

Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs

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ABSTRACT: We explored the role of behaviour and trophic ecology in driving differences in ecosystem function between 2 closely related species. We examined the relationships between diet, feeding rate, alimentary tract structure and patterns of digestion for 2 reef herbivores commonly found on the Great Barrier Reef, *Siganus doliatus* and *S. lineatus*. Despite their similar morphology, the 2 species exhibited distinct feeding behaviours and significantly different feeding rates, diets and movements of digesta through the alimentary tract. *S. doliatus* displayed a typical herbivore diurnal feeding pattern, taking an average 9.7 bites min⁻¹ over the main part of the feeding day and with a diet dominated by red thallose algae (primarily *Laurencia* spp., *Eucheuma* sp., *Halymenia* sp. and *Gracilaria* sp.) and red and green filamentous algae. *S. lineatus* was not observed taking a single bite from the reef substratum in >100 h of underwater observations. The stomach contents of *S. lineatus* were dominated by amorphous organic matter (detritus). Gut passage rates suggest that *S. lineatus* is feeding nocturnally or during crepuscular periods. We suggest that these 2 species have distinct functional roles, with *S. doliatus* being a grazer of reef turf algae and *S. lineatus* primarily a grazer of off-reef detrital aggregates. This versatility of ecosystem function in closely related species provides further evidence that functional roles do not necessarily divide along taxonomic lines. The results highlight the importance of validating ecosystem function on a species-by-species basis.

KEY WORDS: *Siganus* spp. · Ecosystem function · Trophic ecology · Herbivory · Detritivory · Coral reef · Diet

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INTRODUCTION

The species within an ecosystem are increasingly being viewed not in terms of their taxonomic labels, but in terms of their ecosystem function, i.e. the specific role that they play in that system (Steneck & Dethier 1994, Blondel 2003, Nyström et al. 2008). Functional group identity allows the impact of a particular species within an ecosystem to be quantified and, perhaps more pertinently, the likely effect of removal of that species from the ecosystem to be assessed (Nyström 2006, Petchey & Gaston 2006, Slade et al. 2007). Identification of ecosystem function is therefore

an important part of our understanding of the concept of biodiversity (Petchey & Gaston 2006, Wright et al. 2006, Schmitz 2008), especially as it relates to the resilience of ecosystems.

Assessments of ecosystem resilience and of the intrinsic level of functional redundancy within a system frequently assign species from within the same family or genus to a single functional group, often on the basis that they possess similar morphological structures. However, the extent to which one can assume that morphologically and taxonomically similar species have similar functional roles is not well understood (Chalcraft & Reserits 2003, Bjelke & Herrmann 2005),

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and studies investigating differences in functional roles within closely related taxa are limited (for marine exceptions see Bellwood & Choat 1990, Purcell & Bellwood 1993, Duffy et al. 2001, Choat et al. 2002, Norling et al. 2007).

Within coral reef ecosystems, a functional-group approach has been identified as an important diagnostic tool in assessing the overall resilience of, or in predicting the vulnerability of, individual reef systems (Bellwood et al. 2003, 2004, Nyström et al. 2008). The ecosystem services provided by roving herbivorous fishes are widely acknowledged as having a critical role in supporting the resilience of coral reefs (Bellwood et al. 2004, Hughes et al. 2007). Rabbitfishes (Siganidae) are a conspicuous component of reef herbivore assemblages across the Indo-Pacific, but are absent from the Caribbean region and Hawaii (Woodland 1990). Compared to the other, more numerically abundant, families of roving coral reef herbivores (the parrotfishes and surgeonfishes), our understanding of the role of siganids in reef processes is limited. In some locations, however, they can represent a significant component of the herbivorous guild either in terms of abundance or biomass (Bryan 1975, Williams & Hatcher 1983, Fox & Bellwood 2007, Bellwood & Fulton 2008), and there is evidence to suggest that some members of the family may play an important role in preventing shifts of reef systems to undesirable, macroalgal-dominated states (Fox & Bellwood 2008).

The family Siganidae is represented by a single genus, containing ~27 species (Woodland 1990), 12 of which are considered common on the Great Barrier Reef (Randall et al. 1997). Members of the family can be divided into 2 distinct groups based on body shape and habitat: one group comprising the deep-bodied, reef-associated species, and the second comprising the fusiform-shaped species that are more typically associated with seagrass and other off-reef habitats (Woodland 1990). Recent phylogenies of the family have provided evidence of a genetic basis for this dichotomy, with species from each body-shape and habitat group showing the closest phylogenetic relationships (e.g. Kuriwa et al. 2007). The deep-bodied, reef-associated clade exhibits limited morphological variation among species (Woodland 1990), and this morphology appears to have remained stable through time, with fossils of Eocene species displaying very similar body forms and similar bicuspid teeth (Bellwood 1996). In terms of ecosystem function, all current evidence points to this group of reef-associated species belonging to a single functional unit: 'large croppers' (cf. Russ 1984). However, potential variations in functional role between individual members of the group have not been investigated.

