

# Direct versus indirect methods of quantifying herbivore grazing impact on a coral reef

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**Abstract** Two methods were used to assess the grazing impact of roving herbivorous fishes across a coral reef depth gradient within Pioneer Bay, Orpheus Island, Great Barrier Reef. The first technique employed was a method traditionally used to quantify herbivory on coral reefs via the (indirect) inference of herbivore impact from biomass estimates and reported feeding rates. The second method (one of a range of direct approaches) used remote underwater video cameras to film the daily feeding activity of roving herbivores in the absence of divers. Both techniques recorded similar patterns and relative levels of herbivore biomass across five reef zones at the study site. Indirect estimates of the grazing impact across the reef depth gradient of the three predominant species of herbivore broadly coincided with levels quantified directly by remote underwater video, indicating that, to a large extent, presence does correspond to function. However, the video data suggested that, for individual species in particular reef zones, the absolute level of impact may be less than that inferred from presence. In the case of the parrotfish *Scarus rivulatus*, the video recordings suggested that, at the reef

crest, an average of 52% ( $\pm 18$  SE) of each m<sup>2</sup> area of reef would be grazed each month, compared with an area of 109% ( $\pm 41$  SE) suggested by inferring grazing activity from presence alone. Potential biases associated with remote video recorders may explain some of the discrepancy between values. Overall, the results suggest that, for some fish groups, the indirect method of inferring function from presence can provide a good indication of relative levels of herbivore impact across a coral reef.

## Introduction

Much of our understanding of marine ecosystems and the processes that support them are founded on data collected via diver-based underwater visual censuses (UVC). Many studies have highlighted sources of bias that have the potential to affect the accuracy and precision of results obtained via diver censuses (e.g. Brock 1982; Sale and Sharp 1983; Bell et al. 1985; Lincoln-Smith 1988; Thompson and Mapstone 1997; Edgar et al. 2004). Acknowledgement of the limitations of UVCs has led to an examination of the relative merits of alternative methods of quantifying variables within marine ecosystems (e.g. Green and Alevison 1989; Harvey et al. 2001a, b; Tessier et al. 2005), including the use of remote video recorders (Willis and Babcock 2000; Willis et al. 2000; Cappo et al. 2004; Harvey et al. 2004).

Studies examining the relative accuracy and precision of alternative methods have, in all cases, been based on their relative abilities to estimate basic population parameters such as abundance, biomass or species richness (e.g. Davis and Anderson 1989; Schmitt et al. 2002; Watson et al. 2005). However, accurate estimation of the abundance of

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individual species within an ecosystem is only one part of the picture. Management of marine ecosystems also depends on a quantitative understanding of the function of these species in regard to ecosystem processes. For example, it is important to know where they feed, what they feed on and how much they ingest. A neglected area in methodological comparisons has been in assessing the relative ability of methods to quantify the ecosystem function of a particular species or trophic guild.

On coral reefs, herbivorous fishes play a key role in controlling the standing crop of algae (Hatcher and Larkum 1983; Klumpp and McKinnon 1989; Russ 2003) and in determining patterns of benthic community succession (Hay 1981; Scott and Russ 1987; Hixon and Brostoff 1996). As such, the guild has been shown to be of primary importance in maintaining the balance between corals and algae on reefs (Hughes 1994; McClanahan et al. 2003) and in preventing or reversing phase shifts from coral to algal-dominance (Bellwood et al. 2004, 2006; Hughes et al. 2007). The ecosystem function of herbivory on coral reefs is critical and underpins the importance of quantifying the functional impact of herbivorous fishes.

Traditionally, studies aimed at quantifying the grazing impact of roving herbivores have adopted one of two methodological approaches. The first assumes that the location in which a fish is observed on the reef is where it exerts its functional impact, i.e. it infers function from presence (e.g. Bellwood 1995a; Bruggemann et al. 1996; Williams and Polunin 2001; Mumby et al. 2006; Hoey and Bellwood 2007). The abundance of individuals recorded on the reef via underwater visual census is multiplied by a variable which stands for the impact of an individual of that species, giving an estimate of the population-level impact. The traditional alternative to this indirect method of inferring function from presence has been to quantify herbivory in terms of direct observation of bites per unit area by divers (e.g. Klumpp and Polunin 1989; Polunin and Klumpp 1992).

