

Escaping the heat: range shifts of reef coral taxa in coastal Western Australia

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Abstract

One of the most critical challenges facing ecologists today is to understand the changing geographic distribution of species in response to current and predicted global warming. Coastal Western Australia is a natural laboratory in which to assess the effect of climate change on reef coral communities over a temporal scale unavailable to studies conducted solely on modern communities. Reef corals composing Late Pleistocene reef assemblages exposed at five distinct localities along the west Australian coast were censused and the results compared with coral occurrence data published for the modern reefs offshore of each locality. The resulting comparative data set comprises modern and Late Pleistocene reef coral communities occurring over approximately 12° of latitude. For the modern reefs this gradient includes the zone of overlap between the Dampierian and Flindersian Provinces. Modern reef coral communities show a pronounced gradient in coral composition over the latitudinal range encompassed by the study, while the gradient in community composition is not as strong for Pleistocene communities. Tropical-adapted taxa contracted their ranges north since Late Pleistocene time, emplacing two biogeographic provinces in a region in which a single province had existed previously. Beta diversity values for adjacent communities also reflect this change. Modern reefs show a distinct peak in beta diversity in the middle of the region; the peak is not matched by Pleistocene reefs. Beta diversity is correlated with distance only for comparisons between modern reefs in the north and the fossil assemblages, further supporting change in distribution of the biogeographic provinces in the study area. Coral taxa present in modern communities clearly expanded and contracted their geographic ranges in response to climate change. Those taxa that distinguish Pleistocene from modern reefs are predicted to migrate south in response to future climate change, and potentially persist in 'temperature refugia' as tropical reef communities farther north decline.

Keywords: climate change, coral paleoecology, coral reef, Pleistocene, range shifts, Western Australia

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Introduction

As the scientific basis for anthropogenically induced global warming becomes increasingly incontrovertible (IPCC, 2007), many ecologists have begun to document the direct impact of the phenomenon on ecosystems (Parmesan, 2006). Studies have included most major taxonomic groups and an essentially global range of aquatic and terrestrial ecosystems (Parmesan & Yohe, 2003; Lovejoy & Hannah, 2005; Harley *et al.*, 2006;

Parmesan, 2006). Since the trajectory of human-induced climate change is forecasted to continue into the foreseeable future (Stainforth *et al.*, 2005; IPCC, 2007), predicting the impact of climate change on the abundance and distribution of organisms has become increasingly relevant. To date, most studies that predict climate change effects on coral reefs have focused on temperature-induced bleaching (e.g. Hoegh-Guldberg, 1999; Hoegh-Guldberg *et al.*, 2002; Walther *et al.*, 2002), chemically induced changes in calcification rates (Kleypas *et al.*, 2001; Feely *et al.*, 2004), sea level rise (e.g. Buddemeier & Smith, 1988) and observations of a few tropical coral taxa living at higher latitudes than they had been

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previously (Marsh, 1993; Vargas-Ángel *et al.*, 2003; Precht & Aronson, 2004; Precht & Miller, 2006). Here, we utilize the expanded temporal scale provided by the Quaternary fossil record of coral reefs to investigate the impact of climate change since Late Pleistocene time (ca. 125 000 BP) on the geographic ranges of reef coral taxa and the consequences for regional beta diversity among reef coral communities in Western Australia. We then derive predictions of coral community distributions in a future of global warming.

Quaternary paleoecology provides a unique and powerful tool for placing climate change impacts affecting modern reefs into a temporal context that exceeds the scope of traditional ecological studies (Pandolfi, 1999, 2002; Pandolfi *et al.*, 2003). The integration of paleoecological studies of the (long-term) responses to climate change with those focused on modern (short-term) responses potentially allows for more robust predictions of the future for coral reefs. Hence, the Pleistocene marine fossil record has been examined in some detail as a reference datum to gauge the effects of climate change on the distributions and associations of benthic marine invertebrates, primarily bivalves and gastropods (Roy & Pandolfi, 2005). Valentine (1989) and Valentine & Jablonski (1991) demonstrated that numerous molluskan genera expanded their latitudinal ranges along the western coast of North America during Pleistocene time. Moreover, they suggested that such latitudinal migrations were the mechanism by which molluskan species survived extinction during the sea level lowstands that characterize the Pleistocene interval.

The decline in estuarine environments along the Western Australia coast beginning at the end of the Last Interglacial produced similar range shifts in molluskan taxa (Kendrick *et al.*, 1991) as variability in freshwater discharge declined. The conclusions of Valentine & Jablonski (1993, above) were foreshadowed by Kendrick *et al.* (1991) who noted a distinctive enrichment of molluskan faunas as a consequence of the combination of northward and southward overlap of species during the Last Interglacial [135–118 thousand years ago (ka)] in response (at least in part) to the incursion of subtropical faunas south to Cape Leeuwin and then east along the southern continental margin of Australia. Hence, it appears that Pleistocene molluskan faunas avoided extinction during Pleistocene time by adjusting their geographic ranges. As a result, community composition is variable between pairs of modern and Pleistocene molluskan communities.

Similar variability in community composition has been reported when adjacent modern and fossil reef coral communities are compared. Pleistocene reef coral communities exposed in the Key Largo Limestone of

Florida, USA were reported to be different from their extant counterparts offshore (reef tract and patch reef communities) by Precht & Miller (2006). Specifically, the Pleistocene communities lack abundant acroporids relative to their modern counterparts. However, Greenstein *et al.* (1998a) showed that the coral faunas of the modern patch reefs were statistically indistinguishable from the faunas preserved in the Key Largo Limestone. Mid-Holocene reef coral faunas in Japan similarly are lacking abundant acroporids relative to their adjacent counterparts (Veron, 1992). In Western Australia, Playford (1983), Kendrick *et al.* (1991) and McGowran *et al.* (1997) all commented on the difference between the reef coral community preserved in Pleistocene strata of Rottnest Island and the extant coral community offshore.

When temporal patterns in Pleistocene reef building corals are examined, the results are in marked contrast to those obtained by studies of molluskan communities: reef building corals have shown constancy in coral community composition in the face of profound climate cycles. Mesolella (1967) documented that recurrent coral zonation patterns preserved in Pleistocene terraces in Barbados were very similar to those described for modern reef corals in Jamaica by Goreau (1959) and Goreau & Wells (1967). Jackson (1992) analyzed Mesolella's (1967) data and concluded that the same reef coral communities recurred in similar fashion through a 500 ka period encompassing multiple glacial and interglacial intervals that were characterized by wide variation in global sea level, SST and CO₂. Pandolfi & Jackson (2006) tested this model using a hierarchical field sampling design on the Pleistocene terraces of Barbados and found similar results from 220 to 104 ka. Pandolfi (1996) tested whether persistence in community structure characterized reef-building corals preserved in Pleistocene raised reef terraces exposed along 35 km of coastline in the marine terraces of the Huon Peninsula, Papua New Guinea. Coral species composition and diversity were not significantly different among nine distinct reef-building events that spanned a 95 ka interval. Distinctive differences between reefs of the same age were observed at different places along the coast, suggesting that local environmental parameters (in this case discharge of terrigenous materials from a river system) were more important factors determining the composition of reef coral communities than global environmental differences associated with glacial cycles (see also Pandolfi, 1999). However, in all of the cases where tropical corals and mollusks have been studied, comparisons between Pleistocene and modern faunas were made at a single site or reef and latitudinal variability was never examined. This is striking, because latitudinal variation is an important component

in the understanding of the maintenance of coral and fish biodiversity in modern reefs (Bellwood & Hughes, 2001).

In this study, we analyzed reef coral community structure of Pleistocene and modern assemblages present along a latitudinal gradient of 12° in coastal Western Australia that today includes a zone in which temperate and tropical biogeographic provinces overlap, but comprised a single province during the warmer Late Pleistocene time. The study area, thus, enables us to explore the impact of climate change on the geographic ranges of corals and the consequences for regional beta diversity at inter- and intraprovincial levels. Specifically we tested whether: (1) corals underwent changes in their geographic ranges between Late Pleistocene and Holocene time; (2) geographic range shifts observed for corals altered beta diversity; and (3) any differences exist between intra- and interprovincial patterns of beta diversity. We found that tropical-adapted coral taxa contracted their geographic ranges north and this affected regional patterns of beta diversity in the region. These results can be used to erect hypotheses concerning the response of modern reef coral communities to present and future climate change.