Two species of siganid from within the reef-associated clade that are characteristic of and com-

monly found on reefs of the Great Barrier Reef are *Siganus doliatus* and *S. lineatus*. Both are classified as herbivores by virtue of observations of feeding behaviour (Woodland 1990, Randall et al. 1997) or by virtue of intestinal short-chain fatty-acid profiles (Clements & Choat 1995). But no quantitative assessment of diet based on analysis of alimentary tract contents currently exists. Although similar in morphology (e.g. body length:depth ratio), the 2 species have been anecdotally described as exhibiting different patterns of behaviour on the reef (Woodland 1990, Randall et al. 1997). *S. doliatus* often forms strong pair bonds, whereas *S. lineatus* tends to school in groups of 10 to 25 individuals and may occur away from reefs (Woodland 1990). These differences in behaviour and the potential implications for the ecosystem function of the 2 species have not previously been examined. The goal of the present study was therefore to determine whether observed behavioural differences were related to the feeding patterns of the 2 species and whether such differences translated into variation in functional role within coral reef ecosystems. Specifically, the aim of the present study was to describe 5 aspects of the trophic ecology of *S. doliatus* and *S. lineatus*: feeding rate, diurnal pattern of feeding, alimentary tract morphology, pattern of food processing, and diet, in order to evaluate the ecosystem function of these 2 species on coral reefs.

MATERIALS AND METHODS

Feeding rates and diurnal patterns of feeding. The study was conducted in 2007 at Lizard Island (14° 40' S, 145° 28' E), a mid-shelf, continental island located in the northern region of Great Barrier Reef. Three sites (Palfrey Island, Three Beaches Bay, Turtle Beach) on the leeward side of the island were selected for observations of feeding behaviour (rate and diurnal pattern) of *Siganus doliatus* and *S. lineatus*. All observations were conducted on SCUBA over reef-flat, crest and slope habitats to a maximum depth of 6 m. An adult fish was followed for a short period of acclimation (1 to 2 min), then the total number of bites taken over a timed period (2 to 5 min) was recorded. Observations were discontinued if the fish showed a detectable diver response. Fish were observed at the 3 sites over 4 time periods, encapsulating most of the feeding day (Period 1: 06:00 to 07:30 h; Period 2: 08:00 to 11:30 h; Period 3: 13:30 to 16:00 h; Period 4: 16:30 to 18:30 h). A total of 573 observations were collected across the 4 time periods for *S. doliatus* and 383 for *S. lineatus*. Data were converted to bites min⁻¹ and rates averaged to obtain a mean feeding rate for each species in each of the 4 time periods at each of the 3 sites. For *S. doliatus*

tus, differences in feeding rates were tested for using a 2-way ANOVA, with site and time period as fixed factors. Post hoc comparisons of differences among factors were made via Tukey's HSD tests.

Alimentary tract structure and diurnal distribution of tract contents. Adult specimens were collected using a speargun from various leeward sites around Lizard Island (*Siganus doliatus*: mean \pm SE total length [TL] = 191.3 ± 2.3 mm, mean mass = 148.6 ± 5.5 g; *S. lineatus*: mean TL = 290.1 ± 3.9 mm, mean mass = 532.0 ± 21.5 g). Multiple sites (including the 3 at which behavioural observations had been undertaken) were used to avoid bias associated with collection of individuals from a single site. All collections were carried out after the completion of behavioural observations. Approximately equal numbers of specimens ($n = 14$ or 15) were collected for each species at each of 3 times of day: morning (06:00 to 07:30 h), midday (11:30 to 13:00 h) and evening (16:30 to 18:00 h). These time periods were chosen to pinpoint the daily cycle of gut-filling in the 2 species. Specimens were placed on ice and returned to the laboratory within 1 h of capture, where they were weighed and measured (TL and standard length [SL]). The alimentary tract was removed, weighed and uncoiled and the total tract length measured. The alimentary tract was then divided into 5 sections. At the anterior end, the stomach section (S) (up to and including the pyloric cecum) was removed. Since siganids lack a defined hindgut region, the remaining tract was divided into 4 sections of equal length (cf. Clements & Choat 1995, 1997, Choat et al. 2004). The first 3 of these segments were designated intestine (I1, I2, I3) and the posterior segment designated hindgut (H). For each section, the weight with and without contents was recorded. The contents of each section were then placed in separate vials and frozen. Analysis of the mass of alimentary tract contents over the 3 time periods (the temporal pattern of passage of solid material through the 5 regions of the gut) was carried out using canonical discriminant analysis (CDA). The variables used in the analysis were the mass of digesta in each of the 5 regions of the tract (S, I1, I2, I3, H) in each of the 3 time periods (morning, midday, evening) for each of the 2 species. Mean group centroids were plotted for the first 2 canonical variates, along with 95% confidence ellipses (Krzanowski & Radley 1989).

