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RESEARCH PAPER

Fish, coral and community structure: 35 years of change on Wistari Reef, Australia

Gerald B. Goeden[1]*, Mohamad Saupi Ismail[2]

[1*] *Carbon Collectors BV, 9727 KB Groningen, The Netherlands*

[2] *Fisheries Research Institute, Department of Fisheries Malaysia, Batu Maung, 11960 Pulau Pinang, Malaysia*

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Corresponding Author

Gerald B. Goeden
E-mail: gerry@carboncollectors.nl
Tel: +6019-6595494

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Abstract

One hundred sites in 10 grids at Wistari Reef, Queensland were surveyed in 1971, 1999, and again in 2006. The abundance of taxa incorporating 205 fish species were recorded along with estimates of live coral cover and rugosity during each survey. We found that fishes partitioned the reef slope at different scales with more abundant taxa being more patchily distributed within a habitat type but occupying more habitats and a greater share of the reef slope. Rare taxa were more evenly distributed within a habitat type but occupied fewer habitats. Over the 35-year period, there was a decline in fish abundance, rugosity, and coral cover. There were weak relationships between fish abundance and coral cover and stronger relationships between fish abundance and rugosity across the 10 habitat types supporting the idea that fish are more dependent on three-dimensional complexity than on the presence of a healthy coral community.

Introduction

The decline in living coral cover on reefs has been documented since the 1980s throughout the Caribbean and the Indo-Pacific regions (Gardner et al., 2003; Bruno & Selig, 2007; Edmunds and Elahi, 2007) and reported for the Great Barrier Reef (De'ath et al., 2012). This is likely to have had far-reaching impacts on fish abundance and community structure. As a consequence of bio-abrasion and $CaCO_3$ dissolution, there is a gradual reduction in three-dimensional structure that follows the loss of complex corals (Green et al., 2008). This is described by Alvarez-Filip et al. (2009), as "flattening"; a slow collapse of the reef framework into a less complex habitat. Their study was "the first region-wide analysis of changes in reef architectural complexity, using nearly 500 surveys across 200 reefs, between 1969 and 2008"and found that, "The architectural complexity of Caribbean reefs has declined nonlinearly with the near disappearance of the most complex reefs over the last 40 years." It is thought that habitats with greater rugosity facilitate species coexistence through niche partitioning and the provision of important refuges from predators and environmental stressors (Bruno & Bertness, 2001; Willis et al., 2005). Numerous researches have documented the role of rugosity in the structure and composition of fish assemblage (McCormick, 1994; Robertson, 1996; Gratwicke & Speight, 2005a; Kuffner et al., 2007; Komyakova et al., 2013; Newman et al., 2015). Aronson and Precht (1995) used rugosity as a measure of disturbance in reef ecosystems.

The reef predator, *Plectropomus leopardus* (Lacepède, 1802), is one of the more commercially important Great Barrier Reef fish species. The biology of this species, known as the "coral trout", was described by Goeden (1978), and its role in the ecosystem (Goeden, 1982) established this predator as a "keystone species". During this early research, it was observed that the fishes that form the prey of the coral trout were patchily distributed over the reef slope, the major predatory field, as was the predator itself.

Of particular interest was the possible influence of the structural nature of the substrate on the biodiversity and composition of the coral trout prey assemblages (Bradbury & Goeden, 1974). Since those first surveys, this topic has gained considerable attention in the fish ecology literature (Sale, 1977; McCormick, 1994; Szmant, 1997; Komyakova et al., 2013; Darling et al., 2017). Most studies have concluded that high structural complexity is correlated with greater fish species richness (Luckhurst & Luckhurst, 1978; Chabanet et al., 1997; Gratwicke & Speight, 2005b; Paddack et al. 2009) or the abundance of specific trophic groups (Hixon & Beets, 1993; Torres-Pulliza et al., 2020; Russ et al., 2021).

More recently, research has shown that measures of fish biodiversity are correlated with underlying changes in structural complexity, with biodiversity falling as coral loss follows cyclones (Connell et al., 1997) or other stressors (Jones et al., 2004; Wilson et al., 2006; Walker et al., 2009; Darling et al., 2017; Torres-Pulliza et al., 2020). The goal of this study was to compare the relationships among fish community parameters with the reef structural parameters of rugosity and coral cover at Wistari Reef and specifically, to see how these parameters might have changed and interacted over a 35-year period.

Bradbury and Goeden (1974) found that the behavior of the Wistari Reef taxa in partitioning their environment could be explained by common strategies employed on different scales. The rarer taxa were responding to an environmental grain that was different and less coarse than the one to which the common taxa responded. Sale (1977) stated, "Current data indicate that many reef fishes do not finely partition resources of food or living space, that they are often, if not usually, limited by the supply of suitable living space." This study attempts to illuminate the relationships among rare and common taxa, fish abundance, coral cover, and reef rugosity in a changing three-dimensional environment.

MATERIALS AND METHODS

In Bradbury and Goeden (1974), we had originally selected 10 large grids around Wistari Reef, Queensland, Australia. Each grid was divided into ten parallel 5m x 20m belt transects (referred to for brevity as cells) in which were counted the abundance of species, genera, and families with the aim of discovering any differences in habitat utilization among these differentiations.

Data were collected during low tides to minimize the movement, and therefore differences in the fish community, between the reef flat and reef slope at different tides. Initial sampling took place during November, 1971, and was repeated with smaller cells during January-February, 1999, and during January, 2006 all in slight to moderate weather. For the sake of comparison, the taxa list from 1971 was repeated in 1999 and again in 2006. Cells were laid out using marked polyethylene ropes. Their end positions were "permanently" marked with concrete blocks that were readily identified by outline over the 35-year period. The shallowest cells were in about 2m depth at low tide followed by deeper habitat types reaching depths of about 20m. Reef slopes included an exposed windward face, a steeply descending channel with strong currents, and a sandy back reef area. Counting took place 1-2 full days after the cells were laid out so that fish could return. In this study, we use data from 10 cells within each of 10 habitat types (100 cell total) around the perimeter of Wistari Reef in the Capricorn Group, Australia. Each rectangular cell counted during 1999 and 2006 measured 5m x 10m with the long axis parallel to the reef crest. These were smaller than the first samples and corresponded to the center portions of the cells used by Bradbury and Goeden (1974) so that their analysis is replicated in later sampling of cells. The 1971 data was scaled to later cell size. These habitat types are characterized in detail by Bradbury and Goeden (1974).

