

# Survival and dispersal of turf algae and macroalgae consumed by herbivorous coral reef fishes

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**Abstract** The mechanisms by which algae disperse across space on coral reefs are poorly known. We investigated the ability of four common Caribbean herbivorous fish species to disperse viable algal fragments through consumption of macroalgae and subsequent defecation. Fragments of all major algal taxa (Phaeophyta, Rhodophyta, and Chlorophyta) were found in 98.7 % of the fecal droppings of all fish species; however, the ability to survive gut passage and reattach to a substrate differed between algal taxa. While survival and reattachment approached zero for Phaeophyta and Chlorophyta, 76.4 % of the fragments belonging to the group Rhodophyta (mostly species in the order Gelidiaceae) survived gut passage, and were able to grow and reattach to the substrate by forming new rhizoids. Our results thus show that Gelidid algal species are dispersed by swimming herbivores. While the relative contribution of this mechanism to overall algal

dispersal and recruitment in a wider ecological context remains unknown, our findings illustrate a previously undescribed mechanism of algal dispersal on coral reefs which is analogous to the dispersal of terrestrial plants, plant fragments, and seeds via herbivore ingestion and defecation.

**Keywords** Herbivory · Dispersal · Feces · Scaridae · Acanthuridae

## Introduction

Herbivores represent an important structuring factor, either directly or indirectly, in a wide range of ecosystem types around the world (e.g., McNaughton 1985; Collins et al. 1998). Because herbivores consume the biomass produced by autotrophs, they represent a major conduit by which energy enters food webs (Cyr and Pace 1993). Many plant species have evolved defense mechanisms to prevent being grazed (e.g., spines and toxic secondary metabolites), but also strategies to benefit from grazing. For example, by attracting herbivores to fruits or edible seeds, terrestrial plant species use moving herbivores to increase the dispersal range of their offspring (Howe and Smallwood 1982). The dispersal of otherwise motionless plant parts, when they are viable, helps them to escape from local predators, reach more favorable growth sites, and reduce parent-offspring competition (Tiffney 2004). Dispersal of (reproductive) plant parts by animals can occur through external adhesion or by surviving the passage through a herbivore's intestinal tract without losing the capacity to germinate. The latter mechanism was first described for birds (Barton 1812), and has since been found in a wide variety of other vertebrate species (Corlett 1998; Clark

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et al. 2001; Wenny 2001). At present, dispersal of plants and plant parts (e.g., seeds, fragments) through herbivore ingestion and defecation is considered a major factor structuring the composition and distribution of terrestrial plant communities (Tiffney 2004).

Though less well studied, herbivores in aquatic and marine ecosystems are also capable of dispersing plant fragments, fruits, or seeds through defecation. Several freshwater fish species can disperse seeds of terrestrial plants (van der Pijl 1966; Pollux 2011). In addition, invertebrates such as sea urchins (Santelices et al. 1983), mollusks (Santelices and Correa 1985; Santelices and Ugarte 1987), amphipods, and gastropods (Breeman and Hoeksema 1987) disperse viable algal fragments through defecation in marine environments. Thus, plant dispersal via ingestion and defecation by herbivores occurs in a wide variety of terrestrial and marine ecosystems.

On coral reefs, herbivores are important in structuring benthic communities by controlling the abundance of primary producers such as turf and macroalgae (e.g., Ogden 1976; Randall 1961; Hay 1981; Williams et al. 2001; Mumby 2009; Kopp et al. 2010). Some algal species tolerate high levels of herbivory by investing energy in continuous rapid growth rather than costly structural and/or chemical defenses (Duffy and Hay 1990). This strategy is often observed in small filamentous algae, whose biomass production is highest under high levels of herbivory, because continuous cropping prevents self-shading and because herbivore excretion might increase local nutrient availability (Carpenter 1986). Herbivores can also contribute to algal dispersal, i.e., by moving algae or parts thereof away from the adult population or adult plant, respectively. For example, swimming herbivores generate asexually produced algal “offspring” (i.e., fragments) during feeding (Herren et al. 2006) that can adhere to herbivores and become subsequently dislodged in a new habitat (Burgin and Renshaw 2008). Duffy and Hay (1990) described the possibility that algae can offset their losses to herbivory if ingested propagules or vegetative portions remain viable after ingestion and defecation; the authors compared this strategy to that of seed dispersal of terrestrial plants by birds and mammals.

