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Seaweed survival after consumption by the greenbeak parrotfish, Scarus trispinosus

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Abstract We assessed the survival of seaweed (macroalgae and cyanobacteria) after consumption by the greenbeak parrotfish, Scarus trispinosus, in northeastern Brazil. Samples of S. trispinosus feces were collected, inoculated on filter paper, and kept in the laboratory and field for 60 and 30 d, respectively. Comparisons of samples inoculated with feces to those without (controls) revealed a marked increase in the abundance and diversity of seaweed in samples inoculated with feces in both laboratory and field experiments. These results were consistent between summer and winter, although the seaweed species differed. A total of one cyanobacterium and 16 macroalgal taxa (nine rhodophytes, five heterokontophytes, and two chlorophytes) were recorded in the inoculated samples. Rhodophyta also presented the highest abundance across treatments, possibly because of their higher resistance to parrotfish digestion, greater ingestion, or both. The survival of cyanobacteria and macroalgae after consumption by S. trispinosus suggests that parrotfishes may contribute to seaweed dispersion on tropical reefs.

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Introduction

Herbivory is considered as one of the main processes maintaining the structure and diversity of benthic communities on tropical reefs. Reef herbivores may remove up to 90 % of the daily primary production of seaweeds and, therefore, influence the standing biomass of benthic algae (reviewed by Hay 1991). Such intense herbivory has driven the evolution of a range of macroalgal defenses against herbivores, such as morphological adaptations, calcification, production of secondary metabolites, and use of refuges (Hay and Fenical 1988; Duffy and Hay 1990). Furthermore, a number of algal species have been shown to survive following ingestion by sea urchins (Santelices et al. 1983), molluscs (Santelices and Correa 1985), and fishes (Vermeij et al. 2013). This survival ability may be considered as a seaweed dispersal strategy and is dependent on three main factors: (1) the ability of algal tissues that have suffered partial digestion to regenerate and grow; (2) the potential of undigested propagules and fragments to grow; and (3) the induction by herbivory, and release of the cell protoplasts following cell wall digestion (Santelices 1992).

A recent study demonstrated that tropical macroalgae could survive and grow following ingestion by two surgeonfishes (Acanthuridae) and two parrotfishes (Labridae:

Scarini) in the Caribbean (Vermeij et al. 2013); however, limited information was provided on the diversity of algal species. Further, the study reported that while fragments of heterokontophytes survived gut passage, no signs of growth were found following defecation. Therefore, whether the ability to survive and grow following ingestion is widespread, or restricted to a few macroalgal species, is currently unknown. The objective of the present study was to assess the survival of macroalgae following ingestion by the greenbeak parrotfish, Scarus trispinosus, on Abrolhos reefs, northeastern Brazil, and in doing so quantify the diversity of algal species growing in the feces.

Materials and methods

The study was conducted in the Abrolhos Archipelago (17°589S, 38°429W), approximately 70 km off northeastern Brazil. The archipelago is composed of five volcanic islands bordered by fringing reefs, which extend from 0.5 to about 10 m deep. Abrolhos reefs are not remarkable coral constructions, but a veneer of reef organisms growing on hard substratum (Leão 1996). Fieldwork was conducted at Santa Barbara Island, the largest island of the archipelago. During the study, water temperature ranged 23–27 °C and water visibility was 8–15 m.

Seaweed (macroalgae and cyanobacteria) survivorship after passing through the gut of S. trispinosus was assessed by both laboratory and field experiments. Laboratory experiments were conducted during July–August 2008 (austral winter) and December 2008–January 2009 (austral summer), whereas field experiments were restricted to summer due to adverse weather conditions in winter. Scarus trispinosus was chosen because of its abundance in Abrolhos and frequent feeding on the epilithic algal matrix (EAM) and crustose coralline algae (CCA), the dominant benthic components of the studied reefs (Figueiredo 1997; Francini-Filho et al. 2010).