Grid locations were well distributed around the perimeter of the reef (Figure 1). Bradbury and Goeden (1974) had separated these habitat types based on distinctive appearance and these same distinctions are used here. Figure 2 is descriptive of those habitat types.

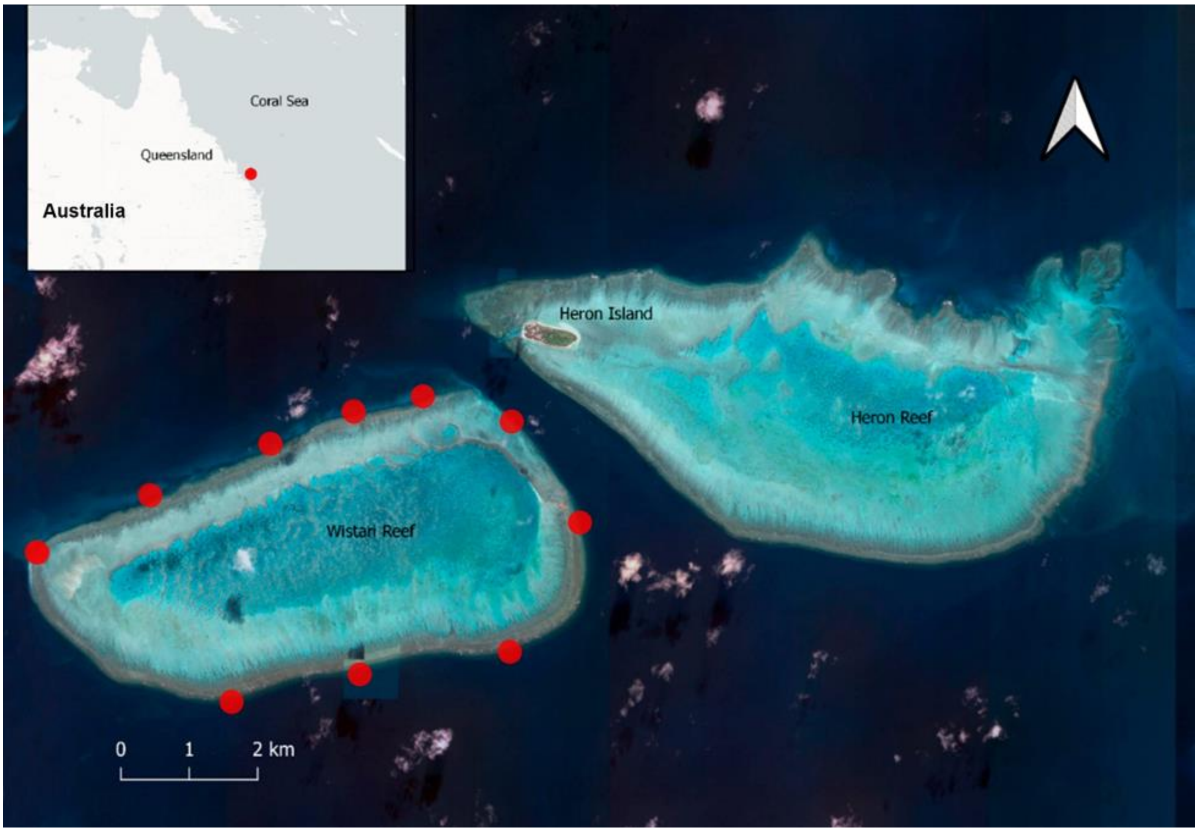
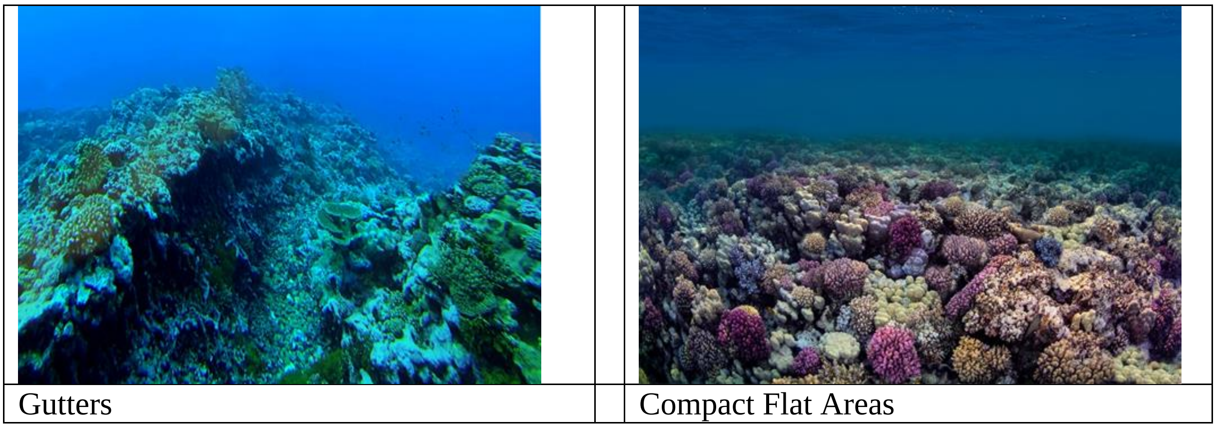


Figure 1. Locations shown on screen shot with superimposed navigational marks (red dots) indicating approximate locations of the sampled areas. (based on Google Earth).

	
Sand/ Rubble	Low Patch Corals
	
Low Stag Thicket	Large Stag Thicket
	
Large Tabular	Smooth Coral Heads
	
Compact Slope	Open Slope



Gutters

Compact Flat Areas

Figure 2. Examples of ten habitat types used in this survey.

Numbers of fish in each of the taxa were assessed through underwater visual counting to an elevation of about 2.5-3m above the substrate; the equivalent of a belt transect as described by Nadon and Stirling (2006).

