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Eriksson, Britas Klemens; Rubach, Anja; Hillebrand, Helmut

Published in:
 Ecology

DOI:
[10.1890/05-0090](https://doi.org/10.1890/05-0090)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2006

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Eriksson, B. K., Rubach, A., & Hillebrand, H. (2006). Biotic Habitat Complexity Controls Species Diversity and Nutrient Effects on Net Biomass Production. *Ecology*, *87*(1), 246-254. <https://doi.org/10.1890/05-0090>

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BIOTIC HABITAT COMPLEXITY CONTROLS SPECIES DIVERSITY AND NUTRIENT EFFECTS ON NET BIOMASS PRODUCTION

BRITAS KLEMENS ERIKSSON,¹ ANJA RUBACH, AND HELMUT HILLEBRAND

Institute for Botany, University of Cologne, Gyrhofstrasse 15, D-50931 Köln, Germany

Abstract. Canopy-forming plants and algae commonly contribute to spatial variation in habitat complexity for associated organisms and thereby create a biotic patchiness of communities. In this study, we tested for interaction effects between biotic habitat complexity and resource availability on net biomass production and species diversity of understory macroalgae by factorial field manipulations of light, nutrients, and algal canopy cover in a subtidal rocky-shore community. Presence of algal canopy cover and/or artificial shadings limited net biomass production and facilitated species diversity. Artificial shadings reduced light to levels similar to those under canopy cover, and net biomass production was significantly and positively correlated to light availability. Considering the comparable and dependent experimental effects from shadings and canopy cover, the results strongly suggest that canopy cover controlled net biomass production and species diversity by limiting light and thereby limiting resource availability for community production. Canopy cover also controlled experimental nutrient effects by preventing a significant increase in net biomass production from nutrient enrichment recorded in ambient light (no shading). Changes in species diversity were mediated by changes in species dominance patterns and species evenness, where canopy cover and shadings facilitated slow-growing crust-forming species and suppressed spatial dominance by *Fucus vesiculosus*, which was the main contributor to net production of algal biomass. The demonstrated impacts of biotic habitat complexity on biomass production and local diversity contribute significantly to understanding the importance of functionally important species and biodiversity for ecosystem processes. In particular, this study demonstrates how loss of a dominant species and decreased habitat complexity change the response of the remaining assembly to resource loading. This is of potential significance for marine conservation since resource loading often promotes low habitat complexity and canopy species are among the first groups lost in degraded aquatic systems.

Key words: *Baltic Sea; biodiversity; canopy cover; coastal ecosystems; ecosystem function; eutrophication; Fucus vesiculosus; macroalgae; marine diversity; subtidal ecology.*

INTRODUCTION

Multivariate approaches to biodiversity show convincing evidence that interacting effects on net production by availability of limiting resources and mortality-inducing disturbances control local diversity (Proulx and Mazumder 1998, Worm et al. 2002). However, few experiments acknowledge that net production also depends on local patchiness of natural communities where biotic habitat complexity and species identities have consequences for local community processes and species interactions (e. g., Jones et al. 1997, Bertness et al. 1999, Bruno et al. 2003). Habitats with high complexity often support higher abundances and diversity of species than less complex neighboring habitats (Heck and Wetstone 1977, Levin and Hay 1996, Thompson et al. 1996). Habitat complexity also influences interactions closely linked to diversity processes,

such as consumption and competition (Heck and Orth 1980, Crowder and Cooper 1982, Diehl 1992).

Canopy-forming species are globally common and important components of habitat complexity because of their often-massive and persistent structures that create variation in resources and thereby influence the distribution of associated species (Dayton 1975, Jones et al. 1997, Jenkins et al. 1999a). An important habitat-modifying property of canopy-forming species is to produce shaded habitat (Jones et al. 1997). The importance of resources for local diversity processes is well recognized, but most experimental diversity studies only consider nutrients as a measure of resource availability (Harley 2002). In many ecosystems, light should be an equally important driving force for primary production (Hill 1996), and light and nutrient availability might also promote strong interactions with grazing since they set different constraints on plant growth (Hillebrand 2005).

On canopy-dominated rocky shores, community structure is determined by disturbances and physical stresses such as grazing, wave exposure, sediment

Manuscript received 21 January 2005; revised 13 May 2005; accepted 27 June 2005. Corresponding Editor: P. D. Steinberg.

