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Consumer versus resource control in rocky shore food webs:

Baltic Sea and Northwest Atlantic Ocean

by

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Glossary: definitions and abbreviations

ANOVA	Analysis of variance
assemblage	A subset of a community chosen for study. This may include only one trophic level
community	A set of species at a geographic location. This should include all species and trophic levels
community structure	Distribution and abundance of species in a community
consumer	Grazer or predator
d	Day(s)
DIN	Dissolved inorganic nitrogen (ammonium + nitrate + nitrite)
DIP	Dissolved inorganic phosphorus (soluble reactive phosphate)
eutrophication	Increasing rate of supply of organic matter to ecosystems (Nixon 1995), typically through an increase in nutrient supply
food web	A set of interacting species which are connected through feeding links
grazer	Organism that consumes living plants (= herbivore)
h	Hour(s)
MANOVA	Multivariate analysis of variance
min	Minute(s)
omnivore	Organism that feeds on several trophic levels (plants and animals)
predator	Organism that consumes living animals (= carnivore)
PSU	Practical Salinity Units
RGR	Relative growth rate
RM-ANOVA	Repeated-measures analysis of variance
SE	Standard error
wk	Week(s)
yr	Year(s)

Photographs



Photo 1. Relatively pristine rocky shore community in the Western Baltic Sea (Eckernförde Bay, June 1998, ca. 0.5 m water depth). The canopy is dominated by large macroalgae (*Fucus vesiculosus*), but numerous species of annual algae and benthic invertebrates co-occur with *Fucus*. Important grazers in this system are littorinid snails, and small crustaceans (isopods and amphipods). Predators include decapod crabs and shrimps as well as fishes. A similar community is found in the low intertidal zone at sheltered sites in Nova Scotia, NW Atlantic.



Photo 2. Typical eutrophic rocky shore site in the Baltic Sea (Hjälpö, Åland Islands, June 1998, ca. 0.5 m water depth). The structurally complex *Fucus* assemblage has been replaced by a uniform turf of fast-growing annual algae (*Pilayella littoralis*) which supports only few consumer species. Photo by C. Boström.



Photo 3. Design of factorial field experiments (Chapter 5 - 7). Rocks (ca. 20 cm diameter) inside cages were colonized by algae and invertebrates. Cages excluded (left) or provided access to grazers and predators (right). Uncaged control plots were also established (not shown). Nutrient supply was manipulated with diffusers (mesh rolls filled with slow-release fertilizer, in the right cage, see also Photo 4).



Photo 4. An experimental nutrient gradient using nutrient diffusers (Chapter 6, 7). Comparative experiments in the Baltic Sea and the NW Atlantic Ocean had 6 different nutrient treatments. Water column nutrient (DIN and DIP) concentrations were a linear function of diffuser length and fertilizer mass. In both experiments, the longest diffuser (left, 80 cm) caused a 200% increase in DIN concentrations, the shortest diffuser (right, 2.5 cm) a 6% increase.



Photo 5. Baltic Sea experiment in June 1997 (Chapter 5). Massive development of green annual algae (*Enteromorpha intestinalis*) occurred on ungrazed and plots (left). Grazers strongly suppressed *Enteromorpha* development (right).



Photo 6. Baltic Sea experiment in October 1998 (Chapter 6). *Fucus* recruitment was low on rocks without grazers and with nutrient-enrichment which were dominated by annual algae in the summer (left). Abundant *Fucus* recruitment occurred on plots with grazers and at ambient nutrient concentrations (right). An 85% increase in DIN concentrations had the same negative effects on *Fucus* recruitment as exclusion of grazers.



Photo 7. NW Atlantic experiment in July 1999 (Chapter 7). Only when grazers were excluded and nutrients were enriched, a dense cover of annual algae developed (left). When grazers were excluded but no nutrients enriched, a sparse macroalgal cover developed (mid). When grazers were present, they strongly suppressed all algae independent of nutrient enrichment (right).



Photo 8. "Grazer-nutrient assay" (Chapter 8). Comparative cage experiments were conducted in 1998 and 1999 at 12 sites in the Baltic and NW Atlantic, involving nutrient-rich and nutrient-poor sites. Ceramic tiles seeded with spores of the fast-growing but grazer-susceptible annual *Enteromorpha* were exposed in open and closed cages and uncaged control plots. This setup was replicated 5 times at each site. Experiments were run for 23 days once in spring and once in summer.

Abstract

Rocky shores are among the most productive ecosystems on the planet. Community biomass and primary productivity are dominated by canopy-forming perennial macroalgae, which fulfill important ecosystem functions including carbon storage, nutrient cycling and the provision of food and habitat for a diverse invertebrate and fish fauna. Recently, perennial macroalgae have severely declined in abundance in the Baltic Sea and other nutrient-rich coastal systems. In this thesis, I analyzed causes and consequences of these changes in a food-web context. Rocky shore food webs are characterized by strong interactions among macroalgae, sessile filter feeders, grazers and predators. Humans alter these webs by harvesting species at various trophic levels (e.g. fish, snails, macroalgae) and by adding plant nutrient resources through coastal eutrophication (dissolved inorganic nitrogen [DIN] and phosphorus compounds [DIP]). My goal was to understand the interactive effects of changes in consumer abundance and nutrient resources on benthic community structure, species diversity and ecosystem functioning. I addressed this through *in situ* nutrient enrichment and caging experiments and large-scale field surveys in the Baltic Sea and the NW Atlantic Ocean, which I used as model systems for nutrient-rich and nutrient-poor ecosystems, respectively.

In the Baltic, I performed a short-term enrichment experiment (25 d) where I exposed single plants of the canopy-forming, perennial macroalga *Fucus vesiculosus* with epiphytes present or removed to pulses of elevated nutrients (DIN and DIP). Repeated 1-h pulses had no effects. A single 5-h pulse increased epiphyte load but not *Fucus* growth rate. However, increasing epiphyte load caused *Fucus* growth rate to decline and attracted higher densities of gastropod grazers. These results indicate that a single nutrient pulse can have strong direct and indirect effects on macroalgae, epiphytes and grazers. Temporal variability of nutrient supply (five 1-h versus one 5-h pulse) plays a significant role in determining the response of primary producers and consumers to elevated nutrients.

Long-term consequences of enhanced nutrient loading and eutrophication were assessed in a growth experiment (1.5 yr) where I transplanted *Fucus* germlings along a nutrient-gradient in Schlei Fjord, Western Baltic Sea. Productivity at the least eutrophied site (Maasholm) was estimated at $4900 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is higher than record values from any other ecosystem. *Fucus* productivity declined by two orders of magnitude along the eutrophication gradient because of reduced growth and increased mortality, probably linked to light competition from phytoplankton.

The relative effects of gastropod and crustacean mesograzers, nutrients and different sources of propagule supply were investigated in a factorial field experiment in Maasholm (Schlei Fjord, Baltic Sea). I followed colonization of rocky surfaces from February - December 1997.

Grazers were manipulated year-round with exclusion cages, nutrient supply was enhanced in the summer with nutrient diffusers (DIN and DIP). Experimental rocks were initially heat-sterilized (propagule supply from dispersal only) or left untreated (supply from a bank of dormant propagules and dispersal). Propagule supply from a propagule bank strongly favored the fast-growing annual alga *Enteromorpha* spp., which then blocked settlement and recruitment of perennial *Fucus*. Grazers reduced abundance of annual algae and thereby favored *Fucus* recruitment. Nutrient enrichment did override grazer control of annual algae and accelerated the decline of *Fucus* only when annual algae had already achieved high densities through the propagule bank. This shows that propagule supply from propagule banks can modify plant competition and the effects of consumers and resources in this community.

In two subsequent experiments (February - December 1998 and 1999), I compared the relative effects of grazers and year-round nutrient enrichment between Maasholm (Baltic Sea) and Bald Rock (Scotian Shelf, NW Atlantic). I established six *in situ* enrichment treatments with 6 - 200% increased DIN concentrations. Grazers were present or excluded with cages. Whereas in the Baltic grazers mostly affected algal species composition but not total abundance (shift from palatable to herbivore-resistant algae), abundance of all macroalgae was strongly reduced by grazing in the NW Atlantic. Nutrient enrichment increased algal abundance and favored annual over perennial algae, which had negative consequences for ecosystem functioning (carbon storage, nitrogen retention) in the Baltic but not the NW Atlantic. Nutrient effects were transmitted through the food web and increased algal, grazer and predator abundance in both experiments ("bottom-up control"). Cascading "top-down" effects of predators on grazers and algae were seen only in the Baltic during summer. Grazers enhanced and nutrients reduced plant species diversity in the Baltic, but these effects were reversed in the NW Atlantic. This appeared to be a predictable result of the much higher nutrient supply and productivity in the Baltic. Increases in productivity (through enrichment) increased species diversity in the NW Atlantic but decreased diversity in the Baltic. This is in accordance with a unimodal productivity-diversity relationship, which was predicted by competition theory.

In an attempt to quantify variability in the effects of grazers and nutrients across multiple sites, I developed a "grazer-nutrient assay" using tiles seeded with spores of the fast-growing but grazer-susceptible annual alga *Enteromorpha intestinalis*. Comparative grazer-exclusion experiments were performed in the Baltic (4 sites) and the NW Atlantic (4 nutrient-poor and 4 nutrient-enriched sites) in spring and summer 1998 and 1999. Results showed that grazers strongly suppressed annual algae in spring. In summer, grazer control weakened in the Baltic but not in the NW Atlantic. At nutrient-rich sites, *Enteromorpha* abundance on the tiles increased 10-fold compared with nutrient-poor sites. Grazers removed a relatively constant fraction of *Enteromorpha* germlings independent of total germling density. This corroborates the experiments in the Baltic and implies that grazers buffer but usually not override the effects of eutrophication.

Large-scale surveys across 25 sites in the Baltic and 16 sites in the NW Atlantic verified key predictions derived from field experiments. Recruitment and abundance of *Fucus* in the Baltic were negative functions of annual algal cover during the time of *Fucus* reproduction. At eutrophied sites in the NW Atlantic, either annual algae or filter feeders (mostly mytilid mussels) had increased and fucoids had decreased abundance compared with nutrient-poor sites. Abundance of grazers correlated negatively with abundance of annual algae. These patterns suggest that current large-scale declines of perennial algae are a consequence of increased nutrient loading causing recruitment inhibition through annual algal turfs (Baltic, NW Atlantic) or mussel beds (NW Atlantic only). Grazers counteract this through selective consumption of annual algae. Therefore, a low abundance of grazers (e.g. through harvesting) likely enhances the effects of eutrophication.

In summary, experiments and observations indicated that grazers and nutrients had strong and antagonistic effects on macroalgal species composition, abundance, carbon and nitrogen cycling in the studied rocky shore food webs. I found evidence for transmission of both “bottom-up” and “top-down” effects through several trophic levels (algae, grazer, and predators). The magnitude and direction of grazer and nutrient effects on species diversity changed predictably with increasing system productivity and sources of propagule supply. Importantly, this study provides detailed experimental evidence that increasing nitrogen loading causes shifts in macroalgal diversity, loss of long-lived perennial algae, increased intensity of destructive algal blooms and the disruption of important ecosystem functions, and that these responses are tightly linked.

Zusammenfassung

Felsküsten gehören zu den produktivsten Lebensräumen der Erde. Die Biomasse und Produktivität der Artengemeinschaft werden meist von mehrjährigen, großwüchsigen Makroalgen bestimmt. Diese erfüllen wichtige Funktionen im Ökosystem. Sie speichern Kohlenstoff und fungieren so als CO₂-Senke, sie sind ein wichtiges Bindeglied im marinen Nährstoffkreislauf, und sie bilden Nahrung und Habitat für eine artenreiche Fisch- und Wirbellosenfauna. In den letzten Jahrzehnten sind mehrjährige Makroalgen jedoch stark zurückgegangen besonders in der Ostsee aber auch in anderen nährstoffreichen Küstensystemen. In meiner Arbeit habe ich die Ursachen und Auswirkungen dieser Veränderungen auf der Ebene von Nahrungsnetzen untersucht. Nahrungsnetze an Felsküsten sind geprägt von starken Wechselwirkungen zwischen Algen, sessilen Filtrierern, Herbivoren und Prädatoren. Menschen greifen nachhaltig in diese Beziehungen ein, zum einen durch Befischung von Arten auf verschiedenen trophischen Ebenen (z.B. Fische, Schnecken, Makroalgen), andererseits durch massive Anreicherung von Pflanzennährstoffen (Eutrophierung mit gelösten Stickstoff- [DIN] und Phosphorverbindungen [DIP]). Mein Hauptanliegen war, die jeweiligen Effekte von Veränderungen der Konsumentenfauna und der Nährstoffressourcen auf die Struktur, Diversität und Funktion küstennaher Lebensgemeinschaften zu verstehen. Dazu habe ich mehrere Freilandexperimente durchgeführt, in denen ich Nährstoffe angereichert sowie die Anwesenheit von Konsumenten manipuliert habe. Ferner habe ich umfangreiche Probennahmen an Hartbodengemeinschaften durchgeführt. Vergleichende Experimente und Surveys fanden in der Ostsee und im kanadischen Teil des NW Atlantik statt. Diese Meere dienten dabei jeweils als Modelle für nährstoffreiche und nährstoffarme Ökosysteme.

Zunächst führte ich in der Ostsee ein Experiment mit kurzzeitigen Nährstoffgaben durch. Dabei wurden Pflanzen des bestandsbildenden Blasenalgens *Fucus vesiculosus* mit und ohne Aufwuchsalgen (Epiphyten) einzelnen (1 x 5 h) oder wiederholten (5 x 1 h) Nährstoffpulsen ausgesetzt (DIN und DIP). Nach 25 Tagen hatten die wiederholten Düngergaben keinen Effekt aber ein 5-h Puls hatte die Epiphytenfracht auf *Fucus* deutlich erhöht. Das führte zum einen zu geringerem Wachstum von *Fucus*, zum anderen siedelten sich mehr Herbivore an. Dies zeigt, daß schon ein einzelner Nährstoffpuls die relative Abundanz von Makroalgen, Epiphyten und Herbivoren im Nahrungsnetz verändern kann und daß dabei die zeitliche Verteilung der Nährstoffgaben eine wichtige Rolle spielt.

Die Langzeitauswirkungen hoher Nährstofffrachten untersuchte ich in einem Wachstumsexperiment, bei dem Keimlinge von *Fucus* entlang eines Eutrophierungs-Gradienten in der Schlei (Westliche Ostsee) ausgebracht wurden. Die Produktion von *Fucus* an dem geringst eutrophierten Standort (Maasholm) betrug 4900 g C m⁻² yr⁻¹ was offenbar einen weltweiten Rekord

darstellt. Entlang des Eutrophierungs-Gradienten ging die Produktion von *Fucus* um zwei Größenordnungen zurück. Dies lag an dem verminderten Wachstum und der erhöhten Mortalität der Pflanzen, die vermutlich auf erhöhte Lichtkonkurrenz durch das Phytoplankton zurückzuführen sind.

Die relativen Einflüsse von Herbivoren, Nährstoffen und der Verfügbarkeit von Algensporen in einer überwinternden "Sporenbank" wurden in einem Experiment in Maasholm (Westliche Ostsee) untersucht. Von Februar - Dezember 1997 folgte ich der Besiedlung von in Käfigen eingeschlossenen Steinen. Herbivore wurden aus Käfigen ausgeschlossen oder hatten Zutritt zu offenen Käfigen. Nährstoffe wurden im Sommer mit Diffusoren angereichert (DIN+DIP). Die als Besiedlungsflächen dienenden Steine wurden zu Beginn entweder sterilisiert (keine Sporenbank, Besiedlung nur aus neu produzierten Sporen) oder unbehandelt gelassen (Besiedlung aus der Sporenbank möglich). In Anwesenheit der Sporenbank erreichte die schnellwachsende einjährige Grünalge *Enteromorpha* spp. sehr hohe Dichten und blockierte damit die Ansiedlung von *Fucus* und anderen Algen, welche weniger von der Sporenbank profitierten. Herbivore fraßen selektiv Grünalgen und förderten damit die Ansiedlung von *Fucus*. Durch Nährstoffanreicherung konnte ich den Herbivoreneffekt auf schnellwachsende Grünalgen teilweise ausgleichen. Dies führte zu weiteren Verlusten bei *Fucus*, dies jedoch nur wenn Grünalgen bereits hohe Dichten aufgrund der Sporenbank aufwiesen. Dies zeigt, daß die Anwesenheit einer Sporenbank sowohl Konkurrenzbeziehungen als auch die Auswirkungen von Herbivorie und Nährstoffanreicherung verändern kann.

In zwei weiteren Experimenten (Februar - Dezember 1998 und 1999) verglich ich die Effekte von Herbivoren und Nährstoffen auf die Besiedlung von Steinen in Maasholm (Ostsee) und Bald Rock (NW Atlantik). Sechs Nährstoffbehandlungen (6 - 200% Anreicherung von DIN) wurden über das ganze Jahr hinweg durchgeführt. Herbivore wurden mit Käfigen ein- oder ausgeschlossen. In der Ostsee hatten Herbivore starke Effekte auf die Artenzusammensetzung (Verschiebung von Grünalgen zu mehr fraßresistenten Braunalgen) aber nicht auf die Gesamtabundanz der Algen. Im NW Atlantik hingegen führte Herbivorie zu starken Verlusten bei allen Algen. Nährstoffanreicherung förderte vor allem annuelle Algen, was negative Auswirkungen auf wichtige Ökosystemfunktionen (Speicherung von Kohlenstoff und Stickstoff in Form von Pflanzenbiomasse) in der Ostsee, nicht jedoch im NW Atlantik hatte. In beiden Experimenten erhöhte die Gabe von Nährstoffen die Dichte von Algen, Herbivoren und Prädatoren ("bottom-up"-Kontrolle). Prädatoren hatten nur in der Ostsee im Sommer deutliche Effekte auf Herbivore und Algen ("top-down"-Kontrolle). Herbivorie erhöhte und Nährstoffanreicherung verringerte die Diversität siedelnder Makroalgen in der Ostsee. Im NW Atlantik hingegen fanden sich genau entgegengesetzte Effekte. Dies erkläre ich mit den extrem nährstoffarmen Verhältnissen und der geringen Produktivität im NW Atlantik. Eine nährstoffbedingte Zunahme der Produktivität erhöhte die Diversität im NW Atlantik, verringerte aber die Diversität in der Ostsee. Auch theoretische

Konkurrenzmodelle sagen voraus, daß der Zusammenhang zwischen Produktivität und Diversität durch eine derartige eingipfelige Kurve zu beschreiben ist.

In weiteren Experimenten untersuchte ich, wie variabel die Effekte von Herbivoren und Nährstoffen zwischen vielen verschiedenen Standorten sind. Dafür entwickelte ich ein "Herbivorie-Nährstoff-Assay", bei dem Kacheln mit der schnellwachsenden aber wenig fraßresistenten Grünalge *Enteromorpha intestinalis* besät und dann in offenen und geschlossenen Käfigen exponiert wurden. Dieses Experiment fand an 4 Orten in der Ostsee und 4 nährstoffarmen und 4 eutrophierten Orten im NW Atlantik statt. Herbivore hatten stets stark negative Effekte auf *Enteromorpha* im Frühjahr. Im Sommer brach der Fraßdruck in der Ostsee, nicht jedoch im NW Atlantik zusammen. An eutrophierten Standorten erreichte *Enteromorpha* eine etwa 10-fach erhöhte Dichte verglichen mit nährstoffarmen Standorten. Herbivore konsumierten einen relativ konstanten Anteil der Algen, unabhängig von deren Gesamtdichte. Dies bestätigte die experimentellen Ergebnisse aus der Ostsee und zeigt, daß Herbivore die Auswirkungen der Eutrophierung zwar bremsen, prinzipiell aber nicht verhindern können.

Probennahmen an 25 Standorten in der Ostsee und 16 Orten im NW Atlantik konnten weitere experimentell gewonnene Aussagen bestätigen. Die Ansiedlung und Abundanz von *Fucus* in der Ostsee wurde stark negativ von der Dichte annueller Algen im Frühjahr (Reproduktionsperiode von *Fucus*) beeinflusst. Auch an eutrophierten Standorten im NW Atlantik zeigte sich, daß annuelle Algen und auch Muscheln die mehrjährigen Algen verdrängen. Die Abundanz annueller Algen ist deutlich negativ mit der Dichte von herbivoren Schnecken korreliert. Die Ergebnisse weisen darauf hin, daß der großskalige Rückgang mehrjähriger Algenbestände auf die erhöhten Nährstofffrachten zurückzuführen ist, welche zur Blockade der Ansiedlung durch schnellwachsende annuelle Algen (Ostsee, NW Atlantik) und Muscheln (NW Atlantik) führen.

Zusammengefasst zeigen meine Experimente und Beobachtungen, wie Nährstoffe und Herbivore antagonistisch die Zusammensetzung, Diversität und Funktion der Felsküstengemeinschaft bestimmen. Weiterhin zeigte sich, daß sowohl "bottom-up" wie "top-down" Einflüsse sich über mehrere trophische Ebenen fortpflanzen können. Die Stärke und Richtung der Effekte von Herbivoren und Nährstoffen auf die Artendiversität der Algen veränderte sich vorhersagbar mit zunehmender Produktivität des Ökosystems und ebenso mit der Verfügbarkeit von Sporen im Frühjahr. Diese Arbeit gibt detaillierte und experimentell abgesicherte Hinweise darauf, daß zunehmende Stickstofffrachten zu starken Veränderungen in der Diversität von Algengemeinschaften, zum Rückgang mehrjähriger Makroalgen, zu destruktiven Massenblüten annueller Algen und zum Verlust wichtiger Funktionen im Ökosystem führen, und daß diese Reaktionen eng miteinander verzahnt sind.

1. General introduction

In all parts of the world, a rocky and partially protected shore perhaps supports, in a given space, a greater number of individual animals than any other station. [...] The number of living creatures of all orders whose existence intimately depends on the kelp, is wonderful.

I can only compare these great aquatic forests [...] with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as here, from the destruction of the kelp.

Charles Darwin, Voyage of the Beagle (1839)

1.1. Coastal ecosystems: the problem

Coastal zones represent only 1 - 2% of the planet's ocean surface area, but they generate more than 20% of oceanic primary production (Charpy-Roubaud & Sournia 1990). High levels of plant productivity sustain high fish and invertebrate biomass, which accounts for almost 20% of the global fishery yield (Pauly & Christensen 1995). Large marine plants such as seagrasses and macroalgae are structurally and functionally important in these systems. In this thesis I discuss factors that regulate the structure and functioning of coastal hard-bottom or rocky shore communities dominated by macroalgae. Here I define rocky shores very broadly, meaning all coastal sites with abundant hard substratum.

Marine macroalgae and seagrasses fulfill important ecosystem functions. They represent up to 40% of the primary productivity of the coastal zone (Charpy-Roubaud & Sournia 1990), and a significant fraction of oceanic plant biomass (Smith 1981). Average macrophyte biomass per unit area is more than 400-fold higher and productivity per unit area is at least 10 times higher than in phytoplankton communities (Mann 1973, Smith 1981). On a local scale, macrophyte detritus can be the dominant energy source in nearshore food webs (Duggins et al. 1989, Vetter 1994). On a global scale, carbon storage by macrophytes may represent a significant sink for anthropogenic carbon dioxide (Smith 1981). In addition to carbon, macrophytes retain and cycle large quantities of plant nutrients (mainly nitrogen and phosphorus), with consequences for nutrient fluxes from the continents to the open ocean (Jickells 1998). Nutrient cycling by coastal macrophytes has been pointed out as one of the most important ecosystem services provided by marine systems and has been valued as US \$ 3.8 trillion (10^{12}) per year globally. This equals the total value of services provided by tropical forests (Costanza et al. 1997). In addition, marine macrophytes play an important structural role. They provide habitat and refuge for diverse communities of associated plant and animals, including juvenile life-stages of many commercially important fish species (Rangeley & Kramer 1995, 1998, Boström & Bonsdorff 1997, Gotceitas et al. 1997). Their forest-like structure

with different layers of canopy, teeming with animal life, easily evokes comparisons with terrestrial rain forests (Darwin 1839).

Another analogy between terrestrial and marine “forests” is that both systems are under intense pressure from human influences. Seventy percent of the human population lives close to the coast. This distribution was likely motivated in part by the high fish yields from coastal waters which still provide a major source of protein for millions of people (FAO 1995). However, increasing demand and high subsidies have increased global fisheries far beyond sustainable levels (Pauly et al. 1998, Casey & Myers 1998). Globally, 66% of all fish stocks are fully exploited or overexploited (Botsford et al. 1997). Collapses of valuable high-trophic level predator stocks (e.g. tuna, cod) caused fishing efforts to shift to successively lower levels in the food web, including primary producers, grazer and detritivores (e.g. rockweed, littorinid snails, sea urchins, sea cucumbers, Pauly et al. 1998, Worm & Lotze 2000). The ecological consequences of these multiple food-web alterations on coastal ecosystems are poorly understood. However, the few well-documented examples are alarming (Estes & Palmisano 1974, Durán & Castilla 1989, Estes et al. 1998, Steneck 1998).

In addition to harvesting of consumers, humans influence marine food webs through changes in resource supply. Nutrient-rich wastes and effluents are often directly disposed into the marine environment or reach the coast via river or atmospheric transport (Carpenter et al. 1998). The problem is exacerbated by exponentially increasing rates of nitrogen fixation and phosphate mining for fertilizers (Vitousek et al. 1997a). Human influences on aquatic nutrient loading are so pervasive that a strong linear correlation between human population density and river water nitrate concentrations has been documented for the worlds major river systems (Peierls et al. 1991). Increasing supply of nutrients and organic matter (eutrophication) has caused changes in plant abundance and species composition, including toxic microalgal blooms, destructive macroalgal blooms and declines of perennial, canopy-forming macrophytes in coastal systems around the world (Orth & Moore 1983, Hallegraeff 1993, Duarte 1995, Schramm & Nienhuis 1996, Valiela et al. 1997). These changes appear to occur on a particularly large scale in the Baltic Sea. Independent observations from several different regions indicate alarming losses of perennial macroalgae (*Fucus vesiculosus*) which formerly dominated most hard-bottom communities from 0 - 10 m depth (Kautsky et al. 1986). Throughout the last decades, *Fucus* became increasingly displaced by turfs of fast-growing annual algae and sometimes filter feeders (Kangas et al. 1982, Kautsky et al. 1986, Baden et al. 1990, Vogt & Schramm 1991). These assemblages are typically less diverse and do not provide the same habitat functions as large, perennial canopies. So far, a number of mechanisms have been proposed in order to explain these changes, but none has been tested experimentally (reviewed by Kautsky et al 1992, Schramm 1996). Although eutrophication undoubtedly plays a major role, both algal blooms and ecological phase-shifts from annual to perennial algae, cannot be predicted from nutrient loading alone (Hallegraeff 1993, Duarte 1995, Valiela et al.

1997). A number of other factors, which may buffer or amplify the effects of eutrophication have been proposed, including changes in consumer abundance and diversity (Duarte 1995, Hauxwell et al. 1998, Lotze 1998, Lotze & Worm 2000). Probably, co-occurring human influences on resource supply and higher trophic levels interact in changing the structure and function of aquatic ecosystems. This proposition has been investigated in lakes and streams (Power 1990, Brett & Goldman 1998) but rarely in coastal systems. Rocky shores, in particular, have been studied for decades with respect to consumer effects, but possible interactions with changes in resource supply remained largely unexplored (Menge 1992, Menge et al. 1997).

This thesis is concerned with the effects of nutrient loading and consumer pressure in rocky shore food webs. My central objectives were (1) to understand how consumers (grazers, predators) and resources (nutrient supply) influence rocky shore community structure across a range of relevant spatial scales and environmental conditions, (2) to analyze potential interactions between these processes, and (3) to predict consequences of increasing resource supply (e.g. through eutrophication) and decreasing consumer pressure (e.g. through harvesting) for coastal hard-bottom communities.

1.2. Theoretical framework

A food web is a map that describes which kinds of organisms in a community eat which other kinds. A web helps picture how a community is put together and how it works, providing a framework for integrating population dynamics, community structure and ecosystem processes. Although food-web research has been a very active field throughout the last decades, the causes for a range of interesting patterns remain controversial (Pimm et al. 1991).

A major line of research has focused on the effects of consumers on lower trophic levels. Much of this was originally inspired by the “green world hypothesis”. In order to explain the dominance of green plants in the world, Hairston et al. (1960) argued that plants are so abundant only because predators limit the density of herbivores to levels at which they are unable to deplete the vegetation. Plants and predators do not suffer from intense predation and are therefore regulated by their resources. In this view, communities are “top-down” controlled: the highest trophic level determines patterns of regulation at lower levels. This hypothesis has been further developed by mathematically analyzing the equilibria of a plant-herbivore-predator food chain (Oksanen et al. 1981). This model predicts that primary productivity limits food-chain length and that food-chain length determines the response of individual trophic levels to increases in productivity. The model assumes that at very low productivity plant density may not be sufficient to maintain herbivores. At intermediate productivity, herbivores are present and control plant density. Increases in productivity in a plant-herbivore chain cause increases in herbivore but not plant density. At high productivity, herbivores are abundant enough to maintain predator populations. Increases in productivity should increase plant density and

predator density, while herbivore density is constant and controlled by predators (Oksanen et al. 1981). These predictions were recently confirmed using simple 2- and 3-level microbial food chains in laboratory microcosms (Kautzinger & Morin 1998).

Many ecologists oppose this body of theory for a number of reasons. Importantly, natural communities are not organized as simple food chains, but species interactions form complicated webs. Trophic levels are not uniform, but consist of species and populations with widely different traits. These traits can be important determinants for the community response to changes in productivity or consumer pressure (Leibold & Wilbur 1992). Many plants are inedible, nutritionally unacceptable, or protected by anti-herbivore defenses and therefore not regulated by herbivores (Coley et al. 1985, Hay & Fennical 1988). Similarly, many herbivores are scarce, hard to catch or have other adaptations to protect themselves against predators (White 1978). Hence, consumers are often unable to control the dynamics of prey populations. In this view, sometimes referred to as the "green desert" hypothesis, communities are "bottom-up" regulated, which means all trophic levels are regulated by their resources and increases in productivity increase the abundance of plants, herbivores and predators. Repeatedly, it has been noted that this "bottom-up versus top-down" controversy is an artificial dichotomy and that food-web research should focus on the interaction of consumer and resource control as structuring forces in natural communities (Sommer 1988, 1994, McQueen et al. 1989, Hunter & Price 1992, Power 1992). In this thesis, I attempted such an analysis of rocky shore food webs in the Baltic and NW Atlantic.

Rocky shore food webs are one of the most important model systems for community ecology (Paine 1977, 1994, Lubchenco 1986, Menge & Farrell 1989). Major practical advantages include that rocky shores are (1) accessible, (2) easy to manipulate experimentally, and (3) they respond rapidly to perturbations. Much experimental work on rocky shores was inspired by R.T. Paine's influential paper "Food web complexity and species diversity", published in 1966. Paine demonstrated that predation by the seastar *Pisaster ochraceus* maintained species diversity in the NE Pacific rocky intertidal by controlling a dominant space competitor, the mussel *Mytilus californianus*. Removal of the "keystone predator" (*P. ochraceus*) transformed a species-rich algal-invertebrate assemblage into a mussel monoculture. A few years before, G.E. Hutchinson (1959) had challenged ecologists with the simple but profound question, why there are so many species that coexist on a small number of limiting resources. Paine's contribution was to demonstrate that consumer pressure constantly maintains species diversity by preventing competitive dominance of a single species (*M. californianus*) on a single limited resource (space). This challenged the prevailing view that ecological communities are usually at competitive equilibrium. According to the new view, "non-equilibrium" factors (such as predation) prevent communities from becoming dominated by a top competitor. Subsequent research showed that herbivory (Lubchenco 1978, 1983, 1986) and physical disturbance (Connell 1978, Sousa 1979, 1984) can play a similar role as predation in structuring rocky shore food webs and maintaining species diversity. Importantly, consumer

effects can in some cases be transmitted across 2 or 3 levels in a “trophic cascade” (Estes & Duggins 1995, Wootton 1995, Estes et al. 1998), which confirmed the “top-down” model of Hairston et al. (1960) and paralleled results from freshwater (Carpenter et al. 1985, Power 1990) and terrestrial ecosystems (McLaren et al. 1994, Letourneau & Dyer 1998).

In contrast to work done in freshwater systems (Sommer 1988, Carpenter et al. 1996, Brett & Goldman 1997, Forrester et al. 1999), studies on rocky shore food webs largely ignored to evaluate the consequences of changes in resource supply and compare these to the effects of consumers (Menge 1992). In his original work, Paine (1966) had speculated on the relative effects of changes in productivity in rocky shore food webs, but it took 25 years until this question was raised again, inspired by the “bottom-up versus top-down” debate (Menge 1992). Since then, few comparative studies (Bustamante et al. 1995, Menge et al. 1997, 1999) and two short-term experimental studies have been conducted, one dealing with phytoplankton in tidepools (Metaxas & Scheibling 1996), the other one with microalgae and micrograzers (Wootton et al. 1996). These data are clearly not yet sufficient to generalize on the relative influences of consumers and resources on rocky shores.

General models of rocky shore food webs postulate that the influences of predation, competition and herbivory depend on propagule supply and successful recruitment of the organisms (Roughgarden 1986, Roughgarden et al. 1988, Menge & Sutherland 1987). Moreover, species interactions can be decisive at the settlement and recruitment stage (Grosberg & Levitan 1992, Vadas et al. 1992, Worm & Chapman 1996, Lotze et al. 1999, 2000). Therefore, the study of rocky shore food-web dynamics should embrace information on propagule supply and on processes affecting recruitment (Underwood & Denley 1984). Recent work has indicated that marine macroalgae, similar to land plants, have two important sources of propagule supply: dispersed, newly produced propagules and dormant propagules, which are stored in a marine propagule bank (Santelices et al. 1995, Lotze et al. 1999, 2000). For these reasons, I included different sources of propagule supply as an additional experimental factor into this study. This enabled me to control for a potential role of propagule supply in modifying the effects of consumers and nutrients.

Finally, in every ecological study there is the problem of scale. This has even been proposed as “the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology” (Levin 1992). It is clear that different physical and biological processes prevail at different scales (Mann & Lazier 1991, Levin 1992, Valiela 1995). As a consequence, small-scale experiments or local observations provide only limited insight into regional or global phenomena. One solution is to incorporate spatial scale explicitly into the experimental and sampling design of field studies to provide a broader, landscape view of ecology (Hughes et al. 1999). However, this is rarely done. For example, most studies on the effects of consumers on rocky shores have been performed at single sites, involving manipulations on cm-scale plots. Similarly, hypotheses on the decline of *Fucus* in the Baltic are based on observations from single sites or regions (Kangas et al. 1982, Kautsky et

al. 1986). In this study, I attempted to test hypothesis concerning the effects of resources and consumers across a range of relevant scales in order to derive valid generalizations about the importance of these factors on rocky shores.

1.3. Questions

In this study, I attempted to answer the following main questions:

- How do changes in nutrient supply and consumer pressure regulate community structure, diversity and ecosystem functioning on rocky shores?
- How do these effects change across temporal and spatial scales and from oligotrophic to eutrophic coastal systems?
- How are these effects modified by different sources of propagule supply?
- How are observed large-scale shifts in rocky shore community structure linked to nutrient loading and changes in consumer abundance?

