

# Epiphyte and herbivore interactions impact recruitment in a marine subtidal system

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**Abstract** Marine assemblages are influenced by the rate and timing of species settlement and recruitment. Both abiotic factors and biotic interactions can impact recruitment rates of marine species in a variety of systems. However, the impacts of species which recruit at the same time upon each other are less well understood. We investigated the relationship between the recruitment of *Lacuna vincta*, a small (<6 mm shell diameter) marine snail, and two species of algal epiphytes, the native *Ceramium virgatum* and the invasive *Neosiphonia harveyi*, in the shallow subtidal zone of Narragansett Bay, Rhode Island. All three species exhibit peak recruitment densities during two months in the summer. We found that the presence of algal epiphytes facilitates the recruitment rate of *L. vincta*, regardless of the epiphyte species composition. We also found a positive relationship between the number of *L. vincta* present and epiphyte recruitment, which is disproportionately driven by higher recruitment of *N. harveyi* than *C. virgatum*. Understanding recruitment dynamics and interactions is

vital to effectively mitigate the effects of and adaptations to changes due to the establishment of non-native species.

**Keywords** *Lacuna vincta* · *Neosiphonia harveyi* · *Ceramium virgatum* · Recruitment · Epiphytes · Herbivores

## Introduction

Recruitment is a key process in the population dynamics of many marine species (Bertness et al. 1992; Gaines and Bertness 1992; Miron et al. 1995; White 2007). Abiotic and biotic factors that influence settlement, and subsequent recruitment, have been examined in a variety of marine systems, including coral reefs (Steele et al. 1998; Schmitt and Holbrook 2000; Mumby et al. 2007), intertidal zones (Osman and Whitlatch 1995; Gribben et al. 2009b), and the marine Antarctic (Siegel and Loeb 1995). The presence or absence of other macrobenthic species on a suitable substratum is one biotic factor that may influence larval settlement dynamics (Rodriguez et al. 1993; Huggett et al. 2005).

One group of macrobenthic species that can influence larval settlement is epiphytic macroalgae (Hall and Bell 1993; Swanson et al. 2006). Epiphytic macroalgae are small, often filamentous species that live attached to larger host macroalgal species. Algal epiphytes can increase the structural complexity of

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their host algal species, which may, in turn, increase the suitability of the host as habitat for small invertebrates, including herbivores (Martin-Smith 1993). Epiphytes can provide these herbivores protection from predators while also serving as a food source (Pavia et al. 1999). The epiphytes can also buffer the associated herbivores from abiotic stress such as desiccation (Salemaa 1986; Bostrom and Mattila 1999). As a result, these herbivores may benefit the host macroalgae by preventing epibiont overgrowth (Stachowicz and Whitlatch 2005) and/or promoting algal growth via nitrogen excretion (Fong et al. 1997; Bracken et al. 2007).

*Lacuna vincta* (Montagu) is a small (< 6 mm shell diameter), ubiquitous, herbivorous snail that feeds and lives on algae within rocky intertidal and subtidal zones of the Northwest Atlantic (Martel and Chia 1991). While *L. vincta* are occasionally found on larger host algae, it has been suggested that the small epiphytes are more accessible and palatable to the herbivores, particularly the newly recruited juveniles (Steneck and Watling 1982; Chavanich and Harris 2002). Adult *L. vincta* tend to move from algal epiphytes to the host macroalga itself.

*Lacuna vincta* is commonly found in shallow rocky subtidal habitats in New England from late spring to early fall (Jones and Thornber 2010). They are found in high densities during juvenile recruitment (>1200 juveniles on algae per cm<sup>2</sup> of rocky substrate; Jones 2007). In these shallow subtidal habitats, *L. vincta* often co-occurs with two species of epiphytic filamentous red algae, the native *Ceramium virgatum* (Roth) and the invasive *Neosiphonia harveyi* (J. Bailey). *N. harveyi* has been present in New England for over 120 years (Farlow 1881) and has invaded areas in which *C. virgatum* frequently occurs (Pederson et al. 2003; Mathieson et al. 2008); both are commonly found in Narragansett Bay (Jones and Thornber 2010).