Note that our comparisons here are between ‘taxa’ rather than species. Bradbury and Goeden (1974) counted an estimated 205 species and then compressed these to genera and families for analysis (1) to overcome possible identification problems, especially in “mixed schools,” and (2) to determine the partitioning at a more ‘functional’ level; i.e., deemed to be functionally similar and paralleling the functional groups of Williams and Polunin (2001). Table 1 lists the taxa included in this study and their functional/trophic group.

Table 1. Description of Taxa counted within cells.

Taxon	**Est. No. of Species**	**Generalized Trophic Group1**	**I.D. This Paper (Taxon No.)**
Abudefdufidae[2]	20	**Planktivore**/Omnivore	1
Acanthuridae (Tangs & Surgeons)	14	**Grazer**	2
Acanthuridae (Unicorns)	5	**Grazer**	3
Chaetodontidae	28	**Invertivore**/Coralivore	4
Chromidae (Chromis)[2]	6	**Omnivore**/Planktivore	5
Chromidae (Dascyllus)[2]	3	**Planktivore**	6
Labridae	45	**Invertivore**/ Carnivore	7
Lethrinidae	5	**Carnivore**	8
Lutjanidae	10	**Carnivore**	9
Pomacanthidae	10	**Invertivore**/Grazer	10
Pomacentridae	12	**Omnivore**/Planktivore	11
Scaridae	20	**Grazer**	12
Siganidae	8	**Grazer**	13
Epinephelidae	19	**Piscivore**	14

[1] Trophic groups in bold type are considered the dominant form.

[2] *Abudefduf*, *Chromis*, and *Dascyllus* were classified in different families at the time of the 1974 surveys but were later moved to the Pomacentridae. We have repeated the earlier taxonomy for continuity.

Six major trophic categories (planktivores, grazers, invertivores, omnivores, carnivores, and piscivores) were distinguished. Although most groups consume more than one category of food, we followed the systems used by others (Paddack et al., 2009; Alvarez-Filip et al., 2011; Froese & Pauly (2021). Abundance was recorded as an estimated number of fish per cell. Coral cover was measured down the center of the long axis of each cell using a 10m tape and the line transect method, as described by Nadon and Stirling (2006). Data was recorded as meters of live coral per 10m tape. These transects amounted to 100m total per Habitat Type.

Rugosity was measured along the same axis as the line transect by using a metal chain with links of 15mm nominal length and 10m long. The chain rugosity method was first described by Risk (1972) for the Caribbean and on the Great Barrier Reef by the author (Goeden, 1971) at Heron Island. In this study, we have used the more convenient mathematical relationship (after Wellington, 1982), as follows:

$Ru = 1-d/L$ where

Ru is rugosity (dimensionless),

d is the horizontal distance the draped chain reached along a horizontal tape, (m)

L is the length of the horizontal tape, (m).

Where rugosity was greater than about 0.3, a second measure was taken along the tape and the two were combined. Since these first studies, rugosity has become an important measure of reef complexity (Luckhurst & Luckhurst, 1978; Carpenter et al., 1981; Turnigan, 1991; McCormick, 1994; Friedlander & Parrish, 1998; Gratwicke & Speight, 2005a; Kuffner et al., 2007; Shumway et al., 2007; Wilson et al., 2007; Purkis et al., 2008; Walker et al., 2009).

Statistical analysis of the data was carried out using one-tailed t-tests. Statistical significance was claimed at ($p<0.10$). Coefficients of determination, R^2, were calculated for all regressions using Microsoft Excel analysis software.

RESULTS

Fish abundance

Bradbury and Goeden (1974) demonstrated that, "The occupancy of habitats at a fine scale was largely indeterminate, but once occupied by a subset of the ensemble, other taxa were not found." We combined the data for 1971, 1999 and 2006 in Figure 3 to see if the three sampling periods followed the same relationship. More abundant taxa did, in fact, occupy a greater number of cells (where 100 was the maximum cells available) than less abundant taxa over the 35-year period. The logarithmic regression of the number of occupied cells on taxon abundance was highly correlated ($R^2=0.8747$), so that taxa abundance explained the majority of the variance in the partitioning of the reef slope in 1971, 1999 and in 2006. The derived mathematical relationship is exponential and likely to explain much larger areas of the Wistari Reef slope and lagoon. The more common taxa (abundance of more than about 2,500 fish in each set of samples or about $0.5m^{-2}$) that would be expected to follow the regression line more closely were limited by the maximum of 100 cells in the samples. Removing these "cell-limited" taxa generated a very similar regression where the number of cells was related to abundance by $y = 21.145\ln(x) - 55.495$ ($R^2 = 0.8998$) and served as a better predictor of abundant taxa distribution over larger areas and more diverse habitats.

