



Herbivory by the Dusky Damsel fish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community

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Abstract

Experiments were carried out on rocky shores at Arraial do Cabo (Southeast Brazil) to evaluate how the dusky damselfish, *Stegastes fuscus* (Cuvier, 1830) affects the benthic community structure. Cage exclusion showed that *S. fuscus* strongly influences the algal community in its territories, keeping it in an early succession stage and preventing dominance by *Jania* spp. Diversity and biomass of the epilithic algal community (EAC) were higher inside territories than outside. These dense mats hold a diverse and abundant cryptofauna ($\cong 72$ ind/100 cm²) that was significantly higher inside territories. Algae comprise 70% of the *S. fuscus* diet, with the remaining 30% composed of animal material. The fish feeds selectively mainly on red filamentous algae, such as *Polysiphonia* spp., *Ceramium* spp. and *Centroceras clavulatum*, albeit it also ingests a great amount of calcareous algae (25% of total algae). Total assimilation and nitrogen assimilation were low in *S. fuscus*. Gut contents turnover varied from 3.7 in summer to 4.1 in winter. The net primary productivity (NPP) values of EAC within territories were intermediate ranging from 0.86 to 2.34 gC day⁻¹ territory⁻¹ in winter and in summer, respectively. Grazing rates did not vary greatly between seasons. In summer damselfish do not appear to affect production on territories, but in winter consumption could remove 100% of primary production, indicating a high turnover rate by EAC. *S. fuscus* plays an important trophodynamic role in this system, since its abundance is high and overall energy flux is enhanced inside its territories. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Herbivory; Damsel fish; Rocky shore; Benthic community; Trophodynamic role

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1. Introduction

Damselfish are well known for their effects on benthic organisms, modifying and influencing communities of algae, mesoinvertebrates and corals, as well as the social structure of other herbivorous fish (see Hixon, 1983). In the last two decades, numerous investigations of the relationships between these fish and their habitats have advanced our knowledge of damselfish and their effects on benthic communities (Lobel, 1980; Montgomery, 1980a; Hixon and Brostoff, 1983; Sammarco, 1983; Klumpp et al., 1987). Most studies were concentrated in tropical areas, mainly coral reefs, a few of them were performed on rock reefs (Montgomery, 1980a,b) and in temperate zone regions (Clarke, 1970; Foster, 1972), whereas tropical rocky shores were not explored. Because damselfish defend their algal gardens from other herbivores, their territories are highly productive and have higher biomass and algal diversity than the areas outside territories (Brawley and Adey, 1977; Lassuy, 1980; Hixon and Brostoff, 1981, 1982; Sammarco, 1983; Hinds and Ballantine, 1987), even though a few studies have found contradictory results (Lassuy, 1980; Montgomery, 1980a; Foster, 1987; Russ, 1987). Damselfish territories are generally dominated by opportunistic, fast-growing and highly productive red and green filamentous algae (Vine, 1974; Brawley and Adey, 1977; Lassuy, 1980; Williams, 1981; Ruyter Van Steveninck, 1984; Russ, 1987). These algae grow rapidly, have high energy and nitrogen content, and recover rapidly from grazing damage (Branch et al., 1992). These characteristics allow them to serve as an optimal food for damselfish and to be relatively tolerant of the fish's feeding. These algae form dense mats that sustain an abundant microfauna of invertebrates; such mats appear to function as a refuge from predation and provide abundant food resources (Lobel, 1980; Hixon and Brostoff, 1982; Klumpp et al., 1988; Zeller, 1988). The trophic importance of these cryptofauna, both as food and as consumers, seems to be widespread consistent when high densities were reported.

Territoriality is primarily suggested as an adaptation to resource limitation (Robertson and Gaines, 1986). In spite of their territoriality, data on consumption/production relationships in damselfish territories have shown that food is apparently not limiting, with the consumption by fish never exceeding primary production (Klumpp and Polunin, 1989). Similar results were found in competition experiments, indicating in some instances that damselfish could tolerate herbivorous blennioid fish in their territories without food limitation (Roberts, 1987). However, schools of roving herbivorous fish could overcome the aggressiveness of damselfish and consume great amounts of algae biomass from territories (Robertson et al., 1976; Klumpp and Polunin, 1989). If resource limitations are locally differentiated, some different processes should occur to maintain the constant supply of algae that the damselfish need to sustain their basic requirements. Local release of waste products by these fish has been one of the processes suggested for the high primary production of algae in their territories (Klumpp et al., 1987). Even though recent experiments showed that damselfish possess a marked diel periodicity of nitrogenous excretion and defecation rates (Polunin and Koike, 1987), no attempt was made to search for what effects these sources of nitrogen would have upon the epilithic algal community.

The main goal of this paper is to expand knowledge of the biology of damselfish,

testing some previous questions concerning them while investigating the Dusky Damselfish, *Stegastes fuscus* (Cuvier, 1830), a conspicuous component of the marine fauna of the Brazilian South Atlantic coast (Meneses and Figueiredo, 1985). Here we tested the herbivory effects by *S. fuscus* on the biomass, diversity and primary production of epilithic algae inside its territories; we compared densities for groups of associated cryptofauna inside and outside territories; we investigated feeding and food assimilation by *S. fuscus* and we also analyzed the effects of local release of the damselfish's waste products upon the epilithic algal communities within territories. We sustain the hypothesis that areas of high densities of *S. fuscus* are sites of high energy flux in the food web and consequently, *S. fuscus* may be considered as playing an important role in trophodynamic processes in the rocky shores studied.

2. Study area

This investigation was conducted at Arraial do Cabo–RJ (23°44'S–42°W), a high latitude tropical region, on the Brazilian southeastern coast during summer and winter periods of 1992 and 1993. Two study sites were chosen for the experiments: one at Forno Inlet and another at Cabo Frio Island (Fig. 1). Both stations are sheltered from wave surge and support large numbers of *Stegastes fuscus* territories in a rocky shore zone ranging from 3 to 5 m water depth. This zone is mainly colonized by adult-sized *S. fuscus* (11–15 cm TL), while juveniles are concentrated in shallower areas where the territories are not clearly defined. The Dusky Damselfish is the most abundant fish at the study sites, occupying more than 70% of the substrate in shallow areas of the rocky shore (Ferreira et al., unpublished data). It is replaced by the omnivorous damselfish, *Stegastes pictus*, in deeper areas. The *S. fuscus* territories are established upon and among granite boulders along the rocky shore (\cong 20 m long: from surface to the sand bottom), and exhibit dense algal turfs 1–3 cm high, dominated by the calcareous algae *Jania* spp. The algal turfs inside and outside territories share space with the 'fire coral', *Millepora alcicornis*, and a conspicuous zoanthid, *Palythoa caribaeorum*. The region of Arraial do Cabo is characterized by a coastal upwelling created by the prevailing northeastern and eastern winds (Valentin, 1984). However, the study sites are not directly affected by the phenomenon, with water temperature ranging from 19 to 25°C over the year. General comments on the environmental conditions of the whole region are given in Valentin (1984) and Gonzalez-Rodriguez et al. (1992).

