Journal of Fish Biology (1998) **53** (Supplement A), 222–235
Article No. jb980824

Seasonal grazing rates and food processing by tropical herbivorous fishes

C. E. L. Ferreira*†‡, A. C. Peret* and R. Coutinho†

**Universidade Federal de São Carlos, Departmento de Hidrobiologia, Via Washington Luiz, Km 235, São Carlos, SP, Cep: 13565 905, Brazil and †Instituto de Estudos do Mar Almirante Paulo Moreira, Departmento de Biologia, Rua Kioto 253, Arraial do Cabo, RJ, Cep: 28930 000, Brazil*

Seasonal variability in grazing rates and food-processing characters were assessed for three abundant fishes in a tropical rocky shore: the damselfish *Stegastes fuscus*, the parrotfish *Sparisoma atomarium*, and the surgeonfish *Acanthurus bahianus*. Significant differences were found in grazing rates among hour of day and seasons, and in food-processing characters among seasons for the three fishes. Grazing rates for *S. atomarium* and *A. bahianus* peaked at 1300 and 1400 hours for *S. fuscus*. Three main periods of different intensity in bite rates, low, intermediate and intense, were identified for all fishes. As expected, total bite rates, ingestion rates and gut fullness were highest in *A. bahianus*, the largest species studied, followed by *S. atomarium* and *S. fuscus*. *S. atomarium* with fused jaw teeth, holds the highest bite size and *S. fuscus* the lowest one. Gut turnover was high for *S. fuscus* and similar for *S. atomarium* and *A. bahianus*. Grazing rates and food-processing characters seem to vary between seasons not only due to changes in temperature, but also affected by other factors. Fishes employ different food-processing mechanisms and bear some differences in food-processing characters to achieve optimal energetic supplies from a poor nutrient food resource.

Key words: grazing rates; food processing; rocky shore; herbivorous fishes.

INTRODUCTION

Herbivory is an important process structuring diverse communities in marine ecosytems (Ogden & Lobel, 1978; Hixon, 1983; Steneck, 1988; John *et al*., 1992).

Fishes, the best group studied among all marine herbivores, are the most important organisms in terms of herbivory pressure (Horn, 1989; Choat, 1991; Hay, 1991; Hixon, 1996), although urchins can exert strong influence in overfished areas (Hay, 1984; McClanahan & Shafir, 1990). Herbivorous fishes can attain large sizes and high biomass in tropical regions (Choat, 1991), consequently, they can take over 100 000 bites m^{-2} (Carpenter, 1986), ingesting almost all or total primary production of algal covering substratum. Such organisms have been the subject of research because of the difficulties they face when feeding on poor nutrient food, and the additional morphological and physiological adaptations they developed (Horn, 1989).

Herbivorous fishes are diurnally active, feeding on a diverse set of epilithic algae and showing a general pattern characterized by a mid-afternoon grazing peak, best explained by photosynthate accumulation in algae by this time of day

---

‡Author to whom correspondence should be addressed at: Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM), Dept. de Biologia, Rua Kioto 253, Arraial do Cabo, RJ, Cep: 28930 000, Brazil. Email: kadu@ax.apc.org

0022–1112/98/53A222+14 $30.00/0

(Tarborsky & Limberger, 1980; Polunin & Klumpp, 1989). In contrast, a temperate herbivorous fish showed a grazing peak at early morning (Choat & Clements, 1993).

Most of the studies performed on feeding and digestive mechanisms of herbivorous fishes have come from temperate or coral reef systems (Klumpp & Nichols, 1983; Clements & Bellwood, 1988; Polunin & Klumpp, 1989, 1992; Horn, 1992; Polunin *et al*., 1995), while tropical rocky shores have received little attention. To date, few studies have examined differences of grazing rates and food processing throughout the year.

This study worked with the three most abundant herbivorous fishes occurring on the rocky shores of Arraial do Cabo (RJ), on the south-east Brazilian coast; the acanthurid *Acanthurus bahianus* (Castelnau, 1855), the scarid *Sparisoma atomarium* (Poey, 1861), and the pomacentrid *Stegastes fuscus* (Cuvier 1830). *S. fuscus* is a strong territorial damselfish that dominates shallow areas, and it was shown to play an important trophodynamic role in that system (Ferreira *et al*., 1998). *S. atomarium* holds larger territories, sometimes overlapped by other males (pers. obs.) and feeds in shallow areas, when damselfishes were not abundant, as well as in deeper areas. Females are transients and feed in groups (three to eight individuals), while males are solitary feeders. *A. bahianus* attain the largest size among fishes examined, feeding either solitary or in larger schools of up to 50 individuals. However, most fishes sampled in the study site were solitary individuals. *S. fuscus* and *A. bahianus* were considered as grazers by Randall (1967). *S. atomarium* can also be classified as a grazer since it ingests great quantities of inorganic material.

This work focused on seasonal differences in grazing rates and food processing (total bites, bite size, ingestion, full gut contents and gut turnover) by these three fishes, as part of a whole study that deals with the relationships between herbivore consumption and primary production at different depth gradients. The hypothesis was that grazing rates and food processing would change seasonally as a function of the temperature regime.