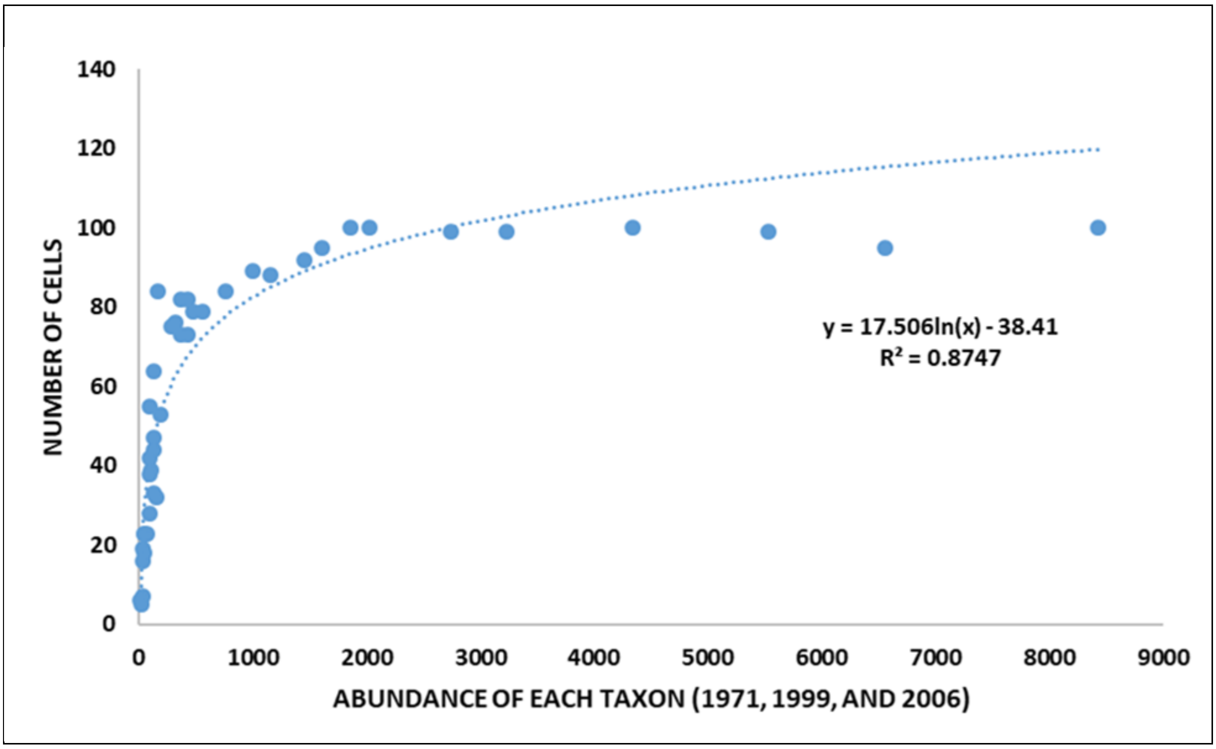


Figure 3. Comparison of the number of cells occupied by rare and common taxa (1971, 1999, and 2006 data are included in the regression).

The abundance of the combined taxa within each of the ten habitat types in 1971 with the same habitat types in 1999 and 2006 was compared for changes in the distribution of fishes over the reef slope with time (Figure 4).

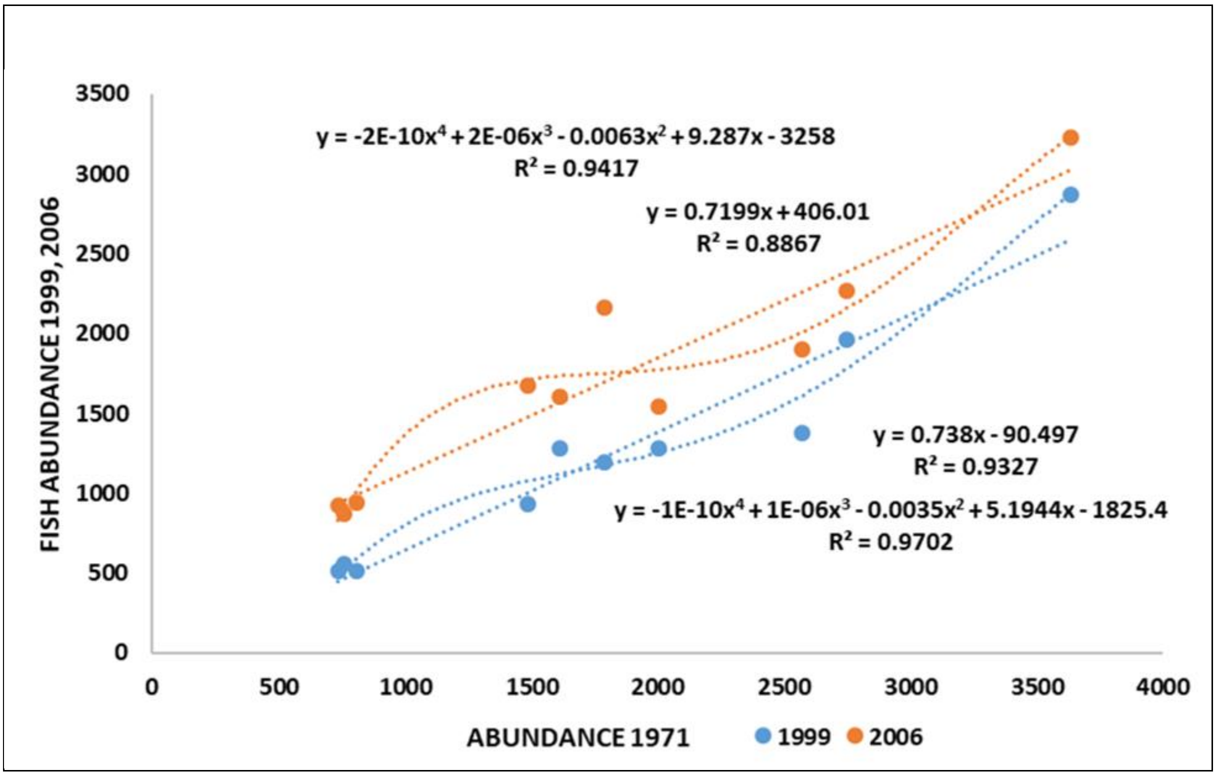


Figure 4. Comparison of fish abundance by habitat type 1999, 2006 vs 1971.

The linear regression line for 1999 on the 1971 data was a good fit ($R^2 = 0.9327$), with the 1971 fish abundance explaining most of the variance during the 1999 survey (Figure 4). This linear relationship demonstrated an overall decrease in fish abundance between the two sampling dates. Abundance during 1999 decreased a little more in the Large Staghorn, Large Tabular, and Smooth Heads. Plotting a 4th order polynomial regression through the data produced a higher correlation ($R^2 = 0.9702$) and supported the view that habitats with lower fish abundances and those with higher fish abundances changed less over the 28-year period than those closer to the mean. The inflexion point was near the 1971 value of ~1,750 fish per Habitat Type (i.e., ~3.5 fish m^{-2}).

The linear regression line for 2006 abundance on the 1971 data was very similar to 1999. The total abundance for 2006 (17,128 fish) appeared to be lower than that for 1971 (18,153 fish) but greater than that for 1999 (12,492 fish). The linear regression of 2006 abundance in 1971 was highly correlated ($R^2 = 0.8867$) with fish abundance in each habitat type during the 1971 survey explaining most of the variance in fish abundance during 2006, some 35 years later. Abundance during 2006 decreased a little more in the Low Patches, Large Tables, and Smooth Heads. Plotting a 4th order polynomial regression through the data produced a higher correlation ($R^2 = 0.9417$). The inflexion point for this regression was (like the 1999 regression) near the 1971 value of ~1,750 fish per Habitat Type (i.e., ~3.5 fish m^{-2}).