¹ E-mail: klemens@ecology.su.se

loads, and air exposure, and by resources such as light, nutrients, and space availability (e. g., Connell 1961, Lubchenco 1983, Schiel and Foster 1986). All these factors are differently influenced by algal canopy cover (reviewed by Bruno and Bertness [2001]). For example, algal canopies increase the mortality of understory organisms from wave exposure by whiplash (Dayton 1975, Hawkins 1983), reduce flow velocity that can increase sediment accumulation and limit space availability, but also enhance propagule retention (Duggins et al. 1990), and reduce physical stresses from high temperatures and desiccation, which facilitate understory recruitment and growth (Bertness et al. 1999). Canopy algae can also attract grazers by providing food, shelter, and protection (e. g., Duffy and Hay 1991, Vadas and Elner 1992), and enclosure experiments indicate that algal canopy cover interacts with grazer effects on algal community structure (Jenkins et al. 1999b). Thus, algal canopy cover may generate strong interaction effects with both local productivity potential and mortality-inducing disturbances. This is supported by many canopy-removal experiments that show significant influences of algal canopy cover on understory species composition and richness (e. g., Dayton 1975, Clark et al. 2004).

In this study we test for interaction effects between resource availability and increased habitat complexity by canopy cover on net biomass production and species diversity of understory macroalgae in a subtidal rocky-shore community. Rocky subtidal communities are patchy, with considerable variation in the abundance of habitat-modifying species (Witman and Dayton 2001). Differences in processes between habitats with or without canopy cover are therefore a natural part of subtidal community dynamics. In the present study area, macroalgal diversity decreases with increased production, and the development of macroalgal cover is strongly enhanced by joint effects of nutrients and overwintering propagules (Lotze et al. 2000, Worm et al. 2001). Thus, depending on nutrient conditions, habitat complexity may interact with community production, both by canopy cover modifying light availability and by propagules enhancing growth rates. Factorial field manipulations of biotic habitat complexity (canopy cover and propagules present or only propagules present or sterile substrates), nutrients (ambient or enriched) and light (ambient or shaded), allowed us to test the following hypotheses: (1) Presence of overwintering propagules (compared with sterile substrates) and nutrient enrichment increase net biomass production and decrease species diversity. (2) Artificial shadings control net biomass production and regulate species diversity. (3) High habitat complexity (canopy cover) limits light availability, controls net biomass production, and regulates species diversity. (4) Effects on net biomass production and species diversity by high habitat complexity and artificial shading are comparable and interdependent (interact), indicating that ef-

fects of habitat complexity on net biomass production and species diversity are generated by limiting light penetration and thereby limiting resource availability.

METHODS

Experimental site

The experiment was performed in a shallow and non-tidal bay at Maasholm in the outer Schlei Fjord (54°41' N, 10°0' E), western Baltic Sea. The macroalgal community grows on numerous stones scattered over a sandy bottom and is dominated by a canopy-forming fucoid, *Fucus vesiculosus* L. (hereafter *Fucus*) that cover ~80% of stone surfaces. The understory consists of 7–9 common macroalgal species, both crusts (mainly *Hildenbrandia rubra* [Sommerf.] Menegh.) and ephemerals (mainly *Ceramium strictum* Harvey, *Enteromorpha* spp., and *Pylaiella littoralis* [L.] Kjellman) with large interannual variations (for detailed species list see Worm et al. [2001]). Salinity (on the practical salinity scale) normally ranges between 12 and 18 in summer and 14 and 20 in winter. Anthropogenic input of nutrients is high and algal production can be up to 5 kg C dry mass·m⁻²·yr⁻¹ (Worm et al. 2002). During the study the nutrient concentrations in plots with ambient nutrient conditions (no enrichment, see below) were 1.46 ± 0.15 and 2.28 ± 0.17 μmol/L [mean ± SE] dissolved inorganic nitrogen (DIN), and 0.38 ± 0.06 and 0.77 ± 0.06 μmol/L phosphate in June and August, respectively. The study site is sheltered from wave action (maximum fetch = 5 km) and water levels fluctuate with an amplitude of ±0.5 m around the mean depending on prevailing winds (Worm et al. 2001).

Field experiment

The experiment was designed in a factorial combination of biotic habitat complexity (three levels), nutrient enrichment, and shading (Fig. 1). Experimental plots were placed at ~1 m depth in three randomized blocks, each block containing all possible combinations of treatment factors, which gave 36 plots in total (three levels of habitat complexity × two nutrient levels × two light levels × three replicates). All plots were separated by at least 3 m and blocks arranged next to each other along the shore. As experimental sampling substrate we used flat natural granite stones (top area ~15 × 20 cm) without macroscopic vegetation that were collected from 0–0.5 m depth at the start of the experiment. The experiment was run from March to August 2004.

