Coral Reefs (2007) 26:53–68
DOI 10.1007/s00338-006-0168-8

REPORT

Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia

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Received: 24 November 2005 / Accepted: 16 October 2006 / Published online: 15 November 2006

Abstract Complex relationships exist between tropical reef ecology, carbonate ($CaCO_3$) production and carbonate sinks. This paper investigated census-based techniques for determining the distribution and carbonate production of reef organisms on an emergent platform in central Torres Strait, Australia, and compared the contemporary budget with geological findings to infer shifts in reef productivity over the late Holocene. Results indicate that contemporary carbonate production varies by several orders of magnitude between and within the different reef-flat sub-environments depending on cover type and extent. Average estimated reef-flat production was 1.66 ± 1.78 kg m^{-2} year^{-1} (mean ± SD) although only 23% of the area was covered by carbonate producers. Collectively, these organisms produce $17{,}399 \pm 18{,}618$ t $CaCO_3$ year^{-1}, with production dominated by coral (73%) and subordinate contributions by encrusting coralline algae (18%) articulated coralline algae, molluscs, foraminifera and *Halimeda* (<4%). Comparisons between the production of these organisms across the different reef-flat zones, surface sediment composition and accumulation rates calculated from cores indicate that it is necessary to understand the spatial distribution, density and production of each major organism when considering the types and amounts of carbonate available for storage in the various reef carbonate sinks. These findings raise questions as to the reliability of using modal production rates in global models independent of ecosystem investigation, in particular, indicating that current models may overestimate reef productivity in emergent settings.

Keywords Calcification · Carbonate production · Reef flat · Torres Strait · Coral · Molluscs

Electronic supplementary material Supplementary material is available in the online version of this article at http://dx.doi.org/10.1007/s00338-006-0168-8 and is accessible for authorized users.

Communicated by Geology Editor P.K. Swart.

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Introduction

Carbonate production by coral reefs located throughout the tropical and sub-tropical oceans is an important component of the global carbon cycle (Vecsei 2004). Recent carbonate studies have focussed on estimating global values of reef production to support climate modelling (Milliman 1993; Kleypas et al. 1999; Vecsei 2004). Such global estimates are dependent on up-scaling from a small number of individual coral reef studies that represent limited coverage of the world's reefs.

At the reef platform scale carbonate production estimates are also of critical importance in understanding the geological and geomorphic development of coral reefs and islands. Production by primary frame builders (corals and encrusting coralline algae) is an important component in reef development (Hubbard et al. 1990). Furthermore, carbonate production by primary frame builders and secondary benthic organisms, along with mechanical and biological erosion, control the generation of detrital sediment on reef platforms, sediment which is subsequently: reincorporated into reef framework (Hubbard et al. 1990); stored on reef surfaces; transported off-reef (Hughes 1999); or transferred to infill lagoons (Macintyre et al. 1987; Kench 1998; Purdy and Gischler 2005) or build islands (Maragos et al. 1973; Hopley 1982; Woodroffe et al. 1999; Yamano et al. 2000, 2002). To date, few studies have attempted to quantify how fine spatial variations in organism density and production influence the character of both reef framework and sediment reservoirs. Notable exceptions include Stearn et al. (1977) and Scoffin et al. (1980) in Barbados; Sadd (1984) and Hubbard et al. (1990) in the Caribbean; and Harney and Fletcher (2003) in Hawaii. Collectively these papers highlight the limited geographical and physiographic coverage of such studies. All were conducted in non-emergent, fringing reef environments potentially influenced by high-island silicate or hydrological inputs so that their results have limited applicability in interpreting the emergent, carbonate environments of Great Barrier Reef (GBR) platforms and Pacific atolls.

Vecsei (2004) identified four principal approaches used to quantify carbonate production on reefs: (1) hydrochemical techniques based on water chemistry changes (Smith and Kinsey 1976, 1978; Davies and Kinsey 1977; Smith and Harrison 1977; Smith 1981, 1983; Kinsey 1985); (2) the census-based approach, which uses data on reef organism cover and extension/production rates (Chave et al. 1972; Stearn et al. 1977; Sadd 1984; Hubbard 1985; Yamano et al. 2000; Vecsei 2001; Harney and Fletcher 2003); (3) geological estimates from net accumulations of carbonate on individual reefs (Ryan et al. 2001); and (4) modelling techniques focussed on net reef accumulation (Kleypas 1997). All these approaches yield aggregate estimates of production at the total reef scale but only the first two, hydrochemical and census-based methods, are applicable at sub-reef scales or in evaluating organism-level production differences.

Productivity rates calculated from hydrochemical (alkalinity-reduction) measurements alone include both the carbonate precipitation and early dissolution occurring in shallow reef waters (Kinsey 1985). These measurements commonly represent carbonate production by entire reef communities and not the relative contributions of different producer types. The widespread adoption of hydrochemical methods over the last three decades has led to significant advances in understanding the productivity of different reef-habitat assemblages (Kinsey 1983; Milliman 1993; Vecsei 2004). These advances have, however, been at the expense of detailed knowledge of the relative contributions of different organism types to gross reef production.

In contrast, census methods afford the opportunity to determine the relative contributions of different carbonate producers to total reef productivity as well as opportunities for detailed spatial comparisons between carbonate contributions and sediment composition, and between patterns of 'framework' versus 'direct-sediment' production (Harney and Fletcher 2003) at sub-reef scales. This study documents detailed patterns of carbonate production on an emergent reef flat as determined using census-based techniques.

Smith and Kinsey (1976) criticised census techniques for their potential for error from the accumulation of contributions by individual biological components. However, there have been sufficient, significant advances in the extent and accuracy of published carbonate producer growth rates to warrant reconsideration of the accuracy of census techniques, and a review of the rates that underlie them. Furthermore, the robustness of census-based results may be easily tested via error estimates and comparisons drawn with hydrochemically determined modal production rates.

This paper presents results from the application of census techniques to construct a high spatial and organism-type resolution budget of carbonate production (types, quantities and distribution) on the emergent reef flat of Warraber Reef, Torres Strait, Australia (10°12′S, 142°49′E). Estimates of production are evaluated via error analyses and comparisons with published estimates from other reef environments. Results highlight the improved spatial resolution that the census approach provides in understanding how several types of reef organisms contribute differently to sediment and framework sinks in reef platform environments. The implications of such differences are explored with regard to the geological development of reef platforms, global carbon budgets and the generation of detrital sediments. While production on the platform slope is likely to rival that produced on the reef top, this paper focuses on the latter environment since the Warraber reef flat is a relatively closed system in terms of carbonate and sediment generation.

Materials and methods

Field setting

Torres Strait consists of a shallow (15–25 m deep) shelf with scattered islands, reefs and shoals, situated between northeastern Australia and southern Papua

New Guinea (Fig. 1). Reefs grow throughout the Strait, fringing high islands, and as large platforms and coral shoals (Woodroffe et al. 2000). Warraber (Sue) Reef comprises a small cay and large platform system, with a total area of 11 km^2, situated in the central Strait. A planar-type reef (Hopley 1982), Warraber is flanked by two parallel, slightly deeper (1–2 m) platforms, Burrar (Bet) and Guijar (Poll) Reefs, which together are referred to as the Three Sisters (Fig. 1b).

