

The importance of structural complexity in coral reef ecosystems

N. A. J. Graham · K. L. Nash

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Abstract The importance of structural complexity in coral reefs has come to the fore with the global degradation of reef condition; however, the limited scale and replication of many studies have restricted our understanding of the role of complexity in the ecosystem. We qualitatively and quantitatively (where sufficient standardised data were available) assess the literature regarding the role of structural complexity in coral reef ecosystems. A rapidly increasing number of publications have studied the role of complexity in reef ecosystems over the past four decades, with a concomitant increase in the diversity of methods used to quantify structure. Quantitative analyses of existing data indicate a strong negative relationship between structural complexity and algal cover, which may reflect the important role complexity plays in enhancing herbivory by reef fishes. The cover of total live coral and branching coral was positively correlated with structural complexity. These habitat attributes may be creating much of the structure, resulting in a collinear relationship; however, there is also evidence of enhanced coral recovery from disturbances where structural complexity is high. Urchin densities were negatively correlated with structural complexity; a relationship that may be driven by urchins eroding reef structure or by their gregarious behaviour when in open space. There was a strong positive

relationship between structural complexity and fish density and biomass, likely mediated through density-dependent competition and refuge from predation. More variable responses were found when assessing individual fish families, with all families examined displaying a positive relationship to structural complexity, but only half of these relationships were significant. Although only corroborated with qualitative data, structural complexity also seems to have a positive effect on two ecosystem services: tourism and shoreline protection. Clearly, structural complexity is an integral component of coral reef ecosystems, and it should be incorporated into monitoring programs and management objectives.

Keywords Coral reef ecology · Coral reef fishes · Ecosystem function · Diversity · Marine protected areas · Ecological methods

Introduction

Structural complexity can be defined as the physical three-dimensional structure of an ecosystem. Much of this structure can be provided by the physical shape and complexity of living organisms, such as trees, grasses, kelp and corals, often termed ecosystem engineers or foundation species (Jones et al. 1994; Bruno and Bertness 2001). However, structural complexity can be provided by other structural elements of the environment, such as geological features and underlying dead matrices formed by organisms (Kleypas et al. 2001). Structural complexity in ecosystems creates manifold microhabitat types and is expected to lead to a greater diversity and abundance of associated organisms (MacArthur and MacArthur 1961; Crowder and Cooper 1982). Indeed, the effects of structural

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N. A. J. Graham (✉) · K. L. Nash
ARC Centre of Excellence for Coral Reef Studies, James Cook
University, Townsville, QLD 4811, Australia
e-mail: nick.graham@jcu.edu.au

complexity on species richness and abundance have been demonstrated in a range of ecosystems, including forests (Spies 1998), seagrass (Heck and Wetstone 1977) and kelp (Russell 1977) beds.

The importance of structural complexity in coral reef ecosystems has been recognised for a number of decades (Risk 1972; Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Grigg 1994). Many of these early studies were fairly descriptive, demonstrating the significance of complexity for reef fish assemblages. However, the increasing prevalence of disturbance and degradation of coral reefs has brought the importance of structural complexity to the fore. A number of studies have found that the initial impacts of disturbances, which cause coral mortality but do not affect the reef structure, can be relatively limited on other components of the system. Whereas, if structural complexity is also lost or subsequently erodes, the impacts on organisms like fish can be much more severe (Sano et al. 1987; Lindahl et al. 2001; Graham et al. 2006). Data on these issues have grown, and meta-analyses of disturbance effects on reef fish have highlighted the importance of structural complexity in mediating declines (Wilson et al. 2006; Pratchett et al. 2008). Critically, the widespread loss of live coral reported for regions such as the Caribbean (Gardner et al. 2003) is being accompanied by a reduction in overall reef structural complexity (Alvarez-Filip et al. 2009). The increasing knowledge of the importance of structural complexity in reef ecosystems and the documented declines has led to a widespread recognition of the critical importance structural complexity will play in the future of coral reef ecosystems (Mumby and Steneck 2008; Pandolfi et al. 2011). However, due to the often disparate, small-scale nature of empirical studies, we have a poor understanding of many of the roles structural complexity plays in coral reef ecosystems.

The best-documented effects of reef structure are for reef fish assemblages, with fish abundance being predicted by reef structure at scales ranging from individual coral colonies (Holbrook et al. 2002) to 100 s of metres (Purkis et al. 2008). The majority of studies have found a positive relationship between structural complexity and the diversity, abundance and/or biomass of reef fishes (Luckhurst and Luckhurst 1978; Grigg 1994; Friedlander and Parish 1998; Wilson et al. 2007; Cinner et al. 2009; Graham et al. 2009); however, the strength of this relationship has varied, and some studies have found no effect or mixed responses among taxa (Jennings et al. 1996; Öhman and Rajasuriya 1998; Harborne et al. 2012). The importance of structural complexity for other components of the ecosystem, such as corals, algae and mobile invertebrate communities, is understudied and much less conclusive, likely due to the influence of variability in small-scale studies. A positive role of structural complexity has generally been documented

for epifaunal mobile invertebrate communities (Vytöpil and Willis 2001; Fraser and Sedberry 2008), whereas the relationship between complexity and urchin population densities on coral reefs has been found to be both positive (Lee 2006) and negative (Weil et al. 2005). Structural complexity can interact with live components of the benthos in complex ways, with evidence of both positive and negative effects on algal cover, possibly mediated through effects on other organisms (McClanahan and Shafir 1990; Lawson et al. 1999). There is also mixed evidence of collinearity between measures of structural complexity and live coral cover (McClanahan and Shafir 1990; Graham et al. 2008, 2009; Wilson et al. 2008a; Alvarez-Filip et al. 2011). Reef structural complexity may also influence ecosystem services, for example, through enhancing fish biomass for fisheries (Cinner et al. 2009) or reducing shoreline erosion through the dissipation of wave energy (Sheppard et al. 2005).