Biotic complexity was manipulated by moving stones with adult *Fucus* to create canopies above the sampling stones from a third of the plots. The *Fucus* stones were smaller than the sampling stones to avoid creating significant rock barriers for water movement. Sampling stones from another third of the plots were heat sterilized at 100°C to remove all overwintering propagules on the surfaces, and the last third of the

a) Experimental design

Sterile substrates (no propagules)				Substrates with propagule bank				Canopy cover (with propagule bank)			
Shade		Ambient light		Shade		Ambient light		Shade		Ambient light	
A	E	A	E	A	E	A	E	A	E	A	E

b) Experimental setup

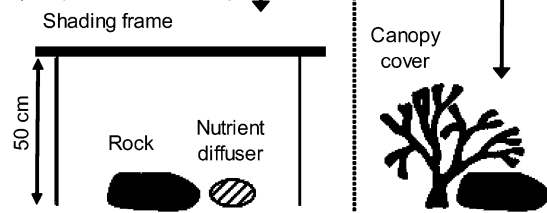


FIG. 1. Schematic of the field experiment performed in a shallow, nontidal bay, at Maasholm in the western Baltic Sea. (a) Experimental design of the factorial field experiment testing for interactions between biotic habitat complexity (manipulating presence of overwintering propagules and canopy cover), light availability ("shade," presence of shading frames; "ambient light," no shading frames), and nutrient availability (A, ambient nutrients; E, nutrient-enriched). Each block of 12 treatment combinations was replicated three times in a randomized-block design ($n = 36$ plots). (b) Examples of two different treatment combinations in the experimental setup; types are indicated by arrows.

sampling stones were left unmanipulated. Thus, twelve of the plots contained experimental substrates with the microscopic community of overwintering propagules intact and canopy cover present (high habitat complexity), 12 plots contained experimental substrates with propagules but no canopy cover (low habitat complexity), and 12 plots contained sterile substrates and no canopy cover (no habitat complexity). This enabled us to compare earlier-described effects of propagules (by comparing pre-seeded vs. sterile substrates; Lotze et al. 2000, Worm et al. 2001) with effects of canopy cover.

Nutrients were manipulated by supplying 60 g of slow-release NPK fertilizer pellets (Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany) to half of the plots (enriched vs. ambient nutrients) following the method described in Worm et al. (2000). Pellets were sewn into plastic net bags, which were changed every 6 to 7 weeks. This method has proved successful in increasing water nutrient concentrations and subsequent biomass production in a number of different habitats (e. g., Hillebrand et al. 2002, Worm et al. 2002, Russell and Connell 2005). Worm et al. (2000) tested the method for predictability in the study area and demonstrated independent nutrient-treatment effects for plots separated by 2 m with enrichment levels up to 320 g, suggesting minimal spillover effects between plots in our experiment (separated >3 m). To control

treatment levels we took water samples from all plots in June and August. Samples were immediately frozen and later analyzed for NO_3^- , NO_2^- , NH_4^+ , and PO_4^{3-} .

Light was manipulated placing separate shading frames over half of the plots (shaded vs. ambient light). The 18 shadings consisted of 0.5×0.5 m wide wooden frames standing on thin steel legs 0.5 m over the bottom. The wooden frames were covered by 0.5-mm-thick black PVC plastic (pond foil) separated in two overlapping pieces to allow water flow-through. To monitor effects of the frames on water circulation at the bottom we used dissolution blocks that dissolve in proportional rate to water flux, following the method described by Harley (2002). The blocks were made of ~ 41 g Lightweight Hydrocal (Woodland Scenics, Linn Creek, Missouri, USA) that had set around a pin in a film-canister box and were applied for two days to all plots without canopy cover. Light was monitored using a Li192 SA flat sensor connected to a Li-1000 data logger (LI-COR Biosciences, Lincoln, Nebraska, USA).

Data collection and analyses

Every month we estimated the cover of all species on the sampling stone in each plot using a 10×15 cm plexiglas sheet with 50 random dots, excluding canopy cover when present (only present in the canopy-cover treatment). In August we brought the sampling stones to the laboratory and carefully scraped off all the vegetation within the 10×15 cm area. Dry mass of all algae was determined after drying at 80°C for 48 h. Species diversity was calculated from the cover data using the Shannon–Wiener index (H'), which is sensitive to diversity changes in this species-poor habitat (total number of recorded species in the plots = 9 species; Worm et al. 2002). Cover and diversity data were analyzed by repeated measures ANOVA, with habitat complexity, nutrient, and light treatments as three orthogonal fixed factors with repeated measures. Biomass data were analyzed by factorial ANOVA. The block factor was never significant and therefore is excluded from all analyses. Homogeneity of variances was tested with Cochran's test. Cover data were arc-sine transformed and biomass data log transformed when necessary.

