Epibiosis on Gastropod Shells in the Rocky Intertidal: Effects of Zonation and Shell Morphology

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Abstract

In a dynamic environment such as the rocky marine intertidal zone, the stresses experienced by epibionts and their hosts may differ when these animals are engaged in symbioses compared with when they are attached alone to the surrounding rock. We compared the species composition of the epibiotic community on gastropod shells to that of colonizers on neighboring rock surfaces to determine whether intertidal zone, wave action, or basibiont identity affected the epibionts present. We examined two tidal heights (a lower *Saccharina sessilis* zone and a higher *Fucus gardneri*/*Semibalanus cariosus* zone) at three sites of varying wave exposure (Westside Preserve, Cattle Point, and Colin's Cove) on San Juan Island, WA. In the lower tidal zone (but not in the higher), the percent of unfouled snails was much greater than predicted based on the surrounding substratum. Fewer than four algal species dominated the substratum at both tidal heights, but the identity of the dominant algae differed between tidal heights and did not match the dominant epibiotic species. Instead, small individuals of the barnacles *Semibalanus cariosus* and *Balanus glandula*, spirorbid worms, an excavating alga, an excavating sponge, and diatoms were the most prevalent epibionts. While the basibiotic gastropods were less fouled than we expected overall, we found heavily-fouled individuals (especially limpets) interspersed among unfouled individuals. We deployed cleaned empty shells, either sanded ("weathered") or intact, of the gastropod species *Tectura scutum*, *Lottia digitalis*, *Nucella canaliculata*, and *Nucella lamellosa* for 3 to 6 weeks in the higher intertidal zone and subtidally at two sites. Differences in settlement of epibionts seemed more due to microhabitat effects than to shell morphology, but it is hard to generalize from such short-term settlement studies.

Introduction

Algae and sessile invertebrates densely colonize the eulittoral zone of the rocky intertidal. Here competition for space is intense, and pelagic larvae and algal spores capitalize on a limited settlement area when they recruit to the rock face to metamorphose. Some species increase their settlement opportunities (and thus chance of survival) by fouling other organisms, a process called epibiosis. Epibiosis is the attachment and settlement of one organism, the epibiont (epizoan or epiphyte), on the body of another called the basibiont. The relationship between the epibiont and basibiont is a multilayered one.

The basibiont can provide a plethora of benefits to its epibionts in addition to providing a substratum for settlement. For example, the hard, stable calcium carbonate shells of gastropods can increase the overall biodiversity of epibionts in a particular area. For example, the infralittoral abalone *Haliotis midae* supports a significantly different community than its rock habitat, and the corallines *Titanoderma polycephalum*, *Mesophyllum engelhartii*, and *Spongites discoideus* exclusively colonize on the shell of this host (Zeeman *et al.* 2013). In another example, epibiont species richness directly correlates with the size of the subtidal limpet basibiont *Turbo torquatus* (Wernberg 2010). Additionally, the basibiont may also provide an escape mechanism from predators. For instance, the epibiotic slipper limpet *Crepidula adunca* favors the marine snail *Calliostoma ligatum* over the morphologically similar species *Margarites pupillus* because of the speed and possible anti-predatory chemical deterrents of *Calliostoma ligatum* (Herstoff and Iyengar 2011). Gastropod shells may also provide a more favorable thermal environment than dark rock substrata, which likely experiences more extreme temperature fluctuations. Taken together, these factors may promote a very different epibiotic community than the fouling community on the surrounding intertidal rocks.

On the other hand, the effects of fouling on the basibiont are more ambiguous, and epibionts may provide benefits, costs, or both simultaneously to the basibiont. For example, the anemone epibiont *Calliactis parasitica* provides a clear positive benefit to the hermit crab *Dardanus arrosor* by protecting it from predatory attacks by cephalopods (Ross and von Boletzky 2009). In a more complex relationship, the lichen *Thelidium litorale* facilitates visual crypsis by disguising an intertidal limpet as less palatable barnacles, but at the same time it erodes the limpet's myostracum (Espoz *et al.* 1995). The epiphytes *Ulva lactuca* and *Acrosiphonia* spp. improve the righting ability and thermal tolerance of the intertidal limpet *Lottia pelta*, but also increase drag (Seaborn 2014). Ephemeral mats of the green alga *Enteromorpha* sp. and the red alga *Porphyra* sp. had no effect on byssal thread production or biomass of the intertidal mussel *Mytilus galloprovincialis*, but decreased survivorship of this host in stormy conditions (O'Connor *et al*. 2004). Drag can become a particularly important detriment in the rocky intertidal where pull stress of the waves comes in erratic, extreme pulses instead of the gradual ebb and flow of the tides.

In other cases, fouling presents a clear negative impact on basibiont fitness and survival. For example, the epibionts *Enteromorpha intestinalis*, *Balanus improvisus*, and *Ectocarpus* sp. significantly increased drag and reduced the growth rate of the limpet basibiont *Littorina littorea* when food was limited (Wahl 1996). The mussel *Mytilus californianus* had significantly lower somatic tissue mass and survivorship when overgrown with the algae *Corallina officinalis*, *Gigartina canaliculata*, and *Gelidium* *coulteri* (Dittman and Robles 1991). Clearly, the effects of the epibiotic community on basibiont survival and fitness when taken as a whole are highly variable and species-specific.