3. Methods

3.1. Characteristics of the damselfish territories

3.1.1. Territory size

The total area of randomly selected damselfish territories ($n = 20$) was estimated by employing a 1-m long rope, divided into 10-cm intervals, with pieces of lead fixed across it. The rope was easily handled, molding perfectly to any territory irregularity,

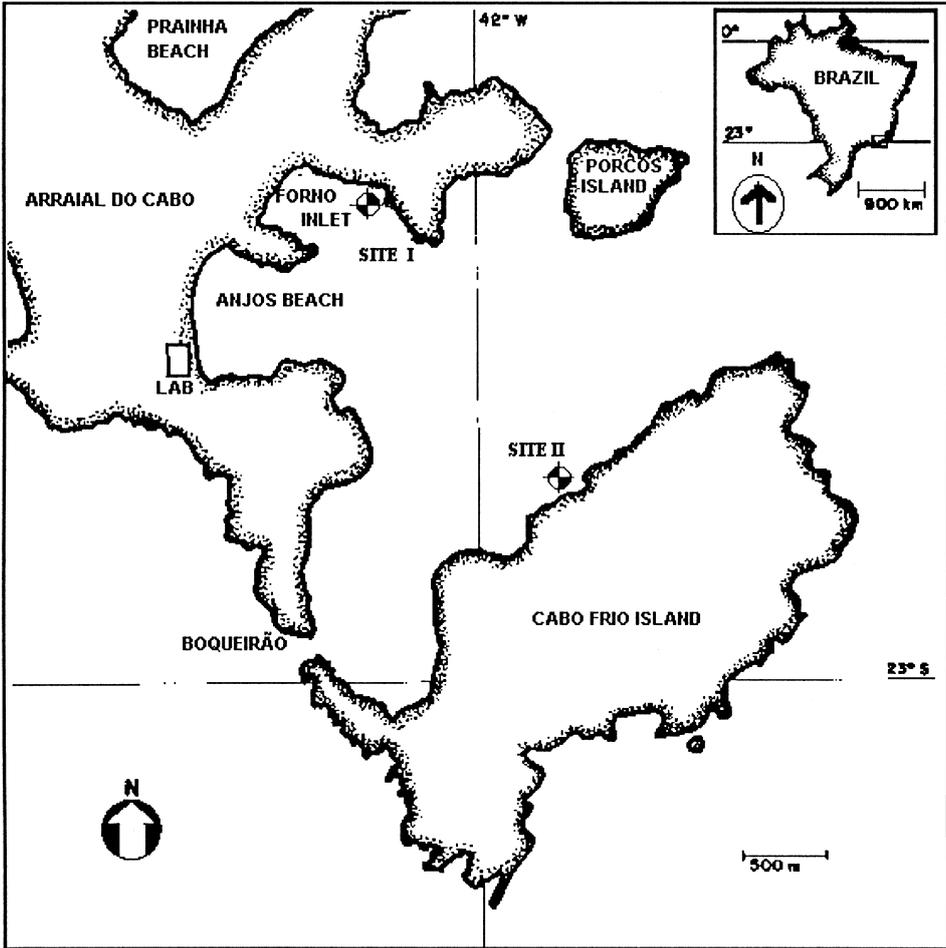


Fig. 1. Map of the region showing the two study sites.

functioning as a chain. The rope was used to follow the contours of the territories, forming circumferences, and afterwards those circumferences were compared to circular frames with approximately the same size, for calculation of the area. Territorially, boundaries were identified through prior observations of the fish's feeding and defensive behavior during successive dives in a 2-week effort (2 h in the morning and 2 h in the evening). Those observations clearly identified territory boundaries since damselfish exhibit marked behavior patterns. When present, boulders had their exposed sides measured and their areas estimated as described above. The base area of each boulder inside territories was calculated and subtracted from the final estimates. The total territory size was estimated by summing up the areas of several circumferences.

3.1.2. Algal biomass

Epilithic algal biomass was compared inside and outside *S. fuscus* territories in winter and in summer. One randomly selected sample of 100 cm² was scraped from the substratum of each territory ($n = 30$) in an adjacent similar rocky shore area, stored in plastic bags and transported to the laboratory. Cryptofauna were separated from algal turf and fixed in 10% formalin for later analysis. Algae were dried in an oven at 105°C for 24 h. All results were converted to gC by prior analysis of the organic carbon content to allow easy comparisons with the available literature. Differences in the epilithic algal biomass inside and outside territories were tested by using the Student's *t*-test (Zar, 1996).

3.1.3. Algal productivity

The net photosynthesis of the territories' epilithic algal community was estimated in situ via simulations using an incubator. It consisted of six transparent Perplex tubes (90 cm long, 10 cm diameter) covered with a plastic net (NORTENE), letting 1, 6, 14, 37, 80 and 100% of incident sunlight pass through each of them. Tubes were supported by a wooden table and interconnected, allowing fresh sea water to circulate across all of them, keeping temperature at constant levels ($24 \pm 1^\circ\text{C}$). Multispecific algal turfs were collected inside territories and transported to the laboratory, where cryptofauna were patiently removed thus avoiding errors due to animal respiration. Algae were separated in turfs of the same size (volume) and inserted into glass bottles (125 ml) with seawater. Four bottles (replicates) and one phytoplankton control were used in each tube. As the tubes had the same angle to the sun, and the same amount of flowing seawater, no significant difference was observed in light and temperature, among replicates of each tube. Therefore, the data variability reflects the natural response of algal turf to the different levels of light used in each treatment. Net photosynthesis and respiration of algae were determined by oxygen changes measured by the Winkler method (Parsons et al., 1984). Two experiments were carried out during a 2-h period, one in winter and the other in summer. Incident sunlight was measured every 10 min with a LICOR quantum sensor. Field light measurements and photosynthesis irradiance relationships (*P*–*I* curves) were used to calculate the daily net production of multispecific algal turfs. Light intensities for the desired depth (3–5 m) were obtained by using values of surface light measured by the staff meteorologists of the Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM), and the extinction coefficients of the water column were measured along the day at the study sites. Daily net production was calculated by using the light intensities occurring at the fish territories, as described above, and photosynthesis rates obtained in the *P*–*I* curve experiments. Values of light and photosynthesis were used to estimate the production modeled by the hyperbolic tangent (Jassby and Platt, 1976), as follows: $P = P_{\max} \cdot \tan h(\alpha \cdot I / P_{\max}) + R$, where *P* (mg C gdw⁻¹ h⁻¹) is the photosynthetic rate, P_{\max} (mg C gdw⁻¹ h⁻¹) is the maximum rate of photosynthesis at saturating irradiance, α (mg C gdw⁻¹ h⁻¹ · (μE m⁻² s⁻¹)⁻¹) is the initial slope of the curve at pre-saturation, *I* (μE m⁻² s⁻¹) is the irradiance, and *R* (mg C gdw⁻¹ h⁻¹) is the rate of respiration. Those values were summed up at every hour during the day to determine daily net production of multispecific algal turfs per biomass and, a posteriori, rates were converted into gC per unit area.

3.1.4. Microfauna

The associated cryptofauna were identified and quantified inside and outside *S. fuscus* territories, by using the same standing-crop samples (100 cm²; $n = 30$). Densities were compared inside and outside by the Student's *t*-test (Zar, 1996). The organisms were manually separated from algal turfs under a stereo-microscope (10×). After trial, samples were homogenized in a Dolphus plate (200 squares = 25 mm² each) and the organisms were scored in each square with a stereo-microscope (50×), after prior identification at the lowest possible taxonomic level.