Warraber Island comprises a 750 m by 1,500 m wide, oval-shaped, low-elevation cay (2–8 m above mean sea level, MSL) fringed by sandy beaches and situated towards the northwestern corner of the reef platform (Fig. 1a). The island and surrounding reef flat are Holocene in origin, having formed over a shallow Pleistocene platform (Woodroffe et al. 2000). The present reef flat comprises two distinct areas separated by differences in gross elevation but both fringed by an elevated, youthful coral-algal rim (Fig. 1c): a large, elevated, central platform in the east, with extensive sand flats covering fossil microatolls and branching coral; and a smaller, lower, western reef flat, characterised by inner muddy sandflats and outer coral patches interspersed with sandy channels and a boat channel, constructed in 1991, dividing the area in two. Woodroffe et al. (2000) interpret the western reef flat as more youthful than the central, emergent fossil reef flat.

Climate and oceanographic regime

Strong tidal currents (up to 4 ms^{-1}) scour the bed of Torres Strait affecting the form of reef development.

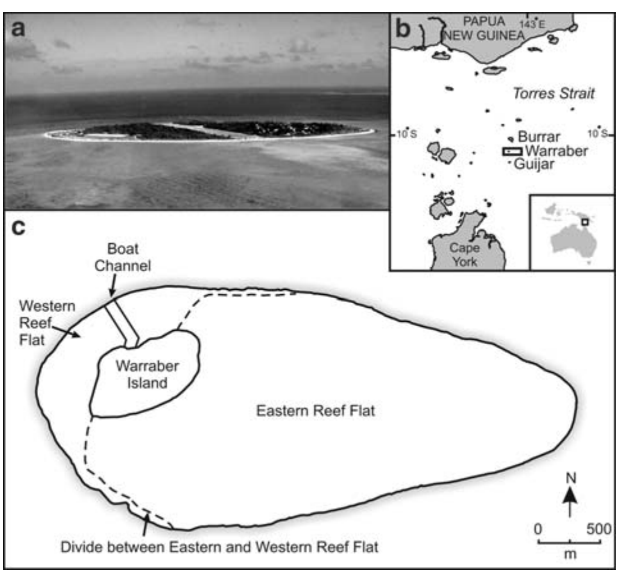


Fig. 1 **a** Oblique aerial photograph of Warraber Island, **b** its location in The Three Sisters reef group, Central Torres Strait, Australia, and **c** the main features of the Warraber Reef platform

The area is also subject to wind-generated surges developed locally, in the Indian Ocean, and in the Coral Sea (Amin 1978). Torres Strait lies north of the main cyclone belt of the GBR, with the central Strait having experienced seven Category 1–2 cyclones since 1910 (Puotinen 2004).

Warraber Reef experiences a semi-diurnal, mesotidal regime with a maximum range of 4 m above the lowest astronomical tide (ALAT). The entire reef flat is submerged at high tide, at which time offshore wave energy propagates across the platform. Conversely, at lower stages of the tide, the elevated central area and reef rim are largely exposed while the outer reef-flat experiences ponding (Brander et al. 2004). Significant wave heights outside the platform range from 0 to 1 m during the wet season, when north-westerly winds prevail, to 0–2 m during the dry season, when south-easterly winds prevail (Young and Holland 1996).

Methodology

Aerial photographs and initial field investigations were used to construct preliminary physiographic maps of the reef flat including a network of seven, 0.6–3.5 km long transects spaced around the island and radiating out to the reef edge. Transects (RT1–RT7) were surveyed using a staff and level and, within sets of three 1 m^2 quadrats at 37 sites along the transects, observations were made of sediment depth and type, and living organism type and planimetric cover or abundance (Electronic Supplementary Material). Rugosity was gauged as the ratio between the length of chain required to cover the cross-sectional profile of a quadrat and the 1 m aerial width of the quadrat profile (with 1–4 indicating flat to very rugose surfaces, respectively). Data from the transects were supplemented with additional quadrat surveys in each broad reef zone between them.

Coral species were identified using Veron (1986, 2000) and Wood (1983) and growth forms recorded. Molluscs were identified using Short and Potter (1987), Cernohorsky (1978), Hilton (1978, 1979) and Wilson and Gillett (1971) while foraminifera were identified using Jones (1994).

Analysis of variance (Single Factor ANOVA and Monte Carlo Randomisation Tests) was performed on the quadrat cover data for each organism type to compare inter- versus intra-site variation (Zar 1999). Cover types were mapped along RT1–RT7 and observations from intervening areas were used to classify the remaining reef flat. A map of ecological zones was constructed and the area occupied by each zone was calculated.

In this paper, the term 'calcification' refers to the potential carbonate production rates (g m^{-2} $year^{-1}$) of individual organisms, while 'production' or 'carbonate production' refers to the estimated rates (g m^{-2} $year^{-1}$) or amounts (t $year^{-1}$) of calcium carbonate ($CaCO_3$) produced. A review of published figures was conducted to determine the calcification rates, skeletal densities and aerial adjustment factors to apply to carbonate-producing organisms found on the reef flat in order to calculate per-quadrat production rates (Electronic Supplementary Material).

Calculated potential production rates for organisms found in each quadrat (average cover >1%) were then summed and results from replicate quadrats were averaged to give gross carbonate production estimates per site (g m^{-2} $year^{-1}$). The quadrat data and calculated zonal areas were summed to produce gross carbonate production rates and standard deviations (σ) (g m^{-2} $year^{-1}$). Maximum, minimum and best-estimate carbonate production figures were compared in order to test sensitivity to variation in species' production rates. This variation was then compared to that which resulted from the patchy nature of cover in survey quadrats (spatial variation).

Results

Reef-flat morphology

Transects RT1–RT6 show marked differences in reef-flat width, elevation and topographic complexity around Warraber Island (Fig. 2). Reef-flat width from island shore to reef rim ranged from 2,700 to 600 m from east to west, with a 0.7–1 m difference in elevation between the elevated eastern (RT1–RT3) and lower western (RT4–RT6) transects. The broad eastern reef can be divided into three morphological components: an elevated inner-reef platform (0–1,000 m from shore, predominantly above MSL) that reflects higher reef growth during the mid-Holocene; a central basin (1,000–2,200 m from shore, predominantly below MSL); and a higher-elevation windward reef rim (2,200–2,700 m from shore, situated above MSL). In contrast, the narrower, deeper, western reef flats do not exhibit distinct morphological differences but rather possess more-varied local-scale topography, reflecting the presence of muddy sandflats versus large live microatolls, interspersed by sandy hollows and dense, branching-coral thickets.

Spatial variability in living cover

The live cover data from quadrats along RT1–RT5 were analysed for spatial variability (Table 1): analysis of variance tests (Single Factor ANOVA and Monte Carlo Randomisation) indicate that for all cover types, except coral-massive and coral-foliose/encrusting/mushroom (coral-fol/encr/mu), data from the three replicate quadrats at each site were more similar than any random combination of quadrats ($P < 0.05$) (Table 1a, b). The non-significance of results for coral-massive and coral-fol/encr/mu reflects the highly variable local distribution patterns of these cover types. For example, massive corals commonly covered 80–100% of quadrats they occupied, but 0% of adjacent replicate quadrats, which frequently contained 100% sandy substrate. Taken alone, neither type of quadrat accurately represents local ecological cover but in combination they indicate the types and densities of organisms present. It was, thus, deemed suitable to group cover data from each set of three replicate quadrats into averaged 'per site' values.