Dietary analysis. Dietary analysis was conducted on a subsample ($n = 10$ to 15 per species) of those individuals with full stomachs. The contents of the stomach portion of the tract were spread onto a Petri dish containing a 50×50 mm grid. The grid consisted of a 10×10 matrix of which a random sample of 60 squares had been blacked out. Contents were viewed under a dissecting microscope and the dietary item in the top left hand corner of each of the remaining 40 squares was

recorded (following Depczynski & Bellwood 2003). Dietary categories (15 in total) were defined following Choat et al. (2002), so as to yield comparative data for the 2 species covered by the present study. Counts for each dietary category were converted to relative proportions (by dividing by 40) and between-species differences in the resulting frequency distributions of each dietary category were assessed using a non-parametric Kolmogorov-Smirnov test, making no prior assumptions about the equality of the distributions of the 2 samples.

RESULTS

Feeding rates and behaviour

Siganus doliatus exhibited a pattern of feeding rate typical of diurnal herbivores, with bite rates increasing through the morning periods, peaking in the mid-afternoon and decreasing again in the late afternoon or early evening (Fig. 1). The feeding rates in all 4 time periods were statistically distinct (Tables 1 & 2a). Early-morning (06:00 to 07:30 h) feeding rates averaged between 0.5 and 0.8 bites min^{-1} across the 3 sites, suggesting that our observations had captured the start of the feeding day. This bite rate increased to a peak of between 9.1 and 12.2 bites min^{-1} in the afternoon (13:30 to 18:00 h)

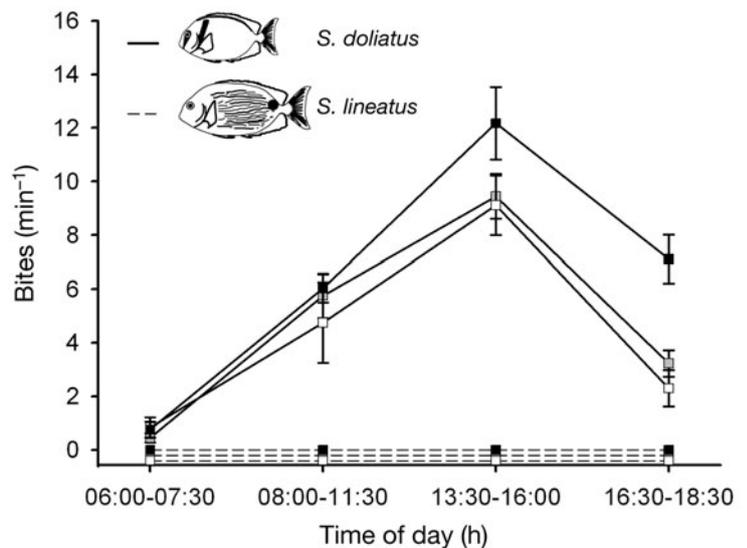


Fig. 1. *Siganus doliatus* and *S. lineatus*. Feeding rates (\pm SE) as a function of time of day. Adult fish from 3 sites (\square : Palfrey Island; \square : Three Beaches Bay; \blacksquare : Turtle Beach) were observed over 4 time periods. Feeding rates for *S. lineatus* at each of the 3 sites had a mean value of zero and no variation about this mean; however, for presentational purposes, data for *S. lineatus* relating to the Palfrey Island and Three Beaches Bay sites have been offset from zero

Table 1. *Siganus doliatus*. Results of 2-way ANOVA of feeding rates (bites min^{-1}) with site (Palfrey Island, Three Beaches Bay, Turtle Beach) and time period (as shown in Fig. 1) as fixed factors. *Significant at the 0.05 level

Source of variation	df	MS	F	p
Site	2	225.6	8.268	<0.001*
Time \times Period	3	1714.7	62.840	<0.001*
Site \times Time \times Period	6	58.0	2.125	0.049*
Error	561	27.3		
Total	573			

16:00 h) (Fig. 1). By the evening (16:30 to 18:30 h), average feeding rates had declined to between 2.3 and 7.1 bites min^{-1} , and in the last 30 min of observations the overall average was 2.5 bites min^{-1} , suggesting that feeding rates were decelerating towards sunset. Turtle Beach displayed a significantly higher feeding rate in the second half of the day than the other 2 sites, leading to a marginally significant interaction between site and time of day (Tables 1 & 2b). However, the overall pattern of an afternoon peak was consistent across sites (Fig. 1).

In contrast to the typical diurnal feeding pattern observed for *Siganus doliatus*, *S. lineatus* exhibited a feeding rate of zero bites min^{-1} at all sites across all time periods (Fig. 1). In none of the 383 observations did the species take a single bite from within the reef habitats surveyed in the present study and therefore the results displayed no variability around the zero bite rate value.

