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Abstract: Coral reefs are hotspots of marine biodiversity, and their global decline is a threat to our natural heritage. Conservation management of these precious ecosystems relies on accurate and up-to-date information about ecosystem health and the distribution of species and habitats, but such information can be costly to gather and interpret in the field. Remote sensing has proven capable of collecting information on geomorphologic zones and substrate types for coral reef environments, and is cost-effective when information is needed for large areas. Remote sensing-based mapping of coral habitat variables known to influence biodiversity has only recently been undertaken and new sensors and improved data processing show great potential in this area. This paper reviews coral reef biodiversity, the influence of habitat variables on its local spatial distribution, and the potential for remote sensing to produce maps of these habitat variables, thus indirectly mapping coral reef biodiversity and fulfilling information needs of coral reef managers.

Key words: coral reefs, fish biodiversity, habitat characteristics, lidar, remote sensing, rugosity.

I Introduction

Coral reefs are the most biodiverse marine ecosystems on the planet, estimated to harbour nearly one million species globally (Reaka-Kudla, 1997: 93). They can be places of extraordinary beauty, and are essential to the livelihoods of people who depend on them for food, coastal protection, tourism-based income and more (Birkeland, 1997: 2). However, the health of coral reefs is declining at a global scale (Wilkinson, 2004: 7), and the threats that have precipitated this decline range from overfishing, nutrient enrichment and coral diseases at the local scale to world-wide ocean warming, acidification, and sea-level rise. Most of these threats are expected to worsen their impact in the coming decades (Hoegh-Guldberg, 1999; Kleypas *et al.*, 1999; Pittock, 1999), leaving an uncertain future for coral reefs. The decline of coral reefs, both past and projected, is of much more than academic interest; it is a serious threat to global biodiversity, an important part of our natural heritage.

Because of the complexity of coral reef ecosystems and the multitude of threats,

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identification of the important threats and the necessary management for a given reef is difficult. Nevertheless, the global area of coral reef under some form of management is growing, and so is the need for information on which to base management measures (Wilkinson, 2004: 1). A manager of a protected area needs assessments of various aspects of reef health, which provide both a basis from which zonation plans and management regulations can be developed, and a baseline from which changes can be assessed.

Reef health is an intangible concept, and is typically mapped and monitored using a number of proxies. Live coral cover is often used for practical reasons (Mumby *et al.*, 2004b), and so is diversity or abundance of ecologically important or vulnerable species (Hodgson *et al.*, 2004). However, owing to the difficulties and expense associated with conducting extensive field surveys under water, spatially distributed data of the appropriate type and detail are rarely available. Remote sensing technologies have therefore been used to map coral reefs since the early days of Landsat (Smith *et al.*, 1975), and research into the use of remote sensing technology continues with the advent of new sensors and data processing methods (Kutser *et al.*, 2006). Classification of broad substrate types is now routinely possible in clear and shallow water, and water depth can be derived from a variety of data sources with varying accuracy. The interference of the water column, however, continues to pose problems for classification accuracy, and so do the similarities in spectral signatures between important substrate types. New technologies show promise for mapping aspects of coral reef health beyond substrate types, including water quality and reef structural complexity, thus providing complementary information for mapping of coral reef biodiversity. In this paper we aim to review coral reef biodiversity and its spatial distribution, the influence of habitat characteristics on biodiversity, and remote sensing approaches to mapping coral reef habitats, with a focus on mapping habitat variables known to influence biodiversity.

II Coral reef biodiversity

Although reefs have been a recurrent phenomenon throughout the history of life on Earth, modern coral reefs only developed in the Triassic (Newell, 1972). The evolution of the *Symbiodinium* group of dinoflagellates and their incorporation into scleractinian corals produced the symbiotic organisms that are still the primary reef-building organisms (Webb, 1998). Important groups of fauna evolved thereafter, notably sea urchins, reef fishes and currently widespread coral genera such as *Acropora*, *Porites* and *Pocillopora* (Wood, 1998). Today, despite covering only between 0.1% and 0.5% of the total area of the oceans (Moberg and Folke, 1999), coral reefs harbour more species than any other marine ecosystem (Dubinsky, 1990: 251; Reaka-Kudla, 1997: 93). The largest groups of known coral reef species are fishes and sponges, the reef-building organisms themselves being relatively few in number. Comprehensive species lists do not exist for any reef area of the world (Paulay, 1997); it is apparent that only a fraction of the existing fauna has been described, and it is likely that small cryptic species outnumber the numerous described fishes and sponges (Moran and Reaka, 1988).

Coral reefs are generally limited to shallow and clear water with a mean water temperature of 18°C or higher, and are thus largely confined to the tropics (Yonge, 1940). Although reefs exist wherever conditions permit, there is profound variation in the number of different species that make up the reef fauna in different parts of the world. At a regional scale, three factors have had a large influence on today's biogeographic patterns. First, the current distribution of land masses and oceans has resulted in upwelling at the eastern margins of the two major oceans, the Atlantic and the Indo-Pacific, and the dominant equatorial currents running east to west (Veron, 1995: 99). Cold nutrient-rich water from upwelling is detrimental to reef growth, and western margins of oceans therefore house larger reef areas than eastern margins (Hubbard, 1997: 52). Second, the closing of the Isthmus of Panama separated the Atlantic and Pacific oceans between 3.1 and 3.5 million years ago (Coates and Obando, 1996), which resulted in different species now being present on either side of the Isthmus. Third, the large area of shallow tropical seas in the Indo-West Pacific has resulted in greater biodiversity of coral reef fauna here than in any other of the recognized biogeographic regions: the Western Atlantic, Eastern Pacific and Eastern Atlantic, in order of decreasing biodiversity (Briggs, 1999; Bellwood and Hughes, 2001). Within the Western Pacific, the species richness of scleractinian corals themselves is greatest in the coral triangle, formed by Indonesia, the Philippines and New Guinea, with more than 450 described. Species richness gradually declines towards the Indian Ocean or the Pacific (Veron, 1995: 140). A similar biogeographic pattern is found for reef fishes (Bellwood and Hughes, 2001; Bellwood and Wainwright, 2002), and for all other taxa for which data are available (Paulay, 1997: 303).