*Ceramium virgatum* and *Neosiphonia harveyi* individuals are present year-round but their peak recruitment period overlaps substantially (early- to mid-summer; Jones and Thornber 2010). They can account for 50-80% of algal epiphytic biomass during the summer months, a period that coincides with peak *Lacuna vincta* recruitment. The remaining biomass is composed of a variety of epiphyte species with no single species accounting for more than of 15% of the algal epiphyte biomass, on average (Jones 2007).

This synchronization of recruitment events may be beneficial to *L. vincta* and host macroalgae (including the native species *Chondrus crispus* and *Fucus vesiculosus* and the invasive species *Grateloupia turuturu* and *Codium fragile* ssp. *tomentosoides*) and detrimental to the epiphytes; at present, however, the relationship between these epiphytes and *L. vincta* recruitment is not well described.

In this study, we investigated interactions between *Lacuna vincta* and the two epiphytes *Ceramium virgatum*, and *Neosiphonia harveyi*. Through a series of field-based manipulations conducted in Narragansett Bay, Rhode Island, we investigated two possible relationships: (1) if the presence of species specific epiphytes influences *L. vincta* recruitment and, alternatively (2) if the presence of *L. vincta* influences species specific epiphytes in terms of their recruitment and/or biomass.

## Materials and Methods

### Study location

We conducted our experiments in the shallow (<1 m below MLLW) rocky subtidal at the University of Rhode Island's Graduate School of Oceanography during the summer of 2008. This zone is characterized by dense stands of macroalgae, primarily *Chondrus crispus*, *Polysiphonia* spp., and *Codium fragile*. We wanted to assess new epiphyte and *Lacuna vincta* recruitment to macroalgae; thus, we used green, nylon rope 0.5 cm in diameter and 13 cm in length (total surface area of 42.4 cm<sup>2</sup>) to mimic natural macroalgae; this rope has been shown to work well for settlement and colonization by algal epiphytes and invertebrates in this system (Jones and Thornber 2010).

We previously conducted a pilot experiment during the summer of 2007; these results indicated that there was no significant caging effect of containers (open or closed) on the recruitment of epiphytes to macroalgal mimics ( $F_{2, 29} = 0.78$ ,  $p = 0.47$ ,  $n=10$ ).

### Impacts of epiphytes on *Lacuna vincta* recruitment

During May of 2008, before recruitment of *Ceramium virgatum* and *Neosiphonia harveyi* occurred, we secured 60 macroalgal mimics by zip-tie to PVC

rings that had been attached to the shallow subtidal with marine epoxy (A-788 Splash Zone Compound). We left the mimics in the field for one month to allow for epiphyte recruitment. One month later, when the first *L. vincta* appeared as recruits in the field, we removed the mimics from the subtidal and brought them to the laboratory in order to manipulate the epiphyte abundance and composition prior to *L. vincta* recruitment. We divided the 60 mimics evenly into six groups of ten each. Three groups were used for epiphyte abundance experiments and three for epiphyte composition experiments. Mimics were removed from the field for a maximum of twelve hours and were stored in ambient temperature, flow-through seawater systems at the URI Graduate School of Oceanography when not being processed.

Within the epiphyte abundance experiments, ten mimics retained a high epiphyte density (75% - 100% of mimic surface area covered with epiphytes), ten were pruned to have a low epiphyte density (25% - 50% of mimic surface area covered with epiphytes), and ten were pruned to remove all visible epiphytes. Within the epiphyte composition experiments, we selectively pruned the mimics such that ten mimics contained only *Ceramium virgatum* epiphytes, ten had only *Neosiphonia harveyi* epiphytes, and ten had a mixture of half *C. virgatum* and half *N. harveyi* epiphytes.

We photographed each mimic and measured its wet mass after blotting off excess moisture. We then reattached the mimics in the shallow subtidal to allow for natural *Lacuna vincta* recruitment. After two weeks, we removed the mimics and brought them to the laboratory for analysis. We photographed each mimic, measured the total wet mass (after blotting the mimics), removed and identified all of the epiphytes, and measured the mass of each epiphyte species. We also removed and counted the *L. vincta* found on each of the mimics. Data were log transformed and analyzed for differences in *L. vincta* recruitment among epiphyte abundance and composition with one-way ANOVAs and post hoc Tukey tests (JMP v. 7; [www.sas.com](http://www.sas.com)).

