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Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia

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Abstract A description of the daily feeding patterns is provided for the two most abundant bioeroding parrotfish species on the Great Barrier Reef: *Chlorurus gibbus* and *C. sordidus*. This study was based at Lizard Island in the northern section of the GBR. Dawn to dusk observations were used to estimate feeding rates and the length of the feeding day. The effects of location and season on these values were also examined. These data are used to estimate erosion rates by the two species. A direct estimate of erosion rates by the two species is provided based on estimated feeding rates and bite sizes. In both species, feeding was characterized by an abrupt initiation and termination with relatively consistent feeding rates throughout the day. Both species spend 83.6 to 91.0% of daylight hours feeding. The proportion of daylight hours spent feeding increases in winter, although the actual length of time spent feeding decreases. Overall, the two species are similar in their general feeding patterns but differ in their seasonal response to time of day effects. *C. gibbus* is conservative with limited site, time of day or seasonal changes in feeding rates. In contrast, *C. sordidus* displayed marked seasonal changes in daily feeding rates and diel feeding patterns, with higher feeding rates in the afternoon and in the summer. Seasonally adjusted estimates of annual erosion rates per individual of the two species were $1017.7 \pm 186.3 \text{ kg yr}^{-1}$ ($0.41 \pm 0.07 \text{ m}^3 \text{ yr}^{-1}$) for *C. gibbus* and $23.6 \pm 3.4 \text{ kg yr}^{-1}$ ($9.7 \cdot 10^{-3} \pm 1.3 \cdot 10^{-3} \text{ m}^2 \text{ yr}^{-1}$) for *C. sordidus*. The likely impact of location and season effects on erosion rates appear to be limited.

Introduction

Since the first note of bioerosion by parrotfishes by Darwin (1842, 1845), there have been numerous records of

their feeding and sediment-producing activities. Records of scarid bioerosion based on observations of gut contents are widespread, with observations from the Red Sea (Al Hussaini 1945, 1947; Gohar and Latif 1959), Indo-Pacific (Cloud 1959; Hiatt and Strasburg 1960; Bakus 1964, 1967; Glynn 1973; Hobson 1974) and Caribbean (Randall and Bishop 1967). Quantitative estimates of scarid bioerosion, however, are largely restricted to the Caribbean (e.g. Gygi 1969, 1975; Ogden 1977; Scoffin et al. 1980). Published estimates of scarid bioerosion on Indo-Pacific reefs rely on indirect estimates based on erosion rates of experimental blocks (Kiene 1985). The present study redresses this imbalance by providing a direct estimate of the extent and variability of bioerosion by parrotfishes on an Indo-Pacific reef.

It has long been recognised that parrotfishes have the capacity to scrape the substratum when feeding, and most parrotfishes have a gut containing large quantities of carbonate sediment. However, few studies have identified the source of this material by distinguishing that which is removed from the substratum during feeding (i.e. eroded sediment) from that existing as sediment on the reef (i.e. reworked sediment). For Indo-Pacific reefs this problem was largely overcome by Bellwood and Choat (1990), who provided a morphological, functional and behavioural basis for identifying those species which excavate (i.e. erode) the substratum during feeding. This has provided a focus for the study of bioeroding species on the Great Barrier Reef.

Bellwood and Choat (1990) identified a number of excavating species, including *Bolbometopon muricatum*, *Cetoscarus bicolor* and a range of “*Scarus*” species. These latter species were all functionally and morphologically distinct from other *Scarus* species and, in a recent phylogenetic study of the Scaridae (Bellwood 1994), these excavating forms have been recognised as a distinct evolutionary lineage and are placed in a separate genus: *Chlorurus*.

In terms of numerical dominance, the two most important *Chlorurus* species on the Great Barrier Reef are *C. gibbus* (previously *Scarus gibbus*) and *C. sordidus* (previously

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Scarus sordidus). *C. gibbus* reaches 450 mm standard length (SL), and is moderately abundant in shallow semi-exposed locations of mid- and outer-shelf reefs. *C. sordidus* is smaller, reaching only 250 mm SL, but is abundant in most reefal habitats on mid and outer-shelf reefs (Russ 1984a, b). *C. gibbus* from the Pacific is identified as *C. microrhinos* by some authors (e.g. Randall et al. 1990, but see Choat and Randall 1986). The other major excavator, *Bolbometopon muricatum*, is relatively uncommon but may be of considerable significance, especially on outer shelf reefs.

The identification of the principal excavating/bioeroding taxa has made it possible to examine the feeding biology of bioeroding scarids in some detail. One of the key steps in evaluating the impact of parrotfishes as bioeroders of coral reefs is to be able to quantify the rate and duration of their daily feeding activities. There have been a number of studies on the feeding biology of parrotfishes in the Indo-Pacific (Choat and Robertson 1975; Bruce 1979; Polunin and Klumpp 1989); however, none provided the detail needed to estimate total daily feeding rates.

The aim of the present study is to provide basic information on the temporal feeding patterns of two of the main bioeroding species on the GBR in terms of behavioural patterns and feeding rates. These data permit a total daily feeding rate to be estimated which, when combined with estimates of bite sizes, will permit a direct estimate of the erosion rates by the two species to be calculated, with confidence intervals based on all major sources of variance. The results will also permit comparisons to be made between the two species in terms of their erosion rates and the extent to which site and seasonal changes affect these estimated values.

Materials and methods

All observations were undertaken on the fringing reefs around Lizard Island, a granitic island in the mid-shelf region of the northern Great Barrier Reef (14°40'S; 145°28'E). Two sites were chosen for the behavioural observations (Fig. 1). Previous work on the behaviour of herbivorous reef fishes at these sites (Choat and Bellwood 1985) has demonstrated that the distance between the sites is sufficient to permit detection of site-related differences in fish-feeding behaviour. A comparison between the two sites therefore, will permit local site-effects to be evaluated. Previous studies have also identified the presence of both time of day and site effects on scarid feeding-patterns (Choat and Clements 1993). These factors were therefore incorporated into the sampling design.

All observations were made during periods when the tides were at least 0.9 m above chart datum. There were three main observation periods; two in summer (6 to 19 December 1991 and 20 to 28 January 1992) and one in winter (9 to 14 July 1992). Sea temperatures during these periods were 28 and 24 °C, respectively (cf. Vail 1987). All time of day values are expressed as Australian Eastern Standard Times (EST).