1.4. Approach

To answer these questions, I chose an approach integrating field experiments and field surveys across a range of relevant spatial scales:

- Small scale (10 cm - 10 m): factorial field experiments with grazer exclusion and nutrient enrichment
- Regional scale (1 - 100 km): comparative experiments at multiple sites
- Large scale (100 - 1000 km): field surveys of rocky shorelines
- Continental scale (>1000 km): experiments and surveys repeated in the Baltic and NW Atlantic

I used exclusively field-based methods in this study. My rationale was that only field studies capture the full range of species interactions, seasonal changes and natural variability of biotic and abiotic factors. Field experiments provide the opportunity to test complex hypotheses under realistic conditions (Paine 1977, 1994, Underwood 1996). Factorial field experiments are particularly valuable because they address independent effects and interactions among several manipulated factors (Underwood 1996). Comparative experiments which are performed at multiple sites are an important tool because they provide an opportunity to test hypotheses across larger scales (McKone 1993). Finally, field surveys can be useful in order to quantify large-scale patterns in the abundance and distribution of organisms and to test experimentally derived predictions (Hughes et al. 1999). Expanding from small to large scales, this thesis also spans several levels of ecological complexity from single organisms to populations, communities, food-webs and ecosystems.

It is important to recognize the limitations of this approach. Field experiments do not provide the same degree of control as laboratory experiments. Often, it is not possible to separate the effects of different species, which therefore have to be treated together (e.g. as “grazers” or “annual algae”). Moreover, the mechanisms, which cause a certain response (e.g. grazer resistance, growth response) can often not be resolved with field experiments. Within the scope of this study, I chose to investigate the relative importance of selected processes in order to explain larger-scale patterns of community structure. Wherever possible, I have attempted to link the results of my experiments to those of more detailed physiological and ecological laboratory studies.

1.5. Thesis outline

This thesis is structured in 9 Chapters, which elucidate patterns of consumer and resource control in study systems of increasing scale and complexity. After the general introduction, I introduce the 2 main study sites and their food webs as well as locations of 41 additional study sites (Chapter 2). In Chapter 3, I present results from a nutrient-pulsing experiment, which revealed consequences of short-term changes in resource supply on single *Fucus vesiculosus* plants, their epiphytes and associated grazers. The effects of increasing nutrient supply on *Fucus* populations, their growth and productivity are treated in Chapter 4. In Chapter 5, I discuss results from factorial field experiments analyzing the relative influences of consumers, nutrients and macroalgal propagule supply on algal recruitment and community structure. The following 2 Chapters reveal the effects of consumers and resources on rocky shore food-web structure (algae, grazers, predators), species diversity and ecosystem functioning in a nutrient-rich environment (Baltic Sea, Chapter 6) versus a nutrient-poor environment (NW Atlantic, Chapter 7). In Chapter 8, predictions that emerged from the previous Chapters are tested in comparative field experiments (12 sites) and field surveys (41 sites) across Baltic and NW Atlantic shorelines. These results are synthesized in Chapter 9, which provides a general discussion and conclusions of this study.

2. Study sites and food webs

In this thesis, I have performed a series of comparative field experiments and surveys in the Baltic Sea and the NW Atlantic Ocean (Fig. 2.1). I used these two oceans as model systems for nutrient-rich (Baltic) and nutrient-poor (NW Atlantic) ecosystems. In this Chapter I describe the physical environments of the two main study sites and the configuration of rocky shore food webs at these sites. In addition, I briefly outline the locations of additional study sites in the Baltic and NW Atlantic.

For taxonomic information on all species in this study refer to the species list at the end of this thesis.

2.1. Baltic Sea

Main study site: Maasholm

Experiments were conducted in the littoral zone close to the Maasholm field station of the Institut für Meereskunde, Western Baltic Sea, Germany (54°41.3' N, 10°0.5' E, Fig. 2.1 A, B). The site is located in a shallow bay at the mouth of the Schlei Fjord, which is a 40 km long inshore water system of glacial origin. Maasholm was chosen as a study site because (1) the benthic community is dominated by marine species which are typical of the N Atlantic Ocean, (2) the site is nutrient-rich with concentrations that are typical for inshore waters in the Baltic Sea, (3) it is protected from severe wave action (maximum fetch is 5 km, maximum wave height is 40 cm), (4) it borders a nature reserve and is therefore largely protected from human disturbance, and (5) Schlei Fjord and the Western Baltic Sea have a history of oceanographic studies, therefore data are available for comparison.

At Maasholm, lunar tides are relatively unimportant compared with irregular wind-driven sea-level changes which reach an amplitude of ± 0.5 m around mean water level. Salinity fluctuates between 12 - 18 PSU (practical salinity units) in summer and 14 - 20 PSU in winter (Fig. 2.2 A). Water temperature ranges between -1 - 5°C in winter and 15 - 21°C in summer (Fig. 2.2 B). Concentrations of dissolved inorganic nutrients in the water column reach 100 - 150 $\mu\text{mol L}^{-1}$ nitrate, 10 - 15 $\mu\text{mol L}^{-1}$ ammonium and 2 $\mu\text{mol L}^{-1}$ phosphate from January to March. From mid-May to mid-August, ammonium and nitrate typically remain close to the detection limit (0.0 - 0.3 $\mu\text{mol L}^{-1}$). Soluble reactive phosphate remains detectable at 0.1 - 0.6 $\mu\text{mol L}^{-1}$ throughout the summer. In September, ammonium regeneration starts and concentrations rise rapidly throughout the fall (Schramm et al. 1996, Chapter 5 and 6).

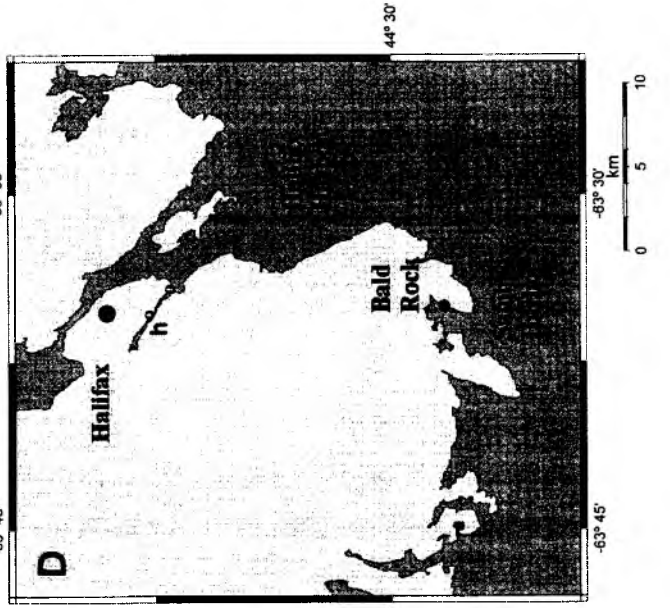
The bottom consists of coarse sand with scattered rocks and boulders. Although this is not a rocky shore in a classical sense (mostly bedrock), there is still abundant stable substratum for macroalgae and sessile invertebrates to colonize. Moreover, the established hard-bottom community is very similar to those found on other rocky shores in the North Atlantic region.

Rocks and boulders at Maasholm are dominated by a dense canopy of the perennial brown seaweed *Fucus vesiculosus* (0.5 - 1.5 m high) which occupies 84 ± 7.3 percent cover on rocks (mean \pm 1 SE, n=10). Because this species is the only fucoid alga of importance in this study, I will mostly refer to *Fucus vesiculosus* simply as *Fucus* hereafter. Annual macroalgae are seasonally abundant and can perform mass blooms in spring and early summer (Lotze et al. 1999, 2000). During this time, the filamentous brown alga *Pilayella littoralis* is the most abundant species, followed by the foliose green *Enteromorpha intestinalis* and the filamentous red *Ceramium strictum*. In winter, the red annual *Dumontia contorta*, green *Ulvopsis grevillei* and brown *Petalonia fascia* are common. Benthic microalgae (mostly diatoms) are abundant in spring. These primary producers are consumed by a species-rich grazer guild, which is consumed by crustacean and fish predators (Fig. 2.3). Among grazers, snails (*Littorina saxatilis*, *L. littorea*) are numerically dominant in the spring, while isopods (*Idotea chelipes*, *Idotea baltica*) dominate in fall. Predators are most abundant in summer and are numerically dominated by the green crab, *Carcinus maenas* and the decapod shrimp *Palaemon adspersus*. Green crabs, fish and shrimps are all preyed upon by gulls (*Larus atricilla*, *L. argentatus*). Mussels and barnacles are not commonly found on rocks, but frequently as epibionts on large, adult *Fucus* plants and mussels are also found occasionally on soft substrata (Reusch 1998). I compiled data from feeding experiments (Sommer 1997, 1999, Lotze & Worm 2000, B. Worm, unpubl.) and >100 h of field observations to map major feeding links in the hard-bottom food web (Fig. 2.3).

Additional sites

In order to test a predictions that emerged from the experiments at Maasholm, I established a number of additional research sites throughout the Baltic Sea (Fig. 2.1 A, B). Maasholm and 2 additional sites in the inner Schlei Fjord were used for a growth experiment with *Fucus vesiculosus* (Chapter 4). Comparative grazer exclusion experiments were run at Maasholm and 3 other sites in Kiel Fjord, Flensburg Fjord and Gelting Cove (Chapter 8). These sites were chosen in order to mimic conditions at Maasholm (shallow, protected from severe wave action and other physical disturbance, abundant rocky substratum). Field surveys were conducted at 15 sites in the Western Baltic, 4 sites at the Swedish coast, 4 sites in the Finnish Åland archipelago, and 2 sites in Lithuania (Chapter 8). These sites were chosen to represent a range of conditions from protected to exposed shorelines. All sites had abundant rocky substratum in the shallow subtidal zone (0 - 2 m).

Fig. 2.1. Study sites in the (A, B) Baltic Sea and (C, D) NW Atlantic Ocean. The main study sites, Maasholm (Schlei Fjord, Kiel Bight, W Baltic Sea) and Bald Rock (Sambro Harbor, NW Atlantic Ocean) are indicated with black dots. Open symbols indicate additional sites. Small letters indicate sites where field experiments were conducted: u=Ulsnis, k=Karschau (see Chapter 4 for details), f=Flensburg Fjord, g=Gelting Noor, ki=Kiel Fjord, p=Passamaquoddy Bay, l=Letang Inlet, h=Halifax Harbor (see Chapter 8 for details). ➡



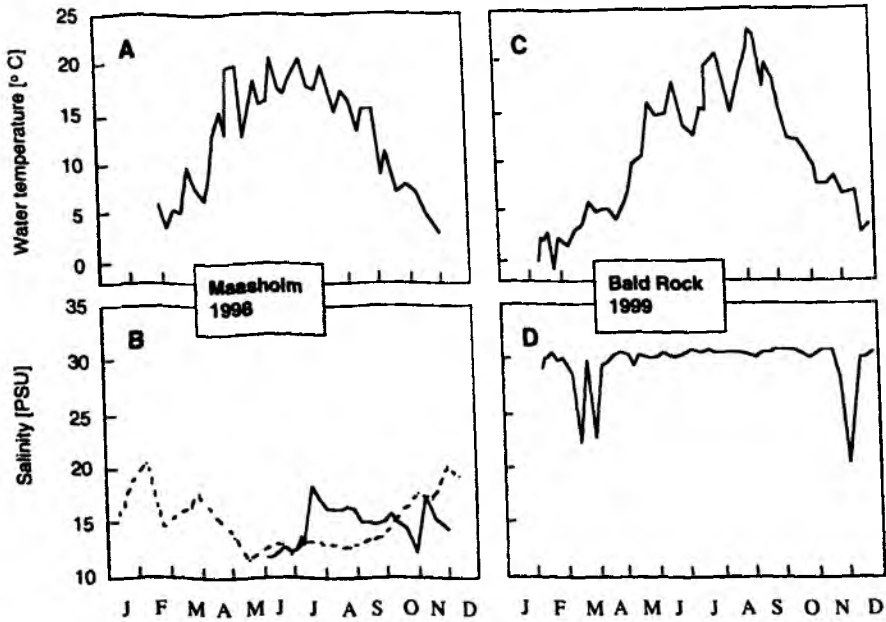


Fig. 2.2. Temperature and salinity trends at the 2 main study sites. Salinity data for Maasholm 1998 (June - December only) are amended by data from 1995 (dashed line, Schramm et al. 1996) for comparison.

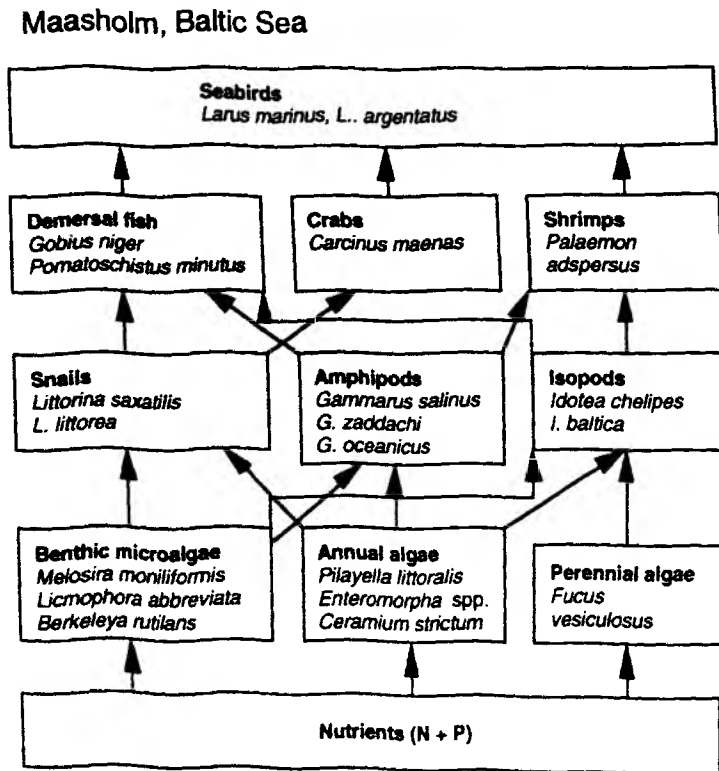


Fig. 2.3. Primary components and feeding links of the hard-bottom food web at Maasholm, the main study site in the Baltic. Different layers represent trophic levels. Boxes represent functional groups. Within each functional group, abundant species are listed before rare species. Filter-feeders (*Mytilus edulis*, *Balanus improvisus*) were present but are not shown because of their low abundance throughout the experiments (Chapters 5 - 6).

2.2. NW Atlantic Ocean

Main study site: Bald Rock

Experiments were conducted in a shallow cove at Bald Rock, Nova Scotia, Canada (44°28.3' N, 63°34.7' W, Fig. 2.1 C, D). The cove lies at the outer reaches of Sambro Harbor, a wide bay 25 km S of Halifax. This site was chosen because (1) it has a very similar species composition as compared with Maasholm, (2) it is flushed by nutrient-poor waters from the open Atlantic, with nutrient concentrations typical for oligotrophic NW Atlantic shorelines, (3) it is privately owned and therefore largely protected from physical disturbance by human activity, (4) Sambro Harbor is a long-term monitoring site for the Bedford Institute of Oceanography (Dartmouth, Nova Scotia, Canada), therefore data are available for comparison. Bald Rock experiences diurnal lunar tides with an amplitude of 1.6 - 2.1 m. The studied food-web, however, was located at the low tide mark and was submerged for >90% of the time, similar to conditions at Maasholm. Temperature ranges between -1 - 4°C in winter and 15 - 22°C in summer (Fig. 2.2 C). Salinity is fairly constant between 29 - 31.5 PSU throughout most of the year, with short periods of lower salinity (21 - 24 PSU) caused by freshwater run-off from melting snow masses (Fig. 2.2 D).

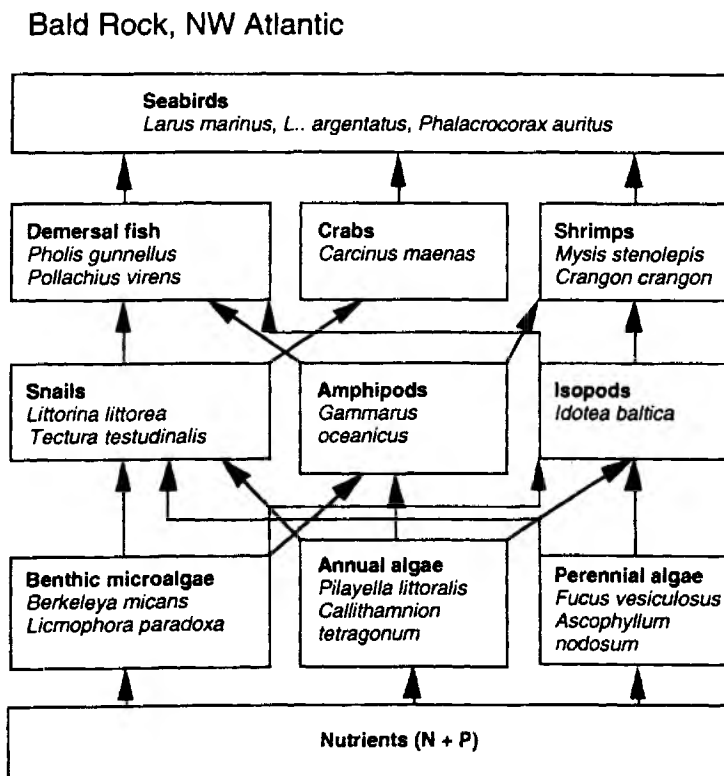


Fig. 2.4. Primary components and feeding links of the hard-bottom food web at Bald Rock, the main study site in the NW Atlantic. Symbols as in Fig. 2.3. Filter-feeders (*Mytilus edulis*, *Semibalanus balanoides*, *Balanus crenatus*) were present but are not shown because of their low abundance throughout the experiments (Chapter 7).

Concentrations of dissolved inorganic nutrients are very low, with maximum concentrations of 2 - 6 $\mu\text{mol L}^{-1}$ nitrate, 1 - 2 $\mu\text{mol L}^{-1}$ ammonium and 0.6 $\mu\text{mol L}^{-1}$ phosphate in January and February. The spring phytoplankton bloom typically occurs in March (Keizer et al. 1996a). From March to October, ammonium and nitrate are largely depleted and typically remain close to the detection limit (0.0-0.4 $\mu\text{mol L}^{-1}$). Concentrations of soluble reactive phosphate remain between 0.3 and 0.6 $\mu\text{mol L}^{-1}$ throughout the year (Keizer et al. 1996a, Chapter 7).

The bottom consists of sand, gravel, boulders and granite bedrock. Hard substrata are colonized by dense stands of perennial brown fucoids (96.8 ± 3.1 percent cover on rocks, mean ± 1 SE, $n=10$). *Ascophyllum nodosum* and *Fucus vesiculosus* dominate in the lower intertidal and upper subtidal, *F. spiralis* dominates the upper intertidal zone. During my study year, more than 20 species of annual seaweeds were found (see species list). Most annual algae had very low abundance (<2 percent cover throughout the year). Higher abundance was only reached by *Pilayella littoralis* (spring and fall), *Dumontia contorta*, *Scytosiphon lomentaria* and *Petalonia fascia* (winter). The grazer fauna was numerically dominated by the periwinkle *Littorina littorea*. Other snails (*L. obtusata* and the small limpet *Tectura testudinalis*) and crustacean grazers (*Gammarus oceanicus*, *Idotea baltica*) occurred at low densities (Chapter 7). As in Maasholm, the green crab *Carcinus maenas* was the most abundant predator in summer. Carnivorous shrimps (*Crangon crangon*) and demersal fish, mainly juvenile pollack (*Pollachius virens*), were present in summer but relatively rare. Omnivorous mysid shrimps (*Mysis stenolepis*) were abundant in summer. Predators were consumed by gulls (*Larus marinus*, *L. argentatus*) and cormorants (*Phalacrocorax auritus*). I compiled data from the literature (Foulds & Mann 1978, Lubchenco 1978, Rangeley & Kramer 1998) and my own field observations to map major feeding links in this rocky shore food-web (Fig. 2.4).

Additional sites

I established a number of additional research sites in the provinces of Nova Scotia and New Brunswick, Canada (Fig. 2.1 C). Based on published information on the concentrations of dissolved nutrients, I selected paired nutrient-enriched and nutrient-poor sites within four larger bays: Halifax Harbor, Annapolis Basin, Letang Inlet and Passamaquoddy Bay. Sites were chosen to represent similar environmental conditions with the exception of their differences in nutrient status (see Table 8.1, Chapter 8). All of these sites were protected from severe wave action and had abundant rocky substratum. Comparative grazer exclusion experiments identical to those in the Baltic Sea were run at the paired nutrient-rich and nutrient-poor sites in the NW Atlantic. In addition, field surveys were conducted at paired sites (2 eutrophied, 2 control) within each of the 4 bays (see Chapter 8 for details).

3. Organisms: Rapid transmission of a single nutrient pulse through a seaweed-epiphyte-grazer system

3.1. Introduction

Nutrient supply in aquatic ecosystems is spatially and temporally extremely variable. Under most conditions, nutrients are supplied as irregular pulses. Such pulses are generated on small scales by animal excretion (Lehmann & Scavia 1982, Williams & Carpenter 1988, Reusch & Chapman 1994), on intermediate scales by leaching of sediment porewater or patches of decomposing organisms (Brennan & Wilson 1993, Hanisak 1993) and on large scales by land run-off and wind-induced mixing and upwelling (Pedersen et al. 1995, Kiirikki & Blomster 1996, Schaffelke & Klumpp 1998). In addition to pulse scale and frequency, pulse concentrations can be extremely variable, ranging from <1 to $>1000 \mu\text{mol L}^{-1}$ (Lehmann & Scavia 1982, Hanisak 1993, Jørgensen 1995, Fong et al. 1996, Schramm et al. 1996). Primary producers have evolved different strategies to exploit heterogeneity in nutrient supply. Microalgae and filamentous macroalgae have a relatively high surface area:volume ratio that allows for high nutrient uptake and growth rates (Rosenberg & Ramus 1984, Hein et al. 1995), but low nutrient storage capacity (2 - 8 d for filamentous algae, Fujita 1985, Pedersen & Borum 1996). Perennial, canopy-forming macroalgae have thick, corticated thalli, and low surface area:volume ratios. They have slower uptake and growth rates (Wallentinus 1984, Duarte 1995) but higher nutrient storage capacities compared with phytoplankton and filamentous algae (up to several months, Chapman & Craigie 1977). It has been hypothesized that because of these physiological differences filamentous, annual macroalgae may be better adapted to use short, frequent pulses while corticated, perennial algae primarily benefit from longer-term (e.g. seasonal) nutrient fluctuations (Rosenberg et al. 1984).

Most work on the effects of nutrient pulses has focused on phytoplankton assemblages (Scavia et al. 1984, Sommer 1985) or single species of macroalgae (Lapointe 1985, Rosenberg et al. 1984, Schaffelke & Klumpp 1998). I asked (1) how small-scale variations in nutrient pulse duration and frequency affect competition between perennial algae and their filamentous epiphytes and (2) whether the effects of short nutrient pulses are transmitted to higher trophic levels. Competition for light and nutrients may be particularly intense between filamentous algal epiphytes and their hosts. Work with seagrass-epiphyte-grazer systems has shown that increased nutrient supply can increase epiphyte loads with negative consequences for the host plant (Sand-Jensen 1977). On the other hand most grazers prefer to feed on filamentous algae and may increase in abundance when food supply increases. Increased grazing pressure may thereby compensate nutrient effects on annual algal growth (Neckles et al. 1993, Williams & Ruckelshaus 1993, Jernakoff et al. 1996). I used the perennial brown algae *Fucus vesiculosus* and its filamentous epiphytes as a model system in order to test the following hypotheses: (1)

Repeated short pulses favor epiphytes, (2) single long pulses favor *Fucus*, (3) effects of nutrient pulses on *Fucus* depend on the cover of epiphytes, and (4) nutrient pulses increase grazer densities.

3.2. Methods

In a (2 x 3) - factorial field experiment, *Fucus* plants with 2 different levels of epiphytes (epiphytes removed every 5 d versus epiphytes not removed) were exposed to 3 different nutrient pulses (no pulses, 5 x 1 h pulses, 1 x 5 h pulse). While pulse frequency and duration were manipulated, pulse concentration was constant at 200 $\mu\text{mol L}^{-1}$ nitrate and 15 $\mu\text{mol L}^{-1}$ phosphate added to ambient seawater. These concentrations mimic conditions in many eutrophic systems where periodic upwelling or mixing with nutrient-rich water deep water occurs (Pedersen et al. 1995, Kiirikki & Blomster 1996). Six replicates were used for each of the six treatments. The experiment was run at Maasholm (see Chapter 2) for 25 d from 22 May 1997 - 15 June 1997. *Fucus vesiculosus* plants were collected from 3 different stands of 1-year old *Fucus* which were 25 - 35 cm high. Plants with small pieces of substratum were chiseled from the rocks. All collected plants had significant epiphyte loads, typical for the time of year (filamentous brown algae *Pilayella littoralis* and *Elachista fucicola*). Plants were transported to the laboratory in a cooler. Epiphytes were cut back with scissors to 3 - 5 mm length in order to standardize epiphyte load among plants and to get an initial reading of *Fucus* wet mass. Initial wet mass was determined to the nearest mg after carefully blotting plants and attached rocks for 10 s between 2 pieces of paper tissue. Plants were fastened on six 1 x 1 m PVC grids with attached plastic clothespins. Clothespins were numbered and treatments were assigned to individual plants using random number tables. One replicate of each treatment was assigned to each grid. Grids were submerged at 0.8 m water depth and anchored with 50-cm steel rods. Individual grids were separated by 2 m, individual plants on a grid were separated by 35 - 50 cm.

All grids were retrieved at day 2, 7, 12, 17 and 22 of the experiment and half of the *Fucus* plants were manually cleaned from epiphyte. Only one plant was damaged and excluded from further analysis. Plants that were assigned to a particular nutrient pulse treatment were placed in a large tub, filled with 30 L freshly collected seawater, enriched with 200 $\mu\text{mol L}^{-1}$ NaNO_3 , and 15 $\mu\text{mol L}^{-1}$ NaH_2PO_4 . The water was exchanged and newly enriched with a concentrated stock solution every 20 min. This was done to keep pulse concentration approximately constant. Plants assigned to 1 h pulses were pulsed 5 times over a 25 d period, plants that were assigned to 5 h nutrient pulses were treated once on day 12.

After 25 d, plants were collected with mesh bags in order to catch all grazers on individual plants. In 2 cases, grazers escaped from the mesh bags while sampling, these plots were excluded from analysis of grazer densities. In the laboratory, grazers were counted,

epiphytes were removed, and *Fucus* was blotted dry for 10 s before determining wet mass. Rocks were removed from all plants and weighed. Epiphytes and *Fucus* plants were dried separately at 80° C for 48 h and dry mass was measured to the nearest mg.

I correlated *Fucus* wet mass (WM) and dry mass (DM) with a linear regression model ($DM=1.1369+0.149 WM$, $r^2=0.89$, $P<0.0001$). Using this model, *Fucus* initial wet mass was transformed into dry mass. I calculated *Fucus* relative growth rate as $RGR=(\ln M_2-\ln M_1)/(t_2-t_1)$, with M =dry mass of *Fucus* [g] and t =time [d]. Data were analyzed by 2-way ANOVA with nutrient pulsing and epiphytes as independent variables and *Fucus* RGR as the dependent variable. Epiphyte dry mass data were normalized to the dry mass of the *Fucus* plant (epiphyte load=epiphyte DM/*Fucus* DM) and analyzed by 1-way ANOVA with nutrient pulsing as the independent variable. Grazer data were also normalized to the mass of *Fucus* plants (grazer density=number of grazers/g DM *Fucus*) and analyzed separately for treatments with and without epiphytes by 1-way ANOVA with nutrient pulsing as the independent variable. This was done because the procedure of epiphyte removal has probably reduced grazer densities precluding direct comparison of treatments with and without epiphytes. Student-Newman-Keuls test (SNK) was used for post-hoc comparisons. All data were log-transformed in order to fulfill the assumption of homogeneous variances tested by Cochran's test. In a subsequent analysis, I used linear regression models to test for correlations among (1) epiphyte loads and grazer densities and (2) epiphyte loads and growth rates of individual *Fucus* plants.

3.3. Results

The mean growth rate of *Fucus* plants in the experiment was $0.016 \pm 0.006 d^{-1}$ (mean \pm 1 SE, $n=35$). Growth rates were not significantly affected by epiphyte removal (ANOVA, $F_{1,29}=0.14$, $P=0.71$) or nutrient pulsing ($F_{2,29}=1.32$, $P=0.28$), but there was a trend towards interactive effects between these two factors (Pulse x Epiphytes, $F_{2,29}=2.81$, $P=0.0766$). This interaction indicated positive effects of nutrient pulsing in the absence of epiphytes (Fig. 3.1 A) but negative effects in the presence of epiphytes (Fig. 3.1 B).

Epiphyte biomass was between 0.2 and 7.4% of *Fucus* biomass at the end of the experiment (mean 3.1% \pm 0.5 SE). Epiphyte species composition was similar to the beginning of the experiment: *Pilayella littoralis* (ca. 70%) and *Elachista fucicola* (ca. 30%). Microscopic examinations revealed that both species were heavily fouled by benthic diatoms (mostly *Tabularia fasciculata*). Nutrient pulses significantly increased epiphyte biomass (Fig. 3.2 A, ANOVA, $F_{2,15}=4.25$, $P=0.0344$), but there were differences among the pulse treatments. Repeated 1 h pulses increased epiphyte biomass by 31% compared with controls, but this increase was not significant (SNK, $P>0.05$). A single 5 h pulse significantly increased epiphyte biomass by 153%, compared with controls (SNK, $P<0.05$).

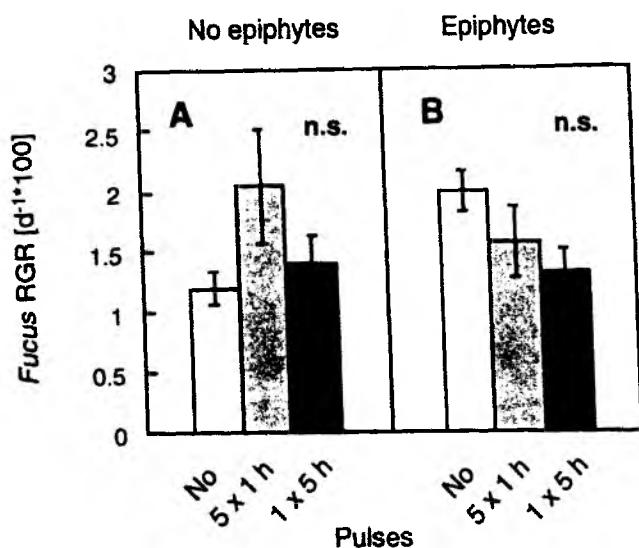


Fig. 3.1. Effects of nutrient pulsing (frequency and duration) and epiphyte removal on the relative growth rate (RGR) of *Fucus* in the experiment. Data are means \pm 1 SE ($n=6$). See text for ANOVA results (n.s.=not significant).

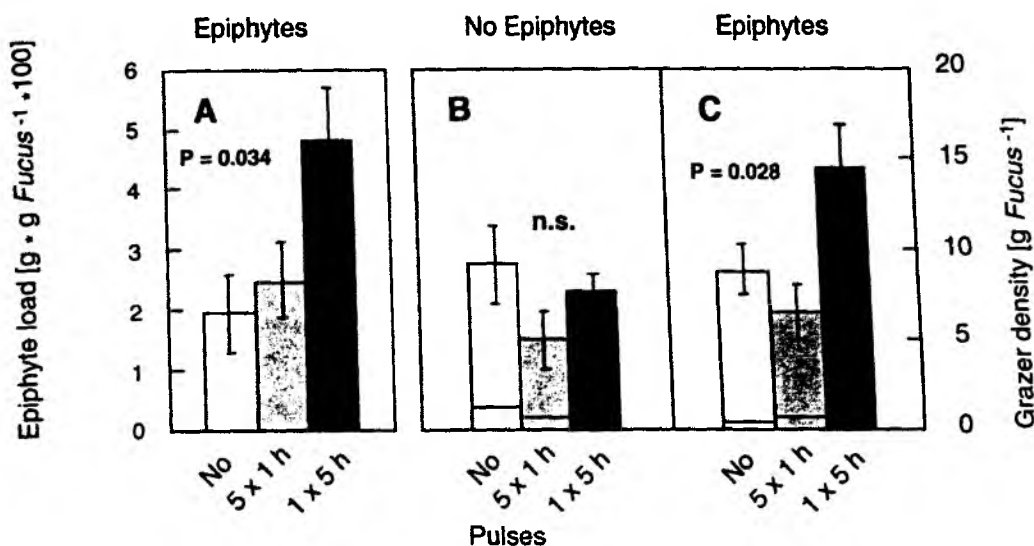


Fig. 3.2. Effects of nutrient pulsing on (A) epiphytes (*Pilayella littoralis*, *Elachista fucicola*), (B) grazer densities in treatments without epiphytes and (C) grazer densities in treatments with epiphytes. Data are means \pm 1 SE ($n=6$). P-levels are derived from 1-way ANOVA models (see text for details). Horizontal lines in grazer density columns indicate the relative proportions of snails (upper column) and crustaceans (lower column).

The grazer fauna (Table 3.1) on the experimental plants was dominated by small snails (*Littorina saxatilis* 43.6% of total, *Hydrobia ulvae* 47.6%) as compared to crustaceans (*Idotea* spp. 5.9%, *Gammarus* spp. 2.2%). Total grazer densities were high, ranging from 9 - 118 individuals per plant (mean 40.2 ± 5.3) or 3 - 22 individuals per g *Fucus* DM (mean 8.6 ± 0.9). Following the increase in epiphyte biomass, grazers occurred at significantly higher densities in nutrient enriched plots (Fig. 3.2 C, ANOVA, $F_{2,13}=4.74$, $P=0.0284$). Differences between controls and 1 h pulse treatments were not significant (SNK, $P<0.05$), but a 62%

increase of grazer densities in the 5 h pulse treatments was significant (SNK, $P < 0.05$). There was no effect of nutrient pulsing on grazer densities in treatments without epiphytes (Fig. 3.2 B, ANOVA, $F_{2,15} = 2.91$, $P = 0.0856$), but this could also be an artifact of the epiphyte removal procedure.

Linear regression models indicated a significant positive relationship between epiphyte load and grazer density ($y = 6.2 + 129.9x$, $r^2 = 0.28$, $P = 0.0354$) and a significant negative relationship between epiphyte load and *Fucus* growth rate ($y = 0.02 - 0.130x$, $r^2 = 0.26$, $P = 0.0371$) in treatments with epiphytes present (Fig. 3.3).

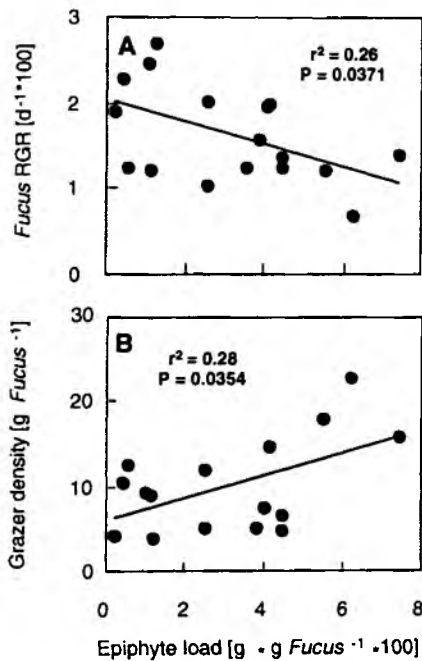


Fig. 3.3. Significant linear relationships between epiphyte load and (A) *Fucus* growth rate and (B) total grazer densities.