At smaller spatial scales, communities form as a subset of the available species of the region, determined by the local physical and biological environment. Within a given coral reef ecosystem several spatial biodiversity patterns have been shown to exist. Biodiversity of corals is greatest at intermediate depth (Huston, 1994: 385; Karlson, 1999: 31), with intermediate disturbance history (Connell, 1978) and fish biodiversity increases close to the reef edge (Friedlander and Parrish, 1998), in areas with high coral cover (Chabanet *et al.*, 1997), and high structural complexity (McCormick, 1994). These relationships, however, are not uniform across taxonomic and functional groups, and are sometimes heavily influenced by stochastic recruitment events (Sale, 1991: 203). Studies have demonstrated spatial covariance of biodiversity for different taxonomic groups, and have confirmed that species with high spatial variation in biodiversity are good indicators of biodiversity across taxonomic groups. This tends to be the case for fish rather than plants (Ward *et al.*, 1999) or coral (Beger *et al.*, 2003), which is unfortunate because fish are not directly mappable using remote sensing. Fortunately, distinguishable habitat categories such as reef, seagrass and sand can predict biodiversity equally well or better than fish, and are more easily mappable (Ward *et al.*, 1999).

III Habitats as indicators of coral reef biodiversity

As noted, several environmental variables have been shown to influence the biodiversity of a given habitat. Mapping such habitat variables could indicate the likely spatial distribution of biodiversity at a local scale and suggest priority areas for conservation, at least for the species for which habitat-biodiversity relationships have been identified. A survey of the literature relating biodiversity and habitat variables yields a complex picture. Studies have focused on a variety of taxonomic or functional groups, have employed different measures of biodiversity, and have measured different habitat variables in different ways. A brief overview is presented in Table 1. Detailed relationships are obscured by the number of different variables used, and the different temporal and spatial scales studied (Jones and Syms, 1998). It can thus be argued that a species-specific approach is more appropriate, as habitat associations of many individual species are well known and well defined (Allen *et al.*, 2003). For a few highly significant species such an approach may be useful but, with approximately 10,000 species of described fish, and a total of one million species in all taxonomic groups estimated to exist on coral reefs, a species-specific approach is unfeasible for studies of general biodiversity patterns.

Despite these problems, several conclusions can be drawn from the literature: (i) several habitat characteristics influence local biodiversity; (ii) the number of studied biodiversity and habitat variables is large

Table 1 Studies demonstrating spatial correlations between habitat and biodiversity variables

Habitat variable	Biodiversity variable	Source
Depth	Fish species richness	Luckhurst and Luckhurst, 1978 Huston, 1994
	Fish species diversity	Friedlander and Parrish, 1998
	Herbivore fish species richness	Ormond *et al.*, 1996
Structural complexity	Fish species richness	Friedlander and Parrish, 1998 McCormick, 1994 Gratwicke and Speight, 2005
	Fish species diversity	Luckhurst and Luckhurst, 1978
	Gastropod abundance	Kohn, 1968
	Gastropod species richness	Kostylev *et al.*, 1997; 2005
Live coral cover	Fish abundance, species richness and diversity	Jones *et al.*, 2004 Chabanet *et al.*, 1997 Garpe and Ohman, 2003
	Corallivore fish species richness	Friedlander and Parrish, 1998
	Sea urchin abundance	McClanahan, 1988
Branching coral cover	Fish species richness	Chabanet *et al.*, 1997
	Fish abundance	Sale and Dybdahl, 1975
Number of holes, total hole volume, mean hole volume	Fish species richness, fish abundance, fish species diversity	Friedlander and Parrish, 1998 Hixon and Beets, 1993
Distance to reef edge	Fish species richness and diversity	Friedlander and Parrish, 1998
Distance to river mouth	Species richness and diversity	Friedlander and Parrish, 1998
Total area	Fish species diversity	Molles, 1978

and relationships are not restricted to a few variables; (iii) some habitat variables, namely depth, live coral cover and reef structural complexity, influence more biodiversity variables than others, and show stronger correlations than others; and (iv) common biodiversity measures, including species abundance, richness and diversity, show correlations with these habitat variables. Several causative mechanisms have been proposed for the relations between habitat and biodiversity. The influence of depth has been cited as an example of intermediate disturbance positively influencing species richness at intermediate depth (Huston, 1994: 383), whereas the influence of live coral cover has been related to larval settlement success and to survival of corallivorous and coral-dwelling species (Jones *et al.*, 2004). Reef structural complexity provides physical heterogeneity and refuge for prey species – spaces big enough for them to enter but too small for their predators (Friedlander and Parrish, 1998). This illustrates the important relation between the body sizes of organisms and the spatial scale of the structure providing refuge. Habitat influences on biodiversity also extend to the temporal domain; loss of fish biodiversity can often be attributed to loss of coral cover (Jones *et al.*, 2004) or loss of physical structure following hurricanes or severe bleaching (Connell *et al.*, 1997; Garpe *et al.*, 2006; Graham *et al.*, 2006). Mapping coral reef habitats can therefore provide coral reef managers with important information on the likely spatial distribution of biodiversity in their area and, in the absence of frequent field surveys, can warn about changes in biodiversity to be expected from changing habitats.

IV Mapping coral reefs with remote sensing

Most coral reef remote sensing research has not been carried out directly in the context of biodiversity, but has focused on mapping geomorphologic zones (Smith *et al.*, 1975; Andréfouët and Guzman, 2005) and characteristic substrate types (Mumby *et al.*, 1997; Andréfouët *et al.*, 2003). Nevertheless, remote sensing has become an important tool for coral reef studies and the existing research has built a foundation from which biodiversity studies can benefit. In addition, new remote sensing technologies have improved the accuracy and spatial scales at which coral reefs can be mapped, so products more relevant for biodiversity research can be developed.