#### Impacts of *Lacuna vincta* on epiphyte recruitment

During May of 2008, before yearly *Lacuna vincta* recruitment occurred, we placed one macroalgal mimic in each of 30 one-liter semi-transparent plastic containers with one-mm mesh sides and lids. These

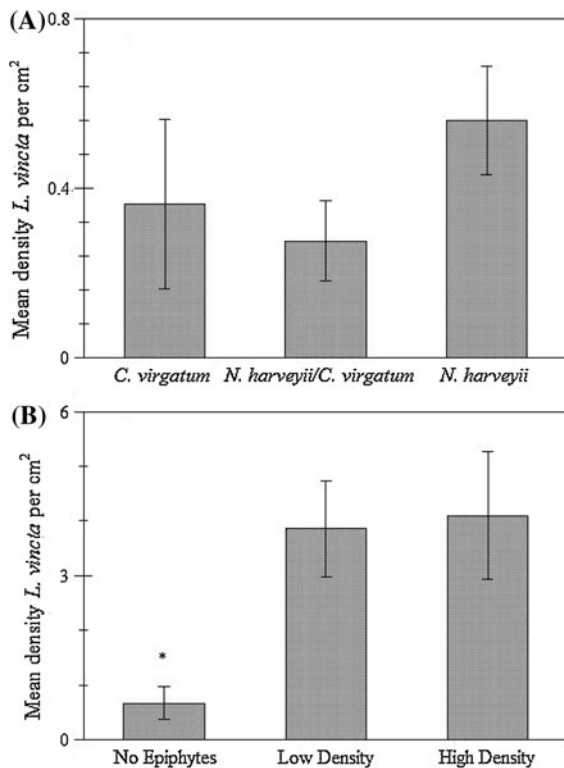
containers were then secured directly to the rocky subtidal, using the same method as described above. In the same manner, we also attached mimics in ten open containers, and ten mimics without containers, to additional PVC rings, as controls. Following the recruitment of *L. vincta* in mid June 2008, we placed 200 *L. vincta* individuals in each of ten closed containers ('high' treatment), 40 *L. vincta* individuals in each of ten closed containers ('low' treatment), and no *L. vincta* in each of ten closed containers ('none' treatment). These treatments were based on *L. vincta* recruitment densities measured during the summer of 2006 (Jones and Thornber 2010). *L. vincta* had free access to the mimics in the open containers and the mimics with no containers.

After *Lacuna vincta* were added, we left the containers and mimics in the field for two weeks (this duration was based on pilot data collected in the summer of 2007) to allow for epiphyte recruitment. After these two weeks, we removed the mimics and containers, placed them in individual plastic bags to retain all *L. vincta*, and brought them to the laboratory. We photographed each mimic, measured its wet mass (mimics were first blotted to remove excess moisture), removed and identified all of the epiphytes, and measured the mass of each epiphyte species. We also removed and counted the *L. vincta* in the closed containers, on the mimics in the open containers, and on mimics with no containers. Data were analyzed for a relationship between *L. vincta* density and epiphyte biomass using correlation techniques (JMP v. 7; [www.sas.com](http://www.sas.com)).

## Results and Discussion

Across all of our treatments, we found a significant positive correlation between the proportion of *Neosiphonia harveyi* ( $0.02 \pm 0.006$  grams per cm<sup>2</sup> of macroalgal mimic) and the total epiphyte mass ( $r = 0.92$ ,  $p < 0.0001$ ). *Ceramium virgatum* densities were never greater than 0.005 grams per cm<sup>2</sup> of macroalgal mimic regardless of total epiphyte mass, indicating that recruitment densities of *C. virgatum* were low or that the *C. virgatum* that did recruit to the mimics was rapidly consumed by *Lacuna vincta*.

