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Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef

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Abstract The biomass of large herbivorous grazing fish on the shallow reef crest of Myrmidon Reef, Great Barrier Reef, is 7.0 times that on the reef slope (15 m depth), and 2.3 times that on the reef flat. Biomass of algal turfs on the crest was only 1.4 and 1.0 times that on the slope and flat, respectively. In contrast, rate of production of algal turfs on the crest was 5.3 and 2.8 times that on the slope and flat, respectively. A multiple correlation between large grazer biomass, algal turf biomass, and algal turf production across the three zones showed that only rate of algal production correlated significantly with large grazer biomass (algal production $p=0.007$, algal biomass $p=0.418$). This result suggests that large grazers may aggregate in zones of highest algal turf production. The mechanisms by which fish respond to habitat-specific differences in food production remain unclear.

Keywords Algal turfs · Biomass · Coral reefs · Grazers · Production

Introduction

Coral reefs are some of the most productive ecosystems known (Hatcher 1988, 1990). The interaction between grazers and algae is possibly the largest trophic flux on coral reefs (Hatcher 1983, 1988; Carpenter 1986). This interaction is also central to the current debate on the relative roles of enhanced nutrients and overfishing of

herbivorous fish in “phase shifts” from coral to algal domination in benthic coral reef habitats (Hatcher 1984; Done 1992; Hughes 1994; McCook 1999). Most relatively undisturbed, oligotrophic coral reefs support a very high biomass of herbivorous grazing fish, but a low biomass of algal turfs on which the fish feed (Hatcher 1988, 1990). The very high productivity of the algal turfs, rather than their standing crop, maintains these high standing stocks of grazers (Hatcher 1983, 1988; Carpenter 1986; McCook 1999). This suggests that the distribution of biomass of herbivorous grazing fish on coral reefs may be influenced more by the rate of production than by the biomass of algal turfs. Few studies have tested this prediction (Hatcher 1988, 1990). This is surprising, given that zonation patterns of reef fish on coral reefs are well documented (Williams 1991).

This study combines information on the abundance of herbivorous grazing fish in the Families Acanthuridae, Scaridae, and Siganidae in three different zones of Myrmidon Reef, the Great Barrier Reef, Australia (Russ 1984b), with information on the biomass, production, and yield to large grazers of algal turfs in these same zones. The study addresses the questions: (1) does grazer biomass correlate with production and biomass of algal turfs? and (2) if so, does grazer biomass correlate more strongly with production or with biomass of algal turfs?

Materials and methods

Study sites

The study was carried out at Myrmidon Reef in the central Great Barrier Reef (GBR), Australia. Myrmidon Reef is a platform reef on the outer continental shelf, approximately 100 km from the Queensland coast [see Fig. 1 in Russ (1984a)]. The study was made in three zones on the northern face of Myrmidon Reef: the reef slope at 15 m depth, the reef crest, and the reef flat, both at 2–3 m depth (see Fig. 1e for a schematic representation).

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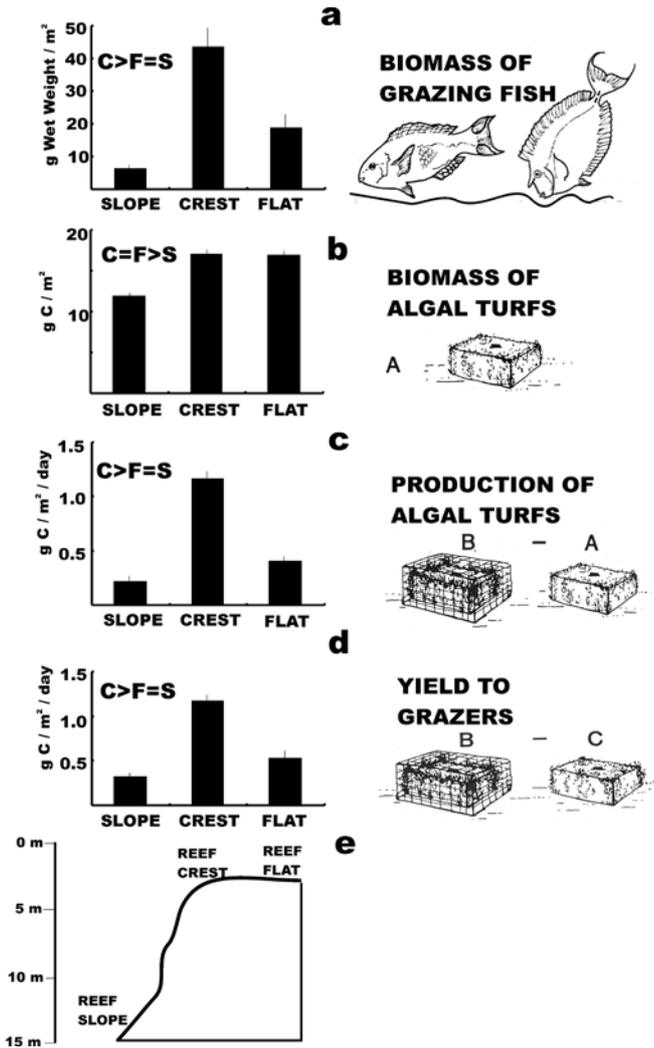