1 Mapping geomorphology and substrate types

Mapping of geomorphologic zones was the first use of remote sensing on coral reefs (Smith *et al.*, 1975) and, despite developments in automated systems (Suzuki *et al.*, 2001), geomorphologic zones are typically still mapped manually – outlined on a plot of original or classified data by an expert user (Andréfouët *et al.*, 2001; Andréfouët and Guzman, 2005). Classes can be limited to the major geomorphologic zones – forereef, reef crest, lagoon, backreef and patch reefs – or they can be arranged in a hierarchy incorporating the major geomorphologic zones and slope, depth, or other variables deemed important (Mumby and Harborne, 1999). Because geomorphologic zones themselves influence biodiversity, their mapping can provide a first insight into likely areas of high biodiversity (Andréfouët and Guzman, 2005).

2 Mapping substrate types

More research effort has gone into mapping substrate types (Mumby *et al.*, 2004b; Kutser *et al.*, 2006). The spectral reflectance properties of various substrate types differ, which enables multispectral and hyperspectral instruments to discriminate between them. The level of detail that can be obtained, typically expressed as the number of classes that can be discriminated and the accuracy of the classification, depends on the platform and sensor type and on environmental factors such as water depth and turbidity, the state of the sea surface, and the atmosphere (Mumby *et al.*, 2004b). Early studies that used Landsat TM and SPOT HRV sensors, for example, only allowed discrimination of broad categories such as coral, sand, seagrass and algae. Even with such broad classes, distinguishing between the coral and algae classes was difficult because the reflectance properties of both are dominated by chlorophyll a; the differences are caused by accessory pigments whose contribution to the spectral reflectance is relatively small (Fang *et al.*, 1995; Hedley and Mumby, 2002; Kutser *et al.*, 2003). In addition, light attenuation with depth reduced differences in spectral reflectance between highly reflecting substrates at depth and less reflecting substrates in shallow water. Landsat TM and SPOT HRV sensors with broad bandwidths (>65 nm full-width half maximum (FWHM) for all water-penetrating wavelengths) were not designed to register the small differences between these substrate types, and classification accuracies are therefore rarely better than 60–70% for the four main classes of coral, sand, seagrass and algae (Green *et al.*, 2000), and as low as 30% for a detailed classification using more than 10 classes (Mumby and Edwards, 2002). The influence of variable depth can be partly mitigated by correcting radiance values for its influence (Lyzenga, 1978; Stumpf *et al.*, 2003), or by stratifying substrate types into depth intervals in the classification (Turner and Klaus, 2005). Specular reflection off the water surface is another source of noise that can be partly eliminated by using radiance values in the near-infrared wavelength range to correct values in the visible range (Hochberg *et al.*, 2003a; Hedley *et al.*, 2005). Another problem with the use of data from Landsat TM and SPOT HRV sensors has been their pixel sizes, 30 m and 20 m, respectively, which result in most pixels containing a mix of substrate types. The better spatial resolution of the IKONOS and Quickbird satellites has reduced, but not eliminated, this problem, and classification accuracies have increased to the 75–85% range using broad substrate classes and around 50% for more detailed classes (Mumby and Edwards, 2002; Andréfouët *et al.*, 2003). The relationship between the sensor type, the number of classes, and the classification accuracy is well developed and can be used to design an optimum mapping strategy for a given application (Mumby *et al.*, 2004b). The development of hyperspectral instruments has improved the degree to which accessory pigments can be used to separate detailed classes, and they have therefore enabled mapping of detailed classes while retaining satisfactory mapping accuracy (Mumby *et al.*, 2004b; Kutser *et al.*, 2006). However, the dominant features of the spectral signatures used to discriminate between typical coral reef substrates are in the part of the visible spectrum where water penetration is lowest, namely 550–700 nm (Mobley, 1994; Kutser *et al.*, 2003). This rapidly reduces the number of distinct substrate types that can be distinguished as depth increases (Holden and LeDrew, 1999; Capolsini *et al.*, 2003; Hochberg and Atkinson, 2003). In a best-case scenario, mapping shallow reefs with the airborne hyperspectral CASI sensor, Mumby *et al.* (1997) mapped nine substrate classes with an overall accuracy of 81%.

V Mapping habitat variables and biodiversity

A few recent studies have related the mapped geomorphologic zones and substrate types to the presence of specific species. These studies do not map individual species directly, but rather reef zones in which particular species are known from field observations to be dominant (Turner and Klaus, 2005; Purkis *et al.*, 2006). As these species assemblages do not have unique properties that are proven both universal and mappable with current technology, these studies require intensive fieldwork to determine the relation between the mapped geomorphologic zones and substrate types and their species composition. The remotely sensed information thus functions more as geolocation of field observations than as the primary information source, and classification algorithms cannot be applied beyond the studied field site.

Habitat variables known to directly influence biodiversity have been mapped surprisingly rarely. Adjeroud *et al.* (2000) used SPOT HRV data to map pinnacle density, surface area, and hydrodynamic aperture of nine atolls in French Polynesia, and found that these explained part of the between-atoll variation in species richness of investigated taxa (corals, molluscs, echinoderms and algae). Andréfouët and Guzman (2005) have found a non-significant correspondence between geomorphologic zones and biodiversity in Panama, which they attribute to variation in reef structural complexity rather than geomorphology *per se*. However, no study has attempted to use remote sensing directly to predict spatial variation in biodiversity from habitat variables.

A review of the literature showed that depth, live coral cover and reef structural complexity all show correlations with several biodiversity variables. Depth is routinely mappable using a variety of remote sensing methods, and algorithms to derive live coral cover from airborne hyperspectral data have been developed. Using remote sensing to map coral reef structure has only recently been explored, and different spatial scales of remote and in-situ measurements remain an unresolved issue. Other habitat variables with known influences on species richness (eg, distance to the reef edge or a nearby river) are also routinely mappable. There is thus ample scope for further exploring the possibility to predict the spatial distribution of biodiversity on coral reefs using habitat maps derived from remotely sensed data.

1 Remote sensing of depth

Water depth can be mapped using acoustic, passive optical, or active optical instruments. Acoustic instruments located at or below the sea surface emit a sound pulse toward the sea floor and measure the temporally resolved return pulse (the echo). With knowledge of the speed and direction of the pulse, the vertical distance between the instrument and the seafloor can be calculated (Preston, 2004). Nadir-pointing acoustic instruments emit pulses at beam angles of 15–25%, and register depth based on the earliest received echo assumed to be directly underneath the instrument (Foster-Smith and Sotheran, 2003). Multibeam instruments emit fan-shaped pulses and employ multiple narrow field-of-view receivers to register the return pulse from several reflecting points on the sea floor (Mitchell and Clarke, 1994). The movement of the instrument as it is towed behind a vessel provides areal coverage and onboard GPS provides each measurement with a coordinate in space. Point spacing is determined by the speed of the towing vessel, water depth, and the proximity of surveyed tracks. Acoustic instruments can function in all but the shallowest depths (<50 cm) (Mumby *et al.*, 2004b).