Observations were restricted to two species: *Chlorurus gibbus* and *C. sordidus* based on the observations of Bellwood and Choat (1990). All observations were made using SCUBA. Data were recorded on underwater paper. To minimise the effects of variability due to observer effects, all feeding observations for each species were recorded by a single observer throughout the study. To minimise the effects of interference by territorial herbivores on feeding behaviour

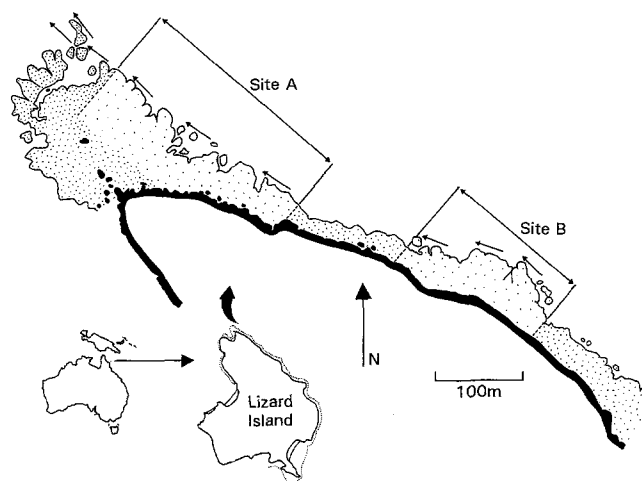


Fig. 1 Location of study sites. Arrows indicate direction of migration at sunset

(cf. Choat and Bellwood 1985), all *C. gibbus* observations were based on individuals >300 mm SL (350 to 440 mm SL) and, to reduce the influence of reproductive activity, all *C. sordidus* observations were based on initial-phase individuals of 150 to 200 mm SL. The sexual status of *C. gibbus* cannot be distinguished externally.

The five main components of the study were:

- (1) to determine the length of the feeding day, in minutes and as a proportion of the daylight hours (defined as the period from sunrise to sunset);
- (2) to determine if there was any significant difference between morning and afternoon feeding rates;
- (3) to estimate the total number of bites taken in a day by each species;
- (4) to estimate bite volumes;
- (5) using (3) and (4), to estimate the daily and annual rates of erosion by the two species.

The methodologies for each of the various aspects of the study are outlined separately below.

Behavioural observations

To estimate daily feeding patterns, feeding rates were recorded during a series of 5 to 6 dives from just after sunrise (to record the first bite) to the point at which all feeding behaviour had ceased (~19.00 to 19.45 hrs). Times were selected to give a relatively even spread throughout the day. Five such daily estimates were made at each study site in the summer period and four daily estimates at North reef in the winter period. These daily values were then used to compare daily feeding rates by the two species between the two sites and between seasons. Logistical constraints precluded a balanced design of sites within seasons, however the results suggest that a single winter site was adequate.

Feeding behaviour was recorded during replicate 5 min feeding-observation periods. Upon arrival at the study site, the observer swam in a rough zig-zag pattern from slope/crest to inner reef flat, until a target individual was located. At this point the fish was given a few minutes to acclimatize to the diver before timed observations commenced. Observations were discontinued if the individual was lost during the 5 min observation period or if the individual showed any signs of disturbance (flight or hiding).

The study area is protected from all spearfishing activity and is regularly visited by researchers and sports divers. There is no fish-feeding and both study species appeared to be diver-neutral. Most observations were undertaken at a distance of 3 to 5 m, occasionally < 3 m if the fish swam towards the observer. Visibility usually

ranged from 7 to 12 m. Observations were discontinued if the visibility fell to < 5 m.

Within each dive, every effort was made to select different individuals for each 5 min observation period. For *Chlorurus sordidus* their abundance ensured a degree of independence, for *C. gibbus* independent sampling within a dive was possible as most individuals could be recognised by size and colour pattern. However, for *C. gibbus* the same individuals were usually observed on successive dives, for *C. sordidus* repeat observations were probably limited. The number of fish observed on each dive was 4 to 8 for *C. gibbus* and 6 to 12 for *C. sordidus*.

During the replicate 5 min feeding observations, the following information was recorded: starting time; bites per minute; principal feeding location(s) [estimated as the distance from the reef crest or in relation to other major features of the reef (gullies, crest, open pits etc.)]; number and location of defaecation events; distance moved between feeding location and defaecation location; additional behavioural notes including the social behaviour of the focal individuals, the size of feeding groups, movement patterns, nature of interactions and swimming behaviour.

Bite areas/volumes

Bite areas and volumes were estimated by following individual fish until the exact location of a bite could be clearly seen. Whilst keeping this location in view, the observer swam to the bite site and measured the size of the bite using vernier callipers. The maximum width, length and depth of the feeding scar was measured to the nearest 0.1 mm. If the feeding mark was composed of two scars, both were measured and the resultant areas/volumes pooled. At least 50 bites were examined for each species at each site.

The accuracy of the measurements was checked by comparing estimated volumes based on measurements with estimated volumes measured directly. To do this, pieces of substratum with scars were collected ($n=11$) and the scars were filled with dental wax. The wax was removed and weighed, and the volume was estimated based on the density of the wax (determined based on the weight of wax in air and the displacement weight in water).

Substratum density

Substratum samples were collected from three locations at North Reef. These were scrubbed and washed and soaked in freshwater to remove epilithic algae, sediment and salt. They were then air-dried to constant weight. Each sample ($n=22$) was sprayed and sealed with a thin coat of acrylic varnish and then dried. The volume of each sample was estimated by measuring the displacement weight in water [volume (cm^3) = weight (g) in air - weight (g) when suspended in water]. The acrylic varnish prevented absorption of water when estimating the volume. Approximately 3 mm of the outer layer of the sample was then removed using a file, and measurements were taken using vernier calipers. The weight and volume of the sample was then estimated as above. A 3 mm depth was chosen as this would encompass the depth of the majority of bites by both *Chlorurus gibbus* and *C. sordidus*. By subtraction of volumes and weights, the density of the outer layer of the substratum could be calculated. This provides a direct estimate of the density of the material removed by excavating scarids, and allows for variation in the density in coral skeletons as a result of growth and/or internal bioerosion.

