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REPORT

Coral colonisation of a shallow reef flat in response to rising sea level: quantification from 35 years of remote sensing data at Heron Island, Australia

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Abstract Observations made on Heron Island reef flat during the 1970s–1990s highlighted the importance of rapid change in hydrodynamics and accommodation space for coral development. Between the 1940s and the 1990s, the minimum reef-flat top water level varied by some tens of centimetres, successively down then up, in rapid response to local engineering works. Coral growth followed sea-level variations and was quantified here for several coral communities using horizontal two-dimensional above water remotely sensed observations. This required seven high spatial resolution aerial photographs and Quickbird satellite images spanning 35 years: 1972, 1979, 1990, 1992, 2002, 2006 and 2007. The coral growth dynamics followed four regimes corresponding to artificially induced changes in sea levels: 1972–1979 (lowest growth rate): no detectable coral development, due to high tidal currents and minimum mean low-tide water level; 1979–1991 (higher growth rate): horizontal coral development promoted by calmer hydrodynamic conditions; 1991–2001(lower growth rate): vertical coral development, induced by increased local sea level by ~12 cm due to construction of new bund walls; 2001–2007 (highest growth rate): horizontal coral development after that vertical growth had become limited by sea level. This unique time-series displays a succession of ecological stage comprising a 'catch-up' dynamic in response to a rapid local sea-level rise in spite of the occurrences of the most severe bleaching events on record (1998, 2002) and the decreasing calcification rates reported in massive corals in the northern part of the Great Barrier Reef.

Keywords Coral growth · Coral community · Great Barrier Reef · Remote sensing · Sea-level rise · Climate change

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Introduction

Coral reef flats are naturally dynamic systems. A large proportion of their area is constituted of shallow and intertidal coral assemblages and habitats. Reef-flat colonisation by corals and their development into reef-flat structures depend on multiple variables: the types of corals present (as adults and incoming larvae), their life histories, their abundance, the frequencies and intensities of physical disturbances, the structures and sediments that they produce (Montaggioni 2005) and prevailing environmental conditions (Done 2011a, b). Biological factors include a timely supply of hard coral propagules (larvae; fragments) and rates of coral survival that allow many individual coral colonies to achieve large size. The primary physical determinants remain adequate ‘accommodation space’ (Spencer 2011) and suitable hydrodynamic conditions (Hearn 2001), i.e. sufficient depth and adequate rates of exchange of water to allow coral occupancy of the area (Morton 1974; Rosen 1975; Connell 1978, Chappell 1980; Done 1983). In some conditions, patch reefs are present (including thickets, hedges, low walls and reticulated structures). Patch reefs may themselves be considered as either transient or persistent outcomes of local constructional and destructive process affecting accretion of reef framework, depending on the time frame of observation (Done 2011a, b).

Once they have formed, reef-flat corals and patch reefs are vulnerable to physical breakage by storms and cyclonic wave action. The shallowest of them can be exposed to air, heat and sunlight at extreme low tides, limiting upward coral growth and killing the tops of coral colonies (Hoegh-Guldberg and Fine 2004; Done 2011a), often resulting in the adoption of the distinctive micro-atoll form once growth to the surface has been completed (Smithers 2011).

Anthropogenic climate change threatens to detrimentally affect coral growth and accretion on reef flats. Projected increases in the frequency of destructive tropical cyclones may not allow enough time for coral recovery between disturbances and may lead to the loss of coral diversity and resilience (Done et al. 2007; Wakeford et al. 2008; Knutson et al. 2010). Warming and acidification of ocean waters may directly diminish the capacity of corals and other calcifiers to build reefs and track rising sea level in coming decades (Hoegh-Guldberg 1999; De’ath et al. 2009; Veron et al. 2009). Such changes may influence the condition, composition and extent of intertidal reef-flat coral communities, whose growth is intimately related to sea level at monthly to decadal and geological scales (Montaggioni and Faure 1980; Buddemeier and Hopley 1988; Buddemeier and Smith 1988; Spencer 2011). Sea-level fluctuations can leave lasting signatures on reef flats. For example, the heights of various Holocene sea-level still-stands have been recorded in the elevation of the dead upper surfaces of micro-atolls (Smithers and Woodroffe 2001; Kench et al. 2009; Yu et al. 2009).

For established individual corals, vertical and horizontal components of growth differ in response to impinging hydrodynamic conditions (Kaandorp and Sloot 2001). Such information acquired at the individual colony scale (such as reviewed in Dullo 2005) is not easily extrapolated to the patch reef and to the reef scale. This scaling-up exercise requires information on the most likely area to be colonised by corals and the time required for them to do so. Addressing these issues necessitates observations and descriptions of coral dynamics to be performed at larger scales than most quadrat and transect-based studies allow to (Connell et al. 2004). Comparable scaling issues were described by Jackson (1991) in relation to scale and diversity patterns in coral communities: they are also valid in relation to occupation of area across reef flats by corals. This scaling-up issue is here addressed by investigating coral growth over a large reef-flat section of Heron Island (Great Barrier Reef, Australia; 23°45′S, 151°92′E) which offers a unique configuration to study reef-flat dynamics.

Observations made at Heron Island (HI) during the 1970s–1990s brought the importance of rapid changes in accommodation space into focus. Vertical accommodation space was first reduced by some tens of centimetres over several hectares of the HI reef flat by blasting and dredging works in the 1940s ; later (1980s and 1990s), sea level increased by a similar amount due to new engineering works undertaken to limit the transport of sediment into a boat channel. Berkelmans et al. (1998) reported changes in coral growth in the now slightly deeper reef-flat area in the years 1993–1997. Rates were all significantly higher than sites away from the influence of the locally induced sea-level rise (>400 m). They included rapid ($\sim$15 cm year^{-1}) growth of branching *Acropora* spp. (mainly *Acropora formosa* and *Acropora aspera*) and less rapid growth of *Montipora* spp and branching *Porites cylindrica* across open sandy areas on the reef flat, reinstatement of vertical growth ($\sim$1 cm year^{-1}) in massive *Porites* spp. micro-atolls previously at equilibrium with earlier lower sea level, strong increases in percentage coral cover ($\sim$3–8% year^{-1}) and more colonies per transect (30–70 colonies inside vs. 20–50 colonies outside the area). The strong coral growth up until 1997 indicated that the prerequisites of propagules, survival and growth had been materially improved by the advent of the locally higher sea level. During the following decade, there were three major coral bleaching events on the Great Barrier Reef (1998, 2002, 2005; Berkelmans 2002; Salih 2002; Ainsworth et al. 2008) and a cold water-induced bleaching on the HI reef flat itself (Hoegh-Guldberg and Fine 2004). Hopley (2011) suggests that while the increased submersion times brought about by climate-change-related sea-level rise will be extremely variable, in places, it could tend to ameliorate the negative effects of extreme temperature volatility on reef flats. However, the degree to which bleaching event and changes in sea level affected, or not, the survival of HI reef-flat corals, and their contribution to reef-flat structures, has not been reported. Therefore, we aim to fill this gap by analysing 35 years of remotely sensed data at reef scale to measure the level of HI coral growth and dynamics. To the best of our knowledge, such goal has never been attempted in the coral reef ecology and remote sensing literature.