3.4. Discussion

In this short-term experiment, epiphyte load on *Fucus* increased significantly after a single 5 h nutrient pulse. This was followed by increases in grazer densities and decreases in *Fucus* growth rates. These results indicate rapid transmission of small-scale variations in resource supply through the benthic food web (epiphytes, seaweeds and grazers). Furthermore, it shows that temporal variability of nutrient supply (5 short versus 1 long pulse) plays a significant role in determining the response of primary producers and consumers to elevated nutrients.

This experiment was conducted in May when epiphyte loads on *Fucus* in the Western Baltic typically reach an annual maximum (Schramm et al. 1996, Lotze et al. 1999, 2000), grazer densities are high and nutrient concentrations decline rapidly towards low summer values ($< 0.5 \mu\text{mol L}^{-1}$ DIN and DIP, Schramm et al. 1996, Chapter 5, 6). Work in freshwater food webs has shown that, at the end of the spring bloom, intense grazing pressure and increasing

nutrient limitation regulate the abundance of phytoplankton (Lampert et al. 1986, Sommer 1989). I was interested whether variations of nutrient supply under these conditions will have effects on the abundance of filamentous epiphytes, and whether this triggers responses in grazers and the perennial host plants. Nutrient pulses such as those simulated in the experiment are common in eutrophic coastal systems. At the study site, irregular nitrate pulses ($70 - 160 \mu\text{mol L}^{-1}$) can occur on a time scale of hours - days between February and May, through wind-driven transport of hypertrophic waters from the inner Schlei Fjord (Schramm et al. 1996). On similar time scales, wind-driven mixing or upwelling of deep water increased total N 10-fold in a Danish fjord (Pedersen et al. 1995) and caused mass occurrences of filamentous epiphytes at the Finnish SW coast (Kiirikki & Blomster 1996).

In the experiment, a single 5 h nutrient pulse increased growth of epiphytes which had indirect effects on grazers and perennial host plants. In contrast, five 1 h pulses had no significant effects. Although nutrient uptake occurs on a time scale of minutes (Thomas & Harrison 1987, Lotze & Schramm 2000) longer exposure to a nutrient pulse appears be necessary to elevate internal nutrient pools to a critical level which is needed to sustain a significant growth response (Fujita et al. 1989, Pedersen & Borum 1996). In 2 other experiments, increases in pulse frequency had positive effects on algal growth rates, but pulse duration was always 6 h (Lapointe 1985, Pickering et al. 1993). My results indicate that pulse duration is a key factor that can be more important than pulse frequency at a time scale of 1 - 5 hours.

Manipulations of epiphyte densities allowed me to test for direct effects of nutrient pulses on *Fucus* as well as indirect effects through increased epiphyte cover. I did not detect significant direct effects on *Fucus* growth rate (Fig. 3.1 A). This could indicate lack of N limitation of *Fucus* in spring because of significant N storage (Schramm et al. 1988). An alternative hypothesis is that *Fucus* responded primarily via storage over the time scale of this experiment and significant growth responses occur on longer time scales. However, a statistically insignificant trend ($P=0.076$) indicated that nutrient pulsing increased growth in the

Table 3.1. Grazer species density [no g *Fucus*⁻¹] in treatments with and without epiphytes (n=18). *Idotea* spp. were *I. chelipes* and *I. baltica*; *Gammarus* spp. were *G. salinus* and *G. oceanicus*.

Species	No Epiphytes		Epiphytes	
	Mean	SE	Mean	SE
<i>Littorina saxatilis</i>	3.494	0.533	4.102	0.730
<i>Hydrobia ulvae</i>	2.895	0.521	5.512	0.920
<i>Littorina littorea</i>	0	0	0.024	0.018
<i>Idotea</i> spp.	0.535	0.113	0.488	0.101
<i>Gammarus</i> spp.	0.242	0.081	0.124	0.045
<i>Jaera albifrons</i>	0.085	0.061	0	0

absence of epiphytes and decreased growth in the presence of epiphytes (Fig. 3.1). Thus, nutrient enrichment may have positive direct effects or negative indirect effects on *Fucus*, depending on epiphyte cover. Indeed, 5 h nutrient pulses increased epiphyte load (Fig. 3.2) and high epiphyte load depressed *Fucus* growth rate by up to 50% (Fig. 3.3). Extrapolation of the regression line in Fig. 3.3 suggests that *Fucus* growth rate approaches zero when epiphyte load exceeds 0.15 g per g *Fucus*. Such loads have been exceeded in other years of study (Schramm et al. 1996). Although deleterious effects of epiphytes on macrophytes have been demonstrated before (Sand-Jensen 1977, Neckles et al. 1993), this is the first evidence that single pulses on a scale of hours can affect epiphyte-macrophyte competition. However, the relative roles of light and nutrient competition have yet to be revealed.

Grazers could be a potentially important ecological force that limits epiphyte biomass and mediates competition between epiphytes and *Fucus*, as shown for seagrass communities (Neckles et al. 1993, Williams & Ruckelshaus 1993). In this experiment, however, grazer density correlated positively with epiphyte biomass (Fig. 3.3) and increased significantly with nutrient enrichment, which indicates prevailing bottom-up effects from nutrients to epiphytes to grazers on the temporal and spatial scale of this experiment. It is important to note that grazers increased through immigration from a large source pool, not through an increase in population growth rate. However, increases in grazer densities with increasing nutrient supply have also been indicated by large-scale evidence, involving comparisons across entire coastlines (Bustamante et al. 1995, Menge et al. 1997, 1999). This study suggests that similar patterns can be found at very small temporal and spatial scales such as single plants subjected to single pulses of elevated nutrients.

4. Populations: Growth and productivity of *Fucus vesiculosus* across an eutrophication gradient

4.1. Introduction

Observations from temperate shorelines in many parts of the world indicate that marine macrophytes (macroalgae and seagrasses) decrease in abundance with increasing eutrophication (Duarte 1995, Schramm & Nienhuis 1996). For example, in the Baltic Sea, a doubling of dissolved inorganic nitrogen and phosphorus concentrations in surface and deep waters has been documented from 1958 - 1990 (Nehring 1987, 1991). Following the increase in nutrient availability, perennial, canopy-forming seaweeds (mostly *Fucus vesiculosus*), which have structurally and functionally dominated the rocky littoral ecosystem, declined in abundance (reviewed by Kautsky et al. 1992, Schramm 1996). However, these observations have been either purely qualitative (Bokn & Lein 1978, Hällfors et al. 1984, Rönnberg et al. 1985, Baden et al. 1990, Eriksson et al. 1998) or focused on sum parameters such as long-term changes in total biomass or percent cover of *Fucus* vegetation in a given area (Kangas et al. 1982, Kautsky et al. 1986, Vogt & Schramm 1991). A number of different mechanisms have been hypothesized, including shading from phytoplankton and epiphytes, negative effects of increased sedimentation, recruitment limitation through space competition from annual algae and filter feeders, overgrazing by herbivores and others (reviewed by Schramm 1996).

Furthermore, it is not clear whether declining *Fucus* populations in the Baltic suffer from increased mortality rate, decreased growth rate, decreased reproductive success or a combination of these factors. A knowledge of these demographic parameters may be fundamental in order to understand and model changes in plant density and biomass (Åberg 1992). Another aspect that needs to be addressed is that changes in *Fucus* abundance have probably important consequences for its functional role in the coastal ecosystem, including productivity and nutrient cycling (Kautsky et al. 1992). To my knowledge, no data are available on how these functional parameters change with increasing eutrophication. Such data would be useful to predict changes in ecosystem function in eutrophied coastal ecosystems (Jickells 1998).

In this Chapter, I focus on the performance of *Fucus* populations under conditions of increased nutrient supply. I followed small, replicated populations of *Fucus vesiculosus* germlings at Maasholm (the main study site in the Baltic Sea, Chapter 2) and two additional sites which are subjected to increased nutrient loading. I tested the following hypotheses: (1) *Fucus* mortality increases, growth and reproductive output decrease with increasing eutrophication, (2) as a consequence, *Fucus* productivity, carbon storage and nitrogen retention (measured as C and N retained in plant biomass at the end of the growth period) decline across a eutrophication gradient.

4.2. Methods

Sites

I transplanted *Fucus* germlings growing on concrete plates across an eutrophication gradient in the Schlei Fjord, Western Baltic Sea. While the outer Schlei Fjord has continuous water exchange with the Baltic, the inner reaches of the fjord experience limited water exchange (Schramm et al. 1996). With increasing distance from the mouth, increasing nutrient concentrations, phytoplankton and zooplankton biomass have been documented (Nellen & Rheinheimer 1970, Gocke & Rheinheimer 1994, Schramm et al. 1996, Table 4.1). I chose to work at 3 sites: Maasholm Germany (54°41.3'N, 10°0.5'E) at the mouth of the fjord, Karschau Germany (54°35.9'N, 9°49.8'E), 13 km from the mouth and Ulsnis Germany (54°33.9' N, 9°46.1' E), 24 km from the mouth (Chapter 2, Fig. 2.1). All sites are sheltered from severe wave action (fetch 3 - 7 km) and experience minimal physical disturbance from humans. Apart from differences in nutrient status, there are differences in salinity but not in temperature (Table 4.1). Differences in salinity likely do not confound the effects of eutrophication, because Baltic *Fucus* populations grow well under a wide range of salinity conditions (6 - 34 PSU, Bäck et al. 1992). Moreover, the entire Schlei Fjord once supported lush *Fucus* cover (Remane 1937). Today, *Fucus* has vanished from the inner Schlei (e.g. Ulsnis), but there is sparse *Fucus* cover in the central Schlei (e.g. Karschau) and high *Fucus* cover in the outer Schlei (e.g. Maasholm).

Table 4.1. The eutrophication gradient in Schlei Fjord (data compiled from Schramm et al. 1996). Lindaunis is 4 km upstream from Ulsnis, Arnis is 5 km upstream from Karschau. Temperature (°C), salinity (PSU), nutrient concentrations ($\mu\text{mol L}^{-1}$) and total N and P ($\mu\text{mol L}^{-1}$) were measured fortnightly from Sep 1994 - Dec 1995.

Site	Lindaunis	Arnis	Maasholm	Lindaunis	Arnis	Maasholm
	Temperature			Salinity		
MEAN	9.7	9.6	9.8	10.3	13.1	16.0
SE	1.3	1.3	1.3	0.3	0.5	0.6
MIN	0.0	0.8	-0.7	7.3	9.3	11.7
MAX	23.2	22.6	23.9	14.7	19.0	20.6
	Nitrate			Total Nitrogen		
MEAN	82.1	56.7	25.6	233.3	165.3	87.3
SE	17.6	12.4	7.7	40.7	28.1	16.7
MIN	0.0	0.0	0.0	29.5	26.4	22.6
MAX	300.1	248.7	161.6	513.6	405.9	301.5
	Phosphate			Total Phosphorus		
MEAN	2.0	1.6	0.9	2.9	2.3	2.1
SE	0.3	0.2	0.1	0.9	0.7	0.7
MIN	0.1	0.1	0.0	0.5	0.4	0.5
MAY	6.1	4.2	2.4	20.0	15.3	14.2

Field experiment

In February 1997, twenty-four concrete plates (15 x 12 x 4 cm) were deployed at Maasholm at 0.8 m water depth. These plates were seeded naturally with *Fucus vesiculosus* during the 1997 reproductive season (April - May, Chapter 5). Recruits became visible to the unaided eye by mid-June. All visible germlings were counted in July and percent cover of *Fucus* and other algae was estimated with a plexiglas frame with 50 random dots. In addition to *Fucus* (32.9 ± 1.4 percent cover, mean \pm 1 SE, n=24), *Pilayella littoralis*, *Ceramium strictum*, and *Enteromorpha intestinalis* were growing on the plates (11.1 ± 1.1 percent cover). All plates were marked with epoxy tags and numbers and randomly assigned to one of 3 sites, Maasholm, Karschau and Ulsnis (n=8 replicates per site). Plates were transplanted to the sites on 15 July 1997 at 0.8 m depth. Individual plates were spaced 3 m apart.

All sites were visited in 3 - 5 month intervals in October 1997, February, June and November 1998. Germling length and density were assessed on all dates except June 1998, when only germling length was assessed. Length was measured by pointing a ruler into the canopy at 8 random points and reading the length of the germling that was growing closest to the base of the ruler. Density was assessed by counting all plants on a central 10 x 10 cm area on the plates. On 1 June 1998, the percentage of reproductive plants was assessed by inspecting 10 randomly chosen plants per replicate for visible receptacles. On 18 November 1998, all plates were scraped with razor blades and *Fucus* biomass was harvested. *Fucus* had practically no epiphytes at this time but some plants at Maasholm had to be cleared from epizootic mussels (*Mytilus edulis*). Samples were dried at 80°C for 48 h and dry mass was determined to the nearest mg. Subsequently, plants were ground to a powder and 2 subsamples per plot were analyzed for carbon and nitrogen tissue content on an automated C:N analyzer (Fisons Instruments, NA 1500 N).

Data analysis

Germling length and density data were analyzed by 1-way repeated-measures (RM)-ANOVA with "Site" (Maasholm versus Karschau versus Ulsnis) as a fixed factor variable and "Time" as repeated measure (4 or 5 sampling dates). This analysis tests the null-hypothesis that there are no differences among the 3 sites or among sampling dates. Biomass and C:N data were analyzed by 1-way ANOVA with "Site" as the fixed factor. Student-Newman-Keuls (SNK) procedure was used for post-hoc comparisons. All data except C:N ratios were log-transformed in order to fulfill the assumption of homogeneous variances, tested by Cochran's test.

4.3. Results

Growth, survival, productivity and C:N tissue ratios of *Fucus* transplants over the experimental period were significantly different among the 3 sites (Table 4.2). Significant Time x Site interactions indicated that some of these differences were not consistent through time (Table 4.2, Fig. 4.1). *Fucus* germling density remained similar among the 3 sites from summer 1997 to spring 1998, despite a 69% overall decrease in germling density (Fig. 4.1 B). From spring to fall 1998, however, *Fucus* density declined by 97% in Ulsnis while in Maasholm and Karschau it declined by 73 - 78%. Final plant densities were not significantly different in Maasholm and Karschau (SNK, $P > 0.05$), but significantly lower in Ulsnis (SNK, $P < 0.0001$). Initial germling length was the same at all sites (ANOVA, $F_{2,21} = 0.26$, $P = 0.7772$). During the first 3 months of the experiment, plants in Maasholm were growing significantly higher than in Karschau and Ulsnis ($F_{2,19} = 40.52$, $P < 0.0001$). During winter (Oct 97 - Feb 98), plant density and length did not change much between the sites. But during the next growth season (Feb - Nov 98) *Fucus* plants in Maasholm grew faster than plants in Karschau which grew faster than those in Ulsnis where plant growth stagnated (SNK, $P < 0.05$). These differences in growth mirrored similar differences in reproduction. In June 1998 (13 months after *Fucus* plants recruited onto the experimental substrata), 58.6 (± 5.3)% of plants in Maasholm were reproductive (showing fertile receptacles). In Karschau, only 3.8 (± 1.8)% of plants were reproductive, while in Ulsnis none of the plants had receptacles.

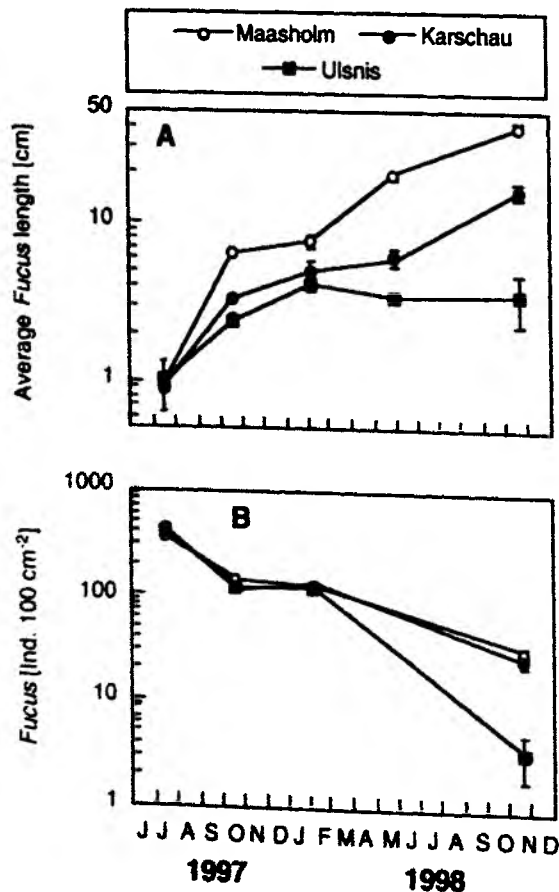


Fig. 4.1. (A) Mean length and (B) mean density of *Fucus vesiculosus* germlings (± 1 SE, $n=8$) throughout the experiment. See Table 4.2 for statistical analysis.

Fucus biomass after 18 months was highest in Maasholm, reaching $16.33 (\pm 2.30, n=8)$ kg dry mass m^{-2} (Fig. 4.2 A). Biomass in Karschau was only 10.5% and in Ulsnis only 0.4% of that in Maasholm. All these differences were significant (Table 4.2). Similar effects occurred for carbon storage (ANOVA, $F_{2,19}=78.25, P<0.0001$, Fig. 4.2 B) and nitrogen retention (ANOVA, $F_{2,19}=186.06, P<0.0001$, Fig. 4.2 B). C:N tissue ratios were significantly lower in Karschau (12.6 ± 0.3) compared with Maasholm (16.8 ± 0.7) and Ulsnis (19.3 ± 1.7) (SNK, $P<0.05$).

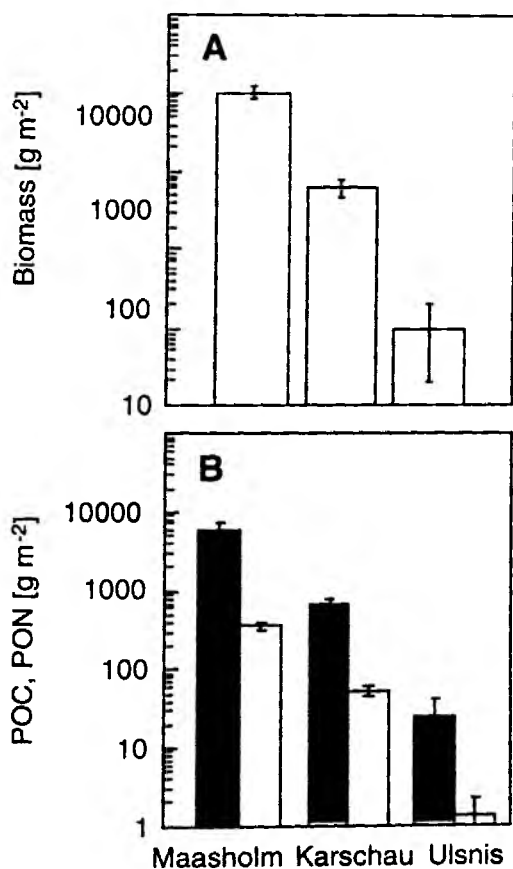


Fig. 4.2. Productivity and tissue composition in *Fucus* at the 3 experimental sites (A) Biomass after 18 months as g dry mass m^{-2} . (B) Carbon storage (POC, dark bars) and nitrogen retention (PON, light bars) in plant biomass at the end of the experiment in November 1998. Data are means ± 1 SE ($n=8$). See Table 4.1 for analysis.

4.4. Discussion

As these results indicate, *Fucus* can reach extremely high growth rates and productivity under eutrophic conditions such as those present in Maasholm. But growth, survival, reproductive output, productivity, carbon storage and nitrogen retention all decline dramatically towards hypertrophic conditions.

Net primary productivity of *Fucus* at Maasholm appeared to be the highest ever recorded in any aquatic or terrestrial system (Fig. 4.3). Because productivity was assessed by the harvesting method which does not include losses to reproduction, grazing, and physical disturbance, this must be even considered a conservative estimate (Sommer 1998). How could this extreme value be explained? Macroalgal assemblages are known to range among the most

productive communities in the world, which may be linked to a continuous nutrient supply through wave action and the ability for carbon and nitrogen storage (Mann 1973, Chapman & Craigie 1977). Productivity at Maasholm, however, is twice the maximum productivity previously reported for macroalgae (Fig. 4.3). Because macroalgal growth is often nutrient limited (Fong et al. 1993, Lapointe 1995, Pedersen & Borum 1996), high nutrient supply at Maasholm may explain high growth rate. However, *Fucus* productivity declined by one order of magnitude from Maasholm to Karschau and by another order of magnitude from Karschau to Ulsnis (Fig. 4.2 A). Although nutrient supply was even higher at these sites (Table 4.1), plant growth was severely reduced compared with Maasholm (Fig. 4.1). This may suggest non-linear responses of *Fucus* to increasing nutrient supply. Mortality of germlings was similar among the 3 sites for the first half of the experiment and probably related to interspecific competition and "self-thinning", as commonly observed in seaweed populations (Cousens & Hutchings 1983, Creed et al. 1996 a, b, Karez 1997). Throughout the second half of the experiment, however, mortality increased at the most eutrophic site (Ulsnis), while it remained similar at the two other sites. In addition, there were striking effects on reproduction, which were probably linked to plant size. Only plants >14 cm length were reproductive, which parallels results from other *Fucus vesiculosus* populations (Knight & Parke 1950, Grützmacher 1984). The largest plants in Ulsnis reached only 11 cm. Hence, no reproduction occurred at Ulsnis. Less than 5% of plants were reproductive in Karschau but more than 50% were reproductive in Maasholm. I conclude that poor performance of *Fucus* populations with increasing eutrophication extends to all important population parameters: growth, mortality and reproduction. With decreasing plant productivity, carbon storage and nitrogen retention in macroalgal biomass were equally reduced (Fig. 4.2 B). This is probably not compensated for by phytoplankton production. Maximum phytoplankton production in the Schlei is $600 \text{ g C m}^{-2} \text{ y}^{-1}$ (Gocke & Rheinheimer 1994), which is still among the highest values ever recorded for marine phytoplankton (Sommer 1998), but small compared to the $4900 \text{ g C m}^{-2} \text{ y}^{-1}$ that I estimated for *Fucus*. Most of the phytoplankton production (50 - 90% depending on water depth) is rapidly recycled in the water column and consequently only a small fraction of the assimilated carbon is permanently stored in sediments (Gocke & Rheinheimer 1994).

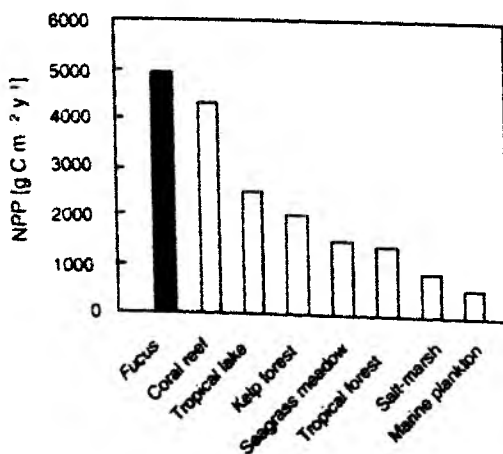


Fig. 4.3. Net primary productivity (NPP) of *Fucus* in Maasholm compared with published record values from other ecosystems. Coral reef data from Sorokin (1995), Tropical lake data from Likens (1975), tropical forest data from Whittaker (1975), plankton data from Gocke & Rheinheimer (1994), others from Mann (1973).

Table 4.2. Analysis of *Fucus* growth parameters and tissue composition across sites (Maasholm, Karschau, Ulsnis). *Fucus* length and density were measured repeatedly throughout the experiment, therefore RM-ANOVA models were used. *Fucus* biomass and C:N ratios were analysed by 1-way ANOVA.

Variable	Source	df	MS	F	P
<i>Fucus</i> length	Site	2	1.77	102.10	0.0001
	Error	17	0.02		
	Time	4	2.07	167.54	0.0001
	Time x Site	8	0.28	22.92	0.0001
	Error	68	0.01		
<i>Fucus</i> density	Site	2	0.47	31.50	0.0001
	Error	16	0.02		
	Time	3	6.33	407.51	0.0001
	Time x Site	6	0.38	24.63	0.0001
	Error	48	0.02		
<i>Fucus</i> biomass	Site	2	18.33	60.87	0.0001
	Error	19	0.30		
<i>Fucus</i> C:N ratio	Site	2	141.62	13.19	0.0003
	Error	17	91.27		

What are the driving mechanisms behind the decline of *Fucus*? Negative physiological effects of enhanced nutrient concentrations (mainly ammonium) on macroalgal growth may become relevant at very high levels ($>500 \mu\text{mol L}^{-1}$, L. Kautsky 1982), which did not occur at my study sites (Table 4.1). Nutrient-stimulated phytoplankton blooms and subsequent light limitation may be a key mechanism in this system. Phytoplankton chlorophyll concentrations increase strongly across the Schlei gradient (Maasholm $9.6 \pm 2.6 \mu\text{g L}^{-1}$ [range 1.1 - 64.0], Arnis $25.6 \pm 3.4 \mu\text{g L}^{-1}$ [4.5 - 81.7], Lindaunis $54.1 \pm 6.8 \mu\text{g L}^{-1}$ [17.5 - 208.5], Schramm et al. 1996). The highest phytoplankton production rates were found directly at the surface (Gocke & Rheinheimer 1994). Productivity in the inner Schlei Fjord declined by 98% in the first 0.7 m depth, indicating strong light limitation of phytoplankton production below the water surface (Secchi depth can be as shallow as 0.4 m, Gocke & Rheinheimer 1994). Because macrophytes have typically lower compensation irradiances than phytoplankton (Duarte 1995), light limitation of *Fucus* photosynthesis and growth at the experimental depth (0.8 m) was probably severe in the inner Schlei Fjord. By comparing phytoplankton biomass, macrophyte depth penetration and total N for

20 Danish estuaries, Sand-Jensen & Borum (1991) found that phytoplankton biomass was a positive linear function of total N and depth penetration of macrophytes a negative function of total N. Fucooids were more sensitive to increased total N than other macroalgae or rooted macrophytes. An empirical relationship predicts that fucooid depth penetration reaches 0 m when average total N exceeds 1.3 mg L^{-1} (Sand-Jensen & Borum 1991). Average total N near Ulsnis was 3.2 mg L^{-1} , near Karschau it was 2.3 mg L^{-1} and at Maasholm it was 1.2 mg L^{-1} (Schramm et al. 1996, Table 4.1). Based on my data, I would predict a slightly higher threshold, between 2 - 3 mg L^{-1} total N, beyond which *Fucus* growth is severely compromised by light competition from phytoplankton. Similarly, decreased depth distribution of *Fucus* in eastern Sweden was attributed to increased nutrient input and phytoplankton densities, which may intensify light limitation of *Fucus* (Kautsky et al. 1986).

However, widespread decline of fucooid macroalgae in the Baltic, the NE Atlantic and the Mediterranean (Schramm & Nienhuis 1996) can not only be attributed to increased competition from phytoplankton. In Kiel Bight for example, 95% of *Fucus* biomass was lost from 1950 - 1990, although nutrient loading and phytoplankton biomass are generally lower than at Maasholm (Gocke & Rheinheimer 1994). Competition from fast-growing ephemeral algae may be another mechanism that leads to a decline of *Fucus* in shallow waters when light competition from phytoplankton is not severe (Duarte 1995, Schramm & Nienhuis 1996, Valiela et al. 1997). Competition between fucooids and other algae may be particularly intense at the recruitment stage (Lubchenco 1986, Vadas et al. 1992, Worm & Chapman 1996, 1998), which was not tested in the experiment. The following questions arise: (1) why is *Fucus* still dominant and extremely productive, albeit high nutrient loadings in Maasholm, (2) how would *Fucus* productivity change at Maasholm if nutrient levels were increased, and (3) how is settlement and recruitment of *Fucus* influenced by increasing nutrient supply and competition from other algae? I will attempt to answer these questions in the following two chapters.

5. Communities: Propagule banks modify plant competition, consumer and resource control in the Baltic *Fucus* community

5.1. Introduction

In the previous Chapters, I have analyzed the effects of variations in nutrient supply on perennial macroalgae and their epiphytes. In this Chapter I ask how the effects of nutrient enrichment on the algal community depend on grazing pressure and on patterns of propagule supply from dormancy and dispersal.

Dispersal and dormancy of propagules are critical processes that contribute to the persistence of plant populations in a variable environment (Harper 1977). Dispersal reduces the risk of local extinction by spreading propagules spatially. Contrary, investment into banks of dormant propagules can provide temporal escapes from adverse conditions. A significant part of the planet's diversity including many protists (Fenchel et al. 1997), insects (Tauber et al. 1986), crustaceans (Hairston & DeStasio 1988, DeStasio 1989), nematodes (Begon et al. 1990), seaweeds (Chapman 1986) and land plants (Leck et al. 1989, Fenner 1992) survives unfavorable periods as cysts, eggs, microscopic stages, seeds or seedlings which can persist over time scales from months to centuries (Leck et al. 1989, Fenner 1992). Although dormant propagule banks occur in all major habitats, they have been studied mostly in higher land plants. Among land plants, differential investment into the propagule bank is related to species life-history patterns: opportunistic annuals invest orders of magnitude more propagules into soil seed banks than most perennial species (Grime 1979) and have more persistent seeds than related perennials (Thompson et al. 1998). Such traits may translate into a competitive advantage for opportunistic annuals in frequently disturbed environments (ruderal strategy, Grime 1979), which has consequences for plant community structure.

On rocky shores, macroalgal propagule banks have been described only recently in some detail (Santelices et al. 1995, Lotze et al. 1999). These "banks of microscopic stages" (Chapman 1986) consist of settled spores, microrecruits or other microscopic forms which suspend growth and survive in a dormant stage for up to 10 months (Hoffmann & Santelices 1991, Schories 1995, Lotze 1998). Whereas the importance propagule supply from dispersal for the dynamics of marine macroalgal populations has been demonstrated (Reed et al. 1988, 1992, Santelices 1990), the relative importance of dormant propagule banks remains unclear. Recently, it has been shown that bloom-forming annual algae use the propagule bank as an important "seed source" for the spring bloom (Schories 1995, Lotze et al. 1999, 2000). I hypothesize that the presence of a dormant propagule bank affects the relative abundance of annual and perennial algae and the relative impacts

of consumers and resources on algal community structure (species composition and diversity). To test these hypotheses, I manipulated the presence of grazers and dormant propagule banks as well as nutrient supply in a factorial field experiment. In order to relate patterns of macroalgal recruitment in the experiment to seasonal patterns of propagule supply, I also monitored settlement and recruitment of macroalgal propagules over a 2-year period.

5.2. Methods

Monitoring of settlement

I applied a recently developed monitoring technique in order to obtain a rough estimate of seasonal patterns of propagule dispersal and settlement at the experimental site (Kiirikki and Lehvo 1997). Propagule settlement was estimated from observations of a sequence of settlement substrata (concrete blocks) which were installed at discrete time intervals at Maasholm, Schlei Fjord, Western Baltic sea (for site description see Chapter 2). Concrete is a suitable substratum for settlement of Baltic macroalgae (Kiirikki & Lehvo 1997). I exposed a sequence of 50 concrete blocks (30 x 30 x 5 cm) at intervals of 14 d (Feb - July 1997) or 10 d (Aug 1997 - Oct 1998). One block per time interval was added to the sequence and installed adjacent to the cage experiment (see below) at 0.8 m water depth. Every 1 - 2 months, all blocks were inspected and average canopy height of each attached species was measured with a ruler in 0.5 cm intervals. In addition, percent cover of all attached species was estimated using a 25 x 25 cm plexiglas sheet with 50 random dots. Algal samples were obtained to verify species identification.

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

Experimental design

I performed a factorial field experiment from February to December 1997 where I manipulated the presence of a macroalgal propagule bank, grazer presence and nutrient enrichment (Fig. 5.1). This was done in cooperation with H.K. Lotze who investigated the effects of these manipulations on competition between *Pilayella littoralis* and *Enteromorpha* spp. (Lotze 1998, Lotze et al. 2000). The experiment was conducted at Maasholm (see site description in Chapter 2) in a natural stand of *Fucus vesiculosus* at 0.8 m water depth. The experimental treatments (propagule bank, grazer, nutrients) were combined in a 2 x 2 x 2 completely crossed design (Fig. 5.1 B) with randomized blocks (4 replicates per treatment combination arranged in 4 blocks of 12 plots each).

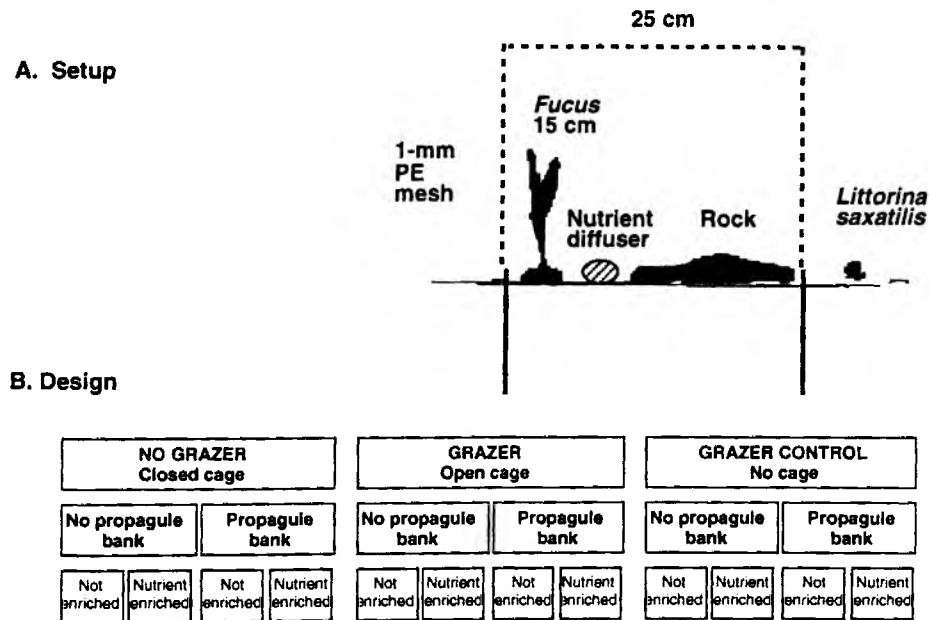


Fig. 5.1. (A) Experimental setup and (B) experimental design of a factorial field experiment testing for interactions among grazers, a macroalgal propagule bank and summer nutrient enrichment. Each of the 12 treatment combinations had 4 replicates. The design allows to test for grazer effects (Main experiment: comparing NO GRAZER and GRAZER treatments) while controlling for cage effects (Control experiment: comparing GRAZER and GRAZER control plots). The experiment was run from February to December, nutrient enrichment was maintained from late June to late August.

Grazers were manipulated with cages (25 x 25 x 25 cm). These were made from a stainless steel frame covered with transparent polyethylene mesh (1 mm mesh size). This mesh size is necessary in order to exclude mesograzers (2 - 15 mm body size), which dominate the grazer fauna of the Baltic Sea. Repeated light measurements indicated that photon flux through the mesh was reduced by only 8% (LI-COR LI-192SA). Half of the cages were completely closed (NO GRAZER

treatment), the other half of the cages had one side cut open to allow free access for grazers (GRAZER treatment). In addition, I established uncaged GRAZER CONTROL plots to test for potential cage artifacts. All plots were 3 m apart from each other. Cages were brushed weekly to prevent fouling and closed cages were checked weekly for grazer intrusion. In July, I compared grazer densities within a central 10 x 10 cm area between GRAZER and GRAZER CONTROL plots to evaluate possible cage artifacts on grazer abundance.