Statistical procedures

For analysis, all times were standardized to minutes after midnight. Sunrise and sunset times for Lizard Island were based on data provided by the Division of Information, Queensland Department of Lands. Day length was taken as the time from sunrise to sunset. The length of the feeding day is defined as the time from the first recorded bite to the last recorded bite on a given day (in minutes). The proportion (%) of the day spent feeding = feeding day length \times 100/day length.

Daily feeding rates

To calculate the total number of bites taken by each species in a day, the feeding rate (adjusted to bites min^{-1}) was plotted against time (min after midnight). As feeding initiation and termination was abrupt, all 0 values were removed at the start and end of the day. A quadratic polynomial line was then fitted to the data. Using this equation the area under the line delineated by the initiation and termination of feeding (first and last value >0 respectively = length of the feeding day), was calculated. This value represents an estimate of the total number of bites taken by that species on that day.

Morning/afternoon feeding rates

Morning and afternoon feeding rates were compared to determine if the two species had a detectable increase in feeding rates during the afternoon, as reported in other herbivorous species. Morning values were based on the mean feeding rate (bites per 5 min) between 07.00 and 11.00 hrs, whilst afternoon values were based on samples between 13.30 and 17.30 hrs. These time periods were chosen to obtain two relatively independent, equal-sized time periods to represent "morning" and "afternoon" feeding periods, which did not include the "turn-on/turn-off" events at the beginning/end of each day.

Erosion rates

Erosion rates were calculated as follows: mean daily erosion rate ($\text{m}^3 \text{d}^{-1}$) = estimated mean daily bite rate (bites day^{-1}) \times mean bite volume (m^3).

Annual rates were calculated by multiplying the result by 365. Erosion rates in kg were estimated by multiplying the result by the estimated substratum density.

Overall means and error terms were calculated using Goodman's estimator following Travis (1982) and an expanded three-term version of Goodman's estimator as follows:

$$\begin{aligned} SE_{(\bar{x} \cdot \bar{y} \cdot \bar{z})}^2 &= (\bar{x} \cdot \bar{y})^2 \cdot SE_z^2 + (\bar{x} \cdot \bar{z})^2 \cdot SE_y^2 + (\bar{y} \cdot \bar{z})^2 \cdot SE_x^2 \\ &+ (\bar{x})^2 \cdot SE_y^2 \cdot SE_z^2 + (\bar{y})^2 \cdot SE_x^2 \cdot SE_z^2 + (\bar{z})^2 \cdot SE_x^2 \cdot SE_y^2 \\ &+ SE_x^2 \cdot SE_y^2 \cdot SE_z^2, \end{aligned}$$

where \bar{x} = mean bites per day, \bar{y} = mean bite volume, and \bar{z} = mean substratum density.

Prior to analysis by ANOVA, homogeneity and normality of variances was tested using Bartlett's test, Cochran's test or Wilk-Shapiro statistics. Heteroscedastic data was \log^{10} or arcsine-transformed prior to retesting and analysis. Consistently heteroscedastic data were analysed, using nonparametric procedures of Zar (1974).

Results

The results are presented in three sections: (a) behavioural observations, (b) feeding rates, and (c) estimates of erosion.

Behavioural observations

Dawn/dusk behavioural patterns and the initiation/cessation of feeding

Chlorurus gibbus. Shortly after sunrise, adult *C. gibbus* slowly migrated from the extreme tip of North Reef to the daily feeding sites. Movement was in groups of 3 to 15 individuals, occasionally accompanied by groups of *Scarus altipinnis* and *S. rivulatus*. These morning migrations appeared to cover distances from 300 to at least 600 m.

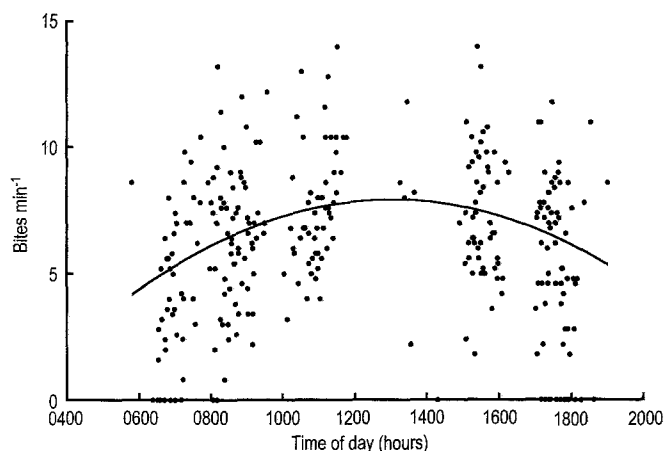


Fig. 2 *Chlorurus gibbus*. Diurnal changes in feeding rates. Each data point represents bite rate based on 5 min observation period. Data are pooled from both study locations and at both seasons (14 d), with quadratic line fitted to pooled data

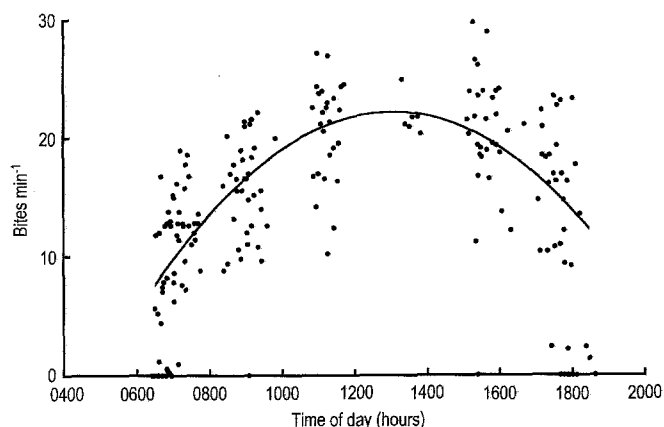


Fig. 3 *Chlorurus sordidus*. Diurnal changes in feeding rates. Each data point represents bite rate based on 5 min observation period. Data are pooled from both study locations during summer period (10 d), with quadratic line fitted to pooled data

Once in the feeding areas the fish usually circled off the reef slope, with occasional forays up on to the reef flat. Initiation of feeding occurred 36 to 51 min after sunrise, usually on one of the forays onto the reef flat. Initiation of feeding was a rapid "switch-on" event, with initial feeding rates usually being within 50% of the maximum recorded during the remainder of the day.