3.2. Exclusion experiment

Two treatments and one control (Fig. 2A–C) were used to assess the effects of herbivory by fish and fertilization, via fish waste products, upon the epilithic algal community inside territories. The cage treatment was composed of an aluminum frame covered with a Nylon net (mesh = 20 mm square, wire diameter = 0.5 mm). This treatment generally encompassed a whole territory. Fish were removed and the Nylon net was attached to the frame, in order to avoid any possible access by fish; the epilithic

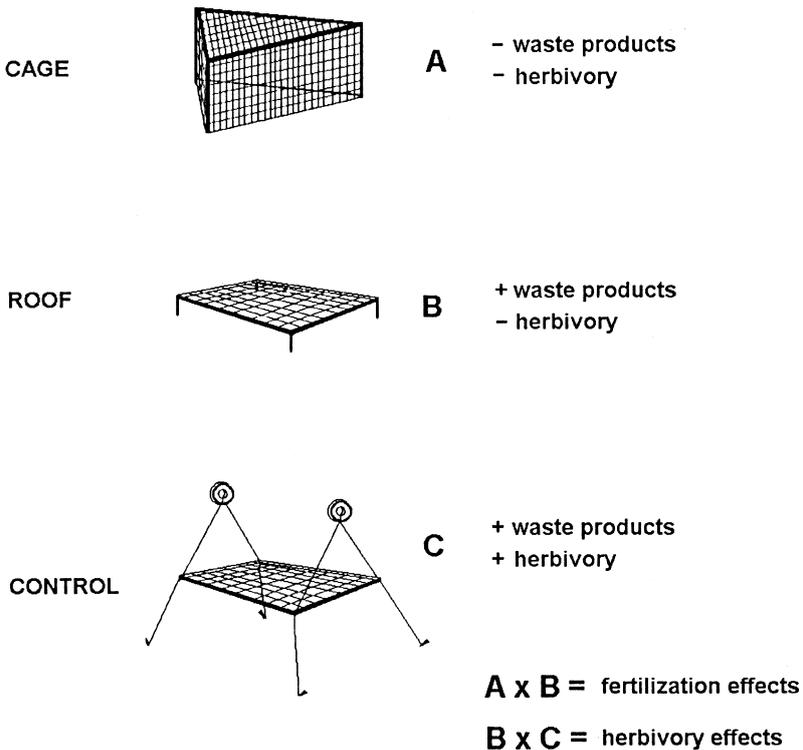


Fig. 2. Treatments and control used to assess herbivory and fertilization effects by *Stegastes fuscus* on epilithic algal community.

algae in this way suffered no influence from fish herbivory or waste products. Secondary effects from waste products of adjacent territories were avoided by establishing the cages in territories where neighbor damselfish were at least 1 m apart. This was possible since in the zone where experiments were developed, territories were surrounded by large patches of *Palythoa caribaeorum*, which functioned as natural borders where no *S. fuscus* inhabit. The roof treatment comprises an aluminum square, $15 \times 15 \times 8$ cm, with the same Nylon net affixed to it, and was cemented on the substratum inside a territory. Resident fish, with this artifact, could not feed on algae, but their waste products could fall upon epilithic algae. The control was made using the same material described above for roof and cage treatments including the same net mesh, and was designed to eliminate the shade effect caused by the Nylon net. Fish could swim underneath the structure and feed normally, while their waste products could fertilize algae. Underwater irradiance measures for each treatment were recorded with a LICOR (Data Logger) utilizing a Li-1000 spherical sensor. Light levels were $378 \mu\text{E m}^{-2} \text{s}^{-1}$ under the cage treatment, $382 \mu\text{E m}^{-2} \text{s}^{-1}$ under the roof treatment, and $392 \mu\text{E m}^{-2} \text{s}^{-1}$ under the control. The treatments and control had the Nylon net changed weekly, in order to minimize algal settlement. Five sets of treatments were randomly placed inside territories between 3 and 5 m deep, and each set included a cage, a roof and a control. Each treatment was approximately 5 m apart from the next, and the distance between each set was 15 m. The experiment was initiated during the winter of 1992 and finished in the summer of 1993 (8-month period). Algal succession and percent cover were analyzed fortnightly (with SCUBA), by quantifying all algae inside the treatments and controls, using the point-intercept method (Chapman, 1989). Shannon–Weaner diversity index (H' – base 2 log) was used to compare algal diversity among treatments and control, and one-factor ANOVA plus Student–Newman–Keuls (SNK) multiple comparisons (Zar, 1996) were used to test significance among algal diversity of treatments and control. Interactions within and among treatments and control concerning algal abundance were analyzed through a MANOVA, since the counts were realized in fixed quadrats, and consequently there was dependence in subsequent counts through time (Sauer-Machado et al., 1996), followed by SNK multiple comparisons (Zar, 1996).

3.3. Feeding habits

Fish were sampled in winter ($n = 40$) and in summer ($n = 40$) months, by using handspears and handnets nearby the study sites. Collections were confined to mid-afternoon, when feeding rates were confirmed to be highest. The length (TL = total length) and weight (wet weight) of each fish was recorded, and gut contents were removed and frozen for later analysis. The gut contents (stomach plus entire intestine) were homogenized on a Dolphus plate and organisms, previously identified at the lowest possible taxonomic level, were counted on 100 random squares with stereo-microscopes ($50 \times$). Percentage composition of diets was compared between winter and summer using the Student's t -test (Zar, 1996). The scores were compared with the results on algal abundance from the enclosure experiment (point-intercept counts), to investigate selectivity (Ivlev, 1961) by *S. fuscus*.

3.4. Grazing rates

Feeding rates were assessed in winter ($n = 15$) and in summer ($n = 15$) according to the frequency of bites taken by a fish during periods throughout the day. The total amount of food ingested by a fish per day was estimated by the product of the daily bite rate and bite size (sensu Klumpp and Polunin, 1989). Two divers (using SCUBA) alternately observed four fish for 10-min periods, at each hour of the day, recording on acrylic sheets the number of fish bites and other behavior patterns (mating, nesting, etc.).

The bite size was estimated in a previous laboratory experiment. Fish were captured with handnets and brought alive to the laboratory, where they were kept in circular tanks (3000 l) with running fresh seawater. The gut contents of fish were extracted after starving them for 18, 20, 22 and 24 h, for verification of when digestive tracts were completely emptied. After 22 h, 90% of the fish ($n = 20$) had empty guts. Therefore, they were kept starved for about 24 h in order to have their digestive tracts totally empty. Another tank was prepared with two masonry blocks placed at opposite sides, containing holes for fish sheltering, and enough space for the establishment of two territories. Two fish were put in this tank for 6 h for acclimatization. Two fish were necessary to stimulate territorial behavior and, thus, a better adaptation to tank conditions. Granite plates (10 cm²) left at the study sites inside the territories for 8 months to allow the development of an epilithic algal community, were offered as a food source and placed (two plates) in front of each masonry block. The experiment required that each fish ($n = 50$) took 50 bites from the plates prior to removal and extraction of the gut contents. The gut contents were dried at 80°C for about 24 h and weighed. The bite size was calculated by dividing the dry weight of the gut contents by the number of bites taken per fish. When defecation was detected, faeces were collected and included in the final analysis for gut contents, as previously mentioned and, assuming that some material would have been lost from these due to assimilation.

3.5. Assimilation efficiency

Food assimilation efficiency by *S. fuscus* was investigated using the total assimilation efficiency ($n = 20$) and the nitrogen assimilation efficiency ($n = 20$) methods used by Montgomery and Gerking (1980). Assimilation was determined by comparing nutrient concentration in stomach with nutrient concentration in faeces using ash as an indigestible marker. Fish were captured with handnets between 10:00 and 11:00 h, when the defecation routine was noted to intensify, and the gut was assumed to be full. The stomach and the first 1 cm of foregut plus faeces (considered as the terminal 5 cm of hindgut), and assuming negligible absorption in these portions, were extracted, dried at 70°C and burned at 550°C for 6 h for ash-free dry weight and total nitrogen analysis.

4. Results

4.1. Territory characteristics

Territories of average-sized fish (13.8 cm \cong 63.10 g wet wt.) had an average total area

Table 1
Description of territory characteristics (mean±S.D.) of *S. fuscus*^a

Total area (m ²)	2.10±0.36 (<i>n</i> = 20)	
Total area covered by algae (m ²)	1.64±0.43	
Area not covered by algae (m ²)	0.47±0.11 ^b	
Total biomass of algae	Winter (<i>n</i> = 15)	Summer (<i>n</i> = 15)
	70.29±21.15 gC m ⁻²	284.09±89.10 gC m ⁻²
Net productivity of multispecific turf algae	115.27 gC territory ⁻¹	465.90 gC territory ⁻¹
	Winter (<i>n</i> = 12)	Summer (<i>n</i> = 12)
	0.52 gC m ⁻² day ⁻¹	1.43 gC m ⁻² day ⁻¹
	0.86 gC day ⁻¹ territory ⁻¹	2.34 gC day ⁻¹ territory ⁻¹

^aAverage size 13.8 cm ± 63.10 g. wet wt.