Many factors drive the species composition of the epibiotic community in the intertidal. Physical zonation height has been shown to affect basibiont size, though in complex and sometimes contradictory ways (reviewed by Vermeij 1972). For example, size of the limpet *Collisella* (formerly *Acmaea*) *digitalis* is positively correlated with zonation height because of decreasing predation and abrasion rates at upper levels (Frank 1965) while the limpet species *Notoacmaea* (formerly *Acmaea*) *scutum*, *Collisella* (formerly *Acmaea*) *pelta*, and *Acmaea mitra* show the opposite trend (Shotwell 1950). Four species of the dogwinkle *Nucella* (formerly *Thais*) had no relationship to intertidal height (Butler 1979). If zonation affects basibiont size, then it may also affect the ecology of the epibionts. Larger size of the basibionts may allow the epibionts to continue to grow to later successional stages as larger—and thus more secure—surfaces are available for attachment.

Shells occupied by the original snail versus a hermit crab may host different epibiotic communities because of the different abiotic stressors imposed by the different behaviors of these organisms. For example, the fouling on *Nucella lapillus* shells occupied by the hermit crab *Pagurus bernhardus* differed significantly from that on shells of the living snail because of decreased emergence time for the hermit crab (Bell 2005).

Inherent in the shell of the basibiont, periostracum may also impact settlement. For example, a thick, hairy periostracum has been shown to inhibit settlement on the gastropod *Fusitriton oregonensis* (Bottjer 1981) and the mussel *Mytilus edulis* (Wahl 1998). Similarly, the marine snail *Trichotropis cancellata* had significantly higher fouling by the barnacle *Balanus* spp. when stripped of its periostracum (Iyengar *et al.* 2008).

Shell morphology in general can have major impacts on the attachment and settlement of epibionts. Most epibiotic larvae and spores start as pelagic organisms, have low Reynolds numbers, and are thus greatly affected by current flow when they attempt to attach to hard substrata and metamorphose. If the epibiont can anchor itself within the boundary layer of a basibiont, such as in the suture line between the whorls of a gastropod shell, it may have a higher chance of long-term attachment and survival. Shell sculpture may alter flow vectors around the basibiont's shell; however, that might preclude effective feeding by the epibionts (Wahl 1996). For example, the periostracum of *Trichotropis cancellata* significantly elevated the arc height—and thus the thickness—of the boundary layer (Iyengar *et al.* 2008), so while the larvae may be able to settle and attach more easily, when they grow they remain in a non-turbulent feeding regime for a longer period of time, which may be unfavorable to filter feeding epibionts.

To determine whether the epibiotic community on gastropod shells differed from the rocky algae and sessile invertebrates fouling the nearby bedrock, we surveyed the dominant algal and gastropod species at different physical zonation heights at three locations around San Juan Island. We then compared the epibiotic communities across the most common gastropod species to see whether they differed from the community on the rocky substratum.

We hypothesized that rugosity of shells and shell morphology would be important factors in determining the degree of shell fouling. Past research has shown that different fouling species prefer to settle on different shell textures. For example, polydimethylsiloxan elastomer (PDMSe) surface modeling has shown that settlement of *Ulva* spp. spores and cyprids of *Balanus amphitrite* are inhibited at different rugosities—surfaces rougher than 2 μm and 20 μm, respectively, were enough decrease settlement (Schumacher *et al*. 2007). We predicted that—as an overall trend—macroscopic axial or spiral ribs on the shell (e.g. as present on *Lottia digitalis*, *Nucella lamellosa*, and *Nucella canaliculata*) would increase fouling because the shelter of the boundary layer of the basibiont's shell would reduce wave-induced dislodgment post-settlement, but rugosity at a microscopic scale would correlate with decreased fouling because it would be harder for the basal attachment surface of the epibiont to gain purchase on the rough surface. Additionally, we predicted that there would be more settlement towards the apex or spire tip of a shell as this positioning improves suspension feeding epibionts' ability to place feeding appendages and chemoreceptors outside of the boundary layer of the surrounding substrata. We also hypothesized that if intertidal zonation was key, then fouling would be greatest in the zone that has shortest emergence time for the lowest level of wave action, as these conditions are the least likely to desiccate and dislodge the fouling species during its vulnerable stages of attachment and early settlement.

The goal of these studies was to determine whether intertidal zonation, gastropod behavior, shell morphology, or a combination of these factors affect the degree of shell fouling across gastropod species, focusing on the dominant gastropods *Tectura scutum*, *Tectura persona*, *Lottia pelta*, *Lottia digitalis*, *Nucella lamellosa*, *Nucella canaliculata*, and *Lirabuccinum dirum*.