Inter-transect variation was not greater than intra-transect variation (Table 1c) with P-values significant ($P = 0.046$) only for the category 'coral-ramose-other', indicating that variation between sites across the reef flat as a whole was no greater than the variation found along each transect for all other cover types. Accordingly, it

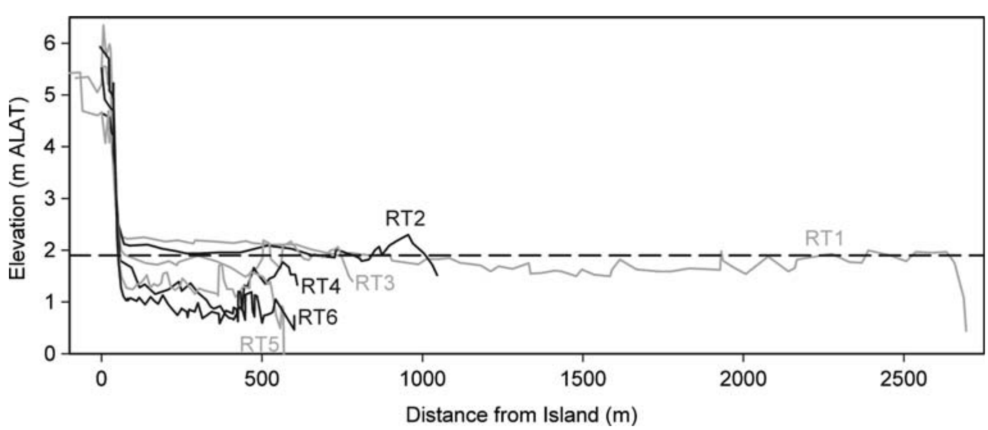


Fig. 2 Topographic surveys of the reef-flat transects in relation to mean sea level (*dashed line* at 1.9 m above the lowest astronomical tide, ALAT)

Table 1 Results from analysis of variance tests for (a) cover by quadrat versus by site, (b) cover by site within transect, and (c) cover by site versus by transect

Cover type	(a) Single factor ANOVA[a]		(a) Monte Carlo randomisation	(b) Single factor ANOVA[a]		(c) Single factor ANOVA[b]		(c) Monte Carlo randomisation
	Site between transect			Site within transect		Site versus transect		
	F	*P*-value	*P*-value	*F*	*P*-value	*F*	*P*-value	*P*-value
Coral-ramose-other	18.079	<0.001	0	15.162	<0.001	2.732	0.046	0.041
Coral-ramose-*Acropora*	2.870	<0.001	0.003	2.578	<0.001	2.022	0.115	0.102
Coral-massive	1.358	0.133	0.089	1.428	0.106	0.559	0.694	0.733
Coral-foliose/encrusting/mushroom	1.007	0.476	0.188	0.948	0.555	1.564	0.208	0.162
Halimeda	1.885	0.011	0.022	1.834	0.017	1.247	0.311	0.298
Coralline algae—encrusting	12.452	<0.001	0	12.566	<0.001	0.919	0.465	0.515
Coralline algae—articulated	3.875	<0.001	<0.001	3.936	<0.001	0.861	0.498	0.493
Mollusc	9.957	<0.001	0	9.138	<0.001	1.807	0.152	0.138
Foraminifera	1.714	0.026	0.039	1.590	0.052	1.701	0.174	0.166
Brown algae	6.125	<0.001	0	5.906	<0.001	1.333	0.279	0.274
Sponge	2.696	<0.001	0.002	2.774	<0.001	0.745	0.569	0.588
Sea grass	1.891	0.011	0.019	2.019	0.007	0.43	0.786	0.902

[a] Degrees of freedom within groups = 74, degrees of freedom between groups = 36, $n = 111$, confidence level = 0.95

[b] Degrees of freedom within groups = 32, degrees of freedom between groups = 4, $n = 37$, confidence level = 0.95

was deemed inappropriate to further group the cover data by transect. This finding indicates a pattern of ecological zones running across, rather than along, the reef transects. For the cover type ‘coral-ramose-other’ the higher inter-transect variation is consistent with the division of the reef flat into a series of elevated eastern and lower western zones, the latter of which is based primarily on variation in the cover of *Montipora digitata*. West of the boat channel *M. digitata* is sparse, occurring in outer reef-flat zones as small to medium sized branching colonies while east of the boat channel *M. digitata* forms a number of tall, wide, dense, monospecific bands mid-way across the reef flat which are replaced by a moderately tall, dense, mixed cover of *M. digitata* and *Acropora* species and massive coral colonies.

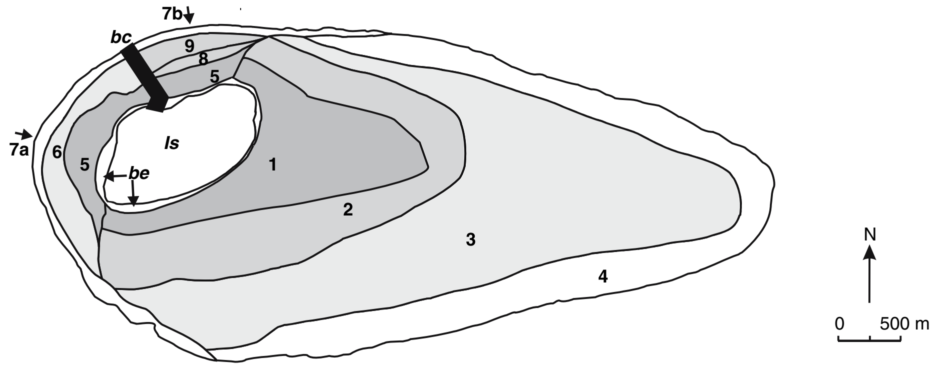
Based on the ‘per site’ census data and observations from intervening areas, ten ecological reef-flat zones were determined according to percentage living cover and substrate type, each zone being characterised by a distinct combination of biological assemblages and substrate types (Fig. 3). All of the eastern zones were >1 km^2, with those in the west and north <0.5 km^2 each, while the total area covered by the zones (i.e. excluding the boat channel and island) was 10.46 km^2. The island, boat channel and whole reef platform cover 0.81, 0.06 and 11.33 km^2, respectively (Fig. 3).

Reef-flat carbonate productivity

Table 2 summarises the organism-level calcification rates used to calculate carbonate production on the Warraber reef flat. The results of these calculations are summarised for each zone in Table 3a, which shows the ‘best estimate’ carbonate production rates (g m^{-2} year^{-1}) of the different assemblages of organisms with standard deviations indicating levels of inter-quadrat variation in each zone.

Productivity estimates vary between the ten zones by two orders of magnitude, from 65 g m^{-2} year^{-1} in Zone 5 to 3,999 g m^{-2} year^{-1} in Zone 6. Such large differences are expected and are due to spatial variability in live cover and the composition of carbonate-producing assemblages found in each zone (e.g. mollusc versus coral dominated). The most productive areas (1,764–3,999 g m^{-2} year^{-1}) are located on the central to outer reef-flat zones characterised by massive and mixed-branching/massive coral cover (Zones 3, 6, 9), while moderate amounts of carbonate (566–1,081 g m^{-2} year^{-1}) are produced in the dense-branching and reef-rim zones (4, 7a–b). The least productive areas of the reef flat (65–161 g m^{-2} year^{-1}) are those dominated by sandy or muddy substrate located close to the island and on the elevated eastern reef flat (Zones 1–2, 5; Table 3a).

