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SHORT COMMUNICATION

Saccate thallus of the red alga *Halosaccion glandiforme* harbor diverse invertebrate fauna

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Abstract Rocky intertidal zones are biologically diverse environments with numerous physical stressors; as such, close associations between organisms often develop to overcome such stressors and enhance survival of associates. As major components of rocky shores, macroalgae support numerous invertebrate species. In this study, we evaluated the habitat-providing role of the red alga, *Halosaccion glandiforme* (S.G. Gmelin) Ruprecht. This alga, also called sea sacs, is commonly found on rocky shores along the West Coast of North America. During emersion, this seaweed holds water within its saccate thallus, which can potentially serve as microhabitat for various organisms. Little is known about the composition of microfauna associated with this seaweed; as such, we documented richness and abundance of species found inside its thallus. Algal specimens were collected from Charleston, Oregon and transported to the laboratory for further analyses. Of the 119 thalli examined, 12 taxa were documented. Nematodes and copepods were the dominant taxa. Other groups represented included ostracods, turbellarians, halacarid mites, bivalves, rotifers, and three larval types (barnacle cyprids, copepod nauplii, mollusc veliger). Diatoms, crustacean molt remnants, detritus, and sand particles were also observed inside thalli. Species richness and abundance were positively correlated with thalli volume, as well as intra-thalli fluid volume. Several feeding and other behaviors of colonizers were noted; they included herbivory, predator–prey interactions, detritivory, and molting. Our findings demonstrate that *H. glandiforme* provide refuge for organisms from harsh environmental conditions during emersion periods, and also serve as feeding and nursery grounds for its diverse invertebrate fauna.

Keywords Sea sacs · Microhabitat · Invertebrate composition · Rocky intertidal community

Introduction

Rocky shores are dynamic environments inhabited by organisms that are able to withstand harsh abiotic and biotic conditions. Some of these organisms, especially macroalgae, provide habitats for many benthic species. These species depend on the physical structure and other resources provided by the seaweeds, thereby enhancing their survival and increasing diversity and abundance (Lilley and Schiel 2006; Wikström and Kautsky 2007).

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Size and morphological features of seaweeds can have a major bearing on the benefits they provide to other species. Numerous invertebrates are dependent on seaweeds with varying morphological features, including the complex three-dimensional *Macrocystis* (Graham 2004), the compact spongy *Codium* (Trowbridge 1998; Bulleri et al. 2006), the fan-like broad thallus of *Chondrus* (Janiak and Whitlatch 2012), the crustose coralline algae *Clathromorphum* (Chenelot et al. 2011) and the calcareous rhodoliths (Foster 2001). Steller et al. (2003) reported that the total number of organisms supported by the coralline red algal rhodoliths significantly increased with both complexity (branching density) and space available (thallus volume) when compared with adjacent sand community. Thus, thallus size/volume can be a factor determining species richness and abundance in associated organisms.

Another morphological trait found in some algae is the presence of saccate or sac-like thallus that retains sea water when exposed to air during low tide. The saccate red alga *Halosaccion glandiforme* grows in clumps in the rocky intertidal areas along the Pacific coast of North America, ranging from the northern Aleutian Isles to southern California (Mondragon 2003). The plant has a short stipe, a discoid holdfast, and thalli measuring 3–4 cm in diameter; it grows to a length of 10–20 cm over the course of a year (Johnson 1994). This seaweed is commonly referred to as the sea sac because its thallus is a cylindrical hollow sac, partially filled with sea water and about a cubic centimeter of gas. Each thallus possesses 5–15 irregularly shaped pores, 10–200 μm in diameter, which allow water into and out of the thallus during exposure and immersion associated with tidal cycles (DePamphilis 1978; Vogel and Loudon 1985). When tides recede, water inside the thallus is retained. Such water reserves reduce desiccation and heating of tissue during periods of emersion (DePamphilis 1978). It has been reported in some field guides that the water-filled sacs of *H. glandiforme* are inhabited by a variety of invertebrates (Mondragon 2003; Lamb and Hanby 2005).

The role of this "sea sac" as a microhabitat for assemblages of small invertebrates has been virtually unexplored. In this study, for the first time, we note the presence of fauna found inside the saccate thallus of *H. glandiforme*. The objectives of this study were to: (1) quantify species richness and abundance (2) determine relationship between species richness/abundance and thallus/seawater volume using multiple regression, and (3) observe miscellaneous ecological interactions between taxa.