The experimental units were flat granite rocks (ca. 15 - 20 cm in diameter). These rocks were collected from the shallow water zone at the study site after break-up of sea ice in February and were initially bare of macroscopic vegetation. To remove the microscopic propagule bank, half of the rocks were heat-sterilized for 48 h at 100°C in order to kill all microscopic macroalgal stages, the other half was left untreated.

Nutrient enrichment was performed on one half of the experimental plots during the period of summer nutrient depletion (20 June - 30 Sep 1997). Therefore, I developed a novel method involving rolls of polyethylene mesh (40 x 2.5 cm, 1 mm mesh size) which were filled with 160 g NPK slow-release fertilizer pellets (Plantacote Depot 6M, Urania Agrochem, Hamburg, Germany). Pellets are covered with a semi-permeable polyurethane membrane and contain 14% N (5.7% NO₃ and 8.3% NH₄), 9%P (P₂O₅) and 15% K₂O, the latter which was assumed to have no effect due to the high K concentrations in seawater. This method is probably the most reliable technique for *in situ* nutrient enrichment of benthic food webs; detailed discussion and comparisons with other methods are provided by Worm et al. (2000a). To control treatment levels, I monitored water column nutrient concentrations on all plots at 3 wk intervals. I obtained water samples with 10 ml polyethylene syringes at a central position within the cages. All samples were immediately filtered over Whatman GF/F filters (pre-combusted at 550°C to remove possible contaminations) and analyzed colorimetrically for ammonium and phosphate (Grasshoff et al. 1986). Release of nitrate was not quantified in this experiment. Independent tests of this enrichment method showed that these diffusers increase nitrate availability on average by 120% relative to background concentrations (Worm et al. 2000a). Using this relationship, I estimated nitrate enrichment levels from water column nitrate levels that were sampled at the experimental site every two weeks. Nitrate samples were obtained with 1 L polyethylene bottles, filtered (Whatman GF/F), frozen and subsequently analyzed on a Technicon autoanalyser.

As the main dependent variable, percent cover of all species on the experimental rocks was estimated monthly with a 10 x 10 cm plexiglas sheet marked with 50 random dots. In June and August, I estimated species diversity using the Shannon-Weaver Index (number of species, weighed by their relative abundance, expressed as percent cover, see Valiela [1995] for formula and constraints). Furthermore, I estimated *Fucus* recruit densities in May, June, August and October in five 2 x 2 cm subsamples within a central 10 x 10 cm area on all experimental rocks.

In addition to *Fucus* recruitment, I was interested to test for treatment effects on growth and survival of adult *Fucus* plants. Therefore I included single *Fucus* plants into all cages and on uncaged plots (Fig. 5. 1 A). I assumed that dormant propagules on *Fucus* plants could not be manipulated in a similar manner as on the experimental rocks without damaging *Fucus*. Instead, I removed all germinating epiphytes on half of the plants during a first sub-experiment from February - June. Hence, during this period grazers and epiphytes were manipulated in a 2 x 2 design. During a second sub-experiment from July - November, grazers and nutrient enrichment were manipulated (2 x 2). Epiphyte cover on *Fucus* remained very low in the second sub-experiment and was not manipulated. In February, I collected *Fucus* plants (12 - 18 cm length) that were growing on small rocks (170 ± 15 g, $n=48$) at Maasholm. Plants were initially free of epiphytes. Plants with rocks were blotted dry with paper tissue for 15 s and weighed. In a first sub-experiment, single *Fucus* plants were added to each experimental plot from February - June. In June, *Fucus* plants were collected, separated from epiphytes and rocks and all 3 parts were weighed separately. The dry mass of *Fucus* and epiphytes was determined after drying at 80°C for 48 h. A second, independent set of *Fucus* plants was run from July - November. Plants were weighed together with their rock substrate in September (no epiphytes occurred at that time). In November, plants were separated from rocks and both parts were weighed separately. Then dry mass of *Fucus* was determined as above. As dependent variables, I estimated *Fucus* relative growth rate in the two sub-experiments as $RGR = (\ln M_2 - \ln M_1) / (t_2 - t_1)$, with M =dry mass of *Fucus* [g] and t =time [d].

Data analysis

All data were analyzed by factorial fixed-factor ANOVA including "Grazers" (GRAZER vs. NO GRAZER) and "Propagule bank" (No propagule bank vs. Propagule bank) as the main effects. "Nutrients" were added as an additional factor to test for the effects of summer nutrient enrichment. The control experiment was analyzed like the main experiment, only that the effect "Cage" (GRAZER vs. GRAZER CONTROL) replaced the "Grazers" effect. When it explained a significant portion of variance, the spatial block effect was included as a non-interactive variable (Mead 1997). Species cover data were angular transformed (Sokal & Rohlf 1995) and analyzed by multivariate MANOVA using the Pillai trace statistic (Johnson & Field 1993). This approach was chosen because it takes cross-correlations among species abundances into account. Two MANOVA runs were performed: pre-enrichment (20 June) and post-enrichment (30 August). In addition, I used univariate ANOVAs to compare changes in the abundance of individual species. *Fucus* recruit density and grazer abundance data were (log+1)-transformed, in order to achieve homogeneity of variances, checked by Cochran's test. Furthermore, I tested for a linear relationship between log (x+1) - transformed *Fucus* recruit densities and the cover of *Enteromorpha* in the experiment by linear regression analysis.

5.3. Results

Monitoring of settlement

Eight species of macroalgae showed dense settlement and recruitment on the settlement blocks (Fig. 5.2). Additional rare species which recruited too sparsely to estimate their settlement periods were *Ceramium nodulosum*, *Polysiphonia violacea*, *Dumontia contorta* and *Chaetomorpha linum*. Among the annual species a clear temporal distinction between 6 species of summer annuals (*Enteromorpha intestinalis*, *E. prolifera*, *E. clathrata*, *Pilayella littoralis*, *Ceramium strictum*, *Cladophora rupestris*) and 3 species of winter annuals (*Ulvopsis grevillei*, *Petalonia fascia*, *Scytosiphon lomentaria*) was observed (Fig. 5.2). The length of the settlement period varied among species and years between 1 and 5.5 months. The only perennial species, *Fucus vesiculosus*, was characterized by a short and intense settlement period from late April to late May in 1997 and from early May to late June in 1998. Some minor *Fucus* settlement occurred on blocks exposed between September to November 1997 and in September 1998. *Fucus* propagules that were generated in fall overwintered as microscopic forms in the propagule bank and recruited to the macrobenthos in the following spring. Similar spring recruitment of overwintering microscopic forms was observed in *Enteromorpha* spp. *Cladophora rupestris* and *Pilayella littoralis*. In addition, adult thalli of *Fucus*, *Ceramium strictum* and (with few individuals) *Cladophora rupestris* overwintered at Maasholm.

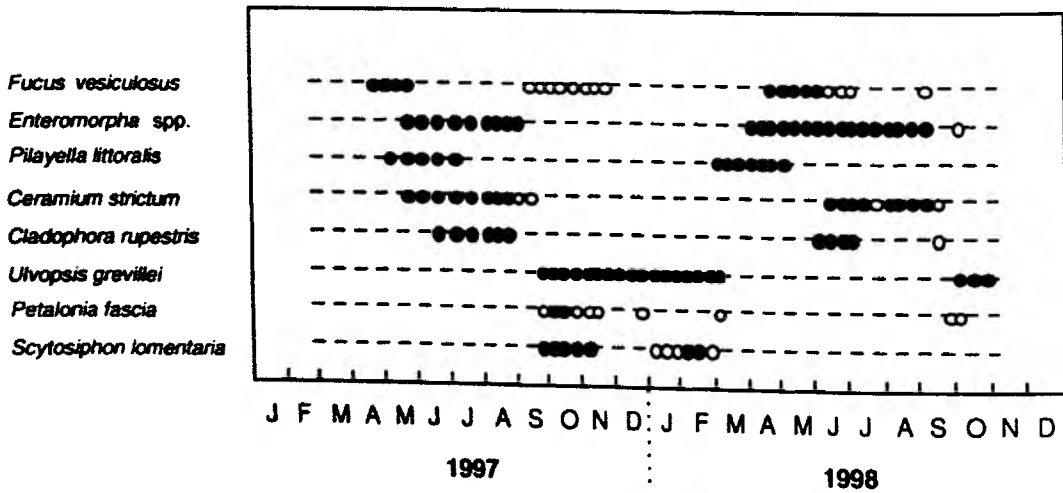


Fig. 5.2. Estimated periods of propagule settlement for eight abundant macroalgal species in Maasholm. Settlement plates were installed at 0.8 m depth at Maasholm every 10 - 14 d from February 1997 to October 1998. Dark circles indicate high settlement (>2% cover), open circles low settlement (<2% cover). *Enteromorpha* spp. was mostly (>80%) *E. intestinalis*. during July and August, *E. prolifera* and *E. clathrata* co-occurred with *E. intestinalis*.

Field experiment: Effects on community structure

Macroalgae were the dominant colonizers on the experimental rocks. Benthic invertebrates (*Mytilus edulis*, *Balanus improvisus*) showed very low recruitment (2% cover or less). Benthic microalgae (mostly tube-dwelling diatoms: *Berkeleya rutilans*) mixed with fine filaments of the winter annual *Ulothrix flacca* occurred abundantly 1 - 2 months after initiation of the experiment, but disappeared thereafter. Depending on the treatment combination, the macroalgal community was dominated by the green annual *Enteromorpha* spp. (Fig. 5.3 A) or *Fucus vesiculosus* (Fig. 5.3 B). *Enteromorpha* spp. (*Enteromorpha* hereafter) was mostly (>80%) *E. intestinalis*. In July and August *E. prolifera* and *E. clathrata* co-occurred with *E. intestinalis*. Diatoms, brown, green and red annual macroalgae colonized the rocks in a successive seasonal sequence at low to intermediate densities (Fig. 5.3 C - E). Other macroalgae that occurred at low densities (<2% mean cover at anytime) were *Chaetomorpha linum* and *Ceramium nodulosum*.

Enteromorpha recruited abundantly from overwintering propagules in March - April and dominated treatments with propagule bank thereafter (Fig. 5.3 A). *Enteromorpha* cover remained significantly lower in treatments without propagule bank (Table 5.1). In contrast, *Fucus* recruited mostly from spring reproduction (April - May, fig. 5.2) and dominated treatments without propagule bank (Fig. 5.3 B, Table 5.1). Similarly, *Pilayella littoralis* and *Cladophora rupestris* were significantly more abundant in treatments without propagule bank (Table 5.1). The winter annual *Ulvopsis grevillei* dominated treatments with propagule bank in February and March (Fig. 5.3 D), but was replaced by *Enteromorpha* thereafter. Grazers had no significant effect on any of the species from February - April, but pronounced effects throughout the following months (Fig. 5.3). *Enteromorpha* and *Pilayella littoralis* were significantly depressed by grazers (Table 5.1), more grazer-resistant species such as *Ceramium strictum* and *Fucus* significantly increased in abundance when grazers were present (Table 5.1).

In the control experiment (GRAZER versus GRAZER CONTROL treatments), I detected significant cage artifacts on half of the colonizing species (Table 5.1). All of these species were also significantly affected by grazers in the main experiment (Table 5.1). The grazer-susceptible species *Enteromorpha* and *Pilayella* had increased cover in GRAZER cages, whereas *Fucus* and *Ceramium strictum* which were indirectly favored by grazing had increased cover on uncaged GRAZER CONTROL plots. This suggests that cage artifacts may be linked to changes in grazer abundance or activity and not by other possible factors such as reduction of photon flux or water flow or increased sedimentation inside cages (this would have reduced the performance of all species inside cages as compared with uncaged plots). In accordance with this hypothesis, grazer counts revealed that the abundance of the snail *Littorina saxatilis* was significantly reduced in the GRAZER compared with GRAZER CONTROL plots (Table 5.2, ANOVA, $F_{1,28}=23.6$, $P<0.0001$). This was most likely an artifact created by the weekly cage brushing procedure, after which slow-moving snails needed time to re-invade GRAZER cages. Fast-moving crustacean grazers (*Idotea chelipes*

Table 5.1. Results of two-way ANOVAs on percent cover of species in the main (above) and control (below) experiment. Values are F-ratios, stars indicate significance levels with $P < 0.05 = *$, $P < 0.01 = **$, $P < 0.001 = ***$, $P > 0.05 = \text{n.s.}$ Analyses was performed for the one month when each species reached its maximum abundance (Table 5.3). Summer nutrient enrichment had no significant effect ($P > 0.1$) on the cover of individual species during these months. Thus this effect was pooled with the error term.

Main experiment	Grazer	Propagule Bank	G x PB	MS block	MS error
Species	df=1	df=1	df=1	df=3	df=28
<i>Enteromorpha</i> spp.	20.50 ***	9.46 **	0.16 n.s.	0.001	0.090
<i>Fucus vesiculosus</i>	18.01 ***	34.23 ***	0.28 n.s.	0.014	0.049
Benthic diatoms	2.70 n.s.	0.66 n.s.	2.48 n.s.	0.017	0.106
<i>Pilayella littoralis</i>	0.12 n.s.	13.03 **	7.37 *	0.013	0.046
<i>Ulvopsis grevillei</i>	0.13 n.s.	9.28 **	0.30 n.s.	0.133	0.076
<i>Cladophora rupestris</i>	0.05 n.s.	4.68 *	1.12 n.s.	0.063	0.028
<i>Ceramium strictum</i>	9.94 **	4.12 n.s.	0.02 n.s.	0.021	0.026
<i>Polysiphonia violacea</i>	1.53 n.s.	3.93 n.s.	1.94 n.s.	0.006	0.019
Control experiment	Cage	Propagule Bank	C x PB	MS block	MS error
Species	df=1	df=1	df=1	df=3	df=28
<i>Enteromorpha</i> spp.	32.16 ***	12.04 **	3.78 n.s.	0.007	0.008
<i>Fucus vesiculosus</i>	17.72 ***	8.382 **	1.24 n.s.	0.052	0.088
Benthic diatoms	0.05 n.s.	0.27 n.s.	0.26 n.s.	0.028	0.111
<i>Pilayella littoralis</i>	30.12 ***	0.401 n.s.	3.52 n.s.	0.196	0.040
<i>Ulvopsis grevillei</i>	0.01 n.s.	5.932 *	0.01 n.s.	0.051	0.088
<i>Cladophora rupestris</i>	1.38 n.s.	0.29 n.s.	0.06 n.s.	0.008	0.057
<i>Ceramium strictum</i>	15.96 ***	1.115 n.s.	1.42 n.s.	0.019	0.024
<i>Polysiphonia violacea</i>	3.62 n.s.	0.006 n.s.	0.55 n.s.	0.004	0.004

Table 5.2. Densities of grazer species in the cage experiment (individuals per 100 cm² ± ISE, n=16). *Gammarus* spp. was *G. salinus*, *G. locusta* and *G. zaddachi*. *Idotea* spp. was *Idotea chelipes* and *Idotea baltica*. GRAZER (open cages) and GRAZER CONTROL plots (no cage) were compared by ANOVA.

Species	Open cage	SE	No cage	SE
<i>Littorina saxatilis</i>	4.46 ***	0.77	13.06	2.27
<i>Littorina litorea</i>	0.04 n.s.	0.04	1.27	0.63
<i>Idotea</i> spp.	4.97 *	1.16	2.12	0.48
<i>Gammarus</i> spp.	3.39 n.s.	0.67	3.02	0.76
All species combined	12.85 *	1.29	18.32	2.40

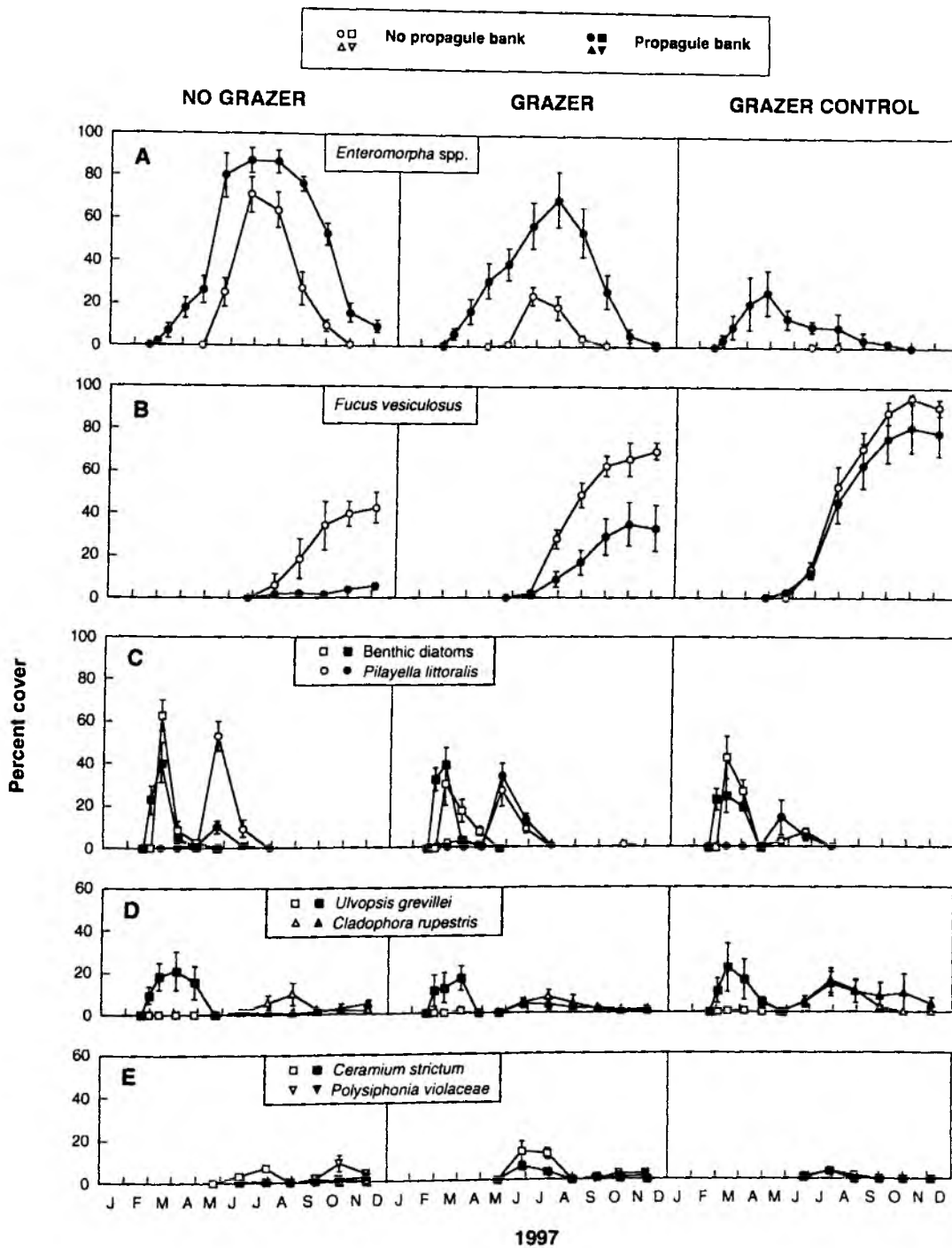


Fig. 5.3. Population development. Effects of grazers and a dormant propagule bank on population development of 8 abundant macroalgal species (means \pm 1SE, n=8). Percent cover is shown throughout the year for (A) the annual green alga *Enteromorpha* spp., (B) the perennial alga *Fucus vesiculosus*, (C) diatoms and ephemeral brown algae, (D) ephemeral green algae, and (E) ephemeral red algae. For ANOVA results see Table 5.1.

Table 5.3. Experimental effects, estimated propagule densities in the propagule bank and maximum cover of macroalgal species in the cage experiment. To compare experimental effects among species, I calculated a simple index $I = (\text{treatment density} - \text{control density}) / \text{control density}$ (Paine 1992) for the one month when the species reached its maximum overall cover. Positive or negative values identify net positive or negative effects of grazers or the propagule bank. ANOVA results are reported in Table 5.1. Propagule density data were compiled from Lotze et al. (1999).

Species	Grazer effect	Propagule effect	Propagule density ($\pm 1SE$)	Max cover [%] ($\pm 1 SE, n=8$)	Month with max cover
<i>Enteromorpha</i> spp.	-0.48	0.52	33000 (± 3000)	87.3 (± 5.8)	June
<i>Ulvopsis grevillei</i>	-0.23	27.8	no data	20.8 (± 9.2)	April
<i>Polysiphonia violacea</i>	-0.21	-0.36	no data	3.5 (± 1.9)	October
<i>Pilayella littoralis</i>	-0.04	-0.58	667 (± 667)	53.0 (± 6.9)	May
<i>Cladophora rupestris</i>	0.91	-0.69	no data	9.5 (± 5.4)	August
<i>Ceramium strictum</i>	1.03	-0.78	no data	13.3 (± 5.1)	June
<i>Fucus vesiculosus</i>	1.55	-0.68	1.7 (± 0.8)	69.8 (± 4.2)	December

Table 5.4. Phosphate and ammonium concentrations [$\mu\text{mol L}^{-1}$] in not-enriched versus enriched plots during summer nutrient enrichment ($n=24, \pm 1SE$). Significance levels for the effect of nutrient enrichment were tested by three-way ANOVA and are indicated by stars as in Table 5.1.

Date	Not enriched	SE	Enriched	SE	Percent increase
Phosphate					
5 July	0.40	0.02	0.71 ***	0.07	76.62
24 July	2.09	0.05	2.74 ***	0.21	30.82
15 August	1.33	0.03	1.55 **	0.08	16.80
12 September	0.68	0.03	0.79 n.s.	0.05	15.50
Mean	1.13	0.07	1.45	0.10	34.94
Ammonium					
5 July	0.11	0.05	0.83 *	0.32	637.20
24 July	4.28	0.14	7.18 ***	0.93	67.81
15 August	0.80	0.15	1.02 n.s.	0.28	27.69
12 September	3.15	0.21	2.94 n.s.	0.32	-6.48
Mean	2.08	0.19	2.99	0.37	181.56

and *I. baltica*) occurred at higher densities in GRAZER compared with GRAZER CONTROL plots (Table 5.2). Gammarid amphipods and the snail *Littorina littorea* were not affected by the presence of cages. Overall, grazer densities were significantly reduced by 30% in the GRAZER compared with GRAZER CONTROL plots (Table 5.2). Weekly examinations revealed that grazer exclusion cages (NO GRAZER treatment) remained practically free of grazers throughout the experiment.

When I compared the effects of grazer exclusion and elimination of the propagule bank among the 7 main colonizing macroalgae I found that grazers and the propagule bank had opposing effects on species abundances: species which were negatively affected by grazers tended to be positively affected by the propagule bank and vice versa (Table 5.3). Also, I found an apparent trade-off between losses to herbivory and microrecruit densities in the propagule bank among the 3 most abundant species (Table 5.3).

Nutrient enrichment from June - September significantly enhanced water column nutrient concentrations on the experimental plots (Table 5.4). Nutrient concentrations were not different among caged and uncaged treatments (ANOVA, $P > 0.2$). Ammonium concentrations were strongly enhanced after one month of enrichment, but declined thereafter. Phosphate remained enriched for two months (Table 5.4). Nitrate background concentrations ranged between 0.77 and 4.3 $\mu\text{mol L}^{-1}$ (mean 1.35 ± 0.29 , $n=21$) during the period of enrichment (June - September). From this, I estimate that nitrate concentrations on enriched plots averaged 2.97 $\mu\text{mol L}^{-1}$ (120% increase, Worm et al. 2000).

I compared algal community structure (species composition, abundance, diversity) before and after nutrient enrichment (Fig. 5.4, Table 5.5). Before enrichment, grazers reduced the total cover of annual algae and prevented space monopolization by *Enteromorpha* spp. (Fig. 5.4 A), thereby maintaining species diversity (Fig. 5.4 B). The presence of propagule banks increased total cover of annual algae and dominance of *Enteromorpha*. Consequently, diversity declined in plots with propagule bank. Grazers and propagule banks had opposite and independent effects on species composition and diversity (Table 5.5) and total plant cover (ANOVA, Grazer $F_{1,28}=13.9$, $P=0.0009$, Propagule Bank $F_{1,28}=6.2$, $P=0.019$, G x PB, $F_{1,28}=2.1$, $P=0.16$).

Nutrient enrichment changed species composition and diversity depending on the effects of grazers and propagule banks, as indicated by 3-way interactions in the analysis (Table 5.5). Enrichment tended to decrease diversity mainly by increasing the relative dominance of *Enteromorpha* on the expense of *Fucus* (Fig. 5.4 C, D). However, this shift only occurred in treatments with both the propagule bank and grazers either present or absent. Nutrients had no effect on diversity if only the propagule bank was present (strong *Enteromorpha* dominance) or if only grazers were present (strong *Fucus* dominance). Presence of the propagule bank increased total plant cover independently of nutrient addition (ANOVA, N x PB, $F_{1,24}=0.7$, $P=0.42$). However, grazers decreased total plant cover only when nutrients were not enriched (ANOVA, N x G, $F_{1,25}=5.5$, $P=0.026$). Comparison of GRAZER and GRAZER CONTROL plots revealed no

cage artifacts on algal diversity (ANOVA, $F_{1,25}=0.9$, $P=0.34$) but on species composition (MANOVA, $F_{4,21}=10.2$, $P<0.0001$) because of increased *Enteromorpha* cover in GRAZER compared to GRAZER CONTROL plots.

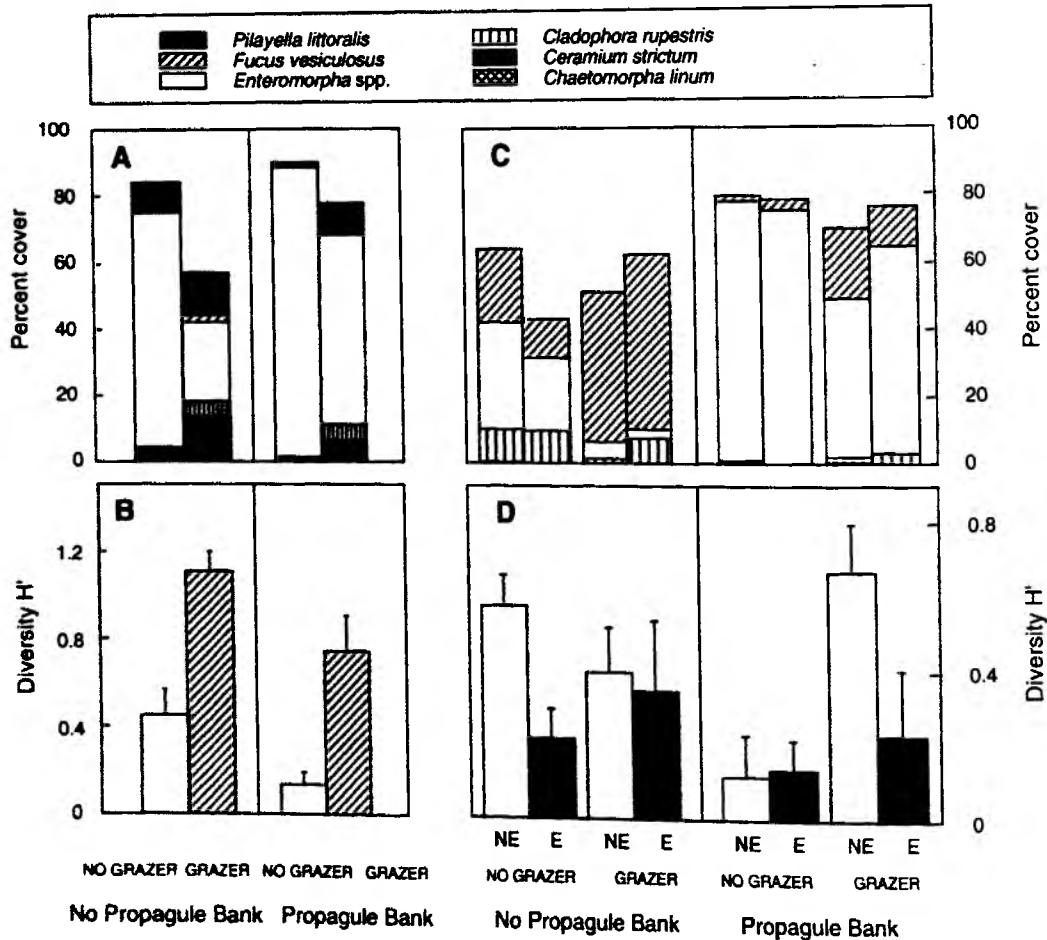


Fig. 5.4. Effects of nutrient enrichment on the established community. (A) Species composition and (B) diversity before nutrient enrichment in June. (C) Species composition and (D) diversity after nutrient enrichment in August (NE=not enriched, E=enriched). Diversity was expressed using the Shannon-Weaver Index. Data are means \pm 1 SE (A, B: $n=8$. C, D: $n=4$). Significant interactions among the 3 experimental factors occurred. For statistical analysis see Table 5.5.

Table 5.5. Analyses of changes in species composition (MANOVA, Pillai Trace statistic) and species diversity (3-way factorial ANOVA) before and after experimental nutrient enrichment. Bold values are $P < 0.1$.

Dependent variable	Source	df	MS	F	P
Species composition before enrichment	Grazing	4, 23	0.51	5.64	0.0028
	Propagule Bank	4, 23	0.36	3.13	0.0352
	G x PB	4, 23	0.13	0.84	0.5130
Species composition after enrichment	Grazing	3, 22	0.42	5.27	0.0068
	Propagule Bank	3, 22	0.66	14.34	0.0001
	Nutrients	3, 22	0.09	0.76	0.5277
	G x PB	3, 22	0.09	0.74	0.5417
	G x N	3, 22	0.12	0.95	0.4326
	PB x N	3, 22	0.04	0.31	0.8166
	G x PB x N	3, 22	0.27	2.72	0.0694
Diversity (H') before enrichment	Grazing	1	3.25	29.55	0.0001
	Propagule Bank	1	0.93	8.41	0.0072
	G x PB	1	0.01	0.04	0.8403
	Residual	28	0.11		
Diversity (H') after enrichment	Grazing	1	0.18	2.83	0.1056
	Propagule Bank	1	0.07	1.13	0.2983
	Nutrients	1	0.34	5.27	0.0307
	G x PB	1	0.24	3.76	0.0644
	G x N	1	0.01	0.18	0.6791
	PB x N	1	0.00	0.00	0.9648
	G x PB x N	1	0.29	4.47	0.0450
Residual	24	0.07			

Field experiment: Effects on *Fucus* recruitment

When I monitored *Fucus* recruitment throughout the experiment (Fig. 5.5 A), I found very low recruitment from the propagule bank in May (1.7 ± 0.8 visible germlings 100 cm^{-2} when grazers were present). Moreover, recruitment from the propagule bank was depressed to 0.2 ± 0.14 germlings 100 cm^{-2} when grazers were excluded (Grazer, $F_{1,25}=3.9$, $P=0.068$). Following spring reproduction, a new cohort of *Fucus* germlings became visible on most plots in June. Densities of new recruits strongly depended on manipulations of grazers and the propagule bank

(Grazer, $F_{1,25}=3.7$, $P=0.064$, Propagule Bank $F_{1,25}=35.6$, $P<0.0001$, $G \times PB$ $F_{1,25}=3.1$, $P=0.091$). Grazer presence increased *Fucus* germling density while the presence of the propagule bank decreased germling density. This pattern did not change throughout the year (June - December, Fig. 5.5 A) which indicates lack of further propagule supply. Summer nutrient enrichment did not significantly affect *Fucus* recruit densities (ANOVA, $P>0.1$). Overall, recruitment of *Fucus* was strongly depressed in treatments dominated by *Enteromorpha*, and highest densities occurred in treatments where *Enteromorpha* cover was low. Regression analysis suggested that recruitment success of *Fucus* was mainly a function of *Enteromorpha* cover during the time of *Fucus* settlement (Fig. 5.5 B).

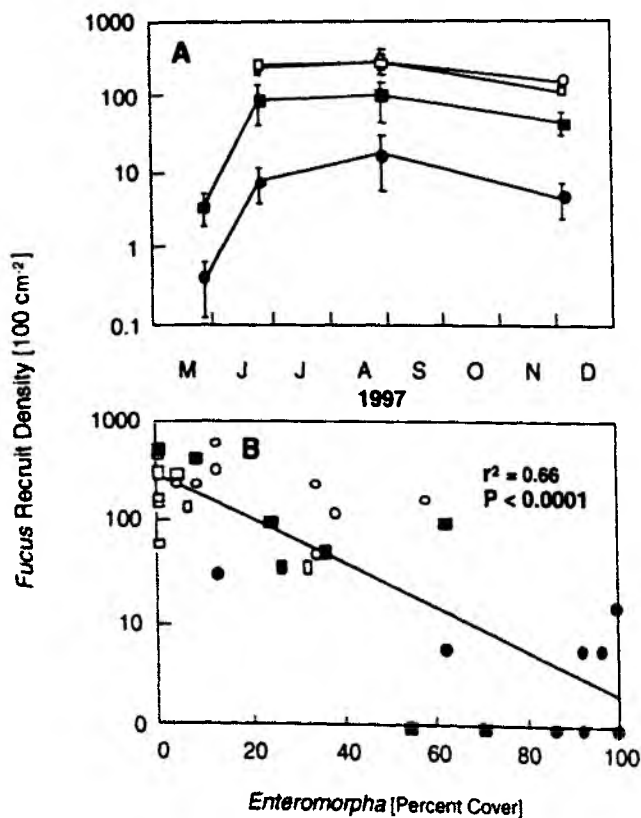


Fig. 5.5. Recruitment of *Fucus vesiculosus*. Symbols identify GRAZER treatments with (■) and without propagule bank (□) and NO GRAZER treatments with (●) and without (○) propagule bank. (A) Effects of grazers and propagule bank on recruit densities on rocks. Recruits in May originate from the propagule bank, recruits on subsequent dates from the propagule bank plus new reproduction. (B) Relationship between *Enteromorpha* cover during the period of *Fucus* settlement (April - May) and *Fucus* recruit densities on the experimental rocks. Linear regression revealed $\log(y+1)=2.436-0.021x$.

Field experiment: Effects on adult *Fucus* plants

The effects of epiphytes (mainly *Pilayella littoralis*), grazers and nutrients on growth of adult *Fucus* plants were weak (Fig. 5.6). All plants in the experiment survived, grew at similar rates and developed fertile receptacles, which apparently released zygotes during spring reproduction. During the spring experiment, I detected a significant interaction between the effects of grazers and epiphytes on *Fucus* growth rate (ANOVA, $G \times E$, $F_{1,25}=6.6$, $P=0.016$). Grazers

slightly reduced *Fucus* growth when epiphytes were removed, but enhanced growth when epiphytes were present (Fig. 5.6 A). However, I could not detect an effect of grazers on epiphyte dry mass, which averaged 0.047 g per *Fucus* plant in June (ANOVA, $F_{1,14}=0.027$, $P=0.84$). In the summer experiment from July - September (Fig. 5.6 B), *Fucus* growth rate averaged $0.015 \pm 0.002 \text{ d}^{-1}$ ($n=24$) which is a 25% decrease compared with the spring experiment ($0.020 \pm 0.003 \text{ d}^{-1}$, $n=32$). Manipulations of grazers and nutrients had no effect on *Fucus* growth rate (ANOVA, $P>0.2$). From September - November, *Fucus* growth rate declined by another 40% ($0.0089 \pm 0.0004 \text{ d}^{-1}$, $n=23$). Experimental treatments had still no effects (ANOVA, $P>0.4$). However, the two latter analyses should be interpreted with caution, because of the loss of eight replicates. Comparison of GRAZER and GRAZER CONTROL plots revealed no cage artifacts in the spring, but a trend towards increased *Fucus* growth rates on GRAZER CONTROL plots in the summer experiment (ANOVA, $F_{1,6}=5.2$, $P=0.064$).