In addition to between-zone differences in estimated carbonate production rates, a large degree of within-zone variation was found as demonstrated by the standard deviations associated with each rate (Table 3a). This variation is explained by the patchy nature of the ecosystems. In Zone 3, for example, quadrats with 100% cover of highly productive massive and branching corals occurred adjacent to quad-



Zone Description	Area (km^2)	Rough (m/m)	Cover (%)	Zone Description	Area (km^2)	Rough (m/m)	Cover (%)
1. sandy reef flat with molluscs	1.3	1	3	8. dense branching coral	0.06	1.3	85
2. sandy reef flat with algae	1.66	1	38	9. mixed coral	0.34	1.5	35
3. sandy reef flat with coral	3.98	1.4	55	be. sand and rock beach		1	<1
4. E raised algal rim	2.13	1.2	68	Is. island	0.81	-	0
5. fine sand reef flat	0.46	1	16	bc. boat channel	0.06	-	<1
6. mixed coral	0.12	1.1	20	Total reef flat zones	10.46	1.2	46.7
7a. W raised algal rim	0.28	1.6	102	Total reef system	11.33	-	-
7b. NW raised algal rim	0.12	1.7	45				

Fig. 3 Map and description of the ten identified ecological zones of the Warraber reef flat, including area, roughness and percentage cover

Table 2 Estimated calcification rates used to calculate carbonate production on the Warraber reef flat as derived from a review of published rates (see Electronic Supplementary Material for details)

Organism	Best-estimate calcification rate (g m^{-2} $year^{-1}$)	Minimum to maximum calcification rates (g m^{-2} $year^{-1}$)	Adjustment factor
Coralline algae	1,872	1,500–2,500	Multiplied by the square of quadrat rugosity for crustose species
Coral massive	16,160	7,680–24,640	
Cora l-foliose/ encrusting/mushroom	17,000	3,000–31,000	
Coral ramose-*Acropora*	19,242	10,818–27,666	Multiplied by an effective cover factor of 0.25
Coral ramose-other	1,394	767–2,021	Multiplied by a branch extension factor of 0.4
Halimeda	1,066	400–1,667	
Foraminifera	120	30–230	Multiplied by a factor of between 0 and 3 depending on organism density
Molluscs	100	10–200	Multiplied by a factor of between 0 and 3 depending on organism density

rats containing only bare sand. Analysis of variance performed on the per quadrat carbonate-production data (One-way ANOVA and Monte Carlo Randomisation Tests) confirm that, despite the high degree of intra-zonal variation, the zonal grouping of quadrats is significant ($P < 0.001$, degrees of freedom between groups = 9 and within groups = 101, $n = 111$).

Total reef-flat carbonate production

The average rate of estimated carbonate production for the reef flat as a whole was 1,663 ± 1,780 g m^{-2} $year^{-1}$ (mean ± SD) (Table 3a) with the total area covered by carbonate-producing organisms 2.41 km^2 or 23% of the total reef flat. These organisms produce an estimated 17,399 ± 18,618 t $CaCO_3$ $year^{-1}$ (mean ±

Table 3 **a** Gross carbonate production rates, and **b** amounts by producer type across the ten ecological zones of the Warraber reef flat calculated using the best-estimate calcification rates

Zone	1	2	3	4	5	6	8	9	7a	7b	Reef flat	Reef flat [cover[b] (%)]
(a) Carbonate production rate (g m^{-2} year^{-1})												
Coral ramose-other	0	0	70	0	0	21	1,046	376	0	0	38	12
Coral ramose-*Acropora*	0	0	321	0	0	994	0	577	321	0	170	4
Coral massive	0	24	2,343	18	13	1,966	0	754	0	0	974	26
Coral foliose/encrusting/mushroom	0	0	57	38	0	453	0	57	0	113	46	1
Coralline algae—encrusting	1	22	234	821	7	541	0	0	586	453	299	43
Coralline algae—articulated	1	6	32	21	0	3	0	0	0	0	18	4
Molluscs	148	61	39	122	17	17	0	0	0	0	69	3
Halimeda	0	19	27	8	8	4	0	0	14	0	16	6
Foraminifera	0	29	33	53	20	0	0	0	160	0	33	1
Framework	1	46	3,026	876	21	3,976	1,046	1,764	906	566	1,527	86
Direct sediment	149	115	131	205	45	23	0	0	174	0	136	14
Average production	149	161	3,157	1,081	65	3,999	1,046	1,764	1,081	566	1,663	100
Standard deviation	115	187	3,931	819	113	1,343	304	887	352	98	1,780	18
(b) Gross carbonate production (t year^{-1})												
Coral ramose-other	0	0	281	0	0	7	66	47	0	0	401	2
Coral ramose-*Acropora*	0	0	1,278	0	0	341	0	72	90	0	1,780	10
Coral massive	0	41	9,335	38	6	674	0	94	0	0	10,187	59
Coral foliose/encrusting/mushroom	0	0	226	81	0	155	0	7	0	13	482	3
Coralline algae—encrusting	1	36	934	1,751	3	185	0	0	164	54	3,128	18
Coralline algae—articulated	1	10	128	44	0	1	0	0	0	0	185	1
Molluscs	193	100	155	261	8	6	0	0	0	0	722	4
Halimeda total	0	32	106	18	4	1	0	0	4	0	165	1
Foraminifera	0	48	133	114	9	0	0	0	45	0	349	2
Framework	1	76	12,053	1,870	9	1,363	66	219	253	67	15,978	92
Direct sediment	194	191	522	437	20	8	0	0	49	0	1,421	8
Total production	195	267	12,575	2,306	30	1,371	66	219	302	67	17,399	100
Standard deviation	150	309	15,660	1,748	51	460	19	110	98	12	18,618	107
Total production (%)	1	2	72	13	0	8	0	1	2	0	100	–

Cover[b] is the percentage of area occupied by carbonate producers, which comprises 23% or 2.41 km^2 of the reef flat

SD) (Table 3b). Total production varies by three orders of magnitude between zones, from 30 t year^{-1} in Zone 5 to 12,575 t year^{-1} in Zone 3, as a function of the area of each zone, as well as of the calcification and cover rates of organisms present.

Table 3b presents estimates of the amount of carbonate contributed annually by the different producer types, highlighting spatial variability in the importance of carbonate producing organisms on the reef surface. Production was dominated by molluscs in Zones 1–2, by coral in Zones 3, 6, 8 and 9 and by encrusting coralline algae in Zones 4 and 7b. Despite the importance of each of these organisms within individual zones, some are quantitatively of little importance to total production. The dominance of coral in Zone 3, for example, represents far more carbonate (11,120 t year^{-1}) than the dominance of molluscs in Zones 1–2 (100–193 t year^{-1}). Total production on the Warraber reef flat is dominated by Zone 3 (70% of total or 12,575 t year^{-1}) while the majority (87%) of carbonate produced on the reef flat is contributed by only three producers: massive corals (59%), encrusting coralline algae (18%), and branching *Acropora* (10%). Other producers contribute ≤4% each to total carbonate production (Table 3b).

Comparisons between the percentage of total carbonate produced by each type of organism and cover[b] (the cover an organism relative to the total area occupied by carbonate producing organisms, 2.41 km^2) reveals a markedly non-linear relationship (Table 3) due to the differential growth and production rates in Table 2. Most notably production by massive, branching-*Acropora* and fol/encr/mu corals is large relative to their areal cover, whilst production by encrusting coralline algae, other branching corals, *Halimeda* and articulated coralline algae is small relative to their cover. Further, the dominant carbonate producer at each site was rarely the dominant cover type. This is due to the predominance of the non-carbonate producing brown algae as well as to the large amount of carbonate produced by corals per unit area compared to encrusting coralline algae.

Sensitivity of production results to growth rates

The sensitivity of carbonate production results to variations in organism growth rates was modelled for the main carbonate producers using mean (best-estimate), minimum and maximum calcification rates (Table 2) which, as indicated in the Electronic Supplementary Material, are conservative and excessive production values, respectively. By comparison with the mean scenario, the proportion of carbonate produced by individual organism types changes by <4 and <2% under the minimum and maximum scenarios, respectively (Table 4), with estimated total carbonate produced under these scenarios 7,726 and 26,347 t year^{-1}, respectively, corresponding to average production rates of 738–2,518 g m^{-2} year^{-1}.