Analysis revealed that there was a significant increase in the abundance of Taxon 2 (Acanthuridae), a significant decrease in Taxon 8 (Lethrinidae), a significant decrease in Taxon 9 (Lutjanidae), and a significant decrease in Taxon 14 (Epinephelidae) over the 35 years from 1971 to 2006 (see Table 2). The taxon that significantly increased its abundance over the 35-year period was classified as a grazer and those that decreased were carnivores and/or piscivores. Apparent changes in the abundance of the remaining taxa were not statistically significant. Statistical analysis of the number of cells occupied by each taxon showed no difference between the two samples and averaged 61.6%., Our data showed (Table 2) an average decrease in recorded abundance of 16.5%, but this was not statistically significant given the high variance among habitat types created by the changing and indeterminate fine scale distribution of taxa.

Table 2. Taxon abundance 1971 vs 2006.

Taxon	**No. of Fish 1971**	**No. of Cells Max =100**	**Density in Cells Fish/M^2**	**No. of Fish 2006**	**No. of Cells Max =100**	**Density in Cells Fish/M^2**	**No. of Fish Change**	**Density in Cells Change**	**2006 vs 1971 Abundance Across Habitats**
(2) **Grazer**	279	75	0.074	477	79	0.121	+71.0%	+63.5%	p<0.10 Acanthuridae
(8) **Carnivore**	65	23	0.057	33	16	0.041	-49.2%	-28.1%	p < 0.05 Lethrinidae
(9) **Carnivore**	94	28	0.067	148	32	0.093	-57.4%	+38.8%	p < 0.10 Lutjanidae
(14) **Piscivore**	171	84	0.041	130	64	0.041	-24.0%	0.0%	p<0.05 Epinephelidae
Totals	18153	AV 61.8%	AV DENS $0.288/m^2$	15154	AV 61.4%	AV DENS $0.250/m^2$	-16.5%	-0.4%	**No differences in totals**

Coral reef decline

In view of the protected status of Wistari Reef, we looked at changes in the physical environment that might have affected the fish community. Our measures for physical change were live coral cover and rugosity and our assumption was that a decrease in either could be reflected as a reduction in the "health" of the reef community. Total coral cover has been commonly used to assess changes in coral-reef ecosystem condition or health (Gardner et al., 2003; Mumby et al., 2007; Ismail & Goeden, 2020; Ismail et al., 2022). By plotting the average coral cover of each habitat type (Figure 5) and the average rugosity of each habitat type (Figure 6), changes in the physical substrate over time were more apparent.

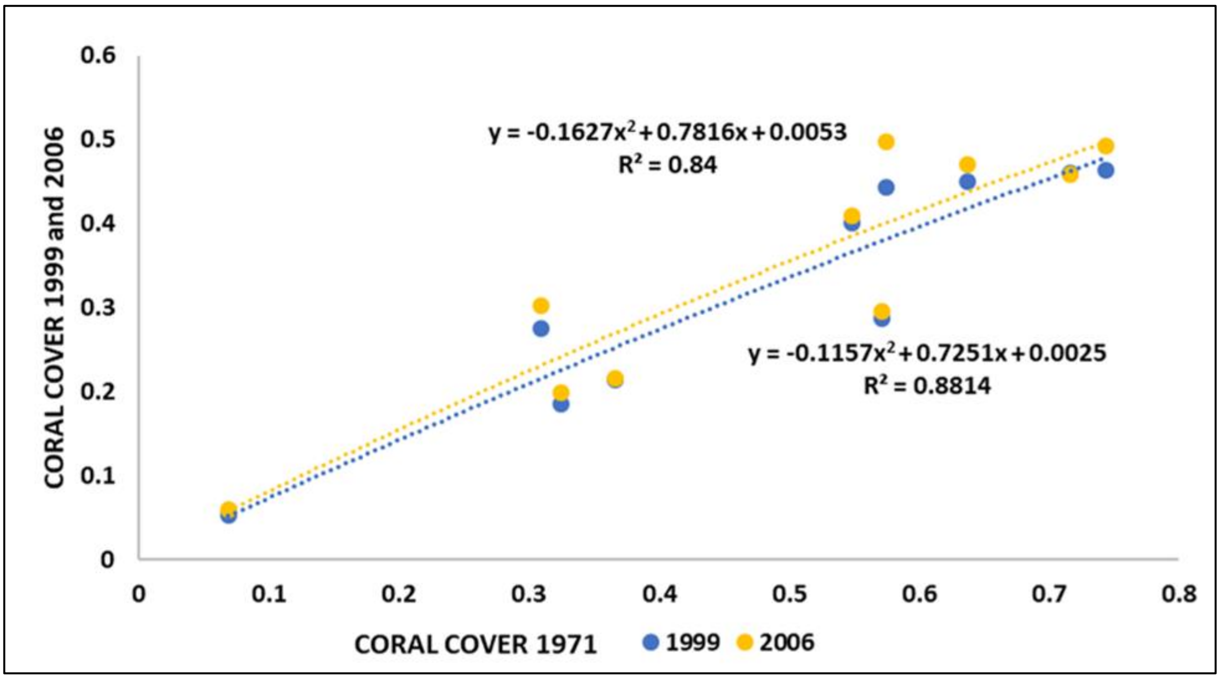


Figure 5. Changes in coral cover by habitat type 1999, 2006 vs 1971.