Methods

Transect Surveys of Intertidal Sites

Transect studies were performed June-July 2014 on San Juan Island, WA. Sampling took place at three sites: (1) Westside Scenic Preserve (hereafter referred to as Land Bank) on the western side of the island (48° 30.339' N, 123° 08.500' W), (2) just north of Colin's Cove on the eastern side (48° 32.985' N, 123° 00.352' W), and (3) Cattle Point on the southern tip (48° 26.991' N, 122° 57.778' W) (see Fig. 1). Land Bank and Cattle Point border the Haro Strait and are exposed to harsher wave conditions than the eastern site near Colin's Cove, and therefore we predicted Land Bank and Cattle Point would have similar epibiotic communities that would differ from those at Colin's Cove. At each site, a transect line was haphazardly placed parallel to the shoreline in each of two intertidal zones. The higher tidal height (hereafter referred to as the *Fucus/Semibalanus* zone) was in the upper midlittoral (0.9-1.2 ft. tidal height) and dominated by the algae *Fucus gardneri* and *Endocladia muricata* and patches of bare rock colonized by the barnacles *Semibalanus cariosus* and *Balanus glandula*. This line ran along the lower tidal extent of *Fucus gardneri* at each site. The lower tidal zone (hereafter referred to as the *Saccharina* zone) was located in the lower midlittoral (0-1 ft. tidal height) in the middle of the *Saccharina sessilis* zone, except at Colin's Cove where the dominant algae was *Ulva* spp. Just below our lower transect line at each site, the large laminarians such as *Laminaria saccharina* and *Alaria* spp. were present. Nine to twelve quadrats (0.5 m x 0.5 m each quadrat, subdivided so each individual cell = 4% of whole) were placed at least 2 m apart along each transect line on relatively flat areas of bedrock. While the angle of incline of the bedrock was not controlled, we stayed on rock benches and avoided areas with deep crevices or boulder/cobble fields. Within each quadrat, the percent cover of algae, and the identity and size of all gastropod species were recorded, and fouled gastropods were transported to the laboratory for identification of each epibiont and total count of each epibiotic species or estimation of amount (categorized as small, medium, large) of basibiont area covered. Specimens with epibionts were processed within 24 hours of collection or were isolated into separate flow-through containers (Toby Tea Boys®) until processed to prevent intra-organismal shell grazing.

The size of gastropods was measured from the tip of the spire along the axis of coiling to the base of the aperature for spired-shell species and from anterior to posterior ends of the aperature for limpet species. Epibionts were classified to the lowest taxonomic or descriptive level possible (e.g. excavating sponge). It was noted if the shell housed the original gastropod, a hermit crab, or was empty.

Measuring Epibiont Settlement in the Field

Live individuals of the limpet species *Tectura scutum* and *Lottia digitalis* and the spired-shell species *Nucella lamellosa* and *Nucella canaliculata* were collected from Land Bank and north of Colin's Cove. Specimens were euthanized via freezing, the bodies extracted, and the shells lightly scrubbed with a soft-bristled toothbrush under a microscope to remove epibionts (barnacles, large algae, and spirorbid worms were completely removed, the diatom *Navicula* spp. and a light film of a thin encrusting bright green alga were impossible to remove without damaging the periostracum/prismatic layers and so were left in place). Eighteen *L. digitalis* and 18 *N. canaliculata* were electrically sanded (Dremel®) to smoothness to test for the effects of a worn shell morphology lacking structures like spiral ribs or axial lamellae. Specimens of each of the

6 treatments (unsanded *T. scutum*, sanded and unsanded *L. digitalis*, unsanded *N. lamellosa,* and sanded and unsanded *N. canaliculata*) were distributed on patches of window screen mesh (fiberglass, mesh size 1.5 mm x 1.5 mm). The marine epoxy Z-Spar was inserted into the aperature and body whorl of each shell and used to anchor the shell to the mesh, and the spired-shell species *N. lamellosa* and *N. canaliculata* also had a nail passed through the mesh and embedded in the Z-Spar to act as an additional anchor. The window mesh was attached (using Z-Spar) directly to rock ledges in the *Fucus/Semibalanus* and subtidal zones in areas close to the lines of our transect studies. The Z-Spar completely filled the body whorl of the shell and the window mesh was flush to the rock substratum to allow transfer of ambient heat from the rock and mimic the thermal warming of the bodies of living specimens, as temperature is likely to impact the survival of epibiotic settlers (Jennifer Burnaford, personal communication). This methodology was supported by Shanks (2009) who found that long-term settlement patches on Plexiglas heated to temperatures lethal to cyprids and much higher than the surrounding rock and thus did not accurately reflect the settlement community of the intertidal. Shells were deployed at two sites: Land Bank and north of Colin's Cove. Arrays were anchored in the *Fucus/Semibalanus* and subtidal *Phyllospadix serrulatus*/*Alaria* spp. (-0.4 ft. tidal height MLLW) zones at Land Bank for 5.5 weeks (29 June-6 August 2014). Due to time constraints, only sanded shells were deployed at the Colin's Cove site. Thus at this site, these shells tested only the effects of gross shell morphology (and not rugosity) on fouling. Eighteen *T. scutum* and 18 *N. canaliculata*—these species chosen due to their maximum morphological differences among our local

possibilities—were electrically sanded (Dremel®, epibiont removal 100%) and replicates were deployed for 3.5 weeks (14 July-6 August 2014).

Results

The average percent cover of the major bedrock species of algae was calculated for the Land Bank, Cattle Point, and Colin's Cove sites (Fig. 2-4). The dominant epibiotic species on gastropod shells were then compared to the major species of algae on the bedrock (Fig. 5-10). Within the higher *Fucus/Semibalanus* zone, the percent of bare rock on the substratum and the percent of unfouled gastropods were within 40 to 60%. However within the lower *Saccharina* zone, while 40-60% of the gastropods remained without epibionts, the percent of the bare bedrock dropped to 5 to 15%. It is worthwhile to note that while percent cover of the algae on the bedrock represents a constantly-sized area, when we discuss the percent of gastropod hosts fouled that represents the number of individuals, without considering the areas that each of their shells provide for settlement and that each individual species can differ in size.