Methods

Study area

Adjacent modern and Late Pleistocene reef coral communities exposed in coastal Western Australia provide a natural laboratory in which to investigate the impact of climate change on reef corals. First, the distribution of coral communities in the region is influenced by the strength of the Leeuwin Current, which bathes the coast of Western Australia with warm, relatively low salinity water derived from the western central Pacific via the Indonesian throughflow (Wyrтки, 1957; McGowran *et al.*, 1997). As a result, elevated sea surface temperatures and low nutrient waters characterize the western coast of Australia in a band approximately 50 km wide (Fig. 1). In response, coral reefs persist over a latitudinal range of approximately 23° (Hatcher, 1991), although species diversity decreases rapidly south of Rottnest Island (Veron & Marsh, 1988). The strength of the Leeuwin Current fluctuates on a variety of temporal scales including seasonally (stronger flow between April and September; Godfrey & Ridgway, 1985) and interannually in response to El Niño–La Niña cycles when it weakens and strengthens, respectively (Griffin *et al.*, 2001). Additionally, eddies of warm water are commonly shed from the current, effectively broadening its reach across the continental shelf of Western Australia (Fig. 1; Griffin *et al.*, 2001).

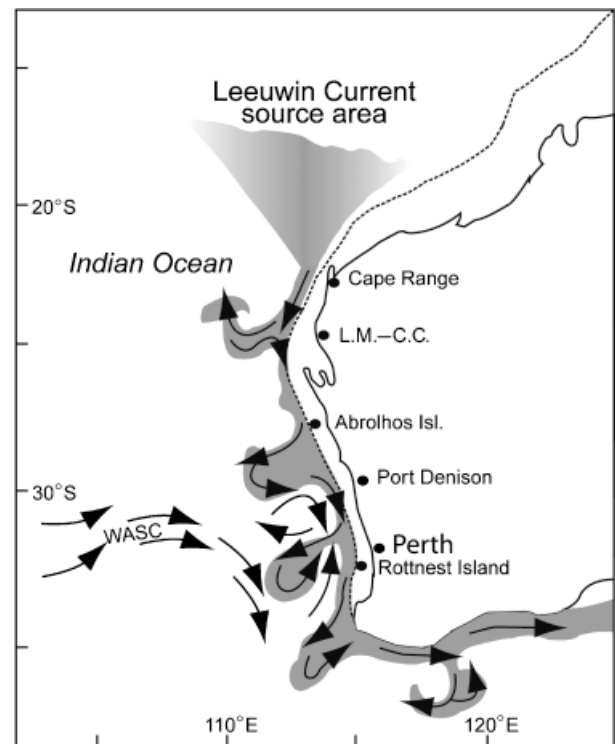


Fig. 1 Disposition of the Leeuwin Current with respect to the Western Australian coast and the Western Australian Summer Current (WASC). Note warm water pool to the north and distinctive eddy cells (after Haig, 2002). L.M.–C.C., Lake Macleod–Cape Cuvier fossil locality. See text and Fig. 2 for further discussion of localities used in this study.

Second, the strength of the Leeuwin current has fluctuated since Late Pleistocene time, potentially impacting the distribution of reef coral communities. Foraminiferal evidence suggests that the Leeuwin Current was present during Late Pleistocene time (Li *et al.*, 1999), and may have been more intense as a result of the southward migration of the west wind drift and subtropical convergence (Kendrick *et al.*, 1991; McGowran *et al.*, 1997). A variety of faunal and geochemical data support this hypothesis. For example, McGowran *et al.* (1997), Kendrick *et al.* (1991) and Playford (1983) noted the extended ranges of coral taxa in Pleistocene outcrops as compared with their modern ranges. Shell beds with abundant warm water bivalve mollusks and large benthic foraminifera have been described from the south-central Australian shoreline (Ludbrook, 1984). Distributions of subtropical planktic foraminifera within the Great Australian Bight (Li *et al.*, 1999), ‘rafted’ shells of *Nautilus* (McGowran *et al.*, 1997) and geochemical analyses of stranded bitumens and resins (McGowran *et al.*, 1997) also suggest that the current was stronger during the Late Pleistocene than today. From the southern extension of stenothermal coral and

bivalve taxa, Kendrick *et al.* (1991) suggested that, during Marine Oxygen Isotope Substage (MIS) 5e, sea surface temperatures along the inner shelf of the Perth region were at least 2 °C higher than present. Wells & Wells (1994) used transfer functions derived from planktic foraminifera to study surface currents of the western margin of Australia at approximately 130, 122–120 and 20 ka [the end of the penultimate glaciation, last interglacial and last glacial maximum (LGM), respectively]. They showed that the Leeuwin Current was intensified during the last interglacial maximum (substage 5e) and shut down during glacial times.

Third, fossil reefs associated with one of the above intervals (MIS 5e), are exposed along the western margin of Australia as a consequence of a combination of a fortuitous sea level history and a variable history of tectonic uplift (Kendrick *et al.*, 1991). Well-preserved exposures of coral reefs are accessible at several localities ranging from south of Rottnest Island to Cape Range, a distance of approximately 1500 km that spans 12° of latitude (Fig. 2). Several workers (Stirling *et al.*, 1995, 1998; Eisenhauer *et al.*, 1996) have obtained precise coral ages within the study area using thermal ionization mass spectrometry (TIMS). Based on the results of over 70 mass spectrometric U-series ages, Stirling *et al.* (1998) constrained the onset and termination of the Last

Interglacial to 128 ± 1 and 116 ± 1 ka, respectively, along the entire Western Australia coastline. Dating of corals within this interval constrained further the major episode of reef building between approximately 128–121 ka. Hence, the fossil reefs examined in this study flourished during contemporaneous reef-building events.

Five Pleistocene/modern reef 'pairs' exposed at separate localities within the region described above have been selected (Fig. 2). The distances separating paired sites range from 1 to 108 km. We have designated these pairs with respect to their location within the study area. 'Northern sites' comprise the two northernmost pairs of localities (Ningaloo-Cape Range and Shark Bay-Lake Macleod/Cape Cuvier); 'Mid-latitude' sites include the modern and Pleistocene sites in the Houtman-Abrolhos Islands and Geraldton-Leander Point; the modern and Pleistocene reefs of Rottnest Island compose our 'southern site.' Critically, our study area includes the modern 'Western Overlap Zone' between the Damperian Province of the Northern Australian tropical region and the Flindersian Province of the Southern Australian temperate region (Wilson & Gillett, 1980; Fig. 2). Hence, our comparative study engages an environmental gradient in which a biogeographic boundary may have migrated in response to changes in the strength of the Leeuwin Current.