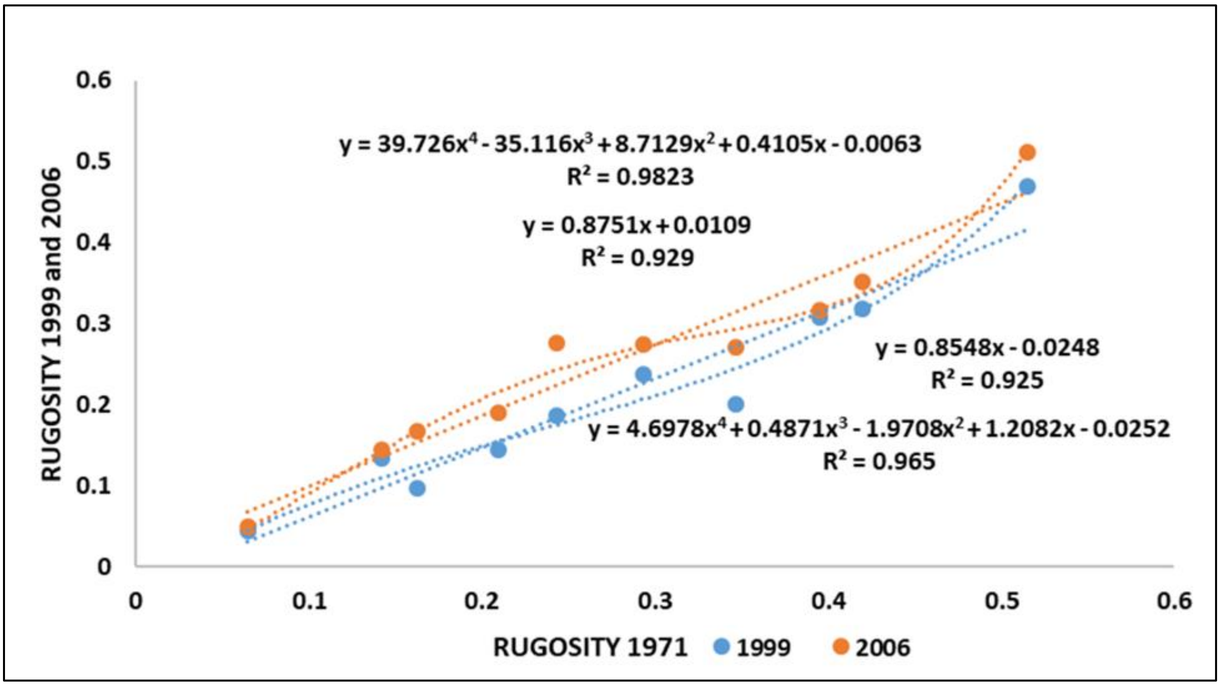


Figure 6. Changes in rugosity by habitat type 1999, 2006 vs 1971.

The polynomial regressions of average coral cover of each habitat type in 1999 and 2006 on our measurements in 1971 demonstrated high correlations between the sampling periods (R^2 = 0.84 and 0.88, respectively). The average coral cover appeared to have declined from 48.65% to 34.04% over the full 35-year period and statistically significant changes (one-tailed t-test) occurred in 7 of the 10 Habitat Types (Table 3). The apparent change in the means of the two data sets (14.6% less) was not statistically significant due to the large variance among Habitat Types.

Table 3. Recorded changes in % coral cover between the 1971 and 2006 samples.

Habitat Type	Change	Direction	Significance
Low Patch Corals	15.1%	Less	$p < 0.05$
Large Stag Thicket	25.1%	Less	$p < 0.01$
Smooth Coral Heads	19.5%	Less	$p < 0.01$
Compact Slope	25.8%	Less	$p < 0.01$
Open Slope	13.9%	Less	$p < 0.05$
Gutters	16.8%	Less	$p < 0.01$
Compact Flat Areas	12.6%	Less	$p < 0.01$
Average	**14.6%**	**~Less**	=

The regressions of average rugosity of each habitat type in 1999 and 2006 on measurements in 1971 showed both very high linear and polynomial correlations between the sampling periods (linear was R^2 = 0.925 and 0.929 respectively; polynomial was R^2 = 0.965 and 0.982 respectively). Habitat Types closer to the average rugosity fared worse over time experiencing a greater decline than those with very low or very high rugosity. Significant changes (one-tailed t-test) over the full 35-year period only occurred in Large Stag Thickets, Large Tabular, Smooth Coral Heads, and Open Slope (Table 4). The apparently contradictory rugosity increase in Large Tabular Habitat Type can be explained by the death and collapse of many corals leaving deep holes between living colonies where plates once overlapped.

Table 4. Changes in rugosity index between the 1971 and 2006 habitat types.

Habitat Type	Change *(Ru)*	Direction	Significance
Large Stag Thicket	0.076	Less	$p < 0.01$
Large Tabular	0.034	More	$p < 0.10$
Smooth Coral Heads	0.069	Less	$p < 0.10$
Open Slope	0.079	Less	$p < 0.05$
Average	**0.024**	**~Less**	=

If rugosity was generated by live coral cover and coral death resulted in structural changes to the reef, then we would expect a close relationship between the two measures. In Figure 7, we compared regression lines of rugosity on coral cover for all of the cells in 1971 and 2006 combined so as to cover the longest time span. We have chosen these two dates to include what we expect would be any long-term changes (e.g., “flattening”) of the physical structure of the reef. The linear regression of rugosity on the coral cover in 200 surveyed cells was not strongly correlated ($R^2 = 0.4641$, N=200).