On the bedrock, *Fucus gardneri* and *Ulva/Ulvaria* spp. were the dominant algal species in the higher zone. In the lower zone, *Saccharina sessilis* dominated at Land Bank and Cattle Point, but *Ulva/Ulvaria* spp. were present in the highest percentage at Colin's Cove, the site with the lowest wave action. While approximately 10 to 15 algal species were present total within each zone (i.e. the diversity of algal species was great), typically only one or two species often exceeded 10% coverage.

The dominant species of algae covering the bedrock did not match the major epibionts present on the gastropod shells (grouped across all gastropod species for the present analysis). Except for the high zone at Land Bank, the diatom *Navicula* spp. was the dominant epibiont on the gastropod shells, but was not a dominant bedrock foulant at any site or zone. While it is possible that we overlooked the presence of *Navicula* spp. on the bedrock and algae, we do not think it was present in as thick aggregations there as on the gastropod shells, or we would likely have noticed. The barnacles *Balanus glandula* and *Semibalanus cariosus* (though rarely exceeding 3 mm), spirorbid worms, an excavating sponge, an excavating alga, and a thin encrusting bright green alga were the most dominant gastropod epibionts. Even when *Fucus gardneri, Saccharina sessilis,* and bare rock were removed from the analysis of the bedrock foulant species, the dominant algae still did not match gastropod fouling. The only fouling species that were present on both the bedrock and the gastropod shells were *Ulva/Ulvaria* spp. and this concordance was only particularly noted at Colin's Cove.

Discussion

The higher percentage of bare rock in the higher *Fucus/Semibalanus* zone was not surprising, as a longer emergence time exerts more extreme thermal and desiccation pressures on the species colonizing that zone. However, the discrepancy between the high number of unfouled gastropod species and low percentage of bare rock in the lower *Saccharina sessilis* zone cannot be explained by emergence time. It is as of yet unclear as to why this incongruity in epibiosis versus algal cover of bedrock exists, perhaps the gastropod specie(s) have behavioral mechanism(s), like migration into higher intertidal zones, to limit the epibiosis on their shells.

The differences in the dominant algal species at Land Bank and Cattle Point versus Colin's Cove can likely be explained by the differences in wave action experienced across sites. It is possible that a higher wave action site supports the

Saccharina sessilis community but the lower wave action site is more favorable to *Ulva/Ulvaria* spp. growth. The overall lack of diversity of algal species across both zones was surprising, as the rocky intertidal is an environment of intense settlement competition for pelagic larvae and algal spores.

The extreme differences between fouling species on the bedrock and gastropod epibionts were also surprising. The rock foulants clearly did not match the species on the gastropod shells. An analysis of epibiosis by specific gastropod species is pending. A note of particular interest was the size of the barnacle epibionts on the gastropod shells. It was rare that *Semibalanus cariosus* or *Balanus glandula* were present on shells at sizes greater than 3 mm, yet they often exceed this size when attached to the bedrock. It is unclear whether the epibiotic barnacles mature at smaller sizes than those individuals that colonize the bare rock face or whether the epibionts mostly die before reaching maturity, thus representing an ecological sink for this species. Future work should investigate this question.

The long-term settlement patches collected from Land Bank and Colin's Cove had limited epibiotic species diversity, likely because of the shorter than ideal duration of deployment. Diatoms, thin encrusting noncalcified algae, and cyanobacteria were the only epibionts observed. The replicates revealed no consistent patterns of epibiosis based on site, zone, or shell morphology. Neighboring settlement patches differed from heavily fouled to unfouled even within a zone. These discrepancies, in combination with the patchiness of epibiosis observed in our transect studies, have led us to believe that fouling is largely determined by microhabitat differences. Future studies with longer deployment periods are necessary to further investigate these claims.

Examining epibiosis on gastropod shells in the rocky intertidal warrants further study, and not only to establish the ecology of this biodiversity hotspot. Many of the species of epibionts examined in this study are also responsible for hull fouling, which is a major concern for the shipping industry. Hull fouling by mucous, calcareous exoskeletons, and algae has been found to increase friction and drag (reviewed by Towsin 2003), resulting in increased fuel expenditure (Schultz *et al.* 2011) and the vectoring of fouling species to nonnative areas (Farrapeira *et al*. 2007). Coating the boat's hull with antifouling biocides like tributyl tin (TBT, now banned), while economically advantageous, has been shown to leech toxic chemicals into the marine environment (Towsin 2003). Studying epibiosis on gastropod shells and the basibionts' antifouling strategies may provide a more benign solution to hull fouling than the self-polishing copolymers (SPCs) currently favored by the shipping industry (Towsin 2003).