MATERIALS AND METHODS

STUDY AREA

This work was conducted at the rocky shores of Cabo Frio Island, located at the town of Arraial do Cabo [(RJ) (23° S, 42° W) (Fig. 1)], during 1996–1997. The marine environment of Arraial do Cabo sustains a very rich reef fauna and flora (Castro *et al*., 1995; Guimaraens & Coutinho, 1996; Ferreira *et al*., 1998) that flourish in embayment conditions upon a granitic rocky shore formation. In such conditions, up to 80 species of reef fishes have been recorded (Ferreira *et al*., unpublished), inhabiting different zones of the rocky shore that is covered basically by a diverse epilithic algal community (Guimaraens & Coutinho, 1996), patches of *Palythoa caribaeorum*, colonies of *Millepora alcicornis*, and four species of hermatypic corals (Castro *et al*., 1995). The study site comprised, a rocky shore of 25–30 m in extent, from the surface of the shore to the sand bottom, with maximum depth range of 15 m at high tides. The whole region is influenced by a coastal upwelling event associated with the local wind regime and bathymetry in summer and spring periods (Valentin, 1984). However, the study site is affected only for short periods, and generally in deeper areas. Additional information about the region can be found in Valentin (1984) and Gonzalez-Rodriguez *et al*. (1992).

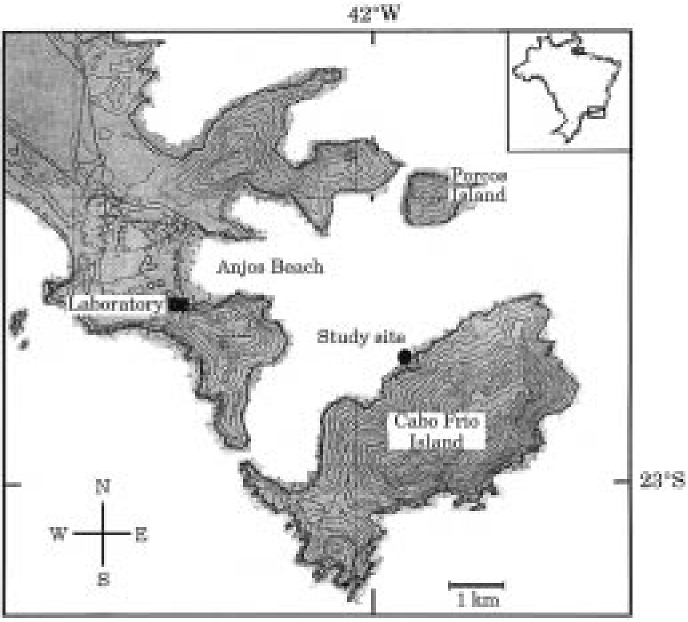


FIG. 1. Map of the region showing the study site at Cabo Frio Island.

DATA COLLECTION

Grazing rates were recorded by observing fishes at 10-min periods throughout the day (0600–1800 hours). A scuba diver chose different individual fishes at different periods of observation. Total daily bites were derived directly from underwater counts. The content mass (mg dry wt) at the point of fullness (gut fullness; *sensu* Polunin, 1988) was calculated by watching routine defaecation and spearing fishes throughout those periods when it was considered that the gut was full: *A. bahianus*, 1100 hours; *S. atomarium*, 1030 hours; and *S. fuscus*, 1100 hours. Fishes were brought to the laboratory (Fig. 1) in <2 h, where the guts were removed, unravelled and the entire contents removed. The contents were wet weighed, then dried at 70° C in an oven. Bite size (mg dry wt) was assessed by dividing mean weight of a full gut by the mean number of bites taken up at this time. Calculation of ingestion (mg dry wt) was obtained by the product of bite size and mean daily total bites. Gut turnover was estimated by dividing ingestion by mean full gut content mass.

STATISTICAL ANALYSIS

Grazing rates were tested for differences in time of day and season by two-way analysis of variance (ANOVA), for each species. Food processing characters were tested for differences among species and among seasons using one-way ANOVA, separately, considering different days of different months of a season as replicates. Even though the three studied species have different mean sizes and it was conceivable that certain food processing characters from those analysed would be clearly different among them, we yet performed ANOVAs in order to achieve better discussions. When homogeneity of variances was not reached (Cochran test), data were log transformed (Underwood, 1997). Additional Student–Newman–Keuls (SNK) multiple comparisons of means test were performed as a *post hoc* test (Zar, 1996). The days when water temperature was too distant from the seasonal mean value were excluded from statistical analysis. Temperature measurements were registered simultaneously with other samples, to make comparisons with grazing data.