Within coral reef communities, algae generally have negative effects on neighboring corals including shading and abrasion (McCook et al. 2001), allelopathy (Rasher and Hay 2010), competition for space and the inhibition of coral recruitment (Vermeij 2006; Vermeij and Sandin 2008), and alteration of microbial communities and dissolved oxygen concentrations on adult and juvenile corals (Smith et al. 2006; Vermeij et al. 2008; Barott et al. 2011, 2012). Grazing by herbivorous fish prevents uncontrolled algal proliferation on coral reefs and thus indirectly benefits coral survival, recruitment, and growth (e.g., Jompa and McCook 2002; Hughes et al. 2007; Burkpile and Hay

2008; Mumby 2009; Kopp et al. 2010; Arnold et al. 2010). Eutrophication, diseases, storms, and overharvesting of herbivores (amongst other factors) synergistically underlie shifts in reef communities from coral to algal dominance; the latter state often becomes reinforced or maintained by positive feedback mechanisms (Scheffer et al. 2001; Mumby and Steneck 2008; Hoey and Bellwood 2011).

Here, we propose that swimming herbivores are capable of dispersing algae in coral reef environments by moving algal fragments away from donor populations. In order to explore this hypothesized mechanism, algal viability after digestion and seeding rates of viable fragments were quantified for several herbivorous Caribbean coral reef fishes. Specifically, we asked the following questions: (1) Do the composition and abundance of algal fragments in fecal pellets differ between herbivore species? (2) Do algal fragments survive the passage through an herbivore’s intestines and retain their ability to grow after defecation? (3) Does the amount of algal fragments released by herbivores differ throughout the day?

## Materials and methods

### Research area

All experiments were carried out on the island of Curaçao between April and July 2010. Fecal sampling and fish behavior surveys occurred at the fringing reefs in front of the Carmabi field station (12°7.337’N, 68°58.111’W) in shallow waters between 3 and 12 m. The area was characterized by low coral cover and high cover of macroalgae and turf algae on dead coral substrates.

### Study species

We focused on four herbivorous fish species that significantly contribute to overall grazing activity on Caribbean coral reefs (Lewis and Wainwright 1985; Bellwood et al. 2004; Kopp et al. 2010): *Sparisoma viride* (stoplight parrotfish) and *Scarus taeniopterus* (princess parrotfish) from the family Scaridae and *Acanthurus bahianus* (ocean surgeonfish) and *Acanthurus coeruleus* (blue tang) from the family Acanthuridae. These species differ in their feeding habits and turn-over rates of ingested food (Ogden and Lobel 1978; Francini-Filho et al. 2010) allowing the investigation of possible effects of different herbivore species on algal fragment viability and relative abundance.

### Collecting and processing fecal samples

Fecal samples were collected in situ on SCUBA at depths from 3 to 12 m. Because *A. coeruleus* and *A. bahianus*

generally defecated high (>1.5 m) above the benthos, samples could easily be collected immediately after release and before they disintegrated while sinking. Because defecation of *S. taeniopterus* and *S. viride* generally occurred close to the bottom, samples were collected from the substrate using a syringe. Fecal droppings that had landed on substrates possibly contaminated with algal fragments (e.g., macro- or turf-algal beds) were avoided. After collection, samples were transported to the laboratory in syringes or 50-ml Falcon tubes within 1 h of collection. Fecal samples were promptly placed in individual Petri dishes filled with filtered seawater (Whatman GF/F). Water temperature and light levels were kept similar to those observed in the field during the same period (28–29 °C and a diurnal light rhythm at 30 % of full sunlight). Due to partial degradation, algal fragments found in the fecal pellets usually could not be classified to the species level. Therefore, algal fragments were classified according to their three main divisions: (1) Chlorophyta: all green algal and green turf-algal structures; (2) Rhodophyta: all red algal structures that are thin and laminar or filamentous with single or branching twigs; and (3) Phaeophyta: all brown algae. Through the course of the study, 20–28 fecal samples per species were collected on different days between 0800 and 1800 hours and analyzed under a dissecting scope to quantify the total number of algal fragments per fecal dropping.

#### Incubation of algal fragments

To determine whether algal fragments collected from feces remained viable and capable of growth and attachment, individual fragments representing each of the three algal groups were collected from the original sample and incubated in filtered seawater as described above. Seawater was refreshed every 2 days to maintain constant nutrient availability and salinity.