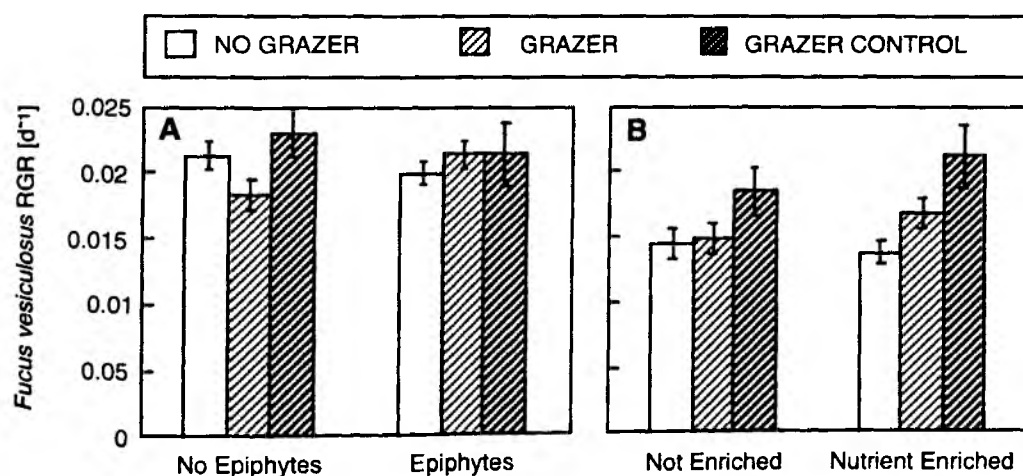


Fig. 5.6. Growth of adult *Fucus* plants in relation to the presence of grazers, epiphytes and nutrient enrichment. (A) Spring experiment from February - June: effects of grazers and epiphytes on relative growth rate (RGR=relative dry mass increase per day) (B) Summer experiment from July - September: effects of herbivory and nutrient enrichment on relative growth rate. For statistical analysis see results section.

5. 4. Discussion

These results suggest that not only propagule supply from the water column (Roughgarden et al. 1988, Reed 1990), but also supply from banks of dormant propagules strongly impinges upon community dynamics. Massive investment into a propagule bank can be a strong competitive advantage, which was mainly exploited by one species, the fast-growing annual *Enteromorpha*. Most importantly, the presence of a propagule bank modified the strong structuring roles of grazers

and nutrients in the community. This implies a novel role of propagule banks for community regulation and ecosystem response to marine eutrophication.

In contrast to terrestrial ecologists who have been fascinated by seed banks for more than a century (Darwin 1855), aquatic ecologists only begin to realize the importance of propagule banks formed by pelagic (Hairston & DeStasio 1989, DeStasio 1989, Madhupratap et al. 1996) and benthic organisms (Hoffmann & Santelices 1991). Examples of macroalgal "banks of microscopic stages" (sensu Chapman 1986) have recently been described in some detail (Santelices et al. 1995, Lotze et al. 1999) but their ecological significance remained unclear. In Chile, a species-rich macroalgal propagule bank (25 taxa) showed low species turnover over the year and removal of the propagule bank had no significant effect on the performance of colonizing species (Santelices et al. 1995, but note that only one replicate per season was analyzed). In California, the presence of a dormant propagule bank did not contribute significantly to recruitment of large kelps, but enhanced spring recruitment of a filamentous annual *Desmarestia ligulata* (Reed et al. 1997). In contrast to these studies, I found strong and persistent effects of a dormant propagule bank on species composition and competitive interactions among annual and perennial algae in the Baltic Sea. In addition, the intensity and species composition of macroalgal blooms were strongly affected by the propagule bank (Lotze et al. 1999, 2000).

Dormancy can occur in winter or summer depending on species life strategies in relation to climatic variability. Most summer annuals (e.g. *Enteromorpha*, *Pilayella littoralis*, *Polysiphonia violacea*) were not or rarely (*Cladophora rupestris*) found as macroscopic thalli during the winter months. In contrast, erect thalli of winter annuals (*Ulvopsis grevillei*, *Petalonia fascia*, *Scytosiphon lomentaria*) were absent over the summer. In addition, I found strong seasonality of spore production and settlement (Fig. 1) in all species at the study site. Thus, most species rely on banks of microscopic forms that persist through unfavorable seasonal conditions. This contrasts with aseasonal (Chile) and less seasonal systems (California) where spore production and settlement occur year-round (Santelices et al. 1995, Reed et al. 1997). Based on these limited comparisons, I hypothesize that the importance of dormancy will increase with increasing seasonality of abiotic and possibly biotic factors that restrict the period of plant growth, reproduction and survival. In addition to pronounced seasonality, strong differences in the abundance of individual species in the propagule bank (Table 5.1, Lotze et al. 1999) may explain the strong effect of the propagule bank. In this experiment, competitive dominance of the opportunistic annual *Enteromorpha* was apparently mediated through its extreme dominance in the propagule bank. This species was 500 - 20000 -fold more abundant in the propagule bank compared with *Pilayella* and *Fucus*. This massive investment into overwintering propagules enabled *Enteromorpha* to recruit in high densities in early spring. During this period, competition from other species was minimal because winter annuals declined in abundance and other summer annuals were absent or rare. Moreover, growing germlings benefit from high nutrient levels in spring while germination is severely nutrient

limited later in the year (Lotze 1998). Most importantly, grazers have no effect on algal cover in May. Thus, recruitment from a propagule bank early in the year can provide a seasonal escape from herbivory for grazer-susceptible species (Lotze et al. 1999, 2000). Overall, recruitment from the propagule bank enabled *Enteromorpha* to use favorable conditions in early spring and to form a dense canopy before perennial *Fucus* initiated reproduction.

This canopy acted as a settlement barrier that strongly interfered with recruitment of perennial algae (*Fucus vesiculosus*). *Fucus* recruited very poorly from the propagule bank (0.005% propagule density compared with *Enteromorpha*). New propagules were generated during a short but intense reproductive period in late spring (Fig. 5.2, Grützmacher 1984). During this period, settlement of *Fucus* zygotes and recruitment to macroscopic germlings depended critically on the degree of space preemption by *Enteromorpha*. Initial differences between treatments persisted throughout the year (independently of the seasonal decline of *Enteromorpha* in summer) and resulted in >20-fold differences in the abundance of *Fucus* among treatment combination in December. I conclude that settlement and recruitment appears to be a population bottleneck for *Fucus*. Qualitatively similar conclusions were obtained in the NW Atlantic, for *Enteromorpha* - *Fucus* competition (Lubchenco 1986) and for *Chondrus crispus* - *Fucus* competition (Worm & Chapman 1996, 1998).

In contrast to early life stages, adult *Fucus* plants appeared to be surprisingly insensitive to experimental manipulations of epiphyte cover, herbivory and nutrients (Fig. 5.6). However, epiphyte loads were relatively low in this experiment compared with plants used in a previous study (Chapter 3), and compared with large adult (1 - 1.5 m) *Fucus* plants, which dominate the canopy at Maasholm. These old plants often carry significant epiphyte loads (Schramm et al. 1996). Most fucoids constantly shed epidermal cells as a defense against epibiosis. Successful recruitment of epiphytes on *Fucus* typically occurs on eroding stipes or injured thallus parts (Russell & Veltkamp 1984, personal observations). Such recruitment foci were largely absent on the relatively young and healthy plants that I used, but more abundant in older plants. I hypothesize that the effects of annual algae on *Fucus* may be highest during the recruitment stage, low at intermediate life stages and again increasing in old plants.

Clearly, crustacean and gastropod grazers played a key role in the studied community. The pronounced effects of grazers in our experiment may be even a conservative estimate of total grazer impact, because of 30% reduced grazer abundances in the open cages compared with uncaged control plots. Through massive and selective consumption of fast-growing annual species grazers prevented their competitive dominance (species- and life-stage specific differences are discussed by Lotze & Worm 2000). This selective grazing pressure indirectly sustained the *Fucus* population and species diversity (Fig. 5.4, 5.5). A large-scale positive relationship between grazer densities and *Fucus* cover and a negative relationship between grazer densities and annual algal cover was also described for the entire Baltic Sea (Worm et al. 1999). These findings provide broad support for

the general concept that selective consumption of a competitively dominant species by grazers (or carnivores, Paine 1966, 1971) favors species coexistence and prevents space monopolization by the top competitor. Indeed, these interactions can shape species distribution patterns over geographical scales (Worm et al. 1999).

Can strong grazer control in this macroalgal community be compensated by other factors? One documented possibility is that carnivores control grazers, releasing plants from grazer control. Cascading effects of carnivores have been demonstrated in river and coastal benthic food webs (Power 1990, Estes et al. 1998) and will be analysed in Chapter 6 of this thesis. Seasonal or spatial escapes from herbivory can be another cause for reduced overall grazer control. The propagule bank provides such a seasonal escape for *Enteromorpha*. When grazers were present, *Enteromorpha* only reached dominance when the propagule bank was present (Fig. 5.3 A). In treatments without the propagule bank, *Enteromorpha* could not compensate grazer pressure despite strong and continuous propagule supply from May to October (5 - 60 million spores settling per m² and day, Lotze et al. 1999). Further, I found a general trade-off among species, comparing losses or gains from grazing with losses or gains from the propagule bank (Table 5.1). Species which were susceptible to herbivory, had high investment into dormant propagules and benefitted from the presence of the propagule bank. Species which were favored by herbivory had low investment in the propagule bank and declined in treatments with the propagule bank present. Based on this evidence, I suggest that propagule banks can serve as an adaptation to seasonal variation in herbivory in addition to their important role for overwintering (Lotze et al. 1999). A similar adaptive value was proposed for small encrusting or boring life stages which alternate with large erect thalli in some grazer-susceptible intertidal species (Lubchenco & Cubitt 1980).

The effects of grazers on plant community structure may also be altered by changes in nutrient supply (Proulx & Mazumder 1998). Anthropogenic nutrient enrichment is a global-scale phenomenon that fundamentally alters the dynamics of the planet's ecosystems (Vitousek et al. 1997a, b, Carpenter et al. 1998). In the marine realm, few studies have experimentally analyzed the effects of nutrient enrichment on plant-animal interactions. In eelgrass (*Zostera marina*) meadows, water column nutrient enrichment promotes epiphytes which suppress eelgrass growth (Neckles et al. 1993, Williams & Ruckelshaus 1993). Isopods alone (Williams & Ruckelshaus 1993) or isopods, amphipods and snails together (Neckles et al. 1993) can increase eelgrass productivity through consumption of epiphytes, but these effects are seasonally variable. These conclusions apply in our system, although grazing effects on epiphytes seemed less important compared with grazing effects on epilithic algae that block *Fucus* recruitment. In a saltmarsh study, grazers increased plant diversity at high but not at low nutrient supply (Gough & Grace 1998). This may be a more general phenomenon across terrestrial and aquatic habitats (Proulx & Mazumder 1998) and is in accordance with our study where grazers maintained species diversity under eutrophic conditions. However, further increases in nutrients can overcompensate grazer control of annual

algae (Lotze et al. 2000) which has negative effects on *Fucus* and other species, thereby reducing diversity. One unexpected result was that the effects of nutrient enrichment depended strongly on manipulations of herbivory and propagule bank. The strongest negative effects of nutrient enrichment on species diversity were seen in treatment combinations with both grazers and propagule bank present (note that this is the natural situation). When the propagule bank or grazers were excluded, nutrients had little effects on species composition and diversity. I conclude that the balance and magnitude of resource ("bottom-up") and consumer ("top down") control can depend on patterns of propagule supply which are linked to dormancy and dispersal strategies of the organisms.

Similar changes in species composition and loss of species diversity following increasing nutrient deposition were found in terrestrial systems (Tilman 1987, Jefferies & Maron 1997, Vitousek et al. 1997a, Bobbink et al. 1998). Do higher-order interactions among soil seed banks, grazers and nutrients play a role for the response of terrestrial communities to eutrophication as they do in our marine system? I propose that this generalization should be critically evaluated, ideally using factorial field experiments. To date, I know of no experiment where soil seed banks and grazers or nutrients were manipulated in combination. Evidence from single-factor experiments suggests that (1) seed banks can be of greater importance than wind-dispersed seeds for plant recruitment in natural grasslands (Thompson 1992) and that annuals have more persistent seeds than perennials, (2) grazers and granivores can strongly affect seed bank dynamics, plant recruitment and plant community composition in desert, grassland and forest ecosystems (overview in Davidson 1993), (3) nutrient enrichment typically increases competitive dominance of one or few fast-growing species and thereby decreases plant diversity in grasslands, forests, wetlands and heathlands (Tilman 1987, Bobbink et al. 1998). Also, nutrient enrichment causes significant shifts in seed bank composition towards increased abundance of a few nutrient-responsive species (Kirkham & Kent 1997). These generalizations are in accordance with results and conclusions from the studied marine macroalgal community. Experimental separation of the effects of dormancy and dispersal, consumers (grazers and granivores) and resources may also be fruitful in terrestrial plant assemblages.

6. Food web I: Benthic food web structure, carbon storage and nitrogen retention regulated by consumer pressure and nutrient loading

6.1 Introduction

Currently, humans are doubling the rate at which nitrogen and phosphorus enter the global biogeochemical cycles (Schlesinger 1991, Vitousek et al. 1997a). Through river, ground water and atmospheric transport, a large fraction of these excess nutrients passes through estuarine and coastal ecosystems (Howarth et al. 1996, Nixon et al. 1996, Jickells 1998). Primary producers in these systems can act as efficient filters and largely control nutrient cycling and the export of nutrients to the open ocean (Jickells 1998). Nutrient cycling has been pointed out as the most important ecosystem service, provided by coastal ecosystems (Costanza et al. 1997). Increasing nutrient loading however, can change primary producer abundance and species composition, with feedbacks on the cycling and processing of nutrients. In this chapter, I asked how the effects of increasing nutrient loading are mediated by food-web interactions in the Baltic Sea coastal system.

Detailed experimental work in freshwater systems showed that nutrients and consumer strongly influence algal abundance, biogeochemical cycling and fisheries production (e.g. Carpenter et al. 1985, Sommer 1985, 1992, Power 1990, Brett & Goldman 1997). In contrast, very few studies in the marine environment considered nutrient and consumer effects simultaneously. Experimental evidence for coastal phytoplankton assemblages (Kivi et al. 1993, Metaxas & Scheibling 1996) and seagrass - epiphyte assemblages (Williams & Ruckelshaus 1993, Neckles et al. 1993) indicates generally strong nutrient and grazing effects on plant species composition and biomass, together with pronounced seasonal variability. Macroalgal assemblages which dominate biomass and productivity of most of the worlds rocky shores (Mann 1973), have been studied intensively for consumer effects (Lubchenco 1986, Menge & Farrell 1989, Paine 1994), but these were rarely weighed against the effects of nutrients (Menge et al. 1997).

Results from the previous experiment (Chapter 5) indicated interactive effects of grazers, nutrients and algal propagule supply during summer nutrient limitation. In this Chapter, I assess the relative effects and possible interactions between nutrients and consumers throughout an entire growth period (February to November) and model changes in species composition and ecosystem function along an experimental nutrient gradient. As important ecosystem functions, I focused on productivity (estimated from total plant cover over the year), carbon storage and nitrogen retention (estimated as C and N retained in plant biomass at the end of the growth period). Using factorial field experiments, I tested the hypotheses that (1) increasing N and P loading and consumers interact in controlling macroalgal abundance and

species composition throughout the year, and (2) that changes in algal and grazer abundance feed back on higher trophic levels. Moreover, I hypothesized (3) that changes in species composition will translate into changes in ecosystem functioning (primary productivity, carbon storage and nitrogen retention) in the coastal zone.

6.2 Methods

Experimental design

Experiments were conducted at Maasholm, Schlei Fjord, Western Baltic Sea (see Chapter 2 for description of study site and food web). The relative effects of grazers and nutrient enrichment on macroalgal abundance and subsequent changes in food-web structure and ecosystem function were investigated throughout one growth period from February - November 1998 at 0.8 m water depth. Grazers (present at natural densities or absent) and nutrient concentrations (NO enrichment, LOW, MED and HIGH enrichment, see below) were manipulated in a (2 x 4) orthogonal design with 4 replicates (Fig. 6.1). This experiment was designed in order to (1) test for the main effects and interactions among nutrient enrichment and grazing by factorial ANOVA and (2) model algal response to nutrient enrichment by regression analysis. For regression analysis, I established a nutrient gradient across 7 levels ($n=2$ for enriched treatments, $n=4$ for controls), corresponding to increasing nutrient diffuser length (2.5 - 80 cm) and nutrient supply. In order to achieve a balanced and statistically powerful ANOVA design, I combined these nutrient enrichment treatments into 4 categories NO (no diffusers), LOW (2.5, 5 cm diffusers), MED (10, 20 cm diffusers) and HIGH (40, 80 cm diffusers) each replicated 4-fold (Fig. 6.1).

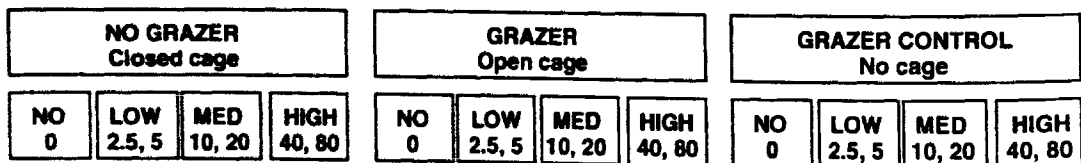


Fig. 6.1. Experimental design. Grazers were manipulated with cages. Open and closed cages were compared to test for grazer effects. Open cages and uncaged plots were compared to test for cage effects. Nutrients were enriched at low, medium and high levels with nutrient diffusers (length of diffusers is given in cm). All 12 treatments were replicated 4-fold.

Grazers were manipulated with exclusion cages (25 x 25 x 25 cm), as described in Chapter 5. Half of the cages were closed (NO GRAZER treatment). Half of the cages had one open side to allow grazer access (GRAZER treatment). All cages were brushed weekly in order to remove fouling algae on the mesh, to check closed cages for grazers and to remove intruders from these cages. To evaluate potential cage effects on algal, grazer or predator density, I

conducted a control experiment where I compared GRAZER treatments with uncaged plots (GRAZER CONTROL). These treatments were also combined with nutrient enrichment and replicated 4-fold.

Nutrient enrichment was performed with a slow-release NPK-fertilizer as described in Chapter 5. Previous tests of this method have shown that release rates in seawater drop after 6 weeks (Chapter 5, Worm et al. 2000), thus I replaced pellets in 6-week intervals. Fertilizer pellets were enclosed in polyethylene mesh rolls (diffusers) of 3.5 cm diameter and 2.5, 5, 10, 20, 40, or 80 cm length (10, 20, 40, 80, 160, 320 g pellets). Diffusers were placed inside cages or fixed with a steel tent pick on uncaged plots. All treatments were arranged in a randomized block design with 2 blocks. Blocks measured 10 x 30 m and were separated by 20 m. Individual plots were separated by 3 - 4 m to avoid interactions.

To monitor nutrient release through time, I collected water samples 10 - 15 cm above a set of control plots with intermediate diffuser length (20 cm) every 3 weeks (n=5). In August, I sampled all plots to reveal how nutrient availability changes with increasing diffuser length. Water samples were obtained with 30-ml plastic syringes, immediately filtered (Whatman GF/F filters) and analyzed within 3 h for dissolved ammonium, nitrate, nitrite and phosphate on a Technicon autoanalyzer.

As experimental substrata, I used granite rocks (ca. 20 cm diameter) from the experimental site. Rocks were collected in the shallow subtidal on 10 Feb 1998, cleared from *Fucus* cover and randomly assigned to the experimental plots. Percent cover of algal species was determined in monthly intervals, using a 15 x 15 cm plexiglas sheet with 50 random dots. Further, I monitored recruitment of *Fucus vesiculosus*, because this species is usually dominant on Baltic rocky shores, but may be particularly vulnerable to competition from other species at the recruitment stage (Worm & Chapman 1996, Chapter 5). *Fucus* recruits became visible in June. Germlings >1 mm length were counted in 5 random 2 x 2 cm subsamples within a central 10 x 10 area on all experimental rocks. Grazer and predator densities were assessed in 4 - 6 wk intervals by visual underwater counts within open cages and around uncaged plots (25 x 25 cm area). Each plot was carefully inspected, including close examinations of the algal canopy and below the rocks (partially buried crabs). These field counts may only represent first-order estimates for some of the smaller amphipods and isopods, however their relative abundance in the various treatments should be assessed accurately.

In order to reveal changes in algal tissue carbon and nitrogen levels in response to nutrient enrichment and grazing, I obtained samples (ca 0.5 g wet mass) of the two most abundant algae, *Fucus* and *Enteromorpha*. Samples were taken in May, July and October from all experimental plots, dried for 48 h at 80°C, ground to powder and analyzed in two subsamples per plot on an automated C:N analyzer. On 26 Oct 1998, the central 10 x 10 cm area was harvested from all plots, sorted by species, dried, weighed and analyzed for tissue C:N ratios as above.

Data analysis

Data were analyzed by factorial ANOVA including "Grazers" (GRAZER vs. NO GRAZER) and "Nutrients" (NO, LOW, MED, HIGH enrichment levels) as the main effects. The control experiment was analyzed like the main experiment, only that the effect "Cage" (GRAZER vs. GRAZER CONTROL) replaced the "Grazers" effect. The spatial block effect did not explain significant portions of the variance ($P > 0.2$) and hence was excluded from the analyses. Species cover data were analyzed by multivariate MANOVA using the Pillai trace statistic (Johnson & Field 1993). This approach was chosen because it takes cross-correlations among species abundances into account. In order to optimize the power of the analysis, the number of variables was limited to species with an average cover $> 1\%$ (across all plots), or $> 5\%$ cover on any plot. Three MANOVA runs were performed for spring (30 March), summer (28 June) and fall (6 October), because different sets of species colonized during these seasons. When MANOVA results were significant, I used univariate ANOVAs to explore changes in the abundance of individual species. Total plant cover, grazer and predator abundances were analyzed by factorial repeated-measures ANOVA, including "Grazers" and "Nutrients" as the main effects and "Time" (monthly sampling Feb - Oct) as the repeated measure. Cover data were angular transformed (Sokal & Rohlf 1995) and consumer abundance data ($\log+1$)-transformed, in order to achieve homogeneity of variances, checked by Cochran's test. Student-Newman-Keuls (SNK) procedure was used for post-hoc comparisons of nutrient treatments. In addition to ANOVA, I modeled the quantitative response of selected dependent variables across all 7 nutrient enrichment treatments. I employed linear and second-order polynomial regression analysis (fitted with a non-linear regression procedure). Polynomial regression results are only reported, if significantly better fits were achieved compared with the linear model.

6.3. Results*Nutrient dynamics*

Throughout the experiment, dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NH}_4^+ + \text{NO}_2^-$) showed strong seasonal trends with generally high concentrations in early spring and fall and low concentrations ($< 1 \mu\text{mol L}^{-1}$) in the summer (Table 6.1). Only on 28 July, DIN showed a strong summer peak (Table 6.1). This was due to high NH_4^+ concentrations following the decomposition of the annual *Pilayella* bloom, which breaks down in late June - July (Lotze et al. 2000). Dissolved inorganic phosphorus ($\text{DIP} = \text{PO}_4^{3-}$) showed less pronounced seasonal patterns than DIN. Throughout the experiment, N:P ratios ranged from 104 in April to 1.5 in August (mean 19.0 ± 9.7 SE). N:P ratios were < 20 from May - Oct and < 10 from May - July. These data strongly suggest nitrogen rather than phosphorus depletion with respect to macroalgal nutrient requirements (average tissue N:P ratios range between 30:1, Atkinson &

Smith 1983, and 49:1, Duarte 1992). Nutrient diffusers filled with coated fertilizers increased nutrient availability for DIN and DIP over the experimental period (Table 6.1). Averaged over the year, medium-sized (20 cm) diffusers increased DIN concentrations by 49.9 (± 17.6) %, and DIP by 68.8 (± 27.5) %, relative to background levels (Table 6.1). N:P ratios in enriched plots averaged 15.0 (± 5.8) and were not significantly different from control plots (ANOVA, $F_{1,18}=0.122$, $P=0.73$). Sampling nutrient concentrations across all diffusers in August revealed that DIN and DIP availability was not affected by the presence of cages or grazers (ANOVA, DIN: $F_{2,30}=2.5$, $P=0.1$, DIP: $F_{2,30}=0.5$, $P=0.61$), but increased with diffuser length and fertilizer mass (Table 6.1, ANOVA, DIN: $F_{2,30}=30.2$, $P<0.0001$, DIP: $F_{2,30}=22.4$, $P<0.0001$). A linear regression model ($y=0.492+0.0118x$, $r^2=0.51$, $P<0.0001$, $n=44$) predicted that DIN availability increased by 51% at intermediate diffuser length (20 cm), which was almost exactly the value I obtained when I averaged relative increases across the whole experimental period (50%, see above). This value doubled with every doubling of diffuser length (100% increase at 160 g fertilizer, 198% at 320 g). DIP availability was predicted to increase by 9% at intermediate fertilizer mass ($y=0.333+0.0015x$, $r^2=0.50$, $P<0.0001$, $n=44$), which did not correspond well with a measured average increase of 68.8%.

Table 6.1. Average concentrations ($\mu\text{mol L}^{-1}$) of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in nutrient-enriched versus control plots during the experiment.

Date	Diffuser length [cm]	Enrichment category	n	DIN control	DIN enriched	DIP control	DIP enriched
02 Mar			5	35.76		0.64	
26 Mar	20	MED	5	10.68	22.90	0.39	0.95
19 Apr	20	MED	5	9.53	10.16	0.09	0.16
18 May	20	MED	5	0.72	1.64	0.21	0.24
10 June	20	MED	5	0.50	0.66	0.10	0.36
09 July	20	MED	5	0.29	0.61	0.10	0.22
28 July	20	MED	5	4.91	5.24	0.31	0.36
12 Aug	20	MED	5	0.46	0.68	0.32	0.35
31 Aug	20	MED	5	1.19	2.27	0.29	0.43
21 Sep	20	MED	5	5.81	6.75	0.73	0.64
14 Oct	20	MED	5	9.54	11.63	0.58	0.62
12 Aug	2.5	LOW	6	0.46	0.50	0.32	0.34
12 Aug	5	LOW	6	0.46	0.44	0.32	0.34
12 Aug	10	MED	6	0.46	0.59	0.32	0.34
12 Aug	20	MED	6	0.46	0.68	0.32	0.35
12 Aug	40	HIGH	6	0.46	1.38	0.32	0.44
12 Aug	80	HIGH	6	0.46	1.25	0.32	0.43

Algal cover and recruitment

Algae were the main space colonizers in the experiment. Sessile invertebrates, although present at the site, only recruited with single individuals (<5% cover on any plot). Grazers and nutrients had strong but seasonally variable effects on macroalgal species composition and abundance (Fig. 6.2). Grazing significantly changed species composition from spring to fall, nutrients had strong effects in summer and weaker effects in fall (Table 6.2). In summer, the impact of nutrients on species composition depended on grazing pressure, as indicated by a significant interaction term (Table 6.2). Together, nutrient enrichment and grazing explained between 44 and 58% of total variance in species composition and 48% of variance in total plant cover throughout the year.

In February - March, tube-forming benthic diatoms (mixed with minor amounts of filamentous green *Ulothrix flacca*) and the green foliose winter annual *Ulvopsis grevillei* colonized (Fig. 6.2). Species composition in early spring was affected by grazers but not by nutrients (Table 6.2). Grazers strongly suppressed the cover of diatoms (ANOVA, $F_{1,24}=16.5$, $P=0.0004$) but had no effects on *Ulvopsis grevillei* ($P=0.94$). In late spring and summer, the bloom-forming macroalgae *Pilayella littoralis* and *Enteromorpha* spp. (>80% *E. intestinalis*) rapidly colonized and dominated most plots (Fig. 6.2). Species composition was strongly influenced by the interactive effects of grazers and nutrients (Table 6.2). *Enteromorpha* dominated NO GRAZER treatments but was strongly suppressed in GRAZER treatments (ANOVA, $F_{1,24}=98.91$, $P<0.0001$). In contrast, *Pilayella* was more abundant in GRAZER treatments ($F_{1,24}=91.18$, $P<0.0001$). Nutrient enrichment strongly increased cover of *Pilayella* in GRAZER treatments and cover of *Enteromorpha* in NO GRAZER treatments respectively (G x N interaction, Table 6.2, *Pilayella* $F_{3,24}=3.7$, $P=0.025$, *Enteromorpha* $F_{3,24}=9.3$, $P=0.0003$). Responses of *Pilayella* to nutrient enrichment in GRAZER and of *Enteromorpha* in NO GRAZER treatments were best described by simple linear models (*Pilayella* cover = $48.22 + 0.16 N$, $r^2=0.21$, $P=0.07$, *Enteromorpha* cover = $35.03 + 0.35 N$, $r^2=0.74$, $P=0.0011$, $n=16$, N = % increase in DIN). The only perennial alga, *Fucus vesiculosus*, recruited in June and dominated all treatments in fall (Fig. 6.2). Species composition in October was significantly affected by grazers (Table 6.2), which increased cover of *Fucus* by an average of 36% ($F_{1,24}=4.68$, $P=0.0408$). In contrast, *Fucus* cover decreased between 18 - 62%, in LOW and HIGH nutrient enrichment levels ($F_{3,24}=4.7$, $P=0.0023$). These effects were independent (Grazer x Nutrient interaction, $P=0.66$). In the control experiment, cages significantly affected species composition in summer ($F_{4,21}=21.2$, $P<0.0001$) and fall ($F_{4,21}=21.2$, $P<0.0001$). Positive grazer effects on *Fucus* and negative effects on *Enteromorpha* tended to be stronger in uncaged GRAZER CONTROL plots compared with caged GRAZER plots (*Fucus*: $F_{1,24}=37.7$, $P<0.0001$, *Enteromorpha*: $F_{1,24}=3.7$, $P=0.067$). Also, the cover of *Pilayella* decreased on GRAZER CONTROL compared with GRAZER plots ($F_{1,24}=5.2$, $P=0.0068$). As in the previous experiment (Chapter 5) these effects were probably caused by the higher density of grazers in GRAZER CONTROL as compared to GRAZER treatments (see below).

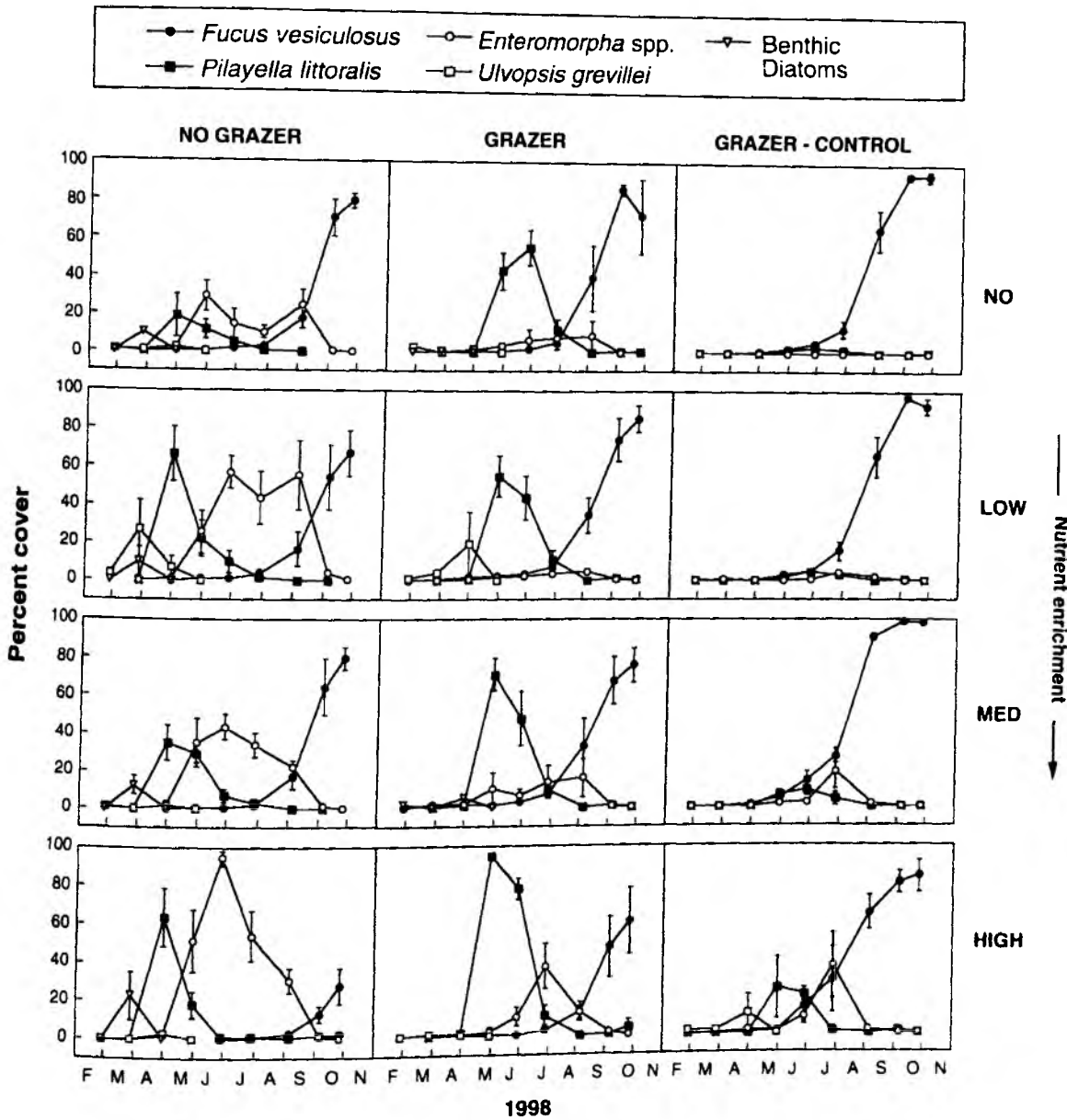


Fig. 6.2. Effects of grazer presence and nutrient enrichment on macroalgal species composition and abundance (mean cover $\pm 1SE$, $n=4$) over time. Shown are NO GRAZER (closed cages, grazer absent), GRAZER (open cages, grazer present) and GRAZER CONTROL (no cage, grazer present) treatments at increasing nutrient enrichment levels. For actual nutrient concentrations refer to Table 6.1. For statistical analysis refer to Tables 6.2 and 6.3.

In addition to species shown in Fig. 6.2, several rare annual species (mean cover <5% at any time) occurred: the green algae *Blidingia minima* (April - June), *Cladophora rupestris* (June - October) and *Chaetomorpha linum* (July - August), the red algae *Ceramium strictum* (June - November) and *Polysiphonia violacea* (September - October) and the brown *Scytosiphon lomentaria* (April - June). Grazer presence and nutrient enrichment had no significant effects on the abundance of any of these species, with the exception of weak positive grazer effects on *Ceramium strictum* in fall ($F_{1,24}=7.8$, $P=0.010$).

Averaged over the year, total plant cover was reduced by grazers (by 8.3% relative to NO GRAZER treatments), but note that this effect represents only an insignificant trend with $P=0.059$ (Table 6.3). In contrast, total plant cover was significantly increased by nutrient enrichment (by 18 - 28% relative to NO enrichment treatments). There were no significant differences among LOW, MED and HIGH enrichment levels on total plant cover (SNK, $P>0.05$). Both, grazer and nutrient effects, changed over time (T x G and T x N interactions, Table 6.3). Graphical inspection of total cover data indicated strong negative grazer effects in March - April, weak effects from May - August and positive effects on total cover in September - October (due to a positive effect on *Fucus*, the dominant species in fall). Nutrient enrichment strongly increased algal cover in May, June and July, but not in the other months. Cages had no effects on total plant cover ($P=0.45$).