Materials and methods

Fronds of *H. glandiforme* were collected from Cape Arago State Park in Charleston, Oregon (43.3062°N; 124.3935°W), USA, between July and September 2015, during low tide. During sampling, the short stipe was gently snipped using a scalpel while making sure the water-filled thalli were intact (Fig. 1). The seaweeds

Fig. 1 Saccate thallus of *Halosaccion glandiforme*, tapering to a short stipe and attached to rocks with small discoidal holdfast. Note the oblong sac partially filled with seawater

were transferred to plastic containers and transported to the laboratory at the Oregon Institute of Marine Biology for further analysis. Any damaged or dehydrated thalli were discarded and not analyzed in our study. All analyses were performed within 8 h of collection, which ensured quantifying and observing live fauna.

Using dissecting scissors, each thallus was carefully removed from the stipe. Assuming that each water-filled thallus was roughly columnar in shape, we measured thallus volume using the formula $V = \pi r^2 h$, where h was the length and r was the width at the widest point on the thallus. The thin seawater-filled sac was held vertically and the tip of the thallus was cut with a scissor. To measure seawater volume, the internal water was withdrawn using a calibrated 5 cc wide mouth syringe. The content of the syringe was transferred into a watch glass and examined for fauna under a binocular stereo microscope (Olympus 10X). Most specimens were identified as close to their taxonomic level as possible using available taxonomic keys (Light and Carlton 2007) and their abundance noted. 10 min were spent observing interactions (if any) between the colonizers for each thallus. Other recognizable intra-thallus components (e.g., phytoplankton, detritus, molt remnants, etc.) were also noted for documenting additional ecological associations.

Multiple regression analyses were performed to determine the relationship between the richness and abundance of the invertebrate fauna and the size of the sea sacs, which included thallus size and fluid volume within each sac. A Kolmogorov–Smirnov test showed the data were not normally distributed, and further transformation did not normalize the data. However, linear regression/correlation might still be robust to non-normality (McDonald 2014), so analyses were performed despite this violation. P values < 0.05 were considered statistically significant.

Results

We examined a total of 119 thalli of *H. glandiforme*. Table 1 lists the different types of invertebrates and their numbers associated with this alga. Of the 119 thalli inspected, 99 (83%) were colonized by 845 individuals

Table 1 Richness, abundance (A), % occurrence (O), mean occurrence (M.O.), range of invertebrate taxa, as well as copepod molts, within the saccate thallus of the red alga *Halosaccion glandiforme*

Invertebrate taxa	A	O (%)	M. O.	Range
Nematoda	598	52.9	9.5	1–107
Order Chromadorida, Fam. Chromadoridae				
O. Monhysterida, Fam. Xyalidae, *Theristus* sp.				
Platyhelminthes				
Class Turbellaria, *Neoplana* sp.	3	2.5	1	1
Arthropoda				
Crustacea				
Acartia sp., *Calanus* sp. (Copepoda: Calanoida)	183	29.4	5.2	1–65
Copepod molt	373	47.9	6.5	1–62
Paradoxostoma sp. (Ostracoda)	4	3.4	1	1
Mystacocaridada (Class Maxillopoda)	3	2.5	1	1
Nauplius larvae	45	17.8	2.8	1–14
Cyprid larvae	4	3.4	1	1
Arachnida	3	2.5	1	1
Marine mites (Fam. Halacaridae)				
Mollusca				
Veliger larva	1			
Unidentified bivalve	1			
Rotifera	nq	18.4		
Foraminifera	1			

Percentages do not add to 100, as occurrence refers to presence of each taxa inside thallus divided by total number of thalli examined ($N = 119$)