The goal of the present study is to extend the current body of literature comparing the relative performance of marine sampling methods to the measurement of ecosystem function, by examining the extent to which our understanding of feeding by roving herbivorous fishes may be shaped by the choice of study methodology. We therefore compare measures of herbivore impact across an entire coral reef provided by traditional indirect methods with a measure that made use of remote underwater video cameras to record the daily feeding activity of roving herbivorous fishes at the whole reef scale. Specifically, the study addresses a single question: to what extent is the quantification of the ecosystem impact of roving herbivorous fishes dependent upon the methodology selected and to what extent does presence equate to function?

## Materials and methods

### Study site and species

All observations were undertaken between October 2005 and January 2006 at Pioneer Bay, Orpheus Island (18°35'S, 146°20'E), in the inner-shelf region of the Great Barrier Reef, Australia. The species of herbivore included in the study were roving herbivorous and “nominally” herbivorous (*sensu* Choat et al. 2002) fishes belonging to the families Labridae (scarids), Acanthuridae, Siganidae and Kyphosidae.

Two sites were used within Pioneer Bay, on the leeward side of the island. Here, the reef flat stretches approximately 150 m from the shoreline to the reef crest and down the reef slope to approximately 20 m. Within each site, the reef was divided into five zones, based on distinct changes in benthic community composition or water depth. The five zones were classified as inner reef flat, mid reef flat, outer reef flat, reef crest and reef slope.

### Sampling methods

Measures of herbivore grazing impact were collected via two contrasting methods. The first method used was one traditionally employed in previous literature examining the impact of herbivorous fishes on coral reefs and was based on the collection of abundance data via underwater visual censuses (timed swims) by divers on SCUBA. Abundance estimates were then multiplied by the grazing impact of an individual of the species. The second method of estimating herbivore feeding impact was a direct estimation method, making use of remote video cameras to film the in-situ feeding activity of herbivores in the absence of divers. A third method of direct estimation of herbivore grazing activity via stationary diver quadrat censuses of feeding activity was conducted, but was rejected as a reasonable comparative methodology based on the low numbers of bites recorded by the diver (see Supplemental Material). This third technique was therefore not included in subsequent methodological comparisons.

#### *Underwater visual censuses (timed swim transects)*

Abundance estimates in the presence of divers were collected using underwater visual censuses techniques (5-min timed swims following the methods of Bellwood and Wainwright (2001)). Within each reef zone, six replicate underwater visual census transects were conducted at each of the two sites (a total of  $2 \times 6 = 12$  replicates within each of the five reef zones). Abundance estimates used in the current study were taken from Fox and Bellwood (2007).

### Remote video recorders

A measure of herbivore abundance and bites taken in the absence of divers for a given area of reef was obtained using remotely deployed video cameras (Sony DCR-TRV950E with an Amphibico 950 underwater housing). Within each of the five reef zones, a 1 m<sup>2</sup> quadrat was placed at random on the reef substratum and a camera mounted on a weighted tripod positioned approximately 2 m from the quadrat. The camera was set to record for a few moments with the quadrat in place in order to provide a frame of reference when viewing the footage. The quadrat was then removed in order to minimise interference with feeding behaviour. Filming commenced at 08:00 h and was continuous until 17:00 h, to coincide with the main portion of the herbivore feeding day. The procedure was repeated for 3 days at each of the two sites (six replicates within each of the five reef zones, giving a total of 30 replicates). The variation in replicate survey numbers between the two methods reflected logistic constraints (time available to process video footage). Footage was replayed at the laboratory to record the species present and the number of bites taken by individual fish. Again, observations for particular species were recorded by size class.

### Calculation of herbivore impact

Estimates of the grazing impact of individual species of herbivore were calculated for each of the two methods. The biomass estimates obtained via both methods revealed that herbivore biomass at the study location was overwhelmingly dominated by three species: *Scarus rivulatus* Valenciennes, 1840, *Chlorurus microrhinos* (Bleeker 1854) and *Siganus doliatus* Cuvier, 1830. Estimates of grazing impact therefore focussed on these three species. In order to account for differences in grazing impact within a particular species by individuals of different sizes, separate impact variables were calculated for “small”, “medium” and “large” individuals and these three components were summed to give a total species-level impact incorporating population size-structure. This approach also allowed us to explicitly incorporate any size-frequency bias shown by a particular method into the measure of herbivore grazing impact. Individuals of the species *Sc. rivulatus* were grouped into categories of small (5–10 cm), medium (11–25 cm) and large (>25 cm). Individuals of the species *S. doliatus* were grouped into categories of small (5–10 cm), medium (11–20 cm) and large (>20 cm). Only one size class (>30 cm) of *C. microrhinos* was examined, as smaller individuals were seldom recorded.

