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REPORT

V.J. Harriott · S.A. Banks

Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs

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Abstract The processes underlying the distributional limits of both corals and coral reefs can be elucidated by examining coral communities at high latitudes. Coral-dominated communities in eastern Australia cover a latitudinal range of >2,500 km, from the northern Great Barrier Reef (11°S) to South West Rocks (31.5°S). Patterns of coral species richness from 11 locations showed a clear separation between the Great Barrier Reef and subtropical sites, with a further abrupt change at around 31°S. Differences in community structure between the Great Barrier Reef and more southern sites were mainly attributable to higher cover of massive corals, branching *Acropora*, dead coral and coralline algae on the Great Barrier Reef, and higher cover of macroalgae and bare rock at more southern sites. The absence of some major reef-building taxa (i.e., staghorn *Acropora* and massive *Porites*) from most subtropical sites coincided with the loss of reef accretion capacity. Despite high cover of hard corals in communities at up to 31°S, only Lord Howe Island contained areas of reef accretion south of the Great Barrier Reef. Factors that have been hypothesized to account for latitudinal changes in coral community structure include water temperature, aragonite saturation, light availability, currents and larval dispersal, competition between corals and other biota including macroalgae, reduced coral growth rates, and failure of coral reproduction or recruitment. These factors do not operate independently of each other, and they interact in complex ways.

Keywords Eastern Australia · High-latitude reefs · Physical and biological processes

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V.J. Harriott (✉) · S.A. Banks
School of Resource Science and Management,
Southern Cross University, Lismore,
New South Wales 2480, Australia
E-mail: vicki.harriott@jcu.edu.au

Present address: V.J. Harriott
CRC Reef Research Centre,
at James Cook University,
Townsville 4811, Australia

Present address: S.A. Banks
Queensland Parks and Wildlife Service,
Performance Management and Monitoring,
P.O. Box 155, Brisbane Albert Street,
Queensland 4002, Australia

Introduction

Because coral reefs are largely restricted to tropical waters, the poleward distribution of coral reefs is generally acknowledged to be limited by water temperature, or one of its environmental or biological correlates (Wells 1957; Johannes et al. 1983; Grigg 1982a, 1982b; Veron 1995; Kleypas et al. 1999, 2002). In eastern Australia, coral communities extend from the northern Great Barrier Reef (11°S) to more than 2,500 km southward, where corals can be a significant component of benthic communities dominated by temperate taxa (Veron et al. 1974; Veron and Done 1979; Harriott et al. 1994, 1995, 1999) but fail to accumulate calcium carbonate (e.g., Buddemeier and Smith 1999).

The wide range of factors suggested as influencing the latitudinal limits of coral-dominated communities and their capacity to form reefs have been reviewed by Johannes et al. (1983), Crossland (1988), Veron (1995) and Kleypas et al. (1999), among others. Such factors include water temperature (Dana 1843; Veron 1974), coral reproduction and recruitment (Yonge 1940; Wells 1957; Harriott 1992, 1999a), competition for space with macro-algae (Johannes et al. 1983; Hatcher and Rimmer 1985; Coles 1988) and other taxa (Birkeland 1977; Holmes et al. 1997; Fairfull and Harriott 1999); oceanographic processes and the physical environment (Veron 1974; Veron and Done 1979; Coles 1988; McGuinness 1990; Jokiel and Martinelli 1992); light availability (Wells 1957; Banks and Harriott 1995; Kleypas et al. 1999); and potential for coral calcification and growth (Crossland 1981; Grigg 1982a, 1982b; Harriott 1999b).

Kleypas et al. (1999) recently reviewed physiochemical factors that limit coral reef development and reported that water temperature, light penetration and aragonite saturation levels are all likely to be significant in determining reef development. They acknowledged that biological factors and regional physical conditions are also likely to be significant locally. In their study, Lord Howe Island and the Solitary Islands in eastern Australia were two sites that showed some inconsistencies with global patterns. Examination of changes in species diversity patterns and community structure along an extensive geographical cline in eastern Australia can contribute significantly to the debate on the factors limiting coral biogeographical patterns and coral reef formation.

The subtropical coral communities south of the Great Barrier Reef have recently been the focus of research interest (Harriott et al. 1994, 1995, 1999; Banks and Harriott 1995). These communities contain a mixture of tropical species near the southern limits of their distribution, and subtropical or temperate coral species that are rare or absent from the Great Barrier Reef (Harriott et al. 1994, 1995, 1999).

In this paper, we analyze surveys of coral species richness and community structure over a wide latitudinal range in eastern Australia. Components of the coral taxa and community structure that distinguish tropical from subtropical locations are identified. Hypotheses on the processes regulating both reef development and coral biogeographical patterns are reviewed, and factors that are likely to limit coral reef development at high latitudes are identified. A qualitative model of the factors controlling the development of eastern Australian coral communities is presented.

Methods

Definitions

Diverse definitions of coral communities and reef formation are possible. In this study, "coral community" is a general term referring to any benthic community with a hard coral component, whether reef-forming or otherwise. In line with the definitions of Buddemeier and Hopley (1988) and Kleypas et al. (2002), a "coral reef community" has the potential for reef production, and reef-building or reef-accretion capacity is defined by the presence of Holocene reef buildup. Absence of reef building is recognized where a coral community grows directly on a rock substrate.

Coral species richness data sources

Data on coral species richness were collated for 11 regions (Table 1). The bibliographic database published by Veron (1993) contained coral species lists for the northern Great Barrier Reef (GBR), central GBR, southern GBR, Flinders Reef, Lord Howe Island, Solitary Islands and south-eastern Australia. These records were updated and supplemented by additional information from published records for Gneering Shoals, Flinders Reef, Solitary Islands, Cook Island, Byron Bay and Julian Rocks, South West Rocks and Lord Howe Island (see Fig. 1 for locations; Harriott et al. 1994, 1995, 1999; Banks and Harriott 1995; Harrison et al. 1998).

Coral community structure data sources

For the multivariate analysis of community structure, data were used from 85 sites covering 11 locations; the northern, central, and southern Great Barrier Reef, Gneering Shoals, Outer Moreton Bay (including Flinders Reef), Cook Island, Byron Bay, Solitary Islands, South West Rocks and Lord Howe Island (Fig. 1). All sites were surveyed using either line transects or video transects.