nq not quantified

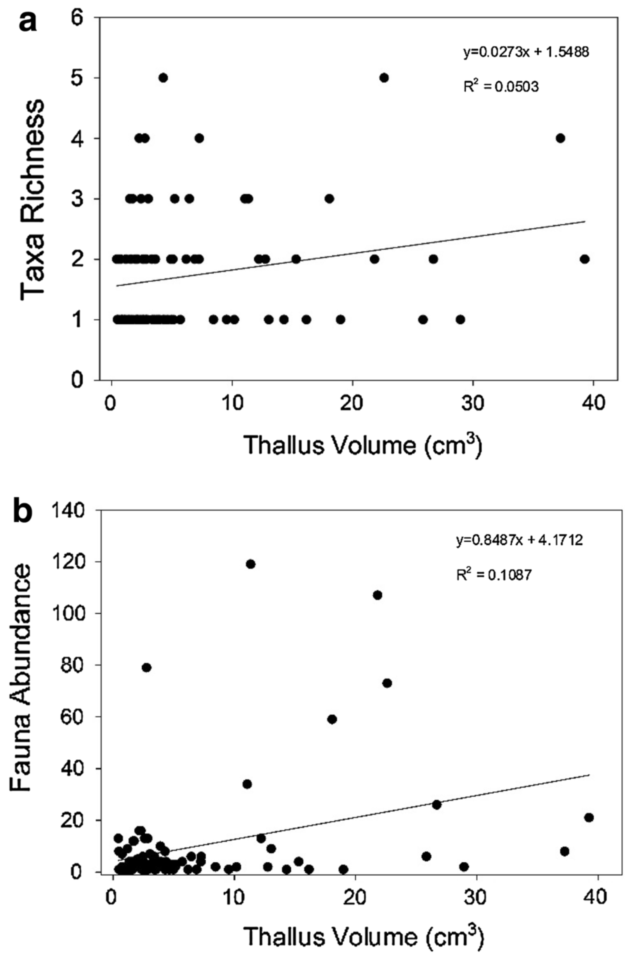

Fig. 2 Linear regression analysis of effect of thallus volume on **a** taxa richness, and **b** fauna abundance

belonging to 12 taxa in total. Up to 5 taxa and 119 individual invertebrates were found inside one sac. Table 1 also lists the percentage occurrence, mean occurrence, and range of all taxa associated with *H. glandiforme*.

Nematoda and Arthropoda were the dominant phyla; they made up over 92% of the total fauna. Nematodes were the most common inhabitants, occurring in 53% of thalli and constituting 70.8% of the total samples. Although the average number of nematodes per thallus was ~10, as many as 107 individuals were found in a single thallus. Copepods were the second most abundant group, occurring in 30% of thalli and comprising of 21.7% of all species. Nematodes and copepods were found to coexist in 26.1% of the samples. Copepods were occasionally found in various states of molting. The other lesser represented groups included ostracods, turbellarians, mites, and bivalves. Numerous copepod nauplii, a few barnacle cyprids, veliger larvae, rotifers, protozoans, diatoms, crustacean molt remnants, detritus, and sand particles were also found inside thalli.

Results of multiple regression analyses were separated in two groups: (a) thallus volume vs. taxa richness and abundance, and (b) fluid volume vs. taxa richness and abundance. The thallus volume and the intra-thallus fluid ranged from 0.42 to 39.27 cm^3 (mean 6.02) and 0.1–8.6 mL (mean 1.10), respectively. Overall, larger thallus volume and greater intra-thallus fluid volume supported higher taxa richness and species abundance. Taxa richness was positively correlated with thallus volume ($F = 4.66$, $P = 0.03$, $R^2 = 0.05$; Fig. 2a) as was species abundance ($F = 10.48$, $P = 0.002$, $R^2 = 0.11$; Fig. 2b). Furthermore, we found positive correlation between fluid volume and taxa richness ($F = 4.25$, $P = 0.04$, $R^2 = 0.05$; Fig. 3a) as well as fauna abundance ($F = 8.75$, $P = 0.004$, $R^2 = 0.11$; Fig. 3b).

A number of feeding interactions between colonizers were noted; they included herbivory, predator–prey interactions, and detritivory. Most of the invertebrates (e.g., copepods, ostracods, nematodes, mystacocaridads, rotifers) fed on diatoms and periphyton, some ingested other invertebrates (e.g., flatworm, nematodes,