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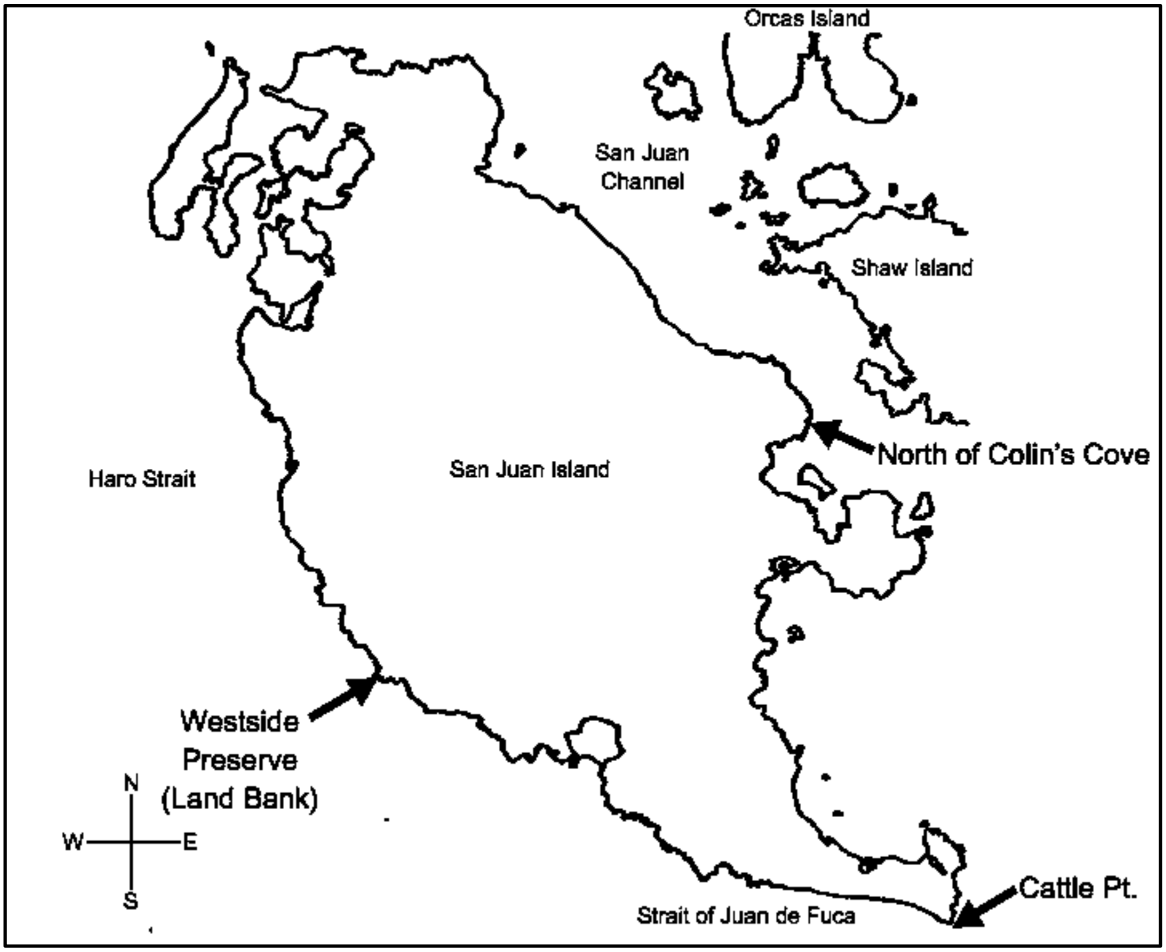

Fig. 1. Location of 3 study sites: at Westside Scenic Preserve (Land Bank) on the western side of the island, just north of Colin's Cove on the eastern side, and at Cattle Point on the southern tip of San Juan Island, WA. Image adapted from TownGraphics.com.

Fig. 2. The dominant species of algae covering the bedrock at Land Bank. The graph on the left shows the higher *Fucus/Semibalanus* zone. br = bare rock, Fg = *Fucus gardneri*, Gf = *Gloiopeltis furcata*, Mb = *Microcladia borealis*, and U = *Ulva*/*Ulvaria* spp. The graph on the right shows the lower *Saccharina* zone. Ss = *Saccharina sessilis*, br = bare rock, rc = red coralline, ENA = encrusting noncalcified algae, and U = *Ulva*/*Ulvaria* spp.

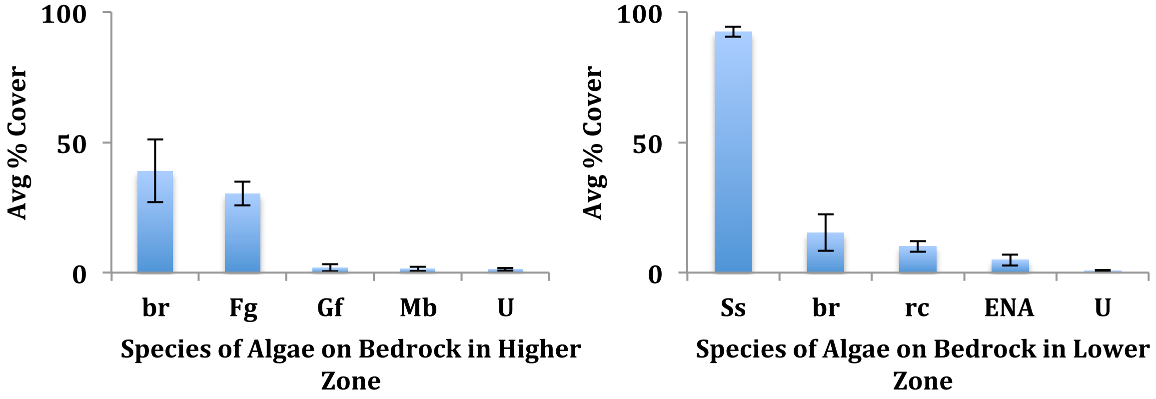

Fig. 3. The dominant species of algae covering the bedrock at Cattle Point. The graph on the left shows the higher *Fucus/Semibalanus* zone. br = bare rock, Fg = *Fucus gardneri*, Gf = *Gloiopeltis furcata*, Mb = *Microcladia borealis*, and U = *Ulva*/*Ulvaria* spp. The graph on the right shows the lower *Saccharina* zone. Ss = *Saccharina sessilis*, br = bare rock, rc = red coralline, ENA = encrusting noncalcified algae, and U = *Ulva*/*Ulvaria* spp.