RESULTS

The shading frames reduced light strongly on sterile substrates and substrates with propagules, but not in the canopy-cover treatment (significant main and interaction effects in factorial ANOVA of light and habitat complexity on instant light values from block 1 and 2 during a sunny day in August, $n = 24$ plots, $P < 0.027$) (Fig. 2). The level of light reduction from shading frames and canopy cover was similar; there was no significant difference in incident light between shaded plots in any habitat-complexity treatment and plots in ambient light with canopy cover (Tukey's HSD post

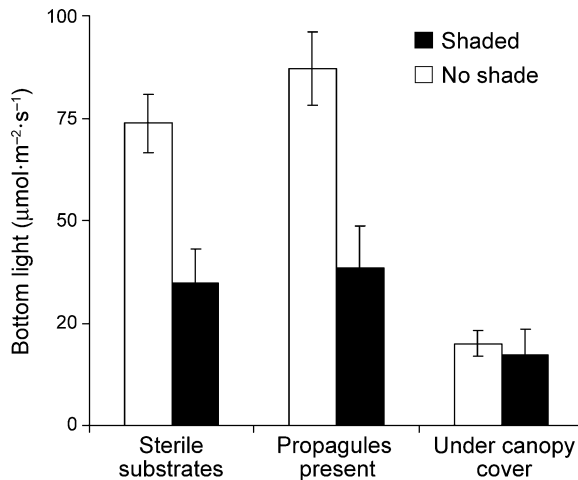


FIG. 2. Bottom light under shading frames compared to ambient light (no shading frames) in the different habitat-complexity treatments (block 1 and 2, $n = 4$ plots for each treatment combination). Data are means \pm SE.

hoc test; $P > 0.40$). The shading frames did not significantly influence water flux on the bottom, judged by percentage mass loss from the dissolution blocks: $22.7 \pm 2.7\%$ (mean \pm SE) per day for shaded blocks and $20.0 \pm 1.8\%$ per day for unshaded blocks (t test; $df = 14$, $t = 0.82$, $P = 0.30$).

Water-column nutrient concentrations of both dissolved inorganic nitrogen (DIN) and phosphate showed strong trends toward statistically significant increases by the nutrient-enrichment treatment: increases of 21.6 and 44.8%, respectively, compared to plots with ambient nutrient conditions (repeated-measures ANOVA of June and August values, main effect of nutrient enrichment, $n = 36$ plots, $P = 0.064$ for DIN and $P = 0.072$ for phosphate). Treatment effects were comparable to predicted values from Worm et al. (2000) and absolute values were well within ambient summer concentrations reported from the study area.

Total net biomass production depended strongly on interactions among habitat complexity, shade, and nutrient enrichment (Table 1). Propagule presence (with-

out canopy cover) strongly enhanced net biomass production in ambient light compared with both sterile substrates and substrates under canopy cover and/or artificial shades (Fig. 3). Net biomass production was also strongly enhanced by nutrients on substrates with propagules, but this effect was eliminated both by presence of canopy cover and/or shades (Fig. 3). The significant experimental effects on total biomass demonstrate that canopy cover and shade limited the rate of net biomass production in the experiment and thereby controlled increases in biomass accumulation generated by nutrients and propagules. Effects of canopy cover and shade were also highly dependent, showing a statistically significant interaction (Table 1). In accordance with the limiting effects of shading, total biomass was linearly correlated with available light (Pearson product-moment correlation using instant light values from block 1 and 2, $n = 24$ plots, $r = 0.67$, $P < 0.001$) but not to nutrient availability ($n = 36$ plots, $P > 0.50$).

Juvenile *Fucus* completely dominated erect biomass on the sampling stones ($96.8 \pm 6.1\%$ of total biomass [mean \pm SD]) and mirrored net production of total biomass (Table 1, Fig. 3). All other commonly occurring erect algae consisted of different ephemerals. Ephemeral biomass was about 75% higher in the propagule treatment (no canopy cover) compared to the sterile treatment, 0.59 ± 0.23 g dry mass (DM)/m² and 0.33 ± 0.09 g DM/m² (mean \pm SE), respectively, an increase that was eliminated by both canopy cover and/or shade generating a trend towards a shade \times habitat complexity interaction (Table 1).

The trajectory of species diversity (H') with time depended strongly on interactions between habitat complexity and shade (significant habitat complexity \times shade \times time interaction, Table 2). Canopy cover and/or shades strongly enhanced the development of species diversity on substrates with propagules (Fig. 4). Species diversity on sterile substrates developed to similar levels as on propagule substrates with canopy cover and/or shades, and was independent of light treatments (Fig. 4). This shows that the same treatment

TABLE 1. Results of ANOVA: effects of shading, nutrient enrichment, and biotic habitat complexity on net biomass production of macroalgae.