^bMainly *Palythoa caribaerum*, corals and bare rock.

of 2.10±0.36 m². Seventy-eight percent (1.64 m²) of the territories were covered by algae and 22% (0.47 m²) were covered by corals, zoanths and bare rock or sand (Table 1). Mean algal standing-crop was 70.29 and 284.09 gC m⁻² in winter and in summer, respectively, accounting for an average standing-crop of 115.27 gC territory⁻¹ in winter and 465.90 gC territory⁻¹ in summer (Table 1). Algal standing-crop within the damselfish territories was significantly greater than outside for both winter (41.91±6.67 gC m⁻²; *t* = 4.25; *P* < 0.05) and summer (146.69±21.88 gC m⁻²; *t* = 25.57; *P* < 0.05).

Production measurements taken in situ with the simulator showed the average net primary productivity (NPP) of multispecific algal turfs inside territories to be between 0.52 gC m⁻² day⁻¹ in winter and 1.43 gC m⁻² day⁻¹ in summer. The NPP for each territory was then 0.86 gC day⁻¹ territory⁻¹ and 2.34 gC day⁻¹ territory⁻¹, respectively, in winter and in summer (Table 1).

Invertebrate microfauna inside territories was abundant and diverse, exhibiting an overall mean of 72 ind/100 cm², accounting for ≈ 11 808 ind/territory covered by algae. The density of cryptofauna inhabiting the multispecific algal community, outside territories, was less dense, with a mean density of 28 ind/100 cm². From the overall density inside territories, amphipods and tanaids made up 57%, and polychaetes, gastropods and bivalves 25%, with the remaining 18% distributed among other groups. Although tanaids were the most abundant groups outside territories, amphipods, tanaids and polychaetes were dominant outside as well as inside (Table 2). Among these dominant groups only tanaids and polychaetes showed total densities not significantly different. From the 15 main groups indicated in Table 2, only five presented densities not significantly different inside and outside territories.

4.2. Exclusion experiment

Algal species inside *S. fuscus* territories were stable during the 8 months of experiment, and there were shifts only in abundance due to ephemeral species blooms. Algal mats were primarily composed of 54.3% filamentous species, mainly rhodophytes, 38.2% red calcareous algae and 7.1% fleshy algae. Table 3 shows all algae observed in the territory boundaries, including tiny algae not assessed with the point–intercept counts.

Table 2
Comparison of cryptofauna density^a (mean±S.E.) inside and outside territories of *S. fuscus*

Taxa	Inside (n = 15)	Outside (n = 15)	Significance level ^b
Crustaceans			
Amphipods	23±6.79	7.3±1.52	<i>P</i> < 0.05
Tanaids	19±4.27	12±2.87	ns
Brachyurans	1.6±0.79	—	<i>P</i> < 0.05
Isopods	1.5±0.58	0.8±0.39	ns
Decapods	0.6±0.27	—	<i>P</i> < 0.05
Caprellids	0.5±0.12	0.1±0.09	<i>P</i> < 0.05
Pagurids	0.3±0.15	0.1±0.09	ns
Cirripeds	0.3±0.22	—	ns
Molluscs			
Gastropods	6.2±2.33	0.8±0.31	<i>P</i> < 0.05
Bivalves	4.8±1.32	0.3±0.2	<i>P</i> < 0.05
Annelids			
Polychaetes	7.1±1.19	6.5±1.26	ns
Cnidarians			
Hydrozoan	2.1±0.82	—	<i>P</i> < 0.05
Echinoderms			
Ophiuroids	1.6±0.49	0.2±0.13	<i>P</i> < 0.05
Urchins	0.6±0.2	—	<i>P</i> < 0.05
Bryozoans	2.5±2.43	—	<i>P</i> < 0.05
Others	0.8±0.20	0.3±0.14	<i>P</i> < 0.05
Total	72	28	

— trace indicate absent.

^aDensity per 100 cm².

^bStudent's *t*-test comparisons between densities inside vs. outside territories.

Dominance by *Jania* spp. upon other algae was evident on roof treatment, affecting abundance of other algae thus decreasing total diversity. Algae excluded from grazing action by *S. fuscus* underwent an abrupt diversity drop (Fig. 3B), consequently, there was a significant difference between algal diversity in roof treatment and control (Table 4). As for diversity, abundance of algae between roof treatment and control was also significantly different in the course of the experiment (SNK, *P* = 0.042). When a fish was present, *Jania* spp. rarely exceeded 50% of the total algal cover (Fig. 3A). Conversely, without fish herbivory, competition among algae was an expressive factor, with *Jania* spp. occupying more than 70% of the substratum. Although *Jania* spp. were dominant even in the control in certain months, the difference in algal density from September to March between roof and control was evident.

Despite cage treatment presenting an algal diversity higher than roof treatment, such a difference was not significant as shown by ANOVA (Table 4). Likewise, algal abundance was kept higher in the cage treatment (Fig. 3C), but not significant during the experiment development (SNK, *P* = 0.96). Such a pattern apparently suggests that fish waste products have no effect upon algal community in roof treatment. *Jania* spp. were once more the dominant algae, nevertheless, they did not exceed 50% of the total cover.

Table 3
Algae observed within territory boundaries of *S. fuscus*

	Common ^a	Uncommon ^b	Rare ^c
Rhodophyta			
<i>Jania adhaerens</i>	x		
<i>Jania capillacea</i>	x		
<i>Amphiroa</i> sp.		x	
<i>Gelidium pusillum</i>	x		
<i>Gelidiella</i> sp.			x
<i>Polysiphonia</i> spp.	x		
<i>Ceramium</i> spp.	x		
<i>Centroceras clavulatum</i>	x		
<i>Herposiphonia</i> sp.		x	
<i>Hypnea</i> spp.		x	
<i>Neogoniolithon</i> sp.	x		
<i>Champia</i> sp.			x
<i>Spyridia</i> sp.			x
Chlorophyta			
<i>Cladophora</i> spp.	x		
<i>Enteromorpha</i> sp.	x		
<i>Bryopsis</i> sp.		x	
<i>Ulva</i> spp.	x		
<i>Chaetomorpha</i> sp.		x	
Phaeophyta			
<i>Sphacelaria</i> sp.		x	
<i>Hincksia</i> sp.		x	
<i>Bachelotia</i> sp.		x	
<i>Colpomenia</i> sp.			x
Cyanophyta			
Diatoms	x		

^aAppeared in more than 70% of point–intercept counts.

^bIn more than 5%.

^cDid not appear in counts.

4.3. Diet and selectivity

The diet of *S. fuscus* was basically composed of algae (70% of the total diet); nevertheless, it ingested some animal material (30% of the total diet). Such a pattern was equally confirmed in winter and in summer (Table 5). As shown in Table 5, fish fed upon various morphological groups of algae and animals. Both food components were seasonally well distributed in guts, with only few groups differing significantly between winter and summer. When comparing the average proportion of algae in stomachs (winter–summer) with that sampled in territories (exclusion experiment), it was clear that *S. fuscus* had the typical selectivity behavior for certain types (Fig. 4). Red filamentous algae, such as *Polysiphonia* spp., *Ceramium* spp. and *Centroceras clavulatum*, were eaten in the same proportion as found in territories (value $\cong 0$). Despite the fact that *Jania* spp. had been eaten in large quantities, they were not preferentially