Active optical (lidar) instruments employ a similar principle, instead emitting and receiving a laser pulse of water-penetrating wavelength, typically 532 nm, using an instrument mounted underneath an aircraft (Guenther, 2001). The temporally resolved return pulse (the waveform) displays reflection peaks from both the water surface and the substrate. Areal coverage is provided by pulses emitted at frequencies up to 3 kHz, a spinning mirror distributing light pulses across the flight path, and the movement of the aircraft. The spatial location of each reflecting surface is determined by an onboard kinematic GPS and an Inertial Measurement Unit, combined with knowledge of the direction of the light pulse and its speed in air and water. Most commercial instruments can achieve a minimum point spacing of 2 m, and can operate at depths up to 70 m, depending on water optical quality (LaRocque *et al.*, 2004; Tenix, 2005). Both acoustic and active optical methods are both so well developed and tested that in-situ verification is typically unnecessary (IHO, 1998).

Water depth can also be mapped with passive optical remote sensing when no better data sources are available. Methods rely on the wavelength dependency of light attenuation in water; within the visible spectrum, longer wavelengths attenuate more rapidly (Mobley, 1994), hence substrates located in deeper water will show a greater proportion of reflected light in shorter wavelengths (Lyzenga, 1978). Variation in substrate spectral reflectance introduces error, but can, at least in theory, be adjusted for using hyperspectral data (Hedley and Mumby, 2003). Water optical properties and substrates with very low reflectance introduce additional complications that can also be partly mitigated (Philpot, 1989; Stumpf *et al.*, 2003). Depth mapping with passive optical remote sensing always requires in-situ calibration, and is rarely possible at depths greater than 25 m (Stumpf *et al.*, 2003).

2 Remote sensing of live coral cover

Mapping of live coral cover has been partly addressed by the substrate classification techniques mentioned above, but the presence of more than one substrate type within a pixel is problematic. Spectral unmixing, routinely used in terrestrial environments to deal with subpixel heterogeneity, is complicated by the effects of the water column in addition to the strong similarity between the spectral signatures of different substrate types. If the diffuse attenuation coefficient of the water column is known, linear spectral unmixing can be modified to include the influence of the water column, as long as all endmember spectra are known (Hedley and Mumby, 2003). However, spatially distributed values of the diffuse attenuation coefficient are rarely, if ever, known, and in practice endmember spectra show strong similarity because of the dominance of chlorophyll a. This approach has not yet been developed into an operational tool (Hedley *et al.*, 2004), though it has been proven useful in conditions of shallow clear water (Mumby *et al.*, 2004a).

Disregarding proportions of non-coral substrate types, Isoun *et al.* (2003) designed a classification scheme based only on percentage live coral cover, and achieved 77% overall classification accuracy using three narrow bands (10 nm FWHM) from an airborne sensor optimized for coral reef benthos discrimination. Going one step further, Joyce (2004) used an index-based approach to investigate correlations between live coral cover and spectral reflectance ratios and derivatives, using hyperspectral data from in-situ and airborne measurements. She found that the optimum band ratio and derivative varied between 'blue' and 'brown' coral types (Hochberg *et al.*, 2003b), and depended on resampling of the hyperspectral data set, depth and water quality. From a survey on Heron Reef, Australia, she obtained a correlation of r = –0.76 between live coral cover and the ratio of reflectances in the 529 nm and 439 nm bands of the airborne sensor.

3 *Remote sensing of reef structure*

The structural complexity of coral reefs has received far less research attention from remote sensing scientists than water depth and live coral cover. Structural complexity is quantified in several ways and exists at scales of varying importance for biodiversity, ranging from regional distribution of reef complexes to the intricate coral skeleton structure. To explore the potential for remote sensing to map structural complexity as it influences biodiversity, it is necessary to review the quantification methods and spatial scales used in field studies that have established the relationship.

Structural complexity on coral reefs has predominantly been measured using the chain-and-tape method. This method yields the measure of rugosity, calculated as the ratio between the contour-following distance between two points on the reef and the distance between the same two points as measured in a straight line (Risk, 1972). Other in-situ measures of structural complexity include vertical relief, fractal dimension, number and volume of holes, percent cover of branching corals, and ordinal scales based on visual estimation. Rugosity is dependent on two scales of its measurement: the total horizontal distance between the two end points and the detail with which the contour-following length is measured. These scales are referred to as spatial extent and grain, respectively, and are key parameters in all quantification of spatial structure (Wiens, 1989; Marceau, 1999; Hay *et al.*, 2001). Finer grain will register more roughness on a surface and greater extent will incorporate larger-scale topography, both leading to higher rugosity values. It is therefore unfortunate that with few exceptions (Luckhurst and Luckhurst, 1978; Kostylev *et al.*, 1997; 2005) this dependence seems to have gone unnoticed in the literature, and that the two scales of measurement vary between studies. Nevertheless, a review of the literature reveals that the measure of rugosity is used more often than any other measure, and that the extent and grain are typically in the regions of 3–10 m and 1–10 cm respectively (Table 2). It therefore seems reasonable that remote sensing of reef structure for biodiversity studies should operate close to these scales.