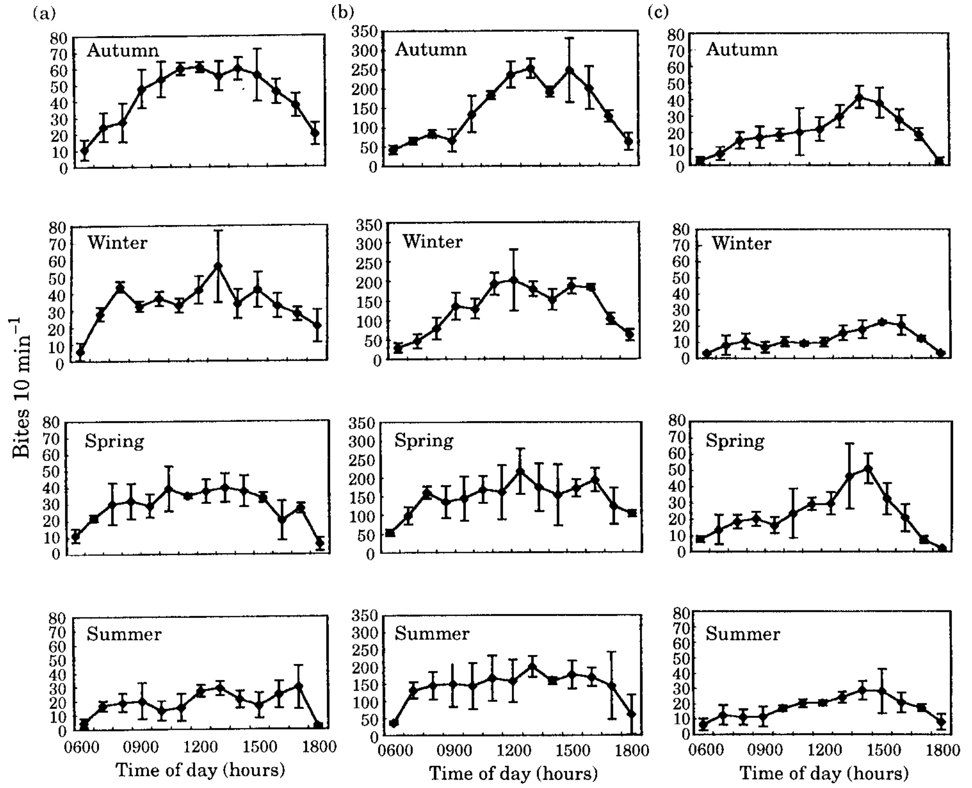
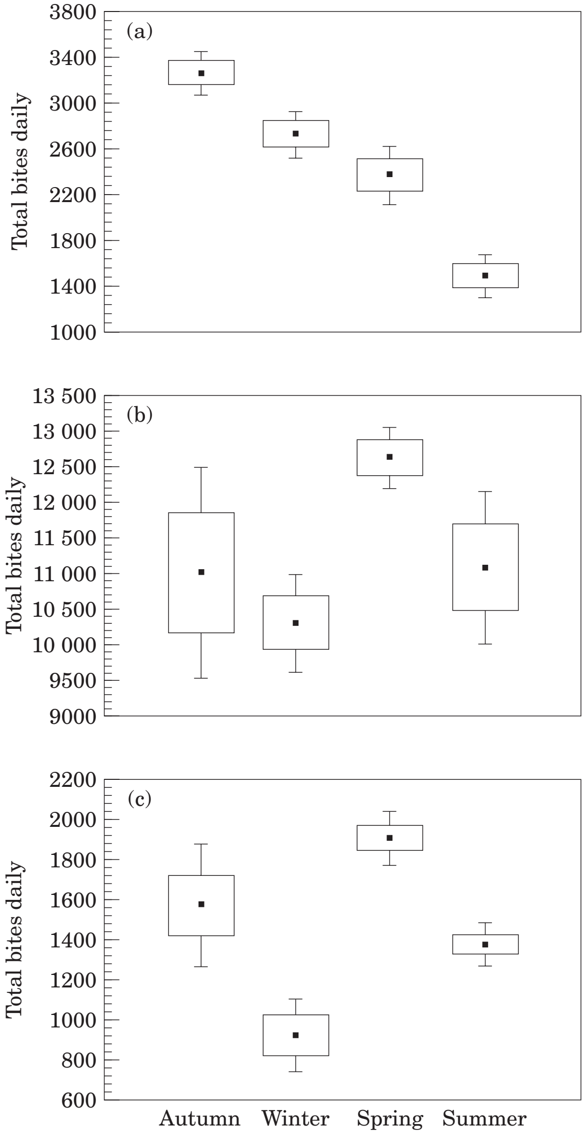


FIG. 2. Seasonal grazing rates (mean ± S.D.) of (a) *S. atomarium*, (b) *S. bahianus*, (c) *S. fuscus*.

RESULTS

GRAZING RATES

The two herbivorous fishes, *A. bahianus* and *S. atomarium*, showed a feeding peak from 1200 to 1300 hours, while the damselfish *S. fuscus*, had feeding peak around 1400 to 1500 hours (Fig. 2). Feeding rates in *A. bahianus* varied significantly during the day (*F*=17·38; *P*<0·001), but not between seasons (*F*=1·66; *P*=0·17). Three main periods of grazing intensity were identified for *A. bahianus* based on ANOVA results: one of low intensity (0600–1800 hours), one of intermediate intensity (0700–1000 hours), and another of maximum intensity (1100–1700 hours). *S. atomarium* feeding rates showed significant differences both for hour of day (*F*=16·24; *P*<0·001) and for season (*F*=60·64; *P*<0·001). Also, three main periods of daily grazing were detected in *S. atomarium*, similar to those of *A. bahianus*: low intensity in early and end of the day (0600 and 1800 hours), intermediate intensity at 0700 hours and a long period of maximum intensity from 0800–1700 hours. Foraging behaviour of *S. fuscus* differed significantly with hour of day (*F*=28·39; *P*<0·001) and with season (*F*=20·75; *P*<0·001). Unlike the other fishes, four periods of grazing activity were identified: low intensity feeding at 0600–0700 hours, two of intermediate intensity at 0800–1300 hours and 1600–1800 hours, and a period of maximum activity at 1400–1500 hours. Total daily bite rates (mean ± S.D. and ± S.E.; plus



	1	2	3	4
Mean	3264	2724	2364	1476
1				
2	0.014*			
3	0.002*	0.071		
4	0.001*	0.001*	0.001*	

	1	2	3	4
Mean	10 996	10 280	12 612	11 084
1				
2	0.407			
3	0.181	0.082		
4	0.936	0.622	0.095	