Laboratory experiments

Five S. trispinosus individuals ([50 cm total length) were speared in the field at midday, when species feeding rates are at maxima (Ferreira and Gonçalves 2006; Francini-Filho et al. 2010). Speared individuals were taken to the laboratory, and the posterior part of their bodies was compressed to expel the final portion of their gut contents. Four samples (3 mL each) of each individual's feces were collected with a pipette, and each sample was inoculated on filter paper and placed in separate aquaria with constant aeration (2 L volume; 5 aquaria). Filter paper without feces was used as a control (n = 4) and kept in the same conditions as the cultures. Seawater used in the aquaria was

filtered (0.45-l m mesh) and sterilized in the microwave for 5 min on full power (following Meneses 1995). Cultures were kept for 60 d under irradiance of 50–70 l mol m^{-2} s^{-1}, photoperiod of 12 h, and temperature of 24 °C. These light and temperature levels are similar to conditions used for growing germlings from temperate systems (e.g., Chapman 1973; Santelices 1992).

The procedure was run in the laboratory in both winter and summer, to account for possible seasonal variations of seaweed availability at the study site (e.g., Figueiredo 1997; Tâmega and Figueiredo 2007) and in S. trispinosus feces. Aquarium temperature was the same (24 °C) for experiments in summer and winter, as this value was observed during both seasons at the study site and, therefore, probably allowed seaweed development during both seasons. Culture medium (ES/2 at 10 mL L^{-1}) was added weekly (following Jones and Woelkerling 1983).

Field experiment

Field experiments were conducted at the reef base (4 m deep) of Santa Barbara Island. Fish collection, sample size, feces extraction, and sample preparation were the same as for the laboratory experiments. Each of the four 3 mL samples of parrotfish fecal contents and controls were placed on separate Petri dishes (8 cm diameter), which had their bottoms previously scraped to provide roughness to facilitate seaweed settlement (following Leukart 1994). Petri dishes were then immersed in trays (eight dishes per tray), filled with 50 mL of sterilized seawater, and gently aerated (following Jones and Woelkerling 1983). Small holes on the sides of the dishes allowed water flow. Trays were kept in a shaded room under constant temperature (27 °C) for five days. After this period, Petri dishes were fixed with epoxy putty to the reef, where temperature ranged between 25 and 26 °C during the experiment. Field experiments were run for 30 d.

Seaweed identification

Macroalgae and cyanobacteria growing in the laboratory and field samples were examined under stereomicroscope (32–5009 magnification) and optical microscope (100–4009 magnification). The abundance and frequency of each seaweed taxon were quantified. For laboratory samples, all seaweed fragments were counted and identified to the lowest taxonomic category possible. For field samples, because of the high seaweed cover on plates, we estimated the relative cover of each taxon using a grid attached to a glass on the top of each Petri dish. For the seaweed cover estimates, the organism immediately below each of the 60 grid points was identified to the lowest taxonomic category possible. Due to difficulties in identifying crustose coralline algae, this group was

collectively termed CCA. Frequency of occurrence of seaweed taxa in the laboratory and field samples was calculated as the number of samples in which a given taxon occurred in relation to the total number of samples.

Results and discussion

This study presents empirical evidence for seaweed survival following ingestion by S. trispinosus on tropical reefs in Brazil. Seaweed growth occurred in all samples inoculated with parrotfish feces in both the laboratory and field experiments. A total of 16 macroalgal taxa (nine rhodophytes, five heterokontophytes, and two chlorophytes) and one cyanobacterium species were observed in inoculated samples (Figs. 1, 2), while only coccoid cyanobacteria were observed in the controls. These results demonstrate that a range of macroalgal species is capable of surviving and growing following ingestion by S. trispinosus, and suggest that this species may contribute to the dispersal of cyanobacteria and macroalgae at the studied reef.

Although it has been previously suggested that animals may act as macroalgal dispersers in the marine environment (e.g., Santelices et al. 1983; Santelices and Correa 1985), only one study has demonstrated that multicellular algae may survive following ingestion by herbivorous fishes (Vermeij et al. 2013). In that study, species from the main macroalgal clades (Chlorophyta, Heterokontophyta, and Rhodophyta) survived ingestion and gut passage by two parrotfishes and two surgeonfishes in the Caribbean (Vermeij et al. 2013). Our study corroborates these findings by showing that cyanobacteria and macroalgal species may survive the passage through the intestinal tract of S. trispinosus in northeastern Brazil. Furthermore, the higher taxonomic resolution of seaweed taxa in the present study revealed that the capacity to survive and grow following ingestion appears to be widespread among macroalgal species. The capacity of seaweeds to survive gut passage, coupled with the behavior of many parrotfish species to defecate away from feeding areas (e.g., Bellwood 1995), suggests that parrotfishes may facilitate the dispersal of seaweeds on tropical reefs. Further studies are necessary to better understand the role of parrotfishes as seaweed dispersers, the scale over which they may disperse algal fragments, and hence their influence on the distribution of macroalgae on coral reefs.