Table 6.2. MANOVA. Analysis of changes in macroalgal species composition in response to grazer removal and nutrient enrichment. Data were angular transformed.

Season	Dominant species	Source	df	Pillai Trace	F	P
Spring	<i>Ulvoopsis grevillei</i> Benthic Diatoms	Grazer	2, 23	0.42	8.18	0.0021
		Nutrients	6, 48	0.37	1.82	0.1144
		G x N	6, 48	0.24	1.09	0.3808
Summer	<i>Enteromorpha</i> spp. <i>Pilayella littoralis</i>	Grazer	4, 21	0.89	43.07	0.0001
		Nutrients	12, 69	0.92	2.56	0.0072
		G x N	12, 69	1.01	2.91	0.0025
Fall	<i>Fucus vesiculosus</i>	Grazer	4, 21	0.36	2.99	0.0420
		Nutrients	12, 69	0.72	1.81	0.0642
		G x N	12, 69	0.57	1.35	0.2138

Table 6.3. Repeated-measures ANOVA. Effects of grazer removal and nutrient enrichment over time (Feb - Oct) on total plant cover. Data were angular transformed.

Source	df	MS	F	P
Grazer	1	0.24	3.93	0.0591
Nutrients	3	0.23	3.83	0.0225
G x N	3	0.13	2.23	0.1104
Error	24	0.06		
Time	8	3.81	74.92	0.0001
T x G	8	0.45	8.84	0.0001
T x N	24	0.26	5.17	0.0001
T x G x N	24	0.06	1.25	0.2472
Error	192	0.05		

Positive grazer effects and negative effects of nutrient enrichment on *Fucus* were most pronounced at the recruitment stage. Nutrient enrichment caused an exponential decline in recruitment success of *Fucus* (Fig. 6.3, Table 6.4), probably because of increased annual algal cover that blocked *Fucus* settlement and recruitment. Counteracting the nutrient effect, grazers favored *Fucus* recruitment. The relative influence of grazers increased with increasing nutrient loading. This was even more pronounced in GRAZER CONTROL compared with GRAZER treatments (Fig. 6.3). A linear regression model (Table 6.4) predicted that a 85% increase in nitrogen concentrations in GRAZER plots caused the same decline in *Fucus* recruitment as grazer exclusion. The same model predicted that a 200% increase in DIN causes a 97.6% drop in *Fucus* recruit densities in NO GRAZER treatments, as opposed to 93.7% in GRAZER treatments and 65.3% in GRAZER CONTROL treatments.

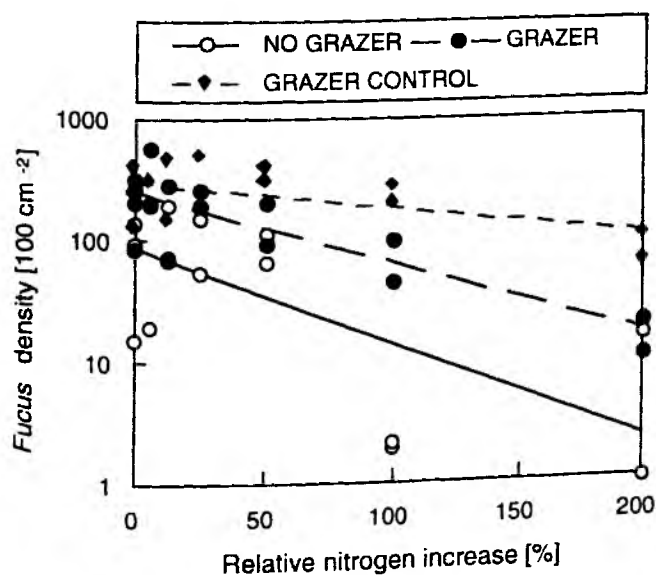


Fig. 6.3. Effects of grazers and nutrient enrichment on *Fucus* recruitment (germling density 100 cm⁻²). Note the logarithmic scale. For regression analyses refer to Table 6.4

Table 6.4. Linear and second-order polynomial regressions of *Fucus* recruit densities (RD), total particulate carbon (POC) and nitrogen (PON) on relative nitrogen increase (N), n=16.

Treatment	Regression	r ²	P
NO GRAZER	log <i>Fucus</i> RD = 1.93 - 0.0081 N	0.52	0.0017
GRAZER	log <i>Fucus</i> RD = 2.39 - 0.0060 N	0.86	0.0001
CONTROL	log <i>Fucus</i> RD = 2.47 - 0.0023 N	0.38	0.0113
NO GRAZER	POC = 68.28 - 0.29 N	0.32	0.0248
GRAZER	POC = 93.18 - 0.36 N	0.46	0.0039
CONTROL	POC = 154.1 + 1.55 N - 0.0085N ²	0.37	0.0131
NO GRAZER	PON = 4.83 - 0.021 N	0.36	0.0149
GRAZER	PON = 6.14 - 0.023 N	0.32	0.0217
CONTROL	PON = 10.262 + 0.067 N - 0.00042 N ²	0.34	0.0183

Carbon storage and nitrogen retention

The two most abundant algae over the experimental period, *Enteromorpha* and *Fucus*, responded similarly to nutrient enrichment with a seasonal increase in N ($P < 0.05$ in May, July, $P > 0.2$ in October) but not C tissue contents ($P > 0.2$ at any time). The increased N content caused tissue C:N ratios to decline with increasing nutrient enrichment (Fig. 6.4). Again, I found weak nutrient effects in spring, pronounced effects in summer and no effects in fall (Fig. 6.4). Grazers and cages had no effects on tissue C:N ratios ($P > 0.2$ at any time).

At the end of the growth period, I harvested all macroalgal biomass from the plots in order to determine how grazing and nutrient enrichment changed total particulate organic carbon (POC) storage and nitrogen (PON) retention by the algal community. I found that almost all (96.7%) of the biomass was *Fucus vesiculosus*, a minor portion was *Ceramium strictum* (2.3%), *Pilayella* (1%) and *Enteromorpha* (0.0003%). Total particulate organic carbon (POC) and nitrogen (PON) in macroalgal biomass increased with the presence of grazers (ANOVA, POC: $F_{1,23}=6.84$, $P=0.015$, PON: $F_{1,23}=4.41$, $P=0.046$, Fig. 6.5). These increases were more pronounced on GRAZER CONTROL compared with GRAZER plots (POC: $F_{1,23}=40.02$, $P < 0.0001$, PON: $F_{1,23}=35.46$, $P < 0.0001$). Nutrient enrichment strongly decreased POC and PON in NO GRAZER and GRAZER treatments. In GRAZER CONTROL treatments POC and PON increased at LOW - MED enrichment but decreased at high enrichment levels (Fig. 6.5, Table 6.4).

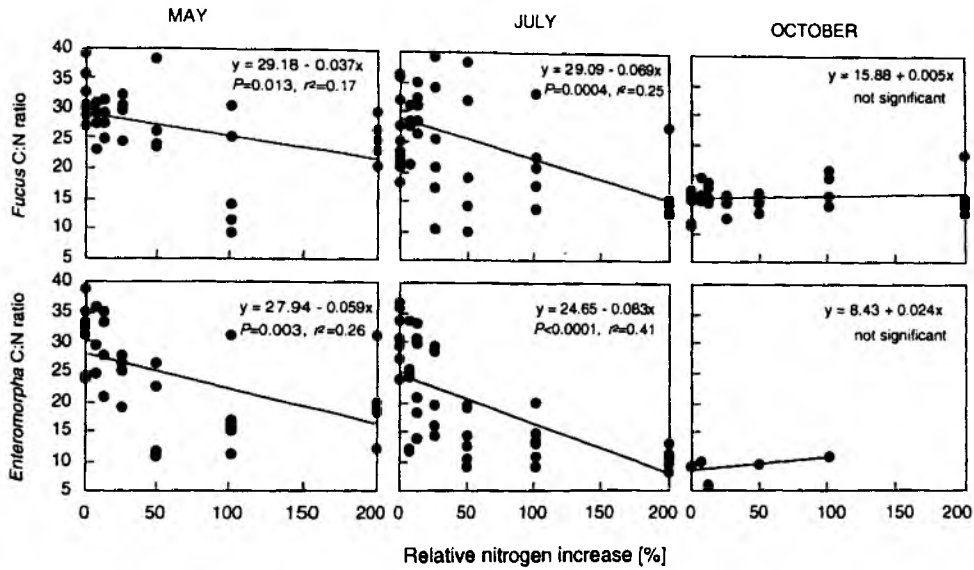


Fig. 6.4. Effects of nutrient enrichment on C:N-tissue ratios of *Fucus vesiculosus* and *Enteromorpha intestinalis* in spring, summer and fall. Nutrient enrichment had significant effects in spring and summer, but not in fall. Grazers and cages had no effects on C:N ratios at any time (ANOVA, $P>0.2$).

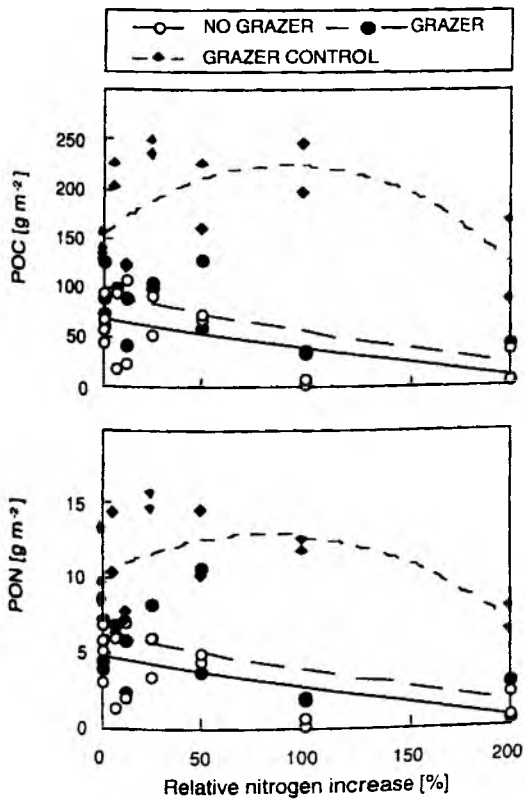


Fig. 6.5. Grazer and nutrient effects on carbon storage and nitrogen retention, measured as particulate organic carbon (POC) and nitrogen (PON) retained in plant biomass at the end of the growth season. For regression analyses refer to Table 6.4.

Grazer and predator densities

Grazers and predators showed strong but contrasting seasonal trends in abundance (Fig. 6.6). Predators were most abundant in summer (10.5 ± 2.5 individuals m^{-2} in July) as opposed to spring and fall ($< 3 m^{-2}$). Grazer densities were low in summer ($44 \pm 14 m^{-2}$ in July) and high in spring ($2671 \pm 341 m^{-2}$ in May) and fall ($1184 \pm 96 m^{-2}$ in October). Snails dominated grazers by number in spring, crustaceans in late summer and fall. Crustaceans (crabs, shrimps) always dominated predators by number as opposed to fish. On average, predators had increased densities in GRAZER compared with GRAZER CONTROL plots (0.56 ± 0.08 vs. $0.28 \pm 0.06 m^{-2}$), while herbivores were more abundant in GRAZER CONTROL treatments, (1080 ± 136 vs. $610 \pm 56 m^{-2}$). These effects tended to change over time (T x C interactions, Table 6.5, graphical inspection revealed strongest effects for grazers in May and July and for predators in April, June and August). Cage effects were most pronounced on slow-moving snails, *Littorina saxatilis* ($731 \pm 141 m^{-2}$ in GRAZER CONTROL versus $302 \pm 51 m^{-2}$ in GRAZER treatments). Small-bodied grazers were rarely found in low numbers (< 5 individuals per cage) in NO GRAZER treatments (checked weekly and grazers removed). Larger individuals and predators were never found in closed cages. This demonstrates the effectiveness of grazer-exclusion cages in this experiment.

Nutrients significantly increased grazer and predator densities in GRAZER and GRAZER CONTROL plots (Table 6.5). Analyzing the responses of individual species to nutrient enrichment, I found overall significant increases in isopods *Idotea* spp. (RM-ANOVA, $F_{3,24}=7.83$, $P=0.0008$), and in shrimps *Palaemon adspersus* (RM-ANOVA, $F_{3,24}=4.33$, $P=0.014$). Increased densities of these species upon nutrient enrichment scaled well to parallel increases in *Enteromorpha* spp. (Fig. 6.7), suggesting a 3-level bottom-up effect.

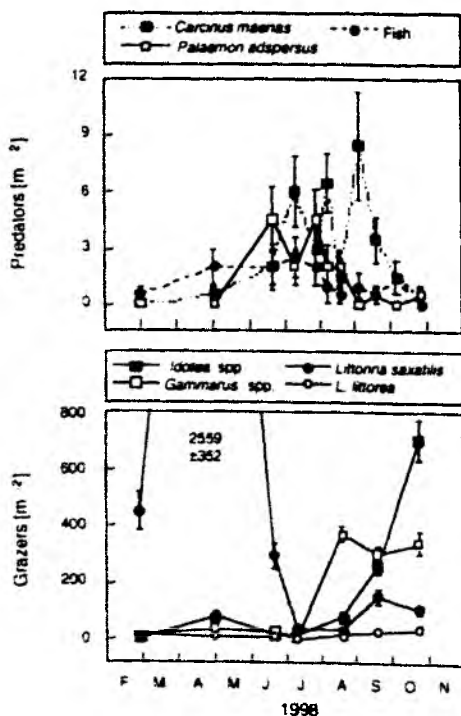


Fig. 6.6. Densities of grazers and predators in the experiment. Data are means (± 1 SE, $n=16$) pooled over GRAZER and GRAZER CONTROL treatments. Crustaceans are represented by square symbols, fish and snails by circles. Weekly examinations showed that NO GRAZER treatments (not shown) remained practically free of grazers and predators throughout the experiment.

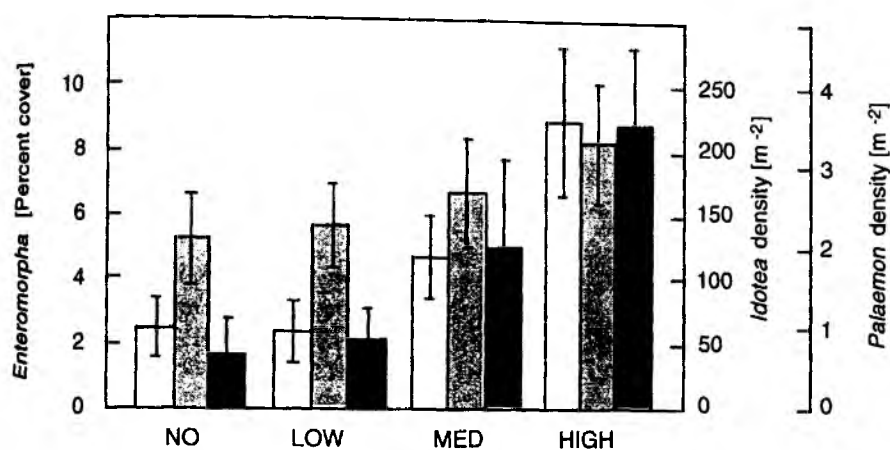


Fig. 6.7. Proportional increases of foliose annual algae (*Enteromorpha* spp., white bars), isopods (*Idotea* spp., gray bars) and shrimps (*Palaemon adspersus*, black bars) with increasing nutrient enrichment. *Enteromorpha* is a preferred food source for *Idotea* (Lotze & Worm 2000) which is consumed by *Palaemon*. Data are means (± 1 SE) pooled over GRAZER and GRAZER CONTROL plots over the experimental period. For ANOVA results refer to Table 6.5. Correlation coefficients (r^2) among trophic levels are 0.980 ($P=0.001$) for nitrogen enrichment - *Enteromorpha*, 0.966 ($P=0.017$) for *Enteromorpha* - *Idotea*, and 0.997 ($P=0.002$) for *Idotea* - *Palaemon*.

Table 6.5. Repeated-measures ANOVA. Effects of cages (open cages versus no cages) and nutrient enrichment on grazer and predator densities in the experiment. Data were ($\log+1$)-transformed.

Variable	Source	df	MS	F	P
Grazer densities	Cage	1	0.56	1.49	0.2344
	Nutrients	3	1.27	3.39	0.0343
	C x N	3	0.06	0.15	0.9299
	Error	24	0.38		
	Time	6	25.40	66.08	0.0001
	T x C	6	0.89	2.31	0.0823
	T x N	18	0.53	1.38	0.2135
	T x C x N	18	0.27	0.69	0.7159
	Error	144	0.38		
Predator densities	Cage	1	0.23	8.427	0.0078
	Nutrients	3	0.10	3.756	0.0242
	C x N	3	0.03	0.9	0.4554
	Error	24	0.03		
	Time	9	0.11	5.492	0.0001
	T x C	9	0.04	1.957	0.0870
	T x N	27	0.02	1.222	0.2623
	T x C x N	27	0.02	1.043	0.4172
	Error	216	0.02		

6.4 Discussion

Grazers and nutrients had strong and antagonistic effects on macroalgal species composition and abundance, carbon and nitrogen cycling in the studied rocky shore food web. Results of this and the previous chapter provide detailed experimental evidence that increasing N-loading causes shifts in macroalgal diversity, loss of consumer control, increased intensity of destructive algal blooms and the disruption of important ecosystem functions, and that these responses are tightly linked.

Algal abundance

This experiment was performed in order to quantify the relative effects of grazers and nutrients in a natural macroalgal community. I found that the magnitude of effects depended on whether populations (cover of individual species) or the entire community (total plant cover) were examined. Species abundance and composition was strongly altered by grazing throughout the experiment. Nutrient effects on species composition were less pronounced and significant only during summer nutrient limitation (Table 6.2). Contrary, despite dramatic changes in species abundances, total plant cover was not significantly reduced by grazers (decline by 8%, $P=0.059$) but increased up to 28% ($P=0.023$) in response to nutrient enrichment. No interaction among the effects of grazers and enrichment on total plant cover occurred, suggesting that these factors have independent effects on algal productivity. However, nutrient effects on species composition can depend on grazing pressure. Nutrient enrichment increased the abundances of fast-growing annual algae, but grazers determined whether *Pilayella littoralis* or *Enteromorpha* spp. were enhanced, corroborating results of an earlier study (Lotze et al. 2000). In contrast, perennial algae (*Fucus vesiculosus*) were independently favored by grazers and suppressed by nutrient enrichment. The magnitude of grazer and nutrient effects changed with season (Table 6.2, 6.3). This was likely driven by seasonal patterns of nutrient supply (Table 6.1) and grazer density (Fig. 6.6). I conclude that grazers represent a seasonal, but overall important ecological force that can partly override the effects of eutrophication on algal community structure. This also holds true for freshwater pelagic food webs, where manipulations of food-web structure are used to suppress phytoplankton biomass under eutrophic conditions (Carpenter et al. 1996). It is however important to realize the limits of this buffering role. In freshwater webs, blooms of grazer-resistant algae (mostly cyanobacteria) can decouple algal growth from grazer control (Gliwicz 1990, Sommer 1992). Similarly, grazer-induced shifts from fast-growing palatable to unpalatable macroalgae and invertebrates have been demonstrated for warm-temperate algal-coral assemblages (Miller & Hay 1996) and tropical coral reefs (Lewis 1986). In this experiment a shift from palatable green algae to more grazer resistant (Lotze & Worm 2000) brown algae occurred from NO GRAZER to GRAZER and GRAZER CONTROL treatments. The brown annual *Pilayella* was still able to perform an

explosive bloom in GRAZER treatments (50-fold cover increase in May). Moreover, the maximum cover of *Pilayella* increased 2- to 12-fold from NO to HIGH nutrient enrichment levels in GRAZER and GRAZER CONTROL treatments, respectively. Nutrient-stimulated blooms of *Enteromorpha* and *Pilayella* lasted from April - September with peak biomass from May - July (Fig. 6.2). This embraces the complete reproductive period of *Fucus* (May - June, Chapter 5, Fig. 5.2). By favoring the intensity and duration of blooms, nutrient enrichment caused exponential declines in *Fucus* recruitment. Grazers indirectly enhanced *Fucus* recruitment at ambient nutrient levels and also slowed the rate of decline with increasing enrichment (Fig. 6.3, Table 6.4). But even though relative grazer effects increased with enrichment, grazers could not overcompensate the nutrient effect. An 85% increase of nitrogen availability in GRAZER treatments had equal effects as the complete exclusion of grazers. The buffer capacity of grazers was greater in GRAZER CONTROL treatments (Fig. 6.3), but the trend of an exponential decrease in *Fucus* recruitment remained. Similar patterns were found for soft-bottom macrophyte assemblages (Neckles et al. 1993, Williams & Ruckelshaus 1993). Grazer enhanced seagrass growth by consuming epiphytes, but nutrient enrichment indirectly reduced seagrass growth by favoring fast-growing epiphytes. In one study, grazer densities and their impact on bloom-forming macroalgae declined across 3 estuaries of increasing nutrient loading (Hauxwell et al. 1998), suggesting an indirect negative effect of nutrient loading on grazers. This could be due to the loss of macrophyte habitat (Salemaa 1987), but may also be caused by other, confounding factors in this comparative study.

In my experiment surprisingly similar effects of nutrient enrichment and grazing on macroalgal abundance and microalgal biovolume occurred. Grazer removal and nutrient enrichment increased microalgal biovolume, but also increased the dominance of single species that were susceptible to grazing but particularly responsive to nutrient enrichment (Hillebrand 1999). Similar growth-resistance trade-offs seem to control the response of coastal micro- and macroalgal and seagrass-epiphyte communities to nutrient enrichment and grazing. Parallel patterns were found in periphyton (Sommer 1997) pelagic (Sterner 1989) and terrestrial plant (Coley et al. 1985) communities.

Carbon storage and nitrogen retention

In addition to changing algal abundance and species patterns, nutrients affected algal tissue chemistry and the ability of the community to retain C and N. Nutrient enrichment increased N content and decreased C:N ratios in *Enteromorpha* and *Fucus* in spring and summer but not in fall. Thus, the effects of nutrients on individual organisms were seasonally transient. Grazers did not affect C:N ratios, which may indicate that no structural (C-based) defenses are induced by herbivory in *Enteromorpha* and *Fucus*. Over the long term, carbon and nitrogen storage on the community level decreased with nitrogen addition but increased in the presence of grazers. In GRAZER CONTROL treatments, there was even an increase in C and N storage at LOW and MED

enrichment levels, but this decreased again at HIGH enrichment (Fig. 6.5). These changes in C and N storage were linked to the species shift from perennial to annual algae. Annual algae are short-lived and their tissue nutrients are rapidly regenerated by grazers and bacterial decomposition (Norkko & Bonsdorff 1996). When the annual *Pilayella* bloom decomposed in July, I found that DIN concentrations increased 17-fold (Table 6.1), which was entirely attributed to increases in ammonium, a product of grazing and decomposition. In contrast, perennial fucoids have a life-span of 3 - 5 years. Measurements on replicate concrete settlement plates at Maasholm revealed that *Fucus* productivity on these surfaces was $13067 \pm 1842 \text{ g m}^{-2} \text{ y}^{-1}$ ($n=8$). Carbon storage was $4920 \pm 675 \text{ g C m}^{-2} \text{ y}^{-1}$ while nitrogen retention was $293 \pm 34 \text{ g N m}^{-2} \text{ y}^{-1}$ (Chapter 4). Because it leads to the decline of perennial macrophytes, nitrogen pollution impairs nitrogen and carbon retention by the coastal macroalgal community, which may result in increased nutrient export to the open ocean. This is most likely the case in the Baltic, where perennial macrophytes have sharply declined on a basin-wide scale (Worm et al. 1999). Qualitatively similar declines in nitrogen retention and carbon storage occurred in experimentally fertilized grasslands (Wedin & Tilman 1996) and declines in nitrogen retention can occur in fertilized forests (Aber 1992). These results suggest that reasonable estimates of increasing carbon storage in response to increasing nitrogen deposition (e.g. Schindler & Bayley 1993) need to incorporate non-linear effects due to changes in species composition.

Higher trophic levels

Nutrient effects in my experiment appeared to be transmitted across 3 trophic levels. With increasing enrichment the densities of isopods and shrimps increased in proportion to *Enteromorpha*, which is a preferred food of *Idotea* (Lotze & Worm 2000). Observations at 15 sites across the Western Baltic corroborated that *Idotea* and shrimps were abundant at sites dominated by *Enteromorpha*, but other consumer species were relatively scarce. Thus, the complex littoral food-web appears to become gradually impoverished with increasing enrichment and *Enteromorpha* dominance. Proportional increases of plants, herbivores and predators are predicted by ratio-dependent predator-prey models, but not by traditional prey-dependent models (Berryman 1992). My results are in line with ratio-dependent models and also in accordance with large-scale comparative studies in marine benthic (Bustamante et al. 1995, Menge et al. 1997) and pelagic (Aebischer et al. 1990) communities. These studies generally showed increasing grazer and predator abundance with increasing algal abundance or productivity. This is the first experimental study to verify these large-scale patterns in a marine benthic community. The only other comparable study I know of (Wootton et al. 1996) found weak effects of nutrient enrichment on micrograzers and no effects on algal biomass, which contradicts my small-scale and other workers large-scale findings (Bustamante et al. 1995, Menge et al. 1997). Wootton et al. (1996) conducted their experiment at relatively short time scales (2-4 months), which may have influenced conclusions about the community response to enrichment.

How do increased predator densities feed back on lower trophic levels? In freshwater food webs, fish predators usually have strong cascading effects on grazer and algal abundance (Power 1990, Brett & Goldman 1997). For marine food webs, there is little evidence for trophic cascades in pelagic webs (Micheli 1999), but accumulating evidence in marine benthic webs (Estes et al. 1998: killer whales - sea otters - urchins - macroalgae, Duffy & Hay 2000: fish - amphipods - macroalgae). In our field experiments, cascading predator effects on grazers and algae appeared to be important in summer. Although I did not manipulate predator densities separately, there were apparent negative correlations between grazer densities and predator densities among seasons and among open plots and closed cages. All grazer species showed parallel population crashes (87 - 100% decline) in June - July when predators reached their highest densities. During this period, the Grazer:Predator ratio decreased from 1068:1 to 4:1 (by number). Grazers recovered again during the fall, when predator numbers declined (Grazer:Predator ratio 1184:1). Equally, grazer densities were reduced by 43% in GRAZER cages, where predators were almost twice as abundant compared with uncaged GRAZER CONTROL plots. In addition to increased predation, periodic removal of grazers by the weekly brushing procedure may have reduced grazer density in the GRAZER cages. Differences in grazing pressure could explain changes in algal species composition among these two treatments. More grazer-susceptible species such as *Enteromorpha* and *Pilayella* had increased cover in GRAZER plots compared with GRAZER CONTROL plots, which were more dominated by grazer-resistant *Fucus*. Because of this replacement of annuals by *Fucus*, no cage effects on total plant cover occurred. The strongest species-specific cage effects occurred on *Pilayella* (Fig. 6.2), which had its maximum development in May, when herbivore densities were extremely high and different between GRAZER and GRAZER CONTROL treatments. Although *Enteromorpha* is more grazer-susceptible than *Pilayella* (Lotze & Worm 2000), this species was less strongly affected by cages (Fig. 6.2). *Enteromorpha* had its maximum cover in July when grazer densities had dropped by 98.4% compared with May. I assume that this decline in grazer densities was partly due to seasonally increased predation, indicating a seasonal cascade from predators to algae in summer. In conclusion, these results demonstrate strong trophic links between nutrients, algae, grazers and predators in this marine benthic food web, and pronounced seasonal shifts in the relative importance of bottom-up and top-down control.

7. Food webs II: Reversal of grazer and nutrient effects on species diversity between nutrient-poor and nutrient-rich rocky shores

7.1. Introduction

In the previous Chapters, I have presented results from a series of experiments manipulating nutrient supply, consumer pressure or both. All investigations were performed in the Baltic Sea, which is a very nutrient-rich system (Nehring 1987, Wulff et al. 1990, Schramm et al. 1996, Worm et al. 2000b). It is difficult to generalize from these results, because it is possible that under nutrient-rich conditions experimental manipulations of nutrient supply have qualitatively different effects compared with nutrient-poor systems. One possible hypothesis is that, in the Baltic, growth of dominant organisms is less nutrient limited (Schramm et al. 1988) compared with nutrient-poor systems, and further increases in nutrient supply have comparatively small effects. On the contrary, the community is already impoverished by a history of eutrophication (Breuer & Schramm 1986, Vogt & Schramm 1991), which may have negative effects on community stability (Tilman & Downing 1994, Johnson et al. 1996). Therefore, small changes in nutrient supply (or grazing pressure) may trigger drastic changes in community composition and ecosystem function in the Baltic (see Chapter 4 - 6). In order to test whether my results from the Baltic can be generalized for nutrient-rich and nutrient-poor rocky shores, I repeated some of my experiments at a very oligotrophic site in the NW Atlantic.

The most important results from the previous chapters were that, in the Baltic, grazers enhanced species diversity, perennial biomass, carbon storage and nitrogen retention. On the contrary, experimental nutrient enrichment (Chapter 5, 6) or larger-scale eutrophication (Chapter 4, Baden et al. 1990, Kautsky et al. 1992) had negative effects on these parameters. Can this be generalized to other systems with different nutrient status? For species diversity, there is often (but not always) a hump-shaped relationship between the number of species and the productivity of a community: species richness first increases, then reaches a plateau, then decreases with increasing productivity (Rosenzweig & Abramsky 1993). In other words, nutrient-stimulated increases in productivity may have positive, no, or negative effects on species diversity, depending on the trophic status of the system. Evidence for this model is accumulating for terrestrial ecosystems (Al-Mufti et al. 1977, Abramsky & Rosenzweig 1984, Tilman 1988), freshwater plankton (Agusti et al. 1991) and coral reefs (Huston 1985).

Could the effects of consumers on species diversity depend on nutrient status as well? Recently, it has been suggested that grazer effects on plant species richness may change predictably between nutrient-poor and nutrient-rich systems ("grazer-reversal-hypothesis", GRH, Proulx & Mazumder 1998). These authors compiled 44 comparisons of plant species richness, under low- versus high-grazing conditions from a wide range of nutrient-rich and

nutrient-poor ecosystems. All 19 comparisons from nutrient-poor systems indicated lower species richness under high grazing pressure, while 14 of 25 comparisons from nutrient-rich systems indicated higher species richness under high grazing pressure (no effect in 9 studies, decline of species richness in 2 studies).

I was interested to test these models on productivity-diversity (Rosenzweig & Abramsky 1993) and nutrients-grazing-diversity (Proulx & Mazumder 1998) in rocky shore food webs. I hypothesized that the effects of both nutrient enrichment and grazing on species diversity may change between a nutrient-rich (Baltic) and a nutrient-poor (NW Atlantic system). Moreover, I was interested whether nutrient and grazer effects on species composition, perennial recruitment, carbon storage and nitrogen retention differ among the Baltic and NW Atlantic. In order to test these hypotheses, I employed a comparative experimental approach (Underwood & Petraitis 1993). I manipulated nutrient enrichment and grazing pressure in a factorial field experiment in the NW Atlantic and compared the outcome of this experiment with results from an identical experiment in the Baltic Sea.

7.2 Methods

Experimental design

A factorial field experiment was conducted at Bald Rock, Nova Scotia, Canada (see Chapter 2 for detailed description of the study site and food web). Using an identical design as in the Baltic Sea, I quantified the relative effects of grazers and nutrient enrichment on the abundance of macroalgae, grazer and predators from February - December 1999. Details of the experimental design are described in the Methods section in Chapter 6 and in Fig. 6.1. The experiment was located at 1 m depth below mean water level. Maximum tidal amplitude was 2.1 m. Thus, the experiment was exposed to air only for brief periods during spring tides. This depth was chosen in order to mimic conditions in the Baltic experiment (0.8 m below mean water level, brief exposure to air during extreme westerly winds).

Grazers were manipulated with exclusion cages (25 x 25 x 25 cm) and nutrient enrichment was performed with nutrient diffusers as described in Chapter 6. All cages were brushed regularly in order to remove fouling algae on the mesh. Closed cages were checked weekly for grazer intrusion and to remove intruders from these cages.

To monitor nutrient release through time, I collected water samples 10 cm above all GRAZER CONTROL plots (NO, LOW, MED, HIGH enrichment levels, n=4). In June and October, I sampled all plots to reveal whether nutrient availability changes between NO GRAZER, GRAZER and GRAZER CONTROL plots (n=16). Water samples were obtained with 30 ml plastic syringes, immediately filtered (Whatman GF/F filters) and analyzed manually within 3 h for dissolved ammonium (Grasshoff et al. 1986). From each water sample, a 15 ml subsample was frozen and analyzed for nitrate, nitrite, and phosphate on a Technicon autoanalyzer.

As experimental substrata, I used granite rocks (ca. 20 cm diameter) from the experimental site. Rocks were collected on 12 Feb 1999 from the lower and middle intertidal zone, occupied by *Fucus vesiculosus* and *Ascophyllum nodosum*. Rocks were scraped free from all macroscopic algae and randomly assigned to the experimental plots. Percent cover of all colonizing species was estimated in monthly intervals, using a 15 x 15 cm plexiglas sheet with 50 random dots. Canopy height was estimated monthly for each species separately with a ruler (0.5 cm intervals). *Fucus* recruits became visible in late July. Germlings > 1 mm length were counted in 5 random 2 x 2 cm subsamples within a central 10 x 10 area on all experimental rocks. Grazer and predator densities were assessed monthly by underwater counts within open cages and around uncaged plots (25 x 25 cm area).

In order to reveal changes in algal biomass, tissue carbon and nitrogen levels in response to nutrient enrichment and grazing, I harvested all plots on 16 Dec 1999 by scraping the entire surface of the experimental rocks with razor blades. Rock surface area was determined with a 20 x 30 cm plexiglas sheet with 1 x 1 cm grid lines. Perennial algal biomass was separated from annual algal biomass and both were dried for 48 h at 80°C, weighed and analyzed for tissue C:N ratios as described in Chapter 6. Data were standardized to 1 m² area.

Diversity and productivity

I compared net primary productivity among the 2 experiments (Maasholm, Chapter 6; Bald Rock, this chapter) using plant cover and average plant height as surrogate parameters for primary productivity. Average plant height was calculated by weighing canopy height of all species by their relative abundance, expressed as percent cover. I analyzed these data during the one month with maximum plant cover and height (June in Maasholm, August in Bald Rock). As diversity measures, I used species richness (S=number of species per plot) and the Shannon-Weaver Index (H'). This index weighs the number of species by their relative abundance (expressed as percent cover) and indicates not only loss of species but also changes in the dominance of single species (see Valiela [1995] for formula and constraints). Species richness and diversity were analyzed during the month with maximum diversity (August in Maasholm, October in Bald Rock).

Data analysis

All data from the experiment were analyzed by factorial ANOVA and MANOVA including "Grazers" (GRAZER vs. NO GRAZER) and "Nutrients" (NO, LOW, MED, HIGH enrichment levels) as the main effects. In addition, I tested for cage artifacts by comparing GRAZER vs. GRAZER CONTROL treatments (details in Chapter 6, Methods section). The spatial block effect did not explain significant portions of the variance ($P > 0.2$) and hence was excluded from the analyses. Cover data were angular transformed and consumer abundance data (log+1)-transformed, in order to achieve homogeneity of variances, checked by Cochran's test. Student-Newman-Keuls (SNK) procedure was used for comparisons among nutrient

treatments. Regression analysis was used to analyze changes in water column nutrient concentrations, tissue C:N ratios, carbon storage and nitrogen retention across all 7 enrichment treatments.