Alimentary tract structure

The 2 species displayed broadly comparable relative gut lengths (to SL) when compared to the range associated with herbivorous reef fishes, although the direct species comparison revealed a statistically significant difference (t -test: $t_{(91)} = 2.627$, $p = 0.01$). For *Siganus*

Table 2. *Siganus doliatus*. Summary of Tukey's HSD post hoc tests to identify (a) times of day and (b) sites that displayed significant differences in feeding rate (bites min^{-1}). *Significant at the 0.05 level

(a)			
Time of day	06:00–07:30	08:00–11:30	13:30–16:00
08:00–11:30	<0.001*	–	
13:30–16:00	<0.001*	<0.001*	–
16:30–18:30	<0.001*	0.004*	<0.001*
(b)			
Site	Palfrey Island	Three Beaches Bay	
Three Beaches Bay	0.583	–	
Turtle Beach	0.046*	0.006*	

doliatus, the alimentary tract was, on average (\pm SE), 4.2 ± 0.05 times SL, and for *S. lineatus* 4.0 ± 0.06 times SL. The 2 species also displayed comparable relative gut weights (empty alimentary tract weight excluding gut contents as a proportion of body weight) compared to the range associated with herbivorous reef fishes, although again the direct species comparison revealed statistically significant differences (*S. doliatus*: $7.6 \pm 0.2\%$ and *S. lineatus*: $6.2 \pm 0.1\%$; t -test: $t_{(87)} = 5.894$, $p < 0.001$). In both species the empty posterior, or hindgut, segment of the intestine made up approximately one-third of the total weight of the intestinal part of the alimentary tract, $36.5 \pm 0.8\%$ in the case of *S. doliatus* and $34.3 \pm 0.8\%$ for *S. lineatus*, despite only being one-quarter of its length. Although both species showed similar levels of investment in the hindgut region as a proportion of the intestine, they displayed marked variation in the overall level of investment in anterior and posterior sections of the overall alimentary tract. *S. lineatus* invested significantly more in the stomach region of its alimentary tract (on average $38.0 \pm 0.7\%$ of the total tract weight) than *S. doliatus* ($28.4 \pm 0.7\%$ of total tract weight; t -test: $t_{(87)} = -9.852$, $p < 0.001$). All values are given in Table 3.

Table 3. *Siganus doliatus* and *S. lineatus*. Relative gut length (total gut length as a proportion of standard length), relative gut weight (weight of empty gut as a percentage of body weight minus gut contents) and relative gut segment investment (empty segment weight as a proportion of total empty intestinal tract weight). Error expressed as SE

	<i>S. doliatus</i> (n = 45)	<i>S. lineatus</i> (n = 44)
Relative gut length	4.2 ± 0.05	4.0 ± 0.06
Relative gut weight (%)	7.6 ± 0.2	6.2 ± 0.1
Relative gut segment investment (% of total empty gut weight)		
Stomach	28.4 ± 0.7	38.0 ± 0.7
Anterior intestine (I1 + I2 + I3)	45.5 ± 0.7	40.8 ± 0.7
Posterior intestine (hindgut)	26.1 ± 0.6	21.2 ± 0.6
Hindgut: intestine (I1 + I2 + I3 + H)	36.5 ± 0.8	34.3 ± 0.8