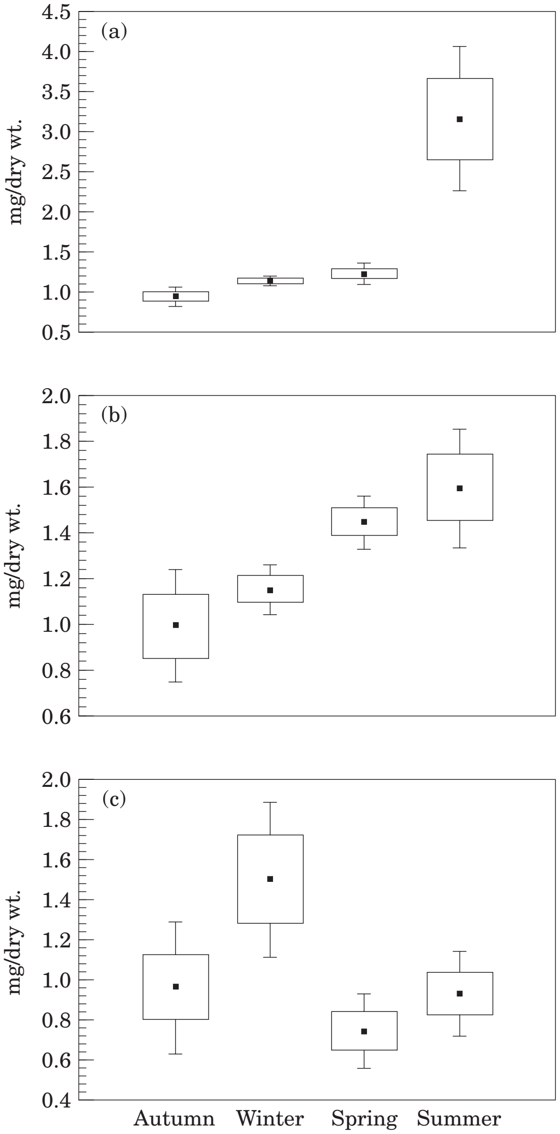
	1	2	3	4
Mean	1563	910.6	1888	1366.5
1				
2	0.005*			
3	0.067	0.001*		
4	0.211	0.016*	0.021*	

FIG. 3. Seasonal variation in total bite rates plus SNK test results (mean ± S.D. ± S.E.). (a) *S. atomarium*, (b) *A. bahianus*, (c) *S. fuscus*. 1, Autumn; 2, winter; 3, spring; 4, summer. *Indicates significant differences.

SNK results) were proportional to the differences cited above for grazing rates between seasons for the three fishes (Fig. 3). Total bite rates were different between seasons for *S. atomarium* (F=37·75; P<0·001) and for *S. fuscus* (F=11·78; P<0·001, but not for *A. bahianus* (F=2·87; P=0·10).

BITE SIZE

All fishes showed bite size values with significant differences between seasons (Fig. 4). *S. atomarium*'s bite size was highest in summer, and consequently ANOVA detected significant differences between summer and other seasons



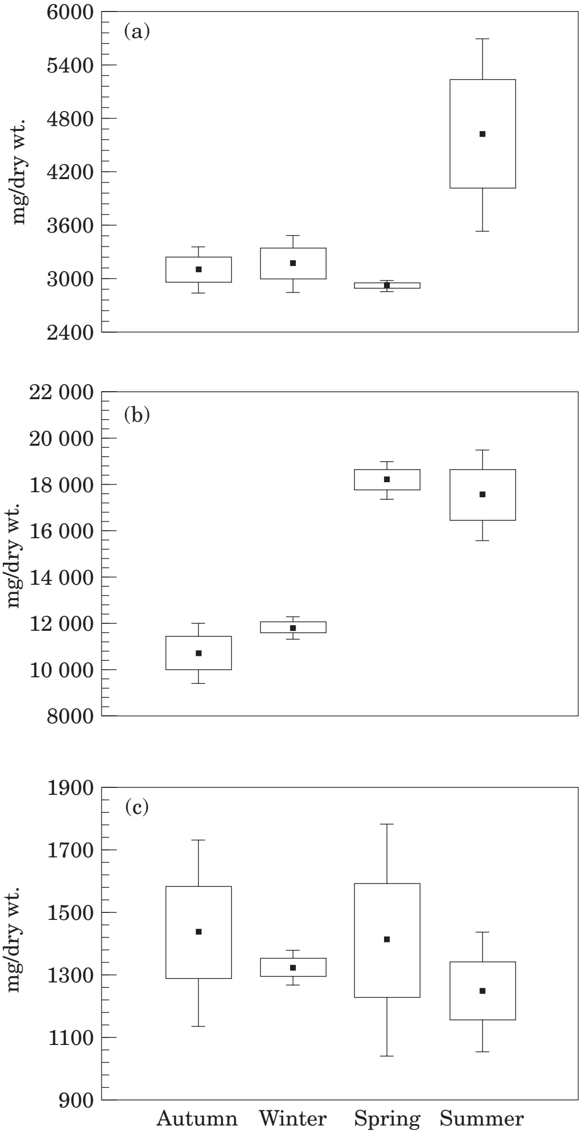
	1	2	3	4
Mean	0.943	1.146	1.220	3.154
1				
2	0.604			
3	0.750	0.849		
4	0.00*	0.002*	0.001*	

	1	2	3	4
Mean	0.994	1.148	1.441	1.593
1				
2	0.356			
3	0.052*	0.101		
4	0.022*	0.053*	0.363	

	1	2	3	4
Mean	0.957	1.498	0.740	0.920
1				
2	0.024*			
3	0.561	0.016*		
4	0.864	0.042*	0.399	

FIG. 4. Seasonal variation in bite size (mean ± S.D. ± S.E.). (a) *S. atomarium*, (b) *A. bahianus*, (c) *S. fuscus*. 1, Autumn; 2, winter; 3, spring; 4, summer. *Indicates significant differences.