Effect	df	Total biomass of all algae		<i>Fucus vesiculosus</i>		Ephemeral algae	
		F	P	F	P	F	P
Shading, S	1	26.12	<0.001	25.97	<0.001	5.48	<0.01
Nutrient enrichment, N	1	0.77	0.390	0.77	0.389	0.01	0.929
Habitat complexity, C [†]	2	15.64	<0.001	15.55	<0.001	5.03	<0.01
S \times N	1	0.87	0.361	0.88	0.359	0.82	0.375
S \times C	2	11.55	<0.001	11.48	<0.001	2.58	0.096
N \times C	2	2.75	0.084	2.75	0.084	0.58	0.567
S \times N \times C	2	3.45	<0.05	3.44	<0.05	0.53	0.595
Error	24						

[†] Canopy cover and propagules present, propagules present, or sterile substrates.

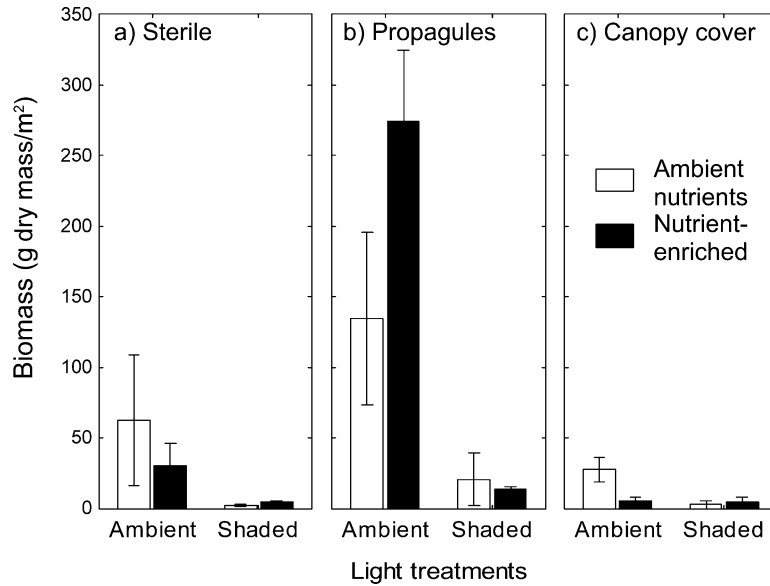


FIG. 3. Net production of macroalgal biomass from March to August on (a) sterile substrates, (b) substrates with overwintering propagules present, and (c) substrates with propagules subjected to canopy cover, for light treatments (under shading frames [shaded] or not [ambient]), and nutrient treatments (nutrient-enriched or not [ambient]). Data are means \pm SE.

combination that significantly enhanced net biomass production, propagule presence in full light (no canopy cover and no shadings), also generated negative experimental effects on species diversity.

Changes in species diversity were paralleled by changes in species dominance patterns. On stones with propagules, *Fucus* cover increased sharply from 1–2% in May to almost 80% in August, but this increase was strongly limited by canopy cover and/or shades (sig-

nificant habitat complexity \times shade \times time interaction, Table 2, Fig. 5). The increase in *Fucus* cover was also present on sterile stones in ambient light, but started later and reached \sim 40% in August. In contrast, two species of crusts (*Hildenbrandia rubra* and *Pseudolithoderma* spp.) were facilitated by shade and/or canopy cover. Crust algae increased continuously with time on stones with propagules, except in full light (no canopy cover and no shadings) where covers were about 4

TABLE 2. Results of repeated-measures ANOVA: effects of shading (*S*), nutrient enrichment (*N*), and biotic habitat complexity (*C*) on species diversity (Shannon-Wiener index) and cover of macroalgae.

Effect	df	Shannon-Wiener Index, H'		<i>Fucus vesiculosus</i>		Crust algae		Ephemeral algae	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Between plots									
<i>S</i>	1	1.14	0.297	10.00	<0.01	1.52	0.229	0.19	0.668
<i>N</i>	1	0.53	0.473	0.33	0.571	0.98	0.332	0.09	0.771
<i>C</i>	2	10.35	<0.001	4.93	<0.05	22.21	<0.001	5.32	<0.05
<i>S</i> \times <i>N</i>	1	0.71	0.408	0.23	0.636	2.06	0.164	0.05	0.833
<i>S</i> \times <i>C</i>	2	0.73	0.493	2.48	0.105	4.21	<0.05	0.14	0.872
<i>N</i> \times <i>C</i>	2	0.80	0.460	0.38	0.687	0.17	0.841	0.66	0.525
<i>S</i> \times <i>N</i> \times <i>C</i>	2	0.07	0.934	0.45	0.642	1.39	0.268	0.71	0.504
Error	24								
Within plots									
Time, <i>T</i>	5	25.44	<0.001	104.42	<0.001	26.52	<0.001	11.92	<0.001
<i>T</i> \times <i>S</i>	5	1.11	0.356	17.61	<0.001	0.10	0.982	1.01	0.418
<i>T</i> \times <i>N</i>	5	0.54	0.747	0.32	0.901	0.46	0.767	0.20	0.961
<i>T</i> \times <i>C</i>	10	4.56	<0.001	13.71	<0.001	1.48	0.173	6.19	<0.001
<i>T</i> \times <i>S</i> \times <i>N</i>	5	1.30	0.268	0.45	0.815	0.03	0.998	0.20	0.963
<i>T</i> \times <i>S</i> \times <i>C</i>	10	2.46	<0.05	2.86	<0.01	1.25	0.280	0.79	0.638
<i>T</i> \times <i>N</i> \times <i>C</i>	10	0.32	0.976	0.73	0.697	0.84	0.568	0.68	0.744
<i>T</i> \times <i>S</i> \times <i>N</i> \times <i>C</i>	10	0.49	0.891	1.04	0.413	0.81	0.595	0.39	0.949
Error	120								

