Diet and trophic plasticity of an herbivorous blenny *Scartella cristata* of subtropical rocky shores

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The goals of the present study were to investigate the feeding rates of *Scartella cristata*, accounting for different water temperature regimes, and to analyse spatial and seasonal variations in its diet. The feeding rate of *S. cristata* was higher in warmer waters and was not correlated with season. A typical herbivorous diel feeding pattern was observed, with a steady increase in bite rate throughout the morning until a plateau in the early afternoon, followed by an abrupt decrease until the end of the daylight period. The gut contents of *S. cristata* included at least 41 different items. Detritus and algae (mainly filamentous) comprised most of the bulk of *S. cristata*'s diet. *Scartella cristata* also exhibited significant seasonal and spatial variability in its diet. This study highlights the importance of detritus within the epilithic algal matrix in the diet of *S. cristata* and pinpoints that, as in coral reefs, the detrital pathway exerts an important role in the trophodynamics of subtropical rocky shores where these fish are abundant. © 2009 The Authors

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Key words: Arraial do Cabo; Blenniidae; detritivory; diet; herbivory; *Scartella cristata*.

INTRODUCTION

Herbivorous fishes (Crossman *et al*., 2005) have received special attention for being the major consumers of macroalgae and for their high biomass in tropical regions (Horn, 1989; Choat, 1991; Floeter *et al*., 2005). Many herbivorous fishes are considered to be keystone species in structuring benthic communities. They can influence primary production, distribution and growth of algae (Carpenter, 1986; Ferreira *et al*., 1998*a*; Bellwood *et al*., 2004; Ceccarelli, 2007), reef bioerosion and sediment transport (Bellwood & Choat, 1990; Hoey & Bellwood, 2008).

Fishes that feed on epilithic algae constitute an important link in the trophodynamics of reef environments (Polunin, 1988; Polunin & Klumpp, 1992; Ferreira *et al*., 1998*a*). The epilithic algal community aggregates invertebrates, micro-organisms, microalgae, detritus and sediment (Wilson & Bellwood, 1997), and as such is better named the epilithic algal matrix (EAM). Thus, EAM-grazing fishes are hardly classified according to their correct feeding status, due the complex and variable composition of the EAM (Choat *et al*., 2002, 2004). Many reef fishes nominally

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classified as herbivores are known not only to ingest but also to target, digest and assimilate detritus aggregates present in EAM instead of algae (Crossman *et al.*, 2001, 2005; Wilson *et al.*, 2003; Choat *et al.*, 2004). The relative importance of different components of the EAM present in the diet of these reef fishes carries vital implications for understanding reef trophodynamics (Wilson *et al.*, 2003).

Many species from diverse families are known to forage on the EAM in reef systems, but damselfishes (Pomacentridae) (Ferreira *et al.*, 1998*b*; Lison de Loma *et al.*, 2000; Ceccarelli *et al.*, 2001), parrotfishes (Scaridae) (Harmelin-Viven *et al.*, 1992; Bonaldo *et al.*, 2006; Ferreira & Gonçalves, 2006) and surgeonfishes (Acanthuridae) (Montgomery *et al.*, 1989; Dias *et al.*, 2001; Ferreira & Gonçalves, 2006) have received the most attention. The Blenniidae can achieve high densities, being the most important fishes inhabiting a great variety of shallow reef systems, including tropical and temperate rocky shores (Kotrschal & Thomson, 1986; Nieder, 1997; Ojeda & Muñoz, 1999; Ferreira *et al.*, 2001; Beldade *et al.*, 2006) and coral reefs (Ackerman & Bellwood, 2000; Depczynski *et al.*, 2007). Recent studies indicate that blennies are a very important link in the trophodynamics of coral reefs (Depczynski & Bellwood, 2003; Wilson *et al.*, 2003), where they reach high biomass (Ackerman & Bellwood, 2000; Townsend & Tibbetts, 2000), are reported to remove a substantial amount of EAM from the substratum (Wilson, 2000; Townsend & Tibbetts, 2004) and have elevated turnover rates (Wilson, 2004).