Such comparisons do not indicate the effect of each organism experiencing different growth conditions, some finding them average, others optimal or sub-optimal. Under these circumstances greater variation in the proportion of carbonate produced by each organism could be expected, with total production somewhere between 7,726 and 26,347 t year^{-1}. Using the maximum coral scenario but minimum scenario for other organisms, the proportion of carbonate produced by coral would increase 14%, while decreasing 8% for coralline algae and 0–4% for other organisms. Total production under this scenario is 12,763 t year^{-1}.

Potential variation in carbonate production with differing growth conditions may be contextualised relative to actual variation resulting from the patchy nature of reef ecosystems (adjacent quadrat cover variation) as indicated by standard deviations in Table 3. Spatial variation in the best-estimate carbonate production on Warraber (i.e. ±SD) is of the order of ±18,618 t year^{-1} (±107%), or ±1,780 g m^{-2} year^{-1}. Thus the potential variation in carbonate production resulting from the patchy nature of reef ecosystems is greater than that which might result from variable growth conditions.

Discussion

The census approach yields estimates of carbonate production by organism-type at a number of spatial scales, including the entire reef platform, eco-morphological zones on a reef platform, and within eco-morphological zones. Of interest are: how these results compare with carbonate rates calculated for reef platforms elsewhere; how the census approach compares with commonly used alkalinity reduction and geological techniques; whether the census approach provides improved accuracy and resolution of carbonate productivity on reefs and; implications for interpreting reef-flat carbonate productivity, geological development of reef platforms and sediment budgets.

Warraber carbonate productivity in global context

Table 5 contains examples of published gross carbonate-production estimates alongside those calculated for Warraber (for a comprehensive review of carbonate-production rates up to 1985 see Kinsey 1985). The estimates of Smith and Kinsey (1976) and Kinsey (1981) are given as examples of rates calculated using alkalinity-reduction techniques, which, as noted, include both carbonate precipitation and early dissolution. In recognition of methodological differences, comparisons focus on the order of magnitude of estimates. The average estimated production rate for the Warraber reef flat, 1.66 kg m^{-2} year^{-1}, is lower than the majority of estimates from other reef environments, which range between 0.8 and 30.5 kg m^{-2} year^{-1}. The Warraber rate is, however, of the same order of magnitude as those from other reef-flat studies (*ca.* 4 kg m^{-2} year^{-1}, Table 5).

A number of factors could contribute to the low-production value for Warraber and reef flats in general.

Table 4 Estimated amounts and proportions of carbonate produced by the different types of organism on Warraber determined using the best estimate (mean), minimum and maximum calcification rates

	$CaCO_3$ production (t year^{-1})			$CaCO_3$ production (%)		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
CA encrusting	3,128	4,177	1,282	18	16	17
CA articulated	185	248	76	1	1	1
Coral ramose-other	401	581	221	2	2	3
Coral ramose-*Acropora*	1,780	2,559	1,001	10	10	13
Coral massive	10,187	15,533	4,842	59	59	63
Coral foliose/encrusting/mushroom	482	879	85	3	3	1
Halimeda total	165	258	62	1	1	1
Molluscs	722	1,444	72	4	5	1
Foraminifera	349	668	87	2	3	1
Total	17,399	26,347	7,726	100	100	100

Table 5 Comparison of carbonate-production estimates for the Warraber reef flat with published rates from several reef environments

Location	Reef environment	Method	Carbonate production (kg $CaCO_3$ m^{-2} $year^{-1}$)	Study area	Total production (t $year^{-1}$)	Source
Warraber Island, Torres Strait	0–4 m deep inter-tidal reef flat	Census-based	1.66	10,462,700 m^2	17,399 ± 18,618	Present study
Green Island, Great Barrier Reef	Reef flat and slope	Census-based	1.6–3.9[a]	410,000 m^2	656–1,606	Yamano et al. (2000)
Mode of several Pacific Reefs	1–3 m deep, seaward reef flat	Alkalinity-reduction	4	–	–	Smith and Kinsey (1976)
Mode of several Pacific Reefs	Protected 5–6 m deep lagoon/bank	Alkalinity-reduction	0.8	–	–	Smith and Kinsey (1976)
Japtan Inter-Island Reef, Eniwetok	Inter-island reef flat	Census-based	30.5	455 m long transect	–	Odum and Odum (1955)
Kailua Bay, Hawaii	Fringing reef with large sand bodies and a diverse benthic community	Census-based	3.18	10,000,000 m^2	74,810 ± 7,440	Harney (2000)
Kaneohe Bay, Hawaii	Shallow (<3 m) reef flat	Alkalinity-reduction	4.7 (3.5–8)	200 m long transect	–	Kinsey (1981)
Discovery Bay, Jamaica	Shallow (<3 m) reef flat	Alkalinity-reduction	4.4 (1.2–10)	200 m long transect	–	Kinsey (1981)
Bellairs Reef, Barbados	5 m deep fringing reef	Census-based	15	10,800 m^2	163	Stearn et al. (1977)
Cane Bay, St. Croix, Virgin Islands	Fringing reef 2–60 m deep incl. hard ground, reef flat and slope	Census-based	1.9 (0.85–5.0)	30,000 m^2	57.5	Sadd (1984)
Cane Bay, St. Croix, Virgin Islands	Fringing reef shelf, 0-40 m deep incl. reef flat, slope and shelf	Census-based	1.21 (0–5.78)	412,200 m^2	499[a]	Hubbard et al. (1990)
Hypothetical	Reef flat	Census-based	3	–	–	Chave et al. (1972)
Hypothetical	Lagoon	Census-based	5	–	–	Chave et al. (1972)
Hypothetical	Algal ridge	Census-based	9	–	–	Chave et al. (1972)
Hypothetical	Upper slope	Census-based	60	–	–	Chave et al. (1972)
Hypothetical	Lower slope	Census-based	8	–	–	Chave et al. (1972)

[a] Calculated from production and areal figures given in the source

First, Warraber is an emergent reef flat where productivity is constrained across broad tracts of elevated reef. Second, it is important to note that Table 5 lists studies undertaken in different reef environments and where production was dominated by different organisms. On the Warraber reef flat, the total estimated carbonate production was dominated by coral (74%), with subordinate proportions produced by encrusting coralline algae (18%) and other organisms in minor proportions (Table 3b).

In reef-flat environments, low-production rates have also been reported by Yamano et al. (2000) on a coral, *Halimeda* and foraminifera dominated reef surface and by Eakin (1996) with production dominated by coralline algae (56%) and coral (44%). A few studies of other environments have found similar low-productivity values: for example, Stearn et al. (1977) on Bellairs fore-reef slope where coral was responsible for 71%, and coralline algae for 29%, of production, and Hubbard et al. (1990) on a shelf-edge reef where coral comprised 93%, and coralline algae 7%, of production.

Comparison of census-based and alkalinity-reduction techniques

From an extensive review of alkalinity-reduction studies, Kinsey (1983, 1985) proposed that a series of absolute carbonate production rates were applicable to reefs in the latitudinal range 23°S to 23°N: 4 kg m^{-2} $year^{-1}$ on high-energy Pacific coral/algal reef-flat and rim environments; 0.5 kg m^{-2} $year^{-1}$ in sheltered sandy back-reef environments; and 2 kg m^{-2} $year^{-1}$ in shallow coral environments.