At dusk, feeding continued until ~20 to 70 min before sunset. Cessation of feeding was rapid. Individuals which stopped feeding early usually moved off the reef flat and "hung" over the reef crest or in gullies in the reef front. Here they remained defaecating for up to 25 min before slowly moving down the reef, in a reverse of the morning migration (Fig. 2). Individuals which continued to feed until later usually stopped feeding abruptly and swam off rapidly, towards the point of North Reef.

This daily migration along the reef was observed during both the summer (December–January) and winter

(July) periods. It did not appear to be associated with reproductive behaviour. Several individuals were followed past the point of North Reef, where they swam off into deeper water (>12 m) away from the reef.

Chlorurus sordidus. The daily behaviour of *C. sordidus* was very similar to that of *C. gibbus*, although there appeared to be no daily migration. Individuals rose from sleeping sites off the reef slope and in gullies 40 min after sunrise. They remained in the immediate vicinity for a few minutes before moving off to the feeding areas. Once in the feeding area, feeding commenced almost immediately and at a relatively high rate. At dusk this process was reversed. The fish stop feeding abruptly and swam off the feeding areas towards the reef slope or into large gullies in the reef. Here they milled around in small groups before diving into shelter to sleep.

Timing of feeding initiation and cessation

The times of initiation and cessation of feeding, and feeding duration in the two species are summarized in Figs. 2 and 3; summary statistics and analyses are given in Table 1. Overall, the two species had very similar feeding times, with distinct seasonal changes in feeding duration. Both species had a shorter feeding day in winter than in summer, despite an increase in the proportion of the day spent feeding. In winter, the time from sunrise to first feeding and from the last bite to sunset decreased in both species, but this did not offset the impact of a shorter day length. Estimates of erosion rates therefore must be seasonally adjusted.

No significant site-effects were detected for any of the four measurements (Table 2), although the probability values suggest that there may have been some site effects.

Feeding rates

Total daily feeding rates

The feeding rates of *Chlorurus sordidus* were consistently higher than those of *C. gibbus* (cf. Figs. 2, 3, 4, 5), resulting in a larger mean daily feeding rate (Table 3). No significant site effect was detected (Table 3). There was, however, a significant species \times season interaction (Table 3). *C. sordidus* showed a marked decrease in feeding rates in winter, whereas *C. gibbus* displayed only a marginal decrease (Table 3; see also Fig. 5).

Morning vs afternoon

Morning and afternoon feeding rates of the two study species were compared to address the question of daily feeding patterns. In particular, to examine the reported increase in foraging rates in the afternoon, as suggested in other studies of herbivorous reef fishes (e.g. Polunin and Klumpp 1989). To maintain adequate sample sizes and to avoid

Table 1 *Chlorurus gibbus* and *C. sordidus*. Effect of season on length of feeding day. All data based on North Reef Site A ($n=5$ for each season) (*CI* confidence interval; *MS* mean square; * $p < 0.05$)

Mean values ($\pm 95\%$ CI)	<i>C. gibbus</i>		<i>C. sordidus</i>	
	summer	winter	summer	winter
% day feeding	83.6 \pm 7.7	90.1 \pm 2.4	88.3 \pm 2.4	91.0 \pm 1.6
sunrise to 1st bite (min)	51.2 \pm 9.6	36.5 \pm 14.4	51.0 \pm 9.8	36.0 \pm 7.8
last bite to sunset (min)	74.2 \pm 61.5	25.3 \pm 5.4	40.8 \pm 12.52	23.3 \pm 25.3
feeding day length (min)	650.8 \pm 60.8	611.5 \pm 15.1	687.4 \pm 19.3	617.8 \pm 9.8

Analyses: two-way ANOVA					
	Effect	MS	df	F	p
% day feeding ^a	species	0.0080	1, 14	3.51	0.082
	season	0.0239		10.55	0.006*
	spp. \times season	0.0030		1.33	0.268
sunrise to 1st bite (min)	species	0.0613	1, 14	0.01	0.924
	season	1102.6		17.04	0.001*
	spp. \times season	0.1125		0.00	0.967
last bite to sunset (min) ^b	species	0.1390	1, 14	3.29	0.091
	season	0.677		16.02	0.001*
	spp. \times season	0.0105		0.25	0.626
feeding day length (min) ^c	species	c	1	1.86	0.172
	season			6.35	0.012*
	spp. \times season			0.28	0.097

^a Arcsine-transformed prior to analysis

^b Log¹⁰-transformed prior to analysis

^c Analysis based on balanced nonparametric ANOVA [Values are Kruskal-Wallis test statistics, *H* (Zar 1974)]

Table 2 *Chlorurus gibbus* and *C. sordidus*. Effect of location on length of feeding day

Mean values ($\pm 95\%$ CI)	<i>C. gibbus</i>		<i>C. sordidus</i>	
	Site A	Site B	Site A	Site B
% day feeding	83.6 \pm 7.7	82.9 \pm 9.3	88.3 \pm 2.4	87.1 \pm 4.6
sunrise to 1st bite (min)	51.2 \pm 9.6	75.2 \pm 23.6	51.0 \pm 9.8	57.0 \pm 29.7
last bite to sunset (min)	74.2 \pm 61.5	45.8 \pm 30.0	40.8 \pm 12.5	44.2 \pm 17.9
feeding day length (min)	650.8 \pm 60.8	637.6 \pm 67.2	687.4 \pm 19.3	678.4 \pm 37.00

Analyses					
	Effect	MS	df	F	p
% day feeding	species	123.65	1, 16	4.79	0.044*
	location	10.24		0.40	0.054
	spp. \times location	0.36		0.01	0.907
sunrise to 1st bite (min)	species	423.20	1, 16	1.60	0.224
	location	1125.00		4.26	0.056
	spp. \times location	405.00		1.53	0.233
last bite to sunset (min)	species	1531.25	1, 16	1.83	0.195
	location	781.25		0.93	0.349
	spp. \times location	1264.05		1.51	0.237
feeding day length (min) ^a	species		1, 16	5.49	0.019*
	location			0.24	0.623
	spp. \times location			0.001	0.970

^a Analysis based on balanced nonparametric ANOVA (cf. Zar 1974; *H* values given)

problems with individual variation in times of feeding initiation and cessation, morning samples were based on observations between 07.00 and 11.00 hrs and afternoon samples between 13.30 and 17.30 hrs. The results were analysed using two three-way ANOVAs to examine the effect of location and season separately. Overall, the two species

displayed consistently higher feeding rates in the afternoon, with *Chlorurus sordidus* showing greater changes than *C. gibbus*. The effect of location and season on daily feeding rates are examined separately below.