The molly miller *Scartella cristata* (L.) is widely distributed along the Atlantic Ocean and Mediterranean Sea coasts. At least four other *Scartella* species inhabit some oceanic islands in the Atlantic, and one species is in the Indo-Pacific (Springer, 1993). *Scartella cristata* is a conspicuous inhabitant of shallow rocky systems and tide pools, and is considered to feed mostly on EAM (Randall, 1967). Although some studies have tried to characterise its diet (Randall, 1967; Tararam & Wakabara, 1982; Nieder, 1997; Mobley & Fleeger, 1999), none has previously dealt successfully with spatial or temporal variations or even described its feeding rate pattern. The goals of the present study were two-fold: (1) to investigate the seasonal variation of feeding rates of *S. cristata* and (2) to analyse spatial and seasonal variations in its diet.

MATERIALS AND METHODS

STUDY SITE

The city of Arraial do Cabo (22° 58′ S; 42° 00′ W) is located on the south-eastern Brazilian coast in the state of Rio de Janeiro. This region is a habitat for organisms with both tropical and subtropical affinities due to the occurrence of a coastal upwelling. The upwelling brings up waters with high nutrient concentrations and temperatures <18° C, in contrast to warmer coastal waters with an average of 22° C. The upwelling waters emerge most frequently and intensively in the spring and summer months (Valentin, 1984). The location of Cabo Frio Island and the cape (Fig. 1) obstruct the occurrence of upwelling to the north, generating sites with tropical and subtropical affinities in a relatively small area (Guimaraens & Coutinho, 1996; Ferreira *et al.*, 2001). This increases local species' richness, making Arraial do Cabo a hot spot for studying the ecology and biogeography of many groups of marine organisms as well as their adaptations to a highly dynamic environment.

This study was carried out at two sites in Arraial do Cabo: Ponta da Cabeça (PC), which is directly affected by the upwelling and Fortaleza (F_Z), which is protected from the upwelling and influenced most of the time by coastal, warm waters throughout the year (Fig. 1).
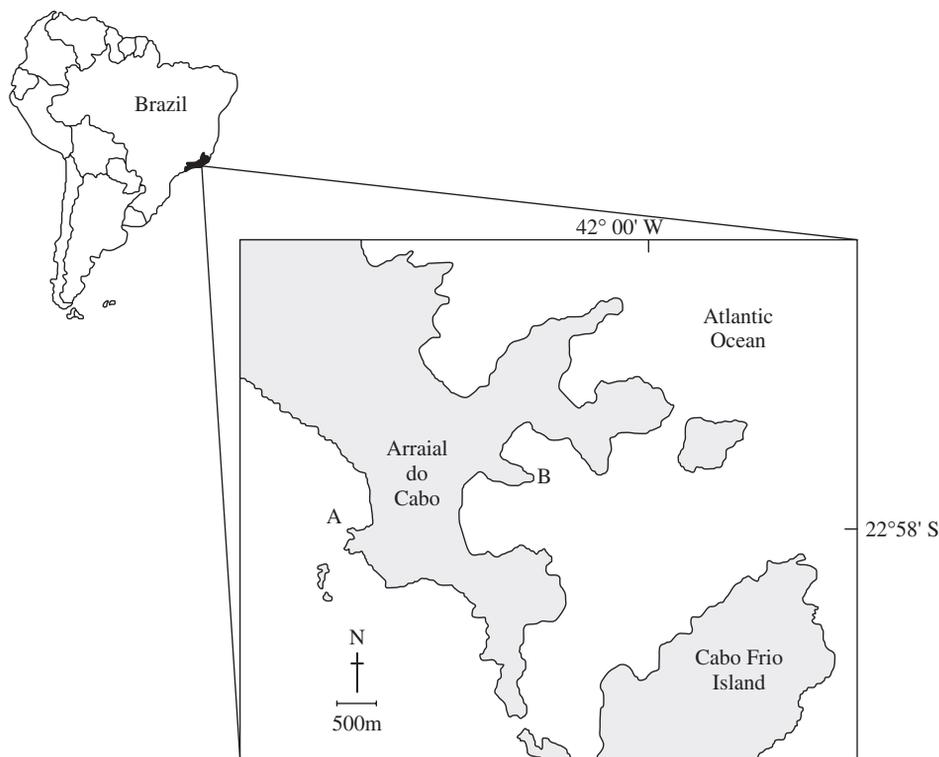
Fig. 1. Location of study sites: A, Ponta da Cabeça (PC) and B, Fortaleza (F$_Z$).