Aerial photographs, airborne sensors and satellite images provide reef-scale (10^1–10^4 m^2) observations of corals, coral communities and coral-built structures. Many reef flats are shallow enough (<5 m) for such passive imaging systems to detect and allow the mapping of reef-top communities. For example, 15 habitat classes (combinations of sediments, pavement, seagrass, algae and corals) were mapped from IKONOS images (Andrefouet et al. 2003), six habitat classes (coral, sand, dense seagrass, mixed coral/sand, mixed seagrass/sand/algae and deep water) were mapped from a Quickbird image in Honduras (Mishra et al. 2006), 17 coral community classes (assemblages of coral morphologies and substratum types) were mapped from a Quickbird image in the Indian Ocean (Scopélitis et al. 2009), and 45 coral community classes were mapped from a Quickbird image in New Caledonia (Scopélitis et al. 2010). These maps have been useful for various monitoring and management applications such as reef productivity, biodiversity, coral bleaching, resource assessment and marine protected area design (Andréfouët and Payri 2001; Yamano and Tamura 2004; Gilbert et al. 2006; Mellin et al. 2007; Dalleau et al. 2010). When used in time-series, high spatial resolution images (from satellite and airborne sensors) have been useful to detect map temporal changes in reef-top substrata and coarse benthic communities (Palandro et al. 2003), infer trajectories of damage and recovery following cyclone impacts (Scopélitis et al. 2009) and estimate changes in physical configuration (Lewis 2002). The ecological resolutions of multitemporal habitat maps thus far remained mostly coarse compared with the diversity of coral communities potentially present on any given reef (Scopélitis et al. 2010). This is mainly due to the spatial resolution of the images itself and the limitations of mapping techniques based on automatic classification rules (Andréfouët 2008). As such, no attempts, to date, have been made to precisely map across time the variability of growth of coral communities (as coral colonies or patch reefs) across an entire reef, using multitemporal above-water imagery.

Heron Reef has been the site of several coral reef remote sensing studies since the mid-1980s, including mapping exercises and spectroscopy studies (e.g. Andrefouet et al. 2003; Joyce et al. 2004; Hedley et al. 2009; Leiper et al. 2009). Earliest studies used Landsat Multispectral Scanner (MSS) to interpret the Great Barrier Reef from space (Jupp et al. 1985a, b), 13 reef zones (including four zones of various coral density) were identified and mapped from Landsat TM (Ahmad and Neil 1994), three classes of macroalgae were mapped by the mean of their chlorophyll a concentration detected on a Landsat TM image (Roelfsema et al. 2002), and attempts were made to define coral cover indexes from Compact Airborne Spectrographic Imager (CASI) to automate coral cover estimates (Joyce 2005). Yet surprisingly, no temporal set of remote sensing images was used at Heron Reef to assess and/or document the changes that occurred over the reef flat.

This paper presents how a succession of vertical and horizontal coral growth regimes over 35 years (1972–2007) was identified, mapped, quantified and monitored on Heron Island (HI) reef flat, Great Barrier Reef, Australia, using remote sensing data.

Materials and methods

Definitions

In the present study, the term 'coral' when used by itself refers to a 'coral-built structure' (patch-reefs, thickets etc.). Over the decadal time scale considered here, corals are likely to die (in whole or in part), possibly remaining in position of growth for years to decades. For example, a reef-top thicket or patch reef may be extensive, whereas the living coral may be confined to its edges. The term 'coral community' is similarly used as shorthand, in this case to describe patch reefs and corals at scales greater than 0.5 m. These are visible in remotely sensed images in which individual pixels usually represent a composite of the living corals, dead fallen and standing corals, and associated algae and substrata.

Study site and history

Heron Reef is a 27-km^2 platform reef rising from 40 m of water and located approximately 60 km from the coast of Queensland. The local tidal range is 1–3 m (Gourlay and Jell 1992). The reef is 11 km long by 5 km wide and has a 0.8 km long vegetated coral cay (Heron Island) at its western end (Fig. 1a). Heron Island has been the site of a tourist resort and a research station since the early 1940s. The reef's geomorphic zones from deeper water towards the cay include the reef slope, the reef rim (or crest), a shallow reef flat and a deeper lagoon with coral patch reefs (Flood 1993). The reef rim emerges from the water on most low tides and retains water on the top of the reef flat as the tide falls, keeping the corals submerged for longer than they would be in the absence of a rim (Berkelmans et al. 1998).

In 1945, water depth over the western reef flat was reduced and local hydrodynamics drastically modified when an entrance was blasted in the reef rim to improve small boat access to the beach. In the mid-1960s, access was further improved by the dredging of a channel across the reef flat (Flood 1984; Gourlay and Jell 1992; Berkelmans et al. 1998). The changes left corals on the western reef flat exposed to air for most of the low-tide cycle and caused elevated rates of sediment export from the cay and reef flat via the channel. In 1982, a series of bund walls consisting of lines of abutting 0.5 m high concrete blocks

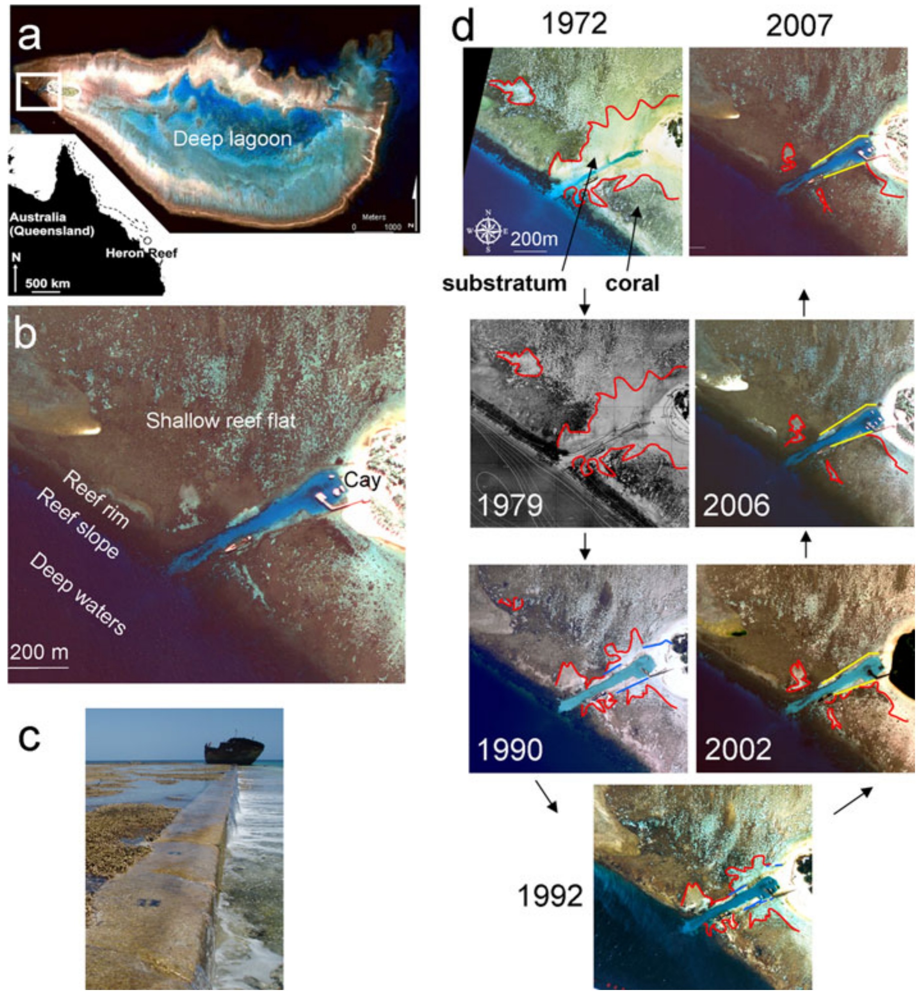

Fig. 1 Heron Island and its western reef flat. **a** Study site overview and surrounding reef: Quickbird 2 satellite image of 2007 showing the location of the study area (*white square*); **b** study area and geomorphic zones: deep waters, reef slope, reef rim, shallow reef flat and deep lagoon (on **a**); **c** 2007 photograph of the southern bund wall at low tide showing the difference in water level between reef flat (*left*) and boat channel (*right*); **d** 1972–2007 time-series of remotely sensed imagery showing the colonisation of the reef flat by corals. The *red lines* show the rough boundary between the colonised and the uncolonised area. The *blue lines* indicate the location of the first set of bund walls (1982–1983). The *yellow lines* indicate the location of the second set of bund walls (1993–1994)

was constructed to reduce the low-tide run-off through the channel, control sediment loss and reduce the frequency of dredging required to maintain navigation safety in the channel. This first series of bund walls only partly restored the original hydrodynamics and minimum low-tide levels. In the mid-1990s, a harbour was dredged and a second set of bund walls made of heavy, sealed concrete blocks was installed. These walls (Fig. 1b) raised the reef flat minimum low-tide water level a further 12–14 cm around the harbour, returning it to pre-blasting levels. The increased mean low-tide reef-flat water levels allowed reef-flat corals to grow taller due to the increase in vertical accommodation space (Hacker and Gourlay 1997; Berkelmans et al. 1998).