For comparison with the census approach used here the Kinsey modes were applied to Warraber, with Zones 1, 2 and 5 classified as sandy back-reef; Zones 4, and 7a, b as high-activity rim; and Zones 8 and 9 as shallow-coral environments. Due to the patchy nature of coral and sand cover in Zones 3 and 6 these were characterised as intermediate between Kinsey's sandy reef-flat and shallow-coral environments. Using these modes, total annual carbonate production for the entire reef flat is 16,540 t $year^{-1}$, with an average production rate of 1.58 kg m^{-2} $year^{-1}$. At the level of the entire reef flat these results compare well with the census-based estimates, providing a first approximation of reef-flat carbonate productivity.

Important differences exist, however, at the individual reef-zone scale. Figure 4a, b compares the census results with those calculated using Kinsey's modes across each zone: major differences occur in zones characterised as reef rim (4, 7a, b) or sandy reef flat with patchy mixed coral cover (3 and 6). Zones 3 and 4, for example, contribute 24 and 52% of total carbonate produced when calculated using Kinsey's modes versus census-based estimates of 72 and 13%. These comparisons highlight the need for more-than-superficial classification of reef ecosystems when using alkalinity-reduction based modes to estimate carbonate productivity and raise questions of accuracy regarding their application in global models of reef productivity independent of ecosystem investigation.

Figure 4a also differentiates the carbonate produced across the reef flat by 'framework' versus 'direct sediment' producers (after Harney and Fletcher 2003), a distinction not possible with alkalinity-reduction results. Direct sediment production is shown to comprise a minor proportion of total carbonate production on the reef flat (8%).

In addition to the above inter-zone insights, the census-based approach provides improved resolution of spatial variations in productivity within individual reef-flat zones. As outlined in the Electronic Supplementary Material, with the exception of molluscs, the contemporary growth rates of carbonate-producing organisms are well documented from a number of reefs and reef environments and show that growth rates vary according to environmental conditions and the age and health or organisms.

However, Scoffin and Garrett (1974) and Vecsei (2001, 2004) show that growth rates are sufficiently similar within species for slight variations in the cover of one species relative to another to drastically alter the constituent composition of carbonate sinks. Both the rates expressed in Table 2, and the comparisons made between productivity variations due to the patchy nature of reef ecosystems and potential variation in growth conditions support this assertion. The potential for variation in carbonate sinks due to variation in species cover rates is ultimately expressed in the estimates summarised in Table 3, which show that productivity varies considerably between the different zones or sub-environments of the reef flat (0.065–3.99 kg m^{-2} $year^{-1}$) depending on the cover of different producers.

For example, these figures are particularly sensitive to the presence of massive coral, which is highly productive and largely limited to the deeper, central to outer reef flat (Zones 3, 6, 9). Within these zones estimated production rates (1.76–3.99 kg m^{-2} $year^{-1}$) approach average rates published for other reef flats (Table 5). In contrast, estimated production rates for the moderately productive, monospecific branching-coral Zone 8 and raised coralgal-rim Zones 4, and 7a, b (0.57–1.08 kg m^{-2} $year^{-1}$) are comparable to those recorded for sand areas (0.4–1.2 kg m^{-2} $year^{-1}$) in

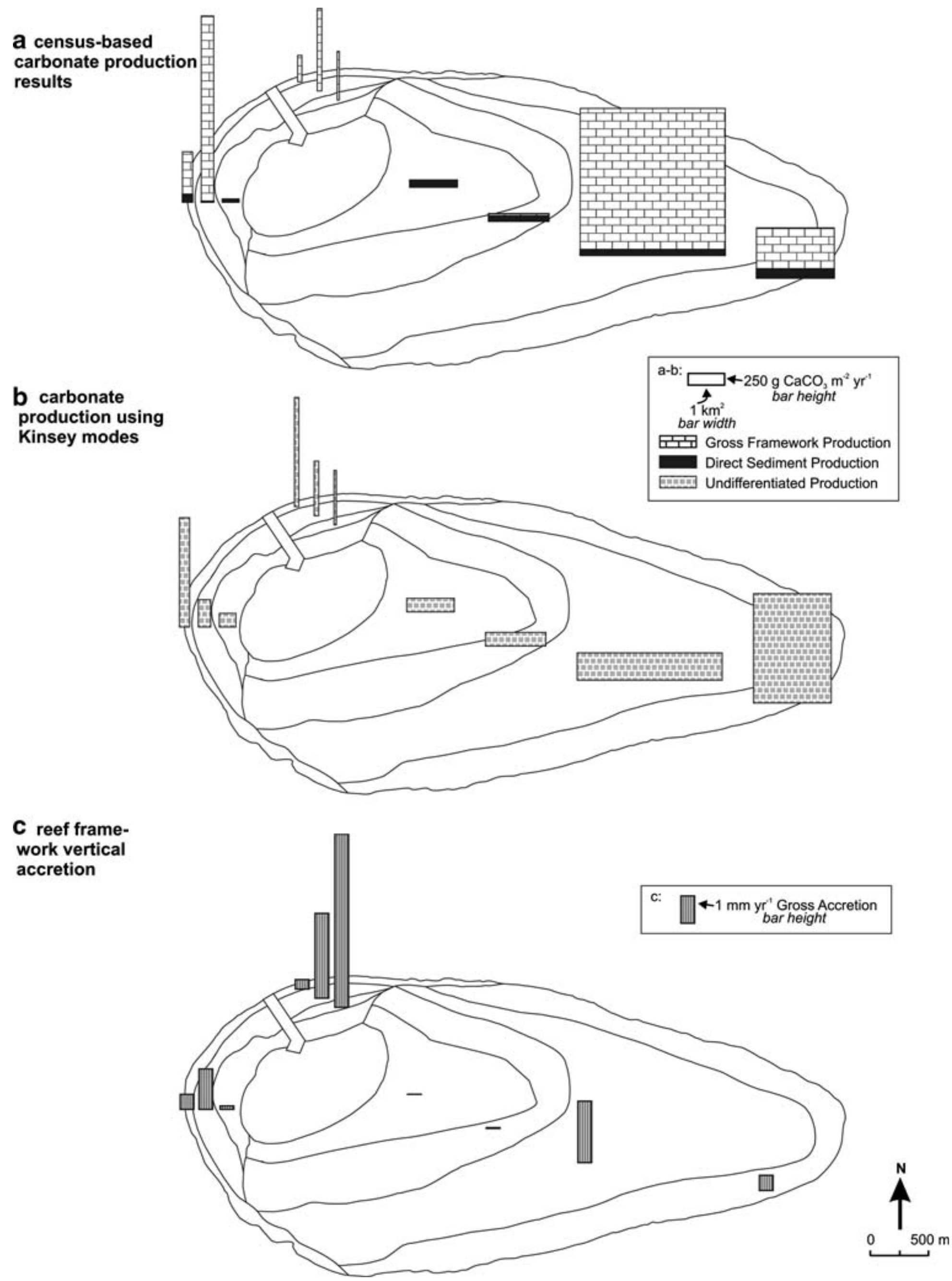


Fig. 4 Carbonate production rates (*bar height*) and amounts (*bar area*) in the ten ecological zones of the Warraber reef flat **a** estimated using census-based techniques, **b** derived from Kinsey's (1983, 1985) alkalinity-reduction review, and **c** gross vertical framework accumulation rates calculated for the ten ecological zones based on framework building organism cover, production and density

Kinsey (1985). Estimates from the least-productive, sandy, inner reef-flat zones on Warraber (0.065–0.15 kg m^{-2} year^{-1}) are amongst the lowest-recorded carbonate production rates.