Note: Habitat complexity is measured as canopy cover and propagules present, propagules present or sterile substrates.

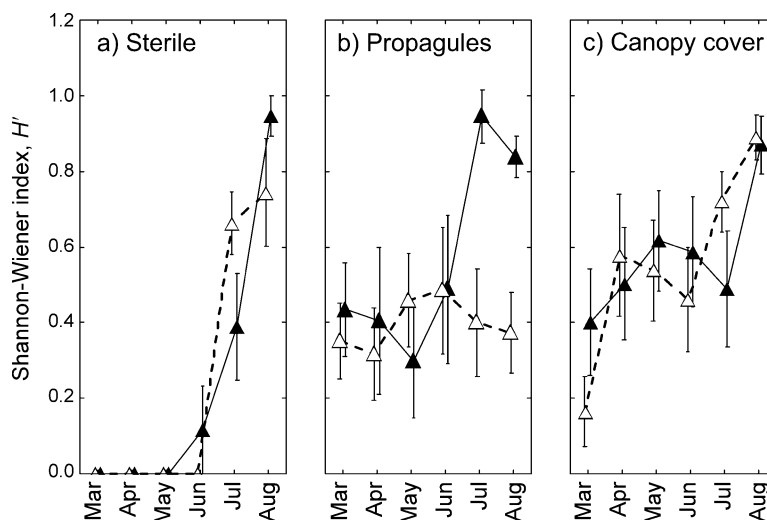


FIG. 4. Species diversity, H' , over time on (a) sterile substrates, (b) substrates with overwintering propagules present, and (c) substrates with propagules subjected to canopy cover, for light treatments: under shading frames (solid symbols) or not (open symbols). Data are means \pm SE.

times lower and similar to covers in the sterile treatments (significant main factor time and a shading \times habitat complexity interaction, Table 2, Fig. 5). Cover of ephemeral algae displayed a significant time \times habitat complexity interaction that depended on large abundances of sheet-like ephemerals (*Monostroma grevillei* [Thuret] Wittrock) on stones with propagules during early samples that were absent in the sterile treatment and diminished with time (Table 2).

DISCUSSION

Our experiments revealed strong impacts of light and habitat complexity on net biomass production and species diversity of understory macroalgae. Without canopy cover in ambient light conditions, overwintering propagules increased biomass accumulation and decreased species diversity significantly compared to sterile substrates. As described by Worm et al. (2001) for the development of algal covers, nutrient enrichment also generated strong enhancing effects on net biomass production in this treatment combination (no canopy cover \times ambient light \times propagules present—partly supporting hypothesis 1, which states that presence of propagules and nutrient enrichment increases net biomass production and decreases species diversity). No effects of nutrient enrichment on species diversity were detected in this study. High habitat complexity (canopy cover) and shade generated similar experimental effects by decreasing available light, limiting net biomass production, and facilitating species diversity, as well as eliminating the propagation of nutrient effects on biomass accumulation detected on substrates with propagules in ambient light (supporting hypotheses 2 and 3, which state that high habitat complexity and artificial shading control net biomass production and regulate species diversity). High habitat

complexity and artificial shade also had similar effects on species covers and changed species-dominance patterns by facilitating crust-forming species and suppressing spatial dominance of *Fucus*. Finally, habitat complexity and artificial shade generated statistically significant interaction effects on biomass, species diversity, and dominant species covers (supporting hypothesis 4, which states that effects on net biomass production and species diversity by high habitat complexity and artificial shading are comparable and interdependent). Net biomass production was positively and significantly correlated to light availability, and earlier studies have demonstrated that community production and species diversity are closely inversely related in the study area (Worm et al. 2002). Thus, the results strongly suggest that high habitat complexity generated by canopy cover controlled declines in species diversity by limiting light and consequently limiting resources for biomass production.