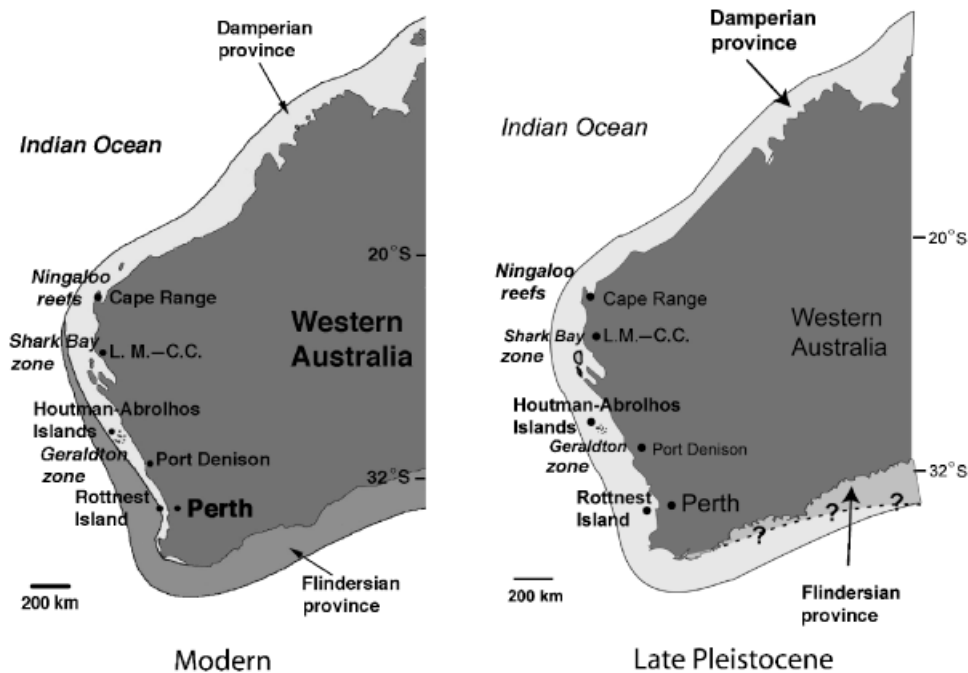


Fig. 2 Modern and Pleistocene localities used for comparative study and their disposition with respect to the Damperian and Flindersian provinces today and during Late Pleistocene time. Disposition of modern provinces after Wilson & Gillett (1980); exact location of the 'overlap zone' during Late Pleistocene time is unknown. Modern reef zones after Veron & Marsh (1988); L.M.-C.C., Lake Macleod-Cape Cuvier. Distances between sites as follows: Ningaloo-Cape Range, 87 km; Shark Bay-Red Bluff, 108 km; Abrolhos Islands, 23 km; Geraldton-Port Denison, 1 km; Rottnest Island, 2 km.

Sampling

Modern Corals. The modern coral fauna of Western Australia has been collected and documented systematically by a number of workers from the University of Western Australia and through a series of field trips sponsored by the Western Australian Museum and/or the National Parks Authority of Western Australia (see Veron & Marsh, 1988 for a review of the history of the collections). Veron & Marsh (1988) synthesized the systematic taxonomy and occurrences of all taxa collected from 1954 to 1986, as well as described *in situ* on numerous expeditions. A series of three expeditions conducted during the 1980s selected diving sites specifically to encompass the full range of hermatypic coral habitats. Additional expeditions in 1984 and 1987 to the Houtman Abrolhos Islands were conducted by CSIRO Marine Laboratories (Perth) and the Australian Institute of Marine Science, respectively. The resulting data set includes locality, habitat and presence/absence data for specimens of 318 species from 70 genera, from the coast, offshore islands and fringing reefs of Western Australia.

The data set was updated (L. M. Marsh and J. Fromont of the Western Australian Museum, personal communication) to include occurrences added by Western Australian staff through 2003. For comparison with the fossil data set four modifications were made to the modern data set: (1) all species of *Acropora* were assigned to the appropriate *Acropora* species group (Wallace, 1999), (2) occurrences of species-rich, nonacroporid genera (e.g. *Montipora*) were reduced to genus-level identification, as this level of identification was most often attained for nonacroporid Pleistocene coral taxa, (3) modern coral taxa that did not occur as fossils anywhere in the study area were removed and (4) modern coral assemblages occurring north or south of the study area were not included in the analyses.

Fossil corals. Fossil reefs were sampled using a nested sampling strategy (Fig. 3). At Cape Range, three sites, separated by a minimum of 500 m were established. Five 25 m transects, separated by 50 m were constructed at each site. All corals encountered on each transect were photographed and identified to the lowest taxonomic level possible; colony orientation and the length of transect intersected by each colony also were recorded. The Lake Macleod–Cape Cuvier region allowed four sites to be established, while the limited extent of exposures in the Houtman-Abrolhos Islands (Turtle Bay, East Wallabi Island), Leander Point, and Rottneest Island each allowed one site consisting of five to seven transects to be sampled. The transect data were pooled within sites before analysis.

The nature of the data

Quaternary fossil reefs do not represent the 'snapshot' that characterizes a living reef (Pandolfi, 2002). Instead they represent 'time-averaged' assemblages, which are amalgams of numerous, once temporally distinct cohorts. The assemblages examined in this study provide a measure of coral community composition over several millennia. For corals, some of which can persist for hundreds to thousands years, time-averaged assemblages might provide a more appropriate temporal scale of analysis than the short-term studies of modern reefs (Pandolfi, 2002). Moreover, subtle differences in community structure have been illustrated for Pleistocene reef coral assemblages (Pandolfi, 2000; Pandolfi & Jackson, 2001) and, for mollusks at least, time-averaged assemblages preserve the rank orders of species found in living assemblages (Kidwell, 2001). Finally, the time-averaged assemblages examined in this study will have dampened any effects of seasonal and/or interannual fluctuations of the Leeuwin Current on coral community composition during the Last Interglacial.

Research on coral preservation (reviewed in Greenstein, 2006) mushroomed in parallel (and in part to justify) the burgeoning literature on Quaternary reef coral paleoecology. Much of this research has demonstrated that while not exact replicates of a living coral reef, Pleistocene reef coral assemblages preserve ecologically reliable data (Pandolfi & Minchin, 1995; Greenstein & Curran, 1997; Greenstein *et al.*, 1998a, b; Edinger *et al.*, 2001), even though not all corals stand an equal chance of being fossilized (Pandolfi & Minchin, 1995; Greenstein & Pandolfi, 1997, 2003; Pandolfi & Greenstein, 1997a, b). Finally, reef corals exposed in Late Pleistocene strata generally preserve sufficient detail to permit identification to low taxonomic levels (e.g. Pandolfi *et al.*, 2002).

We acknowledge the potential for observer bias in that we are comparing relative abundance data collected by us to presence–absence data obtained by earlier workers. We have attempted to minimize this bias by grouping many taxa into higher taxonomic units as discussed above. Finally, our modern–Pleistocene comparisons involve comparative reef zones (shallow fringing reefs), although exact environmental match-up on a site pair basis was not possible.

Data analyses

A Bray–Curtis similarity matrix (Bray & Curtis, 1957) of coral composition was calculated for all modern and Pleistocene localities, and subjected to nonparametric multidimensional scaling (NMDS) to investigate gradients in reef coral community composition. Similarity