7.3. Results

Nutrient dynamics

Throughout this experiment, dissolved inorganic nitrogen (DIN=ammonium, nitrate and nitrite) and phosphorus (DIP=soluble reactive phosphate) showed no strong seasonal trends and generally low background levels ($<1 \mu\text{mol L}^{-1}$ throughout the year, Table 7.1). N:P ratios were very low (<2.5 throughout the year, mean 1.1 ± 0.2) indicating strong nitrogen rather than phosphorus depletion with respect to macroalgal nutrient requirements (average tissue N:P ratios range between 30:1, Atkinson & Smith 1983, and 49:1, Duarte 1992). Nutrient diffusers increased nutrient availability for DIN and DIP throughout the experimental period, with increasing nutrient concentrations in LOW, MED and HIGH enrichment categories (Table 7.1). N:P ratios in enriched plots ranged from 1.24 ± 0.3 (LOW) to 2.2 ± 0.5 (HIGH). When I measured nutrient concentrations across all plots in May, August and October, I found that DIN and DIP availability were not affected by the presence of cages (ANOVA, $P>0.05$). Linear regression models for ammonium ($y=0.582+0.014x$, $r^2=0.08$, $P=0.0002$, $n=181$) and nitrate plus nitrite ($y=0.173+0.005x$, $r^2=0.08$, $P<0.0001$, $n=285$) predicted that DIN concentrations increased linearly with increasing diffuser length from 6% (2.5 cm diffusers) to 201% (80 cm diffusers) over background concentrations. This matches exactly the described relationship between diffuser length and DIN concentrations in the Baltic experiment (6 - 198% increase, Chapter 6). DIP availability was predicted to increase from 2 - 59% ($y=0.404+0.003x$, $r^2=0.09$, $P<0.0001$, $n=285$), which was higher compared with the Baltic experiment (1 - 36% increase).

Algal species composition and recruitment

Grazers and nutrient enrichment had strong effects on macroalgal species composition and abundance throughout the year (Fig. 7.1). In spring and summer, the impact of nutrients on species composition depended on grazing pressure, as indicated by a significant interaction term (Table 7.2). Nutrients strongly enhanced cover of the dominant algal species *Pilayella littoralis* in NO GRAZER treatments, but had little effects when grazers were present. Sessile invertebrates, although present at the site, only recruited with single individuals in the experiment ($<2\%$ cover on any plot).

NO GRAZER treatments were dominated by filamentous brown (*Pilayella littoralis*) and red (*Callithamnion tetragonum*) annual algae and by various species of closely related brown algae (Chordariales, mainly *Sphaerotrichia divaricata* and *Acrothrix gracilis*). *Pilayella* recruitment in spring was strongly enhanced by nutrient enrichment (ANOVA, $F_{3,24}=438.2$,

$P < 0.0001$). The Chordariales recruited in spring and summer and were significantly enhanced by nutrients at MED enrichment levels ($F_{3,24} = 7.9$, $P = 0.0007$, SNK, $P < 0.01$), but not at HIGH enrichment levels (SNK, $P > 0.05$), where *Pilayella* dominated. *Callithamnion* recruited in September and October and was not affected by nutrient enrichment at this time ($F_{3,24} = 0.2$, $P = 0.89$). Filamentous green algae, mostly *Rhizoclonium riparium* and *Enteromorpha intestinalis* became abundant in late summer and fall, but only at HIGH enrichment levels ($F_{3,24} = 20.7$, $P < 0.0001$, SNK, $P < 0.01$).

Table 7.1. Average concentrations ($\mu\text{mol L}^{-1}$) of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in nutrient-enriched versus control plots during the experiment in Bald Rock (NW Atlantic).

Date	n	DIN				DIP			
		NO	LOW	MED	HIGH	NO	LOW	MED	HIGH
03 Mar	4	0.34	0.13	0.23	0.31	0.36	0.36	0.41	0.35
23 Mar	4	0.38	0.51	0.70	0.65	0.44	0.47	0.46	0.45
12 Apr	4	0.38	0.17	0.71	0.40	0.43	0.41	0.43	0.42
03 May	12	0.05	0.12	0.08	0.09	0.40	0.41	0.42	0.45
26 May	4	0.47	0.69	2.52	3.50	0.29	0.30	0.38	0.64
21 Jun	12	0.55	0.61	0.60	2.16	0.25	0.31	0.32	0.63
14 Jul	4	0.15	0.16	0.26	0.53	0.45	0.48	0.52	0.68
06 Aug	4	0.08	0.04	0.30	0.70	0.36	0.37	0.39	0.42
03 Sep	4	0.31	0.65	2.54	1.31	0.31	0.35	0.55	0.55
04 Oct	12	0.85	2.06	3.08	3.98	0.39	0.59	0.76	0.77
01 Nov	4	0.39	0.54	0.73	1.22	0.45	0.47	0.50	0.59
03 Dec	4	0.71	0.76	0.83	1.11	0.53	0.55	0.54	0.58
Mean	72	0.39	0.54	1.05	1.33	0.39	0.42	0.47	0.54

Table 7.2. MANOVA. Analysis of changes in macroalgal species composition (expressed as percent cover) in response to grazer removal and nutrient enrichment. Data were angular transformed.

Season	Dominant species	Source	df	Pillai Trace	F	P
Spring	<i>Pilayella littoralis</i>	Grazer	2, 23	0.95	231.10	0.0001
	<i>Sphaerotrichia divaricata</i>	Nutrients	6, 48	1.02	8.36	0.0001
		G x N	6, 48	0.56	3.14	0.0112
Summer	<i>Pilayella littoralis</i>	Grazer	4, 21	0.86	31.46	0.0001
	<i>Sphaerotrichia divaricata</i>	Nutrients	12, 69	1.27	4.20	0.0001
	<i>Acrothrix gracilis</i>	G x N	12, 69	1.04	3.04	0.0018
Fall	<i>Pilayella littoralis</i>	Grazer	8, 17	0.93	26.55	0.0001
	<i>Callithamnion tetragonum</i>	Nutrients	24, 57	1.57	2.61	0.0016
	<i>Rhizoclonium riparium</i>	G x N	24, 57	1.23	1.65	0.0616

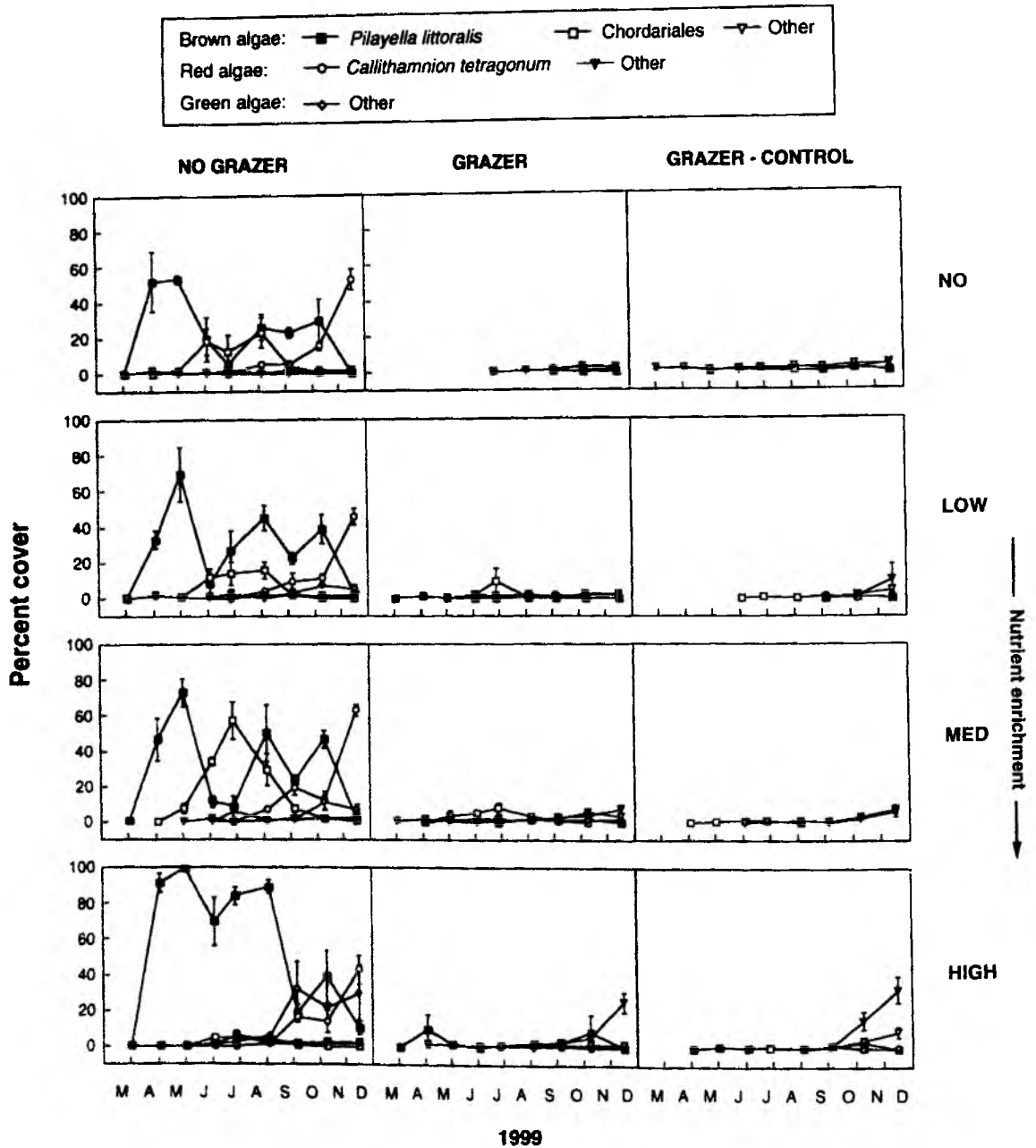


Fig. 7.1. Effects of grazer presence and nutrient enrichment on algal species composition and abundance (mean cover \pm 1 SE) in Bald Rock (NW Atlantic) over time. Shown are NO GRAZER (closed cages, grazer absent), GRAZER (open cages, grazer present) and GRAZER CONTROL (no cage, grazer present) treatments at increasing nutrient enrichment levels. For nutrient concentrations refer to Table 7.1. For MANOVA results refer to Table 7.2. For clarity, similar species were grouped. *Sphaerotrichia divaricata*, *Acrothrix gracilis*, *Eudesme viridis* and *Chorda filum* are morphologically similar brown annual algae and belong to the order Chordariales. Other brown algae were *Scytosiphon lomentaria*, *Petalonia fascia* and *Fucus vesiculosus*. Other red algae were *Dumontia contorta*, *Ceramium nodulosum*, *Audouinella* sp. and *Chondrus crispus*. Other green algae were *Rhizoclonium riparium*, *Enteromorpha intestinalis*, *Cladophora rupestris*, *Ulva lactuca*, *Bryopsis plumosa*, and *Chaetomorpha linum*.

GRAZER treatments had low algal cover from February - October. Only at LOW and MED enrichment, there were small summer peaks (8 - 9.5 percent cover) of Chordariales and at HIGH enrichment there was some recruitment of *Pilayella* in spring and fall. In November and December, the winter annuals *Dumontia contorta*, *Scytosiphon lomentaria* and *Petalonia fascia* recruited to GRAZER plots. *Dumontia* was favored by nutrient enrichment on GRAZER but not on NO GRAZER plots, where other species dominated (ANOVA, Grazer x Nutrients, $F_{3,24}=4.4$, $P=0.0135$). Species composition on GRAZER CONTROL plots was not significantly different from GRAZER plots in spring (MANOVA, $F_{6,48}=0.61$, $P=0.62$), summer ($F_{9,72}=0.79$, $P=0.75$) and fall ($F_{6,19}=2.3$, $P=0.0754$).

Averaged over the year, total plant cover was strongly depressed by grazers (-91%) and increased by nutrient enrichment (+112%), but these effects were interactive and changed over time (RM-ANOVA, Time x Grazer x Nutrients, $F_{24,192}=1.8$, $P=0.0123$). Visual inspection of graphs revealed that nutrient and grazing effects were strongest from May - October and weaker in the other months.

In strong contrast to the Baltic, *Fucus* recruitment in the experiment (Fig. 7.2) was low (7.8 ± 4.4 recruits 100 cm^{-2} , $n=48$) and reduced by grazing (ANOVA, $F_{1,24}=6.8$, $P=0.0152$) but enhanced by nutrient enrichment ($F_{3,24}=4.7$, $P=0.0101$). Following low recruitment, *Fucus* cover remained low on all plots (<10 percent cover). No significant cage artifacts on *Fucus* recruitment occurred ($F_{1,24}=1.7$, $P=0.19$).

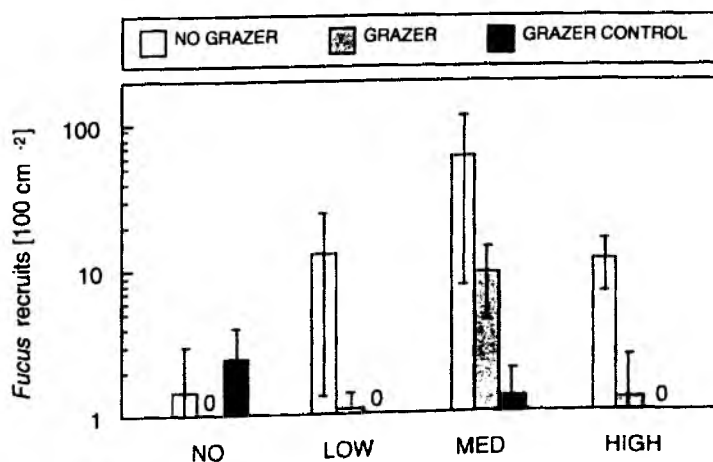


Fig. 7.2. Effects of grazers and nutrient enrichment on recruitment (germling density 100 cm^{-2}) of *Fucus vesiculosus*. Note the logarithmic scale. For analyses refer to the text.

Carbon storage and nitrogen retention

At the end of the growth period, tissue N in annual algal biomass was significantly elevated by nutrient enrichment (ANOVA, $F_{3,30}=3.2$, $P=0.0332$). Tissue C:N ratios were low (8.5 ± 0.2) and declined with increasing enrichment (Fig. 7.3 A). C:N ratios in *Fucus* biomass were higher than in annual algae (18.0 ± 0.8) and not affected by nutrient enrichment (Fig. 7.3 B). Grazers had no effect on tissue C:N ratios ($P>0.1$).

When I harvested all plots in December, I found that most of the biomass was a mix of annual algae (95.8%) and only a minor portion was perennial *Fucus* (4.2%). Total particulate organic carbon (POC) and nitrogen (PON) in macroalgal biomass increased with nutrient enrichment (ANOVA, POC, $F_{3,36}=4.9$, $P=0.0054$, PON, $F_{3,36}=5.4$, $P=0.036$, Fig. 7.3 C, D) but was reduced by grazing (POC, $F_{2,36}=41.6$, $P<0.0001$, PON, $F_{2,36}=46.5$, $P<0.0001$). There were no significant differences between GRAZER and GRAZER CONTROL treatments (SNK, $P>0.2$).

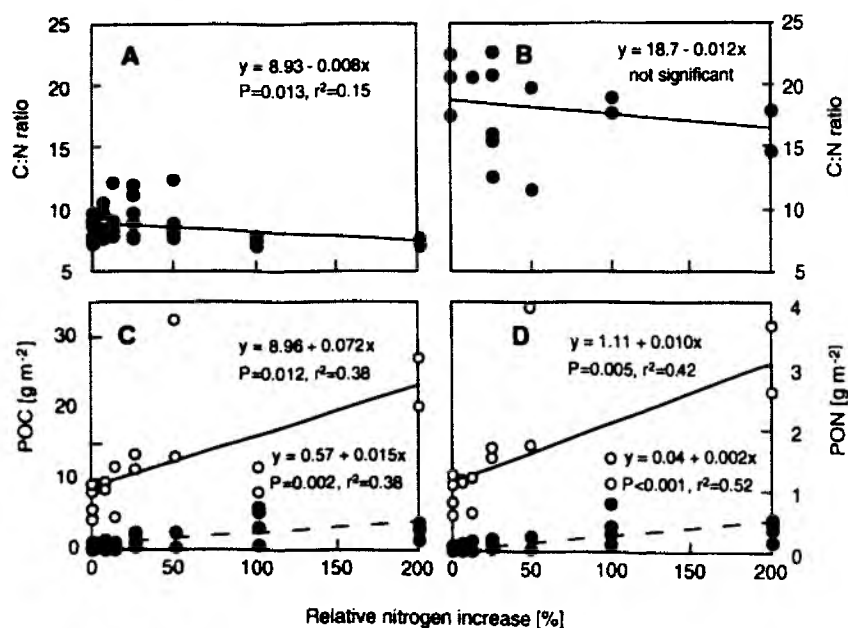


Fig. 7.3. Tissue carbon and nitrogen in algal biomass in relation to nutrient enrichment at the end of the experiment in December. (A) C:N ratio in annual algal biomass, (B) C:N ratio in *Fucus* biomass, (C) carbon storage, and (D) nitrogen retention in total plant biomass. In (C) and (D) only, open symbols represent NO GRAZER treatments, closed symbols GRAZER and GRAZER CONTROL treatments.

Grazer and predator densities

Grazers and predators showed similar seasonal trends in abundance, with high densities in the summer and lower densities in spring and fall (Fig. 7.4). Grazers were mostly the periwinkle *Littorina littorea* and the small limpet *Tectura testudinalis*. Gammarid amphipods were present in spring but disappeared thereafter. Predators were mostly crabs (*Carcinus maenas*) and mysid shrimps (*Mysis stenolepis*). However, *Mysis* is probably not a true

predator, but an omnivore that feeds on small crustaceans as well as on plant detritus (Tattersall & Tattersall 1958, Foulds & Mann 1978).

Nutrient enrichment increased predator densities by up to 83% (NO versus HIGH enrichment), but had no significant effect on grazer densities (Table 7.3). Comparing different species, however, gammarids were significantly more abundant in enriched treatments compared with control treatments (Fig. 7.5, RM-ANOVA, $F_{3,48}=4.3$, $P=0.0153$). Among the predators, crabs ($F_{3,144}=4.5$, $P=0.0116$) and mysids ($F_{3,168}=5.1$, $P=0.0073$) increased in nutrient-enriched treatments (Fig. 7.5). On average, GRAZER plots had 52% higher predator densities compared with GRAZER CONTROL plots, but grazer densities were not significantly different among these treatments (Table 7.3). Among the predator species, only *Mysis stenolepis* increased in abundance on GRAZER plots ($F_{1,168}=22.2$, $P<0.0001$).

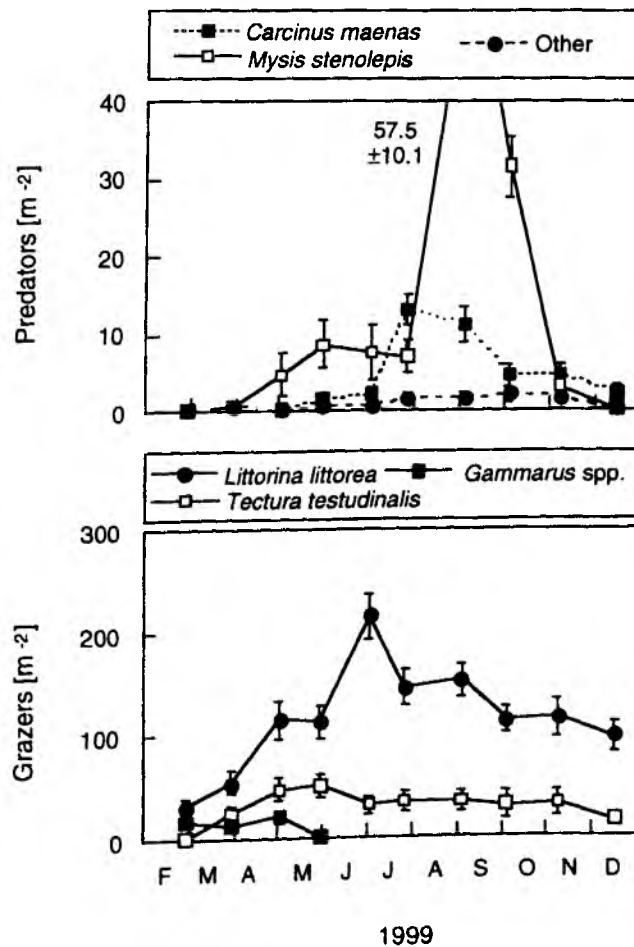


Fig. 7.4. Seasonal trends of grazers and predator abundance in the experiment. Data are means (± 1 SE, $n=16$) pooled over GRAZER and GRAZER CONTROL treatments. Weekly examinations showed that NO GRAZER treatments (not shown) remained practically free of grazers and predators throughout the experiment.

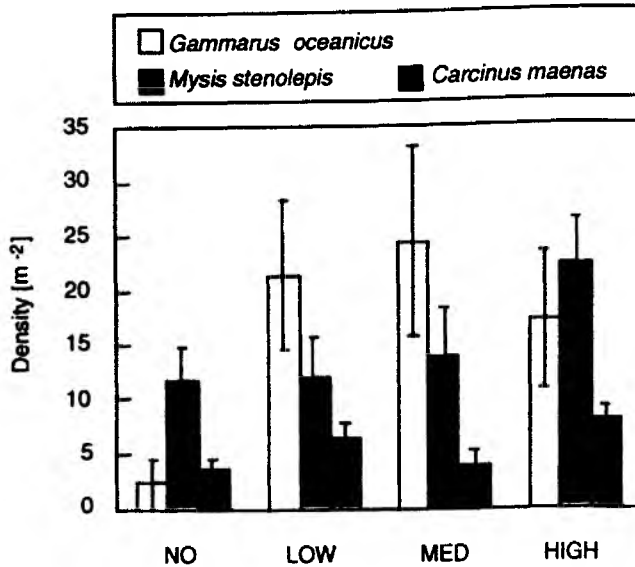


Fig. 7.5. Effects of nutrient enrichment on higher trophic levels. Increases of herbivorous amphipods (*Gammarus oceanicus*), omnivorous mysid shrimps (*Mysis stenolepis*) and carnivorous crabs (*Carcinus maenas*) with increasing nutrient enrichment. Data are means (± 1 SE) pooled over the experimental period. For ANOVA results refer to Table 7.3.

Table 7.3. RM-ANOVA. Effects of cages (open cages versus no cages) and nutrient enrichment (NO, LOW, MED, HIGH) on total grazer and predator densities in the experiment. Data were (log+1)-transformed.

Variable	Source	df	MS	F	P
Grazer densities	Cage	1	0.14	0.19	0.6690
	Nutrients	3	0.95	1.25	0.3148
	C x N	3	1.16	1.53	0.2336
	Error	24	0.76		
	Time	9	4.55	13.55	0.0001
	T x C	9	0.41	1.22	0.3077
	T x N	27	0.33	0.98	0.4805
	T x C x N	27	0.28	0.82	0.6433
Predator densities	Error	216	0.34		
	Cage	1	2.484	6.288	0.0193
	Nutrients	3	1.687	4.271	0.0150
	C x N	3	0.087	0.22	0.8812
	Error	24	0.395		
	Time	8	10.646	38.453	0.0001
	T x C	8	0.425	1.534	0.1767
	T x N	24	0.289	1.042	0.4174
T x C x N	24	0.387	1.399	0.1479	
Error	192	0.277			

Table 7.4. ANOVA. Effects of grazers and nutrient enrichment on primary productivity and species diversity in the NW-Atlantic and Baltic experiments. Total plant cover and canopy height were used as productivity surrogates, species richness and the Shannon-Weaver Index as diversity measures. Cover data were angular transformed, other data were (log+1) transformed to remove heterogeneity of variances.

	df	Percent cover		Canopy height		Species richness		Diversity	
		F	P	F	P	F	P	F	P
NW Atlantic									
Grazer	1	225.9	0.0001	10.12	0.0040	118.0	0.0001	66.3	0.0001
Nutrients	3	9.0	0.0003	6.08	0.0032	19.2	0.0001	22.5	0.0001
G x N	3	2.7	0.0676	4.33	0.0142	1.6	0.2063	5.3	0.0061
Error	24								
Baltic Sea									
Grazer	1	0.1	0.7166	71.1	0.0001	4.1	0.0554	5.8	0.0241
Nutrients	3	15.9	0.0001	13.2	0.0001	0.6	0.5990	3.9	0.0214
G x N	3	5.1	0.0072	9.6	0.0002	2.3	0.1022	3.0	0.0507
Error	24								

Diversity and productivity

The experiments in the Baltic and NW Atlantic revealed strong effects of grazers and nutrient enrichment on plant cover and height, species richness and species diversity (Fig. 7.6, Table 7.4). For species richness and diversity, these effects reversed between the Baltic and the NW Atlantic. As a general patterns, nutrients had more pronounced effects in the Baltic, grazers had stronger effects in the NW Atlantic.

I used total plant cover and plant canopy height as surrogate measures for net primary productivity (NPP). Grazers strongly reduced both plant cover (Fig. 7.6 A) and height (Fig. 7.6 B) in the NW Atlantic. In the Baltic experiment, grazers had little effect on plant cover but reduced plant canopy height. Nutrient enrichment increased plant cover and height in the NW Atlantic and in the Baltic when grazers were absent but had less effects on plant cover when grazers were present as indicated by significant interaction terms (G x N interaction, Table 7.4). Comparisons of GRAZER and GRAZER CONTROL treatments revealed that plant cover and height were reduced on GRAZER CONTROL plots in both experiments, indicating higher grazing pressure on uncaged plots (ANOVA, $P < 0.05$). However, the effects of nutrient enrichment on plant cover and height were similar on GRAZER and GRAZER CONTROL plots (ANOVA, Cage x Nutrient, $P > 0.05$).

In contrast to NPP, grazer and nutrient effects on species richness and diversity reversed between the two experiments (Fig. 7.6 C, D, Table 7.4). Grazer reduced species richness and diversity in the NW Atlantic but had positive effects on species richness) and diversity in the Baltic Sea (note that the effect on species richness represent only a trend with $P = 0.0554$). Nutrient enrichment increased species richness and diversity in the NW Atlantic.

This effect was stronger when grazers were present (G x N interaction, Table 7.4). In the Baltic Sea, nutrient enrichment had no effect on species richness but on species diversity. Diversity was increased at LOW enrichment but then decreased again at MED and HIGH levels. Species richness and diversity were not different among GRAZER and GRAZER CONTROL plots in the Baltic (ANOVA, $P > 0.2$). But in the NW Atlantic, species richness and diversity were lower at NO, LOW, MED enrichment levels in GRAZER CONTROL plots compared to GRAZER plots (Species richness, Cage x Nutrients, $F_{3,24}=4.8$, $P=0.009$, Diversity, C x N, $F_{3,24}=4.6$, $P=0.014$). Nevertheless, the pattern of positive nutrient effects on species richness and diversity remained the same on GRAZER and GRAZER CONTROL plots (Fig. 7.6 C, D).

7.4. Discussion

These results demonstrate that the macroalgal community at Bald Rock is strongly regulated by grazers and strong effects of nutrient enrichment occur only when grazing pressure is reduced. As in Maasholm, the effects of nutrient enrichment were transmitted to higher trophic levels. Further comparisons with experiments from Maasholm indicated a reversal of grazer and nutrient effects on species richness and diversity, carbon storage and nitrogen retention between these two sites. It appears that this pattern is a predictable consequence of differences in nutrient status between the Baltic Sea and NW Atlantic Ocean.

Effects of nutrients and grazer on algae

Grazing pressure was very intense at Bald Rock (Fig. 7.1). Plant cover on grazed plots remained <10% for most of the year. In contrast to the Baltic, where grazing was highly selective (*Enteromorpha* > *Pilayella* > *Fucus*, Chapter 5, 6, Lotze et al. 2000, Lotze & Worm 2000), grazing appeared to be unselective in the NW Atlantic, where all species suffered from grazing. Differences in selectivity could be species-specific (Brendelberger 1997, Lotze & Worm 2000) or could be a consequence of differences in food supply. Only from October - December, when grazer density and activity declined (probably due to decreasing water temperature), winter annuals recruited abundantly on grazed plots. Recruitment of perennials (*Fucus vesiculosus*), which was indirectly enhanced by grazers in the Baltic, was strongly reduced by grazing at Bald Rock. Interestingly, these general patterns (stronger grazer effects compared to Maasholm, mostly unselective grazing) were also found for the microalgal assemblage (H. Hillebrand & B. Worm, unpubl.). Intense grazer pressure is a typical feature of rocky shores in the NW Atlantic (Lubchenco 1980, 1983, 1986, Petraitis 1987, Chapman & Johnson 1990, Worm & Chapman 1998). For example, *Fucus* recruitment on the mid shore level was suppressed by *Littorina littorea* grazing at a semi-exposed site in Maine (Lubchenco 1983). Similarly, grazing strongly reduced *Fucus* recruitment on the low shore level in Maine and Nova Scotia (Lubchenco 1980, Worm & Chapman 1998). On the contrary, *L. littorea* favored *Fucus* and other species recruitment by selectively feeding on fast-growing green algae

at a sheltered site in Massachusetts (Lubchenco 1978, 1983). This site (Canoe Beach Cove) was eutrophied through untreated wastewater from Boston Harbor (Schubel & Levi 1998).

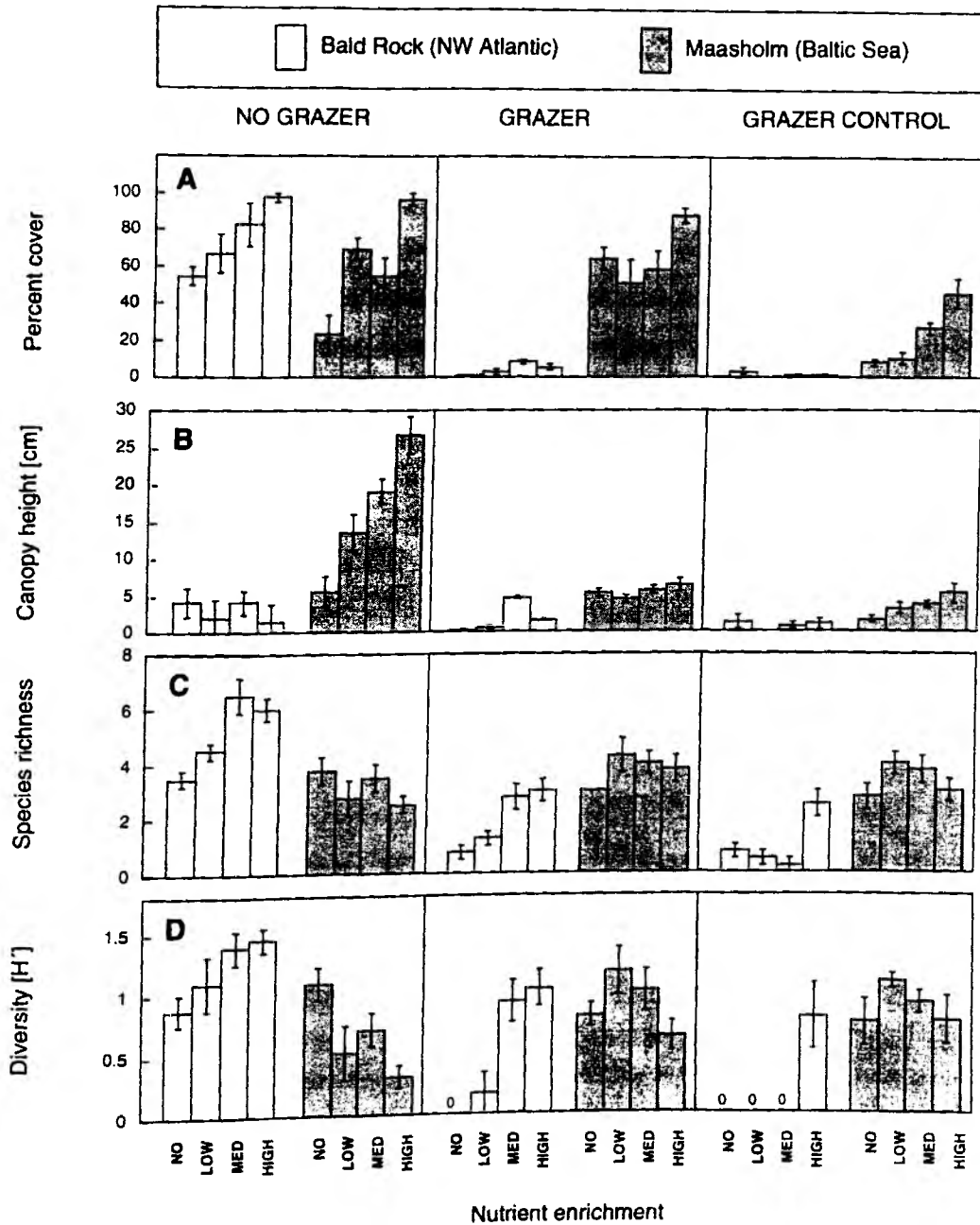


Fig. 7.6. Effects of grazers and nutrient enrichment on (A) total plant cover, (B) plant canopy height, (C) species richness, and (D) diversity in the NW-Atlantic and Baltic experiments. Total plant cover and canopy height were used as productivity surrogates, species richness and the Shannon-Weaver Index (H') as diversity measures.

Under these nutrient-rich conditions, which may be more similar to the Baltic than to other sites in the NW Atlantic, fast-growing annual algae (*Enteromorpha* and *Ulva* spp., Lubchenco 1978, 1983, 1986) can flourish and provide a preferred food source for most herbivores (Lubchenco 1978, Lotze & Worm 2000). As a consequence, grazers have an indirect positive effect on perennial recruitment by cropping fast-growing competitors. I propose that effects of mesograzers on *Fucus* change predictably with increasing nutrient loading and increasing abundance of fast-growing annual algae.

In Bald Rock, however, nutrient enrichment had little effects on species composition and abundance when grazers were present (Fig. 7.1). Even a 200% increase of DIN concentrations could not overcompensate grazer effects on most species (but note that *Fucus* recruitment was increased significantly). Only when grazing pressure declined in late fall, nutrient enrichment enhanced recruitment and growth of winter annuals, which reached up to 50% cover on enriched plots. When grazers were absent, however, nutrient enrichment had strong and year-round effects on species composition and abundance, with high abundance of filamentous brown (spring, summer), green (summer, fall) and red algae (fall). Moreover, internal nitrogen storage in algal tissue was increased (Fig. 7.3 A). Increased plant abundance and tissue nitrogen levels resulted in increased storage of particulate carbon and nitrogen in plant biomass on enriched versus control plots (Fig. 7.3 C, D). Contrary, grazers reduced carbon and nitrogen storage through consumption of algal biomass. Again, this pattern is the reverse of what I found in the Baltic (Chapter 6). This indicates that under nutrient-poor conditions the accumulation of plant biomass and hence C and N storage is strongly limited by intense grazing pressure and low nutrient supply, while under nutrient-rich conditions competition among annual and perennial algae limited C and N storage (see Chapter 6).