### Impact inferred from presence recorded by underwater transects (timed swims)

The inferred daily impact of each species (area of reef grazed per m<sup>2</sup> per day in the case of the two scarid species, or volume of material removed per m<sup>2</sup> per day in the case of *S. doliatus*) was calculated as the product of:

$$\begin{aligned} &\text{mean abundance in visual census (m}^{-2}\text{)} \\ &\quad \times \text{mean daily bite rate (bites day}^{-1}\text{)} \\ &\quad \times \text{mean bite size (m}^{-2}\text{)} \end{aligned}$$

(values taken from Fox and Bellwood 2007).

The three individual size-class impacts for a particular species were summed to give an overall estimate of the daily population impact per unit area of that species, and monthly impact values were calculated by multiplying the daily result by 28. Compound error terms for each size class of the impact variables were calculated using an expanded three-term version of Goodman's estimator (following Bellwood 1995a). Again, individual size class errors were summed to give overall compound error terms for the species-level impact.

### Video estimates of herbivore impact

The remote video recordings of herbivore bites were used to provide direct estimates of herbivore impact for each of the three dominant species at the study site. The directly measured impact (area of reef grazed per m<sup>2</sup> per day, or volume of material removed per m<sup>2</sup> per day in the case of *S. doliatus*) of each size class of each species was calculated as the product of:

$$\begin{aligned} &\text{mean number of bites recorded (m}^{-2}\text{ day}^{-1}\text{)} \\ &\quad \times \text{mean bite size (m}^{-2}\text{)}, \end{aligned}$$

(mean bites sizes for individual species taken from Fox and Bellwood 2007). The three individual size-class impacts for a particular species were then summed to give an overall estimate of the daily population impact per unit area of that species, for each of the five reef zones. Monthly impact values were calculated by multiplying the daily result by 28. Compound error terms for each size class of the impact variables were calculated using Goodman's estimator of the variance of a product of the means of two independent random variables (modified from Travis 1982):

$$SE_{(x,y)}^2 = x^2 \cdot SE_y^2 + y^2 \cdot SE_x^2 + SE_x^2 \cdot SE_y^2$$

where  $x$  = mean bites m<sup>-2</sup> day<sup>-1</sup>,  $y$  = mean bite size.

Individual size class errors were summed to give overall compound error terms for the species-level impact (following Bruggemann et al. 1996).

## Data analysis

Herbivore abundance data collected by the two methods were standardised to a 1 m<sup>2</sup> unit and converted to biomass estimates using published length–weight relationships (Kulbicki et al. 2005). In both cases this involved taking the median size for each size-class. For each method individually, biomass estimates obtained across the reef gradient were compared using a two-way ANOVA (with site and zone as fixed factors). In all cases data were  $\log(x + 1)$  transformed to meet assumptions of normality and homoscedasticity. There was no effect of site on biomass for either the video (ANOVA,  $F_{(1,20)} = 0.01$ ,  $p = 0.923$ ) or UVC transect (ANOVA,  $F_{(1,50)} = 2.335$ ,  $p = 0.133$ ) methods and no significant interaction between factors, therefore data were pooled across the two sites and all subsequent comparisons conducted at the reef zone level. Similarly, there was no effect of site on the total number of bites recorded by the video (ANOVA, square-root transformed,  $F_{(1,110)} = 0.202$ ,  $p = 0.658$ ) method and no significant interaction between site and zone and therefore data were pooled across sites.

The absolute values of biomass estimates collected by the two methods were not directly comparable as units were not identical (value per unit area for underwater visual censuses and value per unit area per unit time for video recordings). Among-method comparisons were therefore made on the basis of the relative proportions of total herbivore biomass recorded within each reef zone by the two methods, using ANOVA, with zone and method as fixed factors. Data were square-root transformed to meet assumptions of normality and heteroscedasticity.

Relative frequencies of individual size classes of *Sc. rivulatus* and *S. doliatus* within overall abundance estimates observed via video and underwater census were compared using non-parametric Mann–Whitney U tests (transformed data were consistently non-normal and heteroscedastic). Since sample sizes were small, exact probabilities are reported.

## Results

### Herbivore presence and biomass

A total of 22 species of roving herbivore were observed across the two census methods (it should be noted that this includes only one *Acanthurus* sp.; *Acanthurus blochii*, *A. nigricauda*, *A. auranticavus*, *A. grammoptilus* and *A. xanthopterus* are all present in this area but they could not be consistently identified and therefore a conservative *Acanthurus* sp. was used). The video recorded a greater number of species than the diver UVCs (Table 1). Four

species, *Chlorurus bleekeri*, *Cetoscarus bicolor*, *Siganus canaliculatus* and *Kyphosus vaigiensis*, were only observed via remote video cameras. Two species, *Siganus corallinus* and *Scarus niger* were only observed during diver UVCs (Table 1). Of the 20 species recorded by the remote video cameras, only 14 were actually observed feeding. The six species noted as present but not observed feeding were: *K. vaigiensis*, *C. bicolor*, *C. bleekeri*, *Siganus lineatus*, *Siganus spinus* and *Naso unicornis* (Table 1).

