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Short research note

Feeding preference of *Littorina* snails (Gastropoda) for bleached and photosynthetic tissues of the seaweed *Mazzaella parksii* (Rhodophyta)

Christine Heaven & Ricardo Scrosati[1,*]
Bamfield Marine Sciences Centre, Bamfield, British Columbia V0R 1B0, Canada
[1]*Present address: University of British Columbia, Department of Botany, Vancouver, British Columbia V6T 1Z4, Canada*
E-mail: scrosati@axion.net
*(*Author for correspondence)*

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Abstract

Marine invertebrate herbivores occasionally prefer particular tissues of a given seaweed depending on tissue age. For the intertidal alga *Mazzaella parksii* (=*M. cornucopiae*), however, important tissue differences result from abiotic stress: distal tissues of many fronds become bleached under strong irradiance and desiccation during spring and summer low tides. Snails of the genus *Littorina* (periwinkles) are significant grazers of *M. parksii*. Through a multiple-choice feeding-preference experiment, we found that periwinkles actively consume bleached tissues, but almost no photosynthetic tissues. This suggests that bleached tissues of *M. parksii* may support *Littorina* populations to a good extent during spring and summer. In addition, since photosynthetic tissues are basal, the impact of periwinkles on frond mortality might be lower than if they preferred photosynthetic tissues. Photosynthetic tissues are actively consumed by periwinkles when they are the only food choice, as shown by other researchers. Therefore, retaining bleached tissues for some time might have evolved in *M. parksii* to divert grazing pressure away from vital tissues.

Intertidal organisms are affected by strong environmental stress, which results from the alternate exposure to aerial and aquatic conditions due to tides (Menge & Branch, 2001). In particular, intertidal seaweeds from temperate habitats are subjected to high desiccation and irradiance during daytime low tides in spring and summer.

In the NE Pacific coast, *Mazzaella parksii* (Setchell & Gardner) Hughey, P. C. Silva & Hommersand (Rhodophyta, Gigartinales; formerly *M. cornucopiae*, according to Hughey et al., 2001) occurs in high intertidal communities from relatively wave-exposed rocky areas. It is a clonal seaweed, composed of a crustose holdfast and several foliose fronds or ramets (see a picture in Scrosati, 2002). In winter, fronds are dark red. In early spring, as the lowest tides switch to daytime, the tips of medium and large fronds turn yellow–green. In late spring and summer, the distal portions of such fronds become bleached, apparently as a result of strong desiccation and irradiance during low tides (Scrosati & DeWreede, 1998). Then, at this time of the year, thousands of fronds show a sharp gradient in color, from dark red in the base, to yellow-green in the middle, to bleached in distal tissues. In unusually warm and sunny years, bleaching can even extend down to the holdfasts (Scrosati, 2001). Bleaching is a disruptive stress (sensu Davison & Pearson, 1996), because the affected tissues are unable to recover and finally die. Such dead biomass is thought to be ultimately lost by a combination of herbivory and wave action.

Laboratory experiments showed that snails of the genus *Littorina* (Gastropoda, Prosobranchia; known as periwinkles) consume frond tissues of *Mazzaella* *parksii* (Kim & DeWreede, 1996), but such experiments were done only with photosynthetic tissues. It is unknown whether *Littorina* actually consumes bleached tissues. Knowing this is important for two reasons. One relates to the understanding of biomass cycles at the intertidal community. If bleached tissues were consumed by periwinkles, then an important amount of algal-generated biomass might remain in the community. If they were not, however, significant exports of algal biomass to other communities would exist, via wave action. The other reason relates to the regulatory effects of periwinkles on *M. parksii* populations. If periwinkles preferred photosynthetic tissues, frond mortality might be higher than if they preferred bleached tissues, since photosynthetic tissues are basal and, hence, vital for frond attachment. Therefore, we investigated the feeding preference of periwinkles for the three *M. parksii* tissue types available in late spring and summer: red, yellow–green, and bleached. It was difficult to predict the outcome of this experiment, though. Bleached tissues are softer to eat than photosynthetic tissues, but it is unknown whether the loss of photosynthetic pigments involves a loss of nutritional value for periwinkles.

Organisms were collected at the east side of Prasiola Point (48° 49′ N, 125° 10′ W), on the Pacific coast of Canada (Fig. 1). This site is described in detail in Scrosati (1998). On 10 July 2002, fronds of *Mazzaella parksii* with the three colors were collected during low tide and kept in seawater inside containers until tested that same day. Simultaneously, periwinkles were collected from *M. parksii* stands and kept in a container, allowing snails to choose between being underwater or above water level. There are four species of *Littorina* in the NE Pacific coast, but identifying them based on shell morphology is difficult (Boulding & Harper, 1998). Kim & DeWreede (1996) stated that specimens from high intertidal algal beds at Nudibranch Point (a similar site 450 m from Prasiola Point) were mostly of one species, which they referred to as *Littorina* sp., now known as *L. subrotundata* (Carpenter) (Boulding & Harper, 1998), with a minor ($<3\%$) occurrence of *L. scutulata* Gould and *L. plena* Gould. Because of the difficulty in identifying all of our periwinkles, we will refer to them only by genus name in this paper, although the taxonomic pattern described by Kim & DeWreede (1996) seemed to hold for our site also.