Geological context of the census-based findings

The spatial variations (intra-reef-flat) in carbonate production highlighted by the census-based estimates provide a basis for evaluating long-term changes in reef production from the mid-late Holocene at the sub-reef scale. Gross vertical framework accretion on Warraber may be estimated using average carbonate production rates for each type of framework builder (corals, encrusting coralline algae) present in a zone divided by their individual densities (listed in Electronic Supplementary Material). This gives a gross vertical framework accretion rate for the reef flat as a whole of 1.15 mm year^{-1}, with rates varying from 2.25 to 6.34 mm year^{-1} on the outer reef flat, from 0.35 to 0.56 mm year^{-1} on the reef rim, and at 0.0 mm year^{-1} on the inner reef flat (Fig. 4c). Accumulation rates vary across the ten ecological zones, independent of zone size, depending on the types of organisms that dominate production and the densities of their skeletons. Alternatively, if gross accumulation is calculated according to Harney and Fletcher's (2003) average framework density (1.48 g cm^{-3}), the reef-flat average is 1.03 mm $year^{-1}$, a similar figure to the 1.15 mm $year^{-1}$ estimate derived using detailed organism densities.

Harney and Fletcher (2003) and Hubbard et al. (1990) report average framework erosion rates (biological plus mechanical) of 27 and 21%, respectively. Using a 25% erosion value for Warraber, the mean net vertical framework accumulation on the reef flat is 0.86 mm $year^{-1}$, the same order of magnitude as Harney and Fletcher's (2003) 0.60 mm $year^{-1}$ rate for Kailua Bay and that calculated from Hubbard et al.'s (1990) results for Cane Bay, 0.61 mm $year^{-1}$, but less than Smith's (1983) 3 mm $year^{-1}$ rate for Holocene margin reefs, Stearn et al.'s (1977) 11 mm $year^{-1}$ rate for a rapidly growing reef, and Buddemeier and Smith's (1988) 10 mm $year^{-1}$ sustained-maximum consensus rate.

Using core samples from the inner reef flat and island, Woodroffe et al. (2000) indicate that the Holocene reef started to grow over Pleistocene foundations 6 m below the present reef surface around 6,700 years ago, reaching its present elevation 5,300 years ago, when sea level was 0.8–1.0 m higher than today, thereafter ceasing vertical accumulation. About 6 m of vertical framework accumulation over the 1,400 years between 6,700 and 5,300 years ago corresponds to a net vertical accumulation rate on the inner reef flat of 4.29 mm $year^{-1}$, including both framework and sediment material. Assuming the ratio of framework to sediment within the reef is around 50:50, as roughly indicated by core composition, and consistent with Buddemeier and Smith (1988), the inner reef flat accumulated framework at an average net rate of 2.14 m $year^{-1}$ from 6,700 to 5,300 years ago. Both the 2.14 mm $year^{-1}$ 'framework' and 4.29 mm $year^{-1}$ 'total' mid-Holocene accumulation rates for the inner-reef flat are well within the range of contemporary gross framework accumulation rates calculated for the outer reef flat but above those of the inner zones (Fig. 4c). The finding that the emergent inner-reef flat is not presently accumulating is consistent with Woodroffe et al.'s (2000) results.

The contrast between the contemporary lack of inner reef-flat accumulation and the core-derived mid-Holocene rates may be explained by intra-platform and regional changes in carbonate production conditions as constrained by sea level and pace of reef development. At the reef scale, Woodroffe et al. (2000) describe how the now-central zones 'caught up' with sea level about 5,300 years ago, followed by stepwise extensions south up to 4,500 years ago, and subsequent infilling of central areas with ongoing extensions northward. This morphological development would have induced intra-platform changes in physical and growing conditions with increasing distance to the rim for inner areas—at the same time as the regional 0.8–1 m fall in sea level led to the emergence of the central reef flat, a characteristic which is common on the fringing reefs of the inner GBR. Together, these changes would have caused the now-central zones to experience a succession from reef-rim, to lagoon, to outer reef-flat and, finally, to emergent inner-reef-flat environment. Results shown in Fig. 4 indicate that such a succession would have been accompanied by large lateral shifts in reef-flat ecology and shifts in carbonate production and framework accumulation.

Determining the high-level of variation in framework accumulation rates that exists across the contemporary Warraber reef flat (Fig. 4c) was only made possible using census-based techniques. Results show that the largely inter-tidal Warraber reef flat produces approximately two orders of magnitude less carbonate than typical back reef (sub-tidal) settings. Largely inter-tidal reef surfaces are common in the Indo-Pacific, particularly where reefs accreted in keep-up or catch-up growth mode in the mid-Holocene, subsequently being emerged through relative sealevel fall in the late Holocene. Given the spatial extent of the emergent reef platform on Warraber (3.76 km^2 or 33% of reef platform surface), results suggest that global estimates of carbonate productivity should be revised in light of the low productivity of these surfaces and the likelihood that such surfaces cover a substantial proportion of Indo–Pacific reefs.

Extending the census-based geological model into the future, it is possible that climate-change induced sealevel and storminess changes could lead to a partial reversal of Holocene changes in growth conditions across Warraber platform. The extent of this reversal will likely be determined by reef community response to the latter two physical factors, to temperature changes (Buddemeier and Smith 1988) and to the sediment accumulations now occupying the mid-Holocene growth surface.

Buddemeier and Smith (1988) establish an apparent global match between reef growth rates and sea level rise, questioning whether this match is coincidental or functional. The variation in growth rates found between the emergent-inner and deeper-outer reef-flat zones on Warraber indicates that the match is, in large part, functional in this setting. This is consistent with Kinsey's (1981) suggestion that the currently shallow and slow-growing Holocene reef flats of the Pacific possess the same potential to increase growth rates in response to accelerated sea level rise as the currently fast-growing Holocene reefs of the Caribbean.

Sediment implications

The results of this study have significant implications for interpreting carbonate sinks and their relationship to detrital sediment budgets within reef systems. Figure 5 contrasts the proportion of total carbonate production contributed by the different reef-flat producers with their occurrence as constituents in the surficial sediments of each zone and, ultimately, in the island beach (Hart 2003). The overall dominance of coral (74%) and small contribution of molluscs (4%) to reef-flat production contrast markedly with their representation in beach sediments (coral 8%, molluscs 55%). *Halimeda* is also over-represented in the beach (7%) relative to its production of carbonate (1%). Coralline algae (19% $CaCO_3$, 16% sediment) and foraminifera (2% $CaCO_3$, 5% sediment) are similar in terms of their carbonate contributions and beach sediment representation. Organism differences between carbonate contributions and surficial reef-flat sediment composition are slightly less than, but of a similar order of magnitude to, those for the island beach (Fig. 5). These differences may be explained by variations in framework accommodation space (Fig. 2), in the spatial distribution of 'direct sediment' and 'framework' production across the reef zones (Fig. 4a), in processes of sediment-particle production (Chave 1964) and taphonomic processes (Scoffin 1992), in particular transportability (Folk and Robles 1964; Maiklem 1968), and by spatial separation between carbonate production and sediment-deposition zones (Yamano et al. 2000; Purdy and Gischler 2005).