Table 1 summarises the chronology of events that affected Heron Reefs since the 1940s.

Image data set and pre-processing

A 900 × 200 m area centred on the harbour (Fig. 1a) was chosen to document and interpret remarkable changes that were observable in seven aerial and satellite images of Heron Reef acquired between 1972 and 2007 (Table 2, Fig. 1c). The 2006 and 2007 Quickbird-2 multispectral images were pansharpened to a spatial resolution of 0.60 m. The aerial photographs for 1972, 1979, 1990, 1992 and 2002 were digitally scanned at a high resolution (up to 600 dpi, depending on the original scale) to achieve a final pixel size (i.e. spatial resolution, ground sample distance) of ~0.5 m. These scans were then resampled to a standard 0.6 m, which approximates the smallest pixel size of the multispectral satellite imagery used in this work (Quickbird-2, 0.60 m).

The 2007 and 2002 images were georeferenced to the 2006 image as a base using the Imagine 9.2® image processing system, a nearest neighbourhood algorithm and 10 ground control points, which gave a root mean square error (RMSE) of <0.5 m (i.e. about the size of a pixel (Jensen 2005)). The 1992, 1990 and 1972 images were georeferenced using ESRI® ArcMap™ from ArcGIS Desktop 9.2® (referred as ArcGIS hereafter) to the 1979 image, which had a precisely surveyed coordinate grid. Using four to six ground control points for each image, an average RMSE of <1 pixel was also achieved for these images.

Table 1 Chronology of natural events and engineering works at Heron Island and their known consequences on the hydrodynamics and corals on the western section of Heron reef flat between 1945 and 2006

Year	Event	Consequence	Reference
1945	Channel blast	Modify the hydrodynamics	Flood (1984)
1967	Rubble walls	Restore minimum low-tide water level	Berkelmans et al. (1998)
1972	Cyclone Emily		
1974	Cyclone Wanda	Breaches in the rubble walls	
1976	Cyclone David		
1979	Bund walls inefficient	Water flows out of the reef flat to the channel for most of tidal cycle.	Hacker and Gourlay (1997), Berkelmans et al. (1998)
		Strong water velocity and very-low-tide water level.	Gourlay and Flood (1981), Gourlay (1982)
		Possible coral mortality.	Endean (1976)
1980	Cyclone Simon	Maintenance work	Hacker and Gourlay (1997)
1982–1983	Concrete block bund walls (1st bund walls)	Partially restore the minimum low-tide level	Berkelmans et al. (1998)
1988	Rubble walls restoration	Restore minimum water level	Berkelmans et al. (1998)
1992	Cyclone Fran	No effect on walls	
		Sediment erosion	Gourlay and Jell (1992)
1993	Heavy, sealed concrete blocks bund walls (2nd bund walls)	Minimum average low-tide water level rose up to 14 cm on reef flat around the channel.	Hacker and Gourlay (1997), Berkelmans et al. (1998)
		Porites sp. and *Acropora* spp. Corals development	
1998	Bleaching		Berkelmans (2002), Salih (2002)
2003	Bleaching		Hoegh-Guldberg and Fine (2004)
			Hoegh-Guldberg et al. (2005)
2005–2006	Bleaching		Ainsworth et al. (2008)

Table 2 Time-series of high spatial resolution remotely sensed images from 1972 to 2007 for Heron Reef: date, type of image, initial resolution or scale before pre-processing

Year	Image type	Initial resolution/scale
2007	Satellite Quickbird	0.60 m
2006	Satellite Quickbird	0.60 m
2002	Aerial photograph	1 m
1992	Aerial photograph	1:6,000
1990	Aerial photograph	1:10,000
1979	Aerial photograph	1:140,000
1972	Aerial photograph	1:12,000

Each image was mapped by manual digitisation of polygons using ArcGIS. Polygon boundaries were identified by visual interpretation of colour and texture. Digitised polygons consisted of spatially contiguous pixels that shared the same colour and together comprised a spatially distinct texture. The entire investigated reef area was partitioned into such polygons. Each polygon was later labelled using a three-level typology. Because mapping was based on visual interpretation, and because the mapped reef area was shallow (<2 m), it was not necessary to perform radiometric corrections to compensate for water column or atmosphere radiative transfer effects. The minimum mapping unit was of 2.4 m^2 (4 pixels) at the finest level of mapping and community description (Level 3).

In situ data set and coral community maps

In September 2007, a field survey was designed using the initial, unlabelled polygon map results for the 2007 Quickbird-2 image. Thirty-seven field stations were chosen based on the locations of map polygons to encompass the entire range of polygon colour and texture patterns. These stations therefore collectively sampled all assemblages of benthic communities and substrate types that were recognisable in the Quickbird-2 image (as in Scopélitis et al. 2009). At each station, the abundance of sessile biota and substrata was estimated using 20-m line intercept transects (LIT), with sampling at every change in feature (English et al. 1997). Attributes recorded included types of substratum, algae, soft corals and hard coral morphologies. Hard coral genus and/or species were also recorded when recognised in situ. Dominant reef-flat species corresponded to previous descriptions (e.g. Berkelmans et al. 1998), especially for branching *Acropora formosa*, *Montipora* spp, branching *Porites cylindrica* and massive forms of *Porites*. Previous in situ long-term studies of coral dynamics in HI (mostly on reef slopes, crests and for one reef-flat area located just on the edge of our study site (Fig. 1)) reported more than 70 species, but with specificities depending on the reef zone (Tanner et al. 1994, Connell et al. 2004). Tanner and Hughes (1994) and Tanner et al. (1996) reduced the taxonomic complexity based on colony morphologies to model HI reef slopes and crests coral dynamics, and we follow the same path here for reef-flat coral community dynamics.

The large number of attribute combinations yielded a 3-level typology of coral communities. At Level 1(L1), communities were characterised according to their dominant benthic feature: hard coral, soft coral and 'no coral' providing only 3 classes at Level 1. For Level 2 (L2), the Level 1 communities were further detailed, considering the dominant types of hard coral morphology, the soft corals (exclusively present in the absence of any other corals on this part of the reef flat) and the dominant types of substratum (hard or soft). The combinations of 15 biological and 4 substratum attributes yielded 19 classes occurring at Level 2. Fast-growing hard coral morphologies were encountered in 3 main growth stages arbitrarily defined as stages 1, 2 and 3. Stage 1 corresponds to the smallest colonies up to a couple of tens of centimetres high; stage 3 corresponded to the ultimate growth stage when the colonies had reached the low-tide water level and formed a platform of eroded and almost cemented thickets; stages 2 corresponded to an intermediate stage. When fast-growing branching corals were encountered dominantly among other coral growth forms, the resulting mixed communities were declined into 4 stages: at stage 1, most of the colonies were small; at stage 4, all colonies had reached the platform stage. In between, at stage 2, most of the colonies, but not all, were at an intermediate stage; at stage 3, most of the colonies, but not all, had reached the platform stage.