Location effects are summarized in Fig. 4, and the analyses in Table 4. In both species, afternoon feeding rates

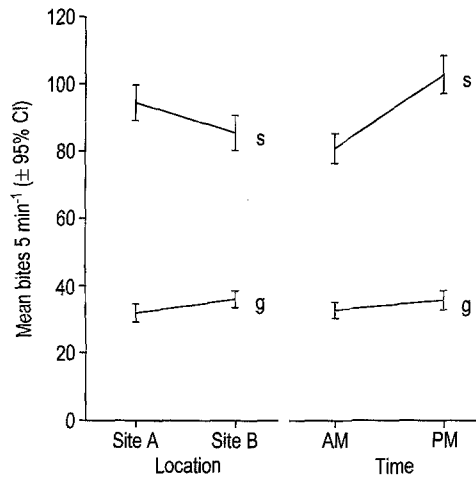


Fig. 4 *Chlorurus gibbus* (g) and *C. sordidus* (s). Effect of location on feeding rates; observations based on summer data only (AM morning; PM afternoon). Analyses in Table 4

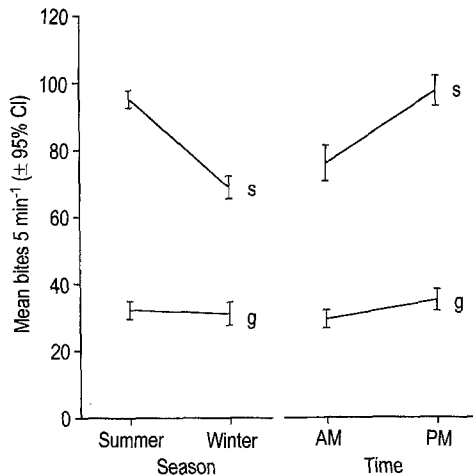


Fig. 5 *Chlorurus gibbus* (g) and *C. sordidus* (s). Effect of season on feeding rates; observations based on Site A data only. Analyses in Table 4

were higher than those in the morning, although this difference was much greater in *Chlorurus sordidus* than in *C. gibbus* (Fig. 4), giving a significant species \times time interaction (Table 4). In addition, there was a significant species \times location interaction, which may be explained by *C. sordidus* having markedly higher feeding rates at Site A than at Site B, whilst *C. gibbus* had marginally higher feeding rates at Site B than at Site A (Fig. 4).

Seasonal effects are summarized in Fig. 5, and the analyses in Table 4. There was a significant time-of-day effect, with both species having a higher feeding rate in the afternoon (Fig. 5). There was no interaction effect with species or season, indicating that this increase was comparable in both species during the summer and winter sampling periods. Season did, however, have a significant interaction with species, as noted above in the analyses of daily feeding rates.

Table 3 *Chlorurus gibbus* and *C. sordidus*. Total daily feeding rates

Mean bites per day \pm 95% CI

Species	Site B		Site A	
	summer (n=5)		summer (n=5)	winter (n=4)
<i>C. gibbus</i>	4,762 \pm 405.6		4,287 \pm 1,001.6	4,171 \pm 1,005.4
<i>C. sordidus</i>	12,575 \pm 2425.9		13,600 \pm 844.8	10,300 \pm 1,344.5

Site effects: two-way ANOVA effect species+location; variable bites per day (for each location $n=5$)

Effect	MS	F	df	p
species	3.66 10^8	290.9	1, 16	< 0.0001*
location	3.75 10^5	0.3	1, 16	0.5928
spp. \times location	2.81 10^6	2.23	1, 16	0.1547

Season effects: two-way ANOVA species+season; variable bites per day (summer $n=5$, winter $n=4$)

Effect	MS	F	df	p
species	2.98 10^8	584.2	1, 14	< 0.0001*
season	1.45 10^7	28.5	1, 14	0.0001*
spp. \times season	1.26 10^7	24.7	1, 14	0.0002*

Table 4 *Chlorurus gibbus* and *C. sordidus*. Daily feeding-rate patterns

Location effects: three-way ANOVA with factors species (*C. gibbus*/*C. sordidus*), location (Site A/Site B) and time (morning/afternoon); for all $df=1, 416$

Effect	MS	F	p
species	34.32 10^4	819.76	0.0001
location	716.61	1.71	0.1915
time	16.42 10^3	39.21	0.0001*
spp. \times location	42.32 10^2	10.11	0.0016*
spp. \times time	95.38 10^2	22.78	0.0001*
location \times time	169.35	0.40	0.5251
spp. \times location \times time	4.44	0.01	0.9180

Seasonal effects: three-way ANOVA with factors species (*C. gibbus*/*C. sordidus*), season (summer/winter) and time (morning/afternoon); for all $df=1, 559$

Effect	MS	F	p
species	24.58 10^4	243.85	0.0001*
season	98.45 10^3	97.66	0.0001*
time	49.39 10^2	4.90	0.0273*
spp. \times season	57.53 10^3	57.07	0.0001*
spp. \times time	12.56 10^2	1.25	0.2647
season \times time	6.47	0.01	0.9363
spp. \times season \times time	16.11 10^2	1.60	0.2067

Erosion rates

Bite volumes

The mean areas and volumes of bites by the two species at the two sites are summarized in Table 5 together with statistical analyses. Significant site effects were only detected

Table 5 *Chlorurus gibbus* and *C. sordidus*. Effect of sites on estimated bite areas and volumes based on direct linear measurements

Mean values \pm 95% CI (n)			
	<i>C. gibbus</i>	<i>C. sordidus</i>	
Bite area (mm ²)			
Site A	194.27 \pm 28.56 (54)	23.04 \pm 1.99 (65)	
Site B	145.25 \pm 20.78 (53)	20.77 \pm 2.08 (59)	
Pooled	169.99 \pm 18.05 (107)	21.60 \pm 1.08 (124)	
Bite vol. (mm ³) ^a			
Site A	296.78 \pm 59.3 (54)	2.25 \pm 0.19 (65)	
Site B	213.73 \pm 52.6 (53)	2.05 \pm 0.21 (59)	
Pooled	256.04 \pm 42.89 (107)	2.20 \pm 0.14 (124)	

Analyses: Student's two-sample *t*-tests examining effect of location (Site A or B) on area/volume estimates

Species	<i>t</i>	<i>df</i>	<i>p</i>
<i>C. gibbus</i>			
area	2.78	96.4 ^b	0.0064*
vol.	2.25	104	0.0268*
<i>C. sordidus</i>			
area	1.58	122	0.1178
vol.	1.52	122	0.1323

^a In the calculations *C. sordidus* scar depths were estimated to be 0.1 mm

^b *df* corrected for heteroskedasticity

in *Chlorurus gibbus*. The smaller bite sizes at Site B were probably a result of the harder substratum and/or a smaller mean fish size.