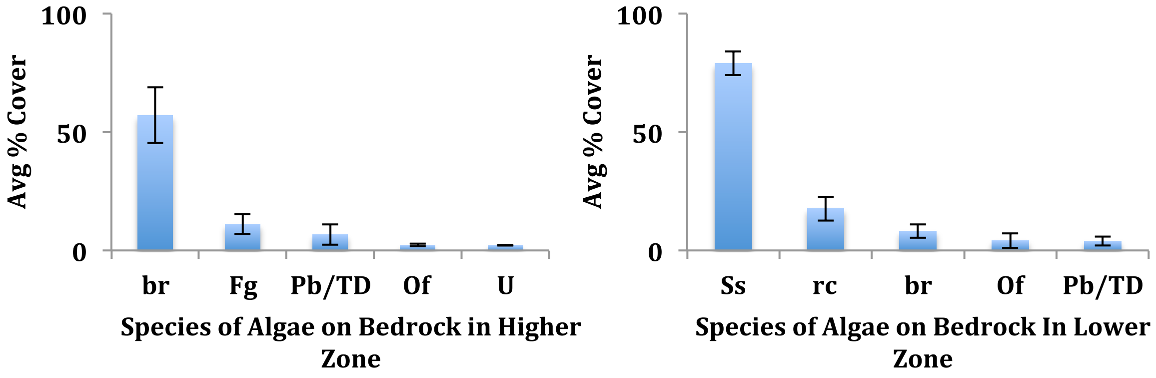

Fig. 4. The dominant species of algae covering the bedrock at Colin's Cove. The graph on the left shows the higher *Fucus/Semibalanus* zone. br = bare rock, Fg = *Fucus gardneri*, U = *Ulva*/*Ulvaria* spp., Ss = *Saccharina sessilis*, and ENA = encrusting noncalcified algae. The graph on the right shows the lower *Alaria*/*Laminaria* zone. U = *Ulva*/*Ulvaria* spp., br = bare rock, Pb/TD = *Pterosiphonia bipinnata*/tube-dwelling diatom, Of = *Odonthalia floccosa*, and ENA = encrusting noncalcified algae.

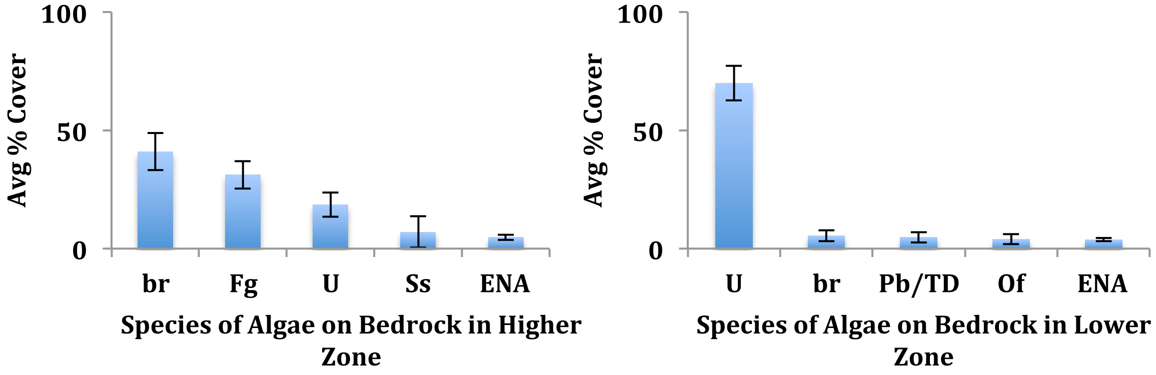

Fig. 5-10. Data of epibionts were combined across all species of basibiotic gastropods. The epibiotic community is likely to vary across basibionts, but we did not have time to tease apart those differences before this paper needed to be submitted. Future work will examine each host species separately.

Fig. 5. Comparison of the dominant species of the algae on the bedrock (disregarding the percent cover of bare rock and the alga *Fucus gardneri*) to dominant epibionts on basibiotic gastropods in the higher *Fucus*/*Semibalanus* zone at Land Bank. The graph on the left shows the algae Gf = *Gloiopeltis furcata*, Mb = *Microcladia borealis*, U = *Ulva*/*Ulvaria* spp., Dl = *Desmarestia ligulata*, and Hg = *Halosaccion glandiforme*. The graph on the right shows the epibionts Bg = *Balanus glandula* (barnacle), ex. a = excavating alga, ex. s = excavating sponge, N = *Navicula* spp. (diatom), and BGA = thin encrusting bright green alga. Note different scale bars on y-axes.