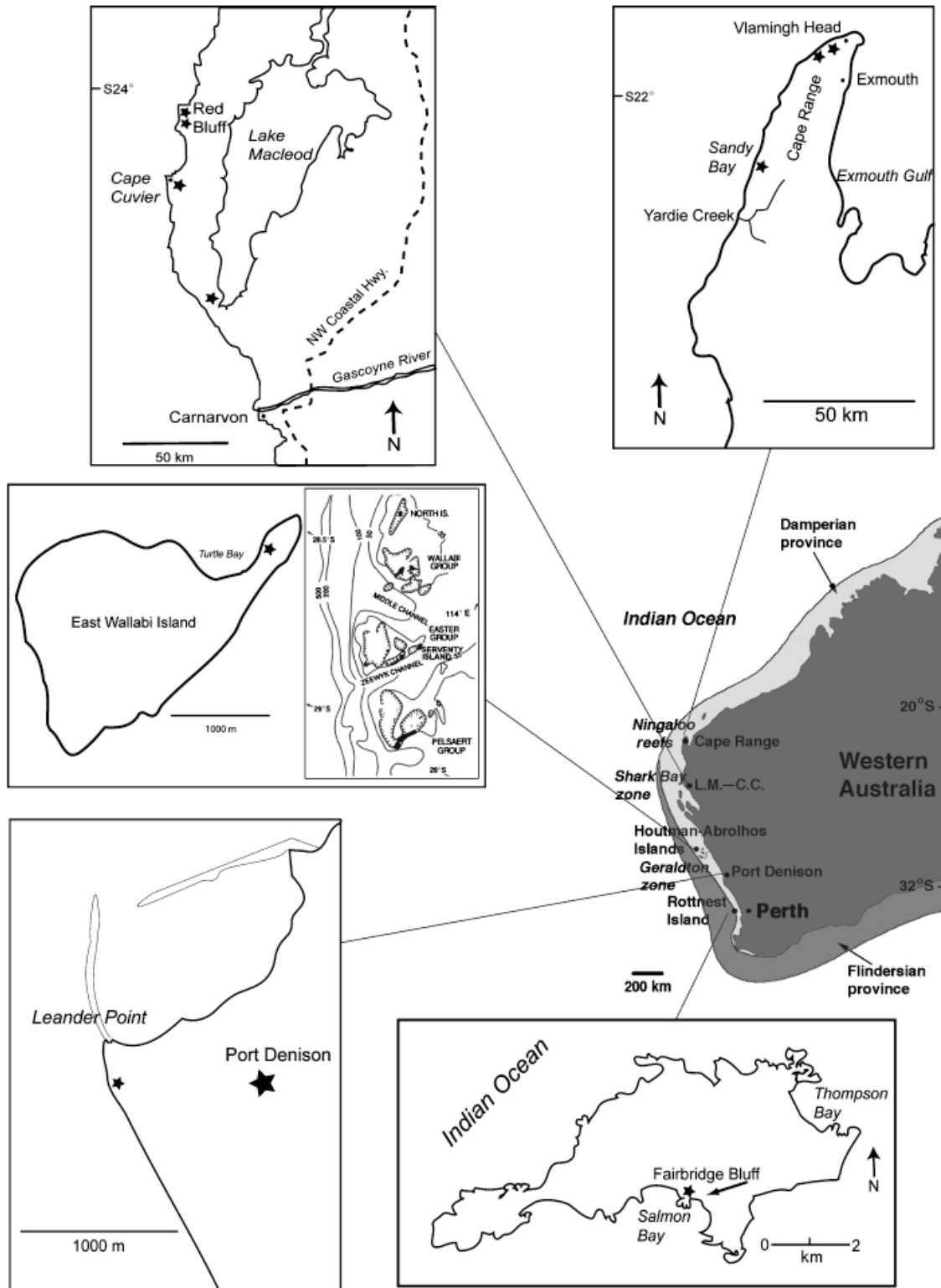


Fig. 3 Sampling design used in this study. Sites at each locality are designated by star symbol.

percentages (SIMPER) were calculated in order to characterize the constituent coral taxa within both modern and Pleistocene samples. The SIMPER procedure also

was used to determine which coral taxa separate modern and Pleistocene samples (both procedures in PRIMER v. 6.15, Clarke & Warwick, 1994).

β turnover (β_T of Wilson & Shmida, 1984, a reliable metric for calculating beta diversity from presence-absence data) was calculated separately for the modern and Pleistocene gradients and for each modern-Pleistocene locality pair along the gradient. We also calculated β_T for the complete list of coral species occurrences published by Veron & Marsh (1988) and updated by us. For each gradient, $\beta_T = g(H) + l(H)/2\alpha$, where $g(H)$ is the number of species gained (i.e. newly encountered) along the habitat gradient, H , and $l(H)$ is the number of species lost along H . This value is standardized by average sample species richness (α). β turnover between all adjacent localities also was calculated. For these pairwise comparisons, $g(H)$ and $l(H)$ become species gained and lost between localities, respectively, and the value is standardized by the sum of the species richness for both localities. Degree of additivity for β turnover was calculated for both modern and Pleistocene gradients by comparing the sum of beta diversity values between adjacent localities with the value obtained for the gradient as a whole. Specifically, percentage error in additivity is defined as $(\beta_{entire} - \beta_{adjacent})/\beta_{entire} \times 100$. Lower additivity values indicate that β -values are the result of community turnover along the gradient (Wilson & Shmida, 1984).

An analysis of covariance (ANCOVA) was performed to explore the effects of distance and region on patterns of beta diversity between modern and Pleistocene localities.

Results

Modern reefs show a clear distinction in the NMDS ordination along Dimension 1, between the high-diversity northern reefs (Ningaloo, Shark Bay Zone) and the mid-latitude reefs of the Abrolhos islands, and lower diversity mid-latitude (Geraldton) and southern (Rottnest) reefs within the study area (Fig. 4). For Pleistocene reefs, the distinction between northern and southern fossil reefs along Dimension 1 is not as clear, as the southernmost reef at Rottnest and the mid-latitude reef at Leander Point are more similar to the northern fossil reefs. Modern and fossil reefs in the northern region have very comparable reef coral assemblages (e.g. fossil reefs at Cape Range and Lake Macleod-Cape Cuvier, and the modern reefs at Ningaloo, Shark Bay and the Abrolhos Islands). For adjacent locality pairs further south in the study area, modern and fossil reefs at similar latitudes comprise distinctive coral faunas (compare, e.g. modern and Pleistocene assemblages at Rottnest Island or the locality pair represented by Leander Point/Geraldton).

Modern reef coral assemblages in the study area are dominated by *Favites*, *Goniastrea australiensis*, *Montipora*, *Pocillopora* and *Symphyllia* (Fig. 5; Table 1). Pleistocene

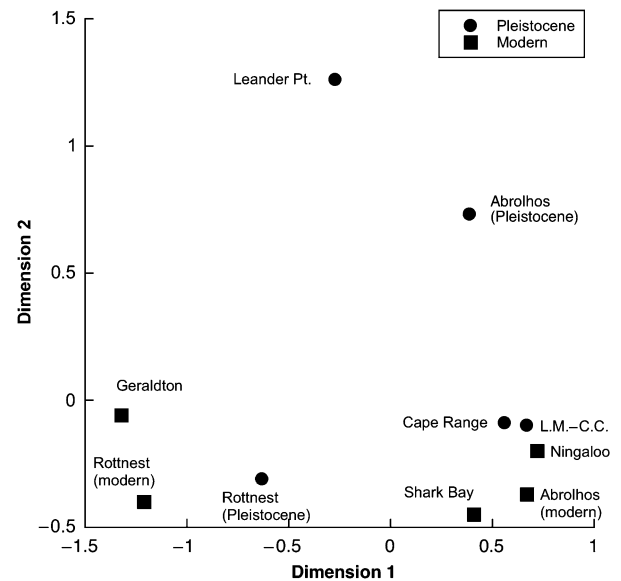


Fig. 4 Results of two-dimensional NMDS of Bray-Curtis similarity values calculated from presence-absence data of coral occurrences in modern and Pleistocene localities. Note a pronounced distinction between northern and southern localities occurs along Dimension 1 for modern reefs only. Minimum stress for the analysis was 0.07. NMDS, nonparametric multi-dimensional scaling.

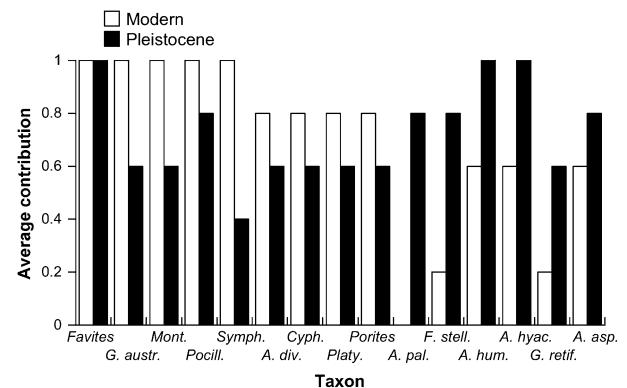


Fig. 5 Graphic comparison of average contributions of important taxa to modern and Pleistocene assemblages. Abbreviations as follows: Mont., *Montipora*; Symph., *Symphyllia*; Cyph., *Cyphastrea*; F. stell., *Favia stelligera*; A. hyac., corals assigned to the *Acropora hyacinthus* group; G. austr., *Goniastrea australiensis*; Pocill., *Pocillopora*; A. div., corals assigned to the *Acropora divaricata* group; Platy., *Platygyra*; A. pal., *Acropora palifera*; A. hum., corals assigned to the *Acropora humilis* group; G. retif., *Goniastrea retiformis*, A. asp., corals assigned to the *Acropora aspera* group.