It was not possible to estimate the depth of many *Chlorurus sordidus* bites with accuracy, as many were < 0.1 mm. A depth value of 0.1 mm was therefore used to permit a volume estimate for further calculations. This has probably resulted in an overestimate of the volume removed.

The accuracy of the volume estimates was supported by the wax impression technique. A total of 11 scars were examined, comparing the volume estimated using linear measurements (mean volume in cm³ = 0.3567 \pm 0.0361 SE) with those derived from wax casts of the scars (mean volume in cm³ = 0.3735 \pm 0.0400 SE). The means suggest that the linear technique may underestimate the volume removed; however, there was no significant difference between the two methods (paired Student's *t*-test: *df*=10, *t*=-1.34, *p*=0.2111).

Substratum density

The estimated density of the outer 3 mm of the grazed substratum was 2.44 g cm⁻³ (\pm 0.067 SE; *n*=22). This was significantly heavier (paired *t*-test, *t*=4.3257, *p*<0.001) than the material as a whole, which had a density of 2.261 g cm⁻³ (\pm 0.034 SE; *n*=22).

Erosion rates

The values calculated above permit the rates of erosion by the two species to be calculated. In both cases, seasonally

Table 6 *Chlorurus gibbus* and *C. sordidus*. Seasonally adjusted bite rates

Species	(n)	kbytes yr ⁻¹ , mean (SE)
<i>C. gibbus</i>	(14)	1615 (61)
<i>C. sordidus</i>	(8)	4396 (253)

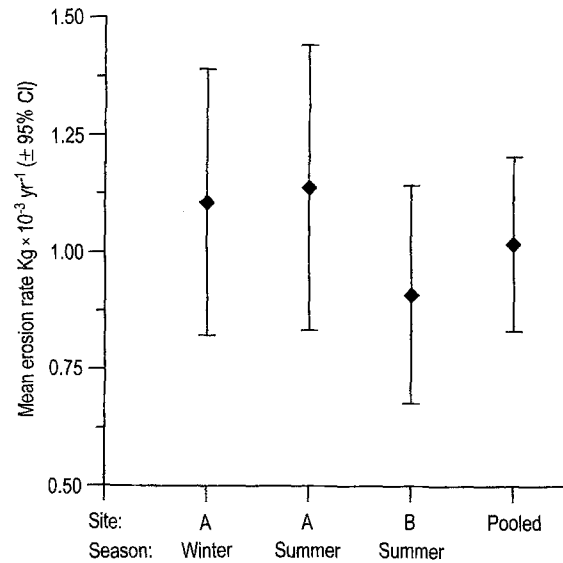


Fig. 6 *Chlorurus gibbus*. Annual bioerosion rates per individual, showing effect of location and season on estimated rates. Bite volumes were determined only in summer. Feeding rates and bite volumes are site- and season-specific. Pooled value is based on seasonally adjusted bite rates (Table 6) and pooled bite volumes (Table 5). Substratum density was taken as 2.44 g cm⁻³ (\pm 0.067 SE) and annual values were estimated by multiplying daily rates by 365. Overall CI values are based on two times total SE value calculated using three-term Goodman equation given in "Materials and methods – Erosion rates"

adjusted bite rates were used. For *Chlorurus gibbus*, all 14 daily bite-rate estimates were pooled as there were no marked differences in daily rates with location or season (Table 3). However, in *C. sordidus* feeding rates appeared to differ significantly with location and season (Table 3). Seasonally adjusted data were therefore based on values from Site A only, incorporating the four winter values and four of the five summer values (chosen at random). The seasonally adjusted annual feeding rate is based on the mean daily feeding rate of these 8 d multiplied by 365, to give an overall estimate of the annual feeding rate. These seasonally adjusted values are given in Table 6.

Estimated mean erosion rates by individuals of the two species are summarized in Figs. 6 and 7. Both species had marginally lower mean erosion rates at Site B, which is a reflection of the site difference in bite volumes (Table 5). As in individual parameters, the overall estimates of annual erosion by *Chlorurus sordidus* varied strongly in relation to site and seasonal effects. In comparison, *C. gibbus* had a relatively consistent erosion rate.

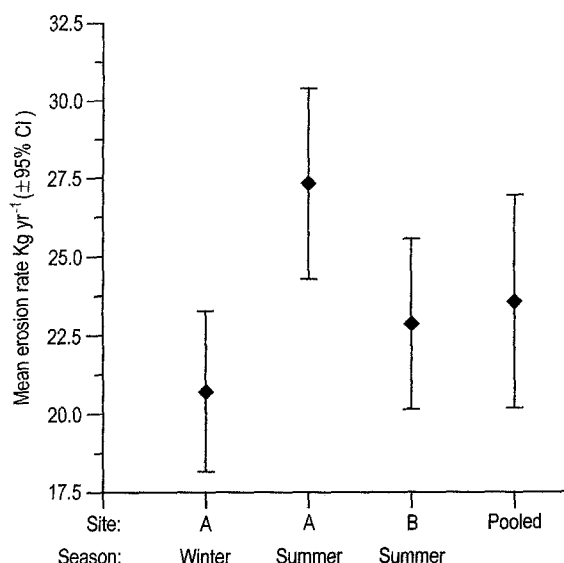


Fig. 7 *Chlorurus sordidus*. Annual bioerosion rates per individual, showing effect of location and season on estimated rates. Calculations follow procedures outlined in legend to Fig. 6