Structural complexity can be quantified from remote sensing data by developing digital elevation models from depth data, and the spatial scale of these models is determined by the instruments used for data collection. Acoustic instruments can obtain data sets with point spacing in the range of centimetres (Weber, 1996), and they are therefore well suited for detailed analyses of reef structure. Although such studies have not yet been conducted, it is likely that remotely sensed rugosity values would correspond closely to those measured in situ, and thus be useful for biodiversity studies. However, this level of detail is achieved at the expense of areal coverage, particularly in the shallow

Table 2 Measures and scales of measurement in the quantification of structural complexity

Measure of structure	Extent (m)	Grain (cm)	Source
Rugosity	3	1.3	Friedlander and Parrish, 1998
Cover of branching corals	n/a		Chabanet *et al.*, 1997
Rugosity	3	10 and n/a	McCormick, 1994
Number and size of holes	n/a		Hixon and Beets, 1993
Microhabitats	n/a		Ormond *et al.*, 1996
Rugosity	3	1.5	Luckhurst and Luckhurst, 1978
Rugosity	?	?	Garpe and Ohman, 2003
Rugosity	10	Nylon line	McClanahan, 1999
Rugosity	14	?	Chapman and Kramer, 1999
Fractal dimension	0.14/0.15	0.1	Kostylev *et al.*, 1997; 2005
Rugosity	1–3.64	n/a	Gratwicke and Speight, 2005
Vertical relief	n/a		Syms and Jones, 2000
Rugosity	10	?	McClanahan, 1988
Visual estimation	n/a		Kohn, 1968; Kohn and Leviten, 1976
Visual estimation	6-point scale		Lara and Gonzalez, 1998
Rugosity	10 (transect)	1.3	Rogers *et al.*, 1991
Vertical relief	n/a		Bainbridge and Reichelt, 1988

waters in which most coral reefs are found (Moyer *et al.*, 2005; Riegl and Purkis, 2005).

Most lidar instruments in operation have been developed for mapping of bathymetry, for which spatial detail is of less concern than depth penetration and areal coverage. As mentioned above, these instruments therefore provide data at a minimal point spacing of 2 m. NASA's Experimental Advanced Airborne Research Lidar (EAARL) is a research lidar able to obtain a point spacing of 80 cm, the best spatial resolution currently offered by an airborne lidar (USGS, 2006). Brock *et al.* (2004) used transects of depth measurements from this instrument to quantify the structural complexity of patch and bank reefs in Florida, and later showed that abrupt depth variations indicate presence of massive stony corals (Brock *et al.*, 2006), the main structural elements on the investigated reefs. These studies show that airborne lidar can provide information about reef structure at the scale of large coral colonies, the main structural elements on coral reefs. However, correlation between the measures produced by Brock *et al.* (2004) and biodiversity variables have proven very weak (Kuffner *et al.*, 2007), and it is questionable whether this may be due to the 80 cm point spacing being inappropriate for this purpose (Knudby and LeDrew, 2007). Nevertheless, Wedding *et al.* (unpublished data), working in Hawaii, have demonstrated that lidar-based rugosity, captured with 4 m point spacing, can predict fish biodiversity variables very accurately, rugosity values explaining more than 60% of the variability in fish biomass between different areas of a reef. It is likely that the obtainable correlations and the optimal spatial scale of rugosity measurements depend on the environment under investigation, and the biodiversity variable investigated (Kuffner *et al.*, 2007).

In terrestrial environments, lidar waveforms have been analysed individually to investigate vertical structure of the surface within the 'footprint' of each pulse. Forest structural variables such as canopy height, aboveground biomass and stem basal area have all been estimated from measures of the shape of lidar waveforms. In marine environments, waveform analysis has been used to derive the Inherent Optical Properties (IOPs) of the water column (Kopilevich *et al.*, 2005) and improve estimates of substrate reflectance

(Tuell *et al.*, 2005). Though not yet tested, it is possible that waveform analysis can be used to derive measures of structural complexity on coral reefs as has been done in forests, enabling such investigation to be undertaken at a smaller spatial scale than possible so far. For example, with an EAARL footprint diameter of 20 cm, waveform analysis of individual footprints would bring the scale of structural complexity measured by remote sensing much closer to that shown by field studies to influence biodiversity on coral reefs.

Passive optical instruments have also been used in situ to document the effect of the structure of coral colonies on their spectral reflectance, which has been attributed to internal shading (Joyce and Phinn, 2002; Minghelli-Roman *et al.*, 2002). However, not all studies have found a significant effect (Holden and LeDrew, 1999), and it is not clear how upscaling to airborne or satellite measurements could be achieved. No studies have successfully mapped reef structure at the scale of coral colonies using data from airborne or spaceborne passive optical instruments.

VI Concluding remarks

Remote sensing is now a standard tool used in coral reef studies, and both sensors and data processing algorithms have become increasingly abundant and sophisticated with time. However, no single instrument type can provide optimum data in all situations and for all purposes; instead, data from the different types of sensors can complement each other. The local distribution of coral reef biodiversity has been shown to be influenced by a number of habitat variables such as depth, live coral cover and structural complexity, each of which can be mapped accurately with one or more remote sensing instruments. Studies that combine the strengths of each instrument type and map multiple habitat variables are needed to test our ability to predict the local spatial distribution of biodiversity, and to map areas of high biodiversity. In addition, studies must investigate in greater detail the optimum spatial scale at which habitat variables should be mapped, in order to make full use of the technology. Ultimately, the usefulness of remote sensing technology for conservation of threatened coral reefs rests upon its ability to map relevant environmental variables, provide a scientific basis for decision-making, and thereby aid effective conservation of coral reef biodiversity.

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References

Adjeroud, M., Andréfouët, S., Payri, C. and **Orempuller, J.** 2000: Physical factors of differentiation in macrobenthic communities between atoll lagoons in the Central Tuamotu Archipelago (French Polynesia). *Marine Ecology-Progress Series* 196, 25–38.

Allen, G.R., Steene, R., Humann, P. and **DeLoach, N.** 2003: *Reef fish identification – tropical Pacific*. Jacksonville: New World Publications.

Andréfouët, S. and **Guzman, H.M.** 2005: Coral reef distribution, status and geomorphology-biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama. *Coral Reefs* 24, 31–42.

Andréfouët, S., Claereboudt, M., Matsakis, P., Pages, J. and **Dufour, P.** 2001: Typology of atoll rims in Tuamotu Archipelago (French Polynesia) at landscape scale using SPOT HRV images. *International Journal of Remote Sensing* 22, 987–1004.

