersion, the characteristic horizontal length, l, over which the sink affects the concentration C is uh/γ. Typical values of γ, h and u are 10^{-4} ms^{-1}, 1 m and 0.1–1 ms^{-1}, respectively, so that l is of order 1–10 km. For dispersion alone, the corresponding distance is $\sqrt{hK_x^3/4\gamma}$ where K_x is the coefficient of horizontal dispersion, and so for a typical range of K_x = 1– 10 $\mathrm{m}^2\ \mathrm{s}^{-1}$, l is of the order 50–1,500 m. This implies that reefs with currents u of the order 1 ms^{-1} are dominated by advection whereas dispersion can be more important to the transport process when u is of the order 0.1 ms^{-1}. We may also be interested in particles that are produced on the reef, and which have (ideally) zero concentration in the outside ocean. Particles drift downstream and diffuse laterally with a half-width of $\sqrt{2xx_K}$ where x is distance from the point source and x_K is the characteristic distance K_x/u. Since x_K is typically 1–100 m so that over a typical reef width of 500 m, the plume will have a half width of 30–300 m depending on the dispersion coefficient and the advective speed.

These results may also be applied to subsystems of the reef using values of residual current and dispersion appropriate to those spatial scales. In some systems, tidal advection dominates flushing and this is important to the dynamics of many larvae (Hamner et al., 2007). A more rigorous approach to finding flushing times is to use the particle-age technique (Hearn, 2006).

Richardson Plot

The detailed surface area of the individual elements of a reef structure (per unit horizontal planar area of the reef) is of major importance to biogeochemical processes and to the role of hydrodynamics in the ecology of the reef. The surface area, and height, of roughness elements also controls friction which is a prime process in reef hydrodynamics. Surface area is a controlling factor in the surface stress imposed on the reef by currents and waves, and so is important to the constant erosion that occurs on reefs (“entry Solution processes/erosion”) and especially to storm damage from extreme currents and waves (“entry Tropical cyclone/hurricane”).

One of the key theoretical tools used to study these structural aspects of reefs is the "Richardson plot" (Hearn, 2008). This is based on the length, *S,* of a chain which is composed of links of size s, and made to fit, as tightly as possible, over the surface of a reef between two points on the reef with a straight-line (not necessarily horizontal) separation s_0. The maximum link size that we could choose is evidently s_0. Experiments with chains are widely used on reefs (e.g., Purkis and Kohler, 2008) and we can also emulate these field experiments with numerical procedures if we have data on the three-dimensional structure of a reef. Numerically, we can also repeat the chain experiment using a net with individual mesh elements each having a surface area of s, fitted tightly over the reef, and compare the total area of the net, S, with the flat projection of that area s_0. These procedures give the linear (or areal) "rugosity" S/s_0 from scale s_0 to s. The decadal rugosity r_{10} refers to the case $s_0/s = 10$.

The Richardson plot is dependent on the position on the reef that we choose for our chain, or net, and will differ greatly between the various zones of the reef. So, we think of the rugosity as a strictly local measure. We can increase the length of the chain, or the total area of the net, until we cover the entire reef. As we increase the value of s_0, in this way, we span a larger part of the reef and so $S(s)$ represents an average over an increasing length, or area, of the reef. In so doing, we do loose strictly local information through this averaging process.

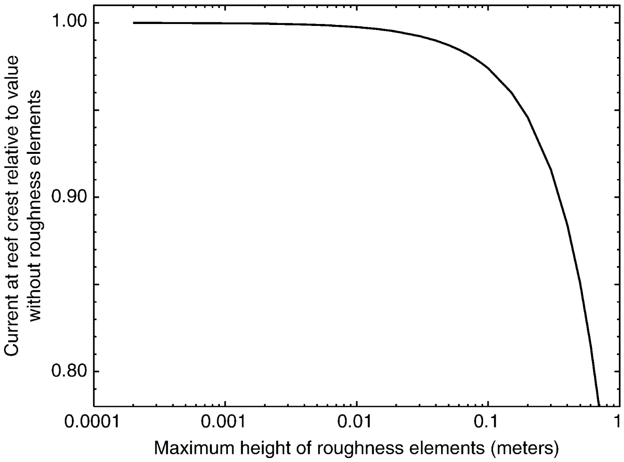
Hydrodynamic models, whether conceptual, analytic, or numerical, use some sort of spatial network of cells which can have a variety of shapes which may not necessarily be the same for all cells. A bathymetry of the reef can be defined at the centers of these cells and this would be the basis of a solid reef model. We can, in principle, make a Richardson plot within each cell with s_0 spanning that cell so that $S(s)$ represents the cell's "individual topography" within a larger scale "bathymetry" of resolution s_0.