The experiment consisted in offering simultaneously the three tissue types to the periwinkles and recording consumption rates after 2 days. This simultaneous offer represented the natural range of choices at the season of collection. Our multiple-choice feeding-preference experiment had eight replicates. Each one consisted of a closed transparent plastic cage with two mesh windows to allow for the passage of water and air, but not of frond tissues or periwinkles. In each cage, we placed 0.3 g (blotted-dry wet biomass) of each tissue type and 40 periwinkles. Another set of eight cages was prepared with the same amount of algal tissues but without periwinkles, thus serving as organism controls, since biomass changes not due to herbivory were recorded in them. The 16 cages were interspersed across a flow-through seawater table. The tidal regime was simulated as follows: low tide between 23:00–08:00 and 10:00–19:00 and high tide between 08:00–10:00 and 19:00–23:00. Low tides were simulated by leaving the cages above water level, while high tides were simulated by submerging them in 2 cm of seawater, making sure that the frond fragments remained underwater. The seawater table was subjected to the natural light regime. We did not starve the periwinkles before the experiment, as this might have artificially stimulated them to discriminate less between food choices (Watson & Norton, 1985; Cronin & Hay, 1996a; Pelletreau & Muller-Parker, 2002).

After 2 days, the blotted-dry wet biomass of the remaining tissue fragments was determined, previously allowing the fragments to rehydrate fully in seawater, since they were collected during ‘low tide’. The percent biomass change was calculated for each tissue type for each cage as:

$$[(B_f - B_i)/B_i]100,$$

where B_f was the final biomass and B_i was the initial biomass. B_i was included as denominator to account for the minor differences (in terms of mg) in initial biomass among replicates, owing to the manual nature of our tissue-cutting technique. Rates of percent biomass change were compared among tissue types through 95% confidence intervals, which are able to detect possible significant pairs in experiments of this kind (Pelletreau & Muller-Parker, 2002). A commonly used statistical technique in multiple-choice feeding-preference studies, Yao’s *R* test (Manly, 1993), only tells whether overall differences exist in the experiment, without identifying which specific means differ significantly, which was our ultimate objective.

For yellow–green and red tissues, biomass changes at the end of the experiment did not significantly differ from zero, regardless of the presence or absence of snails (Fig. 2). Bleached tissues, however, lost a

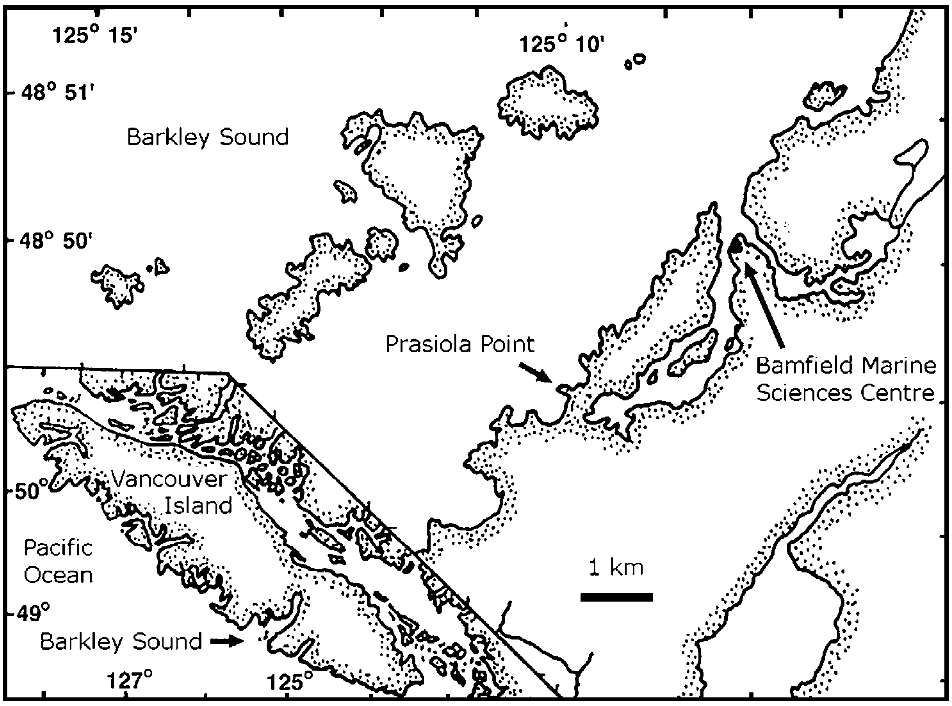

Figure 1. Map showing the location of Prasiola Point.