Andréfouët, S., Kramer, P., Torres-Pulliza, D., Joyce, K.E., Hochberg, E.J., Garza-Perez, R., Mumby, P.J., Riegl, B., Yamano, H., White, W.H., Zubia, M., Brock, J.C., Phinn, S.R., Naseer, A., Hatcher, B.G. and **Muller-Karger, F.E.** 2003: Multi-site evaluation of IKONOS data for classification of tropical coral reef environments. *Remote Sensing of Environment* 88, 128–43.

Bainbridge, S.J. and **Reichelt, R.E.** 1988: *An assessment of ground truth methods for coral reef remote sensing data*. Townsville: AIMS, 439–44.

Beger, M., Jones, G.P. and **Munday, P.L.** 2003: Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biological Conservation* 111, 53–62.

Bellwood, D.R. and **Hughes, T.P.** 2001: Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292, 1532–34.

Bellwood, D.R. and **Wainwright, P.C.** 2002: The history and biogeography of fishes on coral reefs.

In Sale, P.F., editor, *Coral reef fishes: dynamics and diversity in a complex ecosystem*, San Diego: Academic Press, 5–32.

Birkeland, C., editor 1997: *Life and death of coral reefs*. New York: Chapman and Hall.

Briggs, J.C. 1999: Coincident biogeographic patterns: Indo-West Pacific Ocean. *Evolution* 53, 326–35.

Brock, J.C., Wright, C.W., Clayton, T.D. and **Nayegandhi, A.** 2004: LIDAR optical rugosity of coral reefs in Biscayne National Park, Florida. *Coral Reefs* 23, 48–59.

Brock, J.C., Wright, C.W., Kuffner, I.B., Hernandez, R. and **Thompson, P.** 2006: Airborne lidar sensing of massive stony coral colonies on patch reefs in the northern Florida reef tract. *Remote Sensing of Environment* 104, 31–42.

Capolsini, P., Andréfouët, S., Rion, C. and **Payri, C.** 2003: A comparison of Landsat ETM+, SPOT HRV, Ikonos, ASTER, and airborne MASTER data for coral reef habitat mapping in south Pacific islands. *Canadian Journal of Remote Sensing* 29, 187–200.

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G. and **Galzin, R.** 1997: Relationships between coral reef substrata and fish. *Coral Reefs* 16, 93–102.

Chapman, M.R. and **Kramer, D.L.** 1999: Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology-Progress Series* 181, 81–96.

Coates, A.G. and **Obando, J.A.** 1996: The geologic evolution of the Central American Isthmus. In Jackson, J.B.C., Budd, A.F. and Coates, A.G., editor, *Evolution and environment in tropical America*, Chicago: University of Chicago Press, 21–56.

Connell, J.H. 1978: Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199, 1302–10.

Connell, J.H., Hughes, T.P. and **Wallace, C.C.** 1997: A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67, 461–88.

Dubinsky, Z., editor 1990: *Coral reefs*. Amsterdam: Elsevier.

Fang, L.S., Liao, C.W. and **Liu, M.C.** 1995: Pigment composition in different-colored scleractinian corals before and during the bleaching process. *Zoological Studies* 34, 10–17.

Foster-Smith, R.L. and **Sotheran, I.S.** 2003: Mapping marine benthic biotopes using acoustic ground discrimination systems. *International Journal of Remote Sensing* 24, 2761–84.

Friedlander, A.M. and **Parrish, J.D.** 1998: Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224, 1–30.

Garpe, K.C. and **Ohman, M.C.** 2003: Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish-habitat interactions. *Hydrobiologia* 498, 191–211.

Garpe, K.C., Yahya, S.A.S., Lindahl, U. and **Ohman, M.C.** 2006: Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology-Progress Series* 315, 237–47.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. and **Robinson, J.** 2006: Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103, 8425–29.

Gratwicke, B. and **Speight, M.R.** 2005: Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology-Progress Series* 292, 301–10.

Green, E.P., Mumby, P.J., Edwards, A.J. and **Clark, C.D.** 2000: *Remote sensing handbook for tropical coastal management*. Paris: UNESCO.

Guenther, G.C. 2001: Airborne lidar bathymetry. In Maune, D.F., editor, *Digital elevation model technologies and applications: the DEM users manual*, Bethesda: The American Society for Photogrammetry and Remote Sensing, 237–306.

Hay, G.J., Marceau, D.J., Dube, P. and **Bouchard, A.** 2001: A multiscale framework for landscape analysis: object-specific analysis and upscaling. *Landscape Ecology* 16, 471–90.

Hedley, J.D. and **Mumby, P.J.** 2002: Biological and remote sensing perspectives of pigmentation in coral reef organisms. *Advances in Marine Biology* 43, 277–317.

— 2003: A remote sensing method for resolving depth and subpixel composition of aquatic benthos. *Limnology and Oceanography* 48, 480–88.

Hedley, J.D., Harborne, A.R. and **Mumby, P.J.** 2005: Simple and robust removal of sun glint for mapping shallow-water benthos. *International Journal of Remote Sensing* 26, 2107–12.

Hedley, J.D., Mumby, P.J., Joyce, K.E. and **Phinn, S.R.** 2004: Spectral unmixing of coral reef benthos under ideal conditions. *Coral Reefs* 23, 60–73.

Hixon, M.A. and **Beets, J.P.** 1993: Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63, 77–101.

Hochberg, E.J. and **Atkinson, M.J.** 2003: Capabilities of remote sensors to classify coral, algae, and sand as pure and mixed spectra. *Remote Sensing of Environment* 85, 174–89.

Hochberg, E.J., Andréfouët, S. and **Tyler, M.R.** 2003a: Sea surface correction of high spatial resolution Ikonos images to improve bottom mapping in near-shore environments. *IEEE Transactions on Geoscience and Remote Sensing* 41, 1724–29.

Hochberg, E.J., Atkinson, M.J. and **Andréfouët, S.** 2003b: Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. *Remote Sensing of Environment* 85, 159–73.

Hodgson, G., Kiene, W., Mihaly, J., Liebeler, J., Shuman, C. and **Maun, L.** 2004: *Reef check instruction manual: a guide to reef check coral reef monitoring*. Los Angeles: University of California, 92.

Hoegh-Guldberg, O. 1999: Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50, 839–66.

Holden, H. and **LeDrew, E.** 1999: Hyperspectral identification of coral reef features. *International Journal of Remote Sensing* 20, 2545–63.