The "dimensional roughness" σ from scale s_0 to s, is defined as $\log_{10}(r_{10})$, or as the mean negative slope of $\log(S)$ against $\log(s)$. It provides a "filling factor," $0 < \sigma < 1$ for the reef structure at scale s within the space defined by s_0. As an example, a line can be made to completely "fill" a two dimensional space. This is called a "Peano curve" after Giuseppe Peano (1858–1932). The length of a chain fitted over such a line doubles whenever we half the length of its individual links so that $\sigma = 1$. Values of σ at scales of 10–100 m for many coastal structures are of order 0.1–0.3, i.e., $r_{10} = 1.3–2.0$. At scales from a few meters to kilometers, filling factors, σ, for reefs of at least 50% ($r_{10} > 3.2$) are reported by Purkis and Kohler (2008) using Lidar data ("entry roughness"). Note that if σ approached unity at $s = 10$ m, any "holes" in the structure would have a size less than 10 m. Increasing the filling factor increases the surface area and so assists the geochemical processes but does increase the friction and impede flow; it also increases stress, erosion and severity of storm damage.

Rugosity of natural surfaces tends to increase indefinitely as we reduce the spatial scale and this marks their fundamental difference from geometric surfaces. For example, a geometric surface formed from a flat bottom covered with hemispheres fitted tightly together (so that it looks rather like the back of one of the preformed sheets, or boxes, used to pack hens' eggs) is a geometric surface and has a limiting areal rugosity (at all spatial scales less than the diameters of the hemispheres) of $1 + \pi \sim 4$ (relative to a flat plane). This limiting rugosity is otherwise independent of the diameter of the hemispheres. By contrast, natural surfaces do not reach a limiting rugosity at small sales although they may have distinct zones, or ranges, of spatial scales in which limits are effectively reached. In reality, our "egg box" example shows the same phenomenon since at small enough spatial scales we start to see an increase in surface area due to the small-scale structure of the actual material used in its construction. In the same way, most coastal systems are represented by a bathymetry, or topography, which represents the system down to scales of meters. There is then a separation of scales until we see variability at scales that represent sand ripples and sand grains. For these cases, the Richardson plot naturally divides into distinct regions on the s axis and the important hydrodynamic lengths correspond to values of s that separate these regions. For example, the roughness lengths used in most coastal systems is the scale at which sand ripples, or sand grains, start to change the Richardson plot. This separation of scales is important to the structure of hydrodynamic processes.

Topography complexity in reefs stretches from scales of 100's of meters down to millimeters. One very important question is whether there are changes in the Richardson plot which allow some separation of scales. This is likely to occur at the size of individual coral colonies. This scale varies with position in the reef. The basic approach used by Hearn (2010) is to devise an unstructured spatial grid in which one colony occurs in each cell of the grid and cells do not span parts of colonies. Solid reef models incorporate high levels of rugosity at the sub-grid cell scales through increased values of the roughness length. Although simple intuitive estimates can be made of roughness lengths for experimental models, the best approach is to fit the Richardson plot inside a cell to a model of the roughness elements. This involves the form of $S(s)$ averaged over a numerical cell (s_0 = planar area of cell) with minimum s one to two orders of magnitude smaller than s_0. Critical to this fitting procedure is the spatial scales at which the roughness elements start to affect the Richardson plot. For, example, data for individual polyps have been obtained by magnetic resonance imaging from scales of hundreds of microns to centimeters (Zawada et al., 2006).

The Richardson plot for a linear chain can be used to probe the anisotropy of the reef structure. Anisotropy exists in "spur and grove" structures and is common on the windward side of reefs as part of the wave dissipation processes ("entry Spur and groove"). This is important to hydrodynamic processes and is accommodated either by using anisotropic friction or spatially resolving the structure within the bathymetry mesh.



Hydrodynamics of Coral Reef Systems, Figure 5 Variation of current across reef flat shown in Figure 1 as a function of the height of roughness elements.