Fig. 1 a Biomass of large herbivorous grazing fish; b biomass of algal turfs; c rate of algal production; and d yield of algae to grazers in the reef slope, reef crest, and the reef flat zones of Myrmidon Reef, GBR. Algal biomass, production, and yield were measured using preconditioned coral plates, with a standing crop of algal turf. This algae was removed at the beginning of the experiment (treatment A), or left in situ for 1 month, either protected from large herbivores in mesh cages (treatment B) or uncaged (treatment C). Results of Tukey's HSD tests ($p < 0.05$) are shown. A schematic profile of the reef is shown in e. Horizontal distances between zones in this schematic are not to scale. Error bars are standard errors

Fish surveys

The biomass of large, herbivorous grazing fish (all species in the Families Acanthuridae, Scaridae, and Siganidae—which constitute the majority of species of large herbivorous fish on the GBR) was estimated by underwater visual census (UVC) (Russ 1984a, 1984b). A census dive consisted of a 30-min swim on SCUBA through the zone, recording the abundance of each species on a log-3 abundance scale. All individuals within approximately 5 m on either side of the diver were censused. The abundance of a species was recorded cumulatively throughout a census, and all species were censused simultaneously. Juveniles (less than 5–8 cm total length, depending on species) were not counted. Census dives were unidirectional and parallel to the reef crest. Each census covered an area of approximately 4,000 m² (Russ 1984a). Four replicate, non-overlapping

censuses were made in each zone in July 1982 [see Fig. 2 in Russ (1984b) for general location of censuses in each zone of Myrmidon Reef]. Log-abundance data were converted into estimates of number of fish per unit area using the mid-points of the log abundance categories [see Table 2 in Russ (1984a)]. Median lengths were assigned to six different categories (Acanthurid small, Acanthurid large, *Naso* small, *Naso* large, Scarid, Siganid), and wet weights estimated using published length–weight relationships for such fish (Froese and Pauly 1997). This provided an approximate estimate of large grazer biomass (grams of wet weight per square meter) per unit area for each zone.

Algal turf biomass, rate of production, and yield to grazers

Biomass, rate of production, and yield to large grazers of algal turfs were measured in each zone in February and July 1985. Measurements were made at three sites on the reef crest and reef flat, and at two sites on the reef slope, in February 1985. Measurements were made at two sites in all three zones in July 1985. These sites were located haphazardly in the same general areas where the fish censuses were made [see Fig. 2 in Russ (1984b)]. Sites within a zone were approximately 50–100 m apart. Methods were the same as in Russ (1987) and Russ and McCook (1999): preconditioned plates, with a standing crop of algal turf, were removed at the beginning of the experiment (treatment A), or left in situ for 1 month, either protected from large herbivores in mesh cages (treatment B) or uncaged (treatment C) (see Fig. 1). Treatments A and C were taken as initial and final biomass, respectively. Production was estimated