The Great Barrier Reef study used 21 broad benthic life-form categories based on structural attributes (Crown of Thorns-Commonwealth Community Employment Program Team 1986). Approximately 35 benthic categories were used during the various

Table 1. Number of coral species in each scleractinian family for eastern Australia (from Veron 1993) and from regions of eastern Australia (from sources listed in the text). *GBR* Great Barrier Reef

Family	Eastern Australia	Northern GBR	Central GBR	Southern GBR	Gneering Shoals	Flinders Reef	Cook Island	Julian Rocks	Solitary Islands	South West Rocks	Lord Howe Island	South-east Australia
Astrocoeniidae	2	2	2	2	0	0	0	0	0	0	0	0
Pocilloporidae	10	9	10	7	3	4	1	2	2	1	3	0
Acroporidae	127	103	112	78	20	47	7	7	37	0	23	1
Poritidae	42	33	40	22	11	11	3	3	5	0	11	0
Siderastreidae	14	11	10	6	3	4	3	3	4	2	4	2
Agariciidae	20	19	20	16	4	4	0	0	5	0	6	1
Merulinidae	8	7	7	7	2	2	0	1	3	0	4	0
Faviidae	69	63	63	47	17	23	11	5	18	1	20	1
Trachyphylliidae	3	1	1	1	0	0	0	0	0	0	0	0
Fungiidae	34	30	32	18	1	1	0	0	1	0	1	1
Oculinidae	3	3	3	3	0	0	0	0	0	0	0	0
Pectiniidae	10	10	9	7	2	2	0	0	2	0	2	0
Mussidae	22	14	15	14	6	8	3	4	7	1	7	1
Caryphylliidae	9	8	8	7	0	1	0	0	0	0	1	0
Dendrophylliidae	11	11	11	9	8	8	5	5	6	3	5	2
All taxa	384	324	343	244	77	115	33	30	90	8	87	9

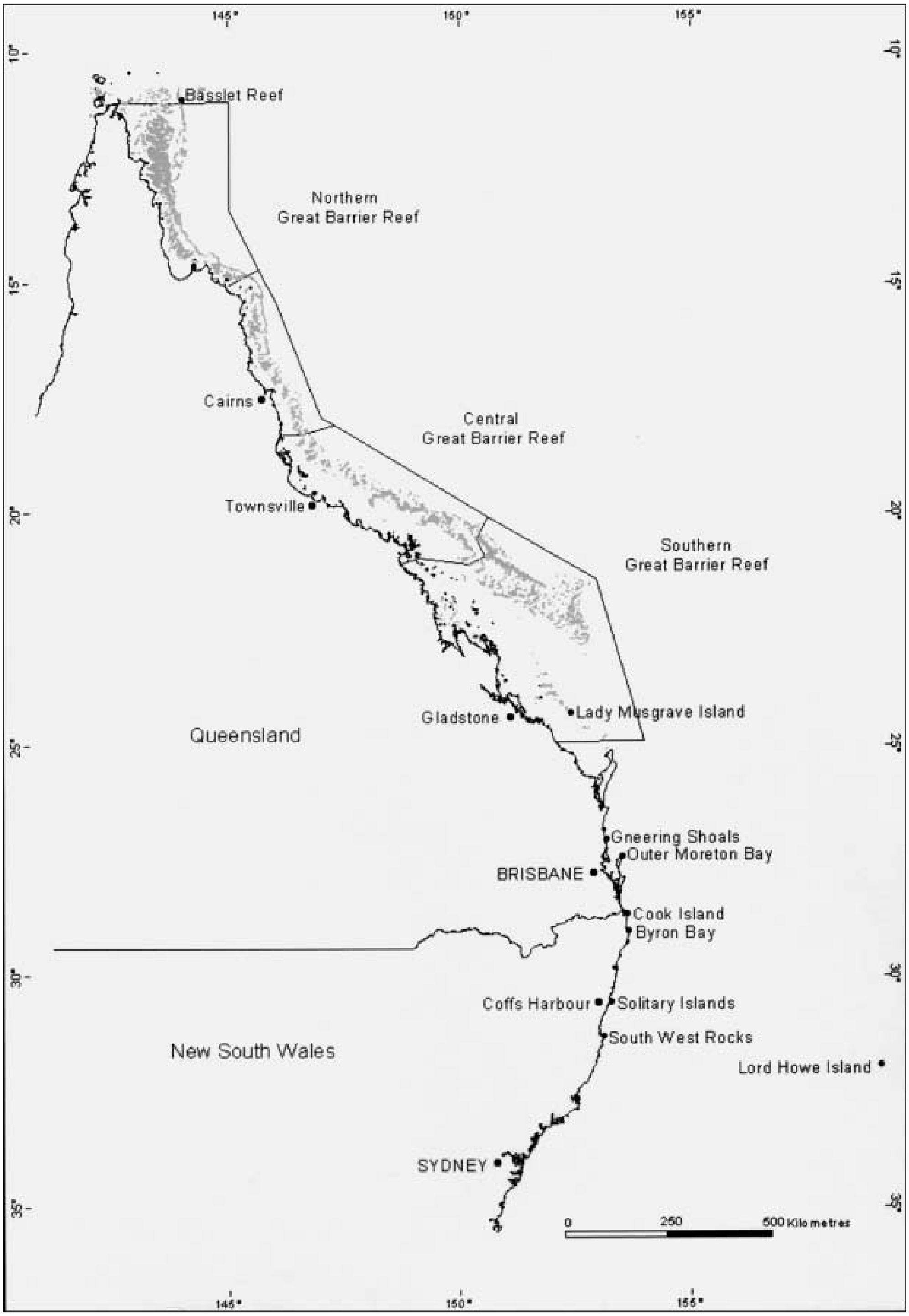

Fig. 1. Map of eastern Australia showing the location of Great Barrier Reef regions and subtropical reefs

surveys of high-latitude reef communities. For the combined data set, the benthic categories used in the original studies were reduced or combined into 20 life-form categories which could be applied consistently across all the studies (Table 2).