Negative effects of propagules on species diversity at ambient light and no canopy cover were confirmed, but species patterns differed strongly from those reported by Worm et al. (2001); they found decreased abundance of *Fucus* by low recruitment success and dominance of ephemeral algae in the presence of propagules. During our present study, ephemeral cover was strongly favored by propagule presence but ephemeral cover during *Fucus* recruitment in April–May was comparatively low ($\sim 6\%$ compared with $\sim 30\%$ reported from the field area in 1997; Lotze et al. 2000, Worm et al. 2001). *Fucus* increased to dominate on all stones in ambient light, but significant increases in cover started a month later on sterile stones compared to stones with propagules. This supports the idea that algal propagules are important for population dynamics by accelerating the rate of recruitment and enabling an

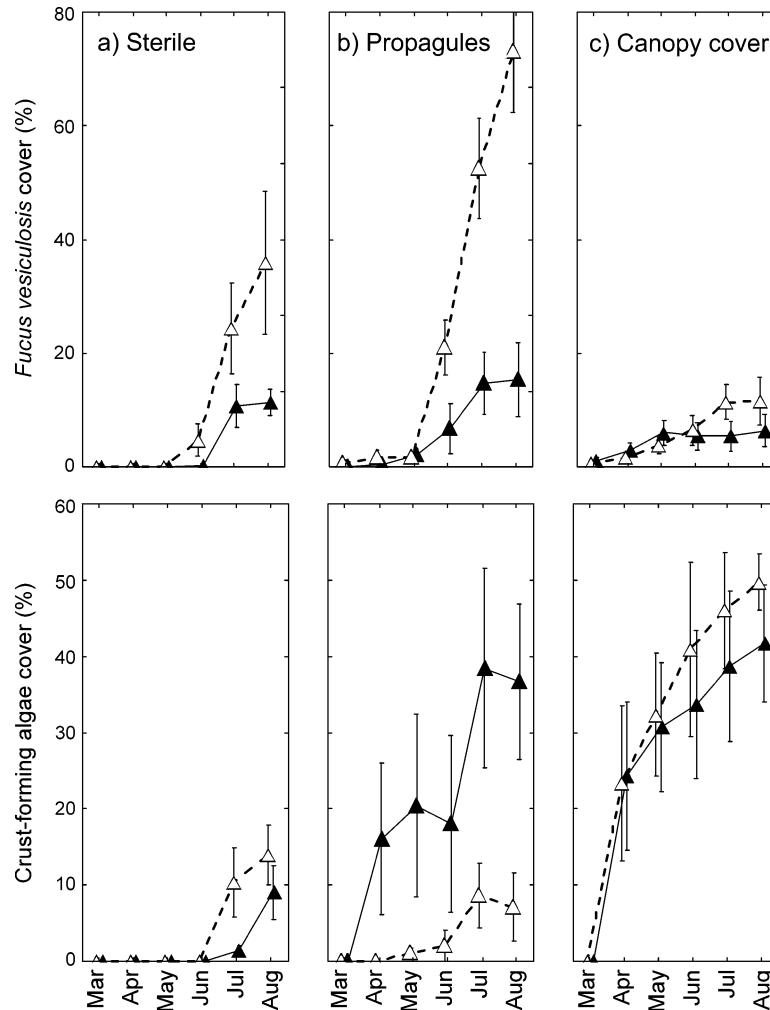


FIG. 5. Percent cover of *Fucus vesiculosus* (upper panels) and crust-forming algae (lower panels) over time on (a) sterile substrates, (b) substrates with overwintering propagules present, and (c) substrates with propagules subjected to canopy cover, for light treatments: under shading frames (solid symbols) or not (open symbols). Data are means \pm SE.

earlier onset of biomass accumulation after winter dormancy (Lotze et al. 2000).

Both high biotic habitat complexity and shading suppressed spatial dominance by *Fucus* and favored the development of macroalgal crusts, thereby increasing evenness of species covers and facilitating species diversity. Crusts are slow-growing stress-tolerant species that proliferate in both areas of high disturbance and/or low productivity, and generally benefit from grazing (Bertness et al. 1983, Steneck and Dethier 1994). They are poor competitors that are easily overgrown, but can survive overgrowth remarkably well (Airoldi 2000). On our stones with a high rate of biomass production, the cover of crusts did not decrease with time by overgrowth but were constrained by decreased growth rate (spatial extension) in the presence of a high number of *Fucus* individuals. The combination of life-history traits of crusts indicates that the facilitation under canopy cover could be mediated by both: (1) increased

disturbance increasing *Fucus* mortality while disturbance-tolerant crusts persist and/or (2) decreased resource availability decreasing the rate of biomass production, suppressing competitive dominance by *Fucus*, and allowing a higher presence of less productive algal crusts.