Here, we conducted a qualitative and quantitative analysis of the available peer-reviewed data on the role of structural complexity in reef ecosystems and associated ecosystem services. This assessment provides a synthetic review of the topic by combining data from multiple small-scale studies to provide greater power to elucidate the importance of structural complexity for various aspects of reef ecosystems, particularly those that were previously poorly understood. Specifically, we first assess the temporal increase in the number of studies assessing this topic, and the range of methods that have been applied. We then provide a qualitative examination of the range of effects of structural complexity on different components of the ecosystem and ecosystem services. Finally, where enough data were available, we quantitatively analyse the relationships between structural complexity and algal cover, total coral cover, branching coral cover, urchin density, and fish density and biomass.

Methods

A comprehensive search of the ISI Web of Science database (1972–2010) was conducted using the following keywords: coral reef AND rugosity OR complexity OR topography OR structur* OR shoreline protection OR matrix AND structur*. The returned literature was thoroughly checked, and only papers specifically related to reef structural components were retained. This resulted in 158 publications examining the role of structural complexity in coral reef ecosystems. Details of the methods used to measure structural complexity were sourced from each of the 140 primary research articles (i.e. excluding review papers); where more than one technique was used to quantify complexity, the publication was classified as using

a mixed method approach. The relationship between structural complexity and components of coral reef communities (e.g. fish density), or with respect to human activities (e.g. tourism), was extracted from each study. These relationships were classified as positive, negative, mixed or neutral based on the relationships in the original papers. Some studies looked at a range of variables, for example, multiple fish families. Therefore, where studies reported positive relationships between some variables and complexity, the study was classified as ‘positive’ if remaining variables were also positively correlated or had no relationship with complexity or ‘mixed’ if some variables were negatively related to complexity. Studies were classified as ‘negative’ using the same criteria. If no link was found between variables and complexity in the study, it was classified as ‘neutral’.

Twenty of the studies, detailing 150 sites, were selected for incorporation into a quantitative analysis. Publications were chosen whether they fulfilled the following criteria: (i) A chain or tape was used to measure rugosity (Luckhurst and Luckhurst 1978), as different methods of assessing complexity may not be directly comparable (McCormick 1994); (ii) A rugosity index (RI) could be calculated from the published data:

$$RI = \text{linear} / \text{surface}$$

where linear is the distance covered when the chain or tape was pulled taught, and surface is the linear distance between the start and end of the chain or tape when it was draped over the contours of the substrate; (iii) The study reported the density, biomass or percentage cover of different components of the reef community; (iv) The location of the data collection did not overlap with other studies quantifying the same variable (e.g. fish density) incorporated in the quantitative analysis. Each site considered as separate by the study’s authors was analysed independently.

Information was extracted on six different components of reef communities potentially related to the structural complexity of the reef: algal cover, coral cover, branching coral cover, urchin density, fish density and fish biomass. We assessed turf algae cover, macroalgal cover and total algal cover. Total algal cover was included as there was greater replication than if assessing these two groups separately, and because turf algae are an early successional stage of macroalgae. Total branching coral cover was inclusive of hard corals, and in some cases, branching soft corals as two of the three individual studies did not separate them. We only included studies that surveyed multi-species assemblages on urchins, as this represented most of the data available. Urchin densities were standardised to 10 m². Fish density was calculated per m² for each site, and further split into the density of individual families, where relevant data were provided. Fish biomass was standardised to kg per hectare. Fish species

richness and other measures of diversity were not included due to the difficulty of standardising these metrics among disparate studies that covered different spatial areas. Care was taken to note potentially important differences in methodology among the individual studies, for example, surveying diurnally active, non-cryptic species of fish, versus including cryptic fish species.

Because reef management (e.g. marine protected areas) can have such a substantial influence on reef fish communities (McClanahan et al. 2007; Russ and Alcala 2010), which may affect the strength of the relationship with structural complexity, we investigated the influence of management status on the relationships between structural complexity and reef fish density and biomass. Four categories of management were included: open access fished areas with no restrictions; areas with restrictions on the types of fishing gears that can be used; locations that had a mix of protected areas and areas open to fishing; and no-take protected areas. Information on the level of protection of the individual sites was sourced from the original studies or from the MPA Global Database (Wood 2007). Because Caribbean coral reefs can function differently to Indo-Pacific coral reefs (Bellwood et al. 2004; Roff and Mumby 2012), these two biogeographic regions were investigated separately where sufficient replication was available (fish density, total algal cover and coral cover), and the mean RI between the regions tested with a one-way ANOVA.