($F=15{\cdot}11$; $P<0{\cdot}001$). For *A. bahianus* a similar pattern of increase in bite size toward the summer was also found, as in *S. atomarium*. The highest values of bite size for *A. bahianus* were in summer and in spring, thus significant differences were detected between these seasons and winter and autumn. *S. fuscus* had the highest bite size values in winter, differing from other fishes. Consequently, the winter bite size of *S. fuscus* was significantly different from that in all other seasons. Ingestion rate in *S. atomarium* follow the same pattern of bite size, increasing toward summer, and with values in summer significantly different from all other seasons (Fig. 5). Ingestion was high in *A. bahianus* in



	1	2	3	4
Mean	3068.2	3126.7	2865.7	4583.6
1				
2	0.905			
3	0.683	0.851		
4	0.031*	0.016*	0.029*	

	1	2	3	4
Mean	10 694.2	11 765.1	18 145.4	17 492.1
1				
2	0.331			
3	0.001*	0.001*		
4	0.001*	0.001*	0.545	

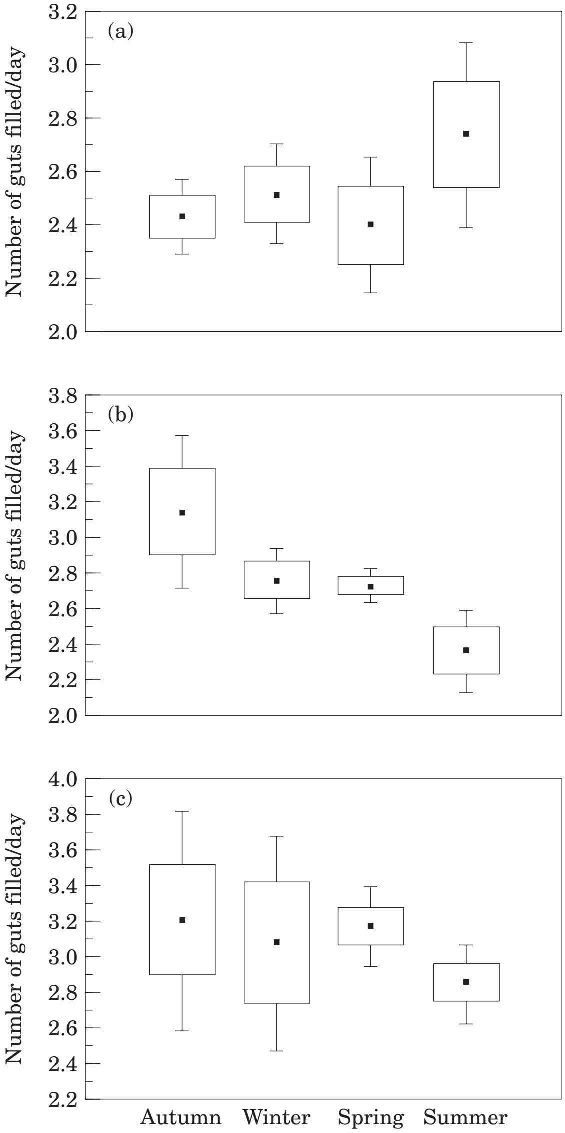
	1	2	3	4
Mean	1431.0	1319.0	1407.7	1241.3
1				
2	0.843			
3	0.909	0.665		
4	0.779	0.704	0.691	

FIG. 5. Seasonal variation in ingestation rates (mean ± S.D. ± S.E.). (a) *S. atomarium*, (b) *A. bahianus*, (c) *S. fuscus*. 1, Autumn; 2, winter; 3, spring; 4, summer. *Indicates significant differences.

spring and summer, following the tendency observed for bite size. Hence, values of spring and summer showed significant differences from those of autumn and winter. *S. fuscus* presented high variation of ingestion rates in autumn and spring, therefore ANOVA could not detect significant differences between seasons.

GUT TURNOVER AND GUT FULLNESS

The total number of guts filled daily in *S. atomarium* and *S. fuscus* was almost constant throughout the year, ranging from 2·4 to 2·7 for the scarid and 2·9 to



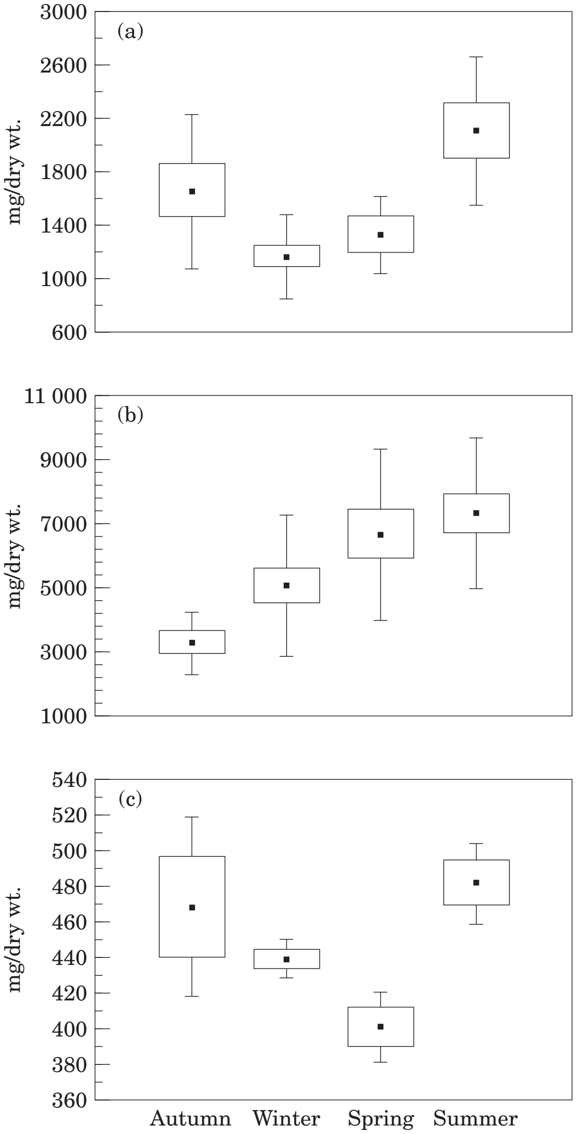
	1	2	3	4
Mean	2.430	2.514	2.394	2.738
1				
2	0.689			
3	0.864	0.828		
4	0.0331	0.299	0.383	