assemblages are dominated by taxa assigned to the *Acropora humilis* group; the *A. hyacinthus* group, *Favites*, *Pocillopora*, *Acropora palifera*, *Favia stelligera* and taxa within the *Acropora aspera* group (Fig. 5; Table 2). When average abundances of corals are compared between modern and Pleistocene assemblages, they illustrate

Table 1 Contributions of individual reef coral taxa to the overall similarity within the modern localities in the study area

Taxon	Average abundance*	Average similarity†	Similarity/SD‡
Favites	1	5.83	1.84
Goniastrea australiensis	1	5.83	1.84
Montipora	1	5.83	1.84
Pocillopora	1	5.83	1.84
Symphylia	1	5.83	1.84
Acropora divaricata group	0.8	2.72	1.08
Cyphastrea	0.8	2.72	1.08
Platygyra	0.8	2.72	1.08
Porites massive	0.8	2.72	1.08
<i>A. aspera</i> group	0.6	1.04	0.62
<i>A. humilis</i> group	0.6	1.04	0.62
<i>A. hyacinthus</i> group	0.6	1.04	0.62
<i>A. latistella</i> group	0.6	1.04	0.62
<i>A. nasuta</i> group	0.6	1.04	0.62
<i>A. robusta</i> group	0.6	1.04	0.62
<i>Goniastrea edwardsi</i>	0.6	1.04	0.62
<i>Goniastrea faulus</i>	0.6	1.04	0.62

Coral taxa (in bold type) with high ratio values are typical for modern reefs.

*Mean abundance for each taxon over all modern reef localities.

†Average contribution for a particular taxon to the overall similarity within the modern assemblages.

‡Ratio of average similarity to its standard deviation, large values indicate the species is typical of the assemblage.

that different coral taxa distinguish the modern and fossil assemblages. A variety of coral taxa distinguish the modern reefs in the study area, including *Symphylia*, *Leptoseris*, *Montastraea*, *Pavona* and acroporids assigned to the *Acropora latistella* and *A. nasuta* groups. In contrast, Pleistocene assemblages are distinguished mainly by acroporids – *A. palifera*, taxa assigned to *A. humilis* and *A. hyacinthus* groups as well as *Goniastrea retiformis* and *F. stelligera* (Table 3).

Total beta diversity values for the gradient range between 1.04 and 2.22, and percent error in additivity is low for all three calculations (Table 4). Beta diversity between adjacent localities along the gradient is plotted in Fig. 6a. The shape of both modern curves is comparable, while the shape of the Pleistocene curve contrasts with that of the modern curves, particularly when adjacent localities in the mid-latitude region are compared. Beta diversity between modern and Pleistocene locality pairs at the same latitude is presented in Fig. 6b. Turnover is low between modern-Pleistocene locality pairs in the northern region of the study area, increases in the mid-latitude region, and remains high in the south.

Table 2 Contributions of individual reef coral taxa to the overall similarity within the Pleistocene localities in the study area

Taxon	Average abundance*	Average similarity†	Similarity/SD‡
Acropora humilis group	1	6.31	4.23
A. hyacinthus group	1	6.31	4.23
Favites	1	6.31	4.23
Pocillopora	0.8	4.26	1.12
A. palifera	0.8	3.44	1.12
Favia stelligera	0.8	3.44	1.12
A. aspera group	0.8	3.38	1.12
<i>Montipora</i>	0.6	2.41	0.61
<i>A. divaricata</i> group	0.6	1.79	0.61
<i>A. robusta</i> group	0.6	1.79	0.61
<i>Favia</i>	0.6	1.68	0.61
<i>Goniastrea australiensis</i>	0.6	1.65	0.61
<i>Goniastrea favulus</i>	0.6	1.65	0.61
<i>Goniastrea retiformis</i>	0.6	1.65	0.61
<i>Platygyra</i>	0.6	1.65	0.61
<i>Cyphastrea</i>	0.6	1.46	0.62
<i>Hydnophora</i>	0.6	1.46	0.62

Coral taxa (in bold type) with high ratio values are typical for fossil assemblages.

*Mean abundance for each taxon over all Pleistocene reef localities.

†Average contribution for a particular taxon to the overall similarity within the fossil assemblages.

‡Ratio of average similarity to its standard deviation, large values indicate the species is typical of the assemblage.

ANCOVA revealed that region had an effect on both the magnitude of β turnover between modern and Pleistocene localities and the relationship between distance and β turnover (Fig. 7). β turnover between modern reefs in the north (Ningaloo, Shark Bay) and all Pleistocene localities is significantly [$F_{(2,20)} = 6.5771$; $P < 0.01$] lower than β turnover between modern mid-latitude or southern reefs and the Pleistocene assemblages (Fig. 7a). β turnover is significantly ($r^2 = 0.45$, $P = 0.03$) correlated with distance between assemblage pairs when modern reefs in the north are compared with the Pleistocene assemblages, while no relationship exists between β turnover and distance between assemblages when modern reefs from either the mid-latitude (Abrolhos Islands and Geraldton) or southern (Rottneest Islands) localities are compared with the Pleistocene assemblages (Fig. 7b).

Discussion

The synoptic view afforded by our analyses is that the coral fauna of Western Australia responded to climate change since Pleistocene time. Specifically, the tropical

Table 3 Contributions of individual reef coral taxa that distinguish modern from Pleistocene assemblages in the study area

Taxon	Pleistocene average abundance*	Modern average abundance†	Average dissimilarity‡	Dissimilarity/SD§
<i>Acropora palifera</i>	0.8	0	2.39	1.45
<i>Favia stelligera</i>	0.8	0.2	2.16	1.18
<i>Symphyllia</i>	0.4	1	1.92	1.01
<i>A. humilis</i> group	1	0.6	1.79	0.76
<i>A. hyacinthus</i> group	1	0.6	1.79	0.76
<i>Goniastrea retiformis</i>	0.6	0.2	1.7	0.95
<i>Favia</i>	0.6	0.4	1.66	0.88
<i>A. aspera</i> group	0.8	0.6	1.63	0.81
<i>A. robusta</i> group	0.6	0.6	1.6	0.82
<i>Goniastrea favulus</i>	0.6	0.6	1.56	0.84
<i>Cyphastrea</i>	0.6	0.8	1.51	0.79
<i>Porites</i> massive	0.6	0.8	1.51	0.79
<i>Hydnophora</i>	0.6	0.6	1.49	0.9
<i>Platygyra</i>	0.6	0.8	1.47	0.77
<i>A. divaricata</i> group	0.6	0.8	1.45	0.76
<i>Goniastrea edwardsi</i>	0.4	0.6	1.42	0.98
<i>Lobophyllia</i>	0.4	0.6	1.42	0.98
<i>A. latistella</i> group	0.2	0.6	1.41	1.01
<i>A. nasuta</i> group	0.2	0.6	1.41	1.01
<i>Goniastrea australiensis</i>	0.6	1	1.38	0.71
<i>Psammacora</i>	0.2	0.6	1.37	1.08
<i>Leptoseris</i>	0	0.6	1.34	1.17
<i>Montastraea</i>	0	0.6	1.34	1.17
<i>Pavona</i>	0	0.6	1.34	1.17
<i>A. muricate</i> group	0.4	0.4	1.3	0.88
<i>Stylophora</i>	0.4	0.4	1.29	0.9
<i>Galaxea</i>	0.4	0.4	1.27	0.9
<i>Porites</i> stout branching	0.4	0.4	1.27	0.9
<i>Montipora</i>	0.6	1	1.02	0.75

Taxa (in bold type) with large discrepancies in average abundance between modern and Pleistocene assemblages and with a high ratio of average dissimilarity to its standard deviation (Dissimilarity/SD) characterize their respective assemblages.

*Average abundance of each taxon over all Pleistocene localities.

†Average abundance of each taxon over all modern localities.