Disturbances from whiplash and sediment scour were probably minor since exposure is low at the field site, but subtidal recruitment of *Fucus* has been shown susceptible to pre-emptying of space by sediment covering the substrate (Eriksson and Johansson 2003). We detected no significant effects on water flux from the shading frames, but sediment load was high and canopies may have trapped resuspended sediment. Disturbance by grazing is a major determinant of biomass and species diversity in the field area (Lotze et al. 2000, Worm et al. 2001), and algal grazers may be attracted to both increased structural complexity and shade (e.g., Burnaford 2004). The major grazers on *Fucus* in

the field area, isopods of the genus *Idotea* spp. (Worm et al. 2001), were rarely found during the course of the experiment (~5 individuals/m²; A. Rubach, *unpublished data*). However, the snail *Littorina littorea* L. that commonly grazes on fucoid germlings and facilitates crusts by limiting overgrowth was abundant (98 individuals/m², A. Rubach, *unpublished data*) (Bertness et al. 1983, Lubchenco 1983). This suggests that part of the lower cover of *Fucus* under canopy cover and shadings potentially could be caused by decreased recruitment, either from increased sedimentation or increased grazer presence. However, separate experiments at the field site showed decreased density of *Fucus* juveniles under canopy cover, but increased density under shades (B. K. Eriksson, *unpublished data*), indicating that effects on net biomass by differences in recruitment should be independent and different between canopy cover and shadings. Considering the dependent and similar effects on biomass, the main effect on species composition was most probably caused by limiting the availability of light and thereby constraining the rate of biomass production. Associated changes of light availability and algal understory species composition on rocky shores have been demonstrated both in artificial shading and canopy-removal experiments (Harley 2002, Clark et al. 2004).

By regulating light and controlling the propagation of nutrient effects, habitat complexity determines the importance of different limiting resources for community production in this system. The proportion of a community that is limited by light or nutrients can have large consequences for ecosystem functioning and resistance to changes in habitat conditions. Firstly, the composition of primary resources (light/nutrient ratio) is likely to have strong effects on organic-matter transfer through trophic levels. Algal resource composition should for example affect algal grazers by the quality (carbon/nitrogen ratio) of algal tissue as food and thereby indirectly affect trophic processes like magnitude of grazing (Urabe et al. 2002). Harley (2002) described a reduction in grazer abundances mediated by changes in algal species composition from limiting light. In aquatic ecosystems both resource availability and grazing rates determine the direction of trophic control (bottom up or top down) of community biomass and structure (Menge 2000, Hillebrand et al. 2002, Worm et al. 2002, Thompson et al. 2004). Changes in resource composition can therefore have additional strong effects on ecosystem function that are mediated by changed grazing rates.

Secondly, by constraining effects of nutrient enrichment on production, high community complexity should increase the resistance of the community to eutrophication. That established communities of canopy algae may prevent or delay effects of nutrient loading was suggested by Bokn et al. (2003), who found limited impacts of nutrient enrichment on primary productivity in fucoid-dominated mesocosms. Accordingly, Russell

and Connell (2005) demonstrated interacting effects between canopy cover and experimental nutrient enrichment on the composition of an understory algal assembly. However, coastal eutrophication is commonly reported to promote low community complexity by reducing the abundance of habitat-forming perennial species such as fucoids, kelps, and seagrasses (Cloern 2001). Although we found no effects of nutrient enrichment on *Fucus* in this study, earlier experiments at the field site have documented significant decreases in the abundance of *Fucus* from nutrient enrichment (Worm et al. 2001). Many other studies suggest that long-term eutrophication also promotes low habitat complexity in the Baltic Sea and demonstrate negative effects on fucoid recruitment both directly from increased nutrient concentrations and indirectly from related processes, such as increased sedimentation and competition from ephemerals (Eriksson and Johansson 2003, Berger et al. 2004). Our results suggest that when nutrient loading decreases the abundance of canopy algae, light limitation decreases in favor of nutrient limitation, which would further enhance effects of nutrient enrichment on the community. Thus, by promoting low community complexity eutrophication may generate self-accelerating cycles.

In conclusion, the demonstrated impact of biotic habitat complexity for biomass production and local diversity contributes significantly to understanding the importance of functionally important species for biodiversity effects on ecosystem function. In particular, the results support the idea that species identity and the contribution to habitat-patch diversity is more important for ecosystem processes than species diversity in coastal ecosystems (see Giller et al. 2004). The results also demonstrate an earlier unappreciated role of light limitation from shading by canopy cover controlling the propagation of nutrient effects.

ACKNOWLEDGMENTS

This study was supported by a post-doctoral grant from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, Formas, through contract 2003-0275 (B. K. Eriksson). We thank the Leibniz Institute for Marine Sciences for access to the field station in Maasholm, T. Hansen for nutrient analyses, W. Schramm for help in the field, P. Plantman for art-work, and P. Steinberg and two anonymous referees for valuable comments on the manuscript.

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