Spearman’s rank correlations were calculated for structural complexity against each component of the reef community. This nonparametric technique was used because in most cases, it was not possible to meet the assumptions of parametric analyses, and because it does not assume a causative relationship. These relationships were also compared between the individual studies and between sites subject to different management regimes for fish density and biomass.

Attempts were made to extract quantitative information on the nature of relationships between structural complexity and tourism outcomes or shoreline protection; however, insufficient data were available to quantify trends in these variables.

Results

There has been an exponential increase in the number of publications discussing the role of structural complexity on coral reefs over the last 50 years, but with a continued emphasis on the interaction between complexity and fish communities compared to other biotic and abiotic aspects of the system (Fig. 1a). A wide range of methods have been used to assess structural complexity on reefs (Fig. 1b). In the last decade, techniques aimed at quantifying structural complexity

at specific scales have proliferated, from studies focused at the colony level to remote techniques such as side-scan sonar which can provide cross-reef assessments of complexity (e.g. Holbrook et al. 2002; Pittman et al. 2009), indicating the strong positive relationship

Qualitatively tallying relationships between increased structural complexity and biotic or ecosystem service attributes indicated predominantly positive effects of structural complexity (79 %; Fig. 2). Only six papers reported a purely negative or negative–neutral relationship, where urchin density decreased with increasing complexity (Weil et al. 2005; Dumas et al. 2007), although a number of papers indicated mixed responses to increased structural complexity (20 %; e.g. Rilov et al. 2007). For tourism and shoreline protection, where sufficient consistent data were not available for further quantitative analyses, the qualitative assessment indicated that structural complexity has a positive effect on both of these ecosystem services.

Structural complexity using the RI method ranged from 1.06 to 3.62 in the 150 sites included in the quantitative analyses, but complexity was generally at the lower end of this range (mean = 1.46). There was a significant difference in RI values reported from the Caribbean (mean = 1.73) and the Indo-Pacific (mean = 1.40) biogeographic regions ($F_{1,128} = 23.1$, $p < 0.01$). Chain or tape length varied from 3 to 50 m in length (mean = 16.98); where chains were used, link size was not always reported but was predominantly under 1.5 cm in length.

There was a strong negative relationship between total algal cover and structural complexity ($n = 25$, $r_s = -0.78$, $p < 0.001$; Fig. 3). The relationship between algae and structural complexity did not hold when assessing macro-algal cover ($n = 18$, $r_s = -0.27$, NS) or turf algal cover separately ($n = 17$, $r_s = -0.39$, NS), or if assessing different biogeographic regions (Caribbean: $n = 6$, $r_s = -0.75$, NS,

Fig. 1 Temporal distribution of publications **a** documenting the role of structural complexity with respect to different aspects of coral reefs and **b** assessing structural complexity on coral reefs using different methodologies

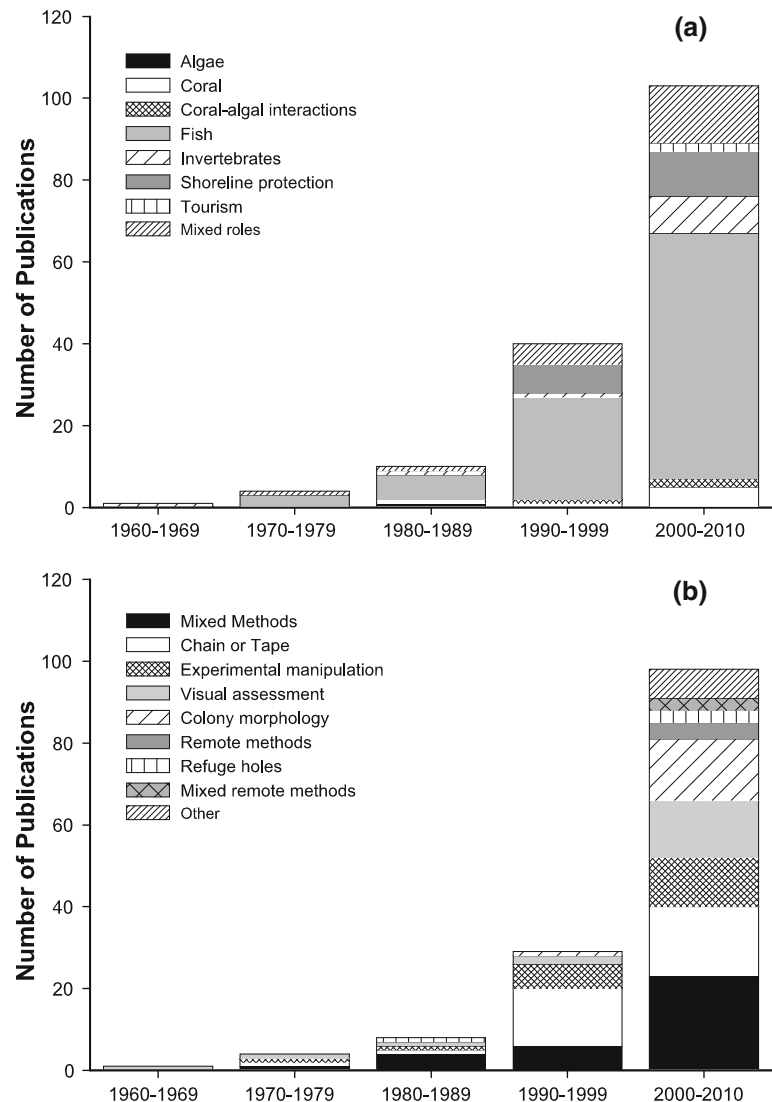


Fig. 2 Number of publications documenting a positive, mixed, negative or neutral influence of structural complexity on different aspects of coral reefs. Classification into categories based on main foci of publication. *Asterisk* indicates positive role with respect to coral dominance. *Plus symbol* indicates negative role with respect to urchin density (Dumas et al. 2007; Weil et al. 2005)