‡Average contribution for a particular taxon to the overall dissimilarity (among all taxa) between modern and Pleistocene localities.

§Ratio of the average dissimilarity to its standard deviation; large values indicate species that discriminate between modern and Pleistocene assemblages.

biogeographic province that constituted the study area during warmer Pleistocene time contracted to the north of the study area and was replaced by a modern temperate/subtropical coral fauna in the south. In the discussion below, we elucidate various aspects of the ecological response to this change, and forecast the response of the modern system to elevated temperatures predicted for the future.

Gradients in reef coral community composition

Results of the NMDS ordination suggest that the distinction of reef coral communities along the latitudinal gradient present in the study area was less robust

during warmer Late Pleistocene time. Fossil reefs flourishing at a latitude of 32°S near Rottneest Island had a coral fauna that was more similar to the fossil reefs exposed at Cape Range (21°48'S), the Lake Macleod–Cape Cuvier region (24°13'S) and the modern reefs in the north than either modern or fossil reefs at more southerly latitudes (Fig. 4). One explanation for this observation is that preservation bias has removed 'indicator' species that would differ between regions. However, work on Pleistocene reefs in the Caribbean (Greenstein *et al.*, 1998a, b; Pandolfi *et al.*, 1999; Pandolfi, 2000; Pandolfi & Jackson, 2001) and the Indo-Pacific (Pandolfi & Minchin, 1995; Edinger *et al.*, 2001) has demonstrated clearly that differences in community

Table 4 Total beta diversity values for each of three coral assemblages present along the gradient represented by the study area

Assemblage	β -value	% additivity
Veron & Marsh (1988)*	2.22	7.7
Modern†	1.04	13.5
Pleistocene	1.53	1.0

*Complete species list, includes taxa reported through 2003.

†Modern species list modified for comparison with Pleistocene data obtained in this study, see text for discussion of modifications.

structure are preserved at local and regional scales. More likely, our results suggest that reef corals have contracted their geographic ranges north since Pleistocene time, coincident with a northward shift in the Flindersian Province. For modern reefs, the NMDS captures a pronounced gradient in coral community composition associated with the transition between the Dampierian and Flindersian provinces. A similar transition between the provinces is not reflected in community composition preserved in the Pleistocene reefs within the study area (we note here that a NMDS ordination of modern coral occurrences at localities north of our study area also did not illustrate a strong gradient in community composition).

Our interpretation is illustrated further by comparison of the ranges of coral taxa found in our study area (Fig. 8) where the northward shift of coral taxa since Late Pleistocene time is evident. Of the 31 total taxa present as fossils in the study area, 22 have the southern terminus of their ranges in the Abrolhos islands or farther north today (Fig. 8a). In Late Pleistocene time seven of those taxa were present south at Rottneest Island, while an additional taxon had extended its range south to Port Denison (Fig. 8b). Evidence of range shifts also is present in the northern portion of our study area, where the northern terminuses of the ranges of five taxa that today occur on Ningaloo reef occurred in Shark Bay in Late Pleistocene time. Additionally, *A. palifera*, which is found as far south as Port Denison in the Pleistocene assemblages, today only occurs north of our study area (Veron & Marsh, 1988). The range shifts illustrated in Fig. 8 had a profound impact on patterns of beta diversity within and between modern and Pleistocene communities; these are discussed in the following section.

Regional beta diversity

The species level resolution provided by the full data set of Veron & Marsh (1988) resulted in the highest total

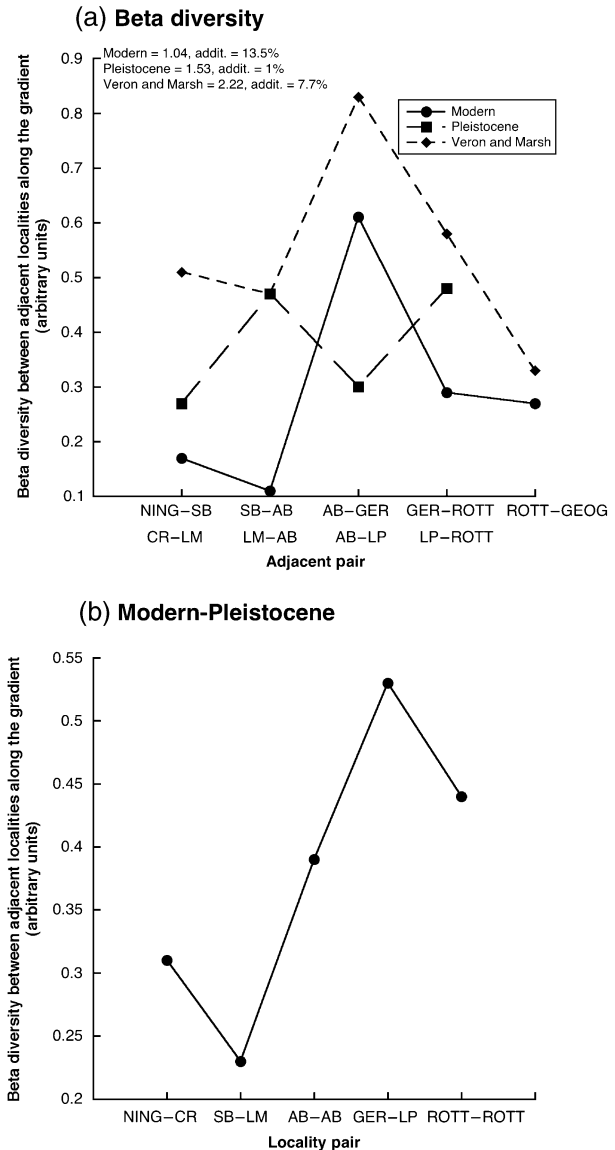


Fig. 6 Analysis of beta diversity. (a) Beta diversity computed between adjacent localities for modern (full data set of Veron & Marsh, 1988; culled data set using only modern taxa that are also represented in Pleistocene reefs) and Pleistocene reef coral communities. A comparison with an additional modern locality south of the study area (Geographe Bay) indicates that lower β turnover resumes within the Flindersian Province. For modern reefs NING-Ningaloo, SB, Shark Bay; AB, Abrolhos; GER, Geraldton; ROTT, Rottneest Island; GEOG, Geographe Bay. For fossil reefs CR, Cape Range; LM, Lake Macleod-Cape Cuvier; AB, Abrolhos; LP, Leander Point; ROTT, Rottneest Island. Gradient beta diversity and additivity are indicated in upper left. (b) Beta diversity between modern and Pleistocene localities present at each latitude, abbreviations as in (a), above.

beta diversity values for the environmental gradient present in the study area. The fact that the modern data set we culled for comparison with our Pleistocene data