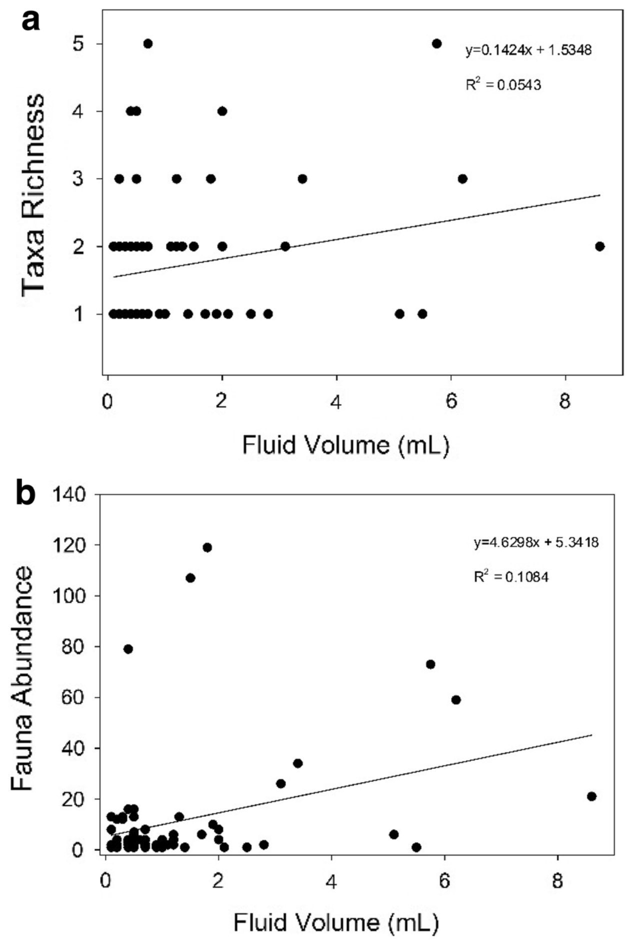

Fig. 3 Regression analysis of effect of fluid volume on **a** taxa richness **b** fauna abundance

copepods, mites), some consumed detritus (ostracods, bivalve, nematodes), and entrapped sediments (mostly nematodes). Nematodes were also found feeding on bacterial films on the copepod molts, which were common in our samples (∼48% occurrence, with up to 201 molts in a single thallus). As crustacean molts were common and nematodes are known detritivores (Heip et al. 1985, and references within), it was unsurprising to find a significant positive relationship between the presence of nematodes and molt remains inside the thallus ($F = 56.77$, $P < 0.0001$, $R^2 = 0.40$; Fig. 4).

Discussion

The importance of seaweeds as habitats has been well studied for many rocky intertidal species; however, that has not been the case for the red alga *H. glandiforme*. Its fronds are annuals; new thalli appear in late winter and early spring, but degenerate after spore production during the following fall and winter (Johnson 1994). With pores as large as 200 µm, microfauna measuring <200 µm most likely enter the fronds via seawater medium and may leave the hollow sacs either during immersion or when the thalli degenerate at the end of the growing season. In this novel algal- invertebrate association study, we characterize this seaweed as a habitat-forming species as it shelters multiple invertebrate groups inside its saccate thallus, and provides multiple benefits for its diverse invertebrate fauna, which in turn, may increase their survivorship and fitness.

Macroalgal traits such as size and morphological complexity can have a large effect on local populations and communities. The presence of multiple pores on the thallus of *H. glandiforme* allows seawater into and out of thalli during tidal cycles and facilitate faunal colonization. Our results show that thallus volume and the

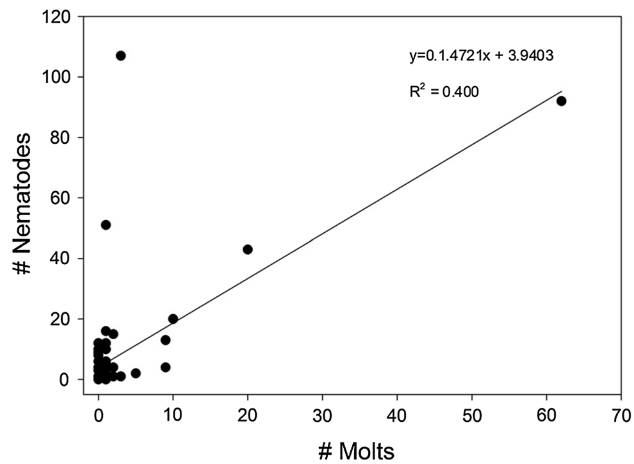

Fig. 4 Relationship between nematode abundance and presence of copepod molts

volume of seawater were important predictors of abundance and richness of invertebrates associated with this alga. Larger thalli possibly contained more resources, including sea water, which allowed them to shelter higher numbers of taxa and greater abundance of organisms. It is likely that bigger thalli have larger pores, which facilitate greater colonization opportunities. These thalli made the coexistence of species with different ecological necessities possible. Other studies have associated algal morphologies with species diversity and abundance. When given a choice between *Gracilaria vermiculophylla* and *Ulva rigida*, the architecturally more complex *G. vermiculophylla* supported higher species richness and diversity of associated macrofauna (Munari et al. 2015). Steller et al. (2003) also reported that the total organisms supported by rhodoliths, another group of benthic red alga, significantly increased with branching density and thallus volume.