Within a given reef zone, overall estimates of total roving herbivore biomass made by the remote video cameras and underwater visual censuses displayed similar patterns across the reef depth gradient (Table 2), with highest herbivore biomass recorded at the reef crest, falling off rapidly down the reef slope and across the reef flat (Fig. 1a). For both methods, the biomass recorded in each zone was overwhelmingly dominated by three species: *Sc. rivulatus*, *C. microrhinos* and *S. doliatus* (Fig. 1b). At the reef crest, these three species made up approximately 90% of the observed biomass (Fig. 1b).

The relative frequencies of individual size classes of *Sc. rivulatus* and *S. doliatus* observed via the two methods varied in just three respects (Fig. 2). For *Sc. rivulatus*, the video recorded a significantly higher proportion of individuals 5–10 cm in length than were censused during the timed swims (Mann–Whitney U,  $Z = -2.25$ ,  $p = 0.02$ ) and a lower proportion of individuals in the 10–15 cm size class than the visual census method (Mann–Whitney U,  $Z = -2.72$ ,  $p = 0.004$ ) (Fig. 2a). For *S. doliatus*, the only significant difference in observed relative frequencies of individual size classes was for the 15–20 cm size class, where the video recorded a higher relative proportion of individuals than did the underwater visual censuses (Mann–Whitney U,  $Z = -3.37$ ,  $p = 0.000$ ) (Fig. 2b).

### Measures of herbivore impact—comparison of video versus inferred estimates

For *Sc. rivulatus*, inferring function from presence tended to yield a larger estimate of species impact than that measured directly by remote video cameras (Fig. 3a). The video recordings suggested that, at the reef crest, an average of 52% ( $\pm 18$  SE) of each m<sup>2</sup> area of reef would be grazed each month, compared with the 109% ( $\pm 41$  SE) of each m<sup>2</sup> area of reef suggested by inferring grazing activity from presence alone. The impact of *Sc. rivulatus* inferred from presence was approximately twice the level recorded by videos in most reef zones (Fig. 3a). For the second scarid species (*C. microrhinos*), inferring function from presence also tended to give a larger estimate of species impact than that measured directly by remote video cameras (Fig. 3b). The main distinction between the two

**Table 1** Species of roving herbivore within Pioneer Bay, Orpheus Island, GBR recorded as (a) present and (b) feeding by the two methods used in the study, remote underwater video cameras (*Video*) and underwater visual census transects (*Timed swim*)

Family	Species	Species present		Species feeding	
		Video	Timed-swim	Video	
Acanthuridae	<i>Acanthurus</i> spp.	✓	✓	✓	
	<i>Naso unicornis</i>	✓	✓		
Kyphosidae	<i>Kyphosus vaigiensis</i>	✓			
Labridae (Scarids)	<i>Hipposcarus longiceps</i>	✓	✓	✓	
	<i>Cetoscarus bicolor</i>	✓			
	<i>Scarus altipinnis</i>	✓	✓	✓	
	<i>Scarus flavipectoralis</i>	✓	✓	✓	
	<i>Scarus ghobban</i>	✓	✓	✓	
	<i>Scarus niger</i>		✓		
	<i>Scarus rivulatus</i>	✓	✓	✓	
	<i>Scarus schlegeli</i>	✓	✓	✓	
	<i>Chlorurus bleekeri</i>	✓			
	<i>Chlorurus sordidus</i>	✓	✓	✓	
	<i>Chlorurus microrhinos</i>	✓	✓	✓	
	Siganidae	<i>Siganus canaliculatus</i>	✓		✓
		<i>Siganus corallinus</i>		✓	
<i>Siganus doliatus</i>		✓	✓	✓	
<i>Siganus lineatus</i>		✓	✓		
<i>Siganus puellus</i>		✓	✓	✓	
<i>Siganus punctatus</i>		✓	✓	✓	
<i>Siganus spinus</i>		✓	✓		
	<i>Siganus vulpinus</i>	✓	✓	✓	
Total		20	18	14	

