Aquatic Botany 95 (2011) 200–206

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Understorey benthic microalgae and their consumers depend on habitat complexity and light in a microtidal coastal ecosystem

Anja Rubach[a], Helmut Hillebrand[a,b,*], Britas Klemens Eriksson[a,c]

[a] Botanical Institute, University of Cologne, Gyrhofstrasse 15, 50931 Cologne, Germany
[b] Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wilhemshaven, Germany
[c] Marine Benthic Ecology and Evolution, Centre for Ecological and Evolutionary Studies, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

ARTICLE INFO

Article history:
Received 10 February 2011
Received in revised form 17 June 2011
Accepted 25 June 2011
Available online 2 July 2011

Keywords:
Canopy cover
Perennial macroalgae
Eutrophication
Benthic microalgae
Consumers

ABSTRACT

Presence of habitat-forming macroalgae is supposed to mitigate effects of altered resources on benthic microalgae and their consumers. In a field experiment in a microtidal area of the Western Baltic Sea, we tested the interactive effects of nutrient enrichment, artificial shading, and habitat complexity on microalgal biomass and diversity as well as invertebrate abundance and richness. Habitat complexity comprised three levels, the presence of macroalgal canopy of *Fucus vesiculosus*, the presence of macroalgal propagules, and the absence of both (=control). Microalgal biomass (and richness) was significantly reduced by canopy presence (−88%, compared to control) and shading (−42%), with the highest biomass in the absence of both canopy and macroalgal propagules at ambient light. Within the microalgal assemblage, higher biomass was related to lower evenness (higher dominance). Density of two main invertebrate groups (snails and amphipods) strongly increased with canopy presence (on average from 53 to 154 individuals m^{-2} stone area for snails, and from 234 to 1203 individuals m^{-2} for amphipods) and so did invertebrate richness (from 4.3 to 10.3). Additionally, snail density doubled with increasing light availability. The snail responses to light and canopy were independent, the former relating to higher availability of microalgal prey, the latter to more structure. Microalgal taxon richness and biomass decreased with increasing invertebrate richness and with density of snails and amphipods. Our experiment thus showed that the presence of habitat-forming macroalgae alters biomass and diversity across trophic levels in benthic coastal communities as well as their response to resource manipulations.

1. Introduction

Coastal benthic communities are strongly affected by interdependent changes in nutrient supply and consumer pressure. Synthesis efforts across the numerous experiments manipulating nutrient supply and grazer presence in coastal areas revealed strong and contrasting effects of both factors on the biomass and diversity of primary producers, including both macroalgae (Worm et al., 2002; Burkepile and Hay, 2006) and microalgae (Hillebrand, 2002). The antagonistic control of autotroph biomass by resource enhancement and grazer control is a very general outcome across ecosystems (Gruner et al., 2008). Moreover, grazing has been suggested to provide the means to prevent negative effects of fertilization on producer diversity, which also appears as a common pattern across ecosystems if those species profiting most from enrichment also suffer highest grazing losses (Hillebrand et al., 2007).

Despite the overall support for this negative feedback mechanism, research on this topic remains lively and recently revealed a number of further aspects needed to understand consumer-resource dynamics in coastal systems. The grazer control over those algal groups profiting from fertilization depends on the diversity of the grazer assemblage (Råberg and Kautsky, 2007). Only if grazers preferring benthic microalgae co-occurred with macroalgae-feeding species, the consumers prevented the fertilization-induced increase in these ephemeral algal groups. Other studies suggest that the nutrient and grazing interaction is altered by depth (Korpinen et al., 2007a,b) and that grazer performance is not only indirectly (through changes in species composition) but also directly (through increased nutrient content) affected by fertilization (Hemmi and Jormalainen, 2002).

---

* Corresponding author at: Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wilhemshaven, Germany. Tel.: +49 4421944199.
E-mail address: hillebrand@icbm.de (H. Hillebrand).

0304-3770/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquabot.2011.06.001

The negative effect of fertilization on benthic producer diversity is often related to the loss of habitat-forming species such as perennial macroalgae (Lotze et al., 2001; Korpinen et al., 2007b). The presence of habitat-forming macroalgae mitigates the fertilization effects on understorey algae if they exert light limitation preventing use of the additional nutrients (Eriksson et al., 2006a, 2007). Furthermore, the presence of habitat-forming species is suggested to maintain higher grazer abundance (Wikström and Kautsky, 2007) and thus to enhance consumer control of autotroph response to fertilization. Habitat-forming species thus represent foundation species sensu Dayton (1975) and potentially play an integral role in the response of benthic coastal ecosystems under altered nutrient cycles, which is especially pervasive in areas of low natural diversity, such as the brackish Baltic Sea (Worm et al., 1999; Nilsson et al., 2004). A second aspect of habitat complexity is the presence of overwintering propagules for macroalgae, which enhances the responsiveness of macroalgae to nutrient enrichment (Lotze et al., 2000; Worm et al., 2001) and might change their interaction with benthic microalgae.