DENSITY

The density and population structure of *S. cristata* at both sites were estimated by utilizing 10 visual censuses in short, replicated, strip transects of 5 m × 1 m at each site. All transects were performed during the summer months with snorkelling by a single trained diver. Fish observed were separated into three size classes: <50 mm, 50–100 mm and >100 mm (total length, L_T).

FORAGING BEHAVIOUR

All field observations of the feeding behaviour of *S. cristata* were carried out at PC. Besides sustaining a higher density of *S. cristata*, this site is under frequent variation of water temperature due to upwelling events. The focal-animal method (Altmann, 1974) was employed, and individuals of *S. cristata* were followed during 5 min intervals at the end of which, bite counts were annotated on a polyvinyl chloride (PVC) sheet. To describe the diel feeding pattern of *S. cristata*, the observations were carried out throughout the diel period from sunrise to sunset. To check the influence of season and superficial water temperature, the observations were carried out in summer and winter, in both seasons under upwelling (mean 18° C) and non-upwelling (mean 22° C) conditions. Individuals that exhibited any behaviour that inhibited feeding, such as aggression (agonistic behaviour) or seeking shelter, were excluded from the analysis. In order to avoid any possible variation in feeding rates related to ontogeny, only adult fish, mean size 8 cm (5–10 cm, L_T) were considered for analysis. This was the most abundant size class at this site. There were at least 6 days of observation for each season along the entire daylight period totalling *c*. 150 h of field observation.

DIET ANALYSIS

Gut contents of 60 individuals (15 at each site per season) were investigated to describe spatial and seasonal variations of the diet of *S. cristata*. Fish were collected using hand-nets or hand spears and killed by pithing. After collection, individuals had their guts fixed with 10% formalin and were transported in alcohol to the laboratory. At the laboratory, fish were measured to the nearest mm with a calliper and had their entire gut content removed. The gut contents were analysed using an optical microscope, where 50 equidistant points were counted, the item under each point was annotated, and the per cent contribution of each item was calculated for each specimen.

DATA ANALYSIS

Differences in abundance were compared using a two-way ANOVA with site (PC and F_Z) and size class (<50, 50–100 and >100 mm L_T) as factors. One-way ANOVAs were performed to compare the diel feeding rate of *S. cristata* among different hours of the day. To test the influence of season and water temperature, a two-way ANOVA with temperature and season as factors was performed. Diets were compared across sites and seasons using a two-way ANOVA for each food category. For all ANOVAs, data were ln or arcsin transformed in order to achieve the basic assumptions, when necessary (Underwood, 1997). Additional Student–Newman–Keuls multiple comparisons of means were performed as a *post hoc* test (Zar, 2006).

RESULTS

DENSITY

The density of *S. cristata* was significantly greater at PC than at F_Z. At F_Z, *S. cristata* reaches a density of almost four individuals m^{-2}, while at PC it can reach almost 10 individuals m^{-2} (Fig. 2). At both sites, the 50–100 mm size class was the most abundant (Fig. 2). For all three size classes, the density of *S. cristata* was significantly higher at PC ($F_{2,54}$, $P < 0.001$).
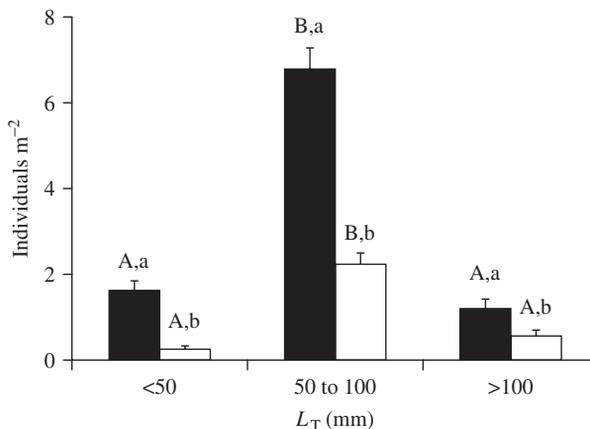

