TURUN YLIOPISTON JULKAISUJA
ANNALES UNIVERSITATIS TURKUENSIS

SAR - SER AII OSA - TOM. 222

BIOLOGICA - GEOGRAPHICA - GEOLOGIA

Nutrient enrichment and water depth modify consumer control in rocky shore macroalgal communities

Samuli Korpinen

TURUN YLIOPISTO
TURKU 2008

Section of Ecology, Department of Biology
University of Turku
Turku, Finland

Supervised by:
Dr. Veijo Jormalainen
Section of Ecology, Department of Biology
University of Turku
Turku, Finland

Reviewed by:
Dr. Christoffer Boström
Miljö och Marinbiologi
Åbo Akademi University
Turku, Finland

Dr. Britas Klemens Eriksson
Department of Marine Benthic Ecology and Evolution
Biological Centre
University of Groningen
Netherlands

Examined by:
Prof. Helmut Hillebrand
Botanical Institute
University of Cologne
Germany

Cover image: The green alga *Cladophora glomerata*, the red alga *Ceramium tenuicorne*, and the blue mussel (*Mytilus trossulus*) on an exposed rocky shore in the Gulf of Finland. © Samuli Korpinen

ISBN 978-951-29-3530-7 (PRINT)
ISBN 978-951-29-3531-4 (PDF)
ISSN 0082-6979

Painosalama Oy - Turku, Finland 2008

To Riikka, my love.

Nutrient enrichment and water depth modify consumer control in rocky shore macroalgal communities

Samuli Korpinen

This thesis is based on the following papers, referred to in the text by their Roman numerals:

I Korpinen S, Jormalainen V & Honkanen T (2007) Effects of nutrients, herbivory, and depth on the macroalgal community in the rocky sublittoral. Ecology 88: 839-852.

II Korpinen S, Jormalainen V & Honkanen T (2007) Bottom–up and cascading top–down control of macroalgae along a depth gradient. Journal of Experimental Marine Biology and Ecology 343: 52-63.

III Korpinen S & Jormalainen V. Grazing effects in macroalgal communities depend on timing of patch colonization. *Submitted*.

IV Korpinen S, Jormalainen V & Ikonen J. Selective consumption and facilitation by mesograzers in adult and colonizing macroalgal assemblages. *Submitted*.

V Korpinen S & Jormalainen V. Grazing and nutrients reduce recruitment success of *Fucus vesiculosus* L. (Fucales: Phaeophyceae). Estuarine, Coastal and Shelf Science, in press.

ABSTRACT

Communities are often generalized as trophic chains of primary producers, herbivores and predators. The objective of my thesis is to assess mechanisms of ecological community control in macroalgal communities in the Baltic Sea. In the top-down model, predatory fish feed on invertebrate mesograzers, releasing algae partly from grazing pressure. Such a relationship is called trophic cascade. In the bottom-up model, nutrient availability determines primary production, thereby affecting biomass at all levels of the food chain. Previous studies have rarely assessed how these regulative mechanisms interact. Because the top-down and bottom-up mechanisms are predicted to depend on environmental disturbances, such as wave stress, and light availability, I have studied these models at two distinct water depths.

The thesis is based on five factorial field experiments, which were all conducted in the Finnish Archipelago Sea. In all the experiments, I studied macroalgal colonization - density, filament length or biomass - on submerged colonization substrates. By excluding predatory fish and/or mesograzers from the algal communities, the studies compared the strength of the top-down control on natural algal communities. A part of the experimental units were, in addition, exposed to enriched nitrogen and phosphorus concentrations, which enabled testing of bottom-up control. These two models of community control were further investigated in shallow (< 1 m) and deep (ca. 3 m) water. Moreover, the control mechanisms were also expected to depend on grazer species. Therefore, in two of the studies, different grazer species were enclosed into experimental units and their specific impacts on macroalgal communities were estimated.

The community control in the Baltic rocky shores was found to follow the general theoretical predictions, some of which have not been confirmed by empirical studies before. Predatory fish limited the impact of grazers on algae; algal communities were more dense and algal filaments longer when fish were present. Nutrient enrichment increased density and filament length of the annual algae and, thus, changed the species composition of the algal community. The brown alga *Fucus vesiculosus* and the red alga *Ceramium tenuicorne* suffered from the increased nutrient availability due to increased alga-alga competition. In general, the enriched nutrient conditions led to denser grazer fauna, thereby causing strong top-down control over both the annual and perennial macroalgae. The strength of the top-down control seemed to depend on the density and diversity of grazers and predators as well as on the structure of macroalgal assemblages. The nutrient enrichment, however, led to weaker limiting impact of predatory fish on grazer fauna, because fish stocks did not respond as quickly to enhanced resources in the environment as the invertebrate fauna.

According to the environmental stress model, environmental disturbances weaken the top-down control. For example, on a wave-exposed shore, wave stress is predicted to hinder consumption by animals close to the surface than deeper on the shore. I found that, although mesograzers were efficient consumers at both the depths, predation by fish was weaker in shallow water. The environmental stress model predicts that the effects of disturbance are the stronger the higher a species stands in the food chain. That prediction was empirically supported in the thesis by the impacts of fish and grazers on algae at the two depths.

This thesis assessed the mechanisms of community control in three-trophic-level food chains and did not take into account higher predators. Such predators in the Baltic Sea are, for example, cormorant, seals, white-tailed sea eagle, cod and salmon. All these predatory species were recently or are currently under intensive fishing, hunting and persecution, and their stocks have only recently increased in the region. Therefore, it is possible that future densities of top predators may yet alter the strengths of the controlling mechanisms in the Baltic littoral zone.

Contents

1. Introduction

1.1. Consumer control in macroalgal communities

Since the green world hypothesis (Hairston, Smith & Slobodkin 1960, hereafter HSS), ecologists have pursued the understanding of trophic control – the theory of who limits or enhances whom in the food web. HSS claimed strong top-down control of predators over herbivores, thus releasing plants from grazer control to resource control (Hairston et al. 1960). Later models challenged this view by bringing forward the role of resource control. These models proposed that bottom-up control (e.g. nutrient availability) not only supports plants but cascades up to consumers as well (Fretwell 1977, Oksanen et al. 1981). The model proposed by Oksanen et al. (1981) is known as the Hypothesis of Exploitation Ecosystems (EEH), sometimes as the Nutrient/Productivity model (N/P model). In productive areas EEH converges with HSS, while in unproductive areas top-down control by predators fails (Oksanen & Oksanen 2000). According to EEH, areas poor in nutrients support only plants and herbivores, and the greatest herbivore pressure on plant growth is exerted only in these communities. In highly productive communities, top-down control by predators is expected to limit herbivory. Experimental evidence has supported EEH predictions in terrestrial and limnetic communities (Fraser 1998, Persson et al. 1992, reviewed in Oksanen & Oksanen 2000). Strong top-down regulation, however, is much more often found in freshwater ecosystems than in marine or terrestrial trophic chains (Polis & Strong 1996, Pace et al. 1999, Shurin et al. 2002, Halpern et al. 2005).

In freshwater ecosystems, top-down control has been found to be particularly strong – the impact of top predators cascades down the food chain to primary producers (Hrbacek et al. 1961, Carpenter et al. 1985, review by Pace et al. 1999, Shurin et al. 2002). This causes reciprocal direct negative and indirect positive effects, when predators suppress the abundance of their prey (herbivores), thereby releasing plants from herbivore control. Quite recently, trophic cascades have also been documented in marine pelagic food chains (Frank et al. 2005, Daskalov et al. 2007). In marine littoral zones, studies on trophic relationships have mainly focused on mussel-starfish (e.g. Paine 1966, Menge 1976) or alga-grazer interactions (e.g. (Lubchenco 1978, Paine 2002); an impact of higher trophic level consumers on food web dynamics has been found only in some cases (e.g. Wootton 1995, Estes et al. 1998, Silliman & Bertness 2002, Shears & Babcock 2003), and evidence for the generality of such relationships in the marine benthic ecosystem is rare (Halpern et al. 2005).

The hypotheses of community regulation are broad and are obliged to bypass details and exceptions, which are produced by dozens of interspecific interactions (Menge 1995). While the primary interactions of species within macroalgal communities and associated grazers include direct consumption and resource competition, the community structure is modified by a number of indirect interactions, such as keystone predation and habitat facilitation (e.g. Wootton 1994, Menge 1995), which may obscure community regulation. Community regulation and trophic cascades are therefore more easily observed in species-poor ecosystems, where trophic regulation cascades via a few dominant species and generalistic feeding strategies of grazers predominate (Polis & Strong 1996).

1.2. Nutrients set the baseline for growth and diversity

Although top-down forces have commonly been found to dominate control of marine communities, a growing body of research has shown the significance of co-occurring bottom-up forces (e.g. Worm et al. 1999, 2002; Nielsen 2001; Marczak et al. 2007). Increased nutrient availability supports a higher biomass of fauna and flora (Menge et al. 1997, 2003; Worm et al. 1999), sometimes seen as macroalgal blooms (Valiela et al. 1997, Sundbäck et al. 2003), and alters the species composition of macroalgal communities (Lotze et al. 2001, Nielsen 2001). As used in this thesis, the term "bottom-up regulation" refers to nutrient availability.

Plant species richness and diversity have sometimes been found to follow unimodal curves in response to productivity (Rosenzweig & Abramsky 1993, Worm et al. 2002), while a recent review underlines a positive relationship (Gillman & Wright 2006). The hypothesis of unimodal response is based on the competitive exclusion theory, which predicts that at low productivity, stress and a lack of resources will limit species richness. As productivity increases the number of species reaches a peak value, until at high productivity species richness is reduced by competitive exclusion, either because competition is more intense (Grime 1973, 1979) or because high productivity leads to a decrease in the heterogeneity of limiting resources (Huston 1979). In some highly productive habitats, however, poor species richness can also be explained by the species pool hypothesis (Taylor et al. 1990), which links species richness to the potential recruitment of species to the site; in some areas the species pool restricts species richness. The explanation for the monotonically increasing species-richness – productivity relationship is based on the energy richness theory (Coleman et al. 1982, Wright 1983). This theory is based on the idea that the probability of avoiding extinction due to stochastic mortality depends on population size (Coleman et al. 1982), and environments with more available energy can support more individuals and more species (Wright 1983). Gillmann and Wright (2006) showed that the positive linear relationship between plant species richness and productivity prevails at all scales, from local to global, but that the tendency toward unimodality is higher at local scales. Their meta-analysis, however, used only terrestrial plant communities; to my knowledge, there has been no equally comprehensive study of aquatic environments.

The productivity-species richness model can be linked to the intermediate disturbance hypothesis (Connell 1978), where disturbances, such as grazing, increase plant species richness by limiting competitively dominant species or by clearing space for new recruitment. In the model proposed by Kondoh (2001), disturbance (e.g. grazing) prevents competitive exclusion by creating resources for subordinate species. The model is based on the unimodal relationship between plant species richness and productivity; it therefore predicts that peak species richness will shift to higher productivity by increasing disturbance. At a mid-productivity site, for example, overly weak disturbance will not enhance species richness while overly strong disturbance will diminish it. Assuming a monotonically increasing relationship between productivity and species richness, grazing effects are likely to vary depending on productivity: at low productivity strong grazing will reduce species richness, at high productivity the reverse is the case (reviews by Proulx & Mazumber 1998 and Austrheim & Eriksson 2001).

The community-level responses of macroalgae to nutrient and disturbance gradients, however, are generalized in that they shadow numerous different and even contradictory species-specific responses (Hunter & Price 1992, Duffy et al. 2005, Darcy-Hall 2006). For example, grazer control over algae in highly productive lakes has been shown to depend on the presence of both inferior and superior competitors in the algal assemblage, so that grazing supports algal abundance through reduced alga-alga competition and the regeneration of nutrients (Darcy-Hall 2006). This may indicate that algal species composition may affect the form of the relationship between productivity and species richness.

1.3. Bottom-up and top-down forces meet in trophic cascades

Grazer-alga interactions depend on the productivity of the environment: in eutrophic environments grazing hardly affects algae, while in oligotrophic environments it modifies the algal community very strongly (Lotze et al. 2001). Also multitrophic top-down control of the plant community has been shown to interact with bottom-up control (Bosman & Hockey 1986, Forrester et al. 1999, Heck et al. 2000, Menge et al. 1999, 2003). Bosman and Hockey (1986) observed that colonial seabirds reduced limpet density and simultaneously fertilized macroalgae by guano inflows in the adjacent littoral zone, the joint impact of which caused a higher algal biomass than on nearby shores. Likewise coastal upwelling areas have been shown to increase mussel recruitment and growth and to maintain higher predator densities (Menge et al. 1997, 1999, 2003). In such areas, strong bottom-up control was found to cooccur with strong top-down control, leading to a high biomass in the community as the high nutrient supply cascades up the food chain and maintains the strong top-down control.

In manipulative experiments, predators have been shown to similarly affect primary producers: the impact of predatory fish in a stream cascaded down, via reduction of insect herbivore density, to the basal level to enhance algal density, which was further enhanced by nutrient enrichment (Forrester et al. 1999). Without the extra nutrient supply grazers were able to reduce the algal biomass quite effectively, despite predation by fish. The models of top-down and bottom-up control by nutrients have been formulated for two-link trophic chains (e.g. review by Menge 2000), but are rather poorly known for multitrophic food chains.