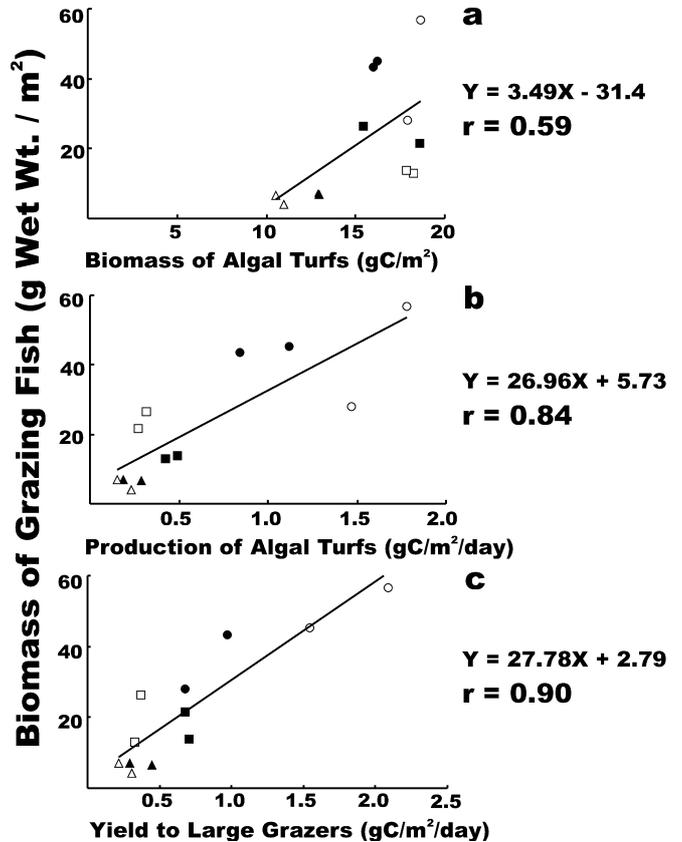


Fig. 2 Linear correlations between biomass of large herbivorous grazing fish and a algal biomass; b rate of algal production; and c yield to grazers. Symbols represent the reef slope (triangles), reef flat (squares), and reef crest (circles). The February experiment is shown as black symbols, the July experiment as white symbols

by growth over a month in the absence of large herbivores (treatment B minus treatment A). Yield to grazers was estimated by that portion of production eaten by large grazers (treatment B minus treatment C).

Flat, coral plates (8×8×2.5 cm, cut from *Porites* spp.) were used as experimental substrata. Flat, square surfaces were chosen because they permitted rapid removal of algal biomass (by scraping) and rapid determination of the upper surface area. Each experimental plate was attached, by a single stainless-steel bolt, directly to the natural substratum at a study site. At each site, 12 plates were placed as four replicate groups of three (treatments A, B, and C), with plates randomly assigned to the three treatments within groups. Plates within groups were placed within 1 m of each other and the four groups in a site were spread over an area of approximately 50–100 m². Plates were immersed at the site 4–5 months before the beginning of each experiment to allow development of an algal turf community that closely approximated that on the natural substratum. The February and July experiments were of 26 and 27 days duration, respectively.

Herbivore exclusion cages used in treatment B were square (12.5×12.5×6.25 cm) and made of galvanized wire mesh (mesh size 12.5 mm square, wire diameter 0.8 mm). These cages excluded all grazers > 12.5 mm minimum dimension (defined as “large grazers”). Previous work, using the methods proposed by Kennelly (1983), found that these cages had no significant effect on algal standing crop (Russ 1987) or species composition (Scott and Russ 1987), other than the effect due to excluding grazers.

At the end of the experimental periods, plates were placed into individual, seal-top plastic bags and frozen immediately. In the laboratory, plates were thawed and the algal turf scraped from the flat, upper surface of each coral plate onto a pre-weighed piece of aluminium foil. A 5-min period of scraping removed all of the algae on the upper surface of the plate, and also removed the top few millimeters of calcium carbonate from the plate. The sample was dried to constant weight and ground in a Wiley mill. The percentage of organic carbon in the sample was determined using the method of Sandstrom et al. (1986) for samples with a high calcium carbonate content. The weight of the dry sample and its percent organic carbon content were used to calculate algal biomass as grams of organic carbon (gC) on each plate. The area of the upper surface of each plate was measured to the nearest 0.1 cm² by digitizing a photocopy of the surface. Algal production and yield to grazers are expressed as areal rates (gC m⁻² day⁻¹; Fig. 1).