Only the remote video cameras were used to directly record feeding activity

**Table 2** Results of two-way ANOVA comparing relative proportions of herbivore biomass recorded across reef zones (*Zone*) by two methods (*Method*) (underwater visual census (UVC) and remote video)

Source of variation	d.f.	MS	<i>F</i>	<i>p</i>
Method	1	0.011	0.601	0.440
Zone	4	1.260	67.241	<b>0.000*</b>
Method × Zone	4	0.003	0.165	0.953
Error	80	0.019		
Total	90			

Data were square-root transformed

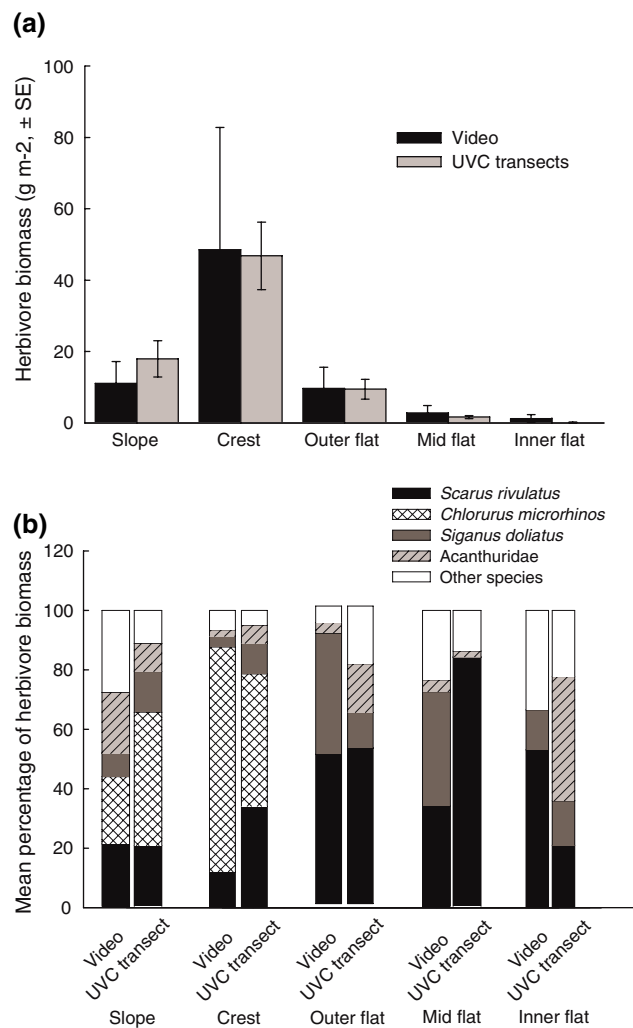
\* Significance at the 0.05 level

methods was on the reef slope where visual censuses suggested that, on average 14% ( $\pm 5.5$  SE) of each m<sup>2</sup> area of reef would be subject to bioerosion activity by *C. microrhinos* in a month, compared to the 1.8% of each m<sup>2</sup> area ( $\pm 0.7$  SE) measured via remote video camera.

In contrast, for the rabbitfish *S. doliatus*, inferring function from presence actually yielded lower estimates of species impact than was recorded by the remote video cameras at the outer and mid-reef flat (Fig. 3c), although at the reef slope and reef crest estimates of the impact of *S. doliatus* inferred from presence were, once again,

greater than those recorded by the video cameras (Fig. 3c).

It was suspected that the compound error terms were so large that the differences in estimated impact between the two methods would be unlikely to be statistically significant. To examine whether this was the case, statistical comparisons of estimates were made based on a decomposed variance (use of the compound error term precluded a direct among-method statistical comparison of mean impact values). The variance associated with bite size was removed, since this was common across both methods and the variance associated with the number of bites taken per day was removed from the inferred estimates of impact. In the case of the indirect visual census method, each replicate count of abundance was multiplied by mean bite size and mean number of bites per day. For the direct video method, each replicate estimate of number of bites per m<sup>2</sup> per day was multiplied by mean bite size. Mean estimates of herbivore species impact provided by the video and visual census methods within each reef zone were then compared using non-parametric Mann–Whitney U tests (transformed data were consistently heteroscedastic and non-normal). Only in the case of the impact of the rabbitfish, *S. doliatus*, on the outer reef flat was there a statistically significant difference between the two methods (Table 3).