Thus, for the Level 3 (L3), communities were characterised considering the developmental stage of the hard coral morphologies, cover of the soft corals and the category of hard and soft substratum (sand, rubble, boulder, dead coral and pavement). Thirty-three biological and 9 substratum types yielded a total of 42 classes at Level 3. Level 3 defines the full diversity of communities present in Heron reef. The combinations are presented in detail in the 'Results' section.

Map accuracy assessment

Additional in situ data were opportunistically collected by one of the authors during an independent project in September 2010. This allowed conducting a posteriori accuracy assessment for the 2007 map, at Level 3. In situ communities were surveyed along five transects. The transects were positioned on both sides of the channel so as to cover the most heterogeneous and dynamics areas from the shore to the crest (see 'Results'). Benthic features were recorded as a set of approximately 100 in-water near vertical photographs (range ~0.8 m) taken at regular interval while swimming along the transects. Taking photographs at regular intervals allowed capturing the continuum of communities. Each underwater photograph was visually assigned either to the thematically closest class from the Level 3 typology or to a new class when the communities had changed noticeably (typically due to coral growth occurring between the image acquisition in 2007 and the ground truthing in 2010). The succession of classes obtained along the transects was then overlaid on the succession of the mapped polygons. When both classes (photograph vs. maps) were matching, this was accounted as an agreement, and when they differed, it was accounted as a disagreement and the difference(s) in community composition compared to the map class was noted aside. This enabled the calculation of the overall accuracy of the map.

Coral colonisation rates

Coral growth rates were computed between each of the six pairs of images, namely 1972–1979, 1979–1990, 1990–1992, 1992–2002, 2002–2006 and 2006–2007. To estimate growth rate variability in space, a single set of 36 image subsets of 51 × 51 pixels was selected according to three criteria: (1) the subsets were to be scattered across the whole reef-flat section; (2) each subset should clearly display a distinguishable pattern of coral and non-coral structure (Level 1); and (3) all of the Level 2 communities should be represented by at least two subsets. With an area of 30.6 m × 30.6 m for each subset, the growth rates were estimated for 19% of the whole study area (33.709 m^2 of 180,000 m^2). The same 36 subsets were used between each pair of images.

A coral growth rate between two consecutive images consisted in the normalised change in the area covered by 'coral pixels' (% cover $year^{-1}$). On the images and regardless of the coral community, dark pixels were identified as 'coral' pixels and light pixels were considered as 'free substratum' pixels, potentially colonisable. 'Coral' included both living hard coral colonies and living soft coral colonies, sometimes merged with dead standing skeletons of hard corals (as typically occurs when corals die off on top due to sub-aerial exposure). The latter are routinely colonised by algae—mostly filamentous with patchy fleshy macroalgae, and encrusting coralline algae. The green band of each image was used to identify corals as it provides the highest contrast between coral and non-coral features (Andréfouët et al. 2002). For each subset, the green band was manually stretched in ENVI 4.6™ from

ITT Visual Information Solutions® to a subset-dependant threshold that differentiated coral and free substratum pixels. This resulted in binary subsets (as in Andréfouët et al. 2002) where coral pixels were displayed in black and substratum pixels in white (Fig. 2).

From each pair of images of coral cover between a year 1 and a year 2, and for each subset (Fig. 2), a *Normalised Areal Colonisation Rate* (NACR; Scopélitis 2010) was computed with Eq. 1:

$$\mathrm{NACR}_{ij} = \frac{(C2 - C1)}{(Y2 - Y1) * N} \tag{1}$$

where $\mathrm{NACR}_{i,j}$ = normalised areal colonisation rate of Level 2 community j for image subset i (% subset i area colonised by community j year^{-1}), $C1$ = number of coral pixels in the subset i in year 1, $C2$ = number of coral pixels in the subset i in year 2, $Y1$ = calendar year 1 of image 1 acquisition, $Y2$ = calendar year 2 of image 2 acquisition and N = number of pixels in the image subset i.

For each community j, the mean rate of change in cover, defined as $\mathrm{NACR}_{o,j}$, was computed across the study area by averaging all subsets i belonging to the j community.

Then, the mean annual rates of change in cover, all communities included, were estimated with Eq. 2. Note that this is equivalent to the computations of a Level 1 community coral growth.

$$\mathrm{NACR}_{o} = \sum_{j=1}^{J} \sum_{i=1}^{K_j} \frac{\mathrm{NACR}_{ij}}{S} \tag{2}$$

where j = index of Level 2 community, K_j = number of subsets for community j on the whole image and J = number of types of Level 2 community present in the calendar period in question (may vary from period to period. In absence of in situ survey prior to the study, we made here the assumption that all communities were present from the start to the end), i = index of image subset, S = total number of subsets over the whole image (with no distinction of community; here $S = 36$).

In the absence of historical field data available prior to the year 2000, it was assumed that the types of substrata and coral communities (Level 2) observed in 2007 could potentially have been present since 1972. This assumption was comforted by the literature review on Heron Reef.

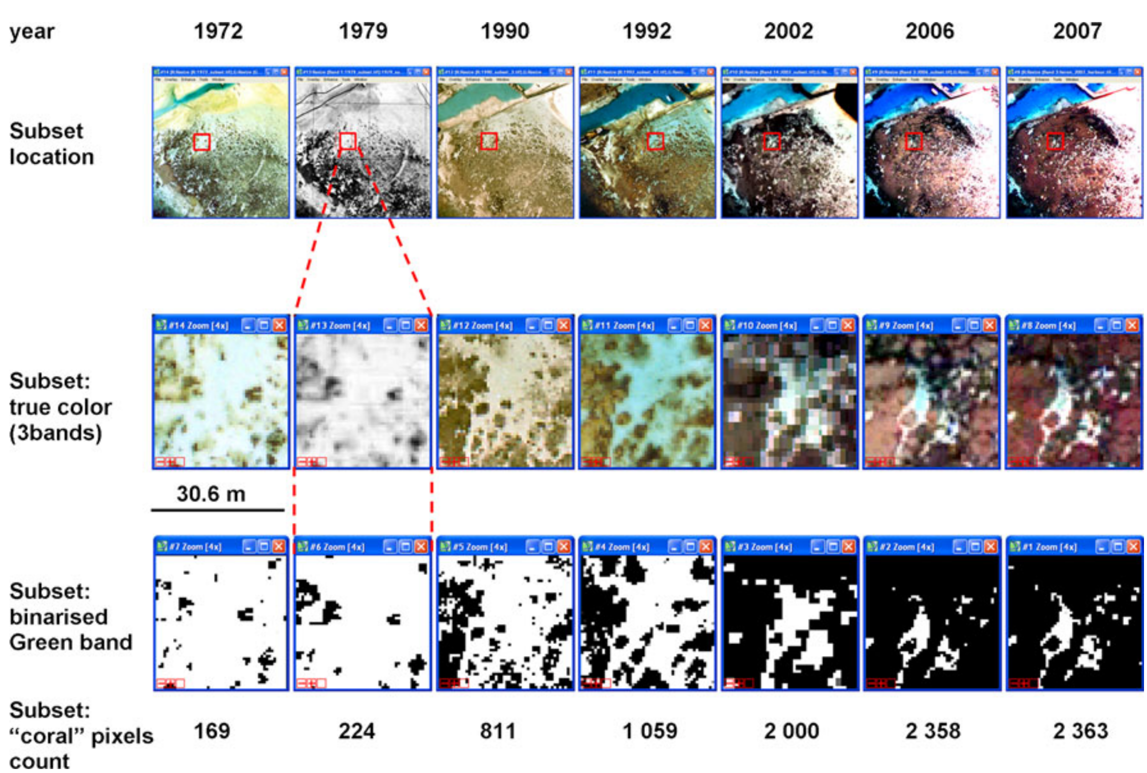

Fig. 2 Coral vs. free substratum multitemporal maps from one of the 36 image subsets for quantifying coral colonisation from series of airborne and satellite images. *Top series* location of the subset (*red square*) on true colour images of the reef flat; *Middle series* zoomed in windows showing the true colour coral patterns of the subset across time; *Bottom series* zoomed in windows showing the binary coral/substratum patterns of the subset across time (*black* coral, *white* substratum); *Bottom line* count of coral pixels for each date (subset size: 2,601 pixels).Windows were resized for illustration only