Data analysis

A one-factor analysis of variance (ANOVA) was used to compare the grazer biomass in the three zones. Two-factor ANOVAs (one fixed factor, zone, with three levels; one nested factor, site(zone), with four levels; four replicate measurements in sites) were used to compare algal biomass, algal production, and yield to grazers in the three zones in February and July combined. Algal data from one of the sites in each of the crest and flat zones sampled in February were eliminated at random to ensure a balanced analysis. Homogeneity of variance ($p < 0.05$) for all analyses was determined using Cochran's test. A posteriori multiple comparisons of means were carried out using the Tukey's Honest Significant Difference (HSD) test ($p < 0.05$).

A multiple correlation was performed between biomass of large grazers, algal biomass, and rate of algal production in the three zones. Simple linear correlations of large grazer biomass with algal biomass, algal production, and yield to grazers were also carried out.

Results

The biomass of large grazers, rate of algal production, and yield of algae to grazers were all significantly higher

on the reef crest than on the reef flat and reef slope, with no significant differences between slope and flat for any of these three variables (Fig. 1; Tukey's HSD results). The biomass of large grazers on the crest was seven times higher than on the reef slope at 15 m depth, and 2.3 times higher than on the shallow reef flat. The rate of production of algal turfs on the crest was 5.3 and 2.8 times higher than on the reef slope and reef flat, respectively. In addition, the yield of algal turfs to large grazers on the crest was 3.7 and 2.2 times higher than on the reef slope and reef flat, respectively. In contrast, the biomass of algal turfs on the reef crest did not differ significantly from that on the reef flat, but was significantly higher than that on the slope (Fig. 1; Tukey's HSD results). Biomass of algal turfs on the reef crest was only 1.44 and 1.0 times that on the reef slope and reef flat, respectively (Fig. 1).

A multiple correlation between biomass of large grazers, algal biomass, and rate of algal production was highly significant ($r = 0.85$, $F_{2,9} = 11.79$, $p = 0.0031$). However, only rate of algal production correlated significantly with large grazer biomass (Beta = 0.738, $t = 3.50$, $p = 0.007$ for algal production; Beta = 0.179, $t = 0.85$, $p = 0.418$ for algal biomass). In simple linear correlations, biomass of large grazers correlated significantly with algal biomass, rate of algal production, and yield to grazers (Fig. 2). However, rate of algal production correlated more strongly with biomass of herbivorous grazing fish than did algal biomass in simple linear correlations ($r = 0.84$, $F_{1,10} = 23.51$, $p = 0.0007$ for algal production; $r = 0.59$, $F_{1,10} = 5.34$, $p = 0.04$ for algal biomass) (Fig. 2a,b). Biomass of large grazers correlated strongly with yield of algal turfs to grazers ($r = 0.90$, $F_{1,10} = 42.68$, $p = 0.00007$) (Fig. 2c).

Discussion

Large herbivorous grazing fish occur in much higher biomass in a zone of a coral reef that has a much higher rate of production, but not a much higher biomass of algal turf food. This study does not establish that the high rate of production of algal turfs on the crest is the cause of the higher biomass of large herbivorous grazing fish on the crest. Other factors not investigated here, such as differences in habitat complexity, predation rates, or recruitment rates between zones, may influence the distribution and abundance of coral reef fish substantially (Williams 1991). However, the data are consistent with the hypothesis that large grazers, which can be highly mobile over scales of hundreds of meters (e.g. Chapman and Kramer 2000), concentrate in a zone of higher rates of algal turf production.