Fragments were monitored for 14 days by photographing the fragments at 0, 5, 9, and 14 days against a background grid for scale. After 14 days, all photographs taken of an individual fragment were analyzed to quantify growth. Growth was defined as observable elongation of the fragment itself or the appearance of new sprouts. Growth potential was quantified as the proportion of fragments that showed signs of growth for each algal category. These data were collected for each of the four herbivore species. To separate the effects of gut passage from fragmentation, we additionally cut 25–35 fragments (0.2–0.8 cm) from individual algae species most often observed in the fecal pellets from the field, and incubated them in the same manner as the fragments collected from the fecal samples; these data were used to determine whether small fragments were capable of growth regardless of whether they had passed through an herbivore's intestines.

#### Field surveys

To quantify the defecation frequency of each herbivore species, random individuals of each species were observed during three-minute intervals at various times of the day so that a total of 30 individuals were followed for each species for each hourly interval between 0800 and 1800 hours. For each fish observed, its length, number of defecations, the substrate on which a fecal dropping landed, and depth at time of defecation were recorded. Divers remained at least 4 m away from each surveyed fish to minimize disruptions in natural fish behavior. In addition, divers noted the benthic surface from which individual fish fed most often during each 3-min observation period.

#### Data analysis

Effective sample sizes for all experiments were determined using power analyses in preliminary experiments. Differences between fecal compositions for different fish species were analyzed as follows: to assess species-specific differences in the number of fragments per fecal droppings, a one-way ANOVA was performed followed by post hoc analyses (Tukey HSD). These analyses were followed by multifactor ANOVAs where the composition of the algal fragments (i.e., the percentage of the total number of fragments belonging to each algal taxon) per fecal dropping was compared among herbivore species. The Tukey HSD test was again used for post hoc analyses. The Z test for proportions was used to assess differences in the proportion of fragments displaying signs of growth among herbivore species and between algal taxa per herbivore species. Growth was simply scored as present (one) or absent (zero). Differences in defecation frequency per fish species could only be analyzed using non-parametric tests (Kruskal–Wallis test) as data were non-normal even after various transformations. Possible relationships between defecation frequency and fish size and time of day were assessed using simple linear regression. Finally, by combining various estimates of fragment abundance, survival, and defecation rates, the total number of viable algal fragments released daily by each fish species was calculated by multiplication of the means of all estimated parameters required. Standard deviations of this composed estimate were calculated by summing the square root of each fractional standard deviation followed by taking the square root of their sum to get the standard deviation for the composed estimate (i.e., the mean number of viable algal fragments released by individual fish measuring 20 cm over a 12-h period). To test whether fish defecated preferentially above certain substrate types, the abundance of substrate types on which fecal droppings landed were compared against their natural abundance at the same site.

Chi-square analyses were used to determine whether this observed distribution of fecal droppings across substrate types differed from the relative abundance of substrate types, thereby testing whether or not fecal pellets landed randomly across the reefscape.

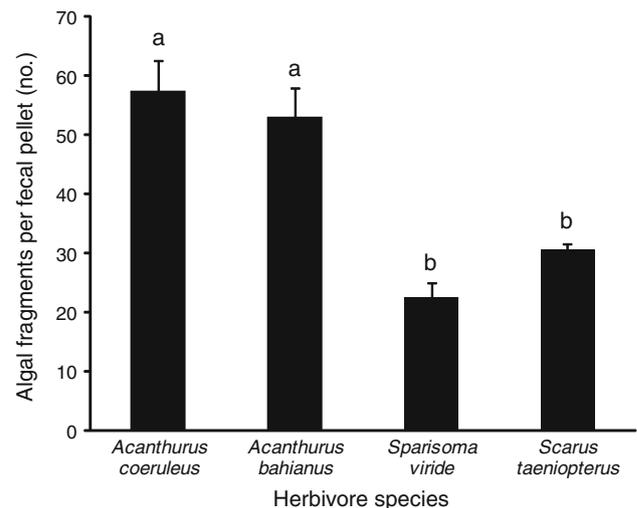
## Results

Do algal fragment composition and algal fragment abundance in feces differ between herbivore species?