FIG. 2. Mean + S.E. density of different total length (L_T) classes of *Scartella cristata* at two different study sites: Ponta da Cabeça (■) and Fortaleza (□). Upper case letters indicate homogeneous groups in *a posteriori* Student–Newman–Keuls test within site, whereas lower case letters indicate differences within same size classes.
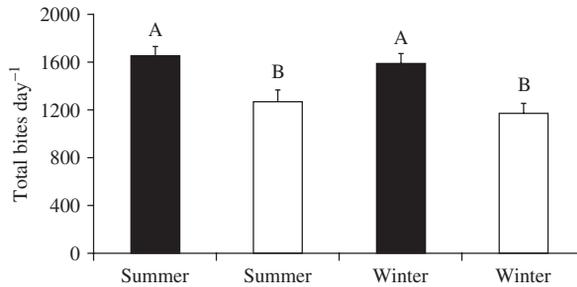
FIG. 3. Mean + S.E. daily feeding rate of *Scartella cristata* at Ponta da Cabeça in summer and winter with different superficial water temperature: warm (22° C average; ■) and cool waters (18° C average; □). Upper case letters indicate homogeneous groups in *a posteriori* Student–Newman–Keuls test.

FEEDING RATES

The feeding rates of *S. cristata* were highly influenced by temperature (Fig. 3). The mean daily number of bites was smaller when the water temperature varied between 16 and 19° C, and was higher in warmer waters (22–25° C) ($F_{3,1436}$, $P < 0.001$). This pattern was prevalent regardless of season.

When considering season and surface water temperature, however, a diel pattern could be observed in the feeding behaviour of *S. cristata*. The feeding process began early in the morning, showed a slight increase during the morning and early afternoon, and peaked always between 1300 and 1400 hours (Fig. 4). Feeding activity decreased abruptly in the afternoon and ceased shortly before sunset (warm
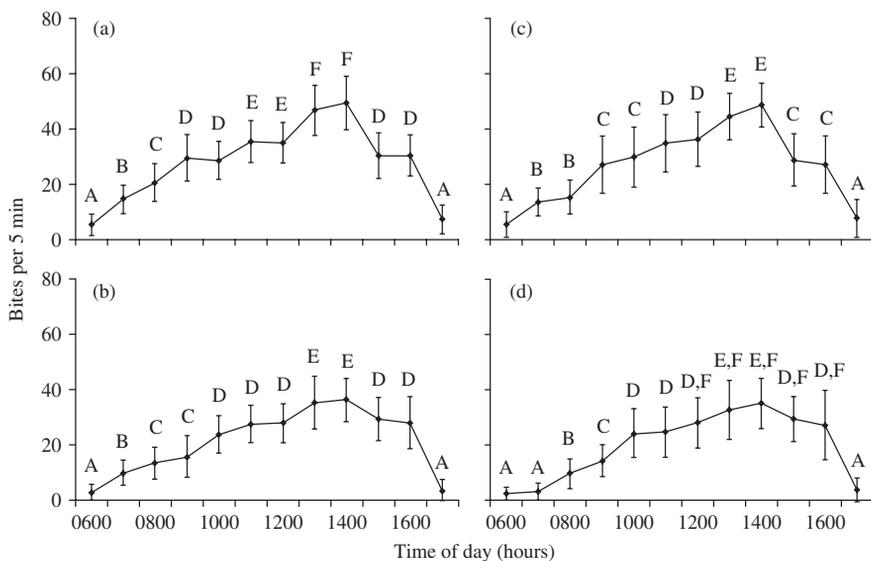

FIG. 4. Variation of the diel feeding behaviour of *Scartella cristata*: (a) summer, water between 22 and 25° C, (b) summer, water between 16 and 19° C, (c) winter, water between 22 and 25° C and (d) winter, water between 16 and 19° C. Values are means ± S.E. Upper case letters indicate homogeneous groups in *a posteriori* Student–Newman–Keuls test.

summer: $F_{11,348}$, $P < 0.001$; cold summer: $F_{11,348}$, $P < 0.001$; warm winter: $F_{11,348}$, $P < 0.001$; cold winter: $F_{11,348}$, $P < 0.001$). No feeding activity was observed after sunset.

DIET

Through gut content analysis, 41 different food items could be identified (Table I). The per cent contribution of each item varied between both sites and season (Table II).