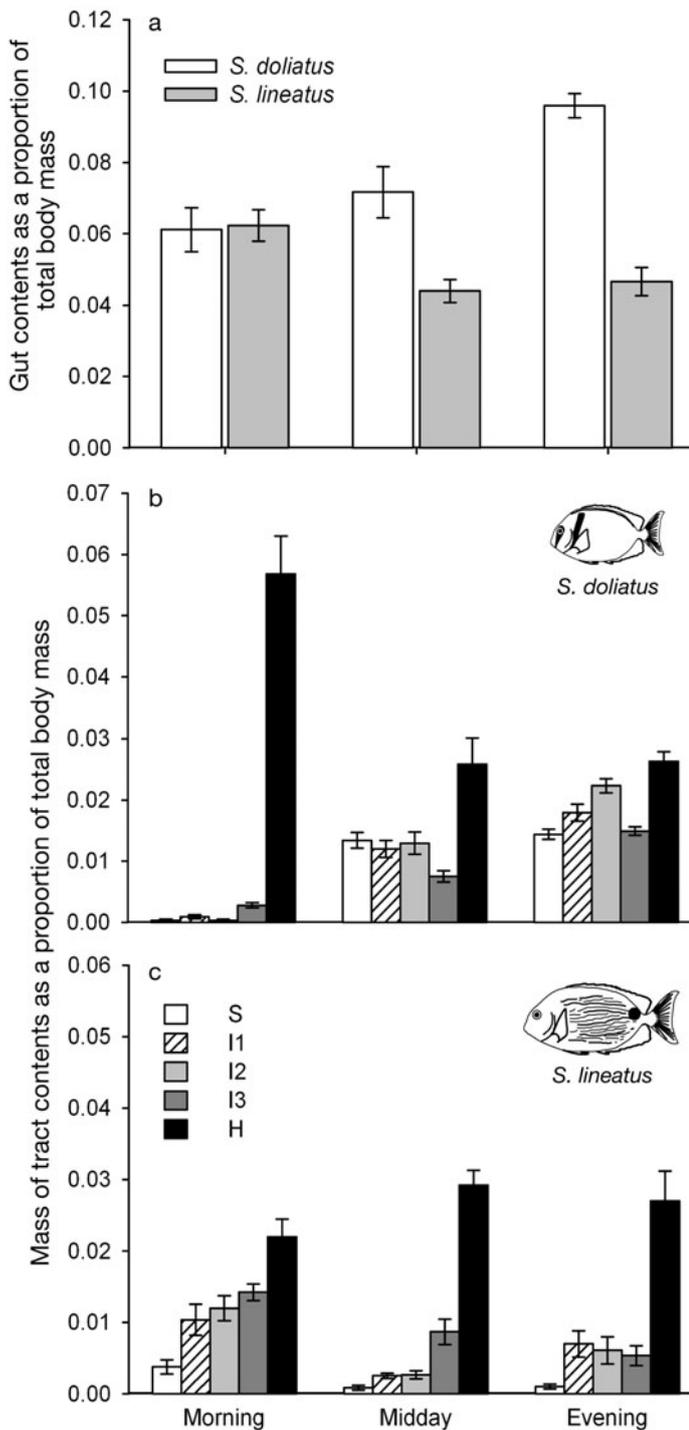


Fig. 2. *Siganus doliatus* and *S. lineatus*. (a) Mean total alimentary tract contents (wet weight) expressed as a proportion of total body weight at 3 times of day, morning (06:00 to 07:30 h), midday (11:30 to 13:00 h) and evening (16:30 to 18:00 h). (b) *S. doliatus* and (c) *S. lineatus*: Wet weight of digesta in 5 regions of the alimentary tract (S: stomach; I1: first intestinal segment; I2: second intestinal segment; I3: third intestinal segment; H: hindgut) expressed as a proportion of total wet weight of gut contents sampled over the 3 times of day referred to in (a). Error bars represent SE

Diurnal distribution of digesta in the alimentary tract

The 2 species exhibited different patterns of gut-filling and -emptying over the day. Total weight of gut contents, as a proportion of body weight, increased from morning (06:00 to 07:30 h) to evening (16:30 to 18:00 h) for *Siganus doliatus* but decreased from morning to evening for *S. lineatus* (Fig. 2a). This supports the results of the behavioural observations and suggests that *S. lineatus* was emptying its gut over the course of the day. For *S. doliatus*, alimentary tract contents ranged (\pm SE) from $6.1 \pm 0.6\%$ of total body weight in the morning to $9.6 \pm 0.3\%$ in the evening (Fig. 2a). Over the 3 time periods included in the present study, *S. lineatus* displayed a lower level of intake and retention in the alimentary tract, with gut contents having their maximum of $6.2 \pm 0.4\%$ of body weight in the morning, declining to $4.4 \pm 0.3\%$ of body weight by midday and remaining at approximately the same level in the early evening (Fig. 2a).

The distribution of digesta through the tract also varied between the 2 species over the day (Fig. 2b,c). The gut contents of *Siganus doliatus* were concentrated in the hindgut region at the start of the feeding day, with $87.7 \pm 5.2\%$ of wet mass found in this region (Fig. 2b). Between early morning and midday, the stomach and intestine of *S. doliatus* filled up and the hindgut emptied (Fig. 2b). In contrast to this, the early-morning alimentary tract of *S. lineatus* showed a more even distribution of contents across all segments, with the hindgut segment at its lowest level of solid content (Fig. 2c). Over the course of the morning, the stomach and intestine of *S. lineatus* emptied and the relative proportion of contents in the hindgut increased (Fig. 2c). Of the 3 time periods observed, the stomach of *S. lineatus* showed its greatest proportional contribution to tract contents during the morning (06:00 to 07:30 h) period (Fig. 2c).

The CDA ordination plot of group centroids for each of the 3 times of day displayed significantly different patterns in distribution of digesta for the 2 species, with each moving in opposing directions along both axes through the day (Fig. 3a). Groups were separated along CV1 and CV2 according to the region of the gut that dominated the contents at a particular time of day (Fig. 3b). Morning observations for *Siganus doliatus* were dominated by hindgut digesta, with midday and evening observations dominated by the stomach and intestine respectively (Fig. 3). The pattern of digesta for *S. lineatus* showed less separation along the axis of the first canonical variate, but still exhibited a significant pattern of morning observations dominated by the stomach and intestine, moving to an evening distribution of digesta dominated by the hindgut (Fig. 3), i.e. the opposite process to that described for *S. doliatus*. For *S. lineatus*, however, the midday and

Table 4. *Siganus doliatus* and *S. lineatus*. Results of Kolmogorov-Smirnov test for equality of frequency distributions of individual dietary items observed in stomachs of the 2 study species. *Significant at the 0.05 level

Dietary category	Z	p
Algae		
Brown thallate	2.205	<0.001*
Green thallate	0.490	0.970
Red thallate	2.449	<0.001*
Brown filamentous	1.143	0.147
Green filamentous	0.980	0.292
Red filamentous	1.470	0.027*
Brown foliose	0.245	1.000
Green foliose	1.470	0.027*
Red foliose	0.898	0.395
Seagrass	0.163	1.000
Animal material		
Foraminifera	0.572	0.900
Microcrustacea	0.490	0.970
Other invertebrates	0.327	1.000
Calcareous sediment	1.143	0.147
Organic matter	2.286	<0.001*

evening distribution of digesta were not significantly different from each other (overlapping 95% confidence ellipses).