In this study, rhodophytes represented the largest number of fragments in laboratory samples (44 and 45 % in winter and in summer, respectively; Fig. 1a, b) and the highest mean cover in field samples (36 %). Similarly, rhodophytes accounted for 76.4 % of the algal fragments growing on parrotfish and surgeonfish feces in a previous study in the Caribbean (Vermeij et al. 2013). This apparent

dominance of rhodophytes may be related to the greater ability of this group to survive gut passage in herbivores, especially compared to Chlorophyta and Heterokontophyta (Santelices and Correa 1985; Vermeij et al. 2013), or greater ingestion of this group by herbivorous fishes. Most parrotfishes feed predominantly on the EAM (Bonaldo et al. 2014), a substratum largely composed of red algae, and which represents one of the main benthic components of Abrolhos reefs (Ferreira and Gonçalves 2006; Francini-Filho et al. 2010). Therefore, the dominance of rhodophytes in the present study may be explained by the higher resistance of this group to parrotfish digestion, by parrotfish feeding preferences, by the higher abundance of this algal group on the reef, or by a combination of these factors.

Despite the dominance of rhodophytes in both Vermeij et al. (2013) and our study, there were differences in the composition of algae between the two studies. Vermeij et al. (2013) reported that 65.1 % of all Rhodophyta fragments were Gelidiaceae species, while the remaining 34.9 % comprised species of Champiaceae, Lomentariaceae, and Ceramiaceae. In contrast, most Rhodophyta fragments growing in our samples were species from the Corallinaceae and Ceramiaceae, with a complete absence of Champiaceae and Lomentariaceae. Further, only one Gelidiaceae species (Gellidiella sanctarum) was recorded during our study, and it was relatively uncommon.

Interestingly, several taxa abundant or common in the present study were rare or absent in samples from fishes in the Caribbean (Vermeij et al. 2013). Cyanobacteria were one of the most abundant taxa in our samples, yet were not reported in the previous study. Vermeij et al. (2013) also observed low survival and growth of chlorophytes and low survival but no growth of heterokontophytes. In contrast, heterokontophytes were among the most abundant species in laboratory and field samples in our study, with Sphacelaria tribuloides as the most abundant alga in the field samples and the summer laboratory (Fig. 2; Electronic Supplementary Material, ESM Fig. S1). These differences may reflect variation in the relative cover of each algal group on the study reefs, variation in feeding preferences of the focal fish species, or methodological differences between the two studies. Irrespective of the reasons driving the differences between the two studies, our results reinforce the view of parrotfishes as potential macroalgal dispersers.