	1	2	3	4
Mean	3.182	2.788	2.753	2.377
1				
2	0.107			
3	0.178	0.872		
4	0.024	0.201	0.122	

	1	2	3	4
Mean	3.216	3.087	3.173	2.846
1				
2	0.925			
3	0.895	0.806		
4	0.661	0.498	0.576	

FIG. 6. Seasonal variation in gut turnover (mean ± S.D. ± S.E.). (a) *S. atomarium*, (b) *A. bahianus*, (c) *S. fuscus*. 1, Autumn; 2, winter; 3, spring; 4, summer. *Indicates significant differences.

3·2 for the pomacentrid (Fig. 6). *S. atomarium* showed high mean values in summer, and *S. fuscus* in autumn. The same occurred with *A. bahianus*, showing the shortest food transit time in autumn, which was significantly different from summer values (lowest values). Gut fullness for the three fishes presented an increased pattern toward the summer. In *S. atomarium*, summer mass contents in a full gut were significantly different from values in spring and in winter (Fig. 7). Gut fullness of *A. bahianus* increased constantly from autumn to summer. The highest values observed in summer and spring differed significantly from those of autumn, the lowest ones. *S. fuscus* contents at the point of fullness



	1	2	3	4
Mean	1699.1	1160.2	1320.2	2096.2
1				
2	0.196			
3	0.223	0.603		
4	0.202	0.022*	0.041*	

	1	2	3	4
Mean	3252.4	5023.9	6607.6	7264.8
1				
2	0.073			
3	0.003*	0.107		
4	0.001*	0.063	0.499	

	1	2	3	4
Mean	468.0	438.3	400.0	480.3
1				
2	0.255			
3	0.054*	0.152		
4	0.624	0.252	0.042*	

FIG. 7. Seasonal variation in gut fullness (mean ± S.D. ± S.E.). (a) *S. atomarium*, (b) *A. bahianus*, (c) *S. fuscus*. 1, Autumn; 2, winter; 3, spring; 4, summer. *Indicates significant differences.

were lowest in the spring. Significant differences were detected between spring values and other season values, and also between summer and winter values (Fig. 7).

COMPARISONS BETWEEN FISHES

As expected, total bites, ingestion and gut fullness increased with increasing fish species size. Therefore, significant differences were detected among all fishes for total bites (F=7·07; P<0·001), for ingestion (F=30·9; P<0·001) and for gut fullness (F=89·9; P<0·001). *S. atomarium* presented the biggest bite size,

TABLE I. Comparative food characters and mean size fish

Mean size fish (range) (cm)	13·5 (11–15) *S. fuscus*	<	19·3 (17–21·5) *S. atomarium*	<	24·2 (18–28·5) *A. bahianus*
Bite size (mg dry wt)*	1·0 *S. fuscus*	<	1·2 *A. bahianus*	<	1·6 *S. atomarium*
Total bites (number day^{-1})*	1434 *S. fuscus*	<	2457 *S. atomarium*	<	11 238 *A. bahianus*
Ingestion (mg dry wt)*	1349 *S. fuscus*	<	3411 *S. atomarium*	<	14 524 *A. bahianus*
Gut turnover (number day^{-1})*	2·5 *S. atomarium*	<	2·7 *A. bahianus*	<	3·0 *S. fuscus*
Gut fullness (mg dry wt)*	424 *S. fuscus*	<	1568 *S. atomarium*	<	5537 *A. bahianus*

*Numbers are annual means.

contrasting with *A. bahianus*, the largest fish of the three, which possesses a delicate mouth. Significant differences were also detected in bite size for the three fishes (F=10·7; P<0·001). Gut turnover was highest for *S. fuscus*, the smallest fish among all, and significantly different from the others (F=8·69; P<0·001), while *S. atomarium* and *A. bahianus* showed similar values. In Table I food-processing characters (annual means) plus mean size of each species were compared roughly.

DISCUSSION

A complete analysis of seasonal grazing rate results in the three species revealed that the prevalent pattern of a foraging peak in the afternoon occurs only for *S. fuscus*, while *S. atomarium* and *A. bahianus* showed feeding peaks by midday and/or early afternoon. Recent studies report similar results of a midday feeding peak (Choat & Clements, 1993), and both patterns observed were explained following the assumptions of photosynthate accumulation in algae at this time (Taborsky & Limberger, 1980; Polunin & Klumpp, 1989).

The upwelling phenomenon bathed the study site with cold water for at least 1 day or a couple of days, during a period of shifting water masses in summer and winter. Despite those typical patterns, different variations in local water temperature could have taken place, as shown during this work (Fig. 8). Even though great variations in temperature were detected in the spring and summer months, the highest means were observed in autumn. However, in addition to the variations of temperature observed in spring and summer, we also observed temperature oscillations even during the days when sampling foraging behaviour. Figure 9 shows clearly the sudden changes in temperature which marine organisms must face in the region and how quickly they respond to it. Grazing intensity is widely known to vary according to water temperature (Hatcher, 1981; Carpenter, 1986; Polunin & Klumpp, 1992). Despite such evidence, our grazing rates and food processing results presented variations both among fishes and seasons, suggesting that factors other than temperature could also be affecting seasonal patterns of grazing and food processing by fishes at this local rocky shore environment.