Diet

The 2 species had an overlapping dietary range, but differed significantly in the relative proportions of the dietary categories consumed (Fig. 4, Table 4). The stomach contents of *Siganus doliatus* contained higher propor-

tions of red thallate algae (in particular, *Laurencia* spp., *Euclima* sp., *Halymenia* sp., *Gracilaria* sp. and *Amphiroa* spp.), brown thallate algae (*Dictyota* spp. and *Padina* sp.), green foliose algae (*Enteromorpha* sp.) and red filamentous algae. The stomach of *S. lineatus* contained significantly higher proportions of organic matter (predominantly amorphous organic matter) (Fig. 4, Table 4), which averaged $50 \pm 8.8\%$ among individuals. A smaller number of individuals had stomach contents dominated by red and brown filamentous algae (Fig. 4), while the stomach of 1 specimen contained a significant proportion of seagrass (*Halophila ovalis*). The stomachs of *S. lineatus* contained, on average, a higher proportion of sediment than those of *S. doliatus*, although the pattern was not sufficiently consistent to generate a statistically significant difference between species (Fig. 4, Table 4).

DISCUSSION

Although broadly similar in external morphology and intestinal structure, the 2 species of siganid examined in the present study were found to exhibit significant differences in feeding rate, feeding behaviour, diet and movement of digesta through the gut. *Siganus doliatus* can be functionally classified as a grazer of epilithic turf algae and *S. lineatus* as a reef-associated grazing detritivore. These results provide the first direct evaluation of the ecosystem function of these 2 species and demonstrate the extent to which functional roles can vary between closely related species within a single genus.

Siganus doliatus was a visible component of the sheltered reef flat and crest fauna and was consistently observed taking regular feeding forays from the reef

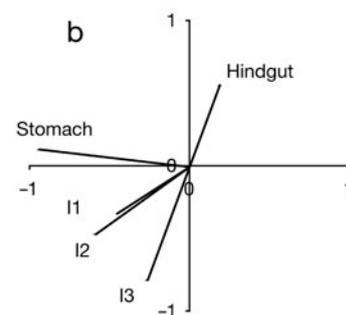
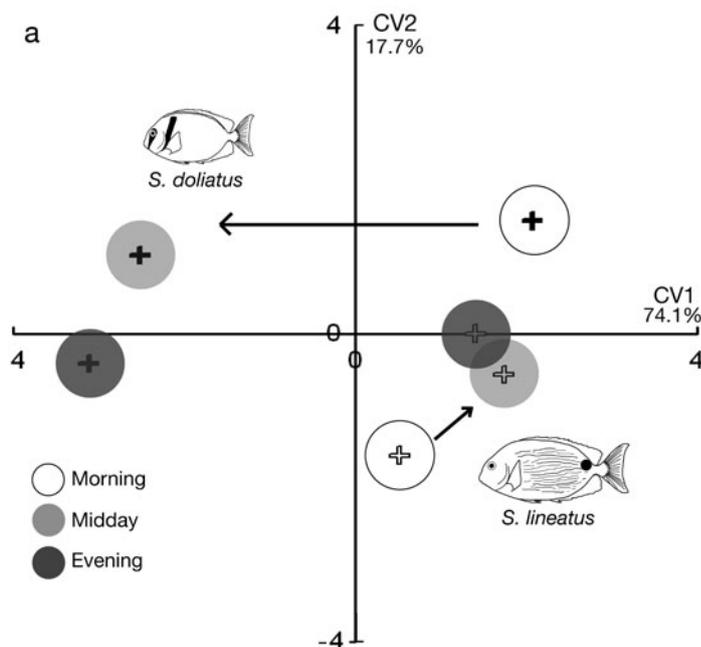


Fig. 3. *Siganus doliatus* and *S. lineatus*. Canonical discriminant analysis (CDA) of amounts of digesta in different regions of the alimentary tract (digesta expressed as a proportion of the individual's total body weight) over 3 times of day, morning (06:00 to 07:30 h), midday (11:30 to 13:00 h) and evening (16:30 to 18:00 h). (a) Ordination plot on CV1 and CV2 of group centroids for each of the 3 times of day for *S. doliatus* (filled cross) and *S. lineatus* (open cross) with 95% confidence ellipses and (b) vector plot based on full correlations between the gut segment response variables and CV1 and CV2