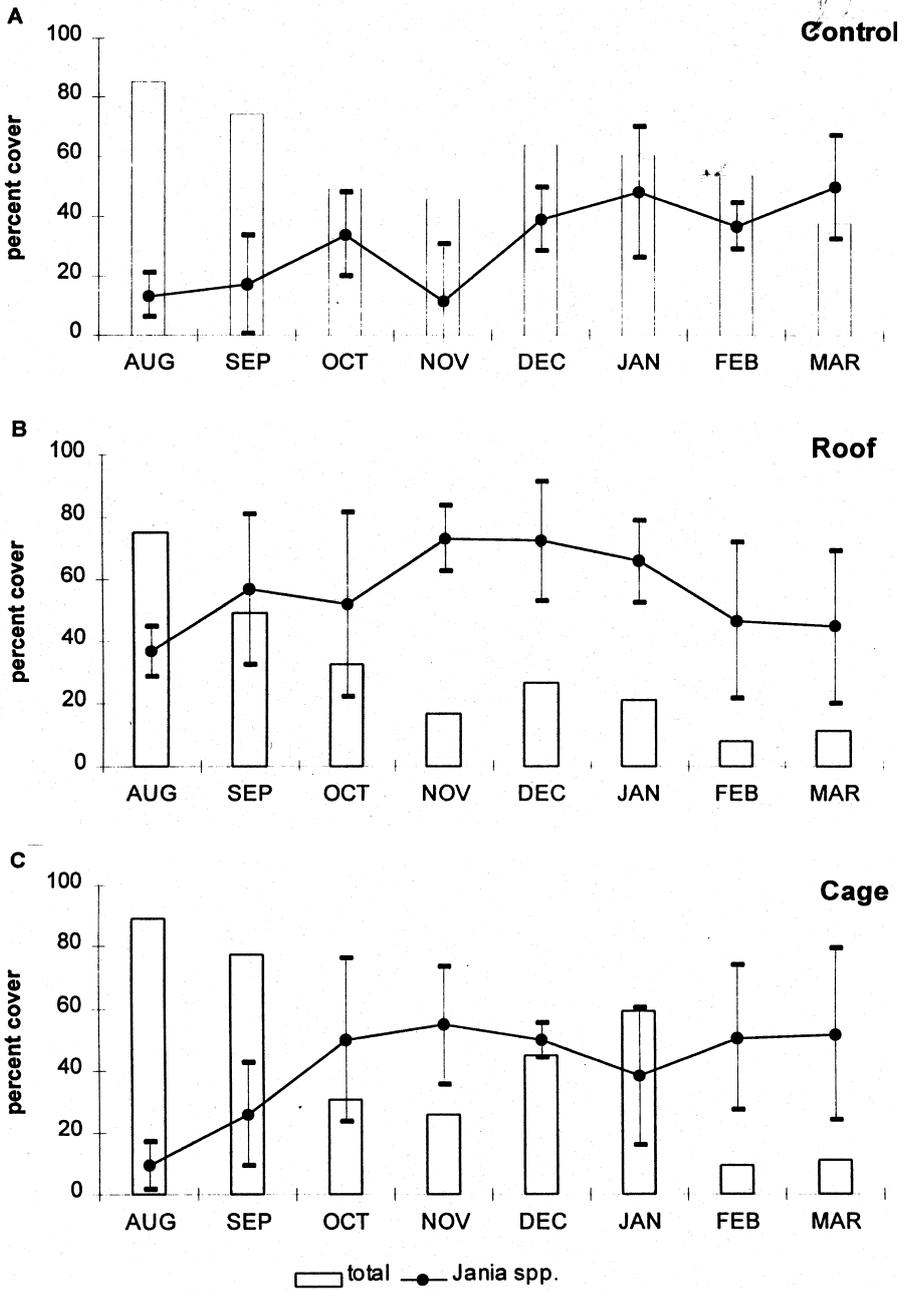


Fig. 3. Algal succession presented as *Jania* spp. percent cover (mean±S.D.) versus total (minus *Jania* spp.) percent cover of other algae on treatments and control. Based on *Gelidium pusillum*, *Polysiphonia* spp., *Ceramium* spp., *Ulva* sp., *Cladophora* spp., *Centroceras clavulatum* and colonial diatoms.

Table 4

Mean diversity and evenness of treatments of the exclusion experiment plus ANOVA and SNK results* among algal diversity of treatments

Treatments	Control	Roof	Cage
H'	2.993	2.135	2.666
Evenness	0.835	0.577	0.720

* $F = 5.216$, $P < 0.05$. Control vs. Roof–SNK, $P < 0.05$. Roof vs. cage–SNK, ns.

selected, as expected from calcareous algae; the same occurring with *Gelidium pusillum*. Other tiny filamentous algae, such as *Herposiphonia* spp., *Briopsis* spp., Ectocarpaceas and Cyanophytes were well accepted by damselfish, while crustose coralline algae were totally avoided. *Ulva* spp. were apparently avoided by the fish, due to unknown reasons,

Table 5

Comparative diet of *S. fuscus* between winter and summer (% of diet)

	Winter ($n = 20$)	Summer ($n = 20$)	Significance level ^a
Algae			
Rhodophyta			
<i>Jania</i> spp.	23.8	14.9	ns
<i>Gelidium pusillum</i>	8.1	5.9	ns
<i>Polysiphonia</i> spp.	4.1	5.5	ns
<i>Ceramium</i> spp.	2.5	13.8	$p < 0.05$
<i>Centroceras clavulatum</i>	3.2	5.1	ns
<i>Hypnea</i> spp.	3.6	2.8	ns
<i>Herposiphonia</i> sp.	1.6	0.1	ns
Chlorophyta			
<i>Cladophora</i> spp.	9.7	10.2	ns
<i>Ulva</i> spp.	1.6	2.3	ns
<i>Bryopsis</i> sp.	6.1	0.9	$p < 0.05$
<i>Enteromorpha</i> sp.	2.1	5.0	ns
Phaeophyta			
Ectocarpaceae ^b	0.5	6.4	$p < 0.05$
Cyanophyta	2.0	1.7	ns
Animals			
Sponges	13.9	4.9	$p < 0.05$
Hidrozoans	7.1	8.9	$p < 0.05$
Amphipods	3.7	0.7	ns
Polychaetes	1.9	3.8	$p < 0.05$
Ostracods	1.3	1.5	ns
Bryozoans	1.1	0.3	ns
Copepods	0.9	1.2	$p < 0.05$
Cirripeds	0.5	0.4	ns
Bivalves	0.4	0.6	ns
Tanaids	0.3	0.1	ns
Caprellids	0.2	0.1	ns
Gastropods	0.2	0.3	ns
Unidentified eggs	0.6	0.3	ns

^a P values for Student's t -test comparisons.

^b*Sphacellaria* sp., *Hincksia* sp. and *Bachelotia* sp.

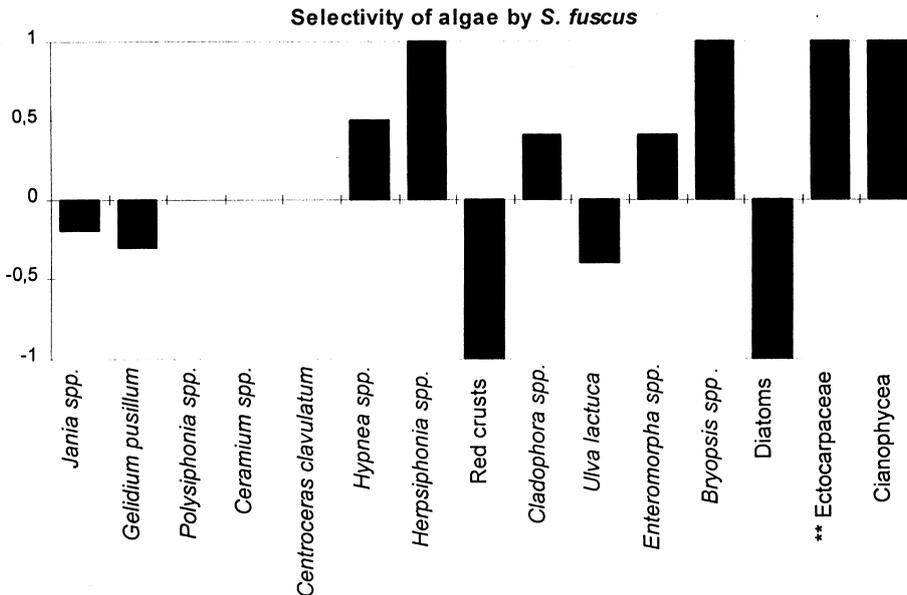


Fig. 4. Algae selectivity by *S. fuscus* presented as comparison between abundance of algae inside territories (point–intercept counts) and abundance of algae in stomach (% of occurrence). *Ivlev index (1961) = ((stomach – territory)/(stomach + territory) × algae abundance in territories). ***Sphacellaria* sp., *Hincksia* sp. and *Bachelotia* sp.

since these algae are usually elected by herbivorous fish. The same shunning pattern was observed for colonial diatoms. Selectivity by *S. fuscus* regarding cryptofauna was not assessed, considering that some groups could be incidentally ingested.