We found nematodes to be the most abundant group in our samples. This is not surprising since they are considered to be among the most abundant organisms on earth. Marine roundworms inhabiting high-energy rocky shores are exposed regularly to changing tidal conditions. Being poor swimmers, they often remain suspended in the water column before re-entering the benthos as passive particles when tides recede; yet, nematodes are efficient in choosing algal habitats (Ullberg and Ólafsson 2003). Nematodes in our algal samples may have entered the saccate thallus via passive or active mechanisms.

The majority of the nematodes we found belonged to the family Chromadoridae (pers. comm. Ashleigh Smythe). In a related study at a Brazilian rocky coast, nematode biodiversity was related to the structural features of macrophyte habitats and the most abundant phytal nematodes were chromadorids (Da Rocha et al. 2006). Chromadorids are often associated with marine macrophytes (Trotter and Webster 1983; Pérez-García et al. 2015). Feeding experiments of the marine nematode *Chromadora* showed that diatoms and chlorophytes were preferred food items (Tietjen and Lee 1973). However, Moens and Vincx (1997) reported that many aquatic nematodes are in fact opportunistic feeders, which may change feeding strategies in response to available food. We also encountered nematodes belonging to the genus *Theristus* in our samples. This free-living marine nematode group has been found in diverse habitats, including degraded algal beds (Olafsson et al. 2013) and exposed sandy beaches (Lee and Riveros 2012). *Theristus* is known to ingest suitably sized food particles like microalgae cells (Moens and Vincx 1997). Diatoms have been shown to be a prominent food resource for *Theristus* (Moens et al. 2014). Diatoms were abundant in our samples and nematodes were frequently observed ingesting them as well as other items inside the thalli.

We found a positive association between the presences of nematodes and remnants of copepod molts. Nematodes were observed feeding on the distinct bacterial films covering these molts. As substrate consumers, nematodes are known to ingest organic substrates along with their associated microflora and microfauna (Moens et al. 2006). Tietjen and Lee (1973) reported that *Chromadora macrolaimoides*, isolated from the collections present on the green alga *Ulva intestinalis*, consumed different types of bacteria.

Copepods were the second most abundant group in our samples. This too is not unexpected as they are considered to be one of the most abundant groups in the marine realm. *Halosaccion glandiforme* belongs to class Rhodophyceae and, according to Fahrenback (1962), rhodophyceans show higher assemblage of copepods than other algal groups. Although the exact reasons why red algae are preferred over brown algae are unknown, Fahrenback (1962) postulates that some red algal fronds are thick enough to accommodate these crustaceans and prevent their dislodgement. Whereas Fahrenback (1962) observed one harpacticoid copepod species (*Diathrodes cystoecus*) in sea sacs collected from Moss Beach, California, we found two genera of planktonic calanoids, *Acartia* sp. and *Calanus* sp. within the algal thalli. They were frequently observed to feed on diatoms and rotifers, which were plentiful in our samples. As omnivores, they were found to graze both on phytoplankton (Paffenhöfer and Lewis 1989) and protozooplankton (ciliates, heterotrophic dinoflagellates, flagellates), and rotifers (Stoecker and Egloff 1987).

In addition to serving as feeding grounds, *H. glandiforme* may also serve as a nursery habitats as gravid copepods and various larval groups were frequently observed. Copepods were found in various states of molting, implying their growth and development inside thalli. The presence of other associated taxa suggested that sea sacs may act as a refuge for multiple species, especially during periods of emersion. According to Lilley and Schiel (2006), habitat-forming species increases spatial complexity and help ameliorate stressful environmental conditions, thereby promoting a diversified assemblage of animals. It is obvious that the use of *H. glandiforme* as a habitat for invertebrates is multifaceted, as it provides refuge from physical stresses and predation, facilitates trophic interactions, and serves as nursery ground. As such, this macroalgae should be addressed in studies dealing with coastal biodiversity conservation.

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