In a broad study program, we analyzed the interactive effects of habitat complexity and resource availability on autotroph biomass production and diversity in a subtidal rocky shore community in the Western Baltic Sea. First, we demonstrated that the presence of a perennial canopy cover by the bladderwrack *Fucus vesiculosus* L. controlled resource availability by limiting light, and thereby decreased net biomass production of understory macroalgae and effects of nutrient fertilization (Eriksson et al., 2006a). Second, we showed that nutrient effects on macroalgae were strongly enhanced by overwintering propagule banks (Eriksson et al., 2006a) and grazer absence (Eriksson et al., 2007). Additionally, canopy cover altered the association between productivity and taxon richness in the annual macroalgae, which switched from negative (without canopy) to positive (with canopy) (Eriksson et al., 2006b). Moreover, we found that the presence of propagules not only enhanced nutrient effects as previously observed, but also promoted light effects on macroalgal biomass (Eriksson et al., 2006a).

Here we extend this previous research by explicitly addressing the interaction of resource supply (nutrients and light) and habitat complexity (presence of propagules or canopy cover) on biomass accrual and diversity of mobile benthic primary consumers and their primary food, benthic microalgae. Thereby, we explored the importance of canopy cover for constraining the effects of fertilization either through preventing resource use by microalgae or by facilitating their consumers. Factorial field manipulations of habitat complexity (canopy cover, propagules present, or sterile substrates), nutrients (ambient vs. enriched) and light (ambient vs. shaded) allowed us to test the following hypotheses:

1. Biomass and diversity of microalgae are controlled by light (artificial shading vs. ambient light) and/or nutrients (enriched vs. ambient).
2. Canopy presence and propagule presence reduce microalgal biomass, which can be due to competition for resources (especially shading) and the attraction of grazers (see hypothesis 3).
3. Density and diversity of mobile consumers increase with the availability of biological habitat complexity (macroalgal canopies) and food (microalgae), which is mediated by resource supply.
4. Canopy-mediated changes in grazer densities (see hypothesis 3) generate negative feedbacks on the microalgal community (i.e., macrofauna density and microalgal biovolume are negatively correlated).

2. Material and methods

2.1. Study site

The experimental study was carried out in a shallow and virtually non-tidal bay in Maasholm in the outer Schlei Fjord (54°41′N, 10°0′E), western Baltic Sea, Germany. The study site has been extensively described elsewhere (Hillebrand et al., 2000; Worm et al., 2001). The brackish water (12–20 PSU (practical salinity units)) is characterized by wind-driven sea level changes (±0.5 m around mean) (Worm et al., 2001) and high anthropogenic nutrient input (Worm et al., 2002). At the end of the experiment (August 2004), ambient nutrient concentrations were 8.02 ± 0.38 (mean ± SE) μM silicate, 2.28 ± 0.17 μM dissolved inorganic nitrogen (DIN), and 0.77 ± 0.66 μM phosphate (Eriksson et al., 2006a). The study site is characterized by sandy bottom but abundant rocks and boulders provide suitable hard and stable substratum for a subtidal community of epilithic macro- and microalgae. The macroalgal community is dominated by the perennial canopy-forming brown seaweed *F. vesiculosus* (hereafter *Fucus*) covering up to 85% of the rock surfaces (Worm et al., 2001), while several ephemeral and crust-forming species complement the understorey (Eriksson et al., 2006a,b). Consumers of micro- and macroalgal biomass are abundant mesograzers dominated by scraping, microphagous gastropods (*Littorina littorea* L. and *Littorina saxatilis* Olivi) and different partly omnivorous and detritivorous amphipods and isopods, such as *Gammarus* spp., *Microdeutopus gryllotalpa* Costa and *Idothea* spp. Predators are numerically dominated by the omnivorous green crab *Carcinus maenas* L., and the decapod shrimp *Palaemon adspersus* Rathke.

2.2. Experimental design

The experiment was designed in a factorial combination of shading, nutrient enrichment and habitat complexity treatments. The 36 experimental plots were arranged in three randomized blocks parallel to the shore line, each block containing one replicate of all possible combinations of treatment factors (three levels of habitat complexity × two light levels × two nutrient levels) (Eriksson et al., 2006a). The plots were placed at approximately 1 m depth, thus always covered by water, and separated by at least 3 m to avoid interactions and guarantee independence of the plots, especially in terms of nutrient enrichment. The rocks for the habitat complexity treatment were flat granite stones collected from shallow water shortly before the start of the experiment, in March 2004 (average area available for growth was 0.065 m^2; approximating a length of 0.2 m, width of 0.15 and height of 0.05 m). For the high habitat complexity level, stones were selected that were covered by a dense canopy of adult *Fucus* (0.3–0.4 m in length). The canopy-covered stones were chosen carefully to minimize differences in canopy biomass at the start of the experiment (average canopy biomass was 82 g dry weight), and then randomly placed into the different nutrient and shading treatments (see below). The stones used for the other habitat complexity treatments were bare of macroscopic vegetation and visible fauna, and half of these were heat sterilized at 100° to remove the microscopic propagule bank. Thus a third of the plots (12 plots) contained stones covered by a dense *Fucus* canopy (hereafter identified as canopy presence), another 12 plots contained stones with a microscopic propagule bank but without a *Fucus* canopy (hereafter identified as propagule presence), and another 12 plots received sterile stones without microscopic propagules and without a *Fucus* canopy (no habitat complexity, hereafter identified as sterile). These stones also served as experimental units for colonization of benthic invertebrates. To test treatment effects on benthic microalgal colonization, we added sterile unglazed ceramic tiles (5 cm × 5 cm) glued on a brick