Our results showed clear seasonal variation in the seaweed species growing from S. trispinosus feces in the laboratory. Species richness of Heterokontophyta and Rhodophyta in summer (four and eight, respectively) was higher than in winter (one and four, respectively; Fig. 1a). Further, the heterokontophyte Ectocarpales sp. and the rhodophyte Ceramiales sp. were exclusive to laboratory samples, while CCA only occurred in field samples. The
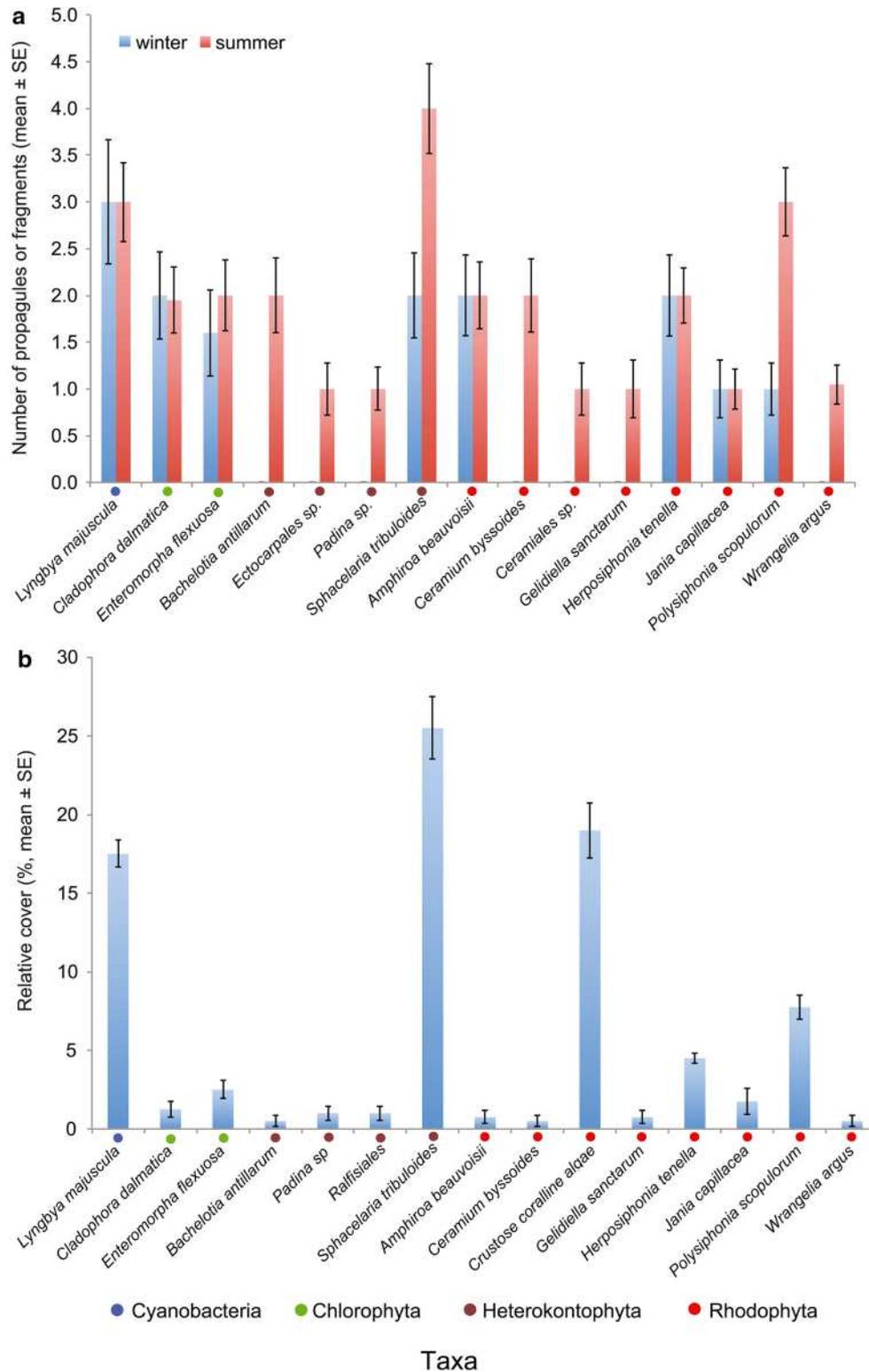
Fig. 1 a Number of seaweed fragments growing in samples inoculated with feces of the parrotfish *Scarus trispinosus* (n = 5) and kept in the laboratory during austral winter (blue) and summer (red), and b seaweed cover (%) in samples kept in the field. Bars represent means, and error bars are SE. Seaweed taxa are color-coded as Cyanobacteria (blue), Chlorophyta (green), Heterokontophyta (brown), or Rhodophyta (red)