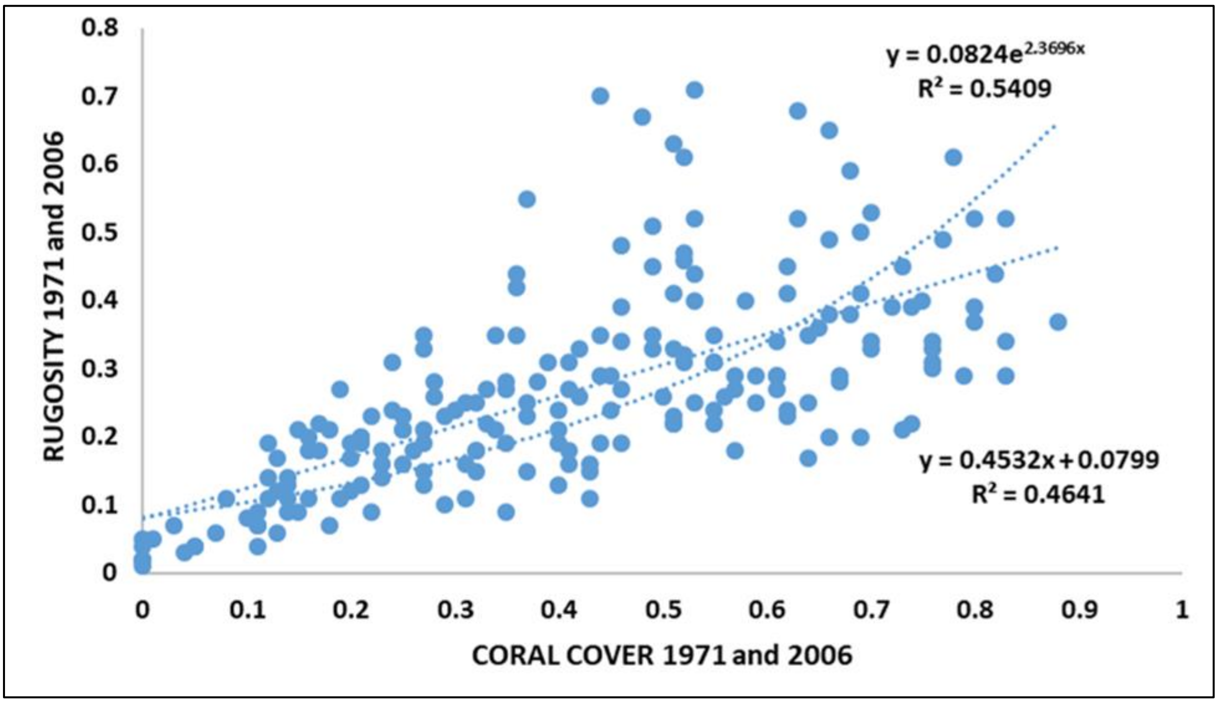


Figure 7. Rugosity vs coral cover 1971 and 2006.

The slightly better R^2 for the combined data was the exponential regression line ($y = 0.0824e^{2.3696x}$, $R^2 = 0.5409$); i.e., increasing coral cover explained about 54% of the variance in rugosity in samples of the same locations 35 years apart.

We compared the abundance of fishes in the Wistari Reef cells with live coral cover using the combined data sets from 1971 and 2006 to include any long-term trends. Both linear and exponential regressions of fish abundance within each cell on coral cover in that cell were poorly correlated ($R^2 = 0.2533$ and $R^2 = 0.3597$, respectively). In both cases, live coral cover explained only about a third of the variance in fish abundance.

By comparing fish abundance with the combined rugosity data for 1971 and 2006 (Figure 8), a linear regression of fish abundance within each cell with the rugosity in that cell was moderately correlated ($R^2 = 0.6636$). A slightly better correlation was found for the exponential regression of fish abundance on rugosity ($R^2 = 0.681$). In both cases, rugosity explained about two-thirds of the variance in fish abundance, i.e., rugosity had about twice the "impact" on the abundance of fishes as live coral cover.

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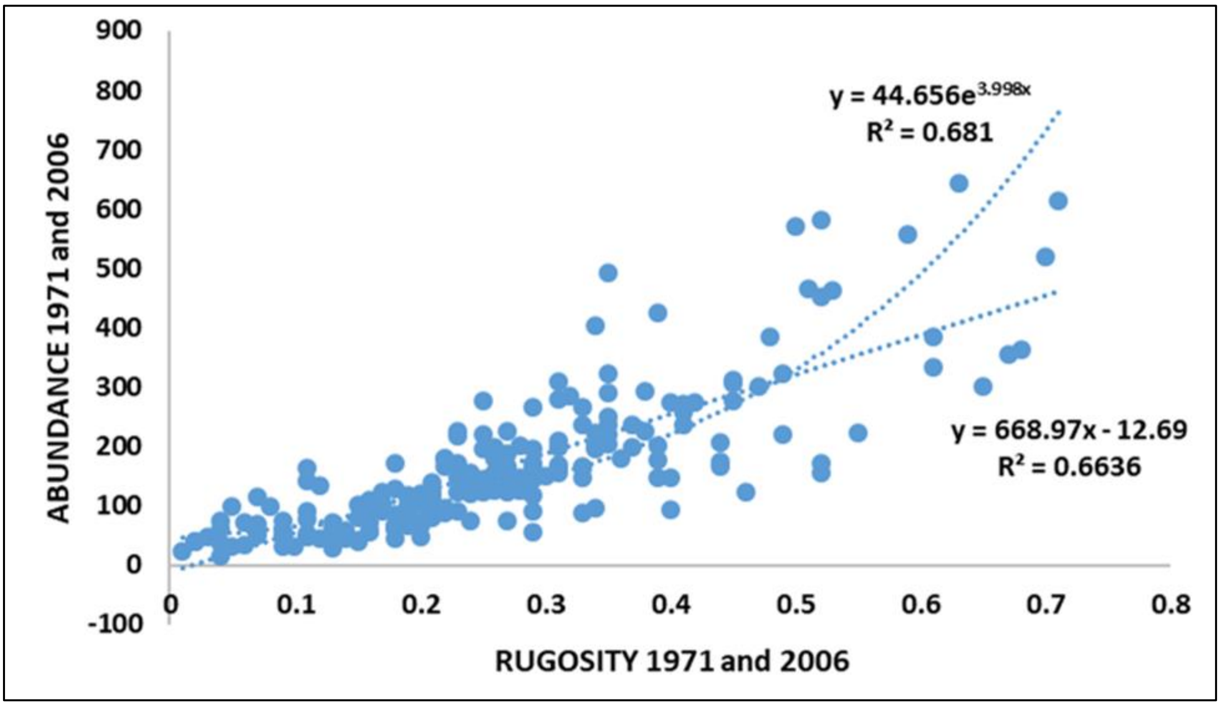

Figure 8. Fish abundance vs rugosity in 1971 and 2006.