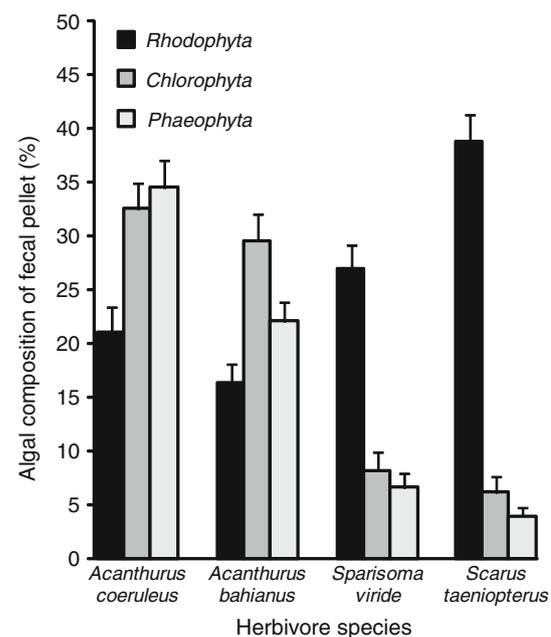
A total of 235 fecal samples were collected from the four herbivorous reef fish studied. Of all fecal samples, 98.7 % ( $n = 232$ ) contained algal fragments. In addition to algal fragments, the fecal samples contained sand and unrecognizable organic debris. The length of fecal pellets differed between species (one-way ANOVA,  $F_{3,730} = 180.11$ ;  $p < 0.001$ ). Average pellet size was similar for both acanthurids species [Tukey HSD; *A. coeruleus*: 1.22 cm (SD 0.90,  $n = 150$ ), *A. bahianus*: 1.29 cm (SD 0.90,  $n = 188$ )], but acanthurid pellets were smaller compared to both scarid species: 2.91 cm (SD 1.46,  $n = 213$ ) for *S. taeniopterus* and 3.58 cm (SD 1.74,  $n = 183$ ) for *S. viride*. Average fecal length was significantly larger in *S. viride* compared to *S. taeniopterus* (Tukey HSD). The number of algal fragments per fecal pellet differed between species (one-way ANOVA,  $F_{3,90} = 18.26$ ;  $p < 0.001$ ). Despite their smaller size, pellets from both acanthurid species contained on average 2.1 times more algal fragments than those from both scarid species, and no significant differences between species within each family were observed based on post hoc analyses (Tukey HSD; Fig. 1). In addition to the mean number of fragments per fecal pellet, the composition of the algal fragments differed between species (MANOVA,  $F_{3,9} = 27.3$ ;  $p < 0.001$ ). Significant differences were observed between the two families but not between species within one family (Tukey HSD; Fig. 2). Fecal pellets of both acanthurid species contained more fragments belonging to the phaeophyta (5.4 times more on average) and chlorophyta (4.3 times more on average) than fecal pellets from scarids, whereas rhodophyte fragments were more abundant in the fecal pellets from the two scarid species when compared to fecal pellets from the two acanthurids (1.8 times more on average).

Do algal fragments survive the passage through an herbivore's intestines and retain their ability to grow after defecation?

Growth was observed in 43 % (total  $n = 1,111$ ) of the algal fragments found in fecal pellets. Among fragments that exhibited growth, the first growth was observed an



**Fig. 1** Average number of algal fragments per fecal pellet for all four herbivore species studied. Letters above the bars indicate significant groupings based on post hoc analyses (Tukey HSD)



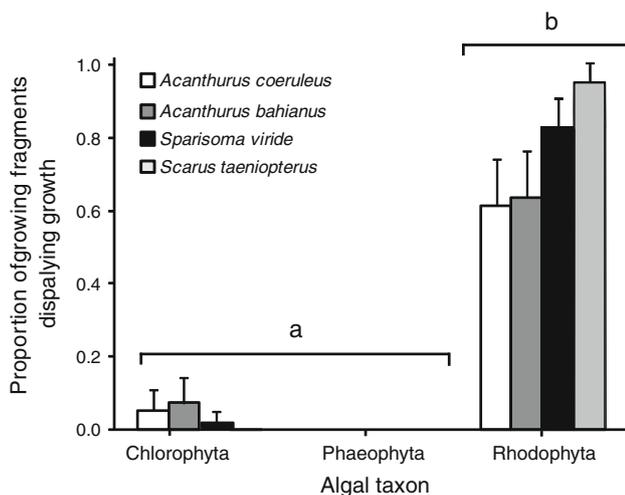
**Fig. 2** Average composition of fecal fragments for all four herbivore species expressed as the relative abundance of fragments belonging to each of three main algal groups

