Abstract We hypothesized that supply from macroalgal propagule banks may influence the relative abundance of annual and perennial algae and that this may alter the effects of grazers and nutrients on species composition. In a factorial field experiment in the Baltic Sea littoral system we tested the effects of manipulating propagule banks, the abundance of crustacean and gastropod grazers, and nutrient supply on recruitment and growth of macroalgae over a year. Moreover, we determined seasonal patterns of macroalgal propagule dispersal at the experimental site and quantified algal abundance and recruitment at 25 locations throughout the Baltic Sea. Experimental manipulations had minor effects on adults of the dominating perennial alga, *Fucus vesiculosus*. Instead, we found that species composition was determined by processes operating at early life stages. Propagule supply from a propagule bank strongly favored the fast-growing annual alga *Enteromorpha* spp. which then blocked settlement and recruitment of *Fucus*. Grazers reduced the abundance of annual algae and indirectly favored *Fucus* recruitment. There was an apparent tradeoff between gains from the propagule bank and losses to herbivory in five of seven colonizing species. Nutrient enrichment overrode grazer control of annual algae and accelerated the decline of *Fucus* only when annual algae had already achieved high densities through the propagule bank. Corroborating the experimental findings, field surveys across the Baltic showed that *Fucus* recruit densities can be predicted from the cover of annual algae during the period of *Fucus* reproduction and settlement. Recruitment inhibition by annual algae, which is driven by the abundance of annuals in the propagule bank, increasing nutrient levels, and declining consumer control, is suggested as a mechanistic explanation of the current decline of perennial algae in the Baltic Sea.

Keywords Dormancy · Eutrophication · *Fucus vesiculosus* · Grazing · Nutrients

Introduction

Dispersal and dormancy of propagules are critical processes that contribute to the persistence of plant populations in a variable environment (Harper 1977). Dispersal reduces the risk of local extinction by spreading propagules spatially. Contrarily, investment into banks of dormant propagules can provide temporal escapes from adverse conditions. Although dormant propagule banks occur in all major habitats, they have mostly been studied in higher land plants (Leck et al. 1989; Fenner 1992). Among land plants, differential investment into the propagule bank is related to species life-history patterns: opportunistic annuals invest orders of magnitude more propagules into soil seed banks than most perennial species (Grime 1979) and have more persistent seeds than related perennials (Thompson et al. 1998). Such traits may translate into a competitive advantage for opportunistic annuals in frequently disturbed environments (ruderal strategy, Grime 1979), which has consequences for the structure of plant assemblages.

In the marine environment, macroalgal propagule banks have only recently been described in detail and little is known about the factors that determine their composition, density, and ecological role (Santelices et al. 1995; Lotze et al. 1999). These “banks of microscopic stages” (Chapman 1986) consist of settled spores, micro-recruits, or other microscopic forms which suspend growth when environmental conditions are unfavorable and can survive for up to 10 months (Hoffmann and Santelices 1991; Schories 1995). It is thought that macroalgal propagule banks are transient in a sense that they persist only for some months (e.g., through winter) until environmental conditions improve and all propagules
germinate or are lost to grazing or other sources of mortality (Lotze et al. 1999). Recently, it has been shown that bloom-forming annual algae use the propagule bank as an overwintering mechanism and as an important “seed source” for the annual spring bloom (Schorie 1995; Lotze et al. 1999, 2000), and that these blooms can interfere with the establishment of perennial algae (Worm et al. 2000a). In addition to propagule supply, nutrient availability and herbivory have strong effects on plant species composition in littoral communities (“bottom-up” versus “top-down” control, Menge 1992; Worm et al. 2000a). The responses of individual species to these forces are linked to life-history patterns: increasing nutrient supply tends to increase the dominance of fast-growing annuals, whereas increasing herbivore pressure favors well-defended perennials (Steneck and Dethier 1994; Duarte 1995; Worm et al. 2000a). However, these effects may rarely be independent, as herbivore effects can depend on nutrient supply (Proulx and Mazumder 1998) and the effects of nutrient enrichment can depend on herbivore abundance (Lotze et al. 2000; Worm et al. 2000a). Therefore we chose to study the effects of a propagule bank in combination with factorial manipulation of grazers and nutrient supply.