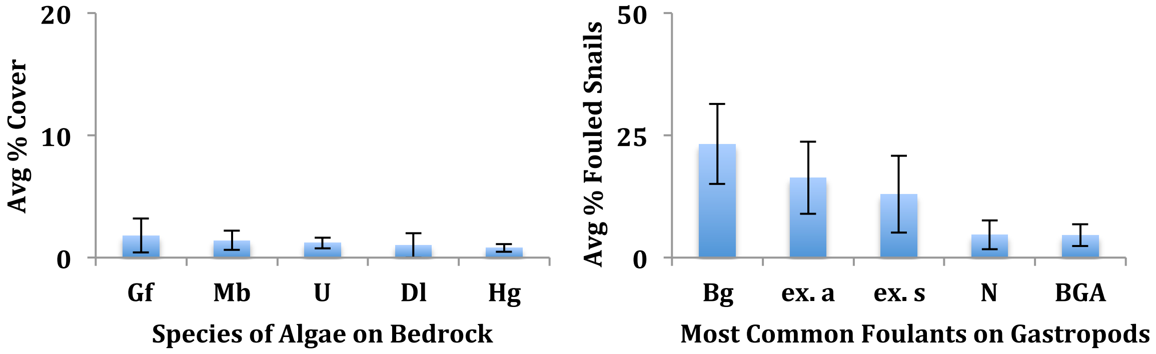

Fig. 6. Comparison of the dominant species of algae on the bedrock (disregarding the percent cover of bare rock and the alga *Saccharina sessilis*) to dominant epibionts on basibiotic gastropods in the lower *Saccharina* zone at Land Bank. The graph on the left shows the algae rc = red coralline, ENA = encrusting noncalcified algae, U = *Ulva*/*Ulvaria* spp., Da = *Desmarestia ligulata*, and Hg = *Halosaccion glandiforme*. The graph on the right shows the epibionts N = Navicula spp. (diatom), ex. a = excavating alga, U = Ulva/Ulvaria spp., BGA = thin encrusting bright green alga, and ex. s = encrusting sponge. Note different scale bars on y-axes.

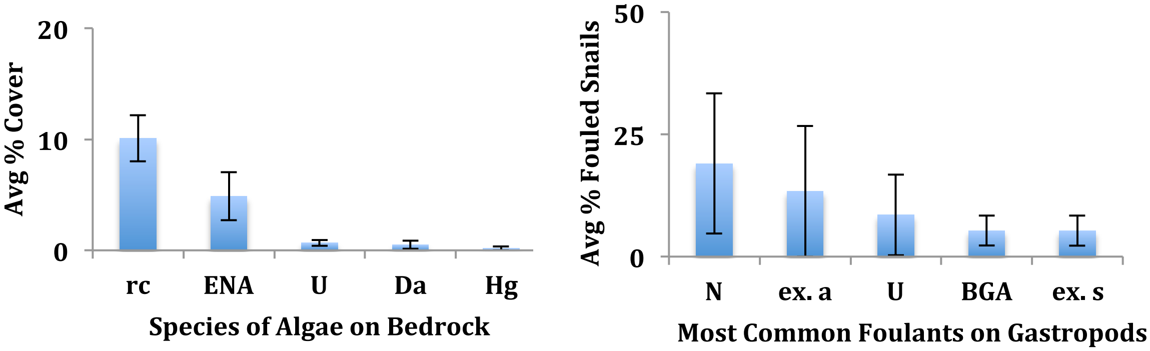

Fig. 7. Comparison of the dominant species of algae on the bedrock (disregarding the percent cover of bare rock and the alga *Fucus gardneri*) to dominant epibionts on basibiotic gastropods in the higher *Fucus*/*Semibalanus* zone at Cattle Point. The graph on the left shows the algae Pb/TD = *Pterosiphonia bipinnata*/tube-dwelling diatom, Of = *Odonthalia floccosa*, U = *Ulva*/*Ulvaria* spp., ENA = encrusting noncalcified algae, and Hg = *Halosaccion glandiforme*. The graph on the right shows the epibionts N = *Navicula* spp. (diatom), Bg = *Balanus glandula* (barnacle), Sc = *Semibalanus cariosus* (barnacle), ex. a = encrusting alga, and spir. = spirorbid worms. Note different scale bars on y-axes.