average of 8 days after the start of incubation (SD = 3;  $n = 487$ ). The highest rate of fragment viability was observed in the Rhodophyta where 76.4 % of all fragments grew within 14 days (Fig. 3). For Chlorophyta, the proportion of fragments displaying signs of growth was indistinguishable from zero because the 95 % confidence intervals of our estimates overlapped with zero. Fragments belonging to the Phaeophyta (mainly *Dictyota* spp.) never

showed any signs of growth (Fig. 3). Within each algal group, the proportion of fragments displaying signs of growth did not differ between the four herbivore species or as a function of increased fragment size ( $Z$  test for proportions;  $p > 0.05$ ). Growing fragments belonging to the Rhodophyta showed enlargement of their thalli, formed new leaves, and produced structures for attachment to the surface of the incubation dish. After fragments displayed some growth, they could be more easily identified under a dissecting scope. Analysis of fragment morphology after growth in the laboratory revealed that 65.1 % of all rhodophyte fragments that grew belonged to the order Gelidiaceae, whereas the remaining 34.9 % comprised species belonging to the Champiaceae, Lomentariaceae, and Ceramiaceae. All four of these rhodophyte taxa are commonly found in turf algal communities on Curaçao (Vermeij et al. 2010). When the capacity to grow was examined in fragments that were artificially created, only fragments from the rhodophyte species (60 %;  $n = 30$ ) showed signs of growth within 14 days. While the potential for growth was quantified for all algal fragments in this study, absolute growth rates were not quantified because these depend heavily on local nutrient and light levels.

Does the number of algal fragments released by herbivores differ throughout the day?

Herbivorous species differed in the number of fecal droppings they produced throughout the day (Kruskal–Wallis test:  $H_{3,1203} = 55.2$ ;  $p < 0.001$ ). Individual analyses between species pairs showed that *A. coeruleus* was solely responsible for the significant difference among species



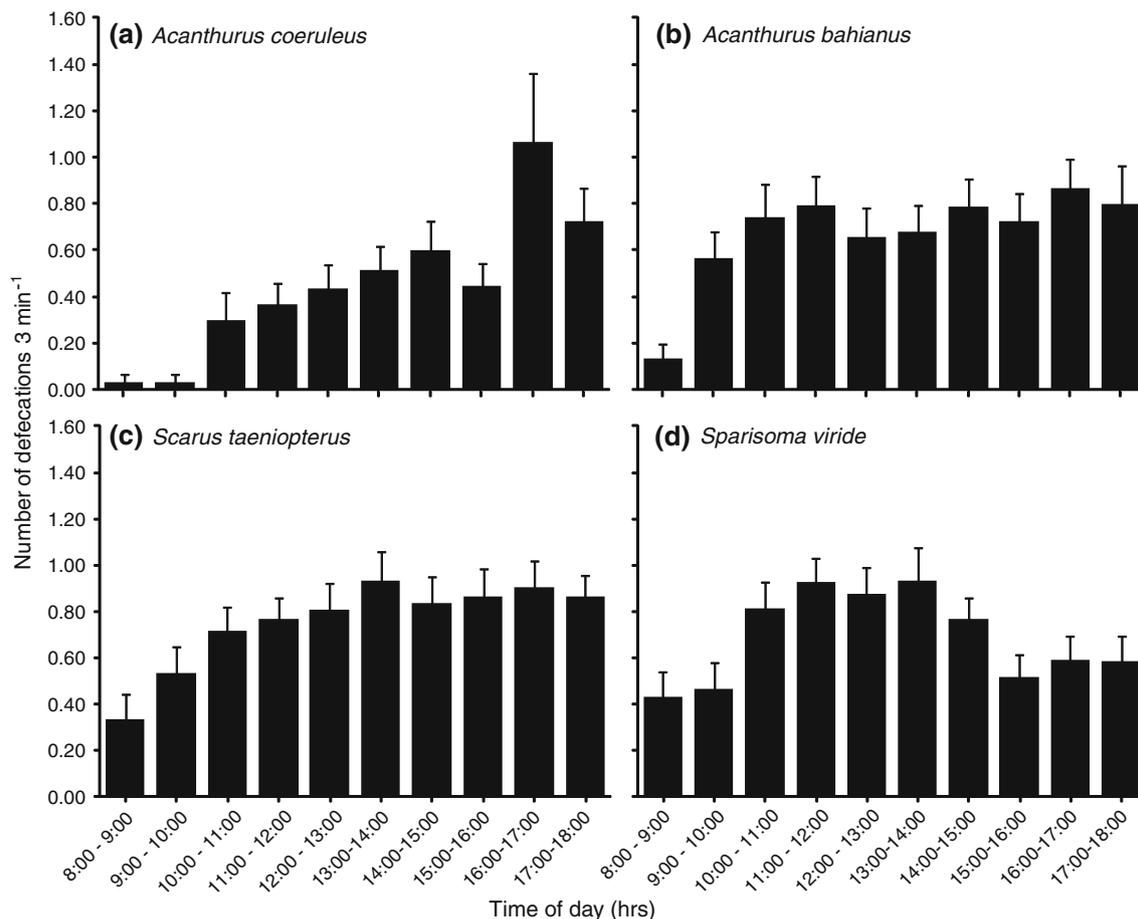
**Fig. 3** Proportion of algal fragments displaying growth within 14 days after defecation shown by algal taxon and herbivore species (mean + 95 % conf. interval). Data for Phaeophyta approaches zero for all herbivore species. Letters indicate significantly similar groups based on post hoc analyses (Tukey HSD)