Results

Reef-flat typology and distribution

From the hierarchical three-level typology of substrata and coral communities, we highlight in Fig. 3 the Level 2 in detail, as this is the level for which we estimate NACR. Level 2 discriminated 19 classes. Each is assigned a colour in Fig. 3 and is named after a dominant coral morphology or dominant substratum type. The combinations of attributes that make up the 19 classes are represented in the histograms in Fig. 3. For example, the class 'Massive' (lime green) is about half dead coral (black in left histogram) and the live coral component is 99% massive growth form (plain grey in right histogram). 'Open branch' (light pink) is nearly half dead (black in left histogram) but the rest is entirely made of live coral of branching growth form (white in right histogram).

The typology also included a more detailed Level 3 that discriminated 42 classes. For concision sake, this typology is not presented in this paper due to the very high number of classes; however, those classes can still be visualised on the map shown in Fig. 4, and details are provided in Scopélitis (2010) available on request to the first author.

The maps of substrata and coral communities present on the western Heron reef flat obtained from the 2007 Quickbird image are displayed in Fig. 4 at the three levels of the hierarchical typology. The dominance by hard corals (dark blue) in 2007 is clearly indicated in Fig. 4a (Level 1). In Fig. 4b (Level 2), the pattern of dominance of different groups is illustrated: e.g. the most widespread were branching hard corals (red and brown); more localised forms (notably '*sub-massive a*' in aqua blue and '*sub-massive a and compact branching*' in purple. Figure 4c (Level 3) portray further complexity within each Level 2 class. It also carries the added information about the stage of vertical development (stages 1–4) in 2007, with older stages (lighter shades) often tending to be more central in polygons of a particular colour and younger stages (darker), more on their margins.

Map accuracy assessment

Although Heron reef flat has been studied intensively, no precisely georeferenced historical in situ data and photographs were available to document the coral assemblages on the study sites to support and validate the classification of the temporal maps. However, no blatant discrepancies

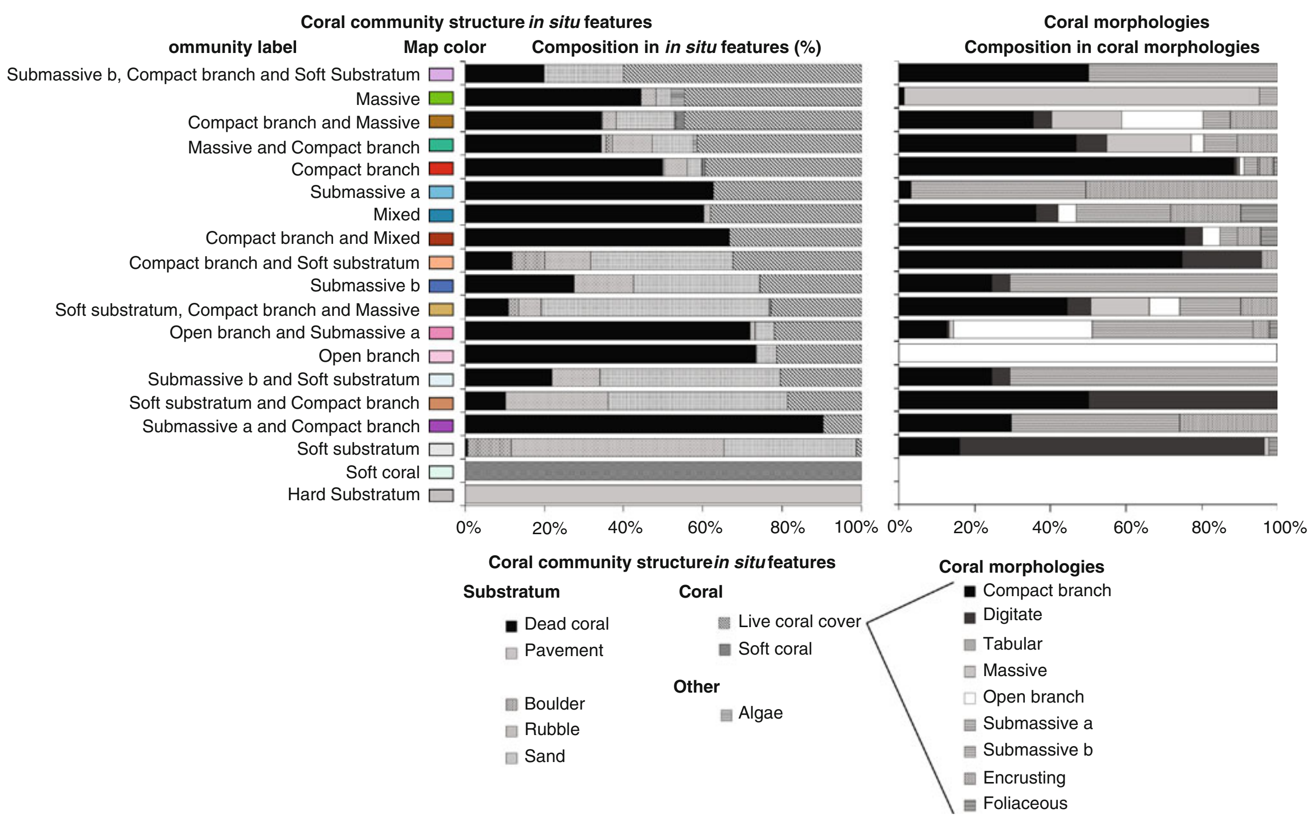

Fig. 3 Coral community typology Level 2 based on field survey of 2007. The combinations of attributes that make up the 19 classes are represented as *grey-scale* histograms. For example, the class 'Massive' (*lime green*) is about half dead coral (*black* in *left histogram*) and 99% massive growth form (*plain grey* in *right histogram*)