TABLE I. List of taxa identified within gut content of *Scartella cristata*

Algae	Diatoms	
	Filamentous	Cianophyceae
		Ceramium spp.
		Centroceras clavulatum
		Polysiphonia spp.
		Deleseriaceae
		Bryothamnion sp.
		Ralfsia sp.
		Ectocarpaceae
		Sphacelaria spp.
		Bryopsis spp.
		Codium spp.
		Boodlea spp.
		Cladophoropsis sp.
		Cladophora spp.
		Enteromorpha spp.
	Calcareous	Crustose coralline
		Jania spp.
		Arthrocardia sp.
		Amphiroa spp.
	Corticated	*Gelidium pusillum*
		Pterocladiella capillacea
		Hypnea spp.
		Gelidiella acerosa
		Colpomenia sinuosa
	Leathery	*Sargassum* sp.
Invertebrates	Foraminifera	
	Porifera	
	Hydrozoa	
	Crustacea	Cirripedia
		Gammaridae
		Caprelidae
		Decapoda Isopoda
	Mollusca	*Brachidontes* sp.
		Perna perna
		Nodilittorina ziczac
		Fissurela sp.
	Echinodermata	*Echinometra lucunter*

TABLE II. Per cent composition of diet (mean ± S.E.), plus ANOVA and Student–Newman–Keuls (SNK) comparison between sites and seasons

		Site and season				ANOVA	SNK results
		PC-SUM	PC-WIN	F_Z-SUM	F_Z-WIN		
Algae	Diatoms	0.79 ± 0.21	5.51 ± 0.9	0	3.78 ± 0.74	$F = 18.74; P < 0.001$	$PC_S = FZ_S < PC_W = FZ_W$
	Filamentous	19.1 ± 0.23	17.74 ± 2.04	38.01 ± 4.46	35.63 ± 1.94	$F = 15.92; P < 0.001$	$PC_S = PC_W < FZ_S = FZ_W$
	Coralline	1.93 ± 0.49	1.4 ± 0.67	8.81 ± 1.27	8.83 ± 1.64	$F = 18.48; P < 0.001$	$PC_S = PC_W < FZ_S = FZ_W$
	Corticated	3.07 ± 0.39	3.2 ± 1.02	6.61 ± 1.19	6.16 ± 1.33	$F = 2.42; P = 0.08$	$PC_S = PC_W = FZ_S = FZ_W$
	Leathery	0	0	1.51 ± 0.65	0	$F = 5.43; P < 0.001$	$PC_S = PC_W = FZ_W < FZ_S$
Invertebrates		8.62 ± 1.85	5.26 ± 1.77	10.04 ± 3.23	10.51 ± 1.16	$F = 2.55; P = 0.06$	$PC_S = PC_W = FZ_S = FZ_W$
Detritus		54.8 ± 2	62.35 ± 1.98	35.02 ± 1.55	35.10 ± 1.57	$F = 50.67; P < 0.001$	$PC_W > PC_S > FZ_S = FZ_W$
Sediment		11.7 ± 1.27	4.54 ± 1.23	0	0	$F = 5.43; P < 0.001$	$PC_S > PC_W > FZ_S = FZ_W$