(Kruskal–Wallis test;  $p < 0.001$ ). *A. coeruleus* produced on average 1.7 times fewer fecal droppings than all other species considered, i.e., 0.45 versus 0.67–0.76 fecal droppings  $3 \text{ min}^{-1}$  for all other species. Defecation frequency was positively correlated, albeit weakly, with fish size for *A. coeruleus* ( $r = 0.17$ ;  $n = 299$ ;  $p < 0.05$ ) and *S. viride* only ( $r = 0.14$ ;  $n = 302$ ;  $p < 0.05$ ). The defecation frequency of all species, except *S. viride* ( $r = 0.01$ ;  $n = 299$ ;  $p = 0.87$ ), increased during the day ( $0.20 < r < 0.34$ ;  $n = 300 \pm 5$ ;  $p < 0.001$ ; Fig. 4). When these data are combined, the mean number of viable algal fragments (all belonging to the Rhodophyta) released by individual fish measuring 20 cm in a day (i.e., over a 12-h period) can be estimated for each species: 804 (SD 1,677) for *A. coeruleus*, 892 (SD 1,213) for *A. bahianus*, 1,428 (SD 1,834) for *S. taeniopterus*, and 1,191 (SD 1,385) for *S. viride*.

Fecal droppings landed non-randomly on the benthos (Fig. 5). While dead coral covered with turf algae dominated the benthos at the study site (68.1 %), the majority of the fecal droppings (i.e., 55.3–77.8 %, depending on species) landed on sand. This is a significantly higher proportion of pellets landing on sand than would be expected by chance if all four of the herbivorous species considered here were releasing fecal pellets randomly over the reef (Chi-square test,  $\chi^2 > 38.0$ ;  $p < 0.001$ ). Finally, more than 80 % of all bites taken by each herbivore species were taken from surfaces dominated by turf algae, and acanthurid species were observed feeding solely on this benthic substrate (Fig. 6).

## Discussion

The main aim of this study was to examine whether or not algal fragments survive gut passage in herbivorous Caribbean reef fishes, to determine whether this mechanism could aid the dispersal of turf algae and macroalgae, i.e., movement away from an existing population or away from the parent organism. For the four fish species studied, we observed that algal fragments occurred in nearly all fecal pellets. Fragments belonging to the order Gelidiaceae (Rhodophyta; for more information on Gelidiaceae, see Guiry and Guiry 2011) were especially capable of growth after gut passage. Our data suggest that these tropical marine algal species can use animal vectors for dispersal, a capability known in some terrestrial plants (Hay 1991). Evidence supporting this idea includes the fact that fragments form exogenous rhizoids for secondary attachment; this capability has been identified in several other species of algae (e.g., Santelices and Varela 1994; Walters and Smith 1994; Perrone and Cecere 1997; Perrone et al. 2006). Successful reattachment in the field is largely dependent on the presence of calcareous substratum (Santelices and