**Fig. 1** **a** Proportion of herbivore biomass (mean  $\pm$  SE) recorded by remote video cameras (*Video*) and by underwater visual censuses (*UVC Transects*) within individual reef zones across a depth gradient at Pioneer Bay, Orpheus Island, GBR. **b** Mean percentage contributions of individual species to the total biomass recorded within individual reef zones by both methods

## Discussion

This study provides the first direct evaluation of methodologies comparing a particular ecosystem function at the whole reef scale. It provides an insight into the degree to which, in the specific case of herbivore feeding, presence equates to function and the degree to which indirect methods of quantifying herbivory may be capable of yielding realistic estimates of herbivore impact across coral reefs. The lack of any clear differences in measured impact of the three dominant species provided by remote video cameras and the indirect method of inference suggests that these species of herbivore are generally censused in proportion to their impact within a given area of the reef and that, in these cases, indirect methods are capable of

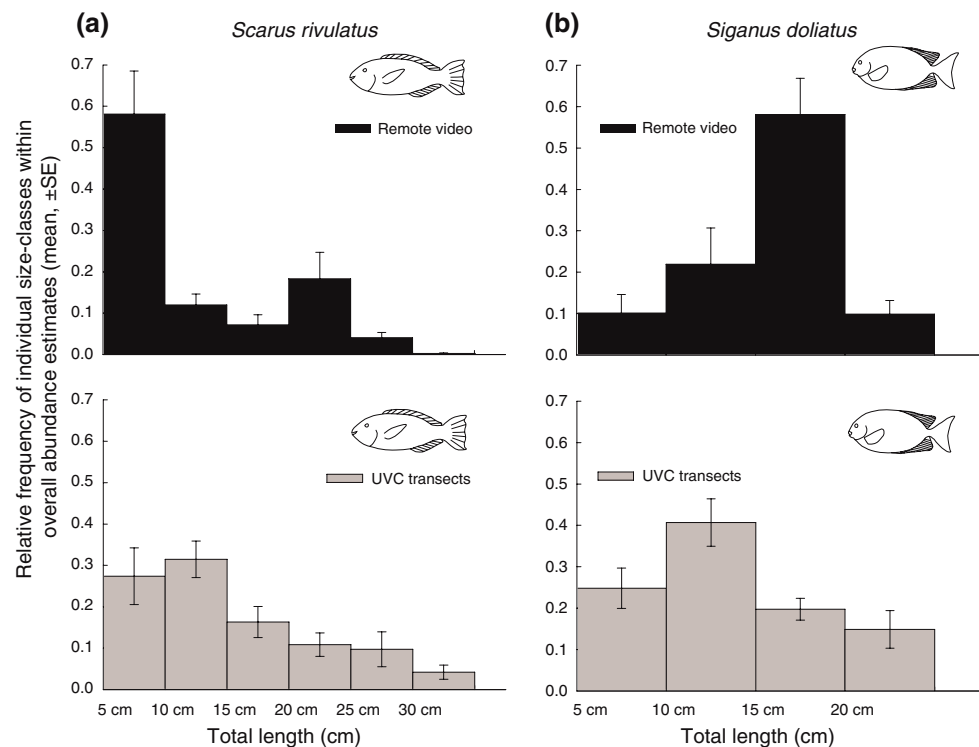
yielding relatively realistic estimates of herbivory across coral reefs.

Previous studies have highlighted the wariness of fish in the presence of divers on SCUBA and its potential to impact on censuses of abundance (Chapman et al. 1974; Kulbicki 1998; Harvey et al. 2004). Avoidance behaviour has been most frequently noted in species that are the target of local fisheries, both commercial and recreational (Davis and Anderson 1989; Kulbicki 1998). In the present study, the similar levels of biomass recorded by the divers and cameras suggest that the presence of the diver did not markedly affect the three main species within Pioneer Bay.

The consistently lower estimates of herbivore impact recorded by videos (relative to direct observations) may suggest the possibility of a “video effect”. It might be expected that the manifestation of this “video effect” would vary between species, with the outwardly more skittish species such as *Sc. rivulatus* and *C. microrhinos* showing the greatest divergence between video and inferred methods and the less wary *S. doliatus* showing more similarity between the two methods. However, in this study no such consistent patterns were observed. For example, although the video recorded a consistently lower impact for *Sc. rivulatus* across the reef slope, crest and outer flat than was inferred from abundance estimates, at the outer flat the video recorded a greater mean number of bites than was inferred from presence. However, many of these bites were by small individuals and therefore did not translate into a higher impact value. Similarly, in terms of the biomass recorded by the two methods, it might be expected that less wary species such as *S. doliatus* would display the greatest consistency between diver and video estimates. However, although the video recorded smaller percentages of *S. doliatus* on the reef slope than the divers, this pattern was reversed on the outer and mid reef flat, with the cameras picked up higher proportions of *S. doliatus* biomass than the divers. This suggests that if there was any aversion to the cameras, it was not consistent across the reef.