Trophic cascades have usually been documented among dominant palatable prey species (Polis & Strong 1996, Murdoch et al. 1998, Polis 1999); in contrast, consumer food preferences, species diversity or predation strategy and on the other hand prey defenses (behavioral, chemical or physical) may dampen or inhibit a trophic cascade (McIntosh & Townsend 1996, Finke & Denno 2004). The occurrences of edible or defended, opportunistic or slow-growing, and ephemeral or perennial macroalgae depend on seasonally varying recruitment times (Kiirikki & Lehvo 1997). Thus finding food web interactions in such an environment requires linking them to species-level dynamics. The ways in which these factors vary among different types of algae and along abiotic gradients have not been yet explored.

1.4. Environmental factors in algal community control

The littoral zone is characterized by inherent gradual change along the depth gradient, causing alterations in abiotic and biotic factors: light intensity decreases, light quality changes, water motion decreases, predation pressure increases (Piazena & Häder 1994, Menge & Sutherland 1987) and the composition of algal and faunal species changes with increasing depth (e.g. Lewis 1964). More specifically, water motion increases photosynthesis (Gonen et al. 1993) and inhibits grazing, predation and the abundance of mobile animal species (e.g. Leonard et al. 1998, Nielsen 2001). Primary producers can utilize nutrients better in flowing than in still water (Hurd 2000, Nielsen 2003), although there is a physical limit to the increase in nutrient uptake (Hurd 2000). Finally, decreased water motion causes increased sedimentation and thus less empty space for algal recruitment (Eriksson & Johansson 2003).

In addition to these vertical gradients of environmental factors, algal communities are also affected by stochastic disturbances (e.g. Dayton 1971, Connell 1978, Sousa 1984). These include boulder turnings, drifting lumber, winter ice, and shadowing or scraping caused by various external sources of disturbance, as well as biotic disturbances such as grazing, predation and trampling. The frequency of these disturbances has been shown to be very important for algal species diversity, as disturbances clear small areas for algal propagules and thereby increase the patchiness of the community (Sousa 1979). Such patchy communities are also called macroalgal mosaics (e.g. Menge et al. 1993), where the patches contain different algal species or assemblages. Sousa (1984) found that small bare patches supported relatively more grazers than large ones, as grazers preferred predator-safe patch margins. His work emphasized the significance of small-scale variability in alga-grazer interactions, which had been often ignored in ecological studies.

Marine ecologists found early that the HSS model was insufficient to explain community control in the marine littoral zone. In 1975 Connell proposed that the abundance and size distribution of prey varies along a gradient of physical harshness; almost at the same time, Menge (1976) showed that the magnitude of top-down control (in a two-link food chain) varied with wave energy. Menge and Sutherland (1976, 1987) presented their environmental stress model (hereafter ESM, see also Menge & Olson 1990, Menge & Branch 2001), which predicts that disturbances will reduce the relative importance of competition in comparison to predation and grazing, and that different trophic levels will respond to a disturbance differently (Menge & Sutherland 1976, 1987; Menge & Branch 2001). ESM differs from the EEH model (Oksanen et al. 1981, Oksanen & Oksanen 2000) in that it explains food chain length by environmental stress rather than by local productivity. According to the ESM, moreover, the higher in the trophic chain the position of the organism, the more environmental stress will inhibit grazing and predation: mesoherbivores, for example, will consume plants in stressful shallow water, but their predators will be inhibited by the environment. According to the ESM, this leads to decreased predation and increased competition at the herbivore trophic level. With weak predation, plant density decreases from intense grazing and can be offset only by enhanced nutrient supply (Fig. 3 in Menge & Sutherland 1987). The ESM has not been thoroughly tested in marine littorals, and in food chains of more than two levels remains mainly a theoretical framework. Despite several examples of trophic cascades (review by Shurin et al. 2002), only a few past studies have dealt with physical abiotic variability together with bottom-up forces and trophic cascades (Proulx et al. 1996, Boyer et al. 2003, Schmitz et al. 2006).

1.5. Objectives of the study

The general objective of this thesis is to examine trophic relationships and the limitation of macroalgal communities on the rocky shores of the northern Baltic. The trophic web in the northern Baltic Sea is rather simple, consisting of predatory fish species, invertebrate mesograzers, and relatively few macroalgal species. In this thesis I manipulated nutrient availability as well as grazer and predator presence in macroalgal communities at two water depths, and have investigated macroalgal responses at both the community and the species level. In the species-poor northern Baltic Sea, understanding species-level macroalgal responses to top-down and bottom-up control may be more important than looking at community-level responses. As the abundances and identities of grazers and algae are known to vary along the depth gradient, both top-down and bottom-up regulation in the food chain is likely to depend on water depth as well.

The thesis is based on two assumptions: (1) that macroalgal control is under both top-down and bottom-up forces, and (2) that interactions between these forces vary with physiochemical conditions such as water depth. More specifically, the following research questions were formulated (references to the main articles in parentheses):

1. Is “top-down” limitation of macroalgae by mesograzers hampered by nutrient enrichment (I, V)?
2. Does predation by littoral fish limit grazing, enhancing algal abundance (II)?
3. Does nutrient enrichment interact with top-down control from fish to algae, leading to dif-

ferent grazing effects at different nutrient availabilities (I, II)?

4. Do the strengths of both the top-down and bottom-up control depend on environmental factors, related to the depth gradient (I, II, III)?

To answer these objectives, I analyzed and/or conducted five field experiments on three islands in the Finnish Archipelago Sea (Fig. 1). Jurmo is situated in the pelagic margin of the Archipelago Sea; the other two islands, Stenskär and Söderland, lie in the outer Archipelago Sea. Experiments I, II, and V compared bottom-up (i.e. nutrients) and top-down (mesograzers and/or fish) control over the macroalgal community. Experiments III and IV were designed to reveal more detailed grazer effects on macroalgae: the effect of colonization time on grazing (III) and the effect on grazing of grazer identity and the age of algal assemblages (IV). In experiments I-II, I also tested the efficacy of top-down and bottom-up controls, and in experiment III the efficacy of top-down regulation alone, comparing two water depths.

2. Material and methods

2.1. Study sites

The northern Baltic Sea, the study area of the thesis, is a tideless sea area, with low salinity (5.5-6.5) and clear seasonality. The studies included in this thesis consisted of field experiments carried out in the Archipelago Sea, SW Finland (Fig. 1). The Archipelago Sea consists of thousands of (mainly) rocky islands of different sizes, forming an archipelago zone tens of kilometres wide. The study sites were chosen in the outer archipelago in order to place the experiments in an environment least affected by anthropogenic nutrient loading. The experiments on the island of Jurmo (59º49.51' N, 21º 35.26' E) (I-III) were conducted in 2003-2004, that on the island of Stenskär (60°02.89’ N, 21°49.19’ E) (IV) in 2004, and that on the island of Söderland (60°6.03’ N, 22°18.37’ E) (V) in 2005. The Jurmo site was moderately exposed to waves, while the other sites were either sheltered (Stenskär) or moderately sheltered (Söderland).

2.2. Macroalgal and faunal communities

The food web structure in the Baltic Sea littoral zone is simpler than those found on oceanic shores. Although the system consists of relatively few species, the abundance and biomass of algae and consumers may be relatively high (Hällfors et al. 1975, Jansson & Wulff 1977). The shallow-water macroalgal community of the outer Archipelago Sea consists of one perennial fucoid species (*Fucus vesiculosus* L.) and about a dozen common filamentous spring and summer-time species, including *Cladophora glomerata* (L.) Kütz., *C. rupestris* (L.) Kütz., *Ceramium tenuicorne* (Kütz.) Waern, *Ulva intestinalis* (L.) Link, *Monostroma* sp., *Pilayella littoralis* (L.) Kjellm., *Ectocarpus siliculosus* (Dillwyn) Lyngbye, *Dictyosiphon foeniculaceus (*Huds.) Grev., *Elachista fucicola* (Velley) Areschoug and *Pseudolithoderma* sp. Most of the perennial red algae grow at deeper depths, and are not included in these studies. Macroalgal communities are commonly dominated by three or four species at a time (I, III, Fig. 2).

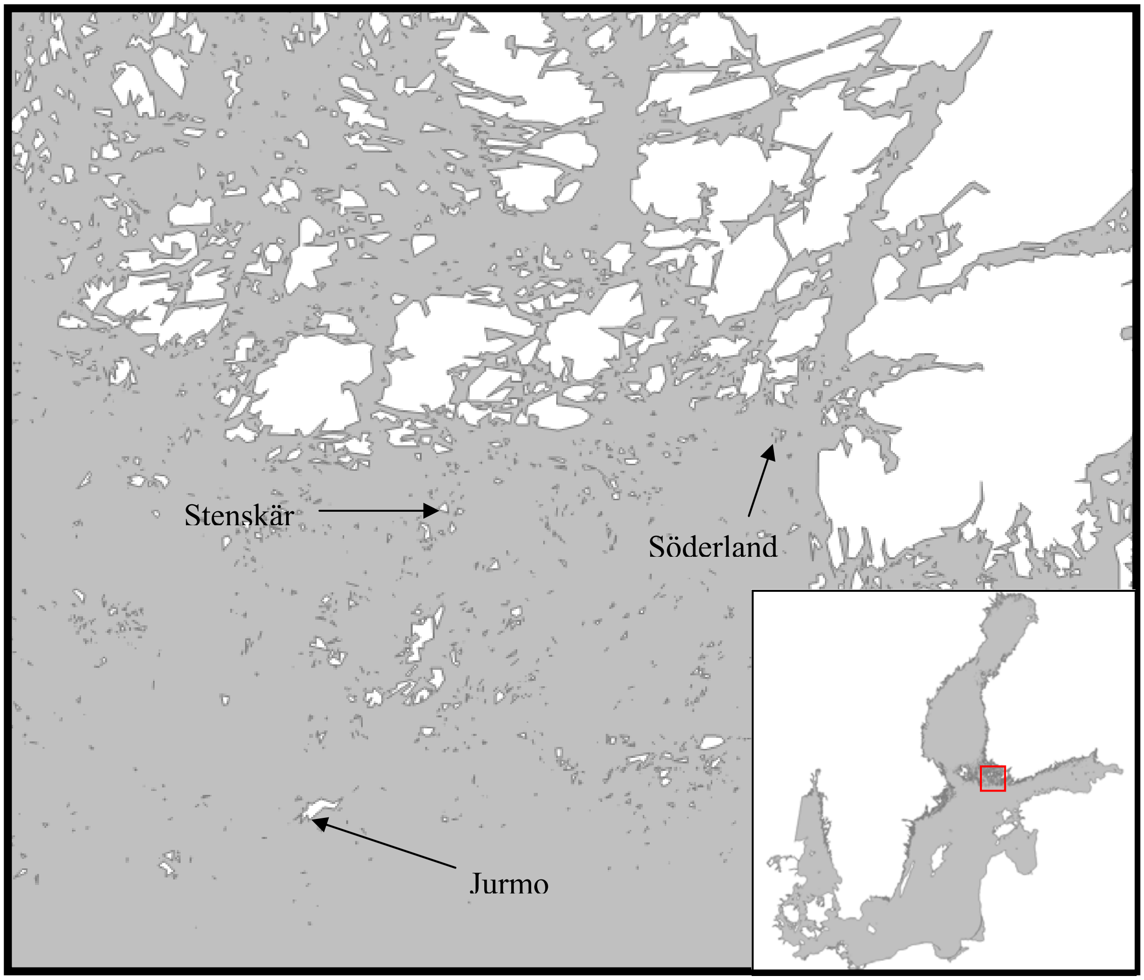

Figure 1. Map of the study area in the Baltic Sea, with study sites shown by arrows. Background map by permission of ESRI Inc.

The macroalgal assemblages of the northern Baltic Sea change gradually along abiotic gradients, such as ice-scouring, wave exposure and the availability of nutrients and light (Kautsky & Kautsky 1989, Bäck & Ruuskanen 2000, Eriksson & Bergström 2005). The most clearly marked zone is formed by the bladderwrack (*F. vesiculosus*), which is a canopy-forming species and commonly dominates at a depth of 0.5-3 m on moderately exposed shores (Bäck & Ruuskanen 2000). On exposed shores, Bäck and Ruuskanen (2000) found the bladderwrack zone to reach to a depth of 5-6 m. In our study region bladderwrack zone flourishes down to two meters depth, after which only single individuals are found.

The herbivores on macroalgae in the northern Baltic Sea consist solely of invertebrate species. The *Gammarus* amphipods (*G. locusta* L., *G. oceanicus* Segerstråle, *G. salinus* Spooner, *G. zaddachi* Sexton), *Idotea* isopods (*I. baltica* Pallas, *I. chelipes* Pallas, *I. granulosa* Rathke), hydrobid snails (*Hydrobia ulvae* Pennant, *H. ventrosa* Montagu, and *Potamopyrgus antipodarum* Gray), and larger snails (*Theodoxus fluviatilis* L. and *Radix peregra* Müller) cause the largest grazing impact on macroalgae, either at their colonization (Lotze et al. 1999, I-V) or in adult phases (Kangas et al. 1982, Engkvist et al. 2000, Jormalainen et al. 2001 *a*, IV). The composition of the invertebrate species assemblage also differs along gradients of wave exposure and depth and among macroalgal assemblages (Hällfors et al. 1975, Salemaa 1987, Kautsky & van der Maarel 1990, I-III). Gammarid amphipods, for example, prefer exposed shores, while *T. fluviatilis* is more abundant at semi-sheltered shores at a shallow depth (Kautsky & van der Maarel 1990). *F. vesiculosus* communities support a biomass of algae and consumers at least ten times higher than communities of annual algae (Jansson & Wulff 1977). Thus *F. vesiculosus* is probably a keystone species on the rocky shores of the Baltic, and its decline due to eutrophication poses the greatest threat to the Baltic littoral food web (e.g. Kangas et al. 1982). Structurally simple filamentous algae cannot support such a diverse and dense algal and faunal community as *F. vesiculosus*.