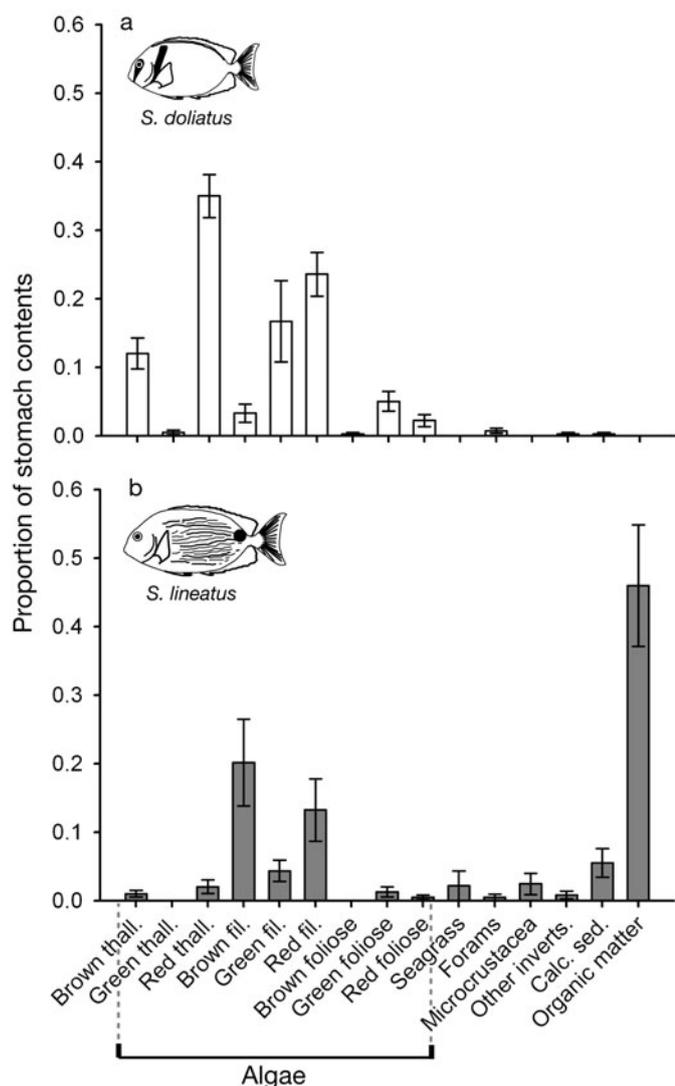


Fig. 4. *Siganus doliatus* and *S. lineatus*. Proportions (mean \pm SE) of individual dietary categories recorded from the stomach contents of (a) *S. doliatus* (n = 10) and (b) *S. lineatus* (n = 15). Algae are divided into 9 categories based on the main taxonomic division and degree of structural complexity (following Choat et al. 2002). Abbreviated dietary categories are provided in full in Table 4

substratum. The average (\pm SE) feeding rate for this species recorded over the period 11:00 to 16:00 h in the present study was 9.7 ± 0.8 bites min^{-1} , a rate similar to that recorded for other grazers of algal turfs such as *Acanthurus lineatus* and *Zebbrasoma scopas* (Choat et al. 2002, 2004). In addition, the diurnal pattern of feeding observed for *S. doliatus*, with a late-afternoon peak in feeding rate, reflects the pattern recorded for *A. lineatus* (Polunin & Klumpp 1989), *Z. scopas* and *A. nigrofuscus* (Polunin et al. 1995). In terms of feeding behaviour, therefore, *S. doliatus* can be described as a typical grazer of the epilithic algal matrix, sensu Wilson et al. (2003).

By contrast, the feeding pattern of *Siganus lineatus* could not be determined from on-reef observations from 06:00 to 18:30 h. Individuals did not display the same gregarious feeding behaviour as *S. doliatus*, nor did the pattern of movement of digesta through the gut of *S. lineatus* match that of a typical, diurnal-feeding reef herbivore. Instead, evidence from gut contents, gut morphology and the passage of digesta through the alimentary tract all suggested that *S. lineatus* exhibits a feeding mode that is intermediate between algal grazing and detritivory. *S. lineatus* possesses low concentrations of short-chain fatty acids within its alimentary tract (Clements & Choat 1995), a characteristic shared by other detrital feeders that appear to rely less on microbial fermentation as a digestive mechanism than typical algal grazers. Yet *S. lineatus* retains a greater proportion of its alimentary tract contents in the hindgut region of its tract than other reef detritivores (Choat et al. 2004). This could be explained by the fact that *S. lineatus* does not have recourse to methods of mechanical trituration (i.e. gizzard or pharyngeal jaw) by which to process its food and may therefore still rely on hindgut processing to a greater degree than its detritivorous trophic equivalents. Certainly, further investigation of the digestive mechanisms employed by this, and other, species of siganid are warranted. For now, the intermediate status of *S. lineatus* between algal grazer and detritivore marks it as functionally distinct from *S. doliatus* and leads us to classify it as a grazing detritivore.