PC, Ponta da Cabeça; FZ, Fortaleza; PC_S and FZ_S, summer; PC_W and FZ_W, winter.
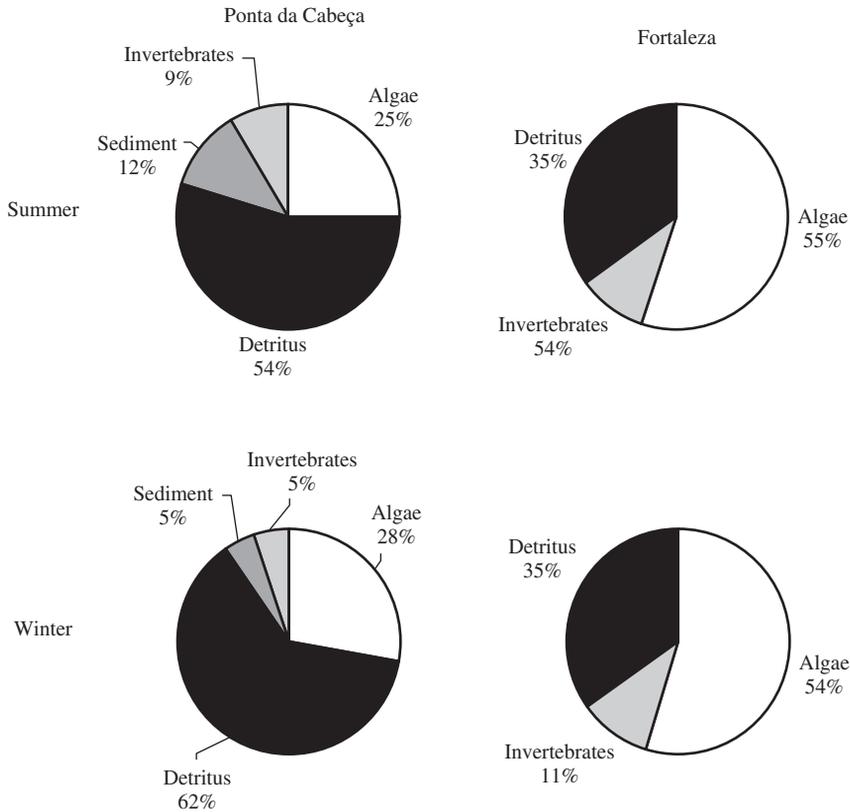
FIG. 5. Comparison of diet of *Scartella cristata* at the two studied sites in different seasons.

Algae and detritus were the most common items identified (Fig. 5). At PC, detritus was the most important item ingested, whereas at F_Z, algae (mainly filamentous) were more abundant in the gut contents (Fig. 5). Although filamentous algae was the most commonly ingested functional group by *S. cristata,* calcareous, corticated and leathery macroalgae were also detected (Fig. 5). Invertebrates, diatoms and sediment were also present but in comparatively smaller quantities.

DISCUSSION

FEEDING RATES

The feeding rate of *S. cristata* was higher in warmer waters (22–25° C) than in cooler ones (16–19° C). It is largely known that metabolic rates in vertebrates increase with increased temperatures (Clarke & Johnston, 1999; Gillooly *et al*., 2001). Temperature is also known to affect many processes related to food acquisition and manipulation in herbivorous fishes, being positively correlated with ingestion (Horn & Gibson, 1990), bite rate (Carpenter, 1986; Polunin & Klumpp, 1989; 1992; Ferreira *et al*., 1998*b*) and foray frequency (Smith, 2008), and also negatively

correlated with gut transit time (Horn & Gibson, 1990). Abrupt decreases in water temperature can promote drastic decreases in feeding rates of herbivorous fishes. Ferreira *et al*. (1998*b*), working on subtropical rocky shores, verified that changes of *c*. 4° C in the surface water temperature during short periods modify the diel feeding pattern of a grazing damselfish *Stegastes fuscus* (Cuvier). Although the feeding rates of *S. cristata* were lesser in cooler water, no short-term changes in its diel feeding pattern could be observed due to temperature, as the water temperature did not change significantly within the days.

Although temperature was observed as the main factor guiding the feeding rate of *S. cristata*, a seasonal trend in resource utilization upon the EAM can be expected. PC is highly influenced by a markedly seasonal upwelling (Valentin, 1984) that causes a negative thermal anomaly. During the non-upwelling months (autumn and winter), the surface water temperature is typically higher, with a consequently greater feeding rate of *S. cristata*, and an expected higher amount of ingested EAM. This increase in feeding rate may provide periods of energy storage that could generate seasonal patterns related to resource allocation (Montgomery & Galzin, 1993). Further studies comparing the condition of *S. cristata* at PC as well as at other sites may unravel this issue.