Hubbard, D.K. 1997: Reefs as dynamic systems. In Birkeland, C., editor, *Life and death of coral reefs,* New York: Chapman and Hall, 43–67.

Huston, M.A. 1994: *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press.

International Hydrographic Organization (IHO) 1998: *IHO standards for hydrographic surveys*. Monaco: International Hydrographic Organization, 1–26.

Isoun, E., Fletcher, C., Frazer, N. and **Gradie, J.** 2003: Multi-spectral mapping of reef bathymetry and coral cover; Kailua Bay, Hawaii. *Coral Reefs* 22, 68–82.

Jones, G.P. and **Syms, C.** 1998: Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* 23, 287–97.

Jones, G.P., McCormick, M.I., Srinivasan, M. and **Eagle, J.V.** 2004: Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* 101, 8251–53.

Joyce, K. 2004: *A method for mapping live coral cover using remote sensing*. Brisbane: School of Geography, University of Queensland, 137.

Joyce, K.E. and **Phinn, S.R.** 2002: Bi-directional reflectance of corals. *International Journal of Remote Sensing* 23, 389–94.

Karlson, R.H. 1999: *Dynamics of coral communities*. Dordrecht: Kluwer Academic.

Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.P., Langdon, C. and **Opdyke, B.N.** 1999: Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284, 118–20.

Knudby, A. and **LeDrew, E.** 2007: Measuring structural complexity on coral reefs. In Proceedings, AAUS Annual Symposium, Miami, USA, 9–10 March.

Kohn, A.J. 1968: Microhabitats abundance and food of *Conus* on atoll reefs in Maldive and Chagos Islands. *Ecology* 49, 1046–62.

Kohn, A.J. and **Leviten, P.J.** 1976: Effect of habitat complexity on population-density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* 25, 199–210.

Kopilevich, Y.I., Feygels, V.I., Tuell, G.H. and **Surkov, A.** 2005: Measurement of ocean water optical properties and seafloor reflectance with Scanning Hydrographic Operational Airborne Lidar Survey (SHOALS): I. Theoretical background. In Proceedings, Remote Sensing of the Coastal Oceanic Environment, San Diego, 31 July, SPIE 5885.

Kostylev, V., Erlandsson, J. and **Johannesson, K.** 1997: Microdistribution of the polymorphic snail *Littorina saxatilis* (Olivi) in a patchy rocky shore habitat. *Ophelia* 47, 1–12.

Kostylev, V.E., Erlandsson, J., Ming, M.Y. and **Williams, G.A.** 2005: The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. *Ecological Complexity* 2, 272–86.

Kuffner, I.B., Brock, J.C., Grober-Dunsmore, R., Bonito, V.E., Hickey, T.D. and **Wright, C.W.** 2007: Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environmental Biology of Fishes* 78, 71–82.

Kutser, T., Dekker, A.G. and **Skirving, W.** 2003: Modeling spectral discrimination of Great Barrier Reef benthic communities by remote sensing instruments. *Limnology and Oceanography* 48, 497–510.

Kutser, T., Miller, I. and **Jupp, D.L.B.** 2006: Mapping coral reef benthic substrates using hyperspectral space-borne images and spectral libraries. *Estuarine Coastal and Shelf Science* 70, 449–60.

Lara, E.N. and **Gonzalez, E.A.** 1998: The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *Journal of Fish Biology* 53, 209–21.

LaRocque, P.E., Banic, J.R. and **Cunningham, A.G.** 2004: Design description and field testing of the SHOALS-1000T airborne bathymeter. In Kamerman, G.W., editor, Proceedings, Laser Radar Technology and Applications IX, SPIE 5412, 162–84.

Luckhurst, B.E. and **Luckhurst, K.** 1978: Analysis of influence of substrate variables on coral-reef fish communities. *Marine Biology* 49, 317–23.

Lyzenga, D.R. 1978: Passive remote-sensing techniques for mapping water depth and bottom features. *Applied Optics* 17, 379–83.

Marceau, D.J. 1999: The scale issue in the social and natural sciences. *Canadian Journal of Remote Sensing* 24, 347–55.

McClanahan, T.R. 1988: Coexistence in a sea-urchin guild and its implications to coral-reef diversity and degradation. *Oecologia* 77, 210–18.

— 1999: Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* 2, 511–23.

McCormick, M.I. 1994: Comparison of field methods for measuring surface-topography and their associations with a tropical reef fish assemblage. *Marine Ecology-Progress Series* 112, 87–96.

Minghelli-Roman, A., **Chisholm, J.R.M.**, **Marchioretti, M.** and **Jaubert, J.M.** 2002: Discrimination of coral reflectance spectra in the Red Sea. *Coral Reefs* 21, 307–14.

Mitchell, N.C. and **Clarke, J.E.H.** 1994: Classification of sea-floor geology using multibeam sonar data from the Scotian Shelf. *Marine Geology* 121, 143–60.

Moberg, F. and **Folke, C.** 1999: Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29, 215–33.

Mobley, C.D. 1994: *Light and water: radiative transfer in natural waters*. San Diego: Academic Press.

Molles, M.C. 1978: Fish species-diversity on model and natural reef patches – experimental insular biogeography. *Ecological Monographs* 48, 289–305.

Moran, D.P. and **Reaka, M.L.** 1988: Bioerosion and availability of shelter for benthic reef organisms. *Marine Ecology-Progress Series* 44, 249–63.

Moyer, R.P., **Riegl, B.**, **Banks, K.** and **Dodge, R.E.** 2005: Assessing the accuracy of acoustic seabed classification for mapping coral reef environments in South Florida (Broward County, USA). *Revista De Biologia Tropical* 53, 175–84.

Mumby, P.J. and **Edwards, A.J.** 2002: Mapping marine environments with IKONOS imagery: enhanced spatial resolution can deliver greater thematic accuracy. *Remote Sensing of Environment* 82, 248–57.

Mumby, P.J. and **Harborne, A.R.** 1999: Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological Conservation* 88, 155–63.

Mumby, P.J., **Green, E.P.**, **Edwards, A.J.** and **Clark, C.D.** 1997: Coral reef habitat-mapping: how much detail can remote sensing provide? *Marine Biology* 130, 193–202.

