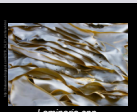
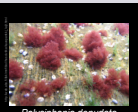
Do macroalgae use allelochemicals to outcompete invertebrates for space in the Gulf of Maine?

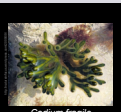
Erica L. Warkus[1], Martine Wagstaff[2], Scott Morello[2], Ron Etter[2]
[1]School of Life Sciences, Arizona State University, Tempe, AZ, [2] Biology Department, University of Massachusetts Boston, Boston, MA

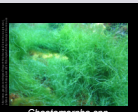

Desmarestia viridis

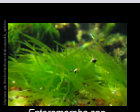

Laminaria spp.


Ulva Lactuca


Polysiphonia denudata


Codium fragile


Chaetomorpha spp.


Enteromorpha spp.


Grateloupia turu turu

Abstract

Macroalgae dominate horizontal surfaces in shallow subtidal habitats, whereas sessile invertebrates dominate vertical surfaces. Prolonged shading of horizontal surfaces in the subtidal allowed sessile invertebrates to colonize areas previously dominated by macroalgae (Miller and Etter 2008). The algaes' competitive advantage on horizontal substrates may be due to a variety of factors including whiplash effects, reduction of accessible food, change in flow dynamics, micropredators sheltering in the algae or allelopathic interactions from secondary metabolites. To explore the possibility of allelopathic effects causing the observed shift in community composition, we reared larval polychaetes with several selected species of macroalgae commonly found in the Gulf of Maine. Survivorship of larval polychaetes was lower in all macroalgae treatments relative to the controls. *Polysiphonia denudata* in particular strongly reduced the survivorship of larvae suggesting the chemicals released by this red algae may inhibit local recruitment. Our results indicate that algal allelopathy may play an important and unrecognized role in structuring temperate shallow subtidal and intertidal marine communities.


Vertical and horizontal surfaces in the subtidal show drastic differences in community composition

Introduction

Allelopathy refers to any process involving secondary metabolites produced by plants, microorganisms, viruses and fungi that influence the growth and development of agricultural and biological systems (International Allelopathy Foundation). Similar to many land plants, macroalgae are capable of producing a variety of chemical compounds such as terpenes, acetogenins and polyphenolics. These secondary metabolites may function as herbivore deterrents or as antifouling and allelopathic agents. The production of allelopathic secondary metabolites is concentrated in genera that predominantly occur in tropical and subtropical regions. Rasher and Hay (2010) found that surface chemicals from a number of tropical macroalgae caused necrosis when placed into contact with the coral, *Porites porites* suggesting allelochemicals may mediate displacement of tropical invertebrate competitors. In the Gulf of Maine, macroalgae displace invertebrates on sunlight horizontal rocky substrates (Miller and Etter 2008). Macroalgae might inhibit invertebrate recruitment in their vicinity via several mechanisms including whiplash effects, harboring micropredators, altering flow required for food and respiration, and exuding allelochemicals. We investigate whether macroalgae in the Gulf of Maine show allelopathic effects on larvae of sessile invertebrates to determine whether algal dominance of unshaded horizontal surfaces in the subtidal reflects chemical inhibition of recruitment. On a broader scale, allelopathy has many medical, agricultural, industrial and environmental implications as well as many potential connotations for understanding ecology and the forces that govern community composition.

Results

Polychaete larval survivorship declined in all algal treatments relative to the experimental controls (Fig. 1 & 2). Survivorship was nearly 100% in the controls throughout both experiments. Steady gradual declines in survivorship occurred in most algal treatments. Rates of mortality were much greater in *Polysiphonia denudata* treatments with almost no individuals remaining by the end of the experiments (Fig. 1 & 2). The trends remained consistent between the experiments with 100 μm and 300 μm nets (smaller and larger larvae) but polychaetes collected with the 300 μm net showed a greater tendency to attach to surfaces and this may have increased the counting error in the second experiment.

Analysis of variance and the Tukey-Kramer t-test on data from Exp. 1 showed that *Codium*, *Enteromorpha* and *Polysiphonia* (highlighted red) all showed significantly lower survivorship from the control ($p < 0.05$). Analysis of variance and the Tukey-Kramer t-test on data from Exp. 2 showed that only *Polysiphonia* (highlighted red) demonstrated significantly lower survivorship from the control ($p < 0.05$).