Among the most common predatory fish species in the Baltic outer archipelago are perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.) (Sundell 1994; Rajasilta et al. 1999; Lappalainen et al. 2000, 2001). Perch feed on crustaceans, while roach feed mainly on gastropods and mollusks (Lappalainen et al., 2001). Other common fish species are gobies (e.g. *Gobius niger* L. and *Pomatoschistus minutus* Pallas), flounder (*Platichthys flesus* L.), white bream (*Blicca bjoerkna* L.), bream (*Abramis brama* L.), eelpout (*Zoarces viviparus* L.), and bullhead (*Cottus gobio gobio* L.) (Sundell 1994; Rajasilta et al. 1999; Lappalainen et al. 2000, 2001; J. Hänninen and M. Kurkilahti, pers. comm.). While second-level predators, such as large fish, seals, cormorants and white-tailed sea eagles, occur in the area, their impact on the littoral food web was not studied.

2.3. Field experiments

The findings of this thesis are based on five field experiments, in which we manipulated nutrient concentration, depth, substrate availability, and the presence or absence of grazers and predatory fish (Table 1). The variables measured included algal biomass (II-IV), macroalgal filament length (II, IV), invertebrate density (I, III-V), and macroalgal density at colonization (I, II, IV, V), early life (III) and adult (IV) stages on rough-faced concrete tiles (10×20 cm) (Table 1). Algal densities were counted on two, four or six 2×2 cm squares, depending on the experiment. Grazer densities were counted on similar but separate 10×20 cm tiles (see methodology in I). In addition, we determined supplementary information, such as nutrient concentrations (I), light intensities (I, IV), parent densities of *F. vesiculosus* (V), and stomach contents of fish (II).

The grazer manipulations were performed by excluding (I-V) or enclosing (IV-V) grazers as well as letting natural grazers freely consume algae (I-V, Fig. 3). The exclosures and open cages compared the pooled natural grazing impact to the no-grazing situation, whereas in the grazer enclosures we quantified the impact of a known grazer species at a known density and compared that to the open cages and grazer exclosures. Caging experiments carry the risk of altering environmental conditions within a cage to such an extent that the phenomena observed no longer reflect natural processes. The risks are often related to clogging of the mesh-net by debris or algae, leading to decreased light intensity, water exchange and oxygen concentration. To control the decrease in light intensity between the grazer exclosures (completely covered by mesh-net) and the open grazing cages, we also had open cages with a mesh-net on the roof (Fig. 3). The differences between these two types of open cage were found to be negligible (I, III). This was also ensured by measuring light intensities within the cages during the experiment (I, IV). Clogging of the mesh-net was further averted by regular cleaning. The frequency of the cleaning depended on the season, as periphyton growth was faster in the summer than in the spring or autumn. The possible effect of cages on water motion was not controlled except for the cleaning, which kept the mesh-nets open for water motion.

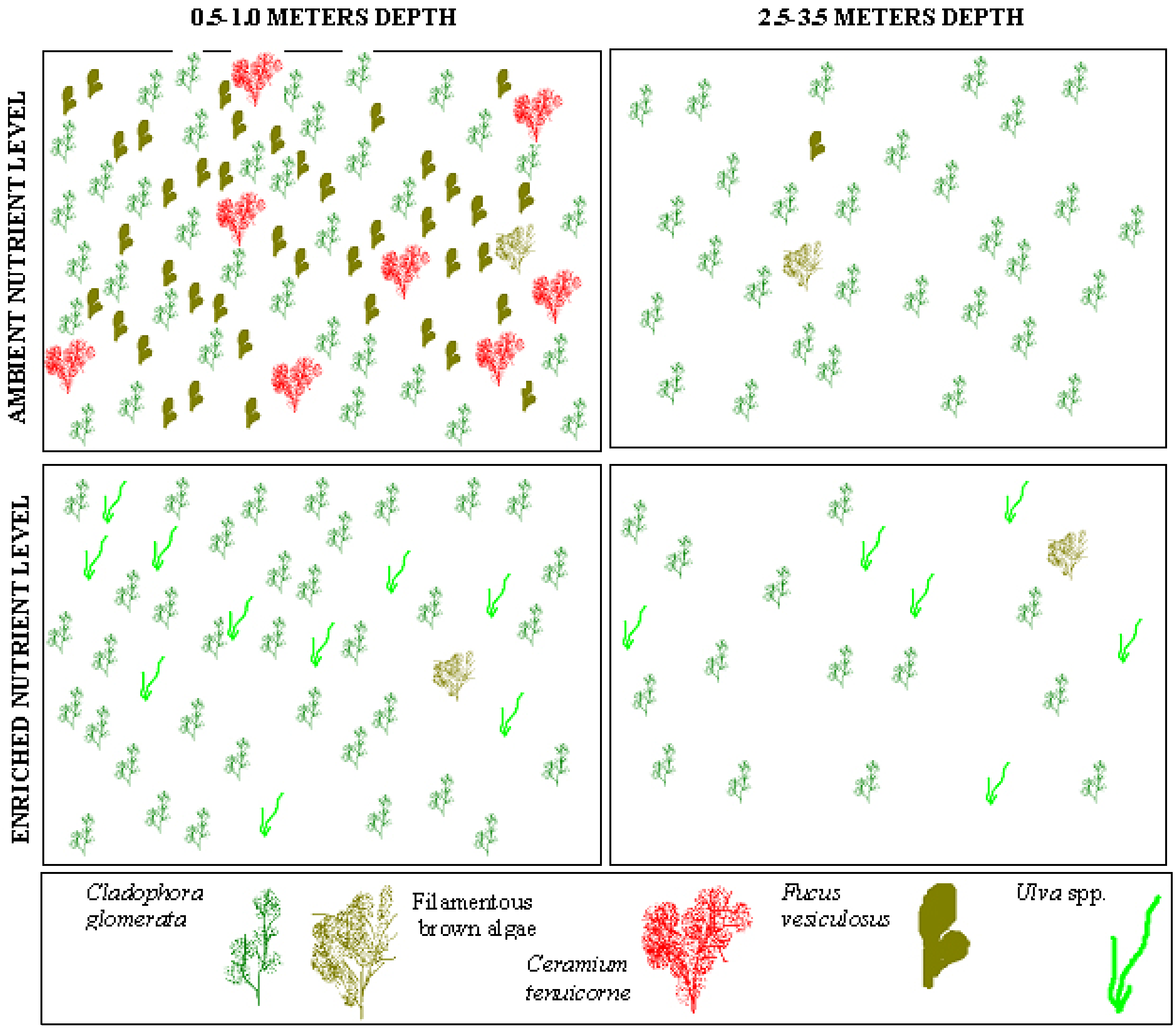

Figure 2. Schematic representation of macroalgal species composition on a moderately exposed shore in shallow (0.5-1.0 m) and deep (2.5-3.5 m) water under ambient and enriched (12×nitrate) nutrient conditions at the island of Jurmo in September 2003. Symbols reflect natural densities of a species in a 10-cm^2 area under natural grazing. Data compiled from Paper I.

To study the effect of the third trophic level, we excluded fish from the macroalga-grazer system and compared that to open cages and cages containing perch (*P. fluviatilis*) as a predatory species (II). The perch enclosure was set to compare the effects of multiple predators in unknown/estimated densities to a single-predator system (with a known density). The 1 cm mesh size allowed the entrance of small fish species or individuals, but these were assumed to exert negligible predation pressure on mesoherbivores.

Figure 3. Roofed and totally covered cages at Jurmo (above) and roofed cage with recruitment substrates on the same shore (below). © Veijo Jormalainen

Table 1. Response variables and manipulations in the field experiments underlying this thesis. Parentheses indicate that a variable was measured but did not involve specific manipulations.

	Paper I	Paper II	Paper III	Paper IV	Paper V
Response variables					
Macroalgae:					
Species richness	×	×	×		
H' diversity	×	×	×		
Biomass	×		×	×	
Total density	×	×	×	×	
Density of separate spe-	×	×	×	×	×
Length of separate spe-		×			
Invertebrates:					
Total density	×	(×)	(×)	(×)	×
Separate species	×	(×)	(×)	(×)	×
Manipulations					
Grazer exclosure	×		×	×	×
Grazer enclosure				×	×
Control for cage effects	×		×		
Fish exclosure		×			
Fish enclosure		×			
Nutrient enrichments	×	×			×
Depth	×	×	×		
Colonization time			×		
Substrate availability				×	×

We manipulated nutrient concentrations by a slow-release 16N:5P:9K fertilizer (Osmocote® Exact Standard 3-4M, Scotts Company) packed into elongate diffusion pouches. The nutrient gradients obtained are temporally stable (over five weeks in our temperature conditions) and spatially restricted (at most some meters) (Worm et al. 2000 *b*, I). We did not find any effect of nutrient enrichment in non-enriched plots four meters (V) or ten meters (I) apart from the nutrient source. The enriched nitrate levels were about fivefold (used in I and V) and 12-fold (I, II), compared to the ambient nutrient level at that time. The enriched phosphate levels were 1.2 and 2.5 times higher than the ambient nutrient level respectively.

Grazer-macroalga interactions were studied at two depths: 0.5-1 meters (shallow) and 2.5-3.5 meters (deep). The depth difference caused evident differences in both physical disturbance and light intensity, as wave and light energies attenuated rapidly along the depth gradient at the study site. The wave motion was clearly perceivable by SCUBA divers at a depth of one but not three meters. The light intensities (mean ± SE), measured on a sunny day in July on the island of Jurmo, were 788 ±21, 677 ± 14 and 143 ± 12 $\mu Em^{-2}s^{-1}$ at the surface and in shallow (1 m), and deep water (3 m) respectively.

To compare grazing between colonizing and adult macroalgae (IV), we placed substrates, either empty or previously colonized, in an experiment. A similar approach was used when we compared the recruitment success of *F. vesiculosus* (V) on unoccupied and previously occupied substrates. The 'occupied' substrates had been either one (V) or three (IV) months in shore water and had been freely colonized by the local algae. The colonization substrates were made of concrete, which may have affected the colonization of algae. To reduce such an effect, the substrates were made rough-faced to create a “natural” microtopography for algal settlement. The resulting macroalgal assemblages closely resembled those in the surrounding environment. Thus the use of the artificial substrates gave rise to sufficiently “natural” algal assemblages.

2.4. Data analyses

The data for macroalgal density, filament length, pooled biomass, species richness, and Shannon-Wiener diversity (H’) were analyzed by either ANOVA, mixed model ANOVA or generalized linear models, the model details depending on the structure of the experimental design and sample distribution. We analyzed the responses of abundant macroalgae species by species and as a pooled total algal density. However, some taxa were pooled at the onset, such as filamentous brown algae consisting of densities of *P. littoralis* and *E. siliculosus*, since they occasionally grew in combination and given their tiny size were difficult to distinguish. The responses of invertebrate grazers to experimental manipulations of depth and nutrient supply were analyzed in order to distinguish these manipulations from that of grazing. In fish manipulations the fish stomach contents were analyzed and compared in order to clarify the top-down effects on macroalgae via mesograzers.

The densities of colonizing macroalgae and invertebrate densities were aggregated, as shown by their negative binomial sample distribution. These analyses were primarily performed by generalized linear models using the SAS GENMOD procedure (SAS Institute 1999). This approach is based on the maximum likelihood method and a χ^2 approximation. Generalized linear models are more flexible than general linear models (GLM) as they allow several sample distributions. The SAS MIXED procedure (SAS Institute 1999) was used when the model contained random factors (V) or repeated measurements (III, V). In these cases, the response variables were (ln+1)-transformed in order to fulfill assumptions of normal distribution and homoscedasticity. The filament length data (II, IV), pooled biomass (II-IV), and diversity parameters (species richness and Shannon-Wiener diversity, H’) (I-III) were analyzed by ANOVA in the SAS GLM procedure (SAS Institute 1999). In this thesis I have combined and reanalyzed data from papers I and II, using the SAS GENMOD procedure, to clarify the trophic cascades from fish to algae (Table 2, Figs. 4 and 5).

The hypotheses in the experiments were often detailed and their testing thus required specific *a priori* hypotheses in the analyses. In the grazing experiments (I), for example, we contrasted open cages (no mesh-net) and roofed cages (open cages, roof covered by net) to grazer exclosures (completely covered by net) and were thereby able to arrive at a reliable estimate of grazing impact. The contrast tests were also used to ensure that the experimental design did not give rise to negative cage effects (I-III).