There was no significant effect of epiphyte composition (*Ceramium virgatum*, *Neosiphonia harveyi*/*C. virgatum*, *N. harveyi*) on *Lacuna vincta* recruitment



**Fig. 1** Effect of epiphytes on recruitment of *L. vincta*. **a** There was no difference in *L. vincta* recruitment among epiphyte composition treatments: *C. virgatum*, *N. harveyii/C. virgatum*, and *N. harveyi* ( $P = 0.1336$ ). **b** There is a significant difference in *L. vincta* recruitment among macroalgal mimics with varying densities ( $P = 0.0009$ , post hoc Tukey–Kramer tests); significant results are indicated. All data are means  $\pm$  1 SE

(Fig. 1a,  $F_{2,17} = 2.24$ ,  $p = 0.14$ ); *L. vincta* recruited to all three epiphyte composition types at similar rates (mean *L. vincta* density =  $0.47 \pm 0.08$  per cm<sup>2</sup> of macroalgal mimic). However, there was an effect of epiphyte presence (high density, low density, and no epiphyte treatments) on *L. vincta* recruitment (Fig. 1b,  $F_{2,23} = 9.58$ ,  $p = 0.0009$ ). Macroalgal mimics containing high or low epiphyte densities had significantly more *L. vincta* ( $4.10 \pm 1.16$  per cm<sup>2</sup> macroalgal mimic and  $3.86 \pm 0.88$  per cm<sup>2</sup> macroalgal mimic, respectively) than mimics with no epiphytes present ( $0.67 \pm 0.30$  *L. vincta* per cm<sup>2</sup> macroalgal mimic; post hoc Tukey–Kramer test), and there was no significant difference between the high and low epiphyte densities. Data are means  $\pm$  1 SE.

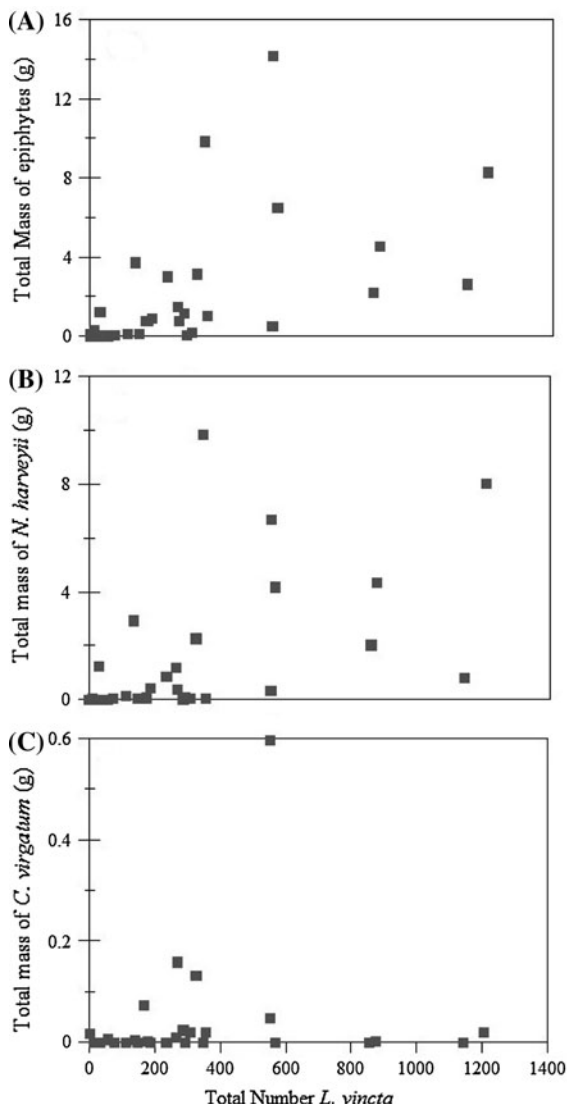
Overall, we found a significant positive correlation between the number of *Lacuna vincta* present and the total mass of epiphytes (the most abundant species being *Neosiphonia harveyi* and a mix of juvenile and

cryptic *Polysiphonia* spp. that could not be identified to the species level) that recruited to macroalgal mimics in all treatments (Fig. 2a,  $r = 0.5$ ,  $p = 0.0058$ ). Unknowingly, some extremely small planktonic *L. vincta* larvae were able to pass through the mesh covering of the containers: recruitment by these ‘accidental’ individuals produced a range of *L. vincta* densities in our closed buckets that reached 5x’s the level of our stocking density. Due to this, we examined the relationship between the number of *L. vincta* and epiphyte density in all of the treatments. When *N. harveyi* and *Ceramium virgatum* were analyzed individually, we found a weak but significant, positive relationship between the number of *L. vincta* and *N. harveyi* recruitment (Fig. 2b,  $r = 0.46$ ,  $p = 0.0026$ ) but no significant relationship between *L. vincta* and *C. virgatum* (Fig. 2c,  $r = 0.26$   $p = 0.14$ ).