Although the present study was able to establish a divergence in ecosystem function between these 2 congeners, exactly when and where *Siganus lineatus* is feeding at our study sites remains to be discovered. The underwater observations reported here can only rule out the diurnal, on-reef feeding that is typical of most roving herbivores. However, the fact that the stomach of *S. lineatus* was full early in the morning (06:00 to 07:30 h) and that the intestine displayed its largest proportional content during this early-morning period would suggest that food had been ingested during crepuscular or nocturnal periods. The filling of the anterior portion of the intestine between the afternoon and evening period suggests that some diurnal feeding was also taking place to top up after the nocturnal or crepuscular feed.

The fact that diurnal feeding was not observed for *Siganus lineatus* in shallow reefal areas indicates that daytime feeding must be taking place in off-reef locations (sand aprons, mangroves or rocky areas associated with the reef) or in deeper reef habitats. Evidence from the stomach contents of *S. lineatus* indicate that this species feeds over sandy areas (significantly higher relative proportions of sediment were observed in the stomach of this species than in the stomach of *S.*

doliatus, which feeds on the reef). Personal observations and anecdotal accounts of bouts of diurnal feeding by *S. lineatus* outside of the present study have all been recorded in off-reef locations; however, the presence of *Halophila ovalis* in the stomach of 1 individual means that feeding in deeper reef habitats cannot be ruled out, as *H. ovalis* is known to grow in patches down to a depth of 15 m at the study site. The presence of substantial proportions of red and brown filamentous algae in the stomachs of some *S. lineatus* could suggest that nocturnal feeding takes place on the reef, although the ingested alga may also be present on hard surfaces in off-reef habitats. We hypothesise that *S. lineatus* is a grazing detritivore, feeding nocturnally or crepuscularly, but with short feeding bouts during the day in off-reef locations, returning to the reef for shelter between bouts. In the present study, groups were frequently seen resting at the edge of the reef adjacent to open sand and in close proximity to, or laying on, colonies of the soft coral *Sinularia* sp., possibly in a deliberate attempt to deter parasites (Bartoli & Boudouresque 1997, Kayser et al. 2003). Further investigation of the feeding behaviour of *S. lineatus* is clearly needed.

The divergence in functional roles between the 2 species examined in the present study not only demonstrates the importance of validating ecosystem function on a species-by-species basis, but also brings into focus the issue of their comparative impacts on the reef ecosystem. To the extent that *Siganus lineatus* may be making greater use of off-reef habitats than its congeneric, its relationship with the reef could be more indirect than that of *S. doliatus*. *S. lineatus* may represent an example of a 'reef-associated' fish (sensu Choat & Bellwood 1991), rather than a coral-reef fish in the strict sense of having an obligate association with the reef. Of course, this assumption raises questions as to where the boundaries of a reef system lie. The distinction between on-reef and off-reef habitats may be blurred when it comes to assessing the ecosystem function of a species and the importance of that species to the overall system (Bellwood 1997, Mumby et al. 2004). Assessments of reef ecosystems therefore need to encompass all reef environments and include those species which may bridge reef and non-reef habitats, such as *S. lineatus*.

The results also highlight the fact that the significance of the functional role of an organism is not necessarily related to its observed presence within the system. While this is now well-established for families such as the Haemulidae and nocturnally active species such as members of the family Muraenidae (Gilbert et al. 2005), it has not generally thought to be the case for 'herbivores'. Recent studies have demonstrated that species that can play a significant role in the process of

herbivory on coral reefs may not be observed during visual censuses of those same reef habitats (e.g. Bellwood et al. 2006, Fox & Bellwood 2008). Now, it appears, the corollary is also true, i.e. that nominally herbivorous species such as *Siganus lineatus* that are censused in reef habitats may not necessarily play a role in the process of herbivory on the reef, or at least not in those habitats in which the individuals are observed. Visual censuses of fish abundance, with their bias towards detecting and observing species that are reef-dependent (i.e. spending all their time on the reef), can therefore be misleading in determining the precise nature of the role that individual species play in reef ecosystems. For roving coral-reef herbivores, the scale over which a species exerts its functional impact will be an important determinant of its ecosystem role and, as shown by the present study, feeding behaviour can be a key driver of the scale of the impact. Determination of ecosystem function must therefore be on a species-by-species basis and must include direct observations of the location and extent of feeding behaviour. Priority species for future investigations of this sort include species that may have the potential to remove macroalgae from reef habitats, such as *Kyphosus vaigiensis* (Cvitanovic & Bellwood 2009) and *S. canaliculatus* (Fox & Bellwood 2008).

Acknowledgements. We thank J. H. Choat and C. Fulton for helpful discussions, the staff of Lizard Island Research Station (an Australian Museum facility) for the provision of essential logistical support and facilities, and E. Graham for field assistance. Financial support was provided by the Australian Research Council (D.R.B.) and an Ian Potter Doctoral Fellowship at Lizard Island (A.S.H.). This study was carried out under JCU Ethics Permit A1072 and GBRMPA Permit G07/23636.1.

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Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA

Submitted: January 16, 2009; Accepted: April 15, 2009
Proofs received from author(s): June 12, 2009