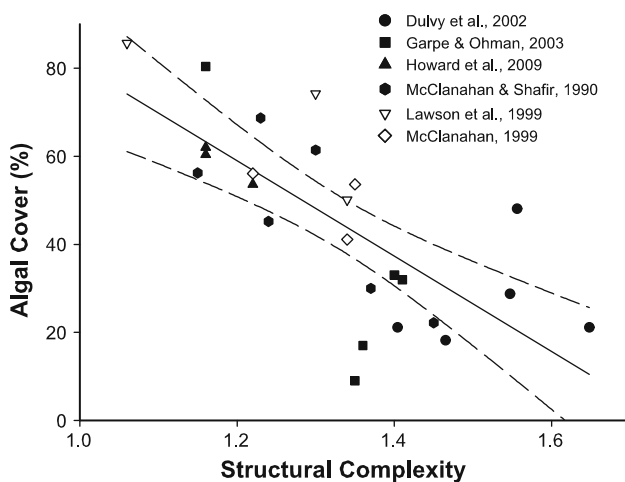
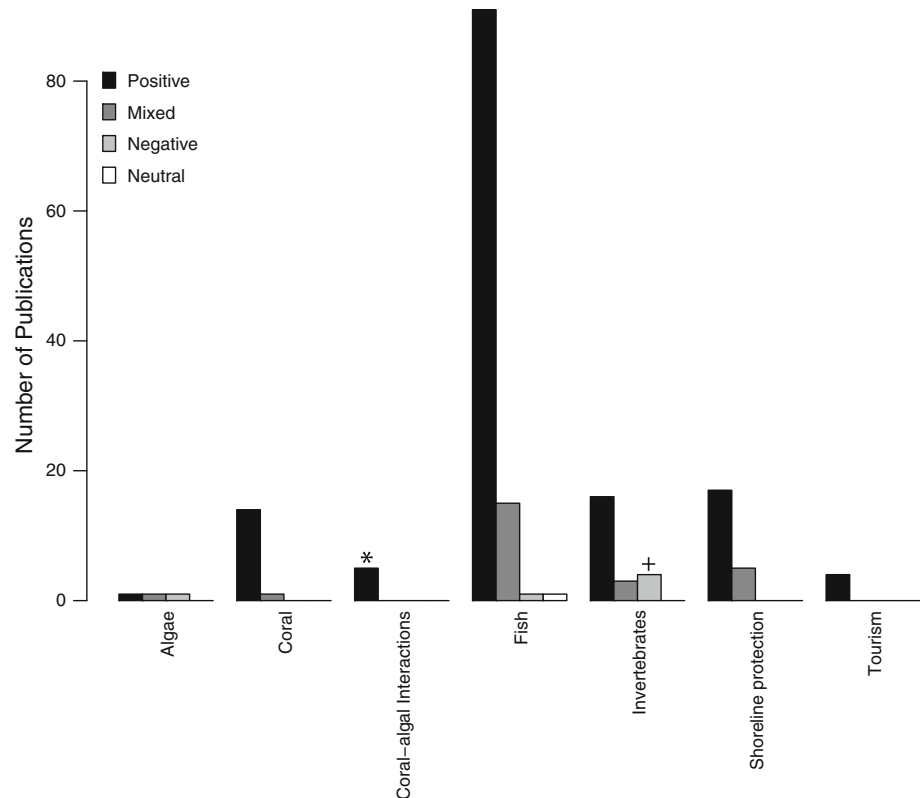


Fig. 3 Relationship between percentage algal cover (turf & macroalgae) and structural complexity (RI). *Open symbols* are studies from the Caribbean, while *closed symbols* are studies from the Indo-Pacific

Indo-Pacific: $n = 27$, $r_s = -0.19$, NS). None of the relationships calculated for individual studies were significant (Electronic Supplemental Material, ESM Table S1).

Coral cover was positively related to structural complexity for all sites ($r_s = 0.26$, $p = 0.023$; Fig. 4a). This relationship only held for the Indo-Pacific region ($n = 60$, $r_s = 0.6$, $p < 0.001$), with the Caribbean showing a flat

relationship ($n = 23$, $r_s = -0.06$, NS). It should be noted that the range of coral cover was generally much higher in the data from the Indo-Pacific (mean = 24.8 %, 3rd quartile = 44.0 %, max = 78.5 %), than the Caribbean (mean = 14.6 %, 3rd quartile = 15.0 %, max = 70.1 %). Almost half the publications had too few data points to permit analysis of study specific relationships (ESM Table S2). Of the remaining seven studies, three displayed a significant positive correlation between coral cover and structural complexity (McClanahan and Shafir 1990; Bergman et al. 2000; Mangi and Roberts 2007). The correlation between structural complexity and branching coral cover was stronger than for total coral cover ($r_s = 0.50$, $p = 0.009$; Fig. 4b). All studies showed a positive correlation between complexity and branching cover when analysed individually (Bergman et al. 2000; Friedlander et al. 2003; Garpe and Ohman 2003), but only data from Bergman et al. (2000) were significant (ESM Table S2).