Seven sites were selected from each of the northern, central and southern Great Barrier Reef, from data published by the Australian Institute of Marine Science in its surveys of crown-of-thorns starfish and corals (Crown of Thorns-Commonwealth Community Employment Program Team 1986). Data used in this study were from front reef sites at both inshore and offshore reefs at a depth of 12 m.

The subtropical rocky reef communities of eastern Australia were surveyed between 1991 and 1997. At most sites, surveys were in the 8- to 12-m-depth range (see original papers for detail). At Lord Howe Island, a few lagoonal and reef top sites were also surveyed. Ten sites were surveyed at Gneering Shoals (26°38′S; 153°08′E) (Banks and Harriott 1995); nine sites at Flinders Reef and Outer Moreton Bay (27°00′S; 153°29′E) (Harrison et al. 1998; Richardson and Banks, unpublished data); two sites at Cook Island (28°12′S; 153°34′E) (Harriott et al. 1999); fourteen sites at Byron Bay (28°38′S; 153°38′E) (Harriott et al. 1999); seven sites at the Solitary Islands (30°10′S; 153°15′E) (Harriott et al. 1994); two sites

Table 2. Mean cover (%) of benthic categories for the major regions in eastern Australia defined from cluster and MDS analysis

Benthic category	Great Barrier Reef	SE Queensland	Byron Bay region	Solitary Islands	Lord Howe Island	Cook Island/ South West Rocks
Branching *Acropora*	5.4	1.9	0.2	0.9	1.3	0.1
Tabulate *Acropora*	2.6	2.5	0.1	2.7	3.9	2.8
Massive *Acropora*	2.4	2.5	0.0	0.0	7.0	0.0
Branching coral	1.3	1.6	0.9	6.4	5.4	2.4
Massive coral	7.1	0.0	0.0	0.0	9.8	2.3
Encrusting coral	5.1	12.3	2.5	9.0	1.1	0.2
Foliose coral	1.3	2.5	0.3	6.7	0.1	7.4
Hard coral total	25.3	23.2	3.9	25.7	28.6	15.2
Soft corals	7.1	17.2	1.8	4.2	9.5	3.7
Soft coral total	7.1	17.2	1.8	4.2	9.5	3.7
Other invertebrates	2.1	8.1	19.9	27.0	1.5	9.5
Barnacle-covered rock	0.0	0.0	11.6	0.0	0.0	19.7
Invertebrates total	2.1	8.1	31.6	27.0	1.5	29.2
Macroalgae	1.4	8.9	41.2	0.0	24.8	4.0
Turf algae	2.5	35.1	7.5	0.0	0.0	32.1
Coralline algae	2.1	0.0	0.4	0.0	0.0	0.0
Halimeda sp.	0.1	0.0	0.0	0.0	0.0	0.2
Algal assemblage	18.5	0.8	0.0	0.0	1.5	0.2
Seagrass	0.0	0.0	0.0	0.0	0.5	0.0
Kelp	0.0	0.0	0.0	11.9	0.0	0.0
Algae total	24.7	44.9	49.1	11.9	26.9	36.4
Sand and rubble	36.0	3.6	9.2	7.1	12.3	8.3
Bare rock	0.0	0.0	4.5	16.1	2.2	5.5
Dead coral	2.8	3.0	0.0	1.6	18.4	0.3
Substrate total	38.8	6.6	13.7	24.8	32.9	14.0

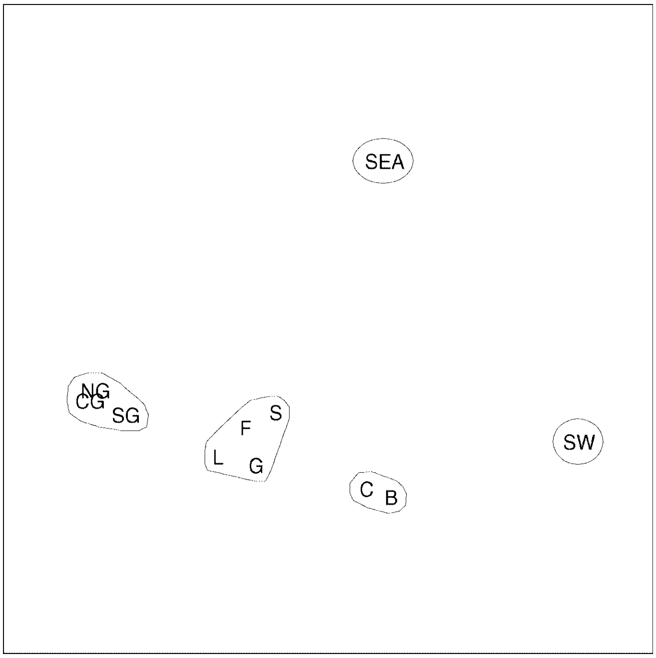

Fig. 2. MDS plot for analysis of species richness patterns of the Great Barrier Reef (GBR) and other locations in eastern Australia. *Lines* connect site groupings derived from cluster analysis at the 80% similarity level. *NG* Northern GBR; *CG* central GBR; *SG* southern GBR; *G* Gneering Shoals; *F* Flinders Reef; *C* Cook Island; *B* Byron Bay; *S* Solitary Islands; *SW* South West Rocks; *L* Lord Howe Island; *SEA* south-east Australia

at South West Rocks (30°56′S; 152°E) (Harriott et al. 1999); and twenty sites at Lord Howe Island (31°33′S; 159°05′E) (Harriott et al. 1995).

Data analysis

Data sets for both coral species richness and community structure were analyzed using the multivariate analysis package Primer v4.0 (Plymouth Marine Laboratories) to perform multidimensional scaling (MDS) ordinations and hierarchical agglomerative cluster analysis. The data were double-square-root transformed and similarities calculated using the Bray-Curtis similarity measure (Bray and Curtis 1957). Cluster analysis aims to find groupings in the sites based on similarities between sites. The MDS ordination was used to illustrate similarities between groups of sites or locations derived from the cluster analysis (Field et al. 1982). SIMPER (SIMilarities PERcentages) analysis (Clarke 1993) was performed to determine the categories that contribute most to the dissimilarities between the groups defined by the analyses.