Our results support the hypothesis that *Lacuna vincta* recruitment is influenced by the presence of epiphytes and lend support to the growing body of evidence on the importance of biotic interactions in recruitment dynamics. This relationship may be explained, in part, by protection from predators provided by the epiphytes’ three-dimensional structure (Williams et al. 2002; Henninger et al. 2009). There may be additional interactions taking place on a shorter time frame than our two-week experiments, but we are primarily concerned with longer-scale, community-wide impacts that persist and ultimately shape the intertidal algal community.

Alternatively, epiphytes may provide a source of food for *L. vincta*. Prior feeding studies in our study location have shown that *L. vincta* preferentially consume native *Ceramium virgatum* over invasive *Neosiphonia harveyi* (Jones and Thornber 2010), even though we found that *L. vincta* recruit to both at the same rates. Chemical defenses in algae can also play a role in herbivore food preferences and selection (Hay and Fenical 1988; Erickson et al. 2006; Lyons et al. 2007); whether defense compounds are present in *C. virgatum* and *N. harveyi* is, however, currently unknown. Our data show correlative support that there is no reciprocal effect of *L. vincta* on epiphyte recruitment, but further research is needed in this area.

Grazers play an important role in controlling epiphyte densities in many marine habitats, including subtidal rocky reefs (Heck and Valentine 2006; Jaschinski and Sommer 2008). On rocky shores,



**Fig. 2** Relationship between *Lacuna vincta* density and epiphyte recruitment. There is a significant positive correlation between the number of *L. vincta* present and **a** the mass of all epiphytes on each macroalgal mimic ( $r = 0.50$ ,  $P = 0.0058$ ) as well as **b** the mass of *N. harveyi* ( $r = 0.46$ ,  $P = 0.0026$ ) on each macroalgal mimic in closed containers. **c** There is no relationship between the number of *L. vincta* present and the mass of *C. virgatum* on macroalgal mimics in closed containers ( $r = 0.26$ ,  $P = 0.1445$ )

grazers are also important in controlling algal growth, and elevated levels of herbivory can increase species diversity (Benedetti-Cecchi 2000; Noel et al. 2008). In coastal areas with subtidal seagrass beds, epiphytes settling on seagrass blades can outcompete the seagrass for resources and eventually cause a decline of seagrass beds (Valiela et al. 1997; Drake et al. 2003; Hauxwell

et al. 2003; Brush and Nixon 2004; Hays 2005). As non-native species continue to become established in coastal marine communities at unprecedented rates (Cohen and Carlton 1998; Grosholz et al. 2000; Grosholz 2002), it is important to understand how these new species could influence recruitment and survival rates of native and other non-native species (Bownes and McQuaid 2009; Gribben et al. 2009b).

It is generally assumed that invasive algae have negative effects on native communities and biodiversity, which is true in many cases (Williams and Smith 2007), but there are instances where invasive algae have either had positive or no effects on native organisms (Gribben and Wright 2006; Gribben et al. 2009a; Jones and Thornber 2010). We found that *Lacuna vincta* recruit in higher densities to macroalgal mimics where epiphytes are present. We also found a positive correlation between the abundance of *L. vincta* and the density of the invasive *Neosiphonia harveyi*, but no correlation between abundance of *L. vincta* and the density of the native *Ceramium virgatum*. When *L. vincta* were present, we found low densities of *C. virgatum* and evidence of severe grazer damage; this is likely because *L. vincta* preferentially consume *C. virgatum* (Jones and Thornber 2010). Thus, our data indicate that *N. harveyi* may facilitate *L. vincta* populations by providing a more complex habitat structure; this may then have a negative, indirect impact on *C. virgatum* density. Determining specific interactions for individual species and communities can be critical to properly mitigating the effects of these species and adapting to the constantly changing marine environment.

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