There was a significant negative correlation between urchin density (10 m^{-2}) and structural complexity ($r_s = -0.68$, $p < 0.001$; Fig. 5). When analysing data from the individual studies, none of the correlations were significant (ESM Table S3).

Fish density was positively correlated with structural complexity for all sites (Fig. 6a) and for those sites open to fishing or subject to gear restrictions (Table 1). There were insufficient data to draw conclusions regarding the

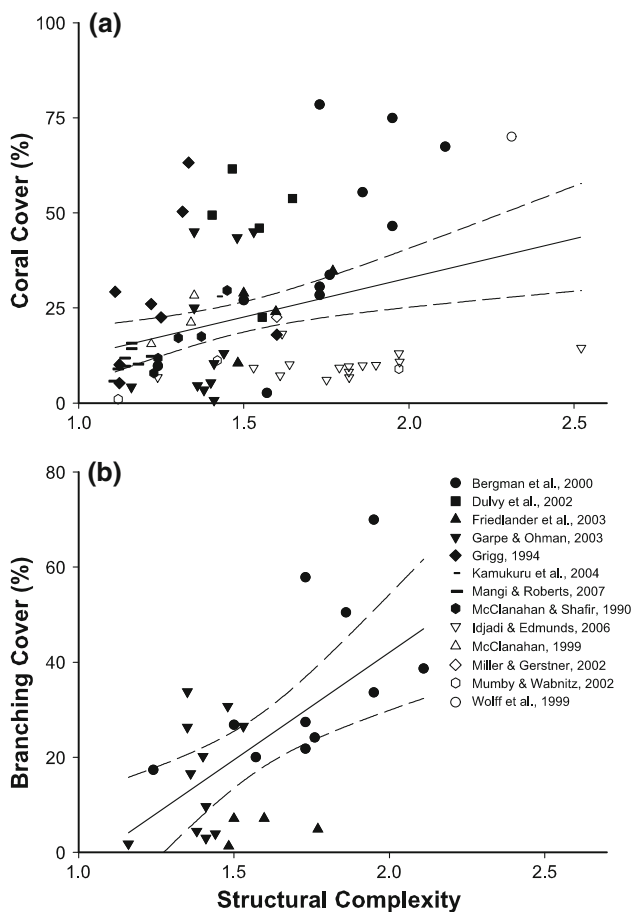


Fig. 4 Relationship between **a** percentage of total live coral cover and **b** percentage of branching coral cover and structural complexity (RI). *Open symbols* are studies from the Caribbean, while *closed symbols* are studies from the Indo-Pacific

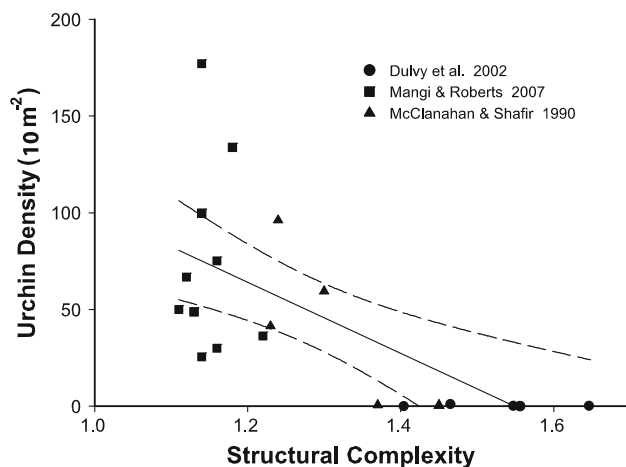


Fig. 5 Relationship between urchin density (10 m^{-2}) and structural complexity (RI)

relationship between complexity and fish density in sites within no-take area or those under mixed management. The significant positive correlation held if the data were

analysed separately for the Caribbean ($n = 12$, $r_s = 0.6$, $p < 0.05$) or Indo-Pacific ($n = 42$, $r_s = 0.67$, $p < 0.001$). Only five of the individual publications surveyed a sufficient number of sites to calculate study specific correlations between fish density and complexity; of these, data from Grigg (1994), Luckhurst and Luckhurst (1978), and McClanahan and Shafir (1990) showed a significant positive relationship (ESM Table S4).

Fish densities recorded by Risk (1972) and Luckhurst and Luckhurst (1978) were considerably higher than those recorded by the other studies (Fig. 6a). Both of these studies were conducted in the 1970s, and cryptic fish were included in surveys. If these two studies were removed, to only include studies published since the 1990s and that surveyed diurnally active or minimally cryptic species, the analyses show a similar correlation between complexity and fish density overall ($r_s = 0.66$, $p < 0.001$) and for different management regimes ($r_s = 0.71$, $p = 0.001$ and $r_s = 0.61$, $p = 0.005$ for open and gear restrictions, respectively), indicating the strong positive relationship between structural complexity and fish density holds regardless of these survey differences.