However, caution should be exercised in attributing all the divergence between video and inferred estimates of herbivory to camera effects. Real differences between the two methods in measurement of herbivore impact may reflect those cases where the functional role of a species is exerted at a narrower scale than its observed range on the reef as reported by visual censuses. For example, in the current study, visual censuses of the presence of *C. microrhinos* on the reef slope led to the inference of a significantly larger impact for this zone than was estimated from video recordings of feeding activity by this species. In fact, it is likely that the record of abundance of *C. microrhinos* on the reef slope relates more to their patterns of defaecation than to any feeding impact. It has been demonstrated (Bellwood 1995b) that the species shows a

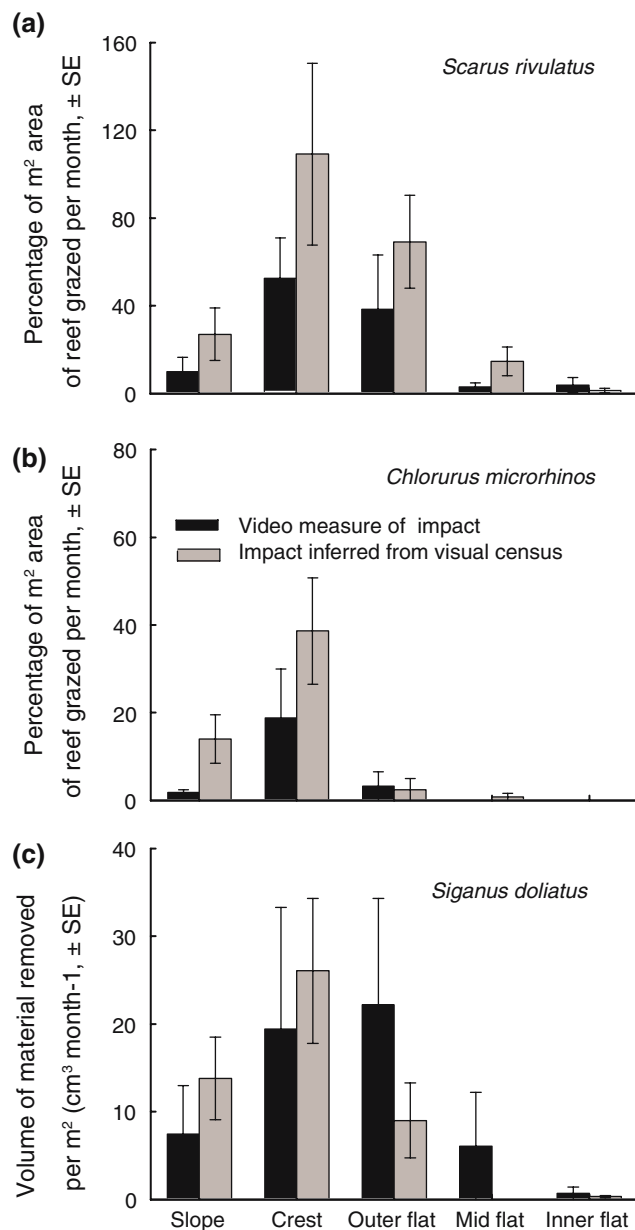
**Fig. 2** Population size-frequency distributions of individuals of the species (a) *Scarus rivulatus* and (b) *Siganus doliatus* across all reef zones as estimated by remote video cameras (*Remote Video*) and by underwater visual censuses (*UVC Transects*)



pattern of moving to specific defaecation sites in deeper water after feeding up on the reef crest. It is likely therefore that the individuals observed on the reef slope in visual censuses were moving between the crest and such sites, leading the over-estimation of inferred grazing impact by *C. microrhinos* on the reef slope.

At the other end of the scale, the results of this study suggest that the impact of *S. doliatus* was underestimated by the indirect method of inferring function from presence. On the outer reef flat, video estimation of the volume of algae removed by *S. doliatus* was almost two and a half times that inferred from the number of individuals of this species sighted during underwater visual censuses. The species does not display skittish behaviour, meaning diver avoidance was unlikely to be behind the underestimation of functional impact. Instead, it suggests that *S. doliatus* may have a greater than average feeding rate within this particular reef zone (either it feeds for proportionately longer periods of time when in this zone or takes a greater number of bites per unit of time). The greater feeding rate may have been a response to higher food quality within this particular zone (Bruggemann et al. 1994). The result re-iterates the fact that the observation of a particular species within a given part of the reef does not necessarily translate to an equivalent grazing impact. The use of remote video cameras can help to illustrate those cases where underwater visual censuses of the presence of a particular species may not tell the whole story in terms of its functional impact.