4.4. Grazing rates and assimilation

In winter, *S. fuscus* exhibited ingestion rates that rose, during the day, up to 4.1 bites/min at 15:00 h, only stopping feeding when there was no sunlight (Fig. 5). Feeding behavior, at the last 30 min of light, was generally very much disturbed, because a great number of roving herbivorous fish were at that time coming from feeding areas, searching for shelter, and *S. fuscus* tended to chase them out. Besides, there was the presence of some predators, such as basses and morays seeking food. Mean total number of bites taken per day, in winter, was 1780. From laboratory experiments it was concluded that an average adult-sized *S. fuscus* (13.8 cm \cong 63.10 g wet wt.) ingested approximately 1 mg dry wt. per bite ($n = 50$; S.E. = 0.08). This represents a total daily ingestion of 1780 mg dry wt. (8.0% of fish dry body weight) in winter. The food eaten by *S. fuscus* comprised 48.7% organic carbon; thereby, 866.8 mgC day⁻¹ were ingested in winter. Such a rate corresponded to 0.8% of biomass and 100% of net primary productivity of an average size territory. Grazing rates in summer were lower than in winter, and accumulated 1586 bites day⁻¹, with a peak of 3.8 bites

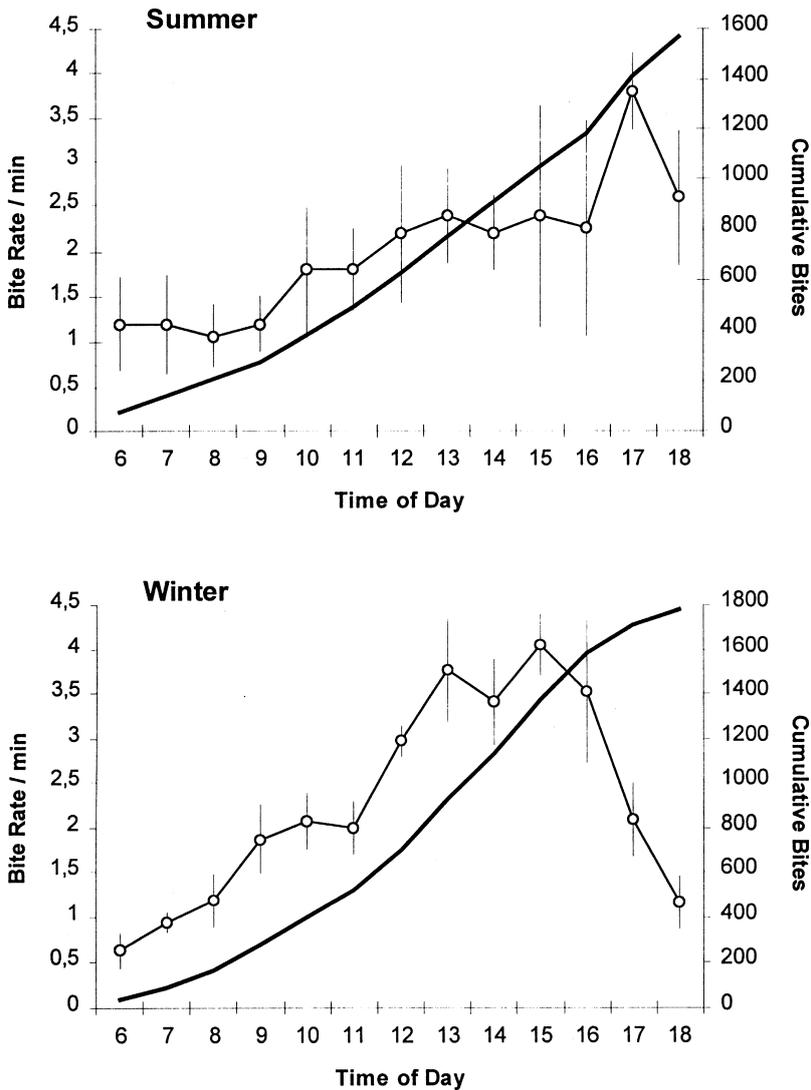


Fig. 5. Grazing rates of *S. fuscus* based on bites rates (mean \pm S.D.) and mean cumulative number of bites winter ($n = 12$) and summer ($n = 12$).

min^{-1} at 17:00 h (Fig. 5). These numbers were equivalent to 1586 mg dry wt. daily ingested (7.5% of fish dry body weight). Therefore, total consumption was 772.3 mgC day^{-1} or 0.2% of biomass and 32% of the primary production of the territory in summer.

A full gut of *S. fuscus* contained 424 mg dry wt. of food, corresponding to 420 bites. Therefore, contents turnover in a gut was 4.1 times day^{-1} (1780 bites day^{-1}) in winter

and 3.7 times day⁻¹ (1586 bites day⁻¹) in summer. Food assimilation efficiency was low in *S. fuscus*, being total assimilation efficiency equal to 28.08% ($n = 12$; S.D. = 9.94) and 57.51% for total nitrogen ($n = 12$; S.D. = 14.08).

5. Discussion

5.1. Resident cryptofauna of territories

Our findings regarding microfauna abundance showed that algal mats inside the *S. fuscus* territories support higher densities of mesoinvertebrates than those outside territories, which are exposed to intense predation. Similar patterns were found in artificial substrata (Hixon and Brostoff, 1982; Zeller, 1988) as well as in natural substrata (Lobel, 1980; Klumpp et al., 1988; Klumpp and Polunin, 1989). Mesoinvertebrate densities inside *S. fuscus* territories (72 ind/100 cm²) were comparable to those found on coral reefs in Panama (Lobel, 1980: up to 80 ind/100 cm²), but lower than those reported in the Central Great Barrier Reef (Klumpp et al., 1988: about 583 ind/100 cm²). Nevertheless, densities in algal mats outside territories (28 ind/100 cm²) were greater than those reported by Carpenter (1986) in the Virgin Islands (10 ind/100 cm²), but still lower than those found in Panama (Lobel, 1980), Hawaii (Brostoff, 1988) and Central Great Barrier Reef (Klumpp et al., 1988). These differences may be explained by factors such as different abundance of herbivores fish, that are the major controllers of algal abundance and biomass (Ogden and Lobel, 1978; Hixon, 1983), as well as abundance of small carnivores (e.g. wrasses). Cryptofauna densities generally increase with an increase in algal biomass and decline with increasing grazing pressure (Vine, 1974; Carpenter, 1986; Klumpp et al., 1988; Hixon and Brostoff, 1996). *S. fuscus* territories established in deeper areas were observed to hold less algal biomass and correlated lower mesoinvertebrate abundance (Ferreira, unpublished data).

Although cryptofauna grazing rates were not assessed, they are expected to affect overall production inside territories, as already demonstrated in experimental works (Brawley and Adey, 1981; Klumpp et al., 1988; Klumpp and Pulfrich, 1989). Dominant groups found on algal mats either outside or inside territories of *S. fuscus* were also dominant in coral reef areas (see Klumpp et al., 1988) with amphipods, the most abundant group inside territories, being known as important grazers (Klumpp et al., 1988).