A strong relationship was found between structural complexity and fish biomass (Table 1, Fig. 6b). The increase in fish biomass with complexity was greater for open sites than those under mixed management; however, for similar levels of structural complexity, greater biomass was generally reported on mixed managed sites than those open to all fishing (Table 1). There were insufficient data to draw conclusions regarding the relationship between complexity and biomass in sites within no-take areas or those with gear restrictions. All of the individual studies with sufficient data for analysis showed a positive correlation between complexity and fish biomass (ESM Table S1; Grigg 1994; Dulvy et al. 2002; Friedlander et al. 2007; Cinner et al. 2009), although this relationship was not significant for the data sourced from Dulvy et al. (2002). Positive relationships were found between individual fish families and structural complexity for the six families where sufficient data existed, but these were only significant for Pomacanthidae, Pomacentridae and Scaridae (Table 2).

Discussion

It is evident that structural complexity is strongly related to many aspects of coral reef ecology and potentially to a range of the ecosystem services coral reefs provide. Combining data from multiple small-scale studies into a larger quantitative analysis provided stronger statistical power to examine some of the effects of structural complexity, clarifying several of the relationships, such as with urchins and algae, where individual studies have been inconclusive. The strongest relationships were for fish

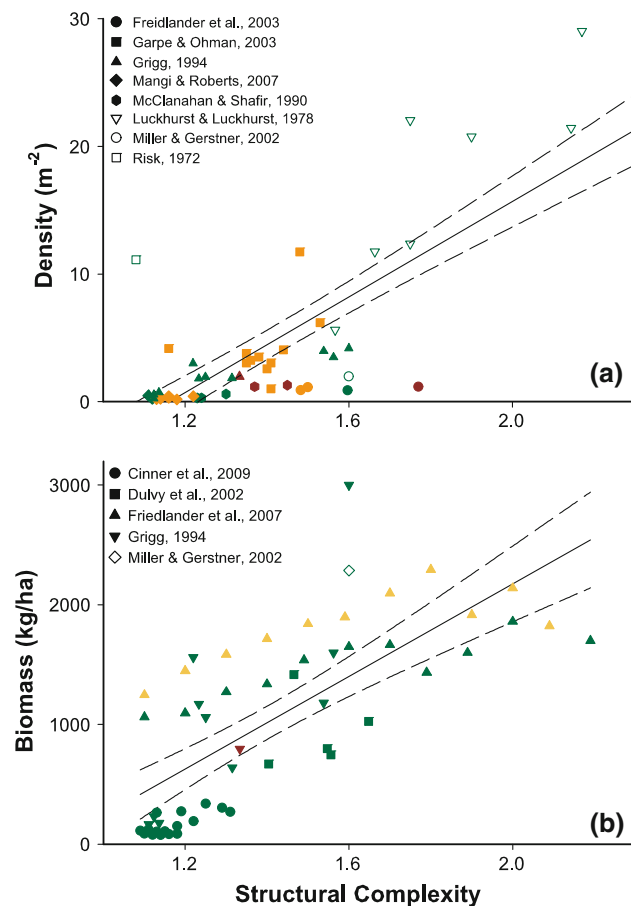


Fig. 6 Relationship between **a** fish density (no. m⁻²) or **b** fish biomass (kg/ha) and structural complexity (RI). Colours represent management regime: *green sites* are open to fishing, *orange sites* are subject to gear restrictions, *yellow sites* have a mix of open and protected areas, *red sites* are no take. *Open symbols* are studies from the Caribbean, while *closed symbols* are studies from the Indo-Pacific. Outlying data point from Luckhurst and Luckhurst (1978; SC = 3.62, Density = 45.42 m⁻²) is not displayed in Fig. 4a but was used in analyses

density and biomass; however, the relationships between structural complexity, and algal cover and urchin abundance were also well correlated, with weaker relationships with live coral cover and branching coral cover. Although we did not have enough consistent data to quantitatively assess the role of complexity on ecosystem service provision, qualitative data indicate positive effects on shoreline protection and tourism.

Very few individual studies have documented an effect of structural complexity on algal cover; however, when combining studies reporting total algal cover here, we have found a strong relationship. Increases in macroalgae are often related to reef degradation (Hughes et al. 2010), with studies showing that as reefs degrade, they typically lose structural complexity and have an increase in algae (Graham et al. 2006; Alvarez-Filip et al. 2009). This pattern may simply be due to the loss of coral and associated

Table 1 Correlation coefficients of fish density (no. m⁻²) and fish biomass (kg/ha) against structural complexity measured using the chain or tape method for all samples and within different management regimes

Management regime	<i>n</i>	Spearman's rank correlation (<i>r_s</i>)	<i>p</i>
<i>Fish density</i>			
Open	28	0.78	<0.001
Gear restrictions	20	0.61	0.005
Mixed management	0	n/a	n/a
No take	4	n/a	n/a
All	52	0.71	<0.001
<i>Fish biomass</i>			
Open	44	0.81	<0.001
Gear restrictions	0	n/a	n/a
Mixed management	11	0.76	0.006
No take	1	n/a	n/a
All	56	0.80	<0.001