The data set used for the analysis of coral species richness was number of species in each genus for each of the 11 locations. Cluster analysis and MDS plots separated sites on the basis of their similarity in species richness for 78 scleractinian genera. The SIMPER analysis defined the taxa that contribute most to differences in species richness between locations.

For the analysis of community structure, mean cover per site in the 20 benthic categories was used for the 85 sites examined. The SIMPER analysis determined the benthic categories that contribute most to similarities within and differences between groups of sites derived from the similarity analyses.

Results

Coral species richness

There was a general decline in coral species richness with increasing latitude on coastal eastern Australia. For brevity, results have been summarized and presented here at Family level (Table 1). Data sets for species richness by genera for each location are available from the authors on request. Two discontinuities

	Group 1	Group 2	Group 3	Group 4
Gr 2	*Acropora* *Goniopora* *Acanthastrea* *Favites* *Favia*			
Gr 3	*Acropora* *Acanthastrea* *Favites* *Goniopora* *Goniastrea*	*Pavona* *Alveopora* *Astreopora* *Scolymia* *Seriatopora*		
Gr 4	*Acropora* *Porites* *Fungia* *Favia* *Goniopora*	*Echinopora* *Fungia* *Pectinia* *Galaxea* *Oxypora*	*Fungia* *Astreopora* *Echinopora* *Alveopora* *Lobophyllia*	
Gr 5	N.A.	*Acropora* *Montipora* *Goniopora* *Pavona* *Favites*	*Acropora* *Montipora* *Favites* *Goniopora* *Montastrea*	*Acropora* *Montipora* *Porites* *Fungia* *Favia*

Fig. 3. Results of SIMPER analysis showing taxonomic categories that contribute most to differences between regions in the cluster and MDS analyses of coral species richness. Categories are listed in order of their contribution to dissimilarities between groups. Categories listed to the *left of each cell* were more abundant in the group listed to the *left*, while those to the *right* were more abundant in those groups listed at *top of column*. *Group 1* South-east Australia; *group 2* Lord Howe Island, Solitary Islands, south-east Queensland; *group 3* Cook Island/Byron Bay; *group 4* Great Barrier Reef; *group 5* South West Rocks

are apparent in the data. Coral species richness declines by more than 50% south of the Great Barrier Reef, and declines abruptly again on coastal Australia south of the Solitary Islands. The number of species recorded declines from 90 at the Solitary Islands to just 9 species at South West Rocks, less than one degree of latitude further south.

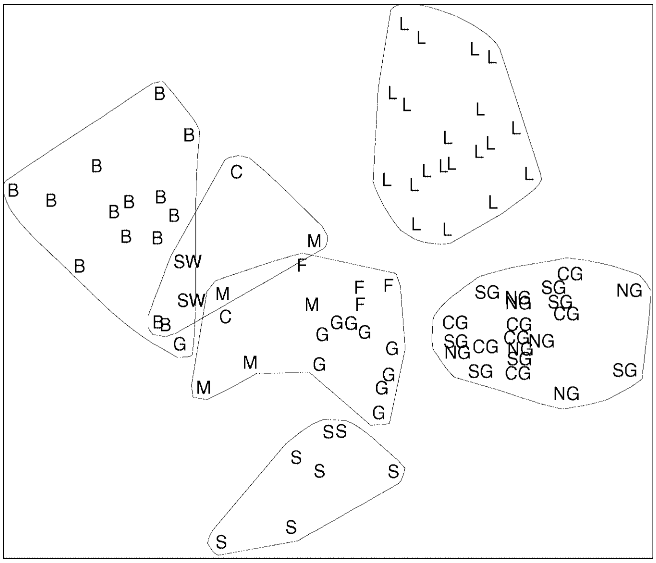

Fig. 4. MDS plot for analysis of community structure patterns of the Great Barrier Reef and other locations in eastern Australia. *Lines* connect site groupings derived from cluster analysis at 63% similarity level. *M* Moreton Bay; for all other site codes see Fig. 2

Eleven of the 15 families and 23% of coral species recorded from eastern Australia were present at the Solitary Islands and Lord Howe Island. For the two most speciose taxa, the Families Acroporidae and Faviidae, 29% of species were recorded at these sites. The Family Dendrophyllidae were better represented at high latitudes with 55% of species present at the Solitary Islands, while in contrast, for the Family Fungiidae, only 3% of species were present at either the Solitary Islands or Lord Howe Island.

In the multivariate analysis of sites according to number of species in each genus, south-eastern Australia and South West Rocks each formed clusters clearly separated from other sites (Fig. 2). Other sites formed three clusters at the 80% similarity level. These were (1) the three Great Barrier Reef locations, (2) Cook Island and Byron Bay and (3) a group comprising Lord Howe Island, Solitary Islands, Gneering Shoals and Flinders Reef.

The taxa that contribute most to the differences between the groups defined by the cluster analysis are presented in Fig. 3. The Great Barrier Reef sites are separated from the four more southern groups primarily by the high species richness of the genera *Fungia*, *Echinopora*, *Acropora* and *Porites*. The South West Rocks and south-eastern Australia groups are distinguished from other groups by the low numbers of *Acropora*, *Montipora*, *Goniopora*, *Porites* and faviid species. The Solitary Islands/Lord Howe Island group are distinguished from the Cook Island/Byron Bay group by the higher species richness of *Pavona*, *Alveopora*, *Astreopora* and other minor genera in the former group.