Table 7 *Chlorurus gibbus* and *C. sordidus*. Total annual erosion rates per individual (*ind*) based on pooled bite volumes (Table 5) and seasonally adjusted bite rates (Table 6). Substratum density was taken as 2.44 g cm^{-3} ($\pm 0.067 \text{ SE}$). Overall CI values based on twice the total SE value calculated using three-term Goodman equation given in "Materials and methods – Erosion rates"

	Mean	95% CI
<i>C. gibbus</i>		
Volume ($\text{m}^{-3} \text{ ind}^{-1} \text{ yr}^{-1}$)	0.413	± 0.068
Mass ($\text{kg ind}^{-1} \text{ yr}^{-1}$)	1017.66	186.34
<i>C. sordidus</i>		
Volume ($\text{m}^{-3} \text{ ind}^{-1} \text{ yr}^{-1}$)	$9.65 \cdot 10^{-3}$	$\pm 1.28 \cdot 10^{-3}$
Mass ($\text{kg ind}^{-1} \text{ yr}^{-1}$)	23.58	3.39

The most striking feature from these data, is the large difference between the two species. Despite the high feeding rates of *Chlorurus sordidus*, *C. gibbus* still removed 43 times more material per individual per year. The size of the bite in *C. gibbus* far outweighed its lower feeding rate. This undoubtedly reflects the much larger size of *C. gibbus* (350 to 440 mm SL) compared to *C. sordidus* (150 to 200 mm SL). The annual erosion rates of the two species in terms of volume and mass are summarized in Table 7.

Discussion

The results of this study on *Chlorurus gibbus* and *C. sordidus* provide the first direct estimate of rates of bioerosion by parrotfishes on the Great Barrier Reef. They emphasise the extent to which erosion rates will be dependent upon the activities of a limited number of species, and pro-

vide a basis for examining these activities in some detail. The results will be discussed in three sections, examining overall erosion rates, sources of variation and methodological considerations.

Relative importance of scarid erosion and regional comparisons

If the erosion rates from the present study are multiplied by scarid abundances, one is able to obtain an estimate of the relative importance of scarid erosion on the GBR. Such calculations suggest that erosion rates by scarids are higher in the Indo-Pacific than in the Caribbean, and provide an explanation for the high rates of variability between sites suggested in previous studies (e.g. Bellwood 1986; Kiene 1985).

Estimates of the erosion rates by scarids are summarized in Table 8. This clearly demonstrates the disparity between Caribbean and Indo-Pacific reefs. In the Caribbean, scarid bioerosion is largely restricted to one species: *Sparisoma viride*. Estimates of erosion by other species such as *Scarus iserti* (Ogden 1977) are probably erroneous, as Caribbean *Scarus* species are functionally "scrapers" sensu Bellwood and Choat (1990) and Bellwood (1994) and are primarily recycling sediment with negligible erosion (Frydl and Stearn 1978).

Even if one allows for overfishing in the Caribbean by using scarid abundance data from the unexploited reefs of Belize (Lewis and Wainwright 1985), scarid erosion rates in the Caribbean are still much lower than the Indo-Pacific estimates (Table 8).

The reasons for the differences appear to be partially historical. The Caribbean has only one significant bioeroding species, *Sparisoma viride*. In contrast, the Indo-Pacific has 16 bioeroding species in three genera (*Bolbometopon*, *Cetoscarus*, *Chlorurus*). These species are widespread and relatively abundant.

The analyses of Bellwood (1994) suggest that the present Caribbean scarid fauna may have been determined largely by the history of the area. It was suggested by Bellwood that reef fish taxa in the Caribbean have a stronger affinity with seagrasses and other non-reef environments than their Indo-Pacific counterparts, possibly as a result of an extensive loss of shallow-water coral communities during the Pleistocene glaciations.

There is a strong possibility that bioeroding scarid species were lost from the Caribbean during this period. The presence of a fossil *Naso* (*N. deani*) in the Caribbean (Tyler 1970), a taxon that is now restricted to the Indo-Pacific, emphasises the fact that reef-fish taxa have been lost from the Caribbean.

The overall result appears to indicate a significant difference in the relative importance of scarids as bioeroders in the two regions. This can be placed in perspective by comparing bioerosion rates by various taxonomic groups in the two regions (Table 9). Details of the various taxa have been discussed by Hutchings (1986).

Although variability in the estimates and the diversity of techniques make comparisons tenuous, it is clearly ap-

Table 8 Summary of estimates of bioerosion rates by scarids at various geographic localities

Species	Rate (kg m ⁻² yr ⁻¹)	Location	Source
<i>Sparisoma viride</i>	0.034	Barbados, Caribbean	Scoffin et al. (1980)
<i>S. viride</i>	0.035	Bermuda, Caribbean	Gygi (1969)
<i>S. viride</i>	0.036	Barbados, Caribbean	Stearn and Scoffin (1977)
<i>S. viride</i>	0.04–0.168	Barbados, Caribbean	Frydl and Stearn (1978)
Scarids – indirect estimate	0.02	St. Croix, Caribbean	Hubbard et al. (1990)
<i>S. viride</i>	0.209	Bermuda, Caribbean	Gygi (1975)
<i>S. viride</i>	0.381	Caribbean	Max. estimate ^a
<i>Scarus iserti</i>	0.490	Panamá, Caribbean	Ogden (1977)
<i>Chlorurus</i> spp.	0.925–5.576	Lizard Island, GBR	(Choat and Bellwood 1985) ^b
<i>Chlorurus</i> spp.	1.990–3.538	Heron Island, GBR	(Choat and Robertson 1975) ^c
Scarids – indirect estimate	0.0–9.11	southern GBR	Kiene (1989)

^a Maximum estimate based on erosion data of Gygi (1975) and maximum estimated fish abundances of Lewis and Wainwright (1985)

^b Calculated using abundance data from Choat and Bellwood (1985)

^c Calculated using abundance data from Choat and Robertson (1975)

Table 9 Bioerosion of coral reef substrata. Taxonomic and regional comparisons. Details of individual erosion rates are given in Trudgill (1983) and Wilkinson (1983), with an overview in Hutchings (1986). As noted by Bak (1990), high erosion rates by echinoids in both Caribbean and Indo-Pacific may be partially due to studies being based in areas with unusually high echinoid numbers as a result of regional anthropogenic stress (overfishing)