The use of video cameras can also get around the well-explored biases imposed by levels of diver experience and removes some of the subjectivity from observations made under water. Video recorders also provide a real methodological alternative for those cases where the variable of interest does not lend itself to real-time measurement or where limitations of diver ability to watch and record are likely to be reached e.g. the ability to accurately record numbers of bites taken by multiple individuals in a school. Of course, the video methodology also imposes the limitation that detection of individuals is reliant on the statistical probability that the swimming pattern of that species brings it into the vicinity of the camera (highlighted by Watson et al. 2005). Period of camera deployment and replicate number of sites are therefore critical to the ability of this method to accurately estimate the presence of particular species. Short deployment times have been demonstrated to be inadequate to estimate species richness and density (Watson et al. 2005). In the current study, however, remote video cameras deployed for longer periods outperformed diver censuses in estimating levels of herbivore species richness within Pioneer Bay. For those species that were not sampled by remote video, the issue remains as to whether this was attributable to their actively avoiding the cameras (i.e. a behavioural feature) or to their relative level of abundance and therefore the probability that they would swim past a particular area (i.e. a feature of experimental replication). Collection of replicate samples



**Fig. 3** Impact of the population of (a) *Scarus rivulatus* (b) *Chlorurus microrhinos* and (c) *Siganus doliatus* within Pioneer Bay, Orpheus Island, GBR as inferred from biomass estimates from UVCs (*Inferred*) and from direct measurement by remote video cameras (*Video*). Impact of scarid species is expressed in terms of the percentage of each m<sup>2</sup> area of reef grazed per month. Impact of *S. doliatus* is expressed in terms of the volume of material removed from each m<sup>2</sup> area of reef per month. Monthly impact values were calculated by multiplying daily values by 28. Compound SEs were calculated using Goodman's estimator (*Video*) and a three-term expansion of Goodman's estimator (*Inferred*)

over a larger number of days would allow for investigation of the relative importance of these factors.

As the scale of our ecological questions increase (Hughes et al. 2005; Mumby et al. 2006), so the need for accurate, unbiased estimates of the components of that

**Table 3** Results of Mann–Whitney U tests comparing estimates of species impact obtained via direct and indirect methods for (a) *Scarus rivulatus* (b) *Chlorurus microrhinos* and (c) *Siganus doliatus*

Reef zone	Z	p <sup>a</sup>
(a) <i>Scarus rivulatus</i>		
Slope	0.937	0.385
Crest	1.311	0.213
Outer flat	0.562	0.616
Mid flat	1.030	0.335
Inner flat	−1.639	0.102
(b) <i>Chlorurus microrhinos</i>		
Slope	1.030	0.335
Crest	1.311	0.212
Outer flat	−0.234	0.820
Mid flat	0.281	0.820
Inner flat	not present	not present
(c) <i>Siganus doliatus</i>		
Slope	1.780	0.083
Crest	1.686	0.102
Outer flat	−2.060	<b>0.041*</b>
Mid flat	−1.124	0.291
Inner flat	0.374	0.750

Comparisons are made within individual reef zones

\* Zones where differences between methods are significant at the 0.05 level

<sup>a</sup> p values reported are exact probabilities adjusted for small sample sizes

system become critical (Thresher and Gunn 1986). Questions related to indices of relative abundance or species composition through time are often robust to the presence of systematic biases in sampling techniques. However, questions relating to the absolute value of ecosystem processes and the extent to which critical levels of those processes may signal the decline of an ecosystem into a new state are reliant on accurate, unbiased measures. At the very least, we need to have an understanding of the sensitivity of those measures to inherent biases in the methodology. For example, if measurements of herbivore impact are systematically biased upwards, the assumed level of herbivore grazing required to maintain a healthy balance between corals and algae will be overestimated and subsequent declines in herbivore populations dismissed as unimportant. Cross-method comparisons are not without their problems, but studies which aim to compare measurements of ecosystem variables made via varying techniques will be critical in increasing our understanding of the extent to which we may be under- or over-estimating particular ecosystem processes. What, then, is the best way of quantifying herbivory? In the case of the three dominant herbivore species within this reef system, the indirect inferred and direct video methods are most likely to yield



an estimate range, albeit imprecise, within which the true value of realised herbivory probably lies. Biases cannot be completely eliminated: the key will be in recognising their potential effect on our understanding of the quantitative impact of individual species on the ecosystem.

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