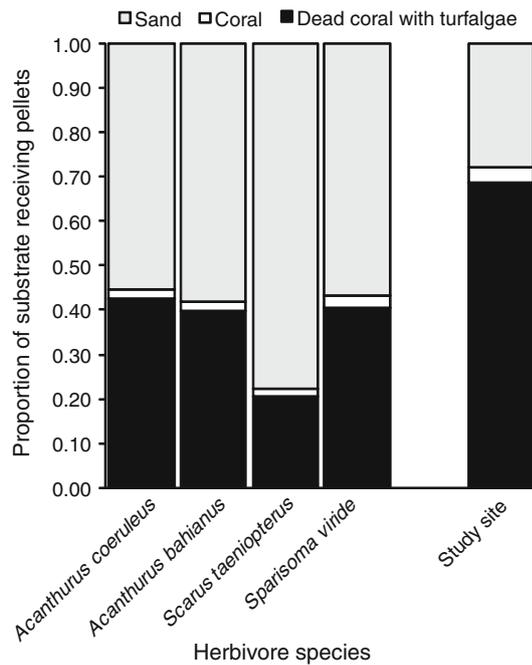


**Fig. 4** Defecation frequency for each herbivore species for hourly intervals throughout the day. *Error bars* standard errors

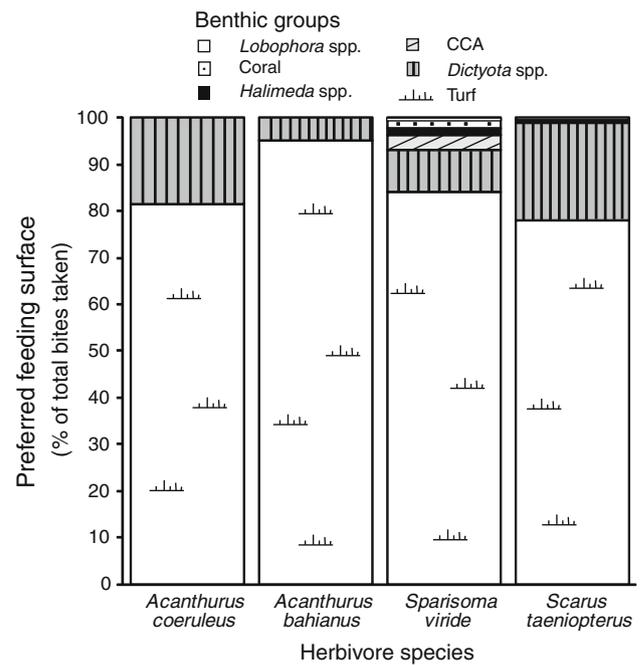
Varela 1994). Secondly, gelidid fragments survive herbivore gut passage far better than the fragments of green and brown algae that co-occurred in the fecal pellets (Fig. 3). The majority of green and brown algal fragments found in the fecal samples were filamentous turf algal species that are 1–5 cells in width. In contrast, branches of the Gelidiales are thicker, and composed of medullary storage cells surrounded by layers of pigmented corticated cells (Guiry and Guiry 2011). The corticated outer layer of gelidid species branches likely protects the storage cells during passage through the herbivore gut, thus reducing the probability that fragments sustain fatal damage. Santelices and Correa (1985) also suggested that cell wall characteristics of gelidid species lowered their sensitivity to digestive enzymes of gastropod grazers. Based on the characteristics of these different algal groups, damage sustained during gut passage is therefore expected to be greater in the turf algal species belonging to the Chlorophyta and Phaeophyta. While the ability of plants and algae to survive consumption and defecation by fish has been described for freshwater fish dispersing terrestrial plant

seeds (van der Pijl 1966; Pollux 2011), and various marine invertebrates dispersing macroalgae (Santelices et al. 1983; Santelices and Correa 1985; Santelices and Ugarte 1987; Breeman and Hoeksema 1987), this is, to the best of our knowledge, the first demonstration that multicellular algae in a marine system can survive gut passage in herbivorous fishes (but see evidence for unicellular autotrophs in Paya and Santelices 1989; Porto et al. 2008; Castro-Sanguino and Sánchez 2012). Our observations thus support the hypothesis that certain marine algae can tolerate or even benefit from herbivory (Carpenter 1986; Duffy and Hay 1990; Hay 1991; Castro-Sanguino and Sánchez 2012).