Group	Rate (kg m ⁻² yr ⁻¹)	Location	Source
Grazers			
<i>Diadema antillarum</i>	4.6	Caribbean	Ogden (1977)
<i>D. antillarum</i>	9.0	Caribbean	Scoffin et al. (1980)
<i>D. antillarum</i>	8.4–15.1	Caribbean	Stearn and Scoffin (1977)
<i>Echinometra lucunter</i>	3.9	Caribbean	Ogden (1977)
Echinoids	0.081–0.325	Enewetak	Russo (1980)
Echinoids	4.5	Moorea	Bak (1990)
Borers			
All borers	2.31	Caribbean	Scoffin et al. (1980)
Sponges	0.190–3.29	Caribbean	Moore and Shedd (1977)
Sponges	0.25–0.30	Caribbean	Rützler (1975)
Polychaetes	0.69–1.79	Great Barrier Reef	Davies and Hutchings (1983)

parent that in the Caribbean the maximum estimated erosion rates by scarids (0.381 kg m⁻² yr⁻¹) are but a fraction of estimates of erosion by borers (2.31 to 3.29) or echinoid grazers (3.9 to 15.1 kg m⁻² yr⁻¹).

In contrast, in the Indo-Pacific scarids, erosion rates (0.925 to 5.576 kg m⁻² yr⁻¹) are comparable to, or greater than, estimates of erosion by other groups such as echinoids (0.325 to 4.5 kg m⁻² yr⁻¹) and boring polychaetes (1.79 to 4.816 kg m⁻² yr⁻¹). Given estimates of coral production rates of 0.3 to 12 kg m⁻² yr⁻¹ (Smith 1983), it is possible that in some areas erosion by scarids may equal or even exceed calcification rates.

However, these comparisons must be made with extreme caution. All estimates have significant error terms. In most cases these are unknown, as is the accuracy of many of the estimating techniques. More importantly, all evidence points to a great deal of spatial variability. Rigorous comparisons must await detailed analyses that consider both spatial and methodological sources of variation.

Species comparisons and sources of variability

Bellwood and Choat (1990) suggested that bioerosion by scarids was probably restricted to a distinctive suite of spe-

cies. These were identified as the “excavating” forms. The present study has demonstrated that within this group of bioeroding species erosion rates may also vary greatly, with one species, *Chlorurus gibbus*, making a disproportionately large contribution to total erosion rates at the sites examined (Table 10).

An individual *Chlorurus gibbus* removes ≈27 times as much material per year than an individual of the smaller *C. sordidus*. Total erosion rates, therefore, will be largely determined by the relative abundance of these two species, with the abundance and feeding patterns of *C. gibbus*, in particular, being of critical importance in determining the rate of erosion at a range of spatial scales.

Bellwood and Choat (1990) indicated that eroding species feed predominantly on convex surfaces. These surfaces will therefore be exposed to disproportionately high erosion rates. This may account for the decrease in topographic complexity in heavily grazed areas reported by Miller (1982). The overall topographic complexity however is probably dependent upon a wide range of factors, including coral growth and turnover rates, herbivore population structure, and bioerosion rates.

The spatial patterns of erosion and sediment release will be considered elsewhere (Bellwood 1995). However, from data currently available, it is clear that bioerosion by scar-

Table 10 *Chlorurus gibbus* and *C. sordidus*. Relative erosion rates ($\text{kg m}^{-2} \text{yr}^{-1}$) by populations on Great Barrier Reef. Lizard Island abundance data were taken from Choat and Bellwood (1985) and Heron Island abundance data from Choat and Robertson (1975)

Species	Lizard Island		Heron Island	
	Site A	Site B	Site A	Site B
<i>C. gibbus</i>	5.47	0.42	3.28	1.01
<i>C. sordidus</i>	0.11	0.50	0.26	0.98
Total	5.58	0.92	3.54	1.99

ids in the Indo-Pacific will be associated with the distribution patterns of a limited number of species and, on a smaller spatial scale, will be determined largely by the feeding behaviour of these species.

The data herein suggest that individual scarid bioerosion rates will vary little with season and have limited small-scale site effects. The two species differed little in their response to site at the scale examined, and had similar feeding patterns in terms of feeding-day length, morning/afternoon comparisons etc. The major differences between the two species is in terms of feeding rate and bite size, which appear to be directly attributable to their relative sizes (*Chlorurus gibbus* 350 to 440 mm SL; *C. sordidus* 150 to 200 mm SL). The larger *C. gibbus* had larger bites and a lower bite rate. Size may also account for the degree to which the two species respond to site and season effects, with the smaller species, *C. sordidus*, showing the strongest changes. Despite overall similarities, behavioural characteristics of the two species within sites in terms of reef-zone and microhabitat-utilization patterns appear to differ markedly (personal observations of DRB). These differences may have important implications for small-scale patterns of erosion (Bellwood 1995).

Methodological considerations

The present study provides the first direct quantitative estimate of erosion by parrotfishes in the Indo-Pacific. It also provides an estimate of total variance.

Previous studies of bioerosion by scarids have produced mean erosion rates either without estimates of variance (e.g. Gygi 1975; Stearn and Scoffin 1977; Frydl and Stearn 1978), with estimates of variance which reflect only a single source of variance (Scoffin et al. 1980; where error terms reflect the variance in daily throughput rates), or variance based on experimental substrata (e.g. *Porites* sp. slabs; Kiene 1989).

In addition, most of the previous studies only provided an indirect estimate of scarid erosion, measuring sediment production and correcting for reworked sediment. Some are probably erroneous, as the extent of reworking is frequently unknown. A few studies have considered site effects, but only Gygi (1975) considered seasonal effects. Gygi, however, did not include the factor season in his calculations.

In comparison to previous studies, the present study permits a more detailed appraisal of erosion by scarids. Accuracy is enhanced by avoiding problems of estimating reworking and throughput rates. Individual erosion rates are based on only three variables (bite rate, bite volume, substratum density). This permits a direct estimate of erosion rates to be made with all major sources of variance taken into account.

The results show the limitations of estimates which are based on the product of several variables. Large confidence intervals are an inherent problem of such procedures. Large sample sizes and comprehensive surveys are therefore essential. However, once the main sources of variation have been identified and taken into account, one is in a strong position to critically examine fundamental processes such as bioerosion on coral reefs.

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