Significant correlations are displayed in bold

Table 2 Correlation coefficients of density of different fish families (no. m⁻²) against structural complexity measured using the chain or tape method

Family	<i>n</i>	Spearman's rank correlation (<i>r_s</i>)	<i>p</i>
Acanthuridae	14	0.49	NS
Chaetodontidae	16	0.38	NS
Labridae	17	0.28	NS
Pomacanthidae	14	0.57	0.032
Pomacentridae	14	0.57	0.032
Scaridae	21	0.47	0.031

Significant correlations are displayed in bold

reductions in complexity, providing free space for colonising algae. However, a possible mechanistic driver of the negative relationship between structural complexity and algal cover could be more fish associating with higher complexity and thus providing critical functions controlling algae where structure is present (Vergés et al. 2011). Indeed, we found a significant positive relationship between Scaridae and complexity in our analysis, a family of fish known to provide a range of critical functional roles regarding the removal of turf and/or macroalgae from reefs (Bellwood et al. 2004; Burkepile and Hay 2008; Hoey and Bellwood 2008; Mumby 2009). Although the relationships were still consistently negative, they were no longer statistically significant when assessing the Caribbean or Indo-Pacific independently; however, the sample size was quite low, particularly for the Caribbean. The negative relationships were also no longer significant when separating algae into the functional groups of turf algae and

macroalgae. This suggests the relationship between structural complexity and algal cover may be quite complex. However, because turf is just an earlier successional stage of macroalgae, and because herbivory by some fishes can be more effective at controlling algal succession (Bellwood et al. 2006; Ledlie et al. 2007), the relationship between structural complexity and total algal cover may capture the dynamics of the system quite well. It must also be noted that the rugosity measure we used for our analyses quantifies the structural complexity of hard reef substratum. Soft flexible benthic cover, for example, macroalgae, can also provide structural complexity (Levin and Hay 1996) and influence associated fish communities in complex ways (Hoey and Bellwood 2011).

Coral cover and particularly cover of branching corals were both positively correlated with structure. It is possible that hard coral cover and the cover of branching corals are contributing a large proportion of the structural complexity being quantified. Indeed, healthier, coral-dominated reefs often have greater structural complexity than more degraded, lower coral cover reefs (Graham et al. 2006; Alvarez-Filip et al. 2009). Interestingly, when the relationship between coral cover and structural complexity was tested independently for biogeographic region, only the Indo-Pacific showed a significant correlation. The Caribbean sites in this study had a much lower overall coral cover distribution which may have influenced this relationship. Indeed, some previous studies have found no correlation between coral cover and complexity where coral cover is low (Graham et al. 2009). Branching coral cover may be particularly likely to contribute fine-scale structural complexity to reefs (Chabanet et al. 1997), which can be important to a range of organisms, such as fish and mobile invertebrates (Wilson et al. 2006; Pratchett et al. 2008; Stella et al. 2011). Interestingly, despite differences in whether a relationship existed between complexity and live coral cover, measures of structural complexity (RI) were higher for the Caribbean than the Indo-Pacific on average. It is possible that this reflects the substantial structure *Montastraea* reefs can afford (Harborne et al. 2012), which are often the focus of Caribbean studies since the loss of most *Acropora* dominated reef habitats. It is possible that reinforcing ecological feedbacks may contribute to the relationship between complexity and coral cover, whereby critical processes such as herbivory may be enhanced by structure and promote successful coral recruitment and increased coral cover (Mumby and Steneck 2008). Indeed, remaining structural complexity following coral mortality events has been suggested as a key factor explaining faster rates of coral recovery at certain sites in both Guam and the Eastern Pacific (Colgan 1987; Guzman and Corte's 2007).

The negative relationship we found between sea urchin density and structural complexity may be explained by a number of mechanisms. High densities of sea urchins on coral reefs can result in substantial bioerosion of reef

structure (Scoffin et al. 1980), driving low complexity at sites where urchin densities are high (McClanahan and Shafir 1990). Alternatively, urchins are vulnerable to predation from fish, particularly species of Balistidae (McClanahan and Shafir 1990). This may lead to gregarious behaviour by urchins in open areas away from structure, where multiple spines and safety in numbers acts to minimise predation (Randall et al. 1964; Hunte and Younglao 1988; Levitan 1988). We restricted our analyses to studies that assessed multi-species urchin assemblages. It should be noted that studies assessing the relationship between structural complexity and individual urchin species density (*Diadema antillarum* in both examples) show contrasting patterns with both positive (Lee 2006) and negative trends (Weil et al. 2005).