3. Results and discussion

3.1. Grazer densities at the study sites

Grazer densities in the Archipelago Sea depend greatly on the season and on environmental factors relating to the site (I, III, IV, V, Hällfors et al. 1975, Boström & Bonsdorff 1997). Commonly, exposed or moderately exposed shores have higher invertebrate densities than protected ones (Leonard et al. 1998, author’s own observations). The low abundance of grazers on sheltered shores may reflect strong predation pressure on them by fish. Predation pressure has been found to be strong in low-disturbance environments, such as wave-protected shores and the deeper end of the littoral zone (Lubchenco & Menge 1978, Menge & Sutherland 1987, Robles & Robb 1993, Leonard et al. 1998, Nielsen 2001). Our results from Jurmo (II) also indicated that fish may limit grazers more at a depth of three meters than closer to the surface. This stronger linkage between trophic levels in a physically more benign environment also modifies the species composition and richness of macroalgal communities (I-III, Kondoh 2001, Svensson et al. 2007).

Grazer densities varied greatly among the three study sites, due to the highly fragmented landscape in our study area, and among seasons. Thus grazer densities are not comparable between experiments, but rather indicate the grazing pressure in each individual case. On the moderately exposed shore on the island of Jurmo, invertebrate densities were high (I-III). Densities of gastropods (means ~33 000 hydrobids and 2 650 *Theodoxus fluviatilis* ind. m^{-2}) were among the highest documented in the northern Baltic Sea (Hällfors et al. 1975, Boström & Bonsdorf 1997), and on the nutrient-enriched substrates the density of hydrobids was even higher (mean ~61 000 ind. m^{-2}). *Gammarus* amphipods had a relatively low density (600 ind. m^{-2}) on the island of Jurmo, while higher densities have been found for the species in the region (Hällfors et al. 1975, Boström & Bonsdorf 1997). The densities of *Idotea* species (750 ind. m^{-2}) were close to the average density found in the northern Baltic Sea (Hällfors et al. 1975, Boström & Bonsdorf 1997). At Stenskär and particularly at Söderland the grazer densities were low (IV, V). At both sites, crustacean densities were c. 500-700 *Gammarus* and 185-200 *Idotea* ind. m^{-2}. Gastropod grazers had densities of 8 500 and 925 ind. m^{-2} for *Hydrobia* and 1 300 and 260 ind. m^{-2} for *T. fluviatilis* at Stenskär and Söderland, respectively. The varying grazer densities were reflected in the grazing intensities among the sites; in Jurmo and Söderland grazing was most and least effective, respectively (I, III, IV, V).

3.2. Grazing modifies macroalgal communities

3.2.1. Grazing intensity

Top-down control by herbivores strongly modified the density and species composition of macroalgal propagules and young macroalgae in the experiments of this thesis (I-V, Fig. 4 a). In the recruitment phase and shortly after it, grazers very strongly reduced the propagules of most macroalgal species (I). The only species clearly avoided by grazers was the red alga *Ceramium tenuicorne*, while filamentous brown algae (*Pilayella littoralis* and/or *Ectocarpus siliculosus*) were avoided only at the time of their peak density (I). The impact of grazers lasted the whole growing season; the algae growing on our colonization substrates were still clearly reduced in density in the late autumn (I). However, each algal species analyzed separately also showed periods of weaker grazing during its growing season. These periods were linked to a low abundance of the species in the assemblage (see appendix C in I), when the few individuals of a species may escape grazers more easily than the temporary dominants. Grazing on spores was regardless of the water depth in the littoral zone (I). Grazers in deep water, consisting mainly of *Hydrobia* spp., were efficient in affecting the densities of *Cladophora glomerata* and filamentous brown algae (III), while the fauna in shallow water, consisting mainly of crustacean mesograzers and the snail *T. fluviatilis*, seemed to be generally more efficient in limiting algal densities (I).

Previous studies on the susceptibility of different algal phases to grazing have shown strong reduction in early life stages (Lubchenco 1983, Lotze et al. 1999, 2001) or the selection of more nutritious phases of algae (Steele and Whittick 1991). In our studies, algal age was reflected in grazing intensity. Grazing on a young macroalgal community, at the age of one year (III), was more selective and context-dependent than during the recruitment phase (I). Exposing mature communities containing long algal filaments to grazing led to very weak results when compared to grazing on algal spores (IV). There was no change in total algal density, filament length or pooled algal biomass with grazing in a mature assemblage. Clearly, both continuous colonization and algal regrowth capacity are enough to override grazing effects in mature communities (cf. Salovius & Bonsdorff 2004). This may be due to the absence of large grazers such as sea urchins and littorinid snails, as well as herbivorous fish species, all of which are responsible for algal biomass loss on oceanic shores (Smith et al. 2001, Shears & Babcock 2002). The mesograzer densities enclosed in our cages reflected those found naturally in the area (IV), which may indicate that only exceptionally high densities are able to reduce the cover of adult macroalgae (Kangas et al. 1982, Engkvist et al. 2000). A similar trophic control, albeit in a very different context, prevails in terrestrial forests, where the regulation of tree species is mainly limited to the sapling phase, while occasional mass folivore outbreaks may defoliate and kill large forest areas (Kallio & Lehtonen 1975). In the Baltic Sea there are examples of mass outbreaks of isopods, *Idotea baltica*, that have wiped out local stands of *Fucus vesiculosus* (Kangas et al. 1982, Engkvist et al. 2000, author's personal observations). These irregular mass outbreaks of grazers indicate that eutrophication has probably destabilized the ecosystem (Rosenzweig 1971).

3.2.2. Grazing in a patchy community

Environmental disturbances maintain mosaic algal communities, consisting of small patches differing in successional stage and algal species composition. Such differences in macroalgal assemblages are caused by the distinct recruitment times and short dispersal distances of algae (Menge et al. 1993, Kiirikki & Lehvo 1997, Dudgeon & Petraitis 2001). We hypothesized that algal mosaics would also differ in the effects of grazing. The outcome of such small-scale variability would be seen, for example, (1) as variation in the density of the same algal species in different patches due to short recruitment periods; (2) as changes in the proportion of algae in a patch due to grazing; and (3) as the emergence of new algal species on patches due to patch-specific variability in grazing (due to selective grazing of some algae or temporally varying abundance of grazer species).

Clearing empty substrates at different colonization times caused distinct macroalgal assemblages, where the occurrence of species or their proportion in the assemblage varied according to colonization time (III). Algal settlement in the Baltic Sea has been found to be strongly seasonal; the highest algal diversity is usually found in the summer (Qvarfordt 2006). Substrates were modified by grazing and competition, but differences among patches lasted over the winter from the previous growing season on both grazed and ungrazed substrates. Thus the mosaic structure is relatively stable in the community. Moreover, we found clear differences in grazing effects; grazers probably select between different algal patches, thereby enhancing the mosaics, which were initially produced by the distinct colonization times of algae. Grazing effects, whether direct (i.e. consumption) or indirect (i.e. positive effect via grazing of competitors), were shown to vary among algal species, and to depend on depth, on the colonization time of the algae, and probably on algal biomass in a patch.

Very obvious differences in grazing were found between the green alga *C. glomerata* and the filamentous brown algae (*E. siliculosus* and/or *P littoralis*) (III). *C. glomerata* in a one-year-old assemblage was effectively reduced in deep water, while in shallow water grazers were unable to reduce its density; in low-biomass patches colonized in August, grazing actually led to an increased density. Filamentous brown algae experienced an opposite grazing pressure between depths: in deep water these algae benefited from grazer presence, while in shallow water grazing reduced the density in the August patches. I suggest that the differences observed in grazing may depend first of all on physical or chemical defenses and nutritional quality in algae and, secondly, on the zonation of grazer species along the depth gradient.

Grazer food preference for an algal species has been shown to depend on its nutritional status (Hemmi & Jormalainen 2002, Boyer et al. 2004) and/or chemical content (Renaud et al. 1990, Jormalainen et al. 2001 *b*, Cruz-Rivera & Hay 2003) of the prey item. The depth gradient may also alter algal chemical content (Renaud et al. 1990, Cronin & Hay 1996, Martínez 1996, Pavia & Brock 2000, Cronin & Lodge 2003, Connan et al. 2004). Chemical or physical defenses against herbivory have been found in several macroalgae (Jormalainen & Honkanen 2007, Toth & Pavia 2007). Although I am not aware of chemical defense against grazers among these two species, *P. littoralis* contains allelopathic chemicals against alga-alga competition (Råberg et al. 2005) and has benefited from grazing in a previous study in the Baltic Sea (Lotze et al. 2001). In this thesis the deterrent effects of algae were not studied specifically, but I found that filamentous brown algae and in particular *P. littoralis* were not reduced by grazers and that sometimes the alga actually benefited from grazing (I, V).

The zonation of grazers along a depth gradient may depend on species' adaptations to their physical environment (Lewis 1964, Kawamata 1998, Nielsen 2001) or on ecological interactions with other species (Lubchenco & Menge 1978, Lubchenco 1980, review by Lubchenco & Gaines 1981, Harley 2003). Such differences in the distribution of grazers also affect the densities of algal prey species. I propose that hydrobid snails, which were very abundant in the deep littoral, probably reduced the spores of *C. glomerata* but avoided feeding on the filamentous brown algae. However, shallow-water grazers (mainly crustaceans and *T. fluviatilis*) reduced the filamentous browns in the low-biomass patch, which was colonized in August (III). In that patch, the filamentous browns may have included more of the species *E. siliculosus* than of *P. littoralis*. *E. siliculosus* reproduces in the late summer (Kiirikki & Lehvo 1997) and has not previously been found to deter grazers. The macroalgal mosaic was clearly maintained by grazing, which enabled species occurrence on the substrate (III). The green alga *Monostroma* sp. was found only on grazed substrates which were colonized in July or August.

3.2.3. Species-specific grazer effects

In order to identify which grazer species caused which effects on macroalgae, I conducted a field-experiment, in which I measured the effects of two snail and two crustacean taxa on macroalgal assemblages (IV). The results showed differences in the grazing effects of the four mesograzer species (IV). While large snails (*T. fluviatilis*) consumed algal spores and the young life stages of *C. glomerata* and *E. siliculosus*, small hydrobid snails (*Hydrobia* spp.) probably fed on periphyton, thereby enhancing the settlement of *C. tenuicorne* and *E. siliculosus*. *T. fluviatilis* enabled the settlement of a crustose alga *Pseudolithoderma* sp. in the mature algal community, which was not present in treatments containing other grazer species. Thus the indirect facilitation performed by the snail cleared space for a new species in the assemblage. Such indirect facilitation has been found commonly in benthic communities. For example predation on blue mussels increases the cover of macroalgae and barnacles (Enderlein & Wahl 2004), while *Littorina* snails increase the cover of *F. vesiculosus* by grazing on ephemeral filamentous algae (Lubchenco 1983). However, we suggested in the Jurmo experiments (I-III) that hydrobids also have a strong impact on macroalgal spores, since macroalgae in deep water were greatly reduced and hydrobid snails were highly abundant at that depth. Macroalgal spores and microalgae are the same size. In the Stenskär experiment (IV), hydrobids did not feed on macroalgal spores, probably due to low hydrobid densities in the manipulations; at very high densities, competition for food may drive hydrobids to accept a wider food spectrum.

Crustacean grazers had only a weak effect on algae: *I. baltica* consumed the spores and microrecruits of *C. glomerata*, whereas *Gammarus* amphipods had no significant effects on the colonization assemblage. The *Gammarus* amphipods, however, reduced the density of *C. tenuicorne* in the mature community. Overall, adult macroalgae were poorly grazed when compared to young recruits in the colonization phase (IV).

3.3. Recruitment inhibition of Fucus vesiculosus

The fifth experiment focused on the responses of a perennial species *F. vesiculosus* to the interactive effects of resource competition and grazing (V). According to recent studies of the decline of *F. vesiculosus* populations in the Baltic Sea, recruitment of the species is vulnerable to sediment cover (Eriksson & Johansson 2003), competition with ephemeral algae (Berger et al. 2003, Råberg et al. 2005), direct nutrient effects on rhizome growth (Bergström et al. 2003), allelopathic metabolites of *P. littoralis* (Råberg et al. 2005), and grazing (Malm et al. 1999); interactions among these factors, however, are poorly known. In addition to the negative main effects of grazing, nutrient enrichment and substrate occupancy, we also found interactive effects among the manipulated factors (V). Nutrient enrichment increased the abundance of filamentous macroalgae, which inhibited the recruitment density of *F. vesiculosus*. Occupied substrates, covered by ephemeral algae, detritus and sediment, also reduced the colonization success of *F. vesiculosus*. The poorest recruitment of *F. vesiculosus* was caused by the combined effect of enhanced nutrient level and pre-occupied substrates (V).

Grazer effects depended on nutrient level: at the ambient nutrient level, neither the enclosed snail grazers (*T. fluviatilis* or *Hydrobia* spp.) nor the natural grazer assemblage had a significant effect on the density of zygotes of *F. vesiculosus*. Although we found negligible grazing at the ambient nutrient level, *T. fluviatilis* has been shown to be a strong grazer of *F. vesiculosus*, particularly during its first summer (Malm et al. 1999). At the enriched nutrient level, however, the lowest densities of *F. vesiculosus* occurred in cages with snails. The interaction between nutrients and grazing led to very low densities of *F. vesiculosus* in both snail treatments.