Regional patterns in community structure

The cluster analysis of community structure grouped the 85 sites along the east coast of Australia into six groups at 63% similarity level. These groups are illustrated on the MDS plot (Fig. 4). Group 1 consists of all the sites surveyed at Lord Howe Island; group 2 includes sites

Fig. 5. Results of SIMPER analysis showing benthic categories that contribute **a** to similarities within groups of sites and **b** to differences between site groupings in the cluster and MDS analyses of community structure. In **b**, categories are listed in order of their contribution to dissimilarities between groups. Categories listed to the *left of each cell* were more abundant in the group listed to the *left*, while those to the *right* were more abundant in those groups listed at *top of column*. *Br* Branching; *Encr* encrusting; *Acrop Acropora*

A

Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Byron Bay	S.W. Rocks Cook Island (mixed)	Solitary Islands	Great Barrier Reef	Gneering Shoals Flinders Reef Moreton Bay	Lord Howe Island
Macroalgae	Barnacles Other invertebrates Sand and rubble	Other invertebrates Encrusting coral Sand and rubble	Algal assemblages Encrusting coral Soft coral Massive coral Branching coral	Turf algae Soft coral Encrusting coral	Macroalgae Dead coral Sand and rubble

B

	Group 1	Group 2	Group 3	Group 4	Group 5
Gr 2	Barnacles Turf algae Macroalgae Rock Br. *Acrop.*				
Gr 3	Macroalgae Rock Tabulate *Acropora* Foliose non-Acrop.	Barnacles Turf algae Macroalgae Rock			
Gr 4	Macroalgae Massive coral Dead coral Rock Br. *Acrop.*	Barnacles Algal assemb. Br. *Acrop.* Dead coral Coralline algae	Algal assemb. Massive coral Rock Br. *Acrop.* Coralline algae		
Gr 5	Turf algae Macroalgae Rock Dead coral Soft coral	Barnacles Encrust. coral Dead coral Rock Soft coral	Turf algae Macroalgae Rock Kelp	Turf algae Algal assemb. Massive coral Coralline algae Br. *Acrop.*	
Gr 6	Dead coral Massive coral Other invert. Massive Acrop. Rock	Barnacles Turf algae Dead coral Massive Acrop.	Macroalgae Massive coral Foliose coral Rock Other inverts.	Macroalgae Algal assemb. Br. *Acrop* Coralline algae Encr. coral	Turf algae Massive coral Encr. coral Massive *Acrop.* Dead coral

located in south-east Queensland (i.e., Gneering Shoals, Flinders Reef and Outer Moreton Bay); group 3 consists of all sites from the Great Barrier Reef; group 4 includes all sites at the Solitary Islands; group 5 consists mostly of the sites at Cook Island and South West Rocks; group 6 consists of most sites from Byron Bay in northern New South Wales. While the groups of sites from Lord Howe Island, the Great Barrier Reef and Solitary Islands were clearly distinguishable from all other groups, there was some overlap between the other three clusters.

The SIMPER analysis shows the benthic categories contributing to the similarities within groups and the differences between groups (Fig. 5). The Great Barrier Reef group shared similar cover of algae, and hard and soft corals, and differed from other groups of sites on the basis of a higher cover of branching *Acropora* coral, massive coral and coralline algae, and lower cover of macroalgae, bare rock and barnacles.

The average cover for each community component for regional groups of sites is summarized in Table 2. Unlike the decline in coral species richness with latitude reported above, there was no clear pattern of declining coral cover with latitude. The coral cover at the Solitary Islands and Lord Howe Island was as high as the coral cover for the Great Barrier Reef and south-east Queensland. However, no surveys were reported for areas south of South West Rocks, where only sparse and isolated coral colonies occur (personal observations).

Soft coral cover was highest for sites in south-east Queensland and was low and similar at all other sites. Invertebrates (mainly ascidians, barnacles and sponges) represented 27–32% of cover at the inshore subtropical reefs (Solitary Islands, Cook Island and South West Rocks, and Byron Bay) but had low cover at both the Great Barrier Reef and Lord Howe Island, so may be representative of inshore sites. Algae represented 12–49% of the communities, but the dominant algal category varied greatly between sites. Solitary Islands was the only region where kelp formed a significant component of the community.

Coral reef accretion

South of the Great Barrier Reef, the only site with significant reef accretion was Lord Howe Island. Even here, carbonate accumulation was largely restricted to the leeward reef in and around the lagoon (Veron and Done 1979; personal observations). On the seaward side of the island, corals frequently grew directly attached to