The diel feeding behaviour of *S. cristata* exhibited a similar pattern during both summer and winter, and with either cold or warm water, with an increase throughout the morning and a plateau in the early afternoon. Although a tremendous variation in the diel feeding behaviour of the nominally herbivorous fishes is commonly observed, a feeding peak or a plateau in the afternoon has been verified in many species (Montgomery, 1980; Lobel & Ogden, 1981; Polunin & Koike, 1987; Montgomery *et al.*, 1989; Polunin & Klumpp, 1989; Zoufal & Taborsky, 1991; Choat & Clements, 1993; Bruggemann, 1994; Polunin *et al.*, 1995; Letourneur *et al.*, 1997; Ferreira *et al.*, 1998*b*; Zemke-White *et al.*, 2002; Townsend & Tibbetts, 2004; Raubenheimer *et al.*, 2005), and may be explained by the presence of a higher concentration in algae photosynthates in the afternoon (Zemke-White *et al.*, 2002). Most of these studies, however, focused on species that are detritivorous or even omnivorous, and thus an explanation based solely on algal characteristics may not be the most suitable. Instead, other factors like establishment of feeding territories in the morning, daily accumulation of detrital resources, hunger and predation must be included to help explain the feeding pattern of these nominally herbivorous fishes. Additionally, it would be possible to infer that detritivory in reef fishes is a secondary characteristic in relation to herbivory and that detritivorous fishes still hold the typical herbivorous diel feeding pattern.

DIET

In the subtropical system of Arraial do Cabo, *S. cristata* exhibited tremendous variation in feeding habits, ingesting from 25 to 55% algae and from 35 to 62% detritus depending on the season and site. Detritus is defined as non-living organic matter derived from a non-fossil living source inhabited by numerous heterotrophic and autotrophic microorganisms such as bacteria, fungi, protozoans and many algae such as diatoms (Wilson, 2000; Crossman *et al.*, 2001; Wilson *et al.*, 2003). Although organic detritus has recently been shown to constitute an important source of nutrients to fishes in coral reefs (Wilson, 2002; Wilson *et al.*, 2003; Crossman *et al.*, 2005),

detritus has not previously been confirmed to play this role in rocky reefs. Chemical analysis in detritus and filamentous algae from coral reefs indicates that although algae tend to have slightly higher protein levels, overall protein contents are similar in both (Wilson & Bellwood, 1997; Crossman *et al*., 2001; Purcell & Bellwood, 2001; Wilson, 2002). The higher protein:energy ratio (Wilson, 2002) and the smaller C:N ratio in detritus (Wilson & Bellwood, 1997; Wilson, 2000; Purcell & Bellwood, 2001), however, indicate that detrital aggregates present in EAM from coral reefs are a relatively more nutritious food source than algae (Wilson *et al*., 2003). Microorganisms colonizing detrital aggregates make this detritus an even richer food source for EAM-feeding fishes (Choat & Clements, 1998).

Detrital aggregates found in the guts of *S. cristata* are potentially colonized by numerous micro-organisms that make this detritus highly nutritious. Choat & Clements (1998) claimed that many reef fishes that ingest detritus and sediment are able to digest bacteria found within these resources to obtain nutrients. Detrital aggregates found in the gut contents of *S. cristata* are composed of small particles with no defined structure, suggesting that they are from amorphic detritus, as proposed by Bowen (1984). According to him, amorphous detritus is composed of small translucent particles <250 μm with no defined structure. Amorphic detritus is more nutritious and more easily digested than morphic detritus (Wilson, 2000). Detrital aggregates found in the gut of *S. cristata* were probably already available within the EAM and were ingested by the fish, owing to the fact that, as with other blennies, *e.g. Salarias patzneri* Bath, the tooth structure and the absence of pharyngeal teeth indicate that *S. cristata* may not be able to macerate food items (Wilson, 2000; pers. obs.). The presence of detrital aggregates in the first part of the gut also suggests that these aggregates are not created by a digestive process. So, it was assumed that all detritus found in the gut of *S. cristata* had been associated with the EAM.

None of the previous studies that investigated the diet of *S. cristata* have been concerned with the amount of detritus ingested, and none have quantified this detritus as an isolated item. According to Randall (1967), the diet of *S. cristata* from the Caribbean was composed of 99·2% macroalgae (*Acanthophora spicifera*, *Amphiroa fragilissima*, *Bryopsis* sp., *Caulerpa* sp., *Ceramium* spp., *Dictyota* spp., *Hypnea musciformis*, *Laurencia* spp. and *Lyngbya* sp.) and organic detritus. The real proportion of each item, however, was not reported. In the Mediterranean Sea, Nieder (1997) mentioned up to 95% algae in the guts analysed, but did not mention the occurrence of detritus. In Florida, *S. cristata* was reported to ingest up to 98·1% 'organic matter' (Mobley & Fleeger, 1999). They considered organic matter, however, as amorphous material, non-differentiated or non-quantifiable, composed of macroalgae, microalgae, sessile organisms and detritus, and once again, the real proportion of each of those categories was not measured. In contrast with these studies that classified *S. cristata* as a herbivorous blenny, Tararam & Wakabara (1982) identified a large amount of invertebrates in the gut content of *S. cristata* from tidepools along the coast of São Paulo (the south-eastern Brazilian coast). A number of observations of *S. cristata* have been made from fish corpses in tide pools and in the subtidal environment of Arraial do Cabo rocky shores (T. C. Mendes & C. E. L. Ferreira, pers. obs.). Along with these previous studies, this work highlights the trophic plasticity of reef-associated fishes and specifically of *S. cristata*. These results suggest that this fish may occupy different food niches depending on specific environmental conditions. This consideration makes trophic definition of these nominally herbivorous fish