A series of water quality tests for pH, salinity, ammonia and nitrate/nitrite levels showed no perceivable difference between the treatments and control. This indicates that polychaete mortality was not caused by algae degradation, which supports the hypothesis that observed mortality was due to secondary metabolites.

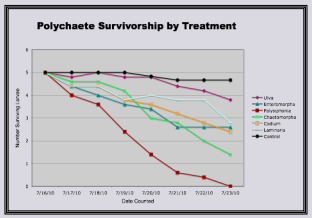


Figure 1. Time series of polychaete Survivorship (Average of five replicates). 7/16/10-7/23/10

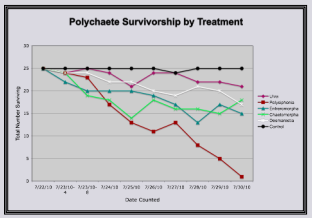


Figure 2. Time series of polychaete survivorship (Total out of 25 individuals). 7/22/10-7/30/10

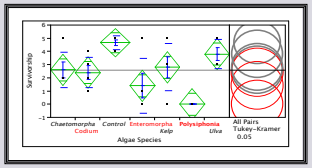


Figure 3. ANOVA and Tukey-Kramer analysis of ending survivorship. Exp. 1 - 7/16/10-7/23/10

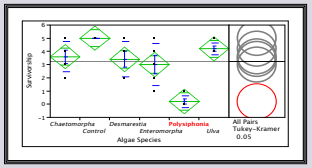


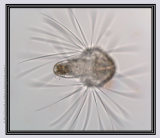
Figure 4. ANOVA and Tukey-Kramer analysis of ending survivorship. Exp. 2 - 7/22/10-7/30/10

Methods

We assessed allelopathic capabilities of temperate algae species by adding macroalgae to populations of planktonic polychaetes and counting survivorship daily. We identified and collected dominant algal species from subtidal habitats. We focused on dominant algal species with the assumption that allelopathic effects would give a competitive advantage. We also tested two species of invasive algae to see if allelopathic capabilities influenced the ability to increase species range.

We selected polychaete larvae to assay the effects of allelochemicals exuded by macroalgae because they were highly abundant in the plankton and because benthic adults interact and compete for space with macroalgae.

Five larval polychaetes were added to small petri dishes that contained seawater (control) or seawater plus one of seven species of macroalgae (treatment). Each treatment and control was replicated five times and the experiment was repeated twice with the second experiment using larger and older larvae. All other organisms living in the algae were removed before the larvae were added. Surviving larvae were counted daily for eight days to determine mortality rates across treatments. At each count, algae were removed and placed in separate trays to more accurately count polychaete larvae. The algae were observed separately to find any individuals carried over. Survivorship data were analyzed using time series plots, ANOVA and Tukey-Kramer HSD.


Polychaete: *Sabellaria cementarium*


Treatment tray with algae and polychaetes


Polychaete: *Spinoidae spp.*

Discussion

Algal exudates, probably involving allelopathic secondary metabolites, have a detrimental effect on larval polychaete survivorship. Our results indicate that allelopathy may be one mechanism used by algae to decrease competition for space and resources from benthic invertebrates. Though bioassays of algae in the tropical oceans have clearly shown allelopathic capabilities (Rasher and Hay 2010), this effect has not been demonstrated in temperate species.

In rocky subtidal habitats worldwide algae dominate on horizontal surfaces while invertebrates (e.g. sponges, bryozoans, anemones, ascidians, barnacles, etc) dominate vertical walls (Miller and Etter 2008). When horizontal rocky substrates are experimentally shaded, invertebrates displace macroalgae and dominate these communities (Miller and Etter 2008) suggesting that macroalgae prevent recruitment of invertebrate larvae or increase post-settlement mortality on sunlight surfaces. The exact mechanism by which algae displace or prevent invertebrates from colonizing horizontal surfaces is unknown but may involve a wide variety of potential forces (Witman and Dayton 2001).

The lack of invertebrates and the dominance of algae on horizontal substrates in temperate subtidal regions worldwide may reflect the deleterious effects of allelopathic chemicals released by various species of macroalgae. Our results indicate that algal allelopathy influences the survivorship of subtidal invertebrates and may affect the ecology, structure and function of shallow subtidal and intertidal ecosystems.


Polychaete: *Spinoidae spp.*


Polychaete: *Spinoidae spp.*

Works Cited

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