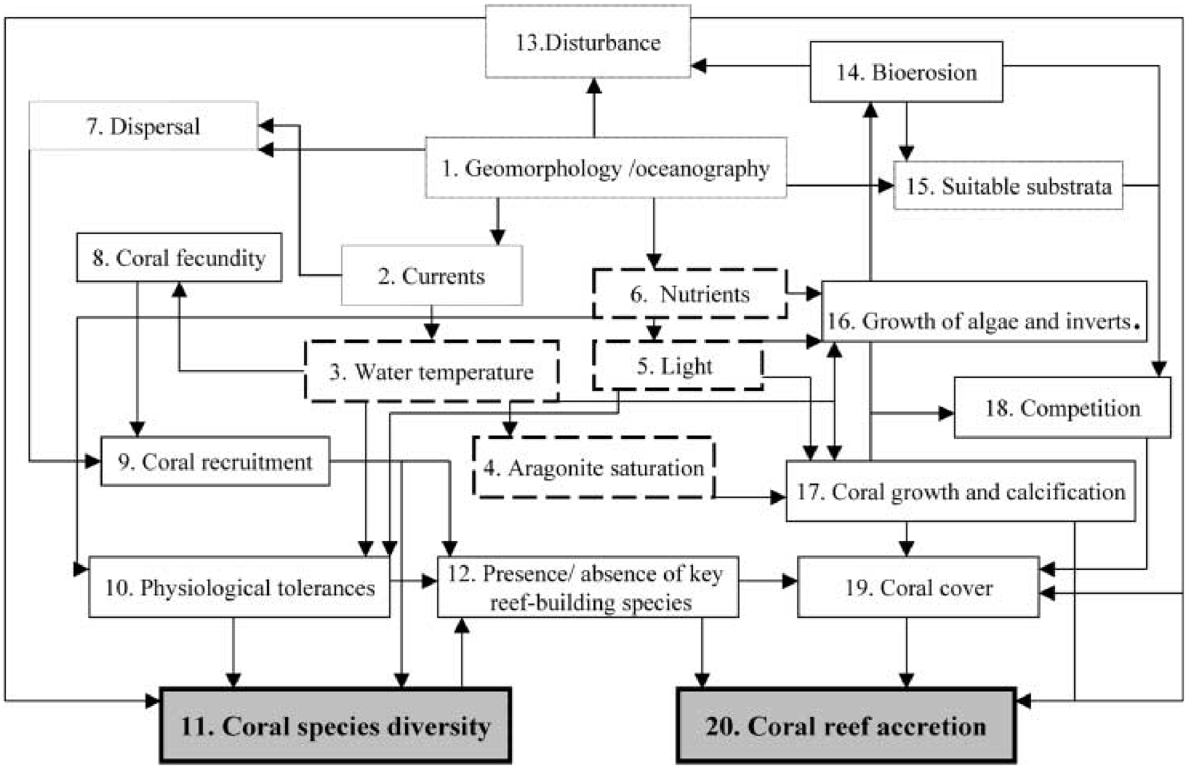

Fig. 6. A qualitative model of the factors and processes that influence the distribution of corals and coral reefs. A brief explanation of each stage is presented in the text. *Dashed boxes 3–6* represent physiochemical factors; *boxes 1*, *2*, *7*, *13*, and *15* represent primarily geophysical processes; *boxes 8–10*, *12*, *14*, and *16–19* represent primarily biological processes and factors; *heavily outlined boxes 11* and *20* represent end points of the model

rocky substrate, indicating a lack of reef buildup (Harriott et al. 1995).

Discussion

The coral communities of eastern Australia

In this first detailed examination of latitudinal clines in coral communities in eastern Australia, the complexity of the relationships between coral species richness, community structure and reef-building capacity is apparent. Locations along a latitudinal cline in eastern Australia were distinguishable on the basis of both patterns of coral species richness and changes in community structure using broad life-form categories.

There was a halving of coral species richness south of the Great Barrier Reef, and a further sharp drop at around 31°S, beyond which only a small number of temperate species were present. It is likely that the abrupt change at 31°S is related to the departure point from the coastline of the East Australian Current, which carries warm tropical water, and potentially tropical larvae, southward along coastal eastern Australia (Godfrey et al. 1980; Cresswell et al. 1983; Harriott et al. 1999).

Coral taxa did not respond consistently to latitudinal gradients. Some families were well-represented in subtropical locations while others were absent. A few species were common in subtropical and temperate locations and rare in the tropics. These patterns almost certainly relate both to variation in physiological tolerances between taxa and to differences in dispersal patterns. For example, differences in larval longevity will determine the maximum potential dispersal distance for corals. Harriott (1992) discusses the effect of reproductive mode (brooding versus broadcast-spawning) on the dispersal of coral larvae to geographically isolated sites.

There was no relationship between coral species richness and coral cover along a latitudinal cline, at least as far as 31°S. Southern sites had high coral cover, despite low species richness, including one site at 31°S, with 8 coral species but 44% cover (Harriott et al. 1999). South of this point, coral communities cease to be identifiable, and the few coral species are represented only by scattered colonies.

The subtropical coral-dominated communities of eastern Australia rarely formed true reefs, despite a coral species richness higher than the coral reefs of Hawaii and the Caribbean [e.g., 90 coral species at Solitary Island (Harriott et al. 1994) and about 45 in Hawaii (Jokiel 1987) and 50 in the Caribbean (Liddell and Ohlhorst 1988)]. Only at Lord Howe Island at 31°S was there significant reef accretion in parts of the back-reef, but corals grew directly on rock on the seaward shores. Dollar and Tribble (1993) and Grigg (1998) report that reef accretion capacity in tropical locations also appears to be related to exposure.

From the present study, the primary biological correlates with the change from carbonate accreting to non-accreting reefs were a change in the representation of staghorn *Acropora* species and massive corals, particularly the large *Porites* colonies which dominate many parts of the Great Barrier Reef, and an increase in macroalgal abundance at high-latitude sites. While coral cover does not decline significantly until >30°S, subtropical coral communities are composed of species with reduced capacity for accretion.

Van Woesik and Done (1997) reported that the absence of both massive *Porites* and branching *Acropora* correlated with the absence of reef accretion capacity in inshore reefs in the southern Great Barrier Reef. This pattern is also consistent with reports of significant reef accretion at Houtman Abrolhos in subtropical Western Australia, where staghorn *Acropora* species are a dominant component of the extant community, growing rapidly (Harriott 1998), and contributing significantly to reef accretion in geological studies (Collins et al. 1993). Lough and Barnes (2000) report a significant decline in growth rates of massive *Porites* species at high latitudes within the Great Barrier Reef. It seems likely, given their distribution patterns, that these species are unable to survive and grow outside the tropics. While recorded as present at Flinders Reef on south-east Queensland (Veron 1993), massive *Porites* are either absent or rare at all subtropical sites (personal observations).

As the world's most southern coral reef, Lord Howe Island provides an interesting case study. The coral reef community is capable of reef formation only in protected parts of the island. While key tropical reef-building species such as *Porites australensis* and *P. lutea*, and large staghorn species such as *Acropora formosa* are absent from Lord Howe Island, other species that are likely to be of intermediate reef-building capacity are abundant. These include the columnar species *Porites lichen* and *P. heronensis*, and the small staghorn species *Acropora yongei* and *A. lovelli*. These species are common in the lagoonal areas (Harriott et al. 1995) where they grow at a rate comparable with tropical species (Harriott 1999b), but are uncommon on the seaward slopes where reef accretion capacity is very limited.

A biophysical model of factors regulating corals and coral reefs

Coral reef formation requires conditions favourable for the dispersal and recruitment of key species, and the presence of environmental conditions suitable for those species to build reefs. One of the difficulties in identifying the factors regulating and controlling coral reef distribution is the high level of correlation among different factors, making it difficult to identify causative agents. Kleypas et al. (1999) reviewed the major physiochemical factors hypothesized to limit coral reef development and concluded that water temperature, light attenuation and aragonite saturation were significant, while nutrient concentration appeared not to significantly affect reef distribution other than locally. They also reported that other regional factors such as storm damage and biological interactions would influence reefs locally, but they did not examine them in detail.

In this section, a qualitative model is presented which incorporates both the physical and biological processes that influence coral distribution and coral reef formation (Fig. 6). Evidence regarding each model parameter (numbered in the text below to correspond with numbers in Fig. 6) is presented and its role in relation to the limitation of coral reefs is discussed briefly. The model focuses in particular on where factors are likely to interact with each other. While developed for eastern Australian corals, the model is likely to have broader applicability both to subtropical and tropical reefs. Factors significant to coral reefs on geological time scales, such as sea level change and climate change, are not considered here.