Carnivorous fish, such as grammistids and serranids, were observed to keep hiding places around boulders within the territories, without any reaction from *S. fuscus*, while most conspecific and interspecific herbivores, and wrasses (mainly *Halichoeres poeyi*), were not allowed to feed within territories. The former take benefit from a well-established resource, while apparently the others cannot. Thus, *S. fuscus* territories serve as nursery sites, exporting a high quality food and also sustaining a great number of fish and macroinvertebrates. Indeed, exhaustive works have shown that the majority of the members of reef fish communities live on a diet of benthic invertebrates (see Jones et al., 1991)

5.2. Herbivory structuring algal community within territories

Algal succession patterns obtained with the enclosure experiment clearly indicated that herbivory by *S. fuscus* exerts a strong influence upon the epilithic algal community of territories. As already cited for other damselfish, herbivory apparently acts preventing any algae from being competitively excluded by others (Montgomery, 1980a; Hixon and Brostoff, 1983; Sammarco, 1983). In our case study, grazing by *S. fuscus* prevents *Jania* spp. from dominating and perhaps overshadowing other species, as commonly observed outside territories, where algal communities are dominated mainly by *Jania* spp., thus retarding the establishment of later successional patterns. Indeed, these algae are also frequently dominant inside territories, as shown in Fig. 3A. Algal communities are kept in an early succession stage, where those species holding a high potential of growth predominate. Such a pattern may well explain why generally only filaments algae and some fleshy algae dominate damselfish territories. Possibly the weeding behavior observed in some damselfish (Lassuy, 1980; Irvine, 1982) may only be necessary where algae are competitively equivalent (including non-palatable species that the damselfish tend to weed out) and/or where herbivory intensity is not efficient to solely promote high productive species. Indeed, the major constraints governing these succession patterns seem to be the competitive ability and correlated algal abundance, as well as herbivore abundance and herbivory intensity. Cropping action, which keeps algae in an exponential growth, is well detectable among damselfish (Klumpp et al., 1987) including *S. fuscus*, although it is not uncommon to see a *S. fuscus* specimen taking a whole turf, including the holdfast. Further investigation is necessary to verify how often this event occurs in search for reliable effects of cropping action.

We used data from an experiment in which the succession of algae was monitored outside the damselfish territories (Gonçalves et al., in preparation) at the same study sites herein described to support the hypothesis of intermediate disturbance (sensu Connell, 1978) applied to some damselfish. Such experiment showed, after a 3-month period in spring–summer, an algal diversity of 1.912 on control, exposed to high levels of grazing, and 2.059 in the caged treatment, excluded from any predation. When compared to our diversity results found inside territories of *S. fuscus* (2.993), algal diversity outside territories zone was significantly lower ($t = 5.51$; $P < 0.001$). These patterns have been reported for other tropical areas (Vine, 1974; Brawley and Adey, 1977; Lassuy, 1980; Sammarco, 1983; Ruyter Van Steveninck, 1984; Kamura and Choonhabandit, 1986; Russ, 1987; Klumpp and Polunin, 1989; Hixon and Brostoff, 1996), with few exceptions (Lassuy, 1980; Montgomery, 1980a). Therefore, algal diversity was maximized at intermediate levels of herbivory (predation) inside territories of *S. fuscus*, whereas at high and low herbivory intensity, diversity was lower.

5.3. Waste products as source of fertilization

The exclusion experiment indicated that fish waste products did not contribute to change significantly diversity or even abundance of epilithic algae inside territories. *S. fuscus* faeces were observed to be released at no determined place, thus it could be deposited in any kind of substratum, not specifically upon algae. Faeces of other

damsel fish species were reported to be far more important than excretion in the generation of nitrogen (Polunin and Koike, 1987). Indeed, faeces of *S. fuscus* as other herbivorous fish that have consistent faeces, would be slowly dissolved releasing nutrients for algal uptake. However, such amount of nutrients was not sufficient to affect significantly algal succession and *Jania* spp. dominance in the roof treatment. Previous works showed that there is a positive contribution of waste products from other herbivorous organisms enhancing primary production (Carpenter, 1988; Williams and Carpenter, 1988). Although our results did not corroborate such effects, evidences deserve future manipulated experiments dealing with the effects of excretion and defecation, separately, upon epilithic algal community in damselfish territories.

5.4. Diet patterns

S. fuscus preference for filamentous algae (50% of ingested algae) follows the habits of most tropical herbivore damselfish (Lassuy, 1980; Lobel, 1980; Montgomery, 1980a,b; Robertson and Polunin, 1981; Kamura and Choonhabandit, 1986; Hinds and Ballantine, 1987; Klumpp and Polunin, 1989), although approximately 25% of algae ingested by *S. fuscus* were calcareous algae (Table 4). Despite the fact that previous studies showed that damselfish occasionally could ingest calcareous algae, they did it in small quantities. In his well-known work on Caribbean fish, Randall (1967) also found fragments of at least two calcareous algae, *Amphiroa* sp. and *Halimeda* sp., on the guts of *S. fuscus*. Calcareous algae, as analyzed by Montgomery and Gerking (1980), are expected to be unselected in favor of more palatable and digestible algae, but such an event does not necessarily take place everywhere. The high abundance and suggested competitive potential exhibited by *Jania* spp. in the current habitat, probably make these algae into an indispensable resource. Actually, food availability and not always food quality are known to be important to other herbivorous fish (Bryan, 1975). This is an expected strategy and well reported from other trophic levels (Longhurst and Pauly, 1987). The same pattern seems to occur with *Gelidium pusillum*, another dominant alga which was consumed in considerable amounts, even though Lobel (1981) had reported that this alga was apparently not digested by the gut enzymes of *S. nigricans*. A possible explanation could be that the low stomach pH of *S. fuscus* would digest these algae making them promptly accessible, thus contrasting with Lobel's suggestion that a fish with an acid stomach avoids calcium carbonate because of the buffering capacity which would increase the pH and interrupt the lysis process of algal cell walls. Other possible evidence of a powerful acid digestion was a conspicuous colonial diatoms possessing a fine cellular wall, observed to be eaten by *S. fuscus*, but whose fragments were not found on guts. Indeed, the stomach pH of damselfish is among the most acid noticed for herbivorous fish (Lobel, 1981; Horn, 1989). Secondly, the majority of these algae (calcareous algae) would be consumed unintentionally, provided that blooms of red filamentous algae, mainly *Ceramium* sp. and *Centroceras clavulatum*, can occur upon or within turfs of *Jania* spp. The former seems to be more plausible, since at least four other damselfish, with approximately the same size, were confirmed to hold selectivity for some algae (Lobel, 1980; Montgomery, 1980a; Kamura and Choonhabandit, 1986; Klumpp and Polunin, 1989). This question lies on what extent the selectivity by *S.*

fuscus is, dealing with problems such as how tiny would algae be, so that the fish could still select it, and must consider factors such as the fish's mouth size.

Like other herbivorous fish, *S. fuscus* includes some animal material in its diet, therefore supporting the idea that cryptofauna would complement nitrogen shortage in algae (Klumpp et al., 1988; Zeller, 1988; Klumpp and Polunin, 1989). Although it is expected that some organisms should be incidentally ingested, it was not uncommon to observe an ambushing behavior, as the fish seeking some more motile invertebrate (e.g. amphipods, copepods). All the guts of juveniles (< 8 cm) analyzed showed 70% of their diet composed by animal material, as compared to only 30% found in adults. Lassuy (1984) also found that juveniles of *S. lividus* had their diets based upon 36% of mesoinvertebrates, and the same pattern was recorded by Emery (1973) working with some Caribbean damselfish. This shift is fundamentally explained by a greater need for a high protein diet during the initial phase of life for fast growth (Mattson, 1980). Whereas some damselfish may display a weeding behavior (Lassuy, 1980; Irvine, 1982), it was not confirmed with *S. fuscus*, although preliminary examinations showed positive preference for some species of algae. Further experiments with replicates are necessary to confirm this trend.