difficult, making evident again the poor comprehension of their digestive processes and nutritional ecology.

The presence of short-chain fatty acids (SCFA) within the gut of fishes was pointed out as an indicator of gastrointestinal bacterial fermentation, enabling the host animal to gain resources from dietary components generally not susceptible to endogenous digestive enzymes (Stevens & Hume, 1998). This fermentation is more pronounced in fishes that feed largely on carbohydrates, which bacteria can break down to produce acetate. This acetate is used as an energy source by the fish, indicating a diet based on carbohydrate-rich algae. On the other hand, species that feed on detritus show little evidence of fermentation (Choat *et al*., 2002, 2004; Mountfort *et al*., 2002). Once the SCFA profiles are concordant with diet and feeding rates (Choat *et al*., 2002), it is possible to infer digestive mechanisms based on the diet of fishes. If so, due to its plastic diet, *S. cristata* would be positioned in the dietary category 2 or 4 (Choat *et al*., 2002), which include medium and low SCFA profiles (Choat *et al*., 2004; Crossman *et al*., 2005). *Scartella cristata* also presents a simple and long gut with no distinct stomach, an apparently rapid turnover of gut contents and an elevated feeding rate, compared with those of detritivorous fishes (Choat *et al*., 2004). Choat *et al*. (2004) showed that distinct phylogenetic species can sustain similar diets, and closely related species can exhibit very different diets. Whether feeding habits may change with environmental conditions is yet to be elucidated. In the subtropical and highly dynamic rocky shores of Arraial do Cabo, *S. cristata* showed a high trophic plasticity, which suggests a great influence of environmental characteristics on the diet of reef fishes.

Detritus can make up a considerable fraction of the diet of *S. cristata*, depending on specific conditions. Other blennies are already known to ingest a large amount of detritus, including *Salarias fasciatus* (Bloch) (Wilson, 2000), *Ecsenius mandibularis* McCulloch (Depczynski & Bellwood, 2003), *Ecsenius lineatus* Klausewitz and *Ecsenius namiyei* McCulloch Jordan & Evermann) (Ho *et al*., 2007), all characterized as detritivorous blennies. Along with these blennies, cryptobenthic Gobiidae compose an important linkage between detrital production and secondary consumers, playing an important role in coral reef trophodynamics. Accordingly with the patterns observed for *S. cristata*, it is hypothesized that cryptobenthic fishes in the subtropical rocky shores probably also exert an important linkage on system trophodynamics by removing great quantities of detritus from the EAM. Most of the studies concerning diet of nominally herbivorous reef fishes have neither identified nor quantified detrital participation, making clear that this issue must be taken in account in future studies.

Owing to the great variation in the composition of its diet, it is possible to classify *S. cristata* as herbivorous-detritivorous fish. In order to determine precisely the trophic status of *S. cristata*, questions concerning the composition of detrital aggregates as well as the digestibility and assimilation capacity of detritus, algae and other items in the diet of *S. cristata* must still be investigated. In summary, this paper highlights the great plasticity of the diet of *S. cristata*, calling attention to the interpretation of punctual gut content analysis to examine fish diet. This is the first study that aimed to quantify the amount of detritus ingested by a rocky reef fish. Detritus was found to be a major component of the diet of *S. cristata*, although filamentous algae and invertebrates can also be important items. This result suggests that, as reported for coral-reef cryptobenthic fishes, along subtropical rocky shores

fishes make up an important link in the detritus-based pathway, playing an important role in reef trophodynamics.

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