Fig. 2 Relative abundance (%, mean ± SE) of fragments (laboratory experiments) and relative cover (field experiment) of seaweed in samples inoculated with Scarus trispinosus feces (n = 5)
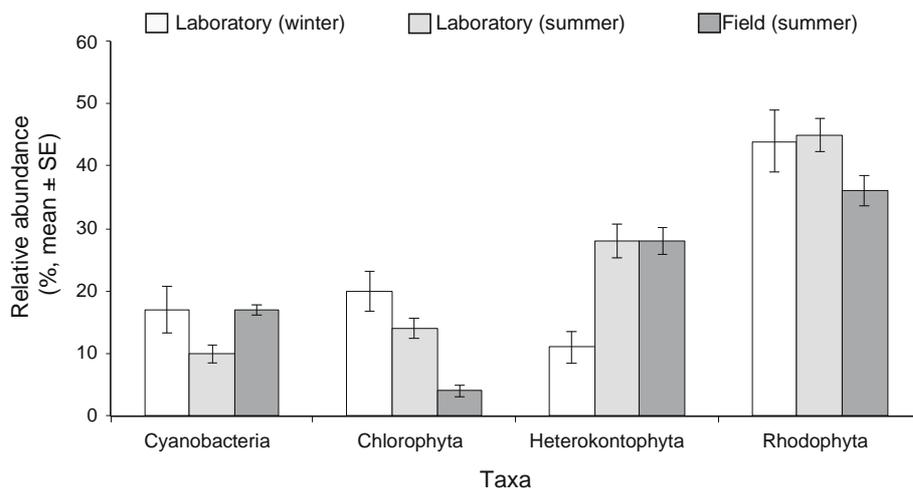
higher species richness in summer accords with previous studies in Abrolhos (Figueiredo 1997; Tâmega and Figueiredo 2007) and may be related to the longer day length and higher temperature during this season, which is known to increase growth and development of some algal species (Lee 2008). However, light and temperature requirements vary greatly among seaweed species (Lee 2008), and further studies on the conditions necessary for the development of seaweeds at our study site are necessary for a better understanding of the observed differences. Furthermore, contrasts between our laboratory and field experiments may have been caused by differences in water movement, temperature, and light exposure between treatments. Alternatively, these differences may have been caused by contamination from the surrounding environment to the field samples, but considering the absence of seaweed in the controls, this appears unlikely.

Although we have not directly measured the contribution of parrotfishes to seaweed dispersion, herbivores can disperse propagules up to five times further than propagules without interference by herbivores (Kinlan and Gaines 2003). The survival of seedlings eliminated through marine invertebrate feces is also increased by the presence of nutrients and viscosity, which enhance the propagules' establishment (Santelices and Paya 1989; Santelices 1992). Additionally, rhodophytes do not have structures that increase their dispersal, such as flagella, and although the dispersion of this group is largely dependent on water movements (Pueschel 1990), herbivores may also contribute, to some extent, to this process.

Our results suggest that seaweed may be dispersed by herbivorous fishes on tropical reefs; however, some caution is warranted when making any generalizations. Herbivorous fishes differ considerably in their digestive processes (e.g., mechanical vs. chemical), gut throughput rates, and feeding preferences, even among closely related species

(e.g., Choat et al. 2002; Hoey et al. 2013). Such differences likely influence the abundance and composition of seaweed ingested, surviving gut passage and growing following defecation.

A recent review recognized parrotfishes as key in seven functional roles in tropical systems: grazing, browsing, coral predation, bioerosion, the production, reworking, and transport of sediment (Bonaldo et al. 2014). The present study presents evidence for a potential new role of parrotfishes on tropical reefs: the dispersal of cyanobacteria and macroalgae. This suggestion is reinforced by the fact that parrotfishes move between different reef areas during the day and may have defecation sites away from their feeding grounds (Bellwood 1995; Vermeij et al. 2013), therefore contributing to the transport of sediment, and potentially viable seaweed fragments, between reef habitats. Clearly, further studies are required to identify the scales at which such dispersal may operate and to determine whether parrotfish defecation sites are suitable for the growth of viable seaweed fragments released in parrotfish feces, especially as many parrotfishes defecate over areas of unconsolidated substrata (Bellwood 1995; Vermeij et al. 2013). The variety of seaweed taxa surviving after parrotfish consumption suggests that these species contribute to the dispersal of seaweeds on reefs. Further studies on parrotfish movements, and observations of seaweed fragments growing in parrotfish feces in the areas in which they are released, can help us to understand to what extent parrotfishes disperse macroalgae on tropical reefs.

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