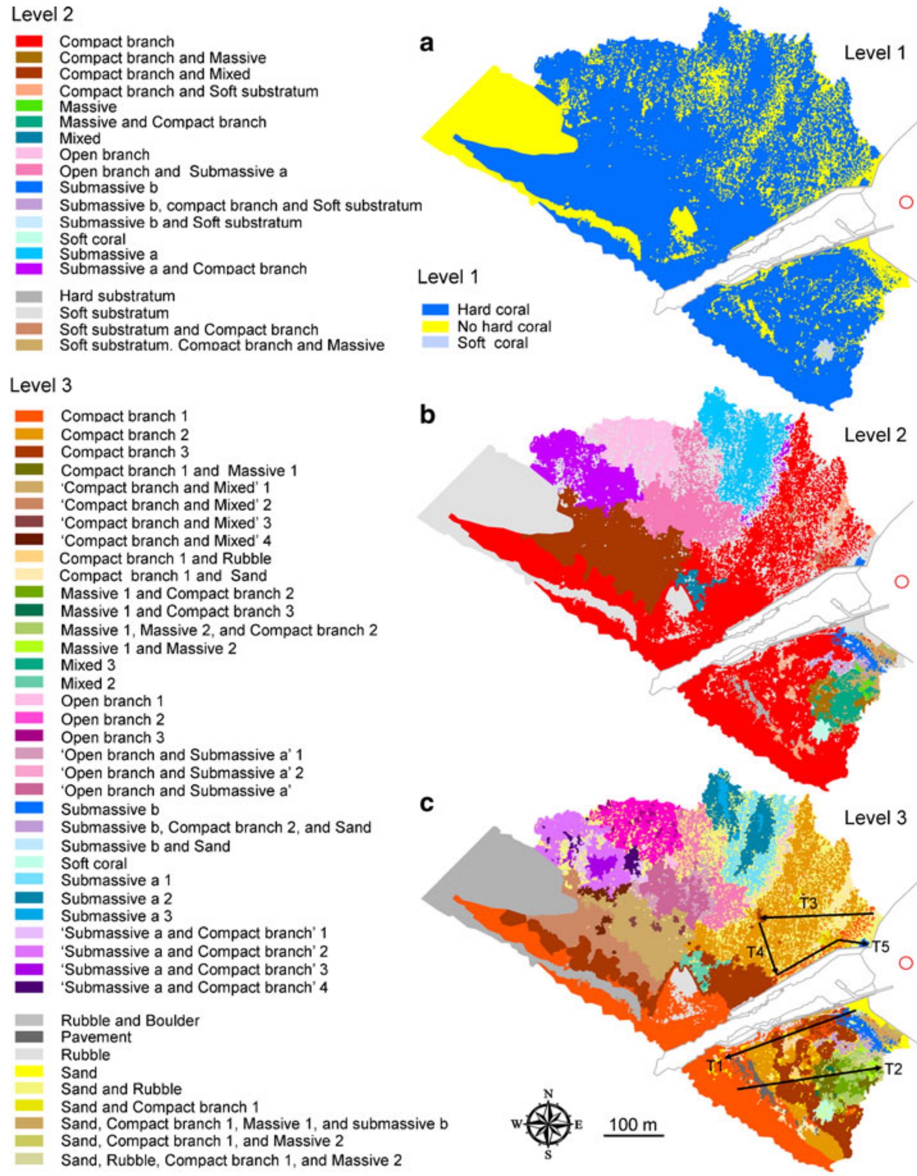

Fig. 4 Hierarchical coral community maps on the western Heron reef flat in 2007. **a** Level 1 showing hard coral, soft coral and free substratum distribution; **b** Level 2 showing 15 classes of living coral assemblages named after their dominant coral morphology and four classes of substratum named after the dominance of soft (e.g. sand, rubble) or hard (e.g. pavement, rock) component; and **c** Level 3 showing 33 classes of living coral assemblages described from their composition in coral morphologies and substratum types and nine classes of substratum described from their combination in soft or hard features. At Level 3, numbers 1–4 appearing after coral morphologies in the legend indicate successive stages of vertical development. *Black arrows* marked as *T1–T5* indicate the location of the five photo-transects surveyed for a posteriori map validation

exist between the previous qualitative reports and our descriptions. The present study benefits from all these past reports. They contribute to provide confidence in the results shown here.

Comparison of the most recent maps (year 2007) at Level 3 with the 2010 in-water photographs provided an average agreement of nearly 80% (79.8 ± 8%, $n = 5$). The location of the five transects is shown in Fig. 4c (T1–T5). Per transect, the agreements were 83, 79, 93, 70 and 73% for T1, T2, T3, T4 and T5, respectively.

This agreement was very good, despite changes that could have occurred between 2007 and 2010. The 20% discrepancy was related to changes in the communities due to the expansion of fast-growing colonies over bare substratum and slow-growing massive corals. Furthermore, a slight 1- to 2-m uncertainty on the exact positioning of the transects is likely and would have induced some error too. This uncertainty relies on in situ information acquired after the latest in situ and imagery data sets were collected and used to constrain the mapping and develop the model. This suggests that the uncertainty is conservative and that it corresponds to a higher limit, a least for the 2007 map.

Coral colonisation

Average coral growth for the entire study site (estimated from the 36 subsets in Fig. 5) is presented in Fig. 6 and Table 3. All six periods were periods of net growth (i.e. increase in the area cover of coral-built structures). However, growth rates were extremely variable among periods (a tenfold variation from 0.23 to 2.4% year^{-1}).

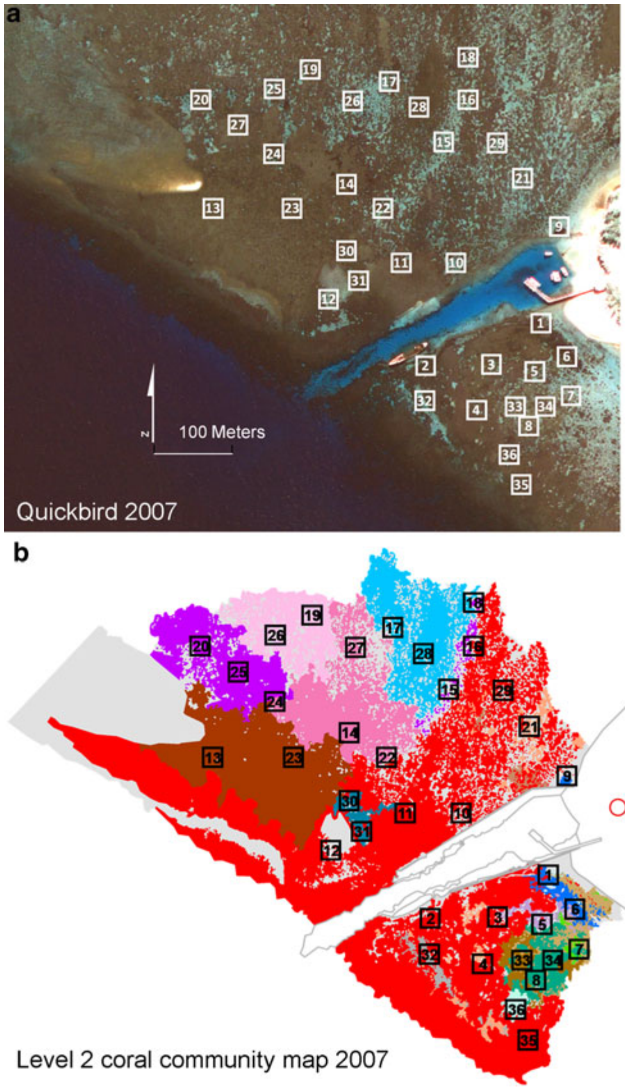

Fig. 5 Subsets (*squares*) stratification for the quantification of the coral growth rates. Subsets superimposed on **a** true colour image pansharpened Quickbird image 2007 and **b** Level 2 map

For each period, the standard deviations were systematically higher than the mean values (Table 3), reflecting variability caused by different coral communities and specifically the spatial differences in the abundance of slow- versus fast-growing corals (Fig. 4). Twelve of the sixteen community types had positive colonisation rates (0.1–5.33% year^{-1}) in all periods. Among the communities that declined (0.1–2.39% year^{-1}), only one (massive coral) did so in more than a single period.

Discussion

Effect of localised sea-level rise on coral growth

Four regimes of coral growth were recognised from 1972 to 2007 (Fig. 6; Table 3).