Why does the biomass of large grazers correlate positively with algal turf production but not biomass? Mobile grazers could be responding to greater food availability (greater amounts of algal turf food over time) in certain zones, or mobile grazers may aggregate in certain zones/habitats for reasons other than food

availability, where they enhance rates of algal production by their grazing. The type of production enhancement is unlikely, however, to cause differences in algal production of the order of 2.8–5.3. Grazing can enhance the productivity of epilithic algal communities by selecting for fast-growing species and growth forms, by reducing self-shading effects and by increasing availability of nutrients (Carpenter 1981, 1986; Hatcher 1983, 1988, 1990; Klumpp and Polunin 1990). The largest enhancement of algal turf productivity on an areal basis that Carpenter (1986) could induce experimentally was a factor of 1.6, and this was not statistically significant. Carpenter (1986) did demonstrate a substantial increase in production per unit algal biomass (i.e. specific productivity) due to urchin grazing. Most evidence suggests that the standing crop of algal turfs on coral reefs is controlled by grazing, whereas the rate of production is controlled by nutrient supply (Hatcher and Larkum 1983; Carpenter 1986; Atkinson 1988; Hatcher 1988; McCook 1999).

It is unlikely that the large grazers are selectively responding to differences in food types (species composition of algal turfs) between zones. The biomass and height of algal turfs is so low in all three zones, relative to the mouth size of most large grazers, that selective feeding on particular algal turf species is unlikely. Thus, it is most likely that grazers are aggregating in zones of highest food availability. Food availability, as measured in this study, is higher on the crest than on the flat and slope due to differences in algal turf production, not biomass. Similarly, the difference in food availability between the flat and slope is due more to differences in production than biomass of algal turfs. If food is affecting the distribution and abundance of large grazers, how do the fish detect this difference? If the differences in food supply among zones were reflected in a large difference in algal biomass, such a difference could be detected visually or tactilely by the grazing fish. Several studies have documented increases in feeding rates (Carpenter 1988; Russ and McCook 1999) and growth rates (Hart and Russ 1996) of herbivorous reef fish in response to increases in algal biomass on coral reefs. It is less clear how fish might detect a difference in the rate of algal production.

Algal productivity has been shown to be two to three times higher on the reef crest than on the reef flat of coral reefs on the Great Barrier Reef (Barnes and Devereux 1984; Klumpp and McKinnon 1989; Klumpp and Polunin 1990). Studies of algal turf productivity on fore-reef slopes of coral reefs are still rare (Hatcher 1990). A consistent pattern in most coral reef studies is that a high proportion of algal turf production is consumed by grazers (Carpenter 1981, 1986; Hatcher 1981, 1983, 1988, 1990; Russ 1987; Klumpp and Polunin 1990; McCook 1999). Studies have demonstrated higher grazing intensities in the shallow zones of coral reefs relative to the deeper zones (Hatcher 1981; Hay 1981). There is often a peak in grazing intensity on the crest, decreasing consistently as one moves across the reef flat

into the lagoon (Hatcher 1981; Hay 1981; Klumpp and Polunin 1990).

Why should the rate of production of algal turfs on the crest be 5.3 and 2.8 times that on the slope and flat, respectively, of Myrmidon Reef? The crest would have higher levels of photosynthetically active radiation (PAR) than the slope (Hatcher 1990). The crest has the greatest water turbulence and mixing and thus supply rate of nutrients to algal turfs (Hearn et al. 2001). Nutrients are consumed as water moves across the crest and reef flat towards the lagoon (Barnes and Devereux 1984; Klumpp and Polunin 1990). Finally, the crest has higher grazing rates than the other zones, thus enhancing production (this study). Given the consistency in the patterns of distribution of large herbivorous grazing fish between zones of coral reefs in the central and southern GBR (Hatcher 1981; Russ 1984a, 1984b), the various factors hypothesized to explain the differences in production and grazing may be generally applicable to many GBR reefs.