I suggest that there may be at least three ecological mechanisms acting interactively and leading to the poor recruitment density of *F. vesiculosus* in nutrient-enriched conditions. Firstly, increased resource competition between *P. littoralis* and *F. vesiculosus* under nutrient enrichment led to the dominance of the opportunistic *P. littoralis* (compare to Steen 2004). Second, the dominance of *P. littoralis* resulted in increased allelopathy (Råberg et al. 2005) and increased grazing pressure on more palatable algae (i.e. *F. vesiculosus*). Finally, the snails probably also fed on other algae, including periphyton, thereby clearing space for the opportunistic settlement of *P. littoralis*. Thus opportunistic ephemeral macroalgae have the potential to rapidly colonize grazer-cleared substrates at enhanced nutrient concentrations, while the narrow recruitment window of *F. vesiculosus* severely inhibits the species' possibilities of finding empty substrates. My previous results in Jurmo (I) showed that grazing also reduced annual algae under nutrient-enriched conditions. In that experiment, however, the density of grazers (i.e. the strength of grazing) was much higher and the diversity of grazers broader than in the experiment in Söderland (V). I therefore suggest that under nutrient-enriched conditions weak grazing cannot limit fast-growing annual algae, which leads *F. vesiculosus* to lose the competition for space to annual algae.

Although the experiments in this thesis were not primarily designed to reveal competitive interactions, the results clearly indicate that such interactions occur. The competition for available space between ephemeral and perennial algae found in the experiment on Söderland is in accordance with previous experiments on the island of Jurmo (I-III), in the southern Baltic Sea (Worm et al. 1999, 2000 a, 2001), and in Skagerrak (Steen 2004). In Jurmo, *F. vesiculosus* and the red alga *C. tenuicorne* did not thrive in grazer exclosures but were rather smothered by annual algae, such as *Ulva* sp., *C. glomerata*, and filamentous brown algae (I). Steen (2004) reported an 80-100% reduction of *F. vesiculosus* due to competition with *U. intestinalis*, while Worm et al. (1999, 2000 a,

2001) found that grazers (littorinid periwinkles) reduced the competition between *F. vesiculosus* and annuals by consuming the latter. Thus the potential of ephemeral algae to rapidly recruit the available space under high nutrient conditions is a severe threat to macroalgae with a short reproductive period.

3.4. Tritrophic cascades from fish to algae

The field experiment, in which we studied the effect of fish on macroalgal colonization, showed a clear trophic cascade, from fish via grazers to algae (Table 2, Fig. 4, II). In the presence of fish the macroalgal colonization and the subsequent growth were enhanced compared to the situation in the absence of fish predation. Similar cascades were found for the slow-growing *F. vesiculosus*, the annual *C. glomerata*, and the filamentous brown algae (Table 2, Fig. 4). The red alga *C. tenuicorne* benefited from grazer presence in the natural tritrophic food chain, while it was reduced in density both by excessive grazing in the "no fish" situation and by excessive competition in the "no grazing" situation (I, II, Fig. 5). The cascading effect was not found for macroalgal diversity or species richness (II).

Table 2. Statistical analyses of trophic cascades from fish via grazers to total macroalgae, the brown alga *Fucus vesiculosus*, the green alga *Cladophora glomerata*, the red alga *Ceramium tenuicorne*, and the filamentous brown algae (*Pilayella littoralis / Ectocarpus siliculosus*) on ambient and enriched (12×nitrate) nutrient levels at depths of 0.5-1 and 2.5-3.5 metres. The ratio of deviance and degrees of freedom (df) indicates the model fit (See *Statistical analyses*). Data compiled from papers I and II and presented in Figures 4 and 5.

		All macroalgae		*F. vesiculosus*		*C. glomerata*		*C. tenuicorne*		Filam. browns	
Deviance / df		39.7 / 24		24 / 23		39.4 / 24		14.98 / 24		29.8 / 24	
	df	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Depth	1	26.80	<0.0001	28.48	<0.0001	18.26	<0.0001	13.02	<0.001	0.01	0.93
Nutrient	1	0.21	0.65	6.15	<0.05	0.96	0.32	17.61	<0.0001	17.38	<0.0001
Top-down	2	41.71	<0.0001	14.74	<0.001	26.66	<0.0001	0.2	0.90	24.52	<0.0001
D × N	1	0.32	0.57	2.97	0.08	0.34	0.56	20.73	<0.0001	0.17	0.68
D × Td	2	1.64	0.44	10.32	<0.01	2.08	0.35	2.91	0.23	12.34	<0.001
N × Td	2	10.88	<0.01	1.27	0.53	8.13	<0.05	1.11	0.57	18.07	<0.001
D × N × Td	2	5.59	0.06	0.12	0.94	7.22	<0.05	0.98	0.61	9.6	<0.01

Trophic cascades have been commonly found in aquatic food chains (Pace et al. 1999, Frank et al. 2005), which has been explained by the general palatability of algae and the simplicity of aquatic food chains (Polis & Strong 1996, Shurin et al. 2006). The Baltic Sea littoral ecosystem is relatively simple, consisting of only few dominant species; this leads to strong species-linkages between trophic levels. The effects of food web complexity, such as high species diversity, omnivory of consumers and prey switching, often inhibit the forming of cascades (Polis & Strong 1996, Heck et al. 2000). In the northern Baltic Sea, second-level consumers in the littoral macroalgae-based food web are carnivorous fish (Lappalainen et al. 2001).

According to the environmental stress model (ESM), consumption increases at lower trophic levels (Menge & Sutherland 1987), meaning that grazers reduce algae more than fish reduce grazers. This is in direct contrast with the HSS model, according to which plants are regulated only by resources. On the other hand, observations by

McQueen et al. (1989) suggest that top-down control does not reach the basal level. In our experiments we found support for the ESM prediction (II). The grazer exclosures (maximal algal recruitment) always produced a higher density of algae than the natural (basically tritrophic) food webs, while the fish exclosures caused maximal grazing pressure (Figs. 4 and 5). The presence of fish partly lessened grazing on algae, but never completely. The differences between grazer exclosures and the two and three-trophic-level systems were greater in deep than shallow water (Fig. 4 a). Nutrient enrichment also enhanced the difference between grazer exclosures and the two and three-trophic-level systems (Fig. 4 a). These results show that environmental conditions and resource availability play a significant role in trophic cascades.

The second Jurmo experiment (II) showed that trophic interactions were stronger in a physically benign environment (here deep water), as predicted by ESM (Menge & Sutherland 1976, 1987; Menge & Olson 1990). ESM predicts that physical disturbance will decrease predation and grazing. Moreover, the model predicts that the role of the inhibitive effect of environmental stress will be greater at higher consumer levels. In accordance with this, we found that a shallow water environment restricted fish more than grazers; the enclosed perch ate more in shallow than in deep water (II). While this was seen in the total

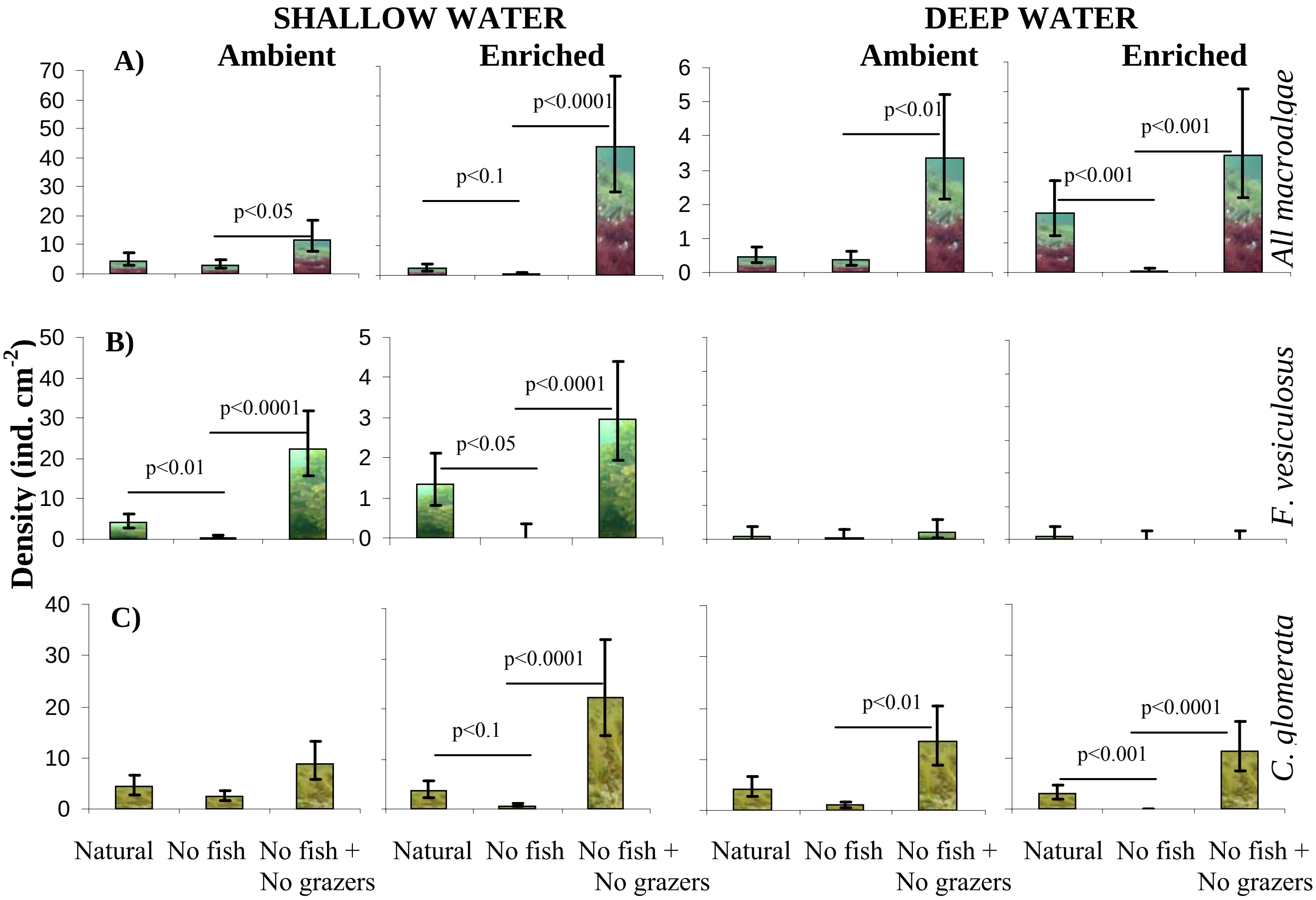

Figure 4. Bottom-up and cascading effects of fish on densities of (A) all macroalgae in September 2003, (B) *Fucus vesiculosus* in July 2003, and (C) *Cladophora glomerata* in September 2003 in shallow (0.5-1 m depth) and deep water (2.5-3.5 m depth) in ambient and enriched (12×nitrate) nutrient conditions. Data combined from papers I and II. Key: Natural = roofed cages, No fish = fish exclosure, No fish, no grazers = fish and grazers exclosure.

amount of eaten prey, the amount of crustaceans did not differ between depths. This is more or less as expected, since the density of crustaceans is lower and fish predation stronger in deep than shallow water (I, III). In limnetic pelagic communities, Proulx et al. (1996) found a similar inhibition of predation by fish in shallow water; phytoplankton biomass increased significantly only in deep water, due to predation of zooplankton by fish.

The risk in caging experiments is that the caging of fish may have affected water flows within the cages, thereby creating altered living conditions for grazers and algae and an artificial shelter for the enclosed fish. The artificial shelter for fish should be seen as an enhanced predation pressure on grazers and increased densities of algae compared to open cages. However, such was not seen in any of the algal species (II). Moreover, all the dominant species grew well in the fully-covered herbivore exclusion cages (I), indicating an absence of cage effects.

The effect of natural fish predation was compared to predation by enclosed perch (II). This single-predator system produced quite similar results to the open multipredator system, but some distinct differences were found. The similarities indicate (1) that the effect seen in the open cages was due to predators, (2) that perch were efficient predators on grazers, and (3) that top predators, such as seals, large fish, white-tailed sea eagle (*Haliaeetus albicilla*) or cormorants (*Phalacrocorax carbo*), did not have a strong impact on the littoral food web at our study site. The differences between the open system and the perch enclosures, on the other hand, occurred only on the nutrient-enriched substrates (II), where hydrobid snails increased greatly (I) but were probably not inhibited by perch, which prefer a diet of crustaceans and insects (Lappalainen et al. 2001). Hydrobids were not found in the stomachs of perch (II). The collapse of top-down control of grazers by perch, due to the narrow food preference of enclosed perch, caused strong grazing of algae in the nutrient-enriched systems, leading to low algal density, diversity and species richness. Indeed, higher predator diversity has been shown to cause greater reduction in herbivore abundance (Gamfeldt et al. 2005, Snyder et al. 2006).

3.5. Role of nutrients in algal assemblages

3.5.1. Nutrients change algal species composition and increase algal abundance

Nutrient availability has been considered the driving force in macroalgal community control (Lapointe 1997, Valiela et al. 1997, Morgan et al. 2003). Indeed, increased concentrations of nutrients have caused blooms of *Ulva intestinalis* and other opportunistic species (Bäck et al. 2000, Sundbäck et al. 2003). However, more often the role of nutrients has been found to change macroalgal species composition (Lotze et al. 1999, Nielsen 2001) and to affect species richness (Worm et al. 2002).