In regime 1 (1972–1979; Fig. 6a), the growth rate was very low in the absence of a bund wall (pre-1979). The presence of the channel had increased tidal current speed and lowered low-tide level by an unquantified amount. Moreover, three cyclones had passed near the reef during this period and changed the drainage of the reef flat (Endean 1976; Table 1). Coral cover in the study area was low (Fig. 1c), and vertical limit of growth was clearly evidenced by dead tops of slow-growing *Porites* micro-atolls (Hacker and Gourlay 1997; Berkelmans et al. 1998).

During regime 2 (1979–1992; Fig. 6b), rapid coral colonisation occurred paralleled with increase in coral cover (Figs. 1c, 2). In this period, the construction of the first concrete bund walls and restoration of the rubble walls (Table 1) led to higher reef-top water level at low tide and thus greater vertical accommodation space for coral growth.

Regime 3 (1992–2002) was triggered by building of the second bund walls in 1993, which raised the mean low-tide water level by an average 12 cm around the harbour (Hacker and Gourlay 1997; Berkelmans et al. 1998). With less exposure to air during the now higher low tides, coral growth was preferentially vertical and marginally horizontal (Fig. 6c). *Acropora* spp. branches produced up to 14.5 cm of vertical growth per year (Hacker and Gourlay 1997). The number of colonies and coral patches also increased significantly around the harbour in 1993–1997 (Figs. 1c, 2), making a major contribution to the increase in coral cover.

Regime 4 covers 2002–2007, when most of the reef-flat study area was colonised and the vertical limit to coral growth imposed by the low tide had been reached (Fig. 6d).

Of the 15 mapped coral communities (Fig. 4b), 11 were positively impacted (exhibited growth) by the first bund walls (increase in cover in Table 3). The exceptions were the sub-massive b corals (constant), mixed corals (declining) and open branch corals (declining). The sub-massive communities were very close to the beach, maximising their exposure to sediments generated by dredging and maintenance of the channel and swing basin. Following the construction of the second set of bund walls (1992–1993), the growth rates of 12 of the 15 recognised coral community types decreased. Horizontal growth was close to zero, both for communities located further than 400 m from the bund walls and for those for which no new substrate was available (Fig. 4b, Table 3). For other communities, growth was likely mostly vertical and thus not detectable in the images.

Coral community succession and reef growth

Five distinct groups of coral morphologies identified at Level 3 characterise the different stages of development of the coral patches: three types of compact branch corals and two types of massive corals.

For the fast-growing corals, 'Compact branch 1' corals correspond to what Piller and Riegl (2003) called the 'initiation' phase of a coral thicket formation: the young colonies develop on a semi-consolidated substratum. 'Compact branch 2' and 'Compact branch 3' corals result from the development of the young colonies into two successive stages of development in the framework formation which eventually form a layer of corals, vertically limited by the low-tide water level and dead on top (Fig 4c). These observations were also in agreement with an earlier observation by Berkelmans et al. (1998) who noticed that branching coral beds were expanding rapidly across sandy area of the reef flat. They also agree with projections by Harriot (1997) who predicted that growth should continue until the new low-tide level was reached and branching coral heads die.

Slow-growing massive corals develop into formations called micro-atolls exhibiting flat-topped circular coral colonies that can reach several metres wide and have a dead core surrounded by a living and growing coral rim (Yu et al. 2009). A massive coral head initially grows both horizontally and vertically, forming a bowl, but when it reaches the lowest water level, the upward growth ceases, the top of the head dies and lateral growth continues.

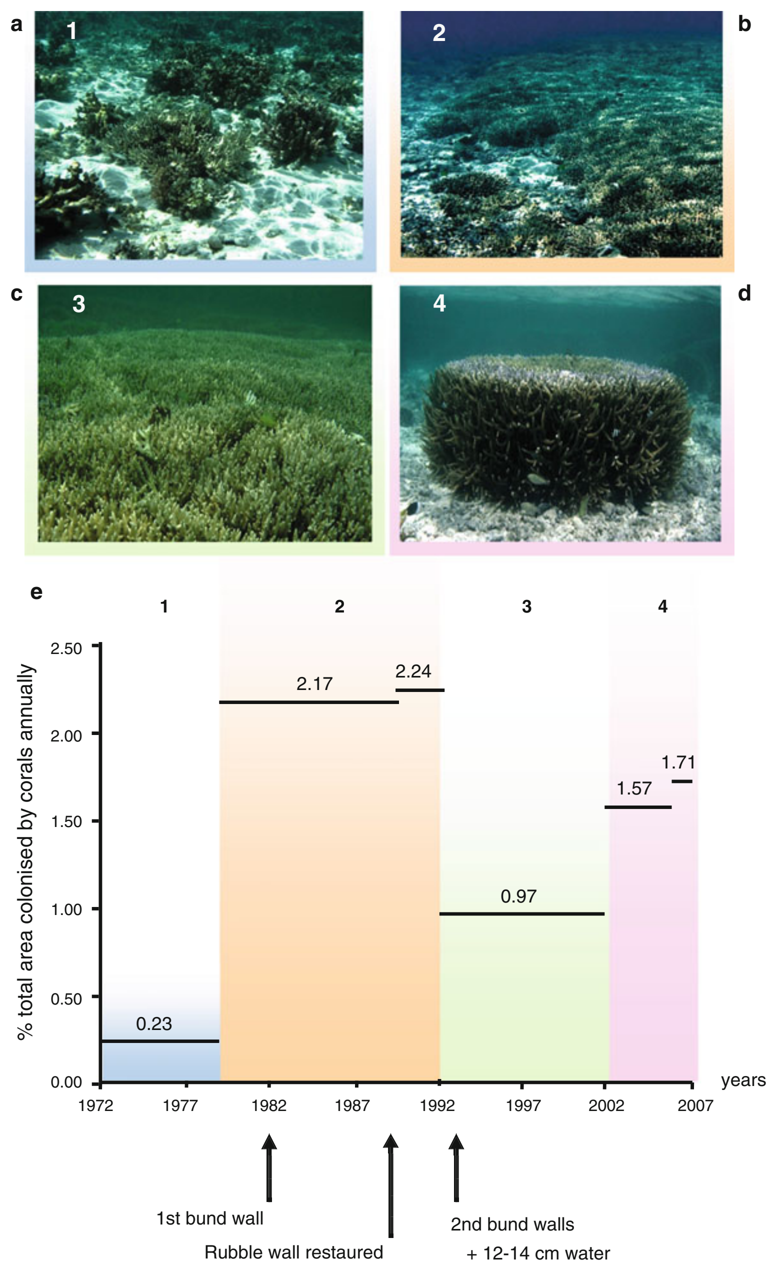

Fig. 6 The four regimes of coral growth. Underwater photographs from September 2007 illustrating variation in coral morphologies during four periods: **a** 1972–1979; **b** 1979–1992; **c** 1992–2002; **d** 2002–2007. *Colours* of borders indicate phases in **e**. **e** Rate of increase in coral cover (mean from 36 subsets)

Table 3 Coral cover and coral colonisation rates extracted from time-series of high spatial resolution images on Heron Island reef flat in the vicinity of the harbour (1972–2007)