Clearly, the caging method used here will underestimate algal production rates. Areal rates of production of algae will decrease as algal biomass accumulates in caged treatments. Furthermore, the technique cannot account for losses of algae caused by small (< 12.5-mm) grazers entering cages, fragmentation, reproduction, or exudation. Such factors may vary between zones, and such variations were not measured. However, such differences across zones are unlikely to change the main conclusions of this study. Another potential criticism of the study is that the biomass of grazers was measured in the zones at a different time to that when the algal biomass, rate of production, and yield were measured. Clearly, a major assumption of this study is that the gross pattern of distribution of biomass of large grazing fish between the three zones is relatively consistent over time. A number of lines of evidence suggest this is true. Russ (1984a, 1984b) reported that the abundance of large herbivorous grazing fish was consistently much higher on the reef crests than on the reef flats or reef slopes of three mid-shelf and three outer-shelf reefs in the central GBR. The consistency of these spatial patterns suggests that it is likely to persist through time. Hatcher (1981) showed that differences in grazer biomass between zones of One Tree Reef on the GBR remained consistent over a 14-month period. Personal observations of the abundance of large herbivorous fish on the reef crests and reef slopes (15 m) of mid- and outer-shelf coral reefs in many different areas of the GBR and various coral reefs of the Philippines over the past 20 years suggest a consistently higher abundance on the reef crest relative to the reef slope and reef flat. This clear pattern of higher biomass of herbivorous fish on the reef crest relative to the slope and flat has also been described on coral reefs in many other parts of the Indo-Pacific, the Red Sea, and the Caribbean [see reviews by Williams (1991) and Russ (1984b)].

In conclusion, grazing fish biomass was shown to correlate more strongly with the production than with

the biomass of algal turfs across three zones of a coral reef. This suggests that large grazers may aggregate in zones of highest algal turf production. The mechanisms by which fish respond to habitat-specific differences in food production remain unclear.

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References

- Atkinson MJ (1988) Are coral reef communities nutrient-limited? Proc 6th Int Coral Reef Symp Invited Rev 1:157–166
- Barnes DJ, Devereux MJ (1984) Productivity and calcification on a coral reef: a survey using pH and oxygen electrode techniques. J Exp Mar Biol Ecol 79:213–231
- Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. J Mar Res 39:749–765
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56:345–363
- Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proc Natl Acad Sci USA 85:511–514
- Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Environ Biol Fish 57:11–24
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132
- Froese R, Pauly D (1997) Fishbase 97: concept, design and data sources. ICLARM, Manila
- Hart AM, Russ GR (1996) Response of herbivorous fish to crown-of-thorns starfish outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. Mar Ecol Prog Ser 136:25–35
- Hatcher BG (1981) The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Proc 4th Int Coral Reef Symp 2:515–524
- Hatcher BG (1983) Grazing in coral reef ecosystems. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouston, Canberra, pp 164–179
- Hatcher BG (1984) A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. Coral Reefs 3:199–204
- Hatcher BG (1988) Coral reef primary productivity: a beggars banquet. Trends Ecol Evol 3:106–111
- Hatcher BG (1990) Coral reef primary productivity: a hierarchy of pattern and process. Trends Ecol Evol 5:149–155
- Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Biol Ecol 69: 61–84
- Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat Bot 11:97–109
- Hearn CJ, Atkinson MJ, Falter JL (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. Coral Reefs 20:347–356
- Hughes TP (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551
- Kennelly SJ (1983) An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. J Exp Mar Biol Ecol 68:257–276
- Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral reef epilithic algal community. J Exp Mar Biol Ecol 131:1–22
- Klumpp DW, Polunin NVC (1990) Algal production, grazers and habitat partitioning on a coral reef: positive correlation between grazing rate and food availability. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Aberdeen University Press, Aberdeen, pp 372–388
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367
- Russ GR (1984a) The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Levels of variability across the entire continental shelf. Mar Ecol Prog Ser 20:23–34
- Russ GR (1984b) The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Patterns of zonation of mid-shelf and outer-shelf reefs. Mar Ecol Prog Ser 20:35–44
- Russ GR (1987) Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? J Exp Mar Biol Ecol 110:1–17
- Russ GR, McCook LJ (1999) Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. J Exp Mar Biol Ecol 235:237–254
- Sandstrom MW, Tirendi F, Nott A (1986) Direct determination of organic carbon in modern reef sediments and calcareous organisms after dissolution of carbonate. Mar Geol 70: 321–329
- Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar Ecol Prog Ser 39:293–304
- Williams DMcB (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 437–474