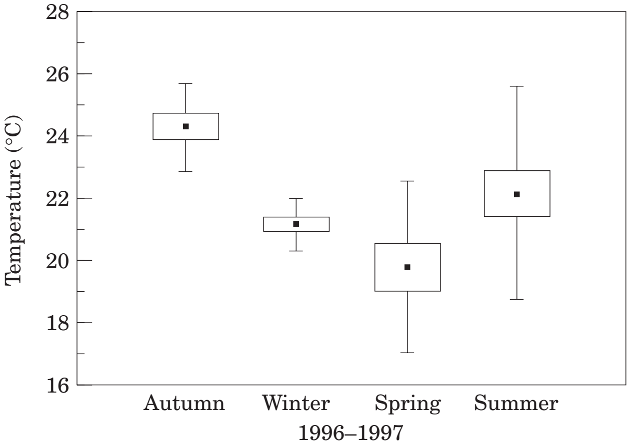


FIG. 8. Seasonal variation (n=15) in water temperature at study site (mean ± S.D. ± S.E.).

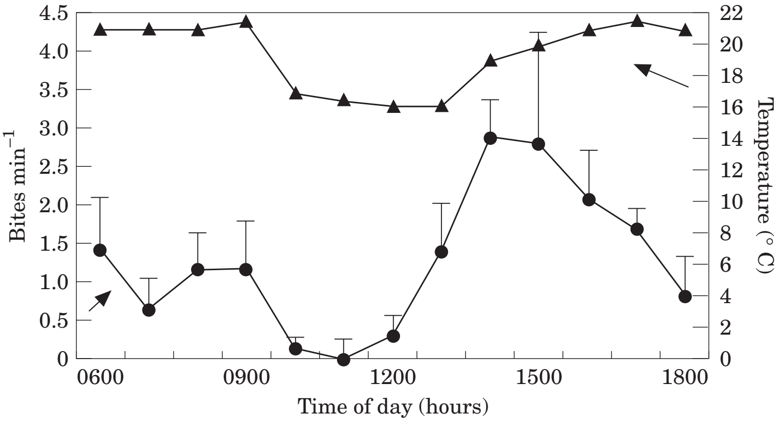


FIG. 9. Changes in *S. fuscus* grazing rates with changes in water temperature due to sudden appearance and mixture of upwelling and non-upwelling water (mean ± S.D. ± S.E.).

Evidence of feeding in relation to food availability could be considered since accumulation of biomass was greatest in summer, followed by autumn and spring months (Ferreira *et al*., unpubl.). Furthermore, blooms of more digestible and nutritious algae, such as red and green filamentous forms, are more common in summer (Guimaraens & Coutinho, 1996; Ferreira *et al*., 1998). Seasonal differences in nutrient content of algae could also drive grazing patterns in directions other than those commonly led by temperature; however, quite a few works have investigated such relationships (Lobban *et al*., 1985). Reproduction has been reported to influence feeding, mainly in those fishes which make spawning migrations (Longhurst & Pauly, 1987). Yet, parental care could affect feeding. As an example, bite counts of *S. fuscus* male individuals which maintained a nest were frequently excluded, because they often spent a lot of time taking care of it and, as a result, fed less.

Comparisons of the food processing characters examined among fishes showed expected differences directly related to species size; nevertheless some differences independent of size were identified (Table I). The scarid *S. atomarium*, with its fused jaw teeth, are able to ingest more food per bite than the others. Indeed, fishes bite size changed seasonally (Fig. 4) and further accurate investigations are needed to search for shifts in bite size in shorter time scales including diel variations.

All fishes studied had a similar food transit time of about 4–5 h, suggesting an adaptation to local food resources. This food transit time was consistent with those existing in literature (Horn, 1989; Polunin *et al*., 1995). Despite a few differences in food preference among the fishes studied, their diets rely on great amounts of dominant algae in the region, such as *Jania* spp., *Amphiroa* spp., *Gelidium pusillum* and *Gelidiella* sp. (Guimaraens & Coutinho, 1996; Ferreira *et al*., 1998). These algae were previously considered as poor in nutrients and difficult to digest (Montgomery & Gerking, 1980). Therefore, fishes fill up their guts 2·5–3·0 times a day (Table I) in order to achieve best assimilation from such a poor nutrient food. Each fish species studied depends on a different mechanical or chemical adaptation to process their food. *A. bahianus* processes a gizzard-like stomach to triturate algae together with inorganic material; *S. atomarium* has a pharyngeal mill to grind algae into small particles; and the damselfish *S. fuscus* employs a highly acidic stomach fluids to lyse algal cell walls (Horn, 1992). Thus, fishes studied rely on different food processing mechansims and have some differences in food processing characteristics to process the same basic, poor nutrient food resource.

In summary, our data indicated that temperature alone was not a good factor to explain seasonal variation in grazing rates and associated food processing characters. Although the fishes here considered shown some degree of selectivity regarding their food, the environment imposes serious constraints, which characterize the opportunistic behaviour and the great capacity of adaptation they sustain.

This work is part of a doctorate thesis from Universidade Federal de São Carlos by CELF. We thank J. E. Gonçalves and Mr Renatão for help with bite counts. Discussions with H. L. Passeri and others improved the manuscript. Financial and logistic support was given by CNPq and IEAPM.

References

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecology Monographs* **56,** 345–363.