We hypothesized that the presence of a propagule bank increases the abundance of annual relative to perennial algae and that this may decrease the relative magnitude of reported strong impacts of grazers and resources on species composition in the Baltic littoral community (Worm et al. 2000a). Moreover, building on previous work from North America (Lubchenco 1986; Worm and Chapman 1996), we hypothesized that annual-perennial competition may be particularly intense at the recruitment stage, rather than at the adult stage. To test these hypotheses, we manipulated the presence of grazers and the propagule bank as well as nutrient supply in a factorial field experiment, monitoring algal recruitment and growth of adult algae. In order to relate patterns of macroalgal recruitment in the experiment to seasonal patterns of propagule supply, we also monitored settlement and recruitment of macroalgal propagules over a 2-year period. In order to test the generality of concepts that emerged from our small-scale field experiments, we conducted a large-scale field survey throughout the Baltic Sea where we quantified patterns of macroalgal abundance and recruitment.

Materials and methods

Study area and species

The experiments and observations were carried out at Maasholm, a shallow embayment which is part of a nature reserve in the outer Schlei Fjord (54°41′N, 10°0′E), western Baltic Sea, Germany. The study area is protected from severe wave action (maximum fetch is 5 km). Lunar tides are unimportant, compared with irregular wind-driven sea level changes with an amplitude of ±0.5 m around mean water level. Salinity fluctuates irregularly following water exchange with the more saline Kattegatt Sea and ranges between 12 and 18 PSU (practical salinity units) in summer and 14 and 20 PSU in winter. Formation of sea ice is common in January and February. Water temperature ranges between –1 and 4°C in winter and 16 and 25°C in summer. Like most regions of the Baltic Sea, the Schlei Fjord is eutrophicated by human activity. Winter concentrations at Maasholm reach 160 µmol l–1 nitrate, 12 µmol l–1 ammonium and 2 µmol l–1 phosphate from January to March (Schramm et al. 1996). From mid-May to mid-August, ammonium and nitrate are largely depleted and typically remain close to the detection limit (0.0–0.3 µmol l–1). Soluble reactive phosphate remains between 0.1–0.6 µmol l–1. In September, ammonium regeneration starts and nutrient concentrations rise rapidly throughout the fall.

In shallow water (0–1 m depth), rocks and boulders provide abundant substrate for seaweed colonization. From a previous study (Lotze et al. 1999), we knew that colonization by various species can either occur from new reproduction (dispersal), or from overwintering banks of microscopic stages (dormancy) which can be found on various substrata, most densely on rocks. The established hard-bottom community at our site is dominated by dense stands (84±7.3% cover on rocks, mean±1SE, n=10) of the perennial brown seaweed Fucus vesiculosus (simply called Fucus hereafter). A suite of annual macroalgae (species names listed in figures and tables, Results), benthic diatoms and benthic invertebrates (Mytilus edulis, Balanus improvisus, various hydroids and bryozoans) co-occur epilithically or epiphytically with Fucus. Important grazers such as urchins or limpets are absent from the Baltic but mesoherbivorous gastropods and crustaceans are common (species names and densities given in tables, Results).

Monitoring of settlement

We applied a recently developed monitoring technique in order to obtain a qualitative estimate of seasonal patterns of propagule dispersal and settlement at the experimental site (Kiirikki and Leho 1997). Propagule settlement was estimated from observations of a sequence of settlement substrata (concrete blocks) which were submerged at discrete time intervals at the research site. Concrete is a suitable substratum for settlement of Baltic macroalgae (Kiirikki and Leho 1997). We exposed a sequence of 50 concrete blocks (30×30×5 cm) at intervals of 14 days (February–July 1997) or 10 d (August 1997–October 1998). One block per time interval was added to the sequence and installed adjacent to the cage experiment at 0.8 m water depth. Every 1–2 months, all blocks were inspected and average canopy height of each attached species was measured with a ruler in 0.5 cm intervals. In addition, percent cover of all attached species was estimated using a 25×25 cm plastic sheet with 50 random dots. Algal samples were obtained to verify species identification.

The beginning of a settlement period can be estimated by comparing the average canopy height of colonizing species over time: blocks which were exposed prior to the settlement period of a species are colonized simultaneously while the following blocks will be colonized in discrete time intervals according to the sequence of exposure. When these colonizing propagules grow into macroscopic recruits, plant height is similar among simultaneously colonized blocks and gradually declines throughout the following sequence of blocks. The last block that is colonized marks the end of the settlement period (Kiirikki and Leho 1997). Comparison of plant cover among blocks may allow a crude estimate of settlement intensity. When only single algae were visible (<2% cover) we classified this as “low settlement”, and higher abundance was classified as “high settlement”. This method allows only minimum estimates of the settlement period and settlement intensity of a species because it requires recruitment and growth of settled propagules to macroscopic germinals of at least 2–3 mm length. However, various factors (herbivory, competition, unfavorable abiotic conditions) can suppress recruitment of settled propagules to macroscopic stages (Vadas et al. 1992; Worm and Chapman 1998).