For example, gastropod tests immediately contribute to the detrital sediment reservoir upon organism mortality and they have higher turnover rates than

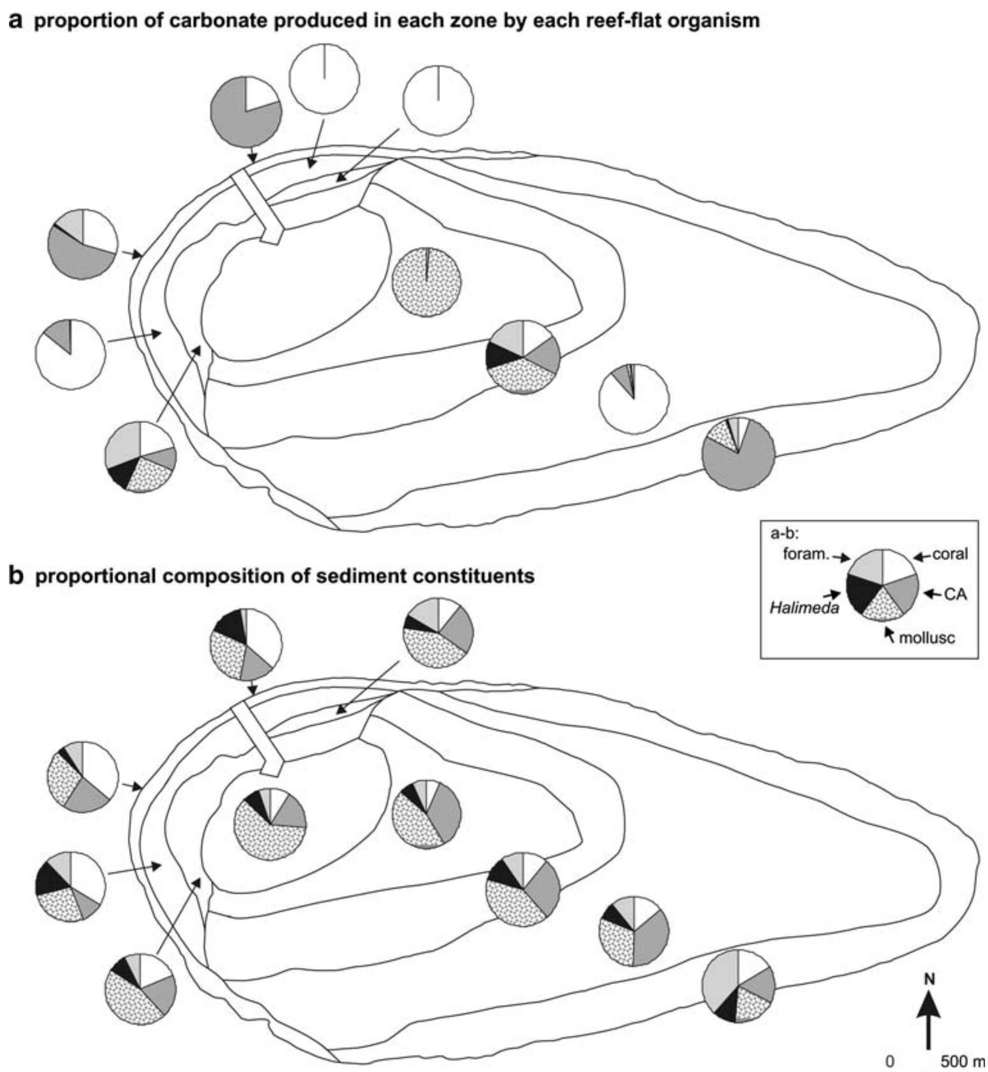


Fig. 5 **a** Proportion of carbonate production contributed by the five main producers compared to **b** the constituent composition of sediments within each ecological zone of the reef flat (*foram* foraminifera, *CA* coralline algae)

coral, helping explain their high abundance in reef-flat sediments. Furthermore, gastropod tests are of a suitable size for beach nourishment, are predominantly produced in areas close to the island (Zones 1, 2, 5) where there is little accommodation space and their skeletal architecture make them highly susceptible to transport (Maiklem 1968; Kench and McLean 1996). Together these factors could explain mollusc dominance of reef-flat and island-beach deposits (Fig. 5) despite their small contribution to total reef-flat carbonate production (Table 3).

In contrast, most carbonate production and the vast majority of coral production on Warraber occurs on the outer reef flat (Fig. 4a), which has up to 1 m of accommodation space (Fig. 2) and, thus, potential for carbonate to be retained as framework. And, although not well quantified, coral has high-durability properties related to its architecture (Chave 1964; Folk and Robles 1964; Scoffin 1987), implying relatively slow conversion rates to sediment, contributing to the dilution of coral in surficial sediments by organisms with higher turnover and sediment-conversion rates (Scoffin 1992).

Furthermore, when coral is eventually broken down it may not be into particle sizes suitable for island-beach nourishment. Coral bioeroders observed on the Warraber reef flat comprised grazing gastropods (Zones 1, 4, 7a, b), boring bivalves (Zone 3, 6) and *Echinometra* urchins (Zones 6 and 9). With the exception of bivalves, which can break off large skeletal blocks, these organisms tend to reduce coral to very fine sediment bypassing the sand sizes that comprise the island beach.

Mechanical erosion of branching coral is more likely to produce sediment suitable for island-beach maintenance on Warraber. West of the island delicate branches of *M. digitata* and *Seriatopora hystrix* were observed to be broken off and swept islandward from Zones 8 to 9 during storm-wave conditions. The amount of carbonate produced on Warraber by branching corals (12%) which may break into sand-sizes particles is, however, small versus that produced by microatolls (59%, Table 3) which likely erode into finer particle sizes and which must traverse up to 2 km of reef surface to contribute to the island deposits.

These initial comparisons indicate that the total amount of carbonate produced on the reef flat is a poor indicator of both the amount and type of carbonate available to be turned into sediment and contribute to sedimentary deposits on reef platforms (e.g. islands, sand aprons and reef-flat sand reservoirs). Clues as to the potential production of beach-nourishing sediment are provided by teasing out the distributions and types of carbonate produced in the different zones of the reef flat. It is recommended that the next step in understanding the relationship between the rates and types of carbonate produced, and the ultimate nature of sink deposits, is to make detailed comparisons between the types, amounts and distribution of carbonate production, and the types and amounts of material found in each reef sink.

Over the longer-term the shifts in reef top ecology discussed and subsequent changes in dominant producers (and rates of production) have major implications for the sediment reservoir and development of geomorphic deposits on reef surfaces. For example, reef islands are unconsolidated accumulations of reef sediment. The accumulation of such islands and their ongoing maintenance is directly dependent on the generation of reef sediments and their transport to island shorelines. However, shifts in reef top ecology and carbonate production as identified at Warraber indicate that sediment type and abundance has likely changed over the past 5,000 years. Such shifts may be critical in 'turning on' and 'turning off' reef island formation and in understanding future changes in reef island stability. As shown by and Yamano et al. (2000) ecological shifts in the late Holocene as a consequence of sea level fall leading to reef flat emergence allowed increased production of foraminifera on the Green Island reef surface, possibly triggering the late Holocene development of this foraminifera-rich island. In contrast, coral is the dominant constituent comprising many reef islands in the Indo-Pacific (Stoddart and Steers 1977). Of relevance is whether or not islands in settings with emergent reef surfaces, such as Warraber, which currently produce only small volumes of coral, are still able to supply sediment to islands in sufficient quantities to maintain island shorelines. In conclusion, the census-based approach examined in this paper has been shown to allow carbonate production values to be established at sub-reef-flat scales, thereby providing critical information for evaluating changes in production and organism type available to contribute to the sediment reservoir at locations proximal to reef islands.

Acknowledgments Research was supported by an Australian Research Council Grant to CD Woodroffe, PJ Cowell, and RF McLean and University of New South Wales ADFA Postgraduate Research Scholarship to DEH. We thank RF McLean for conceptual advice and field assistance, B Billy, B Samosorn, RW Brander, A Coutts-Smith and GA Stewart for field assistance, W Anderson for statistical advice, T Billy, C Tamu and the people of Warraber Island and Beverly and Bill Stephens for their help and hospitality, A Vecsei for supplying raw data from Vecsei (2001), and P Bealing and M Brosnan for assistance with Figs. 1 and 3.

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