Castro, C. B., Echeverria, C. A., Pires, D. O., Mascarenhas, B. J. A. & Freitas, S. G. (1995). Distribuição de Cnidaria e Echinodermata no infralitoral de costões rochosos de Arraial do Cabo, RJ, Brasil. *Revista Brasileira de Biologia* **55,** 471–480.

Choat, J. H. (1991). The biology of herbivorous fishes on coral reefs. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 120–153. San Diego: Academic Press.

Choat, J. H. & Clements, K. D. (1993). Daily feeding rates in herbivorous labroid fishes. *Marine Biology* **117,** 205–211.

Clements, K. D. & Bellwood, D. R. (1988). A comparison of the feeding mechanisms of two herbivorous labroid fishes, the temperate *Odax pullus* and the tropical *Scarus rubroviolaceus*. *Australian Journal of Marine and Freshwater Research* **39,** 87–107.

Ferreira, C. E. L., Gonçalves, J. E. A., Coutinho, R. & Peret, A. C. P. (1998). Herbivory by the Dusky Damselfish, *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: Effects on the benthic community. *Journal of Experimental Marine Biology and Ecology*, in press.

Gonzalez-Rodriguez, E., Valentin, J. L., André, D. L. & Jacob, S. A. (1992). Upwelling and downwelling at Cabo Frio (Brazil): Comparison of biomass and primary production responses. *Journal of Plankton Research* **14,** 289–306.

Guimaraens, M. A. & Coutinho, R. (1996). Spatial and temporal variation of benthic marine algae at the Cabo Frio upwelling region, Rio de Janeiro, Brazil. *Aquatic Botany* **52,** 283–299.

Hatcher, B. G. (1981). The interaction between grazing organisms and the epilithic algal community of a coral reef: A quantitative assessment. *Proceedings of 4th International Coral Reef Symposium* **2,** 515–524.

Hay, M. E. (1984). Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology* **65,** 446–454.

Hay, M. E. (1991). Seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 96–119. San Diego: Academic Press.

Hixon, M. A. (1983). Fish grazing and community structure of reef corals and algae: A synthesis of recent studies. In *The Ecology of Deep and Shallow Coral Reefs* (Reaka, M. L., ed.), NOAA Symposium Series Undersea Research, Vol. 1, pp. 79–87. Maryland: National Oceanic & Atmospheric Administration.

Hixon, M. A. (1996). Effects of reef fishes on corals and algae. In *Life and Death of Coral Reefs* (Birkeland, C., ed.), pp. 230–246. London: Chapman & Hall.

Horn, M. H. (1989). Biology of marine herbivorous fishes. *Oceanography and Marine Biology Annual Review* **27,** 167–272.

Horn, M. H. (1992). Herbivorous fishes: feeding and digestive mechanisms. In *Plant–Animal Interactions in the Marine Benthos* (John, D. M., Hawkins, S. J. & Price, J. H., eds), pp. 339–362. Oxford: Clarendon Press.

John, D. M., Hawkins, S. J. & Price, J. H. (1992). *Plant-Animal Interactions in the Marine Benthos*. Oxford: Clarendon Press.

Klumpp, D. W. & Nichols, P. D. (1983). Nutrition of the southern sea garfish *Hyporhamphus melanochir*: Gut passage rate and daily consumption of two food types and assimilation of seagrass components. *Marine Ecology Progress Series* **12,** 207–216.

Lobban, C. S., Harrison, P. S. & Ducan, M. J. (1985). *The Physiological Ecology of Seaweeds*. Cambridge: Cambridge University Press.

Longhurst, A. R. & Pauly, D. (1987). *Ecology of Tropical Oceans*. Orlando: Academic Press.

McClanahan, T. R. & Shafir, S. H. (1990). Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* **83,** 362–370.

Montgomery, W. L. & Gerking, S. D. (1980). Marine macroalgae as foods for fishes: An evaluation of potential food quality. *Environmental Biology of Fishes* **5,** 143–153.

Ogden, J. C. & Lobel, P. S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* **3,** 49–63.

Polunin, N. V. C. (1988). Efficient uptake of algal production by a single resident herbivorous fish on a reef. *Journal of Experimental Marine Biology and Ecology* **123,** 61–76.

Polunin, N. V. C. & Klumpp, D. W. (1989). Ecological correlates of foraging periodicity in herbivorous reef fishes of the Coral Sea. *Journal of Experimental Marine Biology and Ecology* **126,** 1–20.

Polunin, N. V. C. & Klumpp, D. W. (1992). Algal food supply and grazer demand in a very productive coral-reef zone. *Journal of Experimental Marine Biology and Ecology* **164,** 1–15.

Polunin, N. V. C., Harmelin-Vivien, M. & Galzin, R. (1995). Contrasts in algal food processing among five herbivorous coral-reef fishes. *Journal of Fish Biology* **47,** 455–465.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5,** 665–847.

Steneck, R. S. (1988). Herbivory on coral reefs: A synthesis. *Proceedings of 6th International Coral Reef Symposium* **1,** 37–49.

Tarborsky, M. & Limberger, D. (1980). The activity rhythm of *Blennius sanguinolentus* Pallas, an adaptation to its food source? *Pubbl. Staz. Zool. Napoli (I: Marine Ecology)* **1,** 143–153.

Underwood, A. J. (1997). *Experiments in Ecology*. Cambridge: Cambridge University Press.

Valentin, J. L. (1984). Analyse des parametres hydrobiologiques dans la remotée de Cabo Frio (Bresil). *Marine Biology* **82,** 259–276.

Zar, J. H. (1996). *Biostatistical Analysis*. New Jersey: Prentice Hall.