In the studies on Jurmo (I) and Söderland (V), I found that nutrient enrichment dramatically increased the density of annual species and decreased that of *F. vesiculosus* and *C. tenuicorne* (Fig. 2). Thus nutrient enrichment changed the relative proportion of species in the assemblage in favor of annual species. A large meta-analysis has recently shown that the reason for decreased species richness following nitrogen nutrient enrichment in terrestrial plant communities is both abundance-based, referring to the random loss hypothesis, and trait-based, referring to the hypothesis of competitive exclusion (Suding et al. 2005). The former means that fertilization increases plant biomass, therefore causing community-level thinning and death of small individuals of all species. This random mortality is more likely to lead to the extinction of rare than of common species, thus reducing species richness. The trait-based mechanism works through interspecific competition for resources and is thus based on species' traits to adapt to changing nutrient conditions. In macroalgae the mechanisms may be similar, although given the lack of belowground competition the competition for recruitment space is more relevant (I, V).

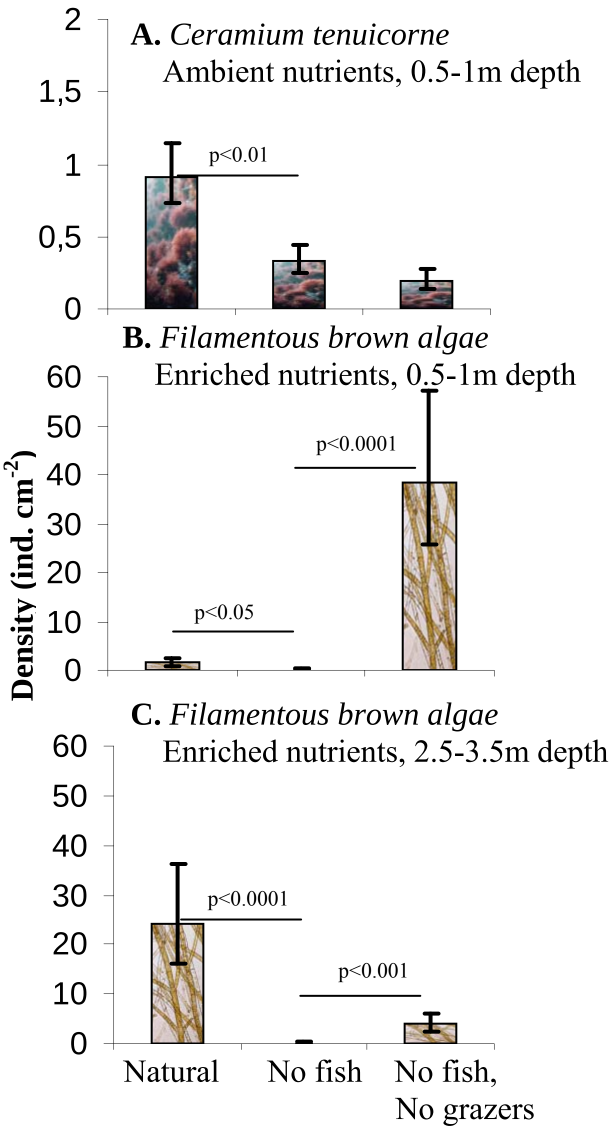

Figure 5. Bottom-up and cascading effects of fish on densities of (A) *Ceramium tenuicorne* on an ambient nutrient level at 0.5-1 m depth in August 2003 and (B, C) filamentous brown algae on an enriched nutrient level at 0.5-1 m depth (B) and 2.5-3.5 m depth (C) in July 2003. The densities of algae at the other treatment levels were too low to be included in the figure. Data combined from papers I and II. Key: see Fig. 4.

In the first experiment, I hypothesized that increased nutrient availability would enhance macroalgal settlement and growth more with higher water motion close to the surface than in the more stagnant waters in the deeper littoral (I). The significantly higher light intensity and broader light spectrum in shallow than in deep water mean higher nutrient assimilation and greater potential for growth. Intermediate water motion has also been shown to enhance nutrient uptake by algae (Hurd 2000). I found that at enriched nutrient levels and in the absence of grazers, annual algae, such as *Ulva* spp., the filamentous brown algae, and *C. glomerata*, were able to increase their density more in shallow than deep water (I, Fig. 2), and that the filament length of *C. glomerata* increased under such conditions (II). Thus bottom-up regulation by nutrients can more effectively enhance the density and growth of annual species in the shallow than the deep-water macroalgal assemblage. As grazing was also weaker in the turbulent shallow water (see 3.2.1), nutrient enrichment, also under grazer presence, caused higher densities of fast-growing annual macroalgae in shallow water (I, II).

3.5.2. The diversity-productivity relationship and disturbances

Hypotheses of the relationship between species richness and productivity may not be well suited to the species-poor macroalgal community in the northern Baltic Sea, as there are only a handful of species and almost as many responses to an excess of nutrients. Nevertheless, I did not find consistent support for the results of the recent meta-analysis by Gillman & Wright (2006), according to whom the relationship of plant species richness and productivity is mostly monotonically positive. Our results rather supported the hypothesis of unimodal relationship (Rosenzweig & Abramsky 1993, Kondoh 2001, Worm et al. 2002). The latter hypothesis predicts that species richness will follow a unimodal curve along a gradient of productivity: maximal species richness is found at mid-productivity, between nutrient limitation and competitive exclusions. Although there were only three nutrient concentrations in the first experiment, I found that the macroalgal species richness, in the absence of grazers, formed a unimodal response curve to nutrient availability in deep water (peak at 5×nitrate level). In shallow water the response was unimodal or monotonically increasing in the summer but monotonically decreasing in the autumn (I). H' diversity followed quite similar trend as species richness (see Appendix B in I).

The shallow-water community showed more temporal variation in algal species richness and diversity than that in deep water. A possible interpretation is that the shallow-water algal assemblage experienced higher disturbance due to water motion, which resulted in the potential for high species richness even at a very high (12×) nitrate level. In more stable conditions in deep water the intermediate nutrient enrichment elevated species richness, but at higher nutrient availability the assemblage was inhabited by competitive dominants, the filamentous brown algae. The response curves, however, should be studied with more than three nutrient concentrations to minimize temporal and spatial variation in species richness. Nevertheless, I suggest that the competitive exclusion hypothesis probably accounts for the reduced diversity and species richness in our experiment, while in the Baltic Sea the species pool is also certainly limiting.

In this thesis, I have assumed that both grazing and water motion are disturbances affecting macroalgal species richness. The grazing effects in our experiments were strong, and can thus be assumed to cause considerable disturbance. Grazers were able to limit colonizing macroalgae in nitrate enrichment as high as 12-fold. The greatest differences in algal density between grazer exclosures and the grazed communities were caused by the combined effect of nutrient enrichment and grazing (I). I did not find consistent enhancement of species richness by grazing along the gradient of productivity; in shallow water, however, macroalgal H' diversity was slightly enhanced by grazers (Appendix B in I). The positive grazer effects on H' diversity indicate that grazing leveled species composition rather than increasing species richness. In the autumn the species pool had even fewer species, which restricted diversity despite grazing. On the other hand, I found that grazers had a positive impact on species richness in patches of lower algal biomass (III). In this specific case grazers enhanced species richness, probably by clearing space for new species from the propagule bank.

3.6. Do nutrients challenge trophic cascades?

The view that resource availability and top-down forces interact in community regulation has recently gained growing attention (e.g. Borer et al. 2006, Burkepile & Hay 2006, Gillman & Wright 2006, Jara et al. 2006, Schmitz et al. 2006, Graff et al. 2007, Heck & Valentine 2007, Marczak et al. 2007, Svensson et al. 2007). Eutrophication of coastal ecosystems and marginal seas is commonly acknowledged to be the result of nutrient overloading to an extent where herbivores cannot consume the plant biomass. External subsidies, such as nutrient loading from adjacent sources, have been found to affect consumer abundance in terrestrial, freshwater and marine communities, if the subsidies are periodic or seasonal and the recipient community at the time is poor in a comparable type of subsidy (e.g. nutrients) (Marczak et al. 2007). Although the Baltic Sea can hardly be called 'nutrient-poor', I found that artificial nutrient enrichment of the community still enhanced plants and herbivores (I, Figs. 4 and 5), thereby also enhancing top-down control over producers (I, II). Nutrient enrichment caused stronger grazing pressure, due to increased grazer abundance, than grazing at the ambient level. The fish were unable to inhibit so strong a grazing impact, even in deep water, where top-down control by fish was evident at the ambient nutrient level (II). I noted that nutrient enrichment increased the density of hydrobid snails as much as tenfold, causing severe grazing pressure on *C. glomerata*, *Ulva* sp. and the filamentous brown algae (II).

I also suspect that nutrient enrichment changed, via altered algal species composition, the food preferences of grazers, to the detriment of perennial algae (V). Selection for high-quality food has been suggested to increase the proportion of inedible food in nutrient-enriched systems (Leibold 1989, Murdoch et al. 1998, Darcy-Hall 2006, Mitra & Flynn 2006). I found that the filamentous brown alga *P. littoralis* increased greatly due to nutrient enrichment and was not inhibited by grazing (I, V, Fig. 5 c). An increase in food availability does not necessarily increase herbivore biomass if the quality of the food is poor, whereas an increase in high-quality food has been suggested to benefit herbivores even under strong predation pressure (Oksanen & Oksanen 2000). Such an increase in resources may lead to oscillatory dynamics in consumer populations, leading in extreme cases to population extinctions (the 'paradox of enrichment'; see Rosenzweig 1971). Since, however, these are not common in nature, Murdoch et al. (1998) suggest that inedible species may act as nutrient sponges and thereby stabilize ecosystems. Likewise Vos et al. (2004) show that inducible defenses (e.g. deterrent chemicals) in prey populations stabilize the trophic chain by dampening oscillations in predator populations. Furthermore, in tritrophic food chains the paradox of enrichment does not lead to grazer extinction if predators inhibit the population density of grazers (Oksanen & Oksanen 2000, Vos et al. 2004). Both of these mechanisms, i.e. the increase in inedible algae and the top-down control of grazers by fish, were found in my experiments (I-III, V).

With regard to multitrophic ecosystems, EEH predicts that top-down effects by predators indirectly control plants, while bottom-up effects indirectly control predators (Oksanen et al. 1981). In food webs with an odd number of trophic levels, increases in primary production should lead to increased biomass for odd-numbered trophic levels and no change in biomass for even-numbered trophic levels. Conversely, in food webs with an even number of trophic levels, increases in primary production should lead to increased biomass for even-numbered trophic levels and no change in biomass for odd-numbered trophic levels (Oksanen et al. 1981). Experimental evidence for the EEH prediction of biomass accrual along gradients of productivity was found in Swedish lakes (Persson et al. 1992). Quite the opposite result has been found in other pelagic freshwater ecosystems, where productivity has more effect at lower levels and top-down control at higher levels of the food web (McQueen et al. 1989, Brett & Goldman 1997). Moreover, a recent meta-analysis by Borer et al. (2006) of manipulative experiments in terrestrial, marine and freshwater ecosystems shows that bottom-up control does not reach herbivores or predators, while top-down control cascades down to primary producers. They claim that community regulation is asymmetric. In this thesis bottom-up control was not measured beyond the grazer trophic level, where the response reflected behavioural aggregation of grazers to resources rather than an increase in grazer abundance. Nevertheless, the enhanced nutrient supply strongly increased densities of both primary producers and mesograzers (I). Thus our results do not support the dampened bottom-up effect by Borer et al. (2006). On the other hand, the top-down effects in our study (II) cascaded from fish to algae, thus also deviating from the conclusion of a limited top-down cascade by Brett and Goldmann (1997). Although our experiments did not assess the population dynamics of grazers, the nutrient enrichments provided grazers with a rich source of food, which was seen as an aggregation of grazers. Such a change in local productivity would soon be seen in the abundance of the grazer population. As we found bottom-up-driven increases at two adjacent trophic levels, our finding is not consistent with the EEH prediction. However, Persson et al. (1992) claim that such a result can be expected if the fourth trophic level cascades weakly, causing lessened predation pressure at the herbivore trophic level and therefore an imperfect trophic cascade.

Even if we accept the conclusion by Borer et al. (2006) of the rapid attenuation of bottom-up control towards higher trophic levels, this does not obviate the fact that an excess of nutrients has led to the eutrophication of many aquatic ecosystems and has dramatically affected the whole trophic web due to the degradation of the breeding, juvenile and feeding habitats of grazers and predators (e.g. review of eutrophication by Cloern 2001, see also Österblom et al. 2001, Karlson et al. 2002, Fernández et al. 2005). This naturally leads to a decreased abundance of consumers as their resources collapse. A novel approach to the world-wide problem of eutrophication has been suggested by Heck and Valentine (2007) in their synthesis of previous work on top-down and bottom-up regulation. They challenge the dogma of bottom-up driven eutrophication process by a top-down view. The authors claim that the well-known outcomes of eutrophication are substantially caused by reduced herbivore abundance rather than by nutrients alone (Heck & Valentine 2007). They base their claim on the fact that grazing is a much stronger regulator of algae than nutrient supply, and that the harvesting of top predators (fish, seals or birds) at the fourth trophic level has led to dampened grazing intensity (see also Burkepile & Hay 2006). In the Baltic Sea the top predators, able to limit small and intermediate-sized fish, are cod (*Gadus morhua*), salmon (*Salmo salar*), grey seal (*Halichoerus grypus*), harbor seal (*Phoca vitulina*), ringed seal (*Phoca hispida*), harbour porpoise (*Phocoena phocoena*) and cormorant (*Phalacrocorax carbo*). The abundances of cod and salmon have declined continuously due to overfishing; all seal species and cormorant have been near extinction for a century due to hunting; and harbour porpoise is nowadays highly endangered and rare in the whole sea area (Helsinki Commission 2003, Strempel 2003). Reports of the abundances of coastal and pelagic fish stocks show that many third-trophic-level species have increased in past decades (Lappalainen et al. 2001, Lappalainen 2002, Ådjers et al. 2006, Helsinki Commission 2006). Grey seals and the white-tailed sea eagle, however, have increased in the northern Baltic Sea in recent years, and cormorants have returned to many coastal areas after a hundred years' absence from the Baltic Sea (Helsinki Commission 2003, Finnish Environment Institute 2007). If their abundance increases in the future, top predators may once again come to limit the third trophic level in the Baltic Sea. This, however, remains a question for further study.