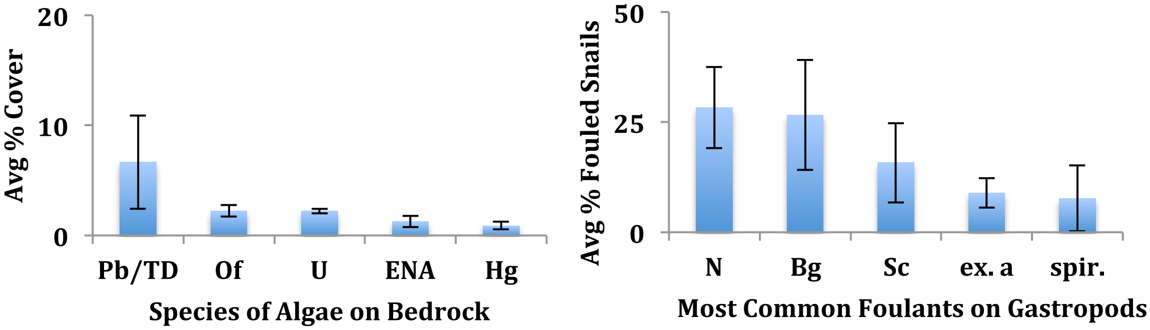

Fig. 8. Comparison of the dominant species of algae on the bedrock (disregarding the percent cover of bare rock and the alga *Saccharina sessilis*) to dominant epibionts on basibiotic gastropods in the lower *Saccharina* zone at Cattle Point. The graph on the left shows the algae rc = red coralline, Of = *Odonthalia floccosa*, Pb/TD = *Pterosiphonia bipinnata*/tube-dwelling diatom, U = *Ulva*/*Ulvaria* spp., v. red = veined red alga, and ENA = encrusting noncalcified algae. The graph on the right shows the epibionts N = *Navicula* spp. (diatom), Bg = *Balanus glandula* (barnacle), spir. = spirorbid worms, Sc = *Semibalanus cariosus* (barnacle), and BGA = thin encrusting bright green alga. Note different scale bars on y-axes.

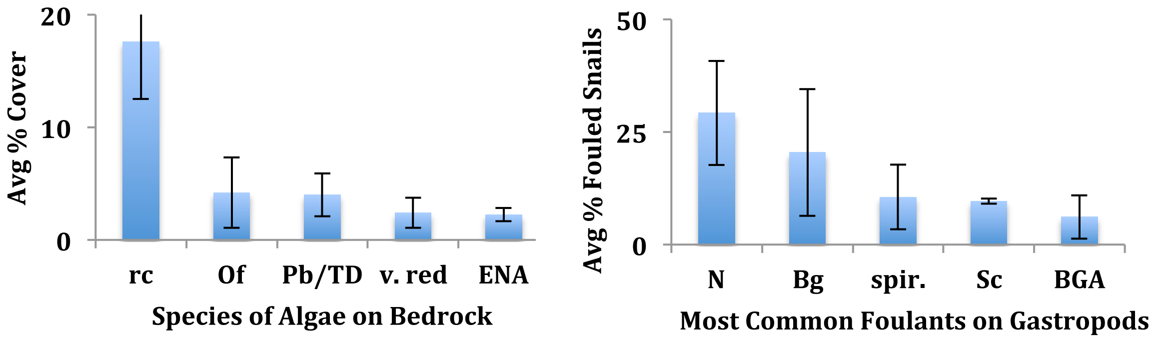

Fig. 9. Comparison of the dominant species of algae on the bedrock (disregarding the percent cover of bare rock and the algae *Fucus gardneri* and *Ulva*/*Ulvaria* spp.) to dominant epibionts on basibiotic gastropods in the higher *Fucus*/*Semibalanus* zone at Colin's Cove. The graph on the left shows the algae Ss = *Saccharina sessilis*, ENA = encrusting noncalcified algae, Pb/TD = *Pterosiphonia bipinnata*/tube-dwelling diatom, Cp = *Callithamnion pikeanum*, and Da = *Desmarestia aculeata.* The graph on the left shows the epibionts N = *Navicula* spp. (diatom), ex. s = excavating sponge, U = *Ulva*/*Ulvaria* spp., spir. = spirorbid worms, and ex. a = excavating algae. Note different scale bars on y-axes.

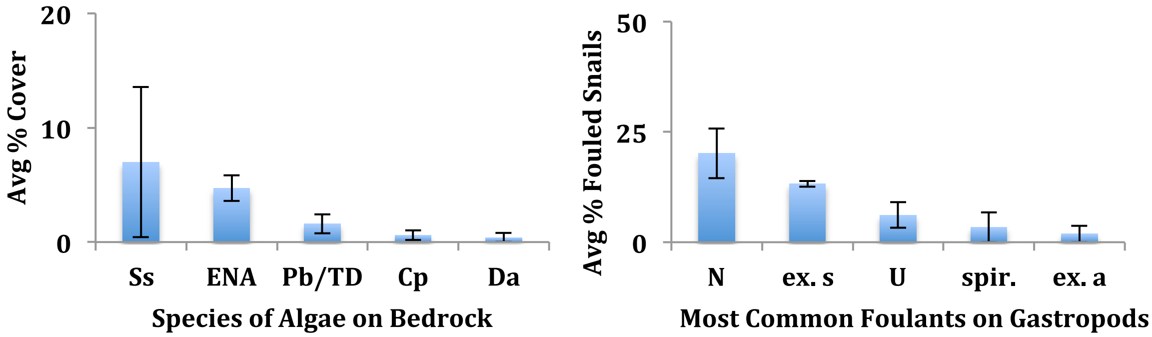

Fig. 10. Comparison of the dominant species of algae on the bedrock (disregarding the percent cover of bare rock and the algae *Ulva*/*Ulvaria* spp.) to dominant epibionts on basibiotic gastropods in the lower *Alaria*/*Laminaria* zone at Colin's Cove. The graph on the left shows the algae Pb/TD = *Pterosiphonia bipinnata*/tube-dwelling diatom, Of = *Odonthalia floccosa*, ENA = encrusting noncalcified algae, Fg = *Fucus gardneri*, and rc = red coralline. The graph on the right shows the epibionts N = *Navicula* spp., ex. a = excavating alga, BGA = thin encrusting bright green alga, spir. = spirorbid worms, and U = *Ulva*/*Ulvaria* spp. Note different scale bars on y-axes.