1. *Geomorphology/oceanography*: the potential for coral reefs to form is limited by the geomorphology of the continental shelf and adjacent terrestrial environment, and by the major oceanographic features imposed by the coastline, such as river runoff (reviewed in Hopley 1982). Where antecedent reef structure is not available, reef formation will be hard-substrate limited. Major oceanographic feature, such as restriction of most reefs to the western edge of oceans where there are significant poleward currents (see 2) delineate the occurrence of reefs world-wide (Dana 1843).
2. *Currents*: current patterns are highly significant to biogeographic patterns of coral distribution. These operate both with respect to major oceanographic features (1) and on a more localized scale. Currents deliver both warm water and tropical larvae, so that currents, water temperature (3) and larval dispersal patterns (7) are inextricably linked (Jokiel and Martinelli 1992; Veron and Minchin 1992). The effects of major currents such as the East Australian Current, Leeuwin Current (Western Australia), Kuroshia Current (Japan) and Gulf Current (Caribbean) in regulating the distribution of reefs and corals have frequently been reported.
3. *Water temperature*: limitation of coral reef distribution by water temperature is the oldest and best-known hypotheses on high-latitude reefs (Dana 1843; Wells 1957; Veron 1974). It is virtual dogma that coral reefs cannot exist when water temperature regularly falls below 18 °C. While lower-than-ambient water temperatures have been demonstrated to kill coral colonies (Glynn and Stewart 1973; Jokiel and Coles 1977), many coral species have been reported to survive temperatures of less than 18 °C for long periods (Coles and Lewis1976; Downing 1985; Tribble and Randall 1986; Coles 1988; Sheppard

1988; Coles and Fadlallah 1991; Veron 1995). Temperature has been hypothesized to limit coral reef formation directly by causing coral mortality as a result of episodes of cold temperatures (10), by reducing the capacity of corals to reproduce successfully (8, 9), and by reducing coral growth rates (17). An indirect effect of cold water temperature is provision of a competitive advantage for coral's competitors (Johannes et al. 1983) (16, 18). As described above, there is also a strong direct correlation between water temperature and larval dispersal (7), since the currents that disperse tropical larvae also carry warm water.

4. *Aragonite saturation*: aragonite saturation is related directly to carbonate ion concentration, temperature and salinity. Smith and Buddemeier (1992), Buddemeier (1994) and Kleypas et al. (2002) have reported on the significance of carbonate saturation in controlling coral calcification. Experiments by Gattuso et al. (1998) and Langdon et al. (1998) indicate reduced calcification of corals and algae with reduced aragonite saturation. The difficulty in determining the relative significance of aragonite saturation and temperature in limiting reef distribution is that the two are generally highly correlated. Australia's Lord Howe Island and Houtman Abrolhos represent two sites with low aragonite saturation where reef formation has been reported (Kleypas et al. 1999).
5. *Light*: just as water temperature declines at higher latitude, so does the availability of light (Grigg 1982a). Average day-length is shorter, light is less intense and the angle of entry of light into the water is shallower. Light availability is also influenced by oceanographic conditions (1) and by nutrient concentrations (6). The major pathway by which light availability is likely to limit coral reefs is by limiting coral calcification and extension (reviewed in Kleypas et al. 1999) (17). Subtropical waters are frequently turbid, and day-length in winter is shorter than for tropical locations. Light may be insufficient to allow significant coral growth or survival (Wells 1957).
6. *Nutrients*: proximity to the coastline and river runoff (1) or to areas of upwelling will affect the nutrient concentrations of waters. In general, inshore and more temperate waters have higher nutrient concentrations than offshore waters (Crossland 1983). Nutrients potentially influence coral reef formation by affecting light availability (5), enhancing the growth of macroalgae and invertebrate fouling communities which compete with corals (16), and by potentially inhibiting coral calcification and growth (17), coral reproduction and recruitment (8, 9), or even survival (10) (Wittenberg and Hunte 1992). However, Kleypas et al. (1999) found no significant relationship between nutrient concentration and reef distribution.
7. *Dispersal* (local and long-distance): geomorphology of the continental shelf (1) or antecedent reefal structure can provide barriers to the local dispersal of recruits. While studies of coral recruitment have indicated the potential for coral larvae to disperse at least on the scale of kilometers (Williams et al. 1984; Willis and Oliver 1988), modelling has indicated that larval densities are greatly diluted with distance (Preece and Johnson 1993; reviewed in Sammarco 1994). While long-distance dispersal is a significant determinant of coral biogeographic patterns (Jokiel 1990; Jokiel and Martinelli 1992; Veron 1995), gene flow between isolated coral reef locations has indicated a strong founder effect for some coral reef taxa, and predominantly local influences on population genetics (e.g., Benzie 1992 for *Acanthaster planci*). In general, brooded larvae have the potential to settle rapidly, but also may survive periods of greater than a month in the water column (Richmond 1987), which may confer an adaptive advantage at high-latitude sites (Harriott 1992). Larvae of broadcast spawned corals generally require a minimum of 4 days to be competent for settlement, and competency declines sharply after 10 days (Babcock and Heyward 1986). The relative dispersal capacity of coral species will be dependent to a large extent on the maximum competency period of their larvae, and on the strength and direction of the prevailing currents (2).
8. *Coral fecundity*: reduction in coral fecundity as a result of low water temperature has been hypothesized as a factor limiting coral reef formation outside the tropics (Yonge 1940; Wells 1957). There have also been reports of reduced coral fecundity as a result of experimentally elevated nutrient levels (6) (Ward and Harrison 2000). Hughes et al. (1999, 2000) reported a decline in coral fecundity with increasing latitude on the Great Barrier Reef. However, Wilson (1998) found no decrease in coral fecundity at the Solitary Islands (30°S), relative to similar tropical species.
9. *Coral recruitment*: attrition in coral larvae numbers due to inter-reefal dispersal (7), and reduced coral fecundity (8) can result in reduced coral recruitment (Veron and Done 1979; Grigg 1983). Harriott and others have demonstrated a pattern of declining recruitment of broadcast spawning corals at high latitudes (Banks and Harriott 1995; Harriott and Simpson 1997; Harriott 1999a). A similar pattern has been reported to the north and south of the Great Barrier Reef by Hughes et al. (1999, 2002).
10. *Physiological tolerances*: to form a part of the established coral community, newly recruited corals must encounter physical conditions within their physiological tolerance range. Where corals are living in conditions close to their physiological limits, a relatively small change in a limiting parameter, for example, water temperature, may cause large-scale mortality. Episodes of water temperatures a degree above normal values have resulted in dramatic world-wide bleaching events (e.g., Berkelmans and