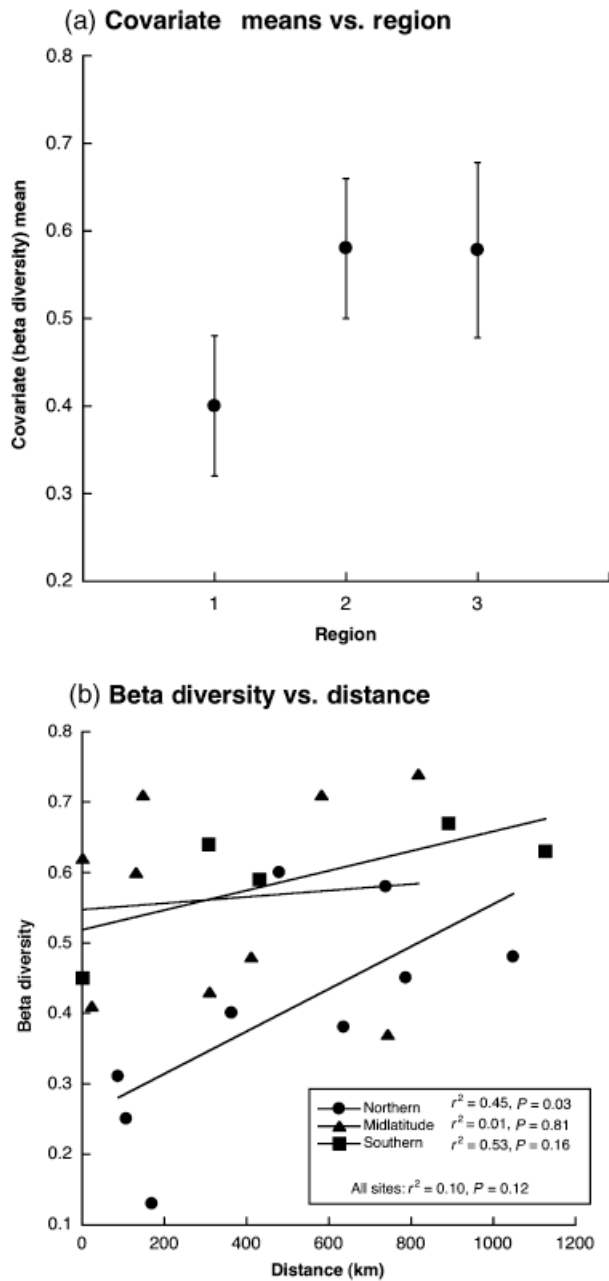


Fig. 7 Results of ANCOVA of region and distance on beta diversity. (a) Effect of region (1, north; 2, mid-latitude; 3, south): Beta diversity between all Pleistocene communities and the two modern northern sites (Cape Range, Shark Bay) is significantly lower than beta diversity between all Pleistocene localities and modern reefs in both the mid-latitude (Abrolhos Islands, Geraldton) and southern (Rottnest Island) regions of the study area. Error bars denote 95% confidence interval; (b) Effect of distance segregated by position along the latitudinal gradient. Distance between communities and beta diversity are significantly positively correlated only for comparisons among modern reefs in the north and the Pleistocene reefs.

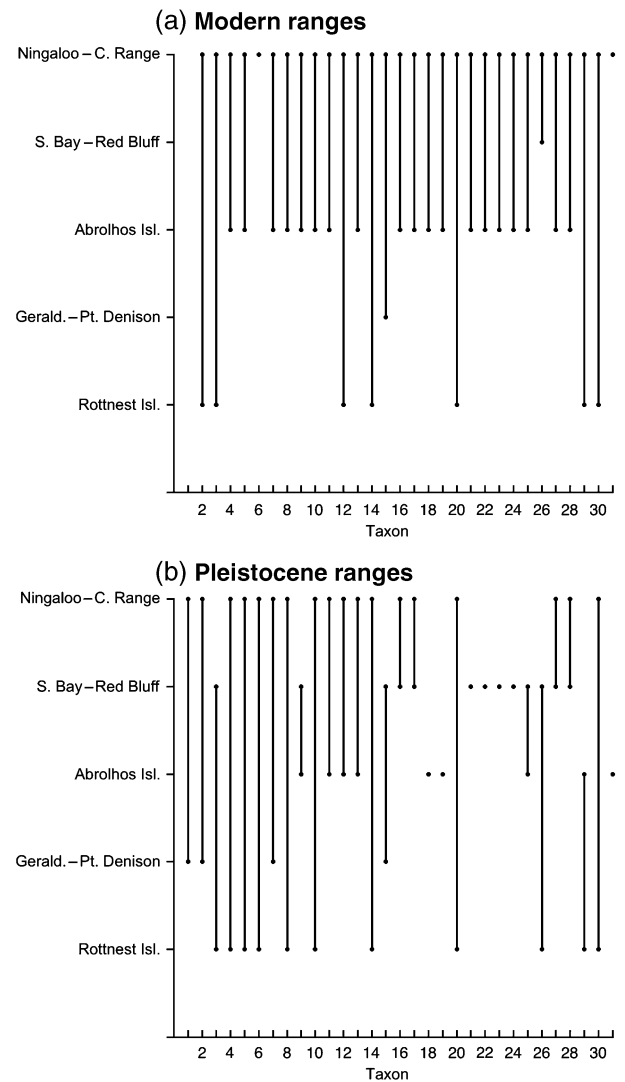


Fig. 8 Ranges of modern and Pleistocene coral taxa within the study area. (a) Modern assemblages, note majority of southern range terminations occur in the Abrolhos Islands; (b) Pleistocene assemblages. The following acroporid species groups: *Acropora humilis*, *A. hyacinthus*, *A. robusta*, *A. aspera*; *Goniastrea retiformis*, *G. favulus* and *Favia* had notably extended ranges in Pleistocene time compared with today. Northern range terminations for modern taxa are largely an artifact of the northern limit of the study area. Northern extent of Pleistocene taxa is unknown. Codes for coral taxa for each graph are as follows: 1, *Acropora palifera*; 2, *Favia stelligera*; 3, *Symphylia*; 4, *A. humilis* group; 5, *A. hyacinthus* group; 6, *Goniastrea retiformis*; 7, *Favia*; 8, *A. aspera* group; 9, *A. robusta* group; 10, *G. favulus*; 11, *Cyphastrea*; 12, *Porites* (massive); 13, *Hydnophora*; 14, *Platygyra*; 15, *A. divaricata* group; 16, *G. edwardsi*; 17, *Lobophyllia*; 18, *A. latistella* group; 19, *A. nasuta* group; 20, *G. australiensis*; 21, *Psammacora*; 22, *Leptoseris*; 23, *Montastraea*; 24, *Pavona*; 25, *A. muricata* group; 26, *Stylophora*; 27, *Galaxea*; 28, *Porites* (stout branching); 29, *Montipora*; 30, *Pocillopora*; 31, *Seriatopora*.

produced a nearly identical curve to that obtained from the full data set (Fig. 6a) indicates that the methodology we employed to compare modern and Pleistocene coral assemblages provided a robust sample for analysis of β turnover.

The shapes of the curves in Fig. 6 represent the changing rates of compositional turnover along the gradient. For the modern coral fauna, the peak in beta diversity between the Abrolhos Islands and Geraldton corresponds to the transition between the Dampierian and Flindersian Province (Fig. 6a). For the Pleistocene coral fauna, the same region produces a drop in beta diversity. Hence, the 'overlap zone' did not exist in the region during Pleistocene time. A further prediction from these results is that different coral faunas within modern and Pleistocene assemblages are now juxtaposed at similar latitudes, hence calculations of beta diversity between adjacent modern and Pleistocene localities should be low in the north, which remains tropical today (hence both modern and Pleistocene assemblages consist of tropical-adapted taxa), and higher in the mid-latitude and southern regions (where cold-water faunas that migrated north since Late Pleistocene time are present adjacent to warm water faunas exposed in fossil reefs). This effect is illustrated in Fig. 6b, in which beta diversity between adjacent modern and Pleistocene assemblages begins to increase in today's 'overlap zone' and remains high south of that region. In summary, the weakening of the Leeuwin Current since Pleistocene time reported by many researchers clearly affected regional patterns of beta diversity for the coral fauna in Western Australia. A final component of our analysis is to gauge the impact of these changes on the spatial relationships of faunal turnover.

Distance between modern and Pleistocene localities is significantly correlated with beta diversity only when the two northern modern localities are compared with the five Pleistocene localities. Additionally, β turnover between modern reefs in the north and all Pleistocene localities is significantly lower than that observed when modern mid-latitude and southern reefs are compared with the Pleistocene localities (Fig. 7). We suggest this pattern is precisely what one would predict had fossil reef coral assemblages contracted their ranges since Pleistocene time. The northward shift of the Dampierian and Flindersian provinces has juxtaposed two modern biogeographic provinces against a single Pleistocene biogeographic province along the Western Australian coastline (Fig. 2) Hence, comparisons between the modern reefs in the north and all of the Pleistocene reefs constitutes an intraprovincial comparison between warm water faunas: β turnover is correlated with distance between reef assemblages within

the province. However, comparison of Pleistocene assemblages to modern reefs in the 'overlap zone,' which support a mixture of tropical- and temperate-adapted taxa (Veron & Marsh, 1988), or the temperate reefs further south, constitutes an interprovincial comparison in which distance and β turnover are largely independent.