The very strong effects of increasing structural complexity on both increasing overall fish density and biomass found here corroborate the findings of the majority of individual studies (e.g. Luckhurst and Luckhurst 1978; Grigg 1994; Friedlander and Parish 1998; Wilson et al. 2007), however, combining the data into a larger quantitative analysis resulted in a much stronger relationship than that presented by most individual studies. The significant relationships for fish density were consistent between the Caribbean and Indo-Pacific regions, suggesting reef fish density is strongly structured by benthic structural complexity in both regions. There are many potential reasons for an increase in fish density and biomass in response to increasing complexity, including the provision of more niche space to mediate density-dependent competition (Holbrook and Schmitt 2002), refuge for prey from predators (Steele 1999), predators accumulating in locations where their prey are abundant (Stewart and Jones 2001), and fish exploiting reductions in strong environmental variables, such as high water flow rates (Johansen et al. 2008). Interestingly, the relationship was strongest for sites open to fishing compared to those subject to gear restrictions, mixed management or no-take restrictions. This was in part the result of increased statistical power for the open access sites, where the sample size in our analyses was greatest. However, there is also the possibility that in fished areas where predatory fish are generally more depleted (Jennings and Polunin 1997), a prey release response can occur where individual prey fish species or all individuals within smaller size classes can increase in abundance (Graham et al. 2003; Dulvy et al. 2004). As fish tend to associate with structural complexity at scales comparable to their body size (Hixon and Beets 1993), a greater abundance of smaller size class fish in the community may be expected to elicit a stronger response to changes in available complexity because complexity on reefs is often at a scale that influences these size classes (Wilson et al. 2007).

When individual fish families were analysed, the strength of the relationship varied considerably. Although all six families examined displayed a positive relationship with increasing structural complexity, only the Pomacanthidae, Pomacentridae and Scaridae displayed significant relationships, whereas trends for the Acanthuridae, Chaetodontidae and Labridae were not significant. This supports previous studies that have indicated variable responses to structural complexity when assessing different components of the fish community (Jennings et al. 1996; Öhman and Rajasuriya 1998). Some of this variation may reflect abundance within different fish families influencing the power to detect relationships, for example, the Pomacentridae tend to be a dominant component of the assemblage based on density, whereas the Chaetodontidae are much less common (Jones et al. 2004). However, some other families, for example, the Pomacanthidae, which is strongly correlated to complexity in our analysis, typically make up a fairly small proportion of the fish assemblage in most reefs (Jones et al. 2004). Individual habitat use studies may elucidate some of these differences, for example, many species of Pomacentridae are known to associate with specific structural features, coral morphologies or genera (Booth and Beretta 1994; Gutiérrez 1998; Wilson et al. 2008b). Alternatively, some fish species or families associate more with alternative reef habitats, such as seagrass, macroalgae and rubble (Dorenbosch et al. 2005; Chong-Seng et al. 2012). Further studies of this nature on a range of fish families will be necessary to fully understand individual fish family and species-level responses to changes in reef structural complexity.

Although there were not enough consistent data across the individual studies to conduct a quantitative analysis of the role of structural complexity for shoreline protection and tourism, the qualitative assessment indicated a positive effect on both of these ecosystem services. Coral reefs are well known to be an important barrier for high wave energy reaching coastlines. Indeed, higher complexity on reef crests and flats is likely to have a dampening effect on shoreline erosion (Sheppard et al. 2005). Dive tourism is an important economic benefit from coral reefs (Moberg and Folke 1999; Hicks 2011), and divers will preferentially dive on reefs of good condition. As our analyses show, high structural complexity is important for the condition of coral reefs. Furthermore, structural complexity enhances the abundance of reef fishes on reefs, which have been identified as one of the principal ecological characteristics dive tourists like to see (Williams and Polunin 2000).

A lot of data from published studies could not be included in our quantitative analysis, partly due to insufficient reporting of methodologies and data, but mainly due to the wide range of methods used to quantify complexity. Using the RI data allowed the most rigorous compilation of data, however,

subtle differences in methodologies, for example, the length of chain used, are still likely to contribute to the variation in the data (Gurevitch and Hedges 1999). Many of the other methods used were for ecological questions at specific spatial scales, such as individual colonies for specific fish–coral interaction studies (Holbrook and Schmitt 2002), or remote sensing data for larger scale habitat mapping (Purkis et al. 2008). Clearly, the scale of measurement is important to the questions being asked or the taxa and size classes being predicted (Wilson et al. 2007; Harborne et al. 2012), and there are many important roles of complexity at different scales that we were unable to elucidate based on the RI. We have tried to only make inferences from the analyses based on the scale of the original studies; however, it should be noted that the relationships we found may be stronger or weaker if complexity and associated variables are assessed at larger or smaller scales. Furthermore, we have focussed on abundances and cover of organisms, rather than changes in ecological processes, which are obviously critical to understanding the role of complexity in ecosystem functioning.

It is clear that structural complexity is an important variable on coral reefs. This importance extends beyond the enhancement of reef fish density and biomass that has received the greatest research attention. As such, quantifying reef structural complexity should be an integral part of coral reef monitoring and research. Furthermore, maintaining or enhancing reef structure should be a key objective of management. This may involve policies to reduce fishing practices such as dynamite or drag nets that damage reef structure (Fox and Caldwell 2006; Mangi and Roberts 2006; Hicks and McClanahan 2012) or controlling areas that dive tourists are permitted to use to reduce accidental damage to vulnerable habitat (Hawkins and Roberts 1993). Management may also focus on areas of robust structure, which are likely to maintain ecological processes and provide refugia for a range of organisms. Future research should focus on the role of structural complexity in maintaining ecological processes and influencing the provision of ecosystem services.

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