DISCUSSION

The original surveys by Bradbury and Goeden (1974) and Goeden (1978) found that the way in which fishes partitioned their environment depended on scale, with the more abundant taxa being patchily distributed within a specific habitat type but occupying space over more kinds of habitat type and so over more of the reefscape. The question arises as to the validity of this relationship over a longer time period; or was the 1974 observation an anomaly? We tested that theory here by comparing data from those same locations at three different times over a period of 35 years and found that, while there have been changes in the relative proportions of taxa, more abundant species continued to occupy more kinds of habitat types and were more widely distributed. Less common taxa were still more evenly distributed within a given habitat type but occupied fewer habitat types. Combined data for 1971, 1999 and 2006 demonstrated this clearly in Figure 3: the common thread in defining the habitat preference of fishes is less about species to species competition (Sale, 1977) and more about the "nature" of the fish's surroundings and the scale at which these are measured by the fish. It is possible that the lumping of species into larger groups could have obscured temporal trends for individual species (Elliott et al., 2018). More targeted approaches may be useful in future studies.

Our results demonstrated a significant decline in the numbers of Lethrinidae, Lutjanidae, and Epinephelidae (all predators) and a significant increase in the Acanthuridae (grazers) over the 35-year period. It is known that fishing can cause trophic cascades through reef fish assemblages (Russ et al., 2021). In the absence of fishing pressure, the observed declines can be interpreted as suggesting that, for many reef fishes, changes in their abundance and distribution were likely to have been linked to changes in their physical environment. Increases in grazer abundance suggest that fish may be responding to reduced predation or increased algal productivity (Nemeth & Appeldoorn, 2009). In fact, recent research suggests that nutritional resources may be more important in structuring herbivorous fish communities than top-down factors (predation risk and shelter availability) (Tootell & Steele, 2016; Tebbett et al., 2020). When we look at how fish abundance changed, we find that the greater changes occurred in those habitat types that supported fish densities nearer the 1971 mean value of ~1,750 fish per surveyed habitat type (i.e., ~3.5 m^{-2}). Habitat types that had supported low numbers of fish continued to support low numbers, while those habitat types that supported large numbers of fish continued to support large numbers, although not as large. We confirm that there were significant changes in both coral cover (7 out of 10 habitat types) and rugosity (4 out of 10) over this period and that all but one of these were decreases. The much lower fish abundance in 1999 may have been influenced by the bleaching event in early 1998 (Hoegh-Guldberg et al., 2007) or cyclone damage. However, Connell et al. (1997), in looking at the impact of cyclones on neighboring Heron Island corals (1967,'72, '76, '80 and '92), stated, "On the deeper transects, cover and density fluctuated only slightly."

Combining the data (200 cells counted) with a span of 35 years between them produced an exponential regression of rugosity on coral cover, but this was poorly correlated (R^2=0.2533). Fuad (2010) found that coral cover was linearly correlated with rugosity in Bunakin National Park (R^2 = 0.321 $p<0.01$). Our results supported the premise that coral cover and rugosity were "mostly independent" and thus provided an opportunity to look at the separate contributions of each to the abundance of coral reef fishes.

We found that the correlation for the linear regression of fish abundance on coral cover for the combined data was weak and was only marginally better for the exponential regression (R^2 = 0.3597). This contrasts to some degree with Komyakova et al. (2013), who found a "critical" relationship between coral richness and cover and fish populations. A linear regression of fish abundance within each cell with the rugosity in that cell was moderately correlated (R^2 = 0.6636). A slightly better correlation was found for the exponential regression of fish abundance on rugosity (R^2 = 0.681). In both of these regressions, rugosity explained about two-thirds of the variance in fish abundance, i.e., rugosity had about twice the "impact" on the abundance of reef fishes as live coral cover. These findings were supported by Nemeth & Appeldoorn (2009), who found that once the effects of depth were minimized, habitat areas of high topographic relief were positively correlated with biomass. Indeed, several recent studies have argued that the relationship should be unimodal because, as complexity increases, the amount of area available for individuals to live declines (Allouche et al., 2012; Paxton et al., 2017; Torres-Pulliza et al., 2020). We postulate that this may be true with the caveats of corals that produce smaller spaces and/or larger inhabitants. We saw no evidence of a unimodal relationship in our results.

While some of the taxa may have had some degree of biological 'interdependence' with living corals, there appeared to be a greater dependence by the fish community on the physical shelter and niche space the coral structures provided, supporting the arguments of Bruno and Bertness (2001) and Willis et al. (2005). In parallel with our results, Nugraha et al. (2020) found a significantly correlated relationship (R^2 = 0.709) between coral reef fish density and rugosity in East Java waters. They found only a weak and surprising inverse relationship between fish density and coral cover (R^2 = 0.108). These results are in contrast to Komyakova et al. (2013), that found that habitat "complexity did not appear to influence overall fish species richness and abundance" as much as coral cover and richness.

Unfortunately, our long-term study revealed that the gradual reduction in rugosity on Wistari Reef was following a long-term decrease in coral cover and leading to the "flattening" (described by

Alvarez-Filip et al., 2009; Elliott et al., 2018) and the slow collapse of the reef framework into less complex habitats. Substantially lower coral cover and rugosity have been reflected in the abundance of many coral reef fishes, but it is the functional role of the 3-dimensional structure that is actually changing (Graham et al., 2015). Newman et al. (2015) stress the importance of “the need to maintain structure above a critical threshold,” and Aragón et al. (2019) suggest a minimum live coral recovery threshold of 10% (in this study, equivalent to Ru>0.1). The continuation of this phenomenon can only lead to a parallel collapse in the fish community and eventual degradation of what was an extraordinarily biodiverse coral reef.

CONCLUSIONS

We can confirm that fishes partitioned the reef slope at different scales, with more abundant taxa being more patchily distributed within a habitat type but occupying more habitats and a greater share of the reef slope in the same habitat types. This continued over a 35-year period despite changes in the physical structure of the reef. Over that same period, there were significant declines in rugosity and coral cover apparently resulting in reduced fish abundance. Of these two metrics, there were stronger relationships between fish abundance and rugosity across the 10 habitat types. We concluded from these results that the three-dimensional complexity of the reef (defined here as rugosity) was central to and more influential than coral cover in supporting a healthy reef fish community. Similarly, we conclude that the decline in rugosity over this period parallels the concurrent “flattening” of the Caribbean reefs (described by Alvarez-Filip et al., 2009; Elliott et al., 2018).

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The authors have read and approved the final manuscript.

Ethical approval

The authors declare that this study complies with research and publication ethics.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Autor Contribution

Gerald B. Goeden: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Review and editing.
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