3.7. Conclusions

Top-down control by fish predators and invertebrate mesograzers plays an important role in limiting littoral plant biomass in the Baltic Sea. From the opposite point of view, increased nutrient availability, representing bottom-up control, enhances recruitment density and early growth of annual macroalgae as well as densities of mesograzers. In this thesis, the interaction of these two opposing forces led to stronger biotic relationships, as numerous mesograzers fed efficiently very dense aggregations of macroalgal propagules and young filaments. Even under conditions of high nutrient availability, grazers were able to reduce total macroalgal density and prevent the bloom-like growth of *Ulva intestinalis*. They were less efficient, however, in limiting the annual brown algae, e.g. *Pilayella littoralis*. Nutrient enrichment also caused significant changes in algal species composition, such as the competitive exclusion of *Fucus vesiculosus* and the red alga *Ceramium tenuicorne*.

Fish predation is an important modifier of the macroalgal community. Top-down control by fish released macroalgae from severe grazing, causing higher density and filament length of algae than in an artificial exclusion of fish predators. Fish predation was stronger in the presence of all naturally occurring fish species than in that of perch alone, suggesting that high natural diversity is needed to maintain the functional ecosystem in littoral waters. High density and diversity of grazer fauna were also found to exert particularly strong grazing pressure on the macroalgal community. On the other hand, grazers fed readily on macroalgal propagules and early life stages, while mature communities experienced only weak reduction due to grazing. Moreover, grazing effects on macroalgae were shown to depend on the colonization time of each algal assemblage. Such small-scale variability in grazing emphasizes the dynamic nature of macroalgal mosaics on rocky shores.

The interactive effects of predation, grazing and nutrients, as well as the species composition of algae and grazers, varied along the depth gradient. Annual algae were able to utilize nutrients better in shallow than in deep water, as seen in their density and filament length. The cascading effects of fish and grazing of macroalgal propagules were strong at both depths, but deep-growing algal assemblages experienced even higher top-down control, probably due to the physically more benign environment. This thesis shows that the regulative impact of fish, grazers and nutrients on macroalgae is strong and varies between sublittoral depths. Such control has not been shown manipulatively in a littoral environment previously.

The Baltic Sea is one of the most extensively studied sea areas in the world, but we still lack large-scale analyses of the roles of top-down and bottom-up control in the Baltic marine ecosystem. The heavy human impact has caused both the excessive nutrient loading and the near extinction of large top-predators in the ecosystem. The results of my studies demonstrate clear trophic cascades from predatory fish to algae and the enriching impact of nutrients on the food chain; thus the impacts of external threats on the ecosystem can be predicted. Although the recent history of top predators in the Baltic is a sad story, the recently observed increase in the numbers of cormorants and grey seals may yet lead to the re-establishment of the fourth trophic level in the eutrophicated Baltic Sea ecosystem. Thus the story may yet turn exciting in the future!

Acknowledgements

First of all, I thank my supervisor Veijo Jormalainen for his ceaseless help during the process of writing this thesis and for the support he has given me during all phases of my work. My referees, Christoffer Boström and Klemens Eriksson, gave valuable comments on and corrections to the summary and welcome encouragement before the dissertation. My second supervisor, Markku Viitasalo, helped me in the beginning to understand experimental work and introduced me to scientific writing; thanks Make! A number of people helped in the field, but I want to make special mention of Veijo Jormalainen, Outi Vesakoski, Meri Lindqvist, Anne Hemmi, Jenni Rautanen, Tuija Honkanen and Joona Ikonen, who were involved in the fieldwork during three summers. Ellen Valle checked the language of the summary, and Ellen and Kevin O’Brien checked the language of the original articles. I express my warm thanks to all these people and colleagues.

Financial support was provided by the Walter and Andrée de Nottbeck Foundation, the Maj and Tor Nessling Foundation, the Ella and Georg Ehrnrooth foundation, and the Academy of Finland, BIREME programme.

4. Literature cited

Ådjers, K., Appelberg, M., Eschbaum, R., Lappalainen, A., Minde, A., Repecka, R. & Thoresson, G. 2006. Trends in coastal fish stocks of the Baltic Sea. Boreal Environment Research 11: 13-25.

Austrheim, G. & Eriksson, O. 2001. Plant species diversity and grazing in the Scandinavian mountains – patterns and processes at different spatial scales. Ecography 24: 683-695.

Bäck, S. & Ruuskanen, A. 2000. Distribution and maximum growth depth of *Fucus vesiculosus* along the Gulf of Finland. Marine Biology 136: 303-307.

Bäck, S., Lehvo, A. & Blomster, J. 2000. Mass occurrence of unattached *Enteromorpha intestinalis* on the Finnish Baltic Sea coast. Annales Botanici Fennici 37: 155-161.

Berger, R., Henriksson, E., Kautsky, L. & Malm, T. 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. Aquatic Ecology 37: 1-11.

Bergström, L., Berger, R. & Kautsky, L. .2003. Negative effects of nutrient enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. European Journal of Phycology 38: 41-46.

Borer, E.T., Halpern, B.S. & Seabloom, E.W. 2006. Asymmetry in community regulation: Effects of predators and productivity. Ecology 87: 2813-2820.

Bosman, A.L. & Hockey, P.A.R. 1986. Seabird guano as a determinant of rocky intertidal community structure. Marine Ecology Progress Series 32: 247-257.

Boström, C. & Bonsdorff, E. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. Journal of Sea Research 37: 153-166.

Boyer, A.G., Swearingen, R.E., Blaha, M.A., Fortson, C.T., Gremillion, S.K., Osborn, K.A. & Moran, M.D. 2003. Seasonal variation in top-down and bottom-up processes in a grassland arthropod community. Oecologia 136: 309-316.

Boyer, K.E., Fong, P., Armitage, A.R., Cohen, R.A. 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs 23: 530-538.

Brett, M.T. & Goldman, C.R. 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275: 384-386.

Burkepile, D.E. & Hay, M.E. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87: 3128-3139.

Carpenter, S.R., Kitchell, J.R. & Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634-639.

Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210: 223-253.

Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y.H. 1982. Randomness, area, and species richness. Ecology 63: 1121-1133.

Connan, S., Goulard, F., Stieger, V., Deslandes, E. & Ar Gall, E. 2004. Interspecific and temporal variation in phlorotannin levels in an assemblage of brown algae. Botanica Marina 47: 410-416.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities; a model and evidence from field experiments. In: Cody, M.L. & Diamond, J. (eds). Ecology and evolution of communities. Belknap, Cambridge, Mass. pp. 460-490.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Cronin, G. & Hay, M.E. 1996. Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology 77: 1531-1543.

Cronin, G. & Lodge, D.M. 2003. Effects of light and nutrient availability on the growth, allocation, carbon/nitrogen balance, phenolic chemistry, and resistance to herbivory of two freshwater macrophytes. Oecologia 137: 32-41.

Cruz-Rivera, E. & Hay, M.E. 2003. Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. Ecological Monographs 73: 483-506.

Darcy-Hall, T.L. 2006. Relative strengths of benthic algal nutrient and grazer limitation along a lake productivity gradient. Oecologia 148: 660-671.

Daskalov, G.M., Grishin, A.N, Rodionov, S. & Mihneva, V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences of the USA 104: 10518-10523.

Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389.

Dudgeon, S. & Petraitis, P. S. 2001. Scale-dependent recruitment and divergence of intertidal communities. Ecology 82: 991-1006.

Duffy, J.E., Richardson, J.P. & France, K.E. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. Ecology Letters 8: 301-309.

Enderlein, P. & Wahl, M. 2004. Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. Journal of Sea Research 51: 145-155.

Engkvist, R., Malm, T. & Tobiasson, S. 2000. Density dependent grazing effects of the isopod *Idotea baltica* Pallas on *Fucus vesiculosus* L in the Baltic Sea. Aquatic Ecology 34: 253-260.

Eriksson, B.K. & Bergström, L. 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. Estuarine, Coastal and Shelf Science 62: 109-117.

Eriksson, B.K. & Johansson, G. 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. European Journal of Phycology 38: 217-222.

Estes, J.A., Tinker, M.T., Wiliams, T.M. & Doak, D.F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473-476.

Fernández, J.M., Selma, M.A.E., Aymerich, F.R., Sáez, M.T.P., Fructuoso, M.F.C. 2005. Aquatic birds as bioindicators of trophic changes and ecosystem deterioration in the Mar Menor lagoon (SE Spain). Hydrobiologia 550: 221-235.

Finke, D.L. & Denno, R.F. 2004. Predator diversity dampens trophic cascades. Nature 429: 407-410.

Finnish Environment Institute. 2007. Cormorant population grew by more than fifty percent from last year. Available at: www.environment.fi > Finnish Environment ... > Current > Press releases > Press releases 2007 > Cormorant population grew by more than fifty percent from last year.

Forrester, G.E., Dudley, T.L. & Grimm, N.B. 1999. Trophic interactions in open systems: Effects of predators and nutrients on stream food chains. Limnology & Oceanography 44: 1187-1197.

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308: 1621-1623.

Fraser, L.H. 1998. Top-down vs bottom-up control influenced by productivity in a North Derbyshire, UK, Dale. Oikos 81: 99-108.

Fretwell, S.D. 1977. The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine 20: 169-185.

Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. 2005. Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. Ecology Letters 8: 696-703.

Gillman, L.N. & Wright, S.D. 2006. The influence of productivity on the species richness of plants: A critical assessment. Ecology 87: 1234-1243.

Gonen, Y., Kimmel, E. & Friedlander, M. 1993. Effect of relative water motion on photosynthetic rate of red alga Gracilaria conferta. Hydrobiologia 260-261: 493-498.

Graff, P., Aguiar, M.R. & Chaneton, E.J. 2007. Shifts in positive and negative plant interactions along a grazing intensity gradient. Ecology 88: 188-199.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344-347.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960. Community structure, population control, and competition. American Naturalist 94: 421-425.

Hällfors, G., Kangas, P. & Lappalainen, A.1975. Littoral benthos of the northern Baltic Sea. 3. Macrobenthos of the hydrolittoral belt of filamentous algae on rocky shores in Tvärminne. Internationale Revue der Gesamten Hydrobiologie 60: 313-333.

Halpern, B.S., Borer, E.T., Seabloom, E.W. & Shurin, J.B. 2005. Predator effects on herbivore and plant stability. Ecology Letters 8: 189-194.

Harley, C.D.G. 2003. Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. Ecology 84: 1477-1488.

Heck, K.L. Jr., Pennock, J.R., Valentine, J.F., Coen, L.D. & Sklenar, S.A. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment. Limnology & Oceanography 45: 1041-1057.

Heck, K.L. Jr. & Valentine J. F. 2007. The primacy of top-down effects in shallow benthic ecosystems. Estuaries and Coasts 30: 371-381.

Helsinki Commission - Baltic Marine Life Protection Commission. 2003. TheBaltic marine environment 1999-2002. Baltic Sea Environment Proceedings 87, 48 pp. Available at: www.helcom.fi.

Helsinki Commission - Baltic Marine Life Protection Commission. 2006. Assessment of coastal fish in the Baltic Sea. Baltic Sea Environment Proceedings 103 A, 28 pp. Available at: www.helcom.fi.

Hemmi, A. & Jormalainen, V. 2002. Nutrient enhancement increases performance of a marine herbivore via quality of its food alga. Ecology 83: 1052-1064.

Hrbacek, J., Dvorakova, M., Kobinek, V. & Prochazkova, L. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Internationale Vereininigung für theoretische und angewandte Limnologie, Verhandlungen 14:192–195.

Hunter, M.D. & Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of top-down and bottom-up forces in natural communities. Ecology 73:724–732

Hurd, C.L. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology 36: 453-472.

Huston, M.A. 1979. A general hypothesis of species diversity. American Naturalist 113: 81-101.

Jansson, B.-O. & Wulff, F. 1977. Ecosystem analysis of a shallow sound in the northern Baltic Sea: A joint study by the Askö group. Contributions from the Askö Laboratory, University of Stocholm, Sweden.

Jara, V.C., Miyamoto, J.H.S., Da Gama B.A.P., Molis, M., Wahl, M. & Pereira R.C. 2006. Limited evidence of interactive disturbance and nutrient effects on the diversity of macrobenthic assemblages. Marine Ecology Progress Series 308: 37-48.

Jormalainen, V. & Honkanen, T. 2007. Macroalgal chemical defenses and their roles in structuring temperate marine communities. In: Amsler, C.D. (ed.) Chemical ecology. Springer-Verlag Berlin Heidelberg.

Jormalainen, V., Honkanen, T. & Heikkilä, N.. 2001 *a*. Feeding preferences and performance of a marine isopod on seaweed hosts: Cost of habitat specialization. Marine Ecology Progress Series 220: 219-230.