The future of reefs in Western Australia

Our study has elucidated a natural experiment on the effect of climate change, specifically cooling, on reef coral community composition. However, the modern and Pleistocene reefs in the study area also provide clues as to how the modern reef fauna might respond to predicted warming associated with global climate change.

Effects on individual corals. Tropical framework-building coral taxa (acroporids) have been observed recently at high latitudes in the Western Atlantic and Indo-Pacific provinces (Vargas-Ángel *et al.*, 2003; Marsh, 1993, respectively). Although Precht & Aronson (2004) interpreted the report by Vargas-Ángel *et al.* (2003) to signify range expansion of *Acropora cervicornis*, it remains to be demonstrated whether or not the populations represent ephemeral or persistent high-latitude assemblages (e.g. Halfar *et al.*, 2005). The genus *Acropora* was reported for the first time from Rottnest Island by Marsh (1993), who attributed the presence of *A. youngi* to both increased temperature, as well as lack of competition from macroalgae. We suggest that range expansions of individual coral taxa may continue as temperature increases over the next century. We predict that certain acroporids may appear in regions south of the Houtman-Abrolhos islands; specifically, those taxa that distinguish Pleistocene from modern assemblages in our study (Table 3) and also exhibit range extensions to the south (Fig. 8a and b). This group includes *A. palifera*, taxa assigned to the *A. humilis*, *A. hyacinthus*, *A. robusta* and *A. aspera* groups; *G. retiformis* and *G. favulus*. Acroporids have been observed (along with Agaricids and Pocilloporids) to be early colonizers of dead coral substrates following bleaching-induced mass coral mortality in the Maldives (Loch *et al.*, 2002). Baird & Hughes (2000) stated that, once established, table colony growth forms (e.g. *A. hyacinthus*) are 'formidable' space competitors on the Great Barrier Reef. Similarly, members of the *A. humilis* group today are often dominant components of reef flats and patch reefs in the Indo-Pacific province (Wallace, 1999; Veron, 2000). Additionally, larvae of *G. retiformis* today preferentially select shallow substrates (Baird *et al.*, 2003) and may become dominant in the intertidal zone (Veron, 2000). *F. stelligera*, also is

common today and often dominant in shallow subtidal environments (Veron, 2000). We predict that the above taxa may return at least as far south as Rottneest Island, where suitable submerged substrates are available (Veron & Marsh, 1988). Our prediction is supported by the observation that today, corals inhabiting reef flats and intertidal environments preferentially survive modern bleaching events (Hoegh-Guldberg & Salvat, 1995). While we do not argue that geographic shifts of coral taxa might mitigate ecological and economic losses resulting from localized mortality, we do suggest that range expansions of important contributors to tropical reef coral communities may allow them to persist in the wake of future climate change.

The Pleistocene reefs in our study area are within 2–4 m of present sea level. However, range shifts of coral taxa commensurate with increasing ocean temperature may not require coincidental sea level rise. The availability of habitable area for coral reefs is highly variable within our study area. For example, the Ningaloo reef system occurs from 200 m to 7 km offshore (May *et al.*, 1983) while reef development in the Shark Bay region is limited to the northwestern portion of Shark Bay, where hydrologic and climate factors permit water of normal marine salinity (Logan & Cebulski, 1970). Fringing reefs occur adjacent to the mainland and on the east side of the islands that enclose the northwest portion of the embayment. The clusters of islands on platforms of the Houtman-Abrolhos archipelago are established on large platforms dissected by channels, lagoons and blue holes (Collins *et al.*, 1996). Hence, a diverse array of reef environments, each yielding a diverse reef coral fauna, is present (Veron & Marsh, 1988). Further south, the continental shelf narrows to 40 km (Veron & Marsh, 1988), with consequent inshore movement of the Leeuwin Current. In response, corals inhabit rocky substrates from the shelf-slope break to the rocky shores developed in the Tamala limestone (Semeniuk & Johnson, 1985). Modern coral reef development offshore from Geraldton all the way to Cape Leeuwin is patchy, with large areas of shallow water along the shelf-supporting sporadic reef development (Veron & Marsh, 1988). Hence, there currently exists a great deal of submerged habitat available for colonization should corals expand their latitudinal ranges to the south.

Regional diversity. Our temporal comparison between communities sampled along a latitudinal gradient has yielded important differences in beta diversity between adjacent localities in modern and Pleistocene time. When compared with the modern coral assemblages, less faunal change occurs between fossil coral communities along the latitudinal gradient in the

study area because we are essentially comparing diversity *within* a province (Pleistocene time) to that present *between* provinces (modern). In response, beta diversity decreases when adjacent communities are compared. This also is reflected by the SIMPER analysis in that fewer coral taxa distinguish the Pleistocene assemblages.

We predict that a similar decrease in beta diversity between communities may occur as tropical-adapted coral taxa expand their geographic ranges south along the coast of Western Australia in the future. This effect may be amplified by preferential survival of particular coral taxa (e.g. Done, 1999). Although the reasons for the correlation are controversial, the role of biodiversity in enhancing ecological stability has been demonstrated on small spatial and temporal scales (e.g. Naeem & Li, 1997; McGrady-Steed *et al.*, 1997; McCann, 2000). Although it remains to be demonstrated whether regional ecological stability and beta diversity are correlated, we suggest that, in a future of decreased regional beta diversity for coral reefs, this question becomes increasingly relevant.

Coda

We recognize that factors other than temperature govern the distribution of reef building corals. We cannot predict how the interplay of light, carbonate saturation state, pollution, disease (e.g. Buddemeier & Smith, 1988) ocean acidification due to CO₂ increase, and associated habitat loss or availability will affect the ability of reef corals to expand their latitudinal ranges over the next century or longer. Moreover, availability of substrate and concentrations of CO₂ (the latter predicted to increase the most at high latitudes, Kleypas *et al.*, 1999) will certainly limit the absolute expansion of the geographical ranges of corals. However, our results demonstrate clearly that important reef coral taxa have expanded their geographic ranges in response to sea surface temperature changes of at least 2 °C during the last interglacial, and that range expansions had a profound effect on regional beta diversity. During the LGM, suitable habitat for coral reefs was reduced 80% compared with modern levels (Kleypas, 1997). Coral reefs persisted in the refugia represented by the remaining 20% and reoccupied shallow marine systems as sea level rose following the LGM. Glynn (1996) and Riegl & Piller (2003) designated specific reef environments, including some high-latitude regions, as potential refugia for corals during times of environmental stress, and observations of the differential response of reefs to past El Niño events (e.g. Jimenez *et al.*, 2001; Reyes Bonilla, 2001) apparently corroborate these hypotheses. We submit that in the wake of predicted future climate change,

reef-building corals might similarly survive in 'temperature refugia' at higher latitudes and serve as sources from which reef corals could potentially expand should conditions favourable to widespread reef development be reestablished.

Conclusions

A comparative study of Late Pleistocene and modern reef coral community composition along a regional latitudinal gradient has allowed for an assessment of the response of reef coral communities to climate change; specifically, the effects of changes in the Leeuwin Current since Late Pleistocene time. The ranges of tropical-adapted reef corals contracted north along the coast of Western Australia. In response, two modern biogeographic provinces occur adjacent to a single biogeographic province preserved in Late Pleistocene strata. Analyses of the effects on reef coral community composition has allowed us to construct hypotheses concerning the response of reef coral communities to future climate change.

- (1) Gradients in Pleistocene reef coral community composition are muted compared with those observed today.
- (2) Migration of coral taxa resulted in higher beta diversity among adjacent communities between Late Pleistocene and, cooler, modern times.
- (3) Certain coral taxa distinguish Late Pleistocene from modern reef coral communities; these are predicted to migrate south in response to predicted global warming.
- (4) The role of regional diversity in enhancing ecologic stability is a critical research issue as reef corals expand their geographic ranges in response to present-day changes in climate.

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