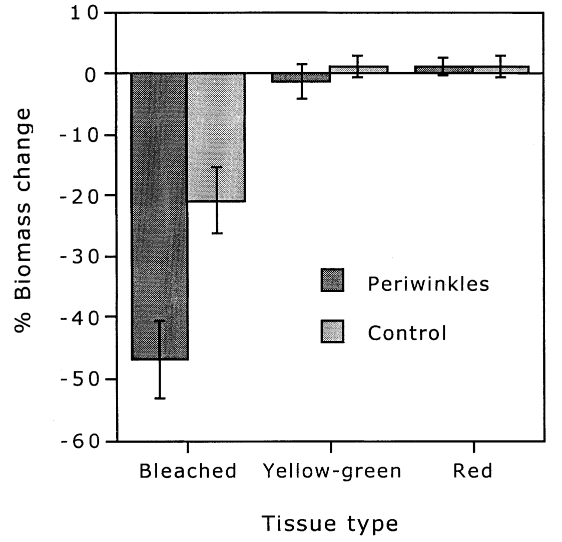

Figure 2. Percent biomass change of *Mazzaella parksii* tissue types with and without *Littorina* snails, expressed as means±95% confidence intervals (n=8).

significant amount of biomass in both treatments. In the control treatment, they lost an average of 20.8%, while they lost an average of 46.9% in the grazing treatment. The lack of overlap of their respective confidence intervals (Fig. 2) indicates that periwinkles actively consumed bleached tissues.

The preferential consumption of certain tissues of the same alga occurs for other invertebrate-alga systems (Watson & Norton, 1985; Poore, 1994; Cronin & Hay, 1996b; Van Alstyne et al., 1999, 2001b; Toth & Pavia, 2002). The feeding preference of such herbivores depends on tissue age, which generally affects tissue biochemistry. For *Mazzaella parksii*, however, the differences between color variants result mainly from differential desiccation and irradiance during spring and summer low tides (Scrosati & DeWreede, 1998). The specific characteristics of bleached tissues that make them more attractive for periwinkles will have to be determined with biochemical and biophysical studies. For the brown seaweed *Dictyota ciliolata* Kützing, tissue bleaching after UV exposure is associated to a decrease in chemical defenses, which results in a slightly higher susceptibility to herbivory by the amphipod *Ampithoe longimana* Smith (Cronin & Hay, 1996a). Red seaweeds have been much less studied than brown seaweeds regarding chemical defenses (Paul et al., 2001; Van Alstyne et al., 2001a), and nothing is known about *M. parksii* on this respect, so specific studies are needed. Tissue toughness is another potential factor to explain our results, as bleached tissues were generally softer than photosynthetic ones.

Mazzaella parksii predominates in many intertidal rocky areas in outer Barkley Sound (Scrosati, 1998). Our finding that *Littorina* snails prefer bleached tissues suggests that such biomass may be an important food source supporting periwinkles and also higher trophic levels. Other invertebrates that might ultimately benefit from *M. parksii* productivity are the shore crab *Hemigrapsus nudus* (Dana), the red rock crab, *Cancer productus* Randall, and the pile perch, *Rhacochilus vacca* (Girard), which prey on periwinkles from Barkley Sound during high tide (Boulding et al., 1999; Rochette & Dill, 2000). The strength of these trophic pathways should be tested through field experiments, since making community-level inferences directly from laboratory experiments has limitations. Other factors to consider are the presence of alternative food sources (possibly diatoms; Voltolina & Sacchi, 1990), algal productivity rates, population attributes of the invertebrates, competition among the invertebrates (Brawley, 1992; Ruesink, 2000), and patterns of local coexistence among the species.

The possible regulatory role of *Littorina* on *Mazzaella parksii* populations was suggested by Kim & DeWreede (1996), although it has yet to be tested in the field. When photosynthetic tissues are the only food choice for periwinkles in laboratory experiments, they are actively consumed (Kim & DeWreede, 1996). However, when the three tissue types are available, bleached tissues are mostly the only ones consumed, as shown here. If these results represent the field situation well, the switch to feeding mostly on distal tissues, once bleaching develops in spring, might decrease frond mortality due to grazing, since photosynthetic tissues are basal and essential for frond attachment. This might ultimately benefit the survival of entire thalli, as holdfasts are protected from abiotic stress by the canopy. *M. parksii* holdfasts are vital for population persistence because they are perennial and produce fronds continuously, which is particularly important given that spore recruitment is low (Scrosati, 1998). Retaining bleached tissues for a given length of time might simply be a fortuitous event resulting from slow cell wall decomposition. However, it might constitute a trait that evolved in response to herbivory. The adaptive value of retaining bleached tissues for some time would be to divert grazing pressure away from healthy tissues. This might add to the known mechanisms that evolved in seaweeds to reduce the impact of herbivores (John & Lawson, 1990). Ultimately, it would even be important for periwinkles, since, in addition to food, they find shelter from abiotic stress in *M. parksii* stands (Boulding & Van Alstyne, 1993).

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