Both solid, and porous, reef models use roughness as part of the structural form of the model and require the model to incorporate some skin friction, i.e., conventional surface friction, and so retain a nominal separation of scales between form and skin friction. An example of this methodology is shown in Figure 5 which is based on the reef illustrated in Figure 1. Roughness elements have been built on the reef flat which has a depth 1 m and itself has quadratic skin friction. The model uses cells of a size of 1 m and within each cell there is a randomly chosen height for a roughness element with a maximum height that is varied in the figure from 0.1 to 700 mm. The figure shows that a reduction of current on the reef flat starts to occur for elements of a height of 10 mm and currents decrease rapidly once the height exceeds 100 mm which is 10% of the height of the water column. The model derives the balance of skin friction, inertia, i.e., momentum advection, and pressure gradient around the roughness elements which constitutes form drag. As with classical experiments in fluid dynamics, some skin friction helps to reduce form drag and prevent separation of the viscous boundary layer (Hearn, 2008). The dominance of friction due to roughness elements, over local skin drag, has been verified by Reidenbach et al. (2006) working in the Red Sea. Drag coefficients were measured via the bottom stress obtained from Acoustic Doppler Velocimeters. It was verified that covering the reef flat with plastic sheets did not significantly change these drag coefficients. So, while some skin drag is important, the friction that we find on reefs comes principally from the larger scale roughness.

Porous reef models

The alternative to the solid reef, or bathymetric, picture of a reef is to treat the reef as a submerged porous system so that water can either pass over the reef or essentially percolate through the structure as in hydrological systems. The porosity parameter $p = 1 - \sigma$, with range $0 < p(s) < 1$, effectively defines the "openness" of the reef structure at scale s. It is also evident that some fore reefs, and reef flats, have structures that contain flow paths that are essentially internal to the reef matrix and have direct surface expression only at the ends of the paths. Measurements of porous flow through reefs are limited. Possible techniques within bore holes have been successfully explored on the Great Barrier Reef by Oberdorfer and Buddemier (1986), on Davies Reef, and by Parnell (1986), on a fringing reef flat at Orpheus Island. They found flow through the reef to be fast although spatially inhomogeneous (Hopley et al., 2007).

Work on porous models is still at very early stages. A major part of the difficulty is measuring the three-dimensional structure of reefs. Optical (Brock et al., 2004) and multi-beam sonar measurements of water depth are providing adequate bathymetry data for solid reef models but do not probe reentrant surfaces of the structure. As such, they determine only "external porosity," or "external roughness." Furthermore, it is important to distinguish, and explore, individual colonies and reef structures (Kuffner et al., 2007). Construction of a porous reef model can be attempted from a knowledge of the variation of dimensional roughness $\sigma(s)$ with scale s. Some limited experimental progress has been made (e.g., Lowe et al., 2008) with artificial reef communities built as very low canopies on the floor of flumes. These experiments are very similar to those conducted with artificial submerged aquatic vegetation (Nepf and Vivoni, 2000) but lack much of the vertical and topographic complexity, of natural systems, which are essential ingredients of their hydrodynamics.

Simple models of reef growth can be devised with "diffusion limited aggregation." Simple codes are given by Hearn (2008) and much more detailed algorithms by Kaandorp and Kübler (2001). These are also valuable for experimental modeling of hydrodynamic processes such as the lattice Boltzmann method which is a class of "computational fluid dynamics" (CFD) techniques for modeling a wide variety of complex fluid flow problems with complex boundaries (Succi, 2001).

Summary

The science of water flow in coral reef systems is a developing area of study and one that is important to much of our understanding of coral reefs. Data on physical processes on reefs is accumulating but still sparse. Much progress is being made in understanding, and measuring, the topographic complexity of reefs. Some of the consequences of that complexity are the nature of friction on reefs and the ways that it can be parameterized. More structural data is needed at spatial scales of meters to centimeters. One of the important properties of reefs that dominates much of reef hydrodynamics is the spatial variability of friction. Considerable progress is being made with models of reef hydrodynamics and our understanding of the roughness and wave boundary layers.

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Cross-references

Boat Channel
Fore Reef/Reef Front
Fringing Reef Circulation
Lagoon Circulation
Lagoons
Reef Structure
Residence Time
Roughness
Sea Level Change and Its Effect on Reef Growth
Sediment Dynamics
Solution Processes/Reef Erosion
Spurs and Grooves
Tidal Effects on Coral Reefs
Tropical Cyclone/Hurricane
Wave Shoaling and Refraction
Waves and Wave-Driven Currents
Wave Set-Up