5.5. Grazing rates

The results of grazing rates by *S. fuscus* showed no marked shifts between winter and summer periods. The greater values of consumption observed in winter (886.8 mg C day⁻¹) rather than in summer (772.3 mg C day⁻¹) could possibly be related to temperature; grazing is known to vary with changes in water temperature (Hatcher, 1981; Carpenter, 1986; Polunin and Klumpp, 1992). Maximum feeding peak in winter occurred in mid-afternoon and later in summer (17:00 h), due to a longer daylight period. Such feeding pattern was reported for a number of damselfish and other herbivorous fish (Montgomery, 1980a; Taborisky and Limberger, 1980; Robertson, 1984; Polunin and Klumpp, 1989; Klumpp and Polunin, 1990), being better explained as an adaptation to photosynthesize accumulation in algae (Polunin and Klumpp, 1989).

Epilithic algal community biomass inside territories of *S. fuscus* exhibited a 4-fold difference between winter and summer, with a correlated high net primary production in summer. Even though we have made several experiments on algal production, but not having estimated the production of EAC outside the territories, NPP of EAC on Arraial do Cabo rocky shores inside damselfish territories is comparable those reported for coral reef areas (Klumpp et al., 1987; Russ, 1987; Klumpp and McKinnon, 1992). Consequently, ingestion rates by *S. fuscus* do not appear to affect the algal community of territories in summer, when both biomass and production were higher. In winter, however, ingestion rates virtually remove total algal production, pointing out that such algae should possess growth adaptations to promote biomass replacement at rates greater than rates of NPP consumption.

Recent studies have demonstrated that a large portion of NPP of the damselfish's territories are taken by other herbivorous organisms (Klumpp and Polunin, 1989, 1990). During all the experiments, we observed few herbivorous fish feeding in *S. fuscus* territories, including an occasional neighbor *S. fuscus* that, once detected, was immedi-

ately chased. Roving herbivores (surgeonfish and parrotfish) were generally observed on the study sites only at the end of the day; these fish usually used these protected areas as sleeping sites, feeding in distant areas (Ferreira, unpublished data). Only some solitary *Sparisoma atomarium* and *Acanthurus bahianus* were frequent at the study sites and were easily kept away from the territories boundaries by *S. fuscus*. Urchins were common at the study sites, but seemed to exert influence only in shallow areas (0.50–2 m) where they are concentrated, whereas herbivorous gastropods were generally tiny and uncommon inside territories. Probably a little of the algal production of territories is lost to other herbivores, although we did not consider mesoinvertebrate influence. Despite the fact that areas of high *S. fuscus* density suggests that herbivory in winter could influence the overall net primary production of such system, the accumulated algal biomass and high turnover rate seem to sustain the balance. One might keep in mind that this event occurs at a random spatial scale, since a high heterogeneity exists in the spatial distribution patterns of organisms on rocky shores at Arraial do Cabo. As an example, our data on community structure indicated that sites which are more exposed to wave pressure appear to sustain higher densities of roving herbivorous fish (Ferreira et al., in preparation) than sites correlated with few or complete absence of *S. fuscus* territories. If we consider those sites with high densities of roving herbivorous fish which are expected to have higher grazing rates (Hixon and Brostoff, 1982; Steneck, 1988; Gonçalves et al., in prep.), grazer demand could also consume great amounts of NPP in winter periods. This would make the comparison of the balance between grazer demand and NPP in such different sites of rocky shores vital to the understanding of how the overall production behaves when facing such grazing pressure.

Our data on *S. fuscus* food acquisition and processing (Table 6) are readily comparable to those presented by Klumpp and Polunin (1989) on comparative grazing rates of herbivorous damselfish. Despite the fact that *Stegastes apicalis* had a similar bite size to *S. fuscus*, daily bite rates and ingestion rates of *S. apicalis* were higher. *Stegastes rectifraenum* has a bite size larger than that of *S. fuscus* and *S. apicalis*. Also, it has a

Table 6
Comparative food acquisition and processing of herbivorous damselfishes ($\cong 70$ g of fish wet weight)^a

Species	Bite size (mg/bite)	Digestive tract size (mg/dry wt.)	Total daily bites	Daily gut fillings	Ingestion rate (mg/dry wt./ fish/day)	Assimilation rate
<i>S. fuscus</i> ^b (southeastern Brazil)	1.0	424	1780 (winter) 1568 (summer)	4.1 (winter) 3.7 (summer)	1787 (winter) 1574 (summer)	Total = 28% <i>n</i> = 57.4%
<i>S. apicalis</i> ^c (central Great Barrier Reef)	1.0	543	2515 (winter) 4685 (summer)	4.0 (winter) 7.4 (summer)	2389 (winter) 4451 (summer)	Total = 35% <i>n</i> = 57%
<i>S. rectifraenum</i> ^d (northern Mexico)	2.6 (winter) 2.9 (summer)	1480	3188 (winter) 2891 (summer)	5.7 (winter) 5.8 (summer)	8436 (winter) 8584 (summer)	Total = 24% <i>n</i> = 67%

^aModified from Klumpp and Polunin (1989).

^bPresent study.

^cFrom Klumpp and Polunin (1989).

^dFrom Montgomery (1980a) and Montgomery and Gerking (1980).

greater gut size, accounting for the higher ingestion rates. Although the average gut contents turnover was similar among the three, it was slightly lower in *S. fuscus*, indicating an adaptation to the food quality that is ingested by this fish and fulfilling its minimal carbon requirements in order to acquire adequate nitrogen and phosphorus (Hay and Steinberg, 1992). Nitrogen assimilation efficiency was similar among the fish, while total assimilation efficiency (TAE) was inversely correlated to the ash contents in food: 82% in *S. rectifraenum* (TAE = 24%), 52% in *S. fuscus* (TAE = 28%) and 40% in *S. apicalis* (TAE = 35%). The differences and similarities of food processing among the three damselfish seem to be justifiable, although better explanations could be achieved with additional information, such as water temperature, changes in food quality and nutritional physiology parameters (Horn, 1989).

6. Conclusions

The data presented here indicated that, as expected, *S. fuscus* share similar features with other damselfish. In addition this species has locally specific adaptations to survive the different damselfish processes and ecological conditions found in the rocky shores studied.

Although we could not confirm a significant effect of fish waste products fertilizing algae, herbivory plays an important role upon algal succession, turning the territories into sites of high algal diversity and biomass. Epilithic algal communities of *S. fuscus* territories provide shelter and food to a rich mesoinvertebrate fauna. Zones of high densities of *S. fuscus* are expected to increase the flux of energy through the rocky shore food web, even though herbivory by these fish in winter could consume the total algal production of the territories, indicating that the overall grazing net estimates in such environments is a very interesting scope of study. *S. fuscus* may be considered as playing an important role in trophodynamic processes on the rocky shores of Arraial do Cabo.

However, Arraial do Cabo rocky shores exhibit a great heterogeneity of patterns of benthic organisms distribution following different gradients of depth and wave exposition. This suggests that the processes and the *S. fuscus* behavior within territories in such particular conditions could be distinct from those results presented here. As emphasized here, and in most studies with damselfish in other tropical areas, the effects of these fish upon the benthic community were analyzed in a single area, zone or depth, generally not considering different abiotic and even biotic gradients. Despite the fact that damselfish tend to have their greater density in shallow zones, and assumptions about whether they chose to live there or not have arisen (Zeller, 1988), such fish can frequently extend their bounds to deeper areas. Thus, it is suggested that subsequent studies should encompass large gradients in a same specific environment to search, for example, if herbivory by damselfish could still control algae diversity at different depths.

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