All four herbivorous fishes considered here had viable algal fragments in their feces; these were primarily species of the Gelidiaceae (Rhodophyta). Chlorophyte species were observed growing after gut passage, but these fragments were far less common. Phaeophyte species were never observed growing after they were defecated (Fig. 3). The observation that algal taxa survive gut passage at different rates has been made in herbivorous molluscs (Santelices and Correa 1985) and sea urchins (Santelices



**Fig. 5** Proportion of each benthos substrate type (sand, coral and dead coral with turf algae) on which fecal droppings landed for each herbivore species (left four bars) in comparison with the natural abundance of these substrate types at the study site (bar on right)



**Fig. 6** Feeding surfaces of the four herbivorous fish species studied: *Scarus taeniopterus* (princess parrotfish), *Sparisoma viride* (stoplight parrotfish), *Acanthurus bahianus* (ocean surgeonfish), *Acanthurus coeruleus* (blue tang). CCA crustose coralline algae

et al. 1983). Given our findings, the differential survival of algal taxa in the herbivore gut appears to be a general phenomenon. Small filamentous turf algae (such as the Gelidiaceae) are generally preferred by herbivores over other algal morphologies such as coarsely branched algae, leathery or rubbery algae, jointed calcareous algae, and crustose coralline algae (Steneck and Watling 1982; Hay 1991). All four herbivore species we observed were most likely to feed on surfaces dominated by turf algae (Fig. 6). Gelidid species are very common in turf algal communities on Curaçao (Vermeij et al. 2010; Fricke et al. 2011), and we observed that these species are capable, at least under laboratory conditions, of surviving, growing, and reattaching to surfaces after gut passage. In contrast to Santelices and Ugarte (1987), who showed that survival and growth of certain algal taxa after defecation depends on the herbivore that ate it, we found no such herbivore effect, but rather that the identity of the algae solely determined its survival and success in growth and reattachment.

The four herbivore species we studied contributed differently to the total amount of viable algal fragments that were released over the reef. Differences in both quantity and composition of algal fragments per fecal pellet were foremost observable between fish families (i.e., Acanthurids vs. Scarids), rather than between species in the same family (Figs. 1, 2). This is likely due to the differences in alimentary tract structure between these families (Horn

1989). Acanthurids possess a stomach in combination with an intestine, whereas scarids possess a pharyngeal mill and an intestine but no stomach (Ogden and Lobel 1978). Generalizations relating a species gut anatomy to its phylogenetic position must still be made with caution, however, because the alimentary anatomy of a herbivorous fish species is not always a reliable guide to its functional capacity (Choat et al. 2004; Horn et al. 2006; Crossmann et al. 2005; Clements et al. 2009), and can even differ among closely related species (Lobel 1981). The differences we observed between fish species in the abundance and composition of algal fragments in their feces is likely to be the result of a number of interacting factors including anatomical characteristics of the gut and feeding apparatus, biochemical characteristics in the gut, species-specific dietary preferences, and perhaps even differences in feeding territories/depths. Similarly, for each species of algae, a combination of factors including inherent structural characteristics (e.g., cell wall thickness) and enzymatic resistance will affect the ability to successfully pass through a herbivore’s gastrointestinal tract.

Interestingly, herbivorous fishes observed in our study fed predominantly on hard substrata dominated by turf algal communities (Fig. 6), but defecated foremost on sand (Fig. 5), a behavior also known from other herbivorous fish species (Polunin and Koike 1987; Bellwood 1995; Krone et al. 2008). It is thought that, by defecating away from their foraging area, herbivorous fish prevent excess

sedimentation on their food sources and reduce infection risks from endoparasites that could still be present in their feces (Krone et al. 2008, and references therein).

Terrestrial herbivores often establish a dual relationship with plants: antagonistic, through herbivory, and mutualistic, through dispersal of seeds or viable fragments. Here, we show that potential for such a relationship exists for herbivores and certain algal taxa in a Caribbean coral reef community. Feces of four common herbivorous fish species contained viable algal fragments from the order Rhodophyta. Admittedly, the relative importance of herbivores to algal recruitment are likely minor as algal fragments in fecal droppings can (1) remain encapsulated within the dropping when it does not completely disintegrate, (2) land or get washed onto unsuitable substrates, and (3) become ingested by coprophagous organisms. Nevertheless, such context-dependent effects of one functional group on another are often neglected in studies on coral reef functioning. These context-dependent ecological factors deserve attention as they could underlie the processes by which undesirable feedback loops and ecological “surprises” occur in coral reef systems.

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