Level	Coral community													Nb subset
	1972	1972–1979	1979	1979–1990	1990	1990–1992	1992	1992–2002	2002	2002–2006	2006	2006–2007	2007	
Level 1														
Generic	42.5	**0.23** ± *0.80*	44.8	**2.17** ± *2.35*	67.7	**2.24** ± *3.35*	70.8	**0.97** ± *1.56*	76.4	**1.57** ± *1 .79*	81.5	**1.71** ± *1.88*	83.3	36
Level 2														
Compact branching	27.9	**0.11** ± *0.14*	28.7	**1.73** ± *2.27*	47.8	**3.34** ± *3.88*	54.5	**1.60** ± *1.21*	70.6	**1.79** ± *1.95*	77.7	**1.36** ± *1.72*	79.1	8
Compact branch and soft substratum	4.5	**0.29**	6.5	**3.88**	49.2	**1.63**	52.5	**1.84**	70.9	**0.83**	74.2	**3.50**	77.7	1
Compact branch and mixed	88.6	**−0.27** ± *0.41*	86.7	**0.71** ± *0.96*	94.6	**0** ± *0*	94.6	**0.29** ± *0.29*	97.5	**0.20** ± *0.07*	98.3	**0.19** ± *0.11*	98.5	2
Submassive a and compact branch	20.5	**0.02** ± *0.01*	20.7	**3.28** ± *3.60*	56.7	**5.33** ± *6.93*	67.4	**0.39** ± *0.29*	71.3	**1.82** ± *1.78*	78.5	**4.35** ± *8.00*	82.9	4
Open branch and submassive a	22.0	**−0.13** ± *0.23*	21.1	**4.61** ± *1.28*	56.7	**1.44** ± *1.83*	67.4	**1.14** ± *0.58*	71.3	**1.00** ± *1.08*	78.5	**0.51** ± *0.87*	82.9	4
Open branch	64.0	**2.72** ± *2.69*	83.0	**0.60** ± *0.44*	89.6	**0.74** ± *1.05*	91.1	**0.10** ± *0.06*	92.0	**0.42** ± *0.07*	93.7	**1.08** ± *0.00*	94.8	2
Submassive a	16.2	**0.03** ± *0.10*	16.8	**0.96** ± *3.07*	46.2	**0.58** ± *1.14*	49.4	**0.36** ± *1.52*	59.4	**1.11** ± *3.17*	71.7	**0.58** ± *0.8*	73.3	3
Mixed	92.9	**0.07** ± *0.02*	93.4	**−0.39** ± *0.93*	89.1	**0.10** ± *0*	89.3	**0.02** ± *0.01*	89.5	**0.97** ± *2.00*	93.0	**2.54** ± *1.58*	95.6	2
Submassive b	5.2	**0.15** ± *0.31*	6.3	**0.16** ± *0.45*	8.0	**3.02** ± *3.27*	14.1	**3.17** ± 2.45	45.8	**3.64** ± *1.90*	60.3	**2.15** ± *1.71*	62.5	*3*
Submassive b, compact branch and soft substratum	8.4	**0.21** ± *0.14*	*9.9*	**3.41** ± *1.92*	*47.4*	**3.80** ± *1.37*	*55.0*	**2.18** ± *2.04*	*76.7*	**2.48** ± *1.36*	*86.6*	**1.06** ± *1.22*	*87.7*	2
Massive and compact branch	47.6	**−2.39** ± *0.14*	48.2	**3.27** ± *3.58*	84.2	**1.36** ± *0.95*	86.9	**1.23** ± *0.18*	89.2	**0.37** ± *0.53*	90.7	**0.33** ± *2.37*	91.0	2
Massive	71.4	**0.52**	75.1	**1.12**	87.4	**−1.08**	85.2	**−1.77**	47.6	**0**	47.6	**0.50**	48.1	1
Soft substratum, compact branch and massive	53.2	**0.75**	58.5	**2.52**	47.8	**0.08**	54.5	**−0.05**	70.6	**0.36**	77.7	**4.31**	79.1	1
Soft coral	71.9	**0.09**	72.5	**1.61**	90.3	**0.10**	90.5	**−0.28**	87.7	**0.98**	91.6	**1.31**	92.9	1

Mean coral cover (underlined), normalised areal colonisation rates (NACR) (bold) and standard deviation (italic) for coral communities at Level 1 (*L1* coral/substratum) and Level 2 (*L2* dominant coral morphology, dominant substratum type). The number of subset for each community is indicated; a single subset allowed no standard deviation

The precise elevation of the dead tops of such micro-atolls is a useful indicator of sea-level fluctuation (Smithers and Woodroffe 2001; Kench et al. 2009; Yu et al. 2009). Micro-atolls that grew together to form a continuum of adjacent massive coral colonies (class'Massive' at Level 2, Fig. 4b) were discriminated from other massive corals associated with fast-growing branching corals that had invaded the vacant surrounding space. At Level 3, the class 'Massive' exhibits two components: 'Massive 1' corresponding to the living rim of the micro-atoll and 'Massive 2' corresponding to their dead, flat sections (Fig. 4c). These observations of micro-atolls were also in agreement with the earlier observations by Berkelmans et al. (1998) who noticed newly formed growth lips on pre-existing micro-atolls.

Significance for reef-flat dynamics in a climate change era

Ocean temperatures and acidification have been rising for the past century, with demonstrated and anticipated deleterious consequences on coral communities, and possible non-return tipping points for coral reefs survival rapidly approaching (Veron et al. 2009). Such pessimistic outlooks have scientists prospecting for 'nuggets of hope' for coral reef survival (Berkelmans and Van Oppen 2006). It was therefore interesting to discover that deleterious effects in terms of reef growth were not detectable over the years covered in this study. Instead, it was shown that there was substantial colonisation of the western section on the Heron reef flat and that spectacular coral development had been facilitated by a local sea-level rise caused by engineering works. The rate of local sea-level rise (~12–14 cm in 10 years) was of the same order as and projected IPCC sea-level rise scenarios for 2100 (~20–90 cm; IPCC 2007).

It thus appears that sea-level rise to date on western Heron reef flat may have offset any potentially negative effects of ocean temperatures (bleaching mortality) and ocean acidification since 1972. From 1972 to 2007, there was a coral colonisation rate of 12 mm year^{-1}. This rate is significant in the light of projected sea-level rise for this century as high as 10 mm year^{-1} (IPCC 2007), which exceeds commonly accepted reef-flat accretion rates (~6 mm year^{-1}; Montaggioni 2005). The rapid rise would cause many of today's inter-tidal reef flats to become subtidal at ecological time scales (Buddemeier and Smith 1988; Hopley and Kinsey 1988; Blanchon et al. 2009). If it could be assumed that there will be an adequate supply of propagules in the future (larvae, viable fragments), colonisation similar to that reported here might be expected to occur on shallow reef flats where present sea level limits coral growth. While the western Heron reef flat (like any other) has specific characteristics (type of communities, local hydrodynamics and perturbation regime) that do not represent all reef flats worldwide, it is pertinent to note that the period of strong growth documented here did bracket the most severe bleaching events on record (1998, 2002) and coincided with decreasing calcification rates in some massive corals on the GBR (De'ath et al. 2009).

Perspectives: towards modelling reef-flat dynamics

The Heron Reef study is localised to a small section of reef flat, but we demonstrated here for the first time that coral patch and communities growth can be finely monitored, especially when they progress over new substratum previously unsuitable and optically bright. Previous studies (Scopélitis et al. 2009, 2010) in combination with the present study demonstrate the feasibility of using remote sensing and in situ observations to monitor reef-flat responses to a variety of stressors across several decades. Detailed quantitative interpretation of such time-series is difficult to achieve due to the lack of past in situ data, but rapid development of monitoring networks should offset this problem in the future. The 1998 bleaching event has triggered many monitoring projects which are still active to date. The applied strategies often lack adaptive capacity (Scopélitis et al. 2010) and stick to the same few limited number of sites, but this is clearly better than nothing. The last methodological steps would be to formalise the various behaviours and responses to design spatially explicit models of reef-flat trajectories following different disturbances (Scopélitis et al. 2007). Calibrated models would enhance our ability to interpret changes in time and space, allow generalisation to other sites and provide more quantitative recommendations for managers in charge of monitoring and maintaining reef resilience.

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