Mumby, P.J., **Hedley, J.D.**, **Chisholm, J.R.M.**, **Clark, C.D.**, **Ripley, H.** and **Jaubert, J.** 2004a: The cover of living and dead corals from airborne remote sensing. *Coral Reefs* 23, 171–83.

Mumby, P.J., **Skirving, W.**, **Strong, A.E.**, **Hardy, J.T.**, **LeDrew, E.F.**, **Hochberg, E.J.**, **Stumpf, R.P.** and **David, L.T.** 2004b: Remote sensing of coral reefs and their physical environment. *Marine Pollution Bulletin* 48, 219–28.

Newell, N.D. 1972: Evolution of reefs. *Scientific American* 226, 54–65.

Ormond, R.F.G., **Roberts, J.M.** and **Jan, R.Q.** 1996: Behavioural differences in microhabitat use by damselfishes (Pomacentridae): Implications for reef fish biodiversity. *Journal of Experimental Marine Biology and Ecology* 202, 85–95.

Paulay, G. 1997: Diversity and distribution of reef organisms. In Birkeland, C., editor, *Life and death of coral reefs,* New York: Chapman and Hall, 298–353.

Philpot, W.D. 1989: Bathymetric mapping with passive multispectral imagery. *Applied Optics* 28, 1569–78.

Pittock, A.B. 1999: Coral reefs and environmental change: adaptation to what? *American Zoologist* 39, 10–29.

Preston, J.M. 2004: *Resampling sonar echo time series primarily for seabed sediment classification*. USA: Quester Tangent Corporation, 12.

Purkis, S.J., **Myint, S.W.** and **Riegl, B.M.** 2006: Enhanced detection of the coral *Acropora cervicornis* from satellite imagery using a textural operator. *Remote Sensing of Environment* 101, 82–94.

Reaka-Kudla, M.L. 1997: The global biodiversity of coral reefs: a comparison with rain forests. In Reaka-Kudla, M.L., Wilson, D.E. and Wilson, E.O., editors, *Biodiversity II,* Washington, DC: Joseph Henry Press, 83–107.

Riegl, B.M. and **Purkis, S.J.** 2005: Detection of shallow subtidal corals from IKONOS satellite and QTC View (50, 200 kHz) single-beam sonar data (Arabian Gulf; Dubai, UAE). *Remote Sensing of Environment* 95, 96–114.

Risk, M.J. 1972: Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* 153, 1–6.

Rogers, C.S., **McLain, L.N.** and **Tobias, C.R.** 1991: Effects of Hurricane Hugo (1989) on a coral-reef in St-John, USVI. *Marine Ecology-Progress Series* 78, 189–99.

Sale, P.F. 1991: Habitat structure and recruitment in coral reef fishes. In Bell, S.S., McCoy, E.D. and Mushinsky, H.R., editors, *Habitat structure – the physical arrangement of objects in space,* London: Chapman and Hall, 438 pp.

Sale, P.F. and **Dybdahl, R.** 1975: Determinants of community structure for coral-reef fishes in an experimental habitat. *Ecology* 56, 1343–55.

Smith, V.E., **Rogers, R.H.** and **Reed, L.E.** 1975: Automated mapping and inventory of Great Barrier Reef zonation with Landsat. OCEANS 7, 775–80.

Stumpf, R.P., **Holderied, K.** and **Sinclair, M.** 2003: Determination of water depth with high-resolution satellite imagery over variable bottom types. *Limnology and Oceanography* 48, 547–56.

Suzuki, H., **Matsakis, P.**, **Andréfouët, S.** and **Desachy, J.** 2001: Satellite image classification using expert structural knowledge: a method based on fuzzy partition computation and simulated annealing. In Proceedings, Annual Conference of the International Association for Mathematical Geology, IAMG, Cancun, Mexico.

Syms, C. and **Jones, G.P.** 2000: Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81, 2714–29.

Tenix 2005: *Laser Airborne Depth Sounder, LADS Mk II*. Retrieved 14 June 2007 from http://www.tenix.com/Main.asp?ID=116

Tuell, G.H., Feygels, V., Kopilevich, Y., Weidemann, A.D., Cunningham, A.G., Mani, R., Podoba, V., Ramnath, V., Park, J.Y. and **Aitken, J.** 2005: Measurement of ocean water optical properties and seafloor reflectance with Scanning Hydrographic Operational Airborne Lidar Survey (SHOALS): II. Practical results and comparison with independent data. Proceedings, Remote Sensing of the Coastal Oceanic Environment, San Diego, USA, 31 July.

Turner, J. and **Klaus, R.** 2005: Coral reefs of the Mascarenes, Western Indian Ocean. *Philosophical Transactions of the Royal Society of London Series A – Mathematical Physical and Engineering Sciences* 363, 229–50.

US Geological Survey (USGS) 2006: *EAARL – Airborne lidar system for high-resolution submerged and sub-aerial topography*. Retrieved 14 June 2007 from http://coastal.er.usgs.gov/remote-sensing/advancedmethods/eaarl.html

Veron, J.E.N. 1995: *Corals in space and time: the biogeography and evolution of the Scleratinia*. Ithaca, NY: Cornell University Press.

Ward, T.J., Vanderklift, M.A., Nicholls, A.O. and **Kenchington, R.A.** 1999: Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* 9, 691–98.

Webb, G.E. 1998: Earliest known Carboniferous shallow-water reefs, Gudman Formation (Tn1b), Queensland, Australia: implications for late Devonian reef collapse and recovery. *Geology* 26, 951–54.

Weber, T. 1996: A new generation of multi-beam sweeping echosounder for surveying – ATLAS FANSWEEP 20. In Proceedings, OCEANS '96, Prospects for the 21st Century, Fort Lauderdale, USA, 23–26 September.

Wiens, J.A. 1989: Spatial scaling in ecology. *Functional Ecology* 3, 385–97.

Wilkinson, C. 2004: *Status of coral reefs of the world*. Townsville: Australian Institute of Marine Science.

Wood, R. 1998: The ecological evolution of reefs. *Annual Review of Ecology and Systematics* 29, 179–206.

Yonge, C.M. 1940: *The biology of reef building corals*. London: British Museum, 353–91.