Oliver 1999). Corals also have well-studied lower temperature tolerance limits (reviewed in Veron 1995). Episodic incursions of cold water have resulted in high coral mortality at many sites (Veron and Done 1979; Porter et al. 1982; Roberts et al. 1982; Burns 1985). While temperature is the physiological limit most commonly encountered, tolerances to other factors such as nutrients and light will also affect coral survival.

11. *Coral species diversity*: the latitudinal decline in coral species richness has been reported here and elsewhere. Key factors are dispersal capacity (7) and physiological tolerances (10). As reported by Harriott et al. (1995), reduced species richness at some high-latitude sites may be the result of turnover of species from a larger potential species pool as a result of sporadic recruitment of rare species and their subsequent local extinction.
12. *Presence/absence of key reef-building species*: where the species absent in a low-diversity community are major reef-builders, as reported in this paper for eastern Australia, and by van Woesik and Done (1997) for inshore GBR sites, reef accretion capacity will decline. Key species in Australia include the massive *Porites* taxa and fast-growing *Acropora* species.
13. *Disturbance*: physical disturbances have been reported to have both positive and negative impacts on coral reefs. For example, intermediate levels of physical disturbance on coral reefs are hypothesized to maximize species diversity (Connell 1978). However, regular, severe storms can limit coral reef accretion (Dollar and Tribble 1993; Grigg 1998; Harriott and Smith, in press). Intact coral skeletons contribute to reef formation, as they form the basis for the accumulation of limestone structure. Coral communities attached directly to rocky substrate are an indication that precedent coral colonies have been removed from the substrate, probably as a result of severe storm and wave conditions (Harriott and Smith, in press). The removal of carbonate material may be hastened by bioerosion (14) (Kleypas et al. 2002).
14. *Bioerosion*: elevated nutrients and cold water favor the growth of fouling communities, and may enhance bioerosion (Birkeland 1977; Hallock and Schlager 1986). At the Solitary Islands, corals were frequently only weakly attached to the rocky substrate, with the joining surface riddled with worms (personal observations). Bioerosion in living or dead corals will accelerate loss of coral skeletons and prevent reef accretion.
15. *Suitable substrata*: availability of suitable substrate may be a factor on several scales. The availability of hard substrate may be limited on broad geographical scales (1), or the substrate may be occupied by competing biota (16). Under conditions of heavy wave action, small islands may lack protected areas suitable for reef accretion (Grigg 1982a, 1982b, 1998; Dollar and Tribble 1993).
16. *Growth of algae and invertebrates*: several authors have reported that competition between corals and macroalgae plays a significant role in regulating high-latitude coral communities (Birkeland 1977; Birkeland and Randall 1981; Johannes et al. 1983; Sheppard 1988; Miller and Hay 1996; Miller 1998) because subtropical conditions favor algae over corals. Other reports, however, have found no relationship between macroalgal growth and coral mortality (Coles 1988; Harriott and Smith, in press). Birkeland (1977) reported that in upwelling conditions, which resemble typical inshore high-latitude environments, fouling communities may outcompete corals with respect to the acquisition of suitable settlement sites. Similarly, Holmes et al. (1997) and Fairfull and Harriott (1999) reported that competition between corals and fouling communities limited coral recruitment (9) in the Solitary Islands.
17. *Coral growth and calcification*: although a review by Buddemeier and Kinzie (1974) reported no direct linkage between coral growth rate and reef-building capacity, there is considerable evidence for reduced coral growth rates at high-latitude sites (Glynn and Stewart 1973; Crossland 1981 ; Lough and Barnes 2000). Harriott (1999b) reviewed evidence on latitudinal limitation of coral growth and reported that growth was within the range for tropical species for some taxa, and significantly reduced at high latitudes in other taxa. As discussed above, the absence of some coral taxa at high latitudes may be a reflection of their failure to grow in such conditions. Grigg (1982a, 1982b) reported that reduced linear extension and calcification poleward in the Hawaiian reef chain results in a failure of coral communities at increasing latitude to accrete at a rate that matches subsidence of the substrate, i.e., at what he termed the “Darwin Point”.
18. *Competition*: limitations in the amount of substrate available (15), in combination with enhanced cover of temperate biota (16) and reduced growth and calcification of corals (17), mean that corals are subject to considerable competitive pressure, and may be outcompeted by other biota, either for settlement space or in the established community (Birkeland 1977; Johannes et al. 1983; Miller and Hay 1996; Holmes et al. 1997; Smith and Harriott 1998; Fairfull and Harriott 1999).
19. *Coral cover*: the combination of reduced coral recruitment (9), low growth and calcification (17), competition with other biota (18) and physical disturbances (13) can result in low coral cover. However, at one site at 31°S in eastern Australia, a coral community of just nine species has sites with 45% hard coral cover but no capacity for reef accretion (Harriott et al. 1999).
20. *Coral reef accretion*: a combination of loss of key species from the community (12), low coral cover (19),

reduced calcification (17) and physical disturbance (13) reduces the capacity for reef accretion.

Summary

This qualitative model includes and integrates many of the biophysical factors that have been hypothesized to contribute significantly to the limitation of coral distribution and coral reef development. The different parameters are likely to interact with each other in complex ways, and will vary in significance at different temporal and spatial scales.

In summary, the factors that limit coral species diversity patterns relate primarily to water currents, water temperature, physiological tolerances and coral dispersal and recruitment processes. Factors that regulate reef-building capacity relate to the presence or absence of key reef-building taxa, as well as to physical disturbance and reduced calcification. While this model is currently qualitative, the potential exists for a numerical model to be developed using known values for many of its physical and biological parameters.

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