Jormalainen, V., Honkanen, T., Mäkinen, A., Hemmi, A., Vesakoski, O. 2001 *b*. Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. Oikos 93: 77-86.

Kallio, P. & Lehtonen, J. 1975. On the ecocatastrophe of birch forests caused by *Oporinia autumnata*. In: F. E. Wielgolaski, ed. Fennoscandian tundra ecosystems. 11. Animals and systems analysis. Ecological Studies 17. Springer, Berlin. pp 174-180.

Kangas, P., Autio, H., Hällfors, G., Luther, H., Niemi, Å. & Salemaa, H. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. Acta Botanicum Fennici 118: 1-27.

Karlson, K., Rosenberg, R., Bonsdorff, E. 2002. Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters - a review. Oceanography and Marine Biology: an Annual Review 40: 427-489.

Kautsky, L. & Kautsky, H. 1989: Algal species diversity and dominance along gradients of stress and disturbance in marine environments. Vegetatio 83: 259-267.

Kautsky, H. & van der Maarel, E. 1990. Multivariate approaches to the variation in phytobenthic communities and environmental vectors in the Baltic Sea. Marine Ecology Progress Series 60: 169-184.

Kawamata, S. 1998. Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin *Strongylocentrotus nudus* (A. Agassiz). Journal of Experimental Marine Biology and Ecology 224: 31-48.

Kiirikki, M. & Lehvo, A.. 1997. Life strategies of filamentous algae in the northern Baltic Proper. Sarsia 82: 259-267.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society of

London Series B - Biological Sciences 268: 269-271.

Lapointe, B.E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and Southeast Florida. Limnology & Oceanography 42: 1119-1131.

Lappalainen, A. 2002. The effects of recent eutrophication on freshwater fish communities and fishery on the northern coast of the Gulf of Finland, Baltic Sea. Department of Limnology and Environmental Protection, University of Helsinki, Finland, and Finnish Game and Fisheries Research Institute. Doctoral Dissertation. 24 pp. Available at: https://oa.doria.fi/handle/10024/3145.

Lappalainen, A., Rask, M., Koponen, H. & Vesala, S. 2001. Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea, in 1975 and 1997: responses to eutrophication? Boreal Environment Research 6: 107-118.

Lappalainen, A., Shurukhin, A. Alekseev, G. & Rinne, J. 2000. Coastal fish communities along the northern coast of the Gulf of Finland, Baltic Sea: Responses to salinity and eutrophication. International Review of Hydrobiology 85: 687-696.

Leibold, M.A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist 134: 922-949.

Leonard, G.H., Levine, J.M., Schmidt, P.R. & Bertness, M.D. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology, 79: 1395-1411.

Lewis, J.R. 1964. The ecology of rocky shores. English Universities Press, London. 323 pp.

Lotze, H.K., Schramm, W., Schories, D. & Worm, B. 1999. Control of macroalgal blooms at early developmental stages: *Pilayella littoralis* versus *Enteromorpha* spp. Oecologia 119: 46-54.

Lotze, H.K., Worm, B. & Sommer, U. 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnology & Oceanography 46: 749-757.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. American Naturalist 112: 23-39.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: An experimental analysis. Ecology 61: 333-344.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64: 1116-1123.

Lubchenco, J. & Gaines, S.D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics 12: 405-437.

Lubchenco, J. & Menge, B.A. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 48: 67-94.

Malm, T., Engkvist, R. & Kautsky, L. 1999. Grazing effects of two freshwater snails on juvenile *Fucus vesiculosus* in the Baltic Sea. Marine Ecology Progress Series 188: 63-71.

Marczak, L.B., Thompson, R.M. & Richardson, J.S. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88: 140-148.

Martínez, E.A. 1996. Micropopulation differentiation in phenol content and susceptibility to herbivory in the Chilean kelp *Lessonia nigrescens* (Phaeophyta, Laminariales). Hydrobiologia 326-327: 205-211.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart T.J., Lean D.R.S. 1989. Bottom-up and top-down impacts on fresh-water pelagic community structure. Ecological Monographs 59: 289-309.

McIntosh, A.R. & Townsend, C.R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108: 174-181.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. Ecological Monographs 46: 355-393.

Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65: 21-74.

Menge, B.A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250: 257-289.

Menge, B.A. & Branch, G.M. 2001. Rocky intertidal communities. *In* M.D. Bertness, S.D. Gaines and M.E. Hay [eds.], Marine Community Ecology, pp. 221-251. Sinauer Associates.

Menge, B.A., Daley,B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G. & Burnaford, J.L. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs 69: 297-330.

Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford E. & Strub, P.T. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences of the United States of America 94: 14530-14535.

Menge, B. A., Farrell, T. M., Olson, A. M., van Tamelen, P. & Turner, T. 1993. Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. Journal of Experimental Marine Biology and Ecology 170: 91-116.

Menge, B.A., Lubchenco, J., Bracken, M.E.S., Chan, F., Foley, M.M., Freidenburg, T.L., Gaines, S.D., Hudson, G., Krenz, C., Leslie, H., Menge, D.N.L., Russell, R. & Webster, M.S. 2003: Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences of the United States of America 100:12229-12234.

Menge, B.A. & Olsen, A.M. 1990: Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5: 52-57.

Menge, B.A. & Sutherland, J.P. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110: 351-369.

Menge, B.A. & Sutherland, J.P. 1987. Community regulation: Variance in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130: 730-757.

Mitra, A. & Flynn, K.J. 2006. Promotion of harmful algal blooms by zooplankton predatory activity. Biology Letters 2: 194-197.

Morgan, J.A., Aguiar, A.B., Fox, S., Teichberg, M. & Valiela, I. 2003. Relative influence of grazing and nutrient supply on growth of the green macroalga *Ulva lactuca* in estuaries of Waquoit Bay, Massachusetts. Biological Bulletin 205: 252-253.

Murdoch, W.W., Nisbet, R.M., McCauley, E., DeRoos, A.M. & Gurney, W.S.C. 1998. Plankton abundance and dynamics across nutrient levels: Tests of hypotheses. Ecology 79: 1339-1356.

Nielsen, K.J. 2001. Bottom-up and top-down forces in tide pools: Test of a food chain model in an intertidal community. Ecological Monographs 71: 187-217.

Nielsen, K.J., Blanchette, C.A., Menge, B.A., Grantham, B., & Lubchenco, J. 2003. Capturing the light fantastic: Oceanographic and tidal influences on intertidal algae. Journal of Phycology 39 S1: 44-45.

Oksanen, L, Fretwell, S.D., Arruda, J. & Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240-261.

Oksanen, L. & Oksanen, T. 2000. The logic and realism of the hypothesis of eploitation ecosystems. American Naturalist 155: 703-723.

Pace, M.L., Cole, J.L., Carpenter, S.R. & Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14: 483-487.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Paine, R.T. 2002. Trophic control of production in a rocky intertidal community. Science 296: 736-739.

Pavia, H. & Brock, E. 2000. Extrinsic factors influencing phlorotannin production in the brown alga *Ascophyllum nodosum*. Maine Ecology Progress Series 193: 285-294.

Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S.F. 1992. Trophic interactions in temperate lake ecosystems: A test of food chain theory. American Naturalist 140: 59-84.

Piazena, H. & Häder, D.-P. 1994. Penetration of solar UV irradiation in coastal lagoons of the southern Baltic Sea and its effect on phytoplankton communities. Photochemistry and Photobiology 60: 463-469.

Polis, G.A. & Strong, D.R. 1996. Food web complexity and community dynamics. American Naturalist 147: 813-846.

Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86: 3-15.

Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79: 2581-2592.

Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B. & Lean, D.R.S. 1996. Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic systems. Ecology 77: 1556-1572.

Qvarfordt, S. 2006. Phytobenthic communities in the Baltic Sea: seasonal patterns in settlement and succession. Doctoral thesis. Department of Systems Ecology, University of Stockholm, Sweden. Available at: http://www.diva-portal.org/su/theses/abstract.xsql?dbid=1153.

Råberg, S., Berger-Jönsson, R., Björn, A.., Graneli, E. & Kautsky, L. 2005. Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment: implications for community composition. Marine Ecology Progress Series 289: 131-139.

Rajasilta, M., Mankki, J. Ranta-Aho, K. & Vuorinen, I. 1999. Littoral fish communities in the Archipelago Sea, SW Finland: A preliminary study of changes over 20 years. Hydrobiologia 393: 253-260.

Renaud, P.E., Hay, M.E. & Schmitt, T.M. 1990. Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. Oecologia 82: 217-226.

Robles, C. & Robb, J. 1993. Varied carnivore effects and the prevalence of intertidal algal turfs. Journal of Experimental Marine Biology and Ecology 166: 65-91.

Rosenzweig, M.L. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. Science 171: 385-387.

Rosenzweig, M.L. & Abramsky, Z. 1993. How are diversity and productivity related. In: Ricklefs, R.E. & Schlutee, D. (eds.) Species diversity in biological communities. pp 52-65. University of Chigaco Press. Illinois, USA.

Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the northern Baltic Sea. Ophelia 27: 1-15.

Salovius, S. & Bonsdorff, E. 2004: Effects of depth, sediment and grazers on the degradation of drifting filamentous algae (*Cladophora glomerata* and *Pilayella littoralis*). Journal of Experimental Marine Biology and Ecology 298: 93-109.

SAS Institute. 1999. SAS/STAT User's Guide, Version 8. SAS Institute Inc., Cary, NC., USA.

Schmitz, O.J., Kalies, E.L. & Booth, M.G. 2006. Alternative dynamic regimes and trophic control of plant succession. Ecosystems 9: 459-472.

Shears, N.T. & Babcock, R.C. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132: 131-142.

Shears, N.T. & Babcock, R.C. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series 246: 1-16.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Andersson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5: 785-791.

Shurin, J.B., Gruner, D.S. & Hillebrand, H. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society of London Series B - Biological Sciences 273: 1-9.

Silliman, B.R & Bertness, M.D. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences, USA 99: 10500-10505.

Smith, J.E., Smith, C.M. & Hunter, C.L. 2001: An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19: 332-342.

Snyder, W.E., Snyder, G.B., Finke, D.L. & Straub, C.S. 2006. Predator biodiversity strengthens herbivore suppression. Ecology Letters 9: 789-796.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. Ecology 60: 1225-1239.

Sousa, W.P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65: 1918-1935.

Steele, D.H. & Whittick, A. 1991. Seasonal variation in *Pilayella littoralis* (Phaeophycae) and its consequences as a food source for the amphipod, *Gammarus lawrencianus*, in the intertidal of Newfoundland. Journal of the Marine Biological Association of the United Kingdom 71: 883-889

Steen, H. 2004. Interspecific competition between *Enteromorpha* (Ulvales: Chlorophycaceae) and *Fucus* (Fucales: Phaeophyceae) germlings: effects of nutrient concentration, temperature, and settlement density. Marine Ecology Progress Series 278: 89-101.

Strempel, R. 2003. The ASCOBANS Jastarnia plan: Towards a new lease of life for Baltic harbor porpoises. Journal of Internationsl Wildlife Law and Policy 6: 53-55.

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America 102: 4387-4392.

Sundbäck, K., Miles, A., Hulth, S., Pihl, L., Engström, P, Selander, E. & Svenson, A. 2003. Importance of benthic nutrient regeneration during initiation of macroalgal blooms in shallow bays. Marine Ecology Progress Series 246: 115-126.

Sundell, J. 1994. Dynamics and composition of littoral fish fauna along the coast of SW Finland. Aqua Fenn 24: 37-50.

Svensson, J.R., Lindegarth, M., Siccha, M., Lenz, M., Molis, M., Wahl, M. & Pavia, H. 2007. Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. Ecology 88: 830-838.

Taylor, K.L., Aarssen, L.W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. Oikos 58: 239-250.

Toth, G.B. & Pavia, H. 2007. Induced herbivore resistance in seaweeds: a meta-analysis. Journal of Ecology 95: 425-434.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D. & Foremani, K. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology & Oceanography 42: 1105-1118.

Vos, M., Kooi, B.W., DeAngelis, D.L. & Mooij, W.M. 2004. Inducible defences and the paradox of enrichment. Oikos 105: 471-480.

Wootton, J.T. 1994: The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25: 443-466.

Wootton, J.T. 1995. Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. Ecoscience 2: 321-328.

Worm, B., Lotze, H.K., Boström, C., Engkvist, R., Labanauskas, V. & Sommer, U. 1999. Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. Marine Ecology Progress Series 185: 309-314.

Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417: 848-851.

Worm, B., Lotze, H.K. & Sommer, U. 2000 a. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. Limnology & Oceanography 45: 339-349.

Worm, B., Lotze, H.K. & Sommer, U. 2001. Algal propagule banks modify competition, consumer and resource control on the Baltic rocky shores. Oecologia 128: 281-293.

Worm, B., Reusch, T.B.H. & Lotze, H.K. 2000 *b*. In situ nutrient enrichment: Methods for marine benthic ecology. International Review of Hydrobiology 85: 359-375.

Wright, D.H. 1983. Species-energy theory: An extension of species-area theory. Oikos 41:496-506.

Österblom, H., Bignert, A., Fransson, T. & Olsson, V. 2001. A decrease in fledging body mass in common guillemot *Uria aalge* chicks in the Baltic Sea. Marine Ecology Progress Series 224: 305-309.

Erratum

Paper II, Fig. 3 a: The title of the vertical axis should read: Stomach content (ind. per stomach).