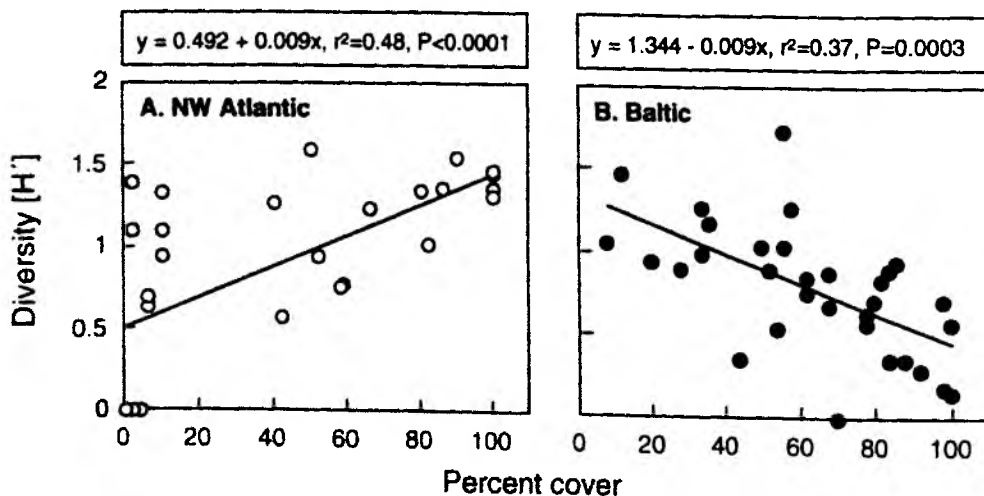


Fig. 7.7. Productivity - diversity relationships in the NW Atlantic and Baltic experiments. Percent cover was used as productivity surrogate, the Shannon-Weaver Index as diversity measure. Similar relationships were found if species richness was used as diversity measure (NW Atlantic: $y=1.86+0.042x$, $r^2=0.64$, $P<0.0001$; Baltic: $y=4.29-0.014x$, $r^2=0.12$, $P=0.049$).

Higher trophic levels

While grazers regulated plant abundance at Bald Rock, there was no evidence for top-down control of grazers. In contrast to Maasholm, where grazer populations crashed in summer (Chapter 6, Fig. 6.6), grazers in Bald Rock reached their highest abundance in summer when predators were most abundant as well (Fig. 7.4). This pattern between the two sites seems in accordance with a generalized food-web model that predicts that herbivores control plant abundance at low productivity and predators control herbivores at high productivity (Oksanen et al. 1981). However, predator abundance and species composition were similar at Bald Rock and Maasholm, which is not predicted by the model (Oksanen et al. 1981). Possibly, grazers at Bald Rock were better defended against predation. While small, thin-shelled *Littorina saxatilis* and crustaceans dominated the grazer assemblage in Maasholm, large, thick-shelled *L. littorea* dominated at Bald Rock. Similar to Maasholm, nutrient effects were transmitted to higher trophic levels: gammarids, crabs and shrimps all increased in abundance in nutrient-enriched plots. Plant abundance, however, did not increase. This may indicate that nutrient enrichment increased plant productivity but not plant abundance on grazed plots because of a rapid response of higher trophic levels. Note however, that this response was through immigration into plots, not through increased growth of consumer populations.

Diversity and productivity

Changing patterns of biological diversity along environmental gradients represent an important problem for ecologists (Hutchinson 1959, Connell & Orias 1964, Huston 1979, Tilman 1982, Abramsky & Rosenzweig 1984, Abrams 1995). In my experiments, I addressed the question how plant species diversity develops along an experimental productivity gradient and how grazers modify this response. I found that nutrient-stimulated increases in primary productivity had opposite effects on species richness and diversity in the Baltic and NW Atlantic (Fig. 7.7). This is consistent with theoretically predicted and empirically documented unimodal productivity - diversity relationships in other ecosystems (Tilman 1982, Abramsky & Rosenzweig 1984, Rosenzweig & Abramsky 1993, but see critique in Abrams 1995).

In the Baltic, diversity decreased with increasing enrichment and plant cover (Fig. 7.7 B). This pattern was driven by the dominant annual alga *Enteromorpha*, which through rapid nutrient uptake and growth responded strongly to nutrient enrichment and monopolized space under high-nutrient conditions. Consequently, diversity declined with increasing plant cover and productivity. This may indicate that (space) competition intensified with enrichment and that at high resource availability single species tend to monopolize the limited resource (Rosenzweig 1971, Rosenzweig & Abramsky 1993). Under these nutrient-rich conditions, moderate physical or biotic disturbance (e.g. wave action, grazing) increases diversity because plant biomass is removed, space becomes available and competitive exclusion is prevented. This is predicted by the predation hypothesis (Paine 1966) and the intermediate disturbance hypothesis (Connell 1978). However, comparisons with the NW Atlantic experiment suggest

that these models may have limited application for nutrient-poor ecosystems. Under low-nutrient conditions, enrichment increased diversity and grazer decreased diversity (Fig. 7.6 D). This pattern seems to be driven by a positive productivity-diversity relationship (Fig. 7.7 A), where higher productivity allows coexistence of more species. This suggests that nutrient competition is the driving force and space does not become limiting at the nutrient levels applied in this experiment. At highest enrichment levels however, no significant increases in diversity were observed as plant cover approached 100% (Fig. 7.6 A, C, D). Probably, nutrient limitation switches to space limitation with increasing enrichment. Similarly, in pelagic communities, increasing productivity and phytoplankton density switches the community from nutrient limitation to light limitation (Duarte 1995). This has also severe effects on benthic diversity because macro- and microphytes that can not grow up to the water surface become outcompeted by phytoplankton and free-floating macroalgae (Duarte 1995).

To my best of knowledge, this is the first experimental study where both the effects of grazers and nutrient enrichment on species diversity were compared between a nutrient-rich and a nutrient-poor ecosystem. Two important bodies of ecological theory are combined, one emphasizing productivity (Rosenzweig 1971, Tilman 1982, Rosenzweig & Abramsky 1993) and one emphasizing predation and herbivory (Paine 1966, 1994, Lubchenco 1978). Qualitatively, these results were predicted by Proulx & Mazumder (1998) who first conceptualized the "grazer-reversal-hypothesis" (GRH). Their meta-analysis of grazing effects in terrestrial, freshwater and marine ecosystems indicates that the pattern of reversing grazer effects on plant species richness with increasing productivity may be a general feature of ecosystems.

8. Ecosystems and large scales: a test of experimental predictions across Baltic and NW Atlantic rocky shores

8.1. Introduction

In the previous Chapters, I have concluded that grazers and nutrients interactively determine the structure and functioning of rocky shore plant assemblages (abundance of annual and perennial algae, diversity, productivity, carbon storage and nitrogen retention). Some of these effects reversed between a nutrient-rich site in the Baltic and a nutrient-poor site in the NW Atlantic. For higher trophic levels, I found that nutrient enrichment increased grazer and predator densities (transmission of bottom-up effects) and that grazer impacts on algae in the Baltic were reduced in summer, probably because predators reduced grazer density (transmission of top-down effects). Most of these conclusions were based on results from small-scale field experiments at 2 sites (Maasholm, Baltic Sea and Bald Rock, NW Atlantic). Clearly, these data are not yet sufficient to generalize upon interactions among nutrients, algae, grazers and predators on rocky shores, because (1) sample size is low ($n=2$ sites) and (2) the results may be confounded by the small scale of the experiments. Many ecological processes are scale dependent (Mann & Lazier 1991, Levin 1992) and spatial scale should be incorporated into the design of field studies in order to derive valid generalizations (Hughes et al. 1999). In this Chapter, I attempt to test the generality of my experimental results through comparative experiments and field surveys at a large number of sites. I tested the following predictive hypotheses that were derived from my previous experiments:

- (1) Grazer impact: Grazers strongly reduce colonization of annual algae (Chapter 5 - 7).
- (2) Seasonality: In the Baltic, grazer impacts are stronger in spring than in summer (Chapter 6), in the NW Atlantic grazer impacts are similar in spring and summer (Chapter 7).
- (3) Bottom-up versus top-down: Nutrient enrichment can override grazer control of annual algae (Chapter 5, 6).
- (4) Perennial-annual competition: The abundance of annual algae should be negatively correlated with the cover of perennial algae (Chapter 5, 6).
- (5) Nutrient effects on perennial-annual competition: Nutrient-rich sites have lower perennial and increased annual algal cover compared with nutrient-poor sites (Chapter 3 - 6).
- (6) Grazer effects on perennial-annual competition: Grazer density is positively correlated with perennial algal cover in the Baltic (Chapter 5 - 6), but not in the NW Atlantic (Chapter 7).
- (7) Transmission to higher trophic levels: Grazer and predator abundance increases at nutrient-rich sites (Chapter 3, 6, 7).

In order to test predictions 1 - 3, I conducted grazer-exclusion experiments in spring and summer 1998 - 1999 at 12 sites in the Baltic Sea and the Canadian NW Atlantic Ocean. I used tiles seeded with spores of the green annual *Enteromorpha intestinalis* as a "grazer assay" (*sensu* Hay et al. 1983, Worm & Chapman 1998) in order to compare changes in grazing pressure ("top-down") across gradients in nutrient supply and algal productivity ("bottom-up"). Detailed experimental evidence (Chapter 5 - 7, Lotze 1998, Lotze et al. 2000) indicated that high abundance of *Enteromorpha* is indicative of high nutrient supply, low grazing pressure or both. Especially early life stages (spores and germlings) are extremely responsive to changes in these parameters (Lubchenco 1986, Lotze et al. 1999, 2000, Lotze & Worm 2000). These traits suggest that *Enteromorpha* could be used as an indicator organism in order to assay changes in productivity and grazing pressure. As a further advantage, *Enteromorpha* thrives under a wide range of salinity, temperature and light conditions (Woodhead & Moss 1975, Reed & Russel 1979), which facilitates comparisons across different regions.

In addition to field experiments, I performed comparative field surveys across 41 sites in the Baltic and NW Atlantic in order to test (1) how rocky shore community structure changes with increasing nutrient supply and productivity, and (2) how the abundance of perennial and annual algae, grazers and predators are correlated (predictions 4 -7).

8.2. Methods

Field experiments

Grazer-exclusion experiments were conducted at 12 sites in spring and summer 1998 and 1999 in the Baltic Sea and the NW Atlantic (Fig. 8.1, Table 8.1, see also maps in Fig. 2.1, Chapter 2). These sites were chosen to represent similar hydrographic conditions, low-moderate wave exposure and abundance of hard substratum and algal cover. Consequently, the results can only be generalized for these conditions. In the Baltic Sea, 3 large fjords (Flensburg Fjord, Schlei Fjord, Kiel Fjord) and one small bay (Gelting Noor) were chosen as study regions. Experimental sites were located at the mouth of these fjords and had high nutrient loading typical for inshore regions in the Baltic Sea (Table 8.1., data from Chapter 6, Schramm et al. 1996, Hillebrand 1999, and the coastal resource data base of the Landesamt für Natur und Umwelt, Kiel, Germany). In the NW Atlantic, 4 large bays were chosen as study regions. Within the NW Atlantic regions, 4 nutrient-poor and 4 nutrient-rich sites were selected based on published long-term monitoring data of plant nutrient concentrations and chlorophyll concentrations (Dalziel et al. 1991, Keizer et al. 1996 a,b, Strain & Clement 1996, and data base of the phytoplankton monitoring group, Bedford Institute of Oceanography, Dartmouth, NS, Canada). "Nutrient-poor" and "nutrient-rich" represent relative, not absolute categories in this study. Nutrient-rich sites have been eutrophied by human activity. Sources of nutrient input in these areas included municipal wastewater, salmon aquaculture and agricultural run-off. To

compare hydrographic conditions of the sites, water temperature and salinity were recorded every time the sites were visited.

Table 8.1. Positions and site characteristics of the 12 experimental sites in the Baltic Sea and the NW Atlantic (NWA). DIN, DIP and chlorophyll averages (May - August), water temperature (Spring: May - June, Summer: July - August) and salinity (May - August) at the experimental sites are given.

Ocean	Region	Lat. (N)	Long. (E)	DIN $\mu\text{mol L}^{-1}$	DIP $\mu\text{mol L}^{-1}$	Chl.a $\mu\text{g L}^{-1}$	T _{spring} °C	T _{summer} °C	Sal PSU
Baltic Sea	1 Flenburg Fjord	54°46.0	09°52.8	1.14	0.93	2.10	13.1	15.4	15.8
Baltic Sea	2 Schlei Fjord	54°41.3	10°00.5	1.35	0.23	6.71	16.1	18.8	14.5
Baltic Sea	3 Kiel Fjord	54°22.4	10°14.8	3.04	4.52	nd	14.0	16.2	15.1
Baltic Sea	4 Gelting Noor	54°45.7	09°54.1	nd	nd	nd	16.0	19.0	15.9
NWA - Nut-rich	1 Halifax Harbor	44° 28.3	-63° 35.4	0.78	0.81	1.15	8.4	18.4	30.1
NWA - Nut-poor	1 Halifax Harbor	44° 28.3	-63° 34.7	0.44	0.34	0.55	10.7	16.8	30.1
NWA - Nut-rich	2 Annapolis Basin	44° 41.7	-65° 36.1	6.00	0.75	3.50	12.4	17.7	30.0
NWA - Nut-poor	2 Annapolis Basin	44° 39.8	-65° 56.0	4.84	0.45	2.28	9.7	13.5	31.8
NWA - Nut-rich	3 Letang Inlet	45° 02.4	-66° 48.4	13.29	1.14	2.10	8.7	16.1	31.0
NWA - Nut-poor	3 Letang Inlet	45° 04.9	-66° 46.9	7.28	0.90	1.69	10.0	16.0	30.7
NWA - Nut-rich	4 Passamaquoddy Bay	45° 07.4	-67° 02.2	5.97	0.62	nd	11.3	16.5	30.2
NWA - Nut-poor	4 Passamaquoddy Bay	45° 03.7	-66° 44.1	4.84	0.45	nd	9.4	15.1	30.8

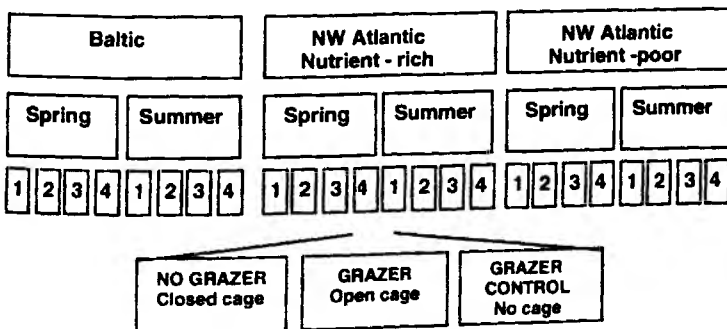


Fig. 8.1. Design of grazer exclusion experiments in the Baltic and NW Atlantic. Experiments were run in spring and summer at 4 regions in the Western Baltic and 4 regions in the NW Atlantic. In the NW Atlantic, nutrient-rich and nutrient-poor sites were compared within each region. At each site, ceramic tiles seeded with green algal spores were exposed in closed cages, open cages and uncaged plots ($n=5$ per site).

At each site, plant productivity and grazer impact were assayed by following germination of spores of the green alga *Enteromorpha intestinalis* on tiles in replicated cage experiments. Heat-sterilized, unglazed ceramic tiles (5 x 5 cm) were seeded with *Enteromorpha*

spores. Seeding was done using 1 kg of fertile *Enteromorpha intestinalis* harvested from the shallow subtidal in Maasholm, Baltic Sea (54°41.3'N, 10°0.5'E) and from tide pools in Duncan's Cove, NW Atlantic (44°29.9'N, 63°31.7'W). Plants were dripped dry and stored overnight in the dark at 8°C, then immersed in freshly collected seawater (8°C) and exposed to natural daylight. Water temperature slowly increased to 20°C. This initiated release and fertilization of spores which were allowed to settle on tiles for 30 h. Seeded tiles were stored for 1 - 2 d in filtered seawater in the dark at 10°C until they were used in the experiment. During each experimental run, 5 tiles were cultivated in the laboratory in order to quantify the initial density of *Enteromorpha* spores on the tiles. Each tile was placed in 500 ml filtered and Provasoli-enriched seawater and cultured for 23 d at 10°C and 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in a 14:10 h light:dark cycle, according to Lotze et al. (1999).

For the experiment, tiles were enclosed into circular cages (closed cages: NO GRAZER, open cages: GRAZER) or exposed on uncaged plots (GRAZER CONTROL) with 5 replicates per treatment per site. Cages were simple polyethylene mesh bags (15 x 15 cm) made from the same 1-mm mesh that was used to exclude mesograzers in previous experiments (Chapter 5 - 7). Bags were closed at one end. The open end was put over a 8 cm diameter polypropylene base made from sanitary tubing ends. A strong rubber ring (4 mm thickness) sealed the cage against the base. Half of the cages had two 4.5 x 4.5 cm openings to provide access to grazers. In the Baltic Sea, cages were placed in the *Fucus vesiculosus* zone between 0.6 - 0.9 m water depth and secured with two tent picks. In the NW Atlantic, cages were also placed in the *Fucus vesiculosus* / *Ascophyllum nodosum* zone which spans the lower to mid intertidal. The chosen shore level corresponded to approximately 8 - 9 h of immersion per tidal cycle. In order to fasten cages on sloping intertidal shorelines, I inserted 4 cm wedge anchors into holes that were drilled with a gasoline-powered hammer drill. The end of the wedge anchor was inserted through a hole in the cage base and secured with a nut.

Tiles were exposed for 23 d at the experimental sites (Baltic: 3 - 26 May and 6 - 29 July 1998, NW Atlantic 16 May - 8 June and 2 - 25 Aug 1999), then collected and analyzed in the laboratory. I determined *Enteromorpha* germling density at 25 x magnification under a dissecting microscope. Germlings were counted in 10 random 4 x 4 mm subsamples per tile. Other macroalgal germlings were relatively rare and were not quantified.

Field surveys

Detailed field surveys were conducted at 25 sites in the Baltic and 16 sites in the NW Atlantic in spring and summer 1998 - 1999. Spring surveys were performed during the peak period of *Fucus* reproduction because I hypothesized that annual algal cover during this time would be the best predictor for *Fucus* cover and recruitment (see Fig. 5.5., Chapter 5). The peak period of *Fucus* reproduction was in May in the western Baltic, June in the central Baltic, July in the eastern Baltic and from May - June in the NW Atlantic (Grützmacher 1984, Fig. 5.1, Chapter 5, R. Engkvist, C. Boström, G. Sharp, personal communications). All 12

experimental sites (Table 8.1) were included in the survey. In addition, I sampled 11 more sites in the German Kiel Bight (54°12'N, 11°03'E - 54°55'N, 9°48'E), 4 sites at the Swedish East coast (56°14'N, 16°02'E - 57°21'N, 16°37'E), 4 sites in the Åland archipelago, Finland (60°20'N, 19°36'E - 60°23'N, 19°43'E) and 2 sites along the Lithuanian open shore (55°50'N, 21°03'E - 55°55'N, 21°02'E). For locations of sites see Fig. 2.1 (Chapter 2). These 4 regions were 400 - 1000 km apart, sites within regions were at least 5 km apart. At each site, 10 replicate frames (25 x 25 cm) were placed randomly along 100 - 150 m transects at 0.8 - 1.2 m depth. Percent cover of attached algae and sessile invertebrates on rocky surface (no epiphytes or drifting plants) was determined using a plexiglas frame with 50 random points. Grazers were removed by shaking the algae within a framed sampling net and counted by species. However, no reliable estimates of predator densities could be gained using this sampling protocol. All sites were revisited after 3 months and the density of visible (>2 mm) *Fucus* recruits was determined with a 10 x 10 cm frame.

In the NW Atlantic, I sampled all 8 experimental sites in spring and in summer. In addition, I sampled 8 other sites in spring only: 4 nutrient-poor control sites and 4 sites that were located close (0.5 - 2 km) to a nutrient point source (sewage outfall, salmon aquaculture operation, fish processing plant). These sites were included in the survey in order to check whether patterns observed at nutrient-rich versus nutrient-poor sites may become even more apparent near a nutrient point source. At all sites, I sampled 100 - 200 m transects which spanned the mid eulittoral zone which is normally dominated by *Fucus vesiculosus* and *Ascophyllum nodosum*. Each transect was sampled with 10 randomly placed 50 x 50 cm quadrates. Percent cover of all plants and sessile animals was determined with a 50 x 50 cm plexiglas sheet with 50 random dots. The only group that was excluded from the analysis because of taxonomic uncertainty were red algal crusts. I sampled epiphyte cover, secondary space cover and primary space (understorey) cover. The latter was determined after removing *Fucus* and *Ascophyllum* from the sample plots. Removed plants were shaken vigorously over a bucket in order to sample grazers and predators. These and the remaining animals on the sample plots were counted by species.

Data analysis

The purpose of this investigation was to evaluate the generality of patterns and processes in rocky shore food webs across multiple sites and regions. This type of experiment should be analyzed using mixed-model ANOVA with "Site" or "Region" as a random factor and the experimental manipulation as a fixed factor (Sokal & Rohlf 1995, Underwood 1996). This analysis tests the general hypothesis that the outcome of the experimental manipulations can be generalized across all sites within the sampled population of sites, in this case the Baltic and Canadian NW Atlantic shorelines. Thus, I analyzed *Enteromorpha* germling density on the tiles as a function of grazer presence (fixed factor: open versus closed cages), season (fixed factor: comparing spring and summer), trophic status (fixed factor: nutrient rich versus nutrient

poor sites, NW Atlantic only) and region (random factor, region 1 - 4) in a factorial mixed-model ANOVA. Results from the Baltic need to be interpreted with caution, because of an unbalanced design (4 sites in spring, 3 sites in summer, loss of replicates at one site). In a separate analysis, I tested for cage artifacts by comparing open cages versus uncaged plots. Subsamples from individual tiles were pooled for analysis. Data were log-transformed in order to achieve homogeneity of variances tested by Cochran's test.

Similarly, I analyzed the abundance of perennial algae, annual algae, filter feeders, grazers and predators as a function of season (fixed factor, spring versus summer, NW Atlantic only), trophic status (fixed factor: nutrient rich versus nutrient poor sites, NW Atlantic only) and region (random factor, region 1 - 4). Percent cover data were angular transformed (Sokal & Rohlf 1995). Grazer and predator data were (log+1)-transformed.

Finally, I used linear regression models (Sokal & Rohlf 1995) in order to test for correlations (1) among germling abundance on grazed and ungrazed tiles in the experiment and (2) among annual and perennial algal cover, filter feeder, grazer and predator abundance across all sites (n=25 in the Baltic, n=16 in the NW Atlantic, only spring data). Replicates were pooled for each site.

8.3. Results

Field experiments

Cultivation of the seeded tiles in the laboratory showed that the seeding procedure was successful. Spores settled at high densities on the experimental tiles ($2210 \pm 308 \text{ cm}^{-2}$, mean \pm 1 SE, n=20) and spore densities were not significantly different among the four runs of the experiment (spring and summer in the Baltic and NW Atlantic, ANOVA, $F_{3,16}=2.5$, $P=0.098$). These densities are representative of daily settlement densities of *Enteromorpha* spores on ceramic tiles in the Baltic ($1000 - 6000 \text{ cm}^{-2} \text{ d}^{-1}$ from May - August, Lotze et al. 2000).

In the field, only a fraction of settled spores developed into germlings. Averaged across all experiments, germling density after 23 d in the field was $174 \pm 25 \text{ cm}^{-2}$ (range 0 - 2665, n=259). In the Baltic experiments, grazers strongly reduced germling abundance in spring but not in summer (Fig. 8.2, Table 8.2, S x G, $P=0.062$). On average, grazers consumed 97% of germlings in spring, but only 43% in summer. At 2 out of 3 sites, germling abundance was not reduced by grazers at all (Fig. 8.2 B). In the absence of grazers, germling density was higher in the spring ($433 \pm 176 \text{ cm}^{-2}$) than in summer ($91 \pm 39 \text{ cm}^{-2}$), in the presence of grazers germling density was lower in spring ($13 \pm 5 \text{ cm}^{-2}$) than in summer ($52 \pm 11 \text{ cm}^{-2}$). This may indicate high nutrient supply and algal productivity and high grazing pressure in spring and low nutrient supply and low grazing pressure in summer. Among the 4 regions, algal productivity in spring increased 65-fold from region 1 to 4. No clear pattern among sites was evident in summer. The control experiment (GRAZER versus GRAZER CONTROL treatments) revealed no significant cage artifacts (ANOVA, $F_{1,3}=0.004$, $P=0.95$).

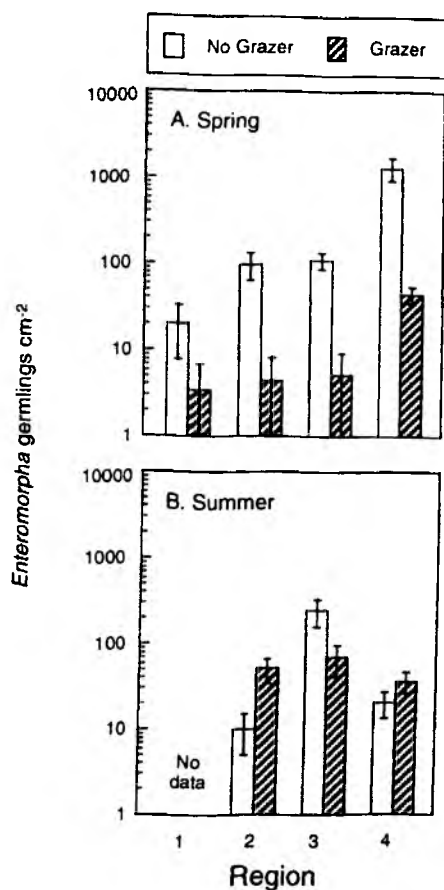


Fig. 8.2. Baltic Sea experiment. Effects of grazers on the densities of green algal germlings (*Enteromorpha intestinalis*) in 4 different regions in (A) spring and (B) summer. Data are means \pm 1 SE (n=5). GRAZER CONTROL treatments were not significantly different from GRAZER treatments and are not shown.

In the NW Atlantic experiments, grazers strongly reduced *Enteromorpha* germination (Fig. 8.3, Table 8.2, $P=0.0026$), independent of season (S \times G, $P=0.14$) and trophic status (G \times T, $P=0.84$). In the absence of grazing, germination was higher in spring (326 ± 70 cm⁻²) than in summer (242 ± 93 cm⁻²). When grazers were present, germination was similar in spring (105 ± 41 cm⁻²) and summer (107 ± 46 cm⁻²). Nutrient-rich sites had on average 9-fold higher germling densities than nutrient-poor sites (287 ± 4 cm⁻² versus 32 ± 5 cm⁻²). However, this effect varied among seasons and regions as indicated by a significant interaction term (Table 8.2, S \times T \times R, $P=0.0007$). This interaction indicates that nutrient-rich sites had higher germling densities in all regions and seasons, except region 2 in summer where this effect was reversed, possibly due to upwelling of nutrient-rich deep water from the Bay of Fundy. These results suggest that grazing pressure and algal productivity are similar in spring and summer in the NW Atlantic. Among the 4 regions, nutrient-poor sites showed increasing productivity in spring from region 1 - 4, whereas this pattern was reversed in nutrient-rich sites. The control experiment revealed no significant cage artifacts (ANOVA, $F_{1,3}=1.3$, $P=0.33$).

When I plotted germling densities in GRAZER versus NO GRAZER treatments, I found a striking linear relationship (Fig. 8.4). This indicates that in these experiments grazers removed a relatively constant proportion of germlings (80%) independent of algal productivity across 3 orders of magnitude in germling density.

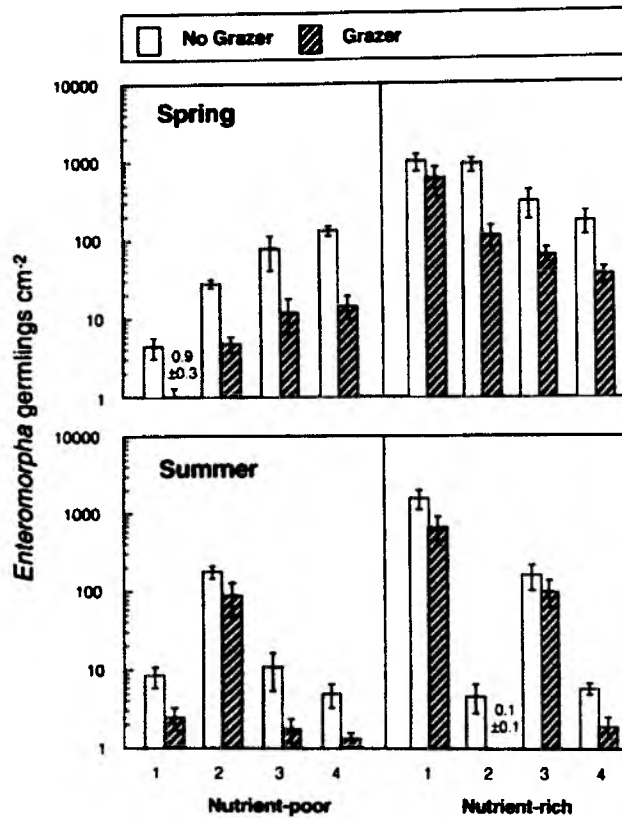


Fig. 8.3. NW Atlantic experiment. Effects of grazers on the densities of green algal germlings (*Enteromorpha intestinalis*) at nutrient-poor and nutrient-rich sites in 4 different regions. (A) Spring experiment. (B) Summer experiment. Data are means \pm 1 SE (n=5). GRAZER CONTROL treatments were not significantly different from GRAZER treatments and are not shown.

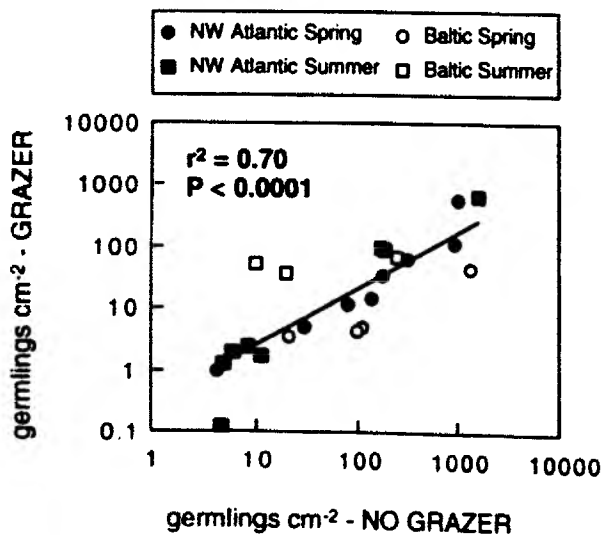


Fig. 8.4. Relationship between *Enteromorpha* germling densities in closed cages (NO GRAZER) and germling densities in open cages (GRAZER) at all experimental sites in the Baltic and NW Atlantic ($\log y = -0.829 + 1.037[\log x]$). Each point represents the mean of 5 replicates.

Field Surveys

Benthic community structure varied strongly among the 4 experimental regions in the Baltic (Fig. 8.5, Table 8.3 A). As productivity increased from regions 1- 4, perennial algal cover decreased, annual algal and filter feeder abundance increased, and grazer density remained similar. Region 2 (Schlei, Fjord, Maasholm) was an exception from this pattern, showing much higher grazer densities and perennial algal cover but lower annual algal cover than the other regions. In the NW Atlantic, perennial algal cover was lower at nutrient-rich sites than at nutrient-poor sites (Fig. 8.6 A), but this effect varied among regions as indicated by a significant interaction (Table 8.3 B, T x R, P=0.0011).

Table 8.2. Mixed-model ANOVA. Effects of season, grazer presence and region in the Baltic (above) and effects of season, grazer presence, trophic status and region in the NW Atlantic (below) on *Enteromorpha* germlings density in the experiment. Data are (log+1) - transformed. Effects with $P < 0.1$ are printed bold.

Source	df	MS	F	P
Season	1	0.25	0.08	0.8061
Grazer	1	5.10	6.14	0.0894
Region	3	2.66	0.74	0.7945
S x G	1	7.37	14.48	0.0626
S x R	2	3.25	6.38	0.1355
G x R	3	0.83	1.63	0.4021
S x G x R	2	0.51	1.95	0.1524
Residual	51	0.26		
Season	1	9.05	4.20	0.1330
Grazer	1	12.85	86.65	0.0026
Trophic Status	1	24.55	1.92	0.2598
Region	3	1.53	0.17	0.8925
S x G	1	0.59	21.62	0.1349
S x T	1	4.17	0.68	0.4689
G x T	1	0.01	0.05	0.8369
S x R	3	2.16	0.35	0.8056
G x R	3	0.15	0.80	0.7236
T x R	3	12.78	2.06	0.2583
S x G x T	1	0.03	0.84	0.4270
S x G x R	3	0.10	3.01	0.1949
S x T x R	3	6.10	187.64	0.0007
G x T x R	3	0.12	3.74	0.1539
S x G x T x R	3	0.03	0.26	0.8576
Residual	128	0.13		

Annual algae (Fig. 8.6 B) and filter feeders (Fig. 8.6 C) were on average more abundant at nutrient-rich sites. This effect was more evident in summer and dependent on the region (Table 8.3 B, S x T x R, $P_{\text{Annuals}} = 0.0161$, $P_{\text{Filter feeder}} = 0.0007$). There was an interesting pattern among the 4 regions. Nutrient-rich sites in region 1 and 3 had low cover of filter feeders but high cover of fast-growing annual algae (mostly *Enteromorpha* spp. and *Ulva* spp.). Nutrient-rich sites in region 2 and 4 showed very high cover of mussels and barnacles and low cover of annual algae. Grazer density showed no clear response to increases in nutrient supply (Fig. 8.6 D). There were both increases and declines at nutrient-rich compared to nutrient-poor sites (Table 8.3 B, S x T x R, $P = 0.029$). Predator density also showed no clear pattern

between nutrient-poor and nutrient-rich sites (Fig. 8.6 E). However, as a general trend, nutrient-rich sites that were dominated by filter feeders had high grazer abundance (Region 2, 4, Fig. 8.6 C, D). Nutrient-rich sites dominated by annual algae had low grazer abundance (Region 1, 3, Fig. 8.6 B, D).

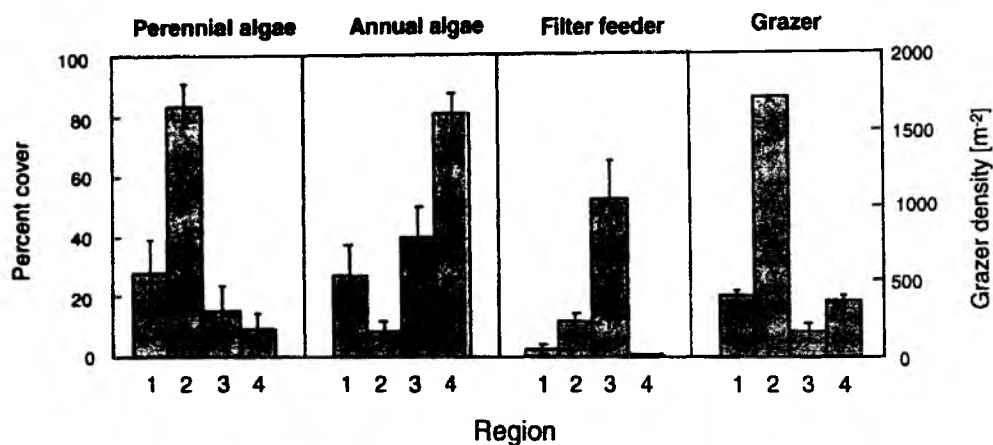


Fig. 8.5. Community structure in the 4 Baltic experimental regions in spring. Data are means \pm 1 SE (n=10).

Table 8.3. Mixed-model ANOVA. Effects of region, season and trophic status on the abundance of 5 food-web components in the Baltic and NW Atlantic. Algal and filter-feeder data were angular transformed, grazer and predator data were log-transformed. Raw data in Fig. 8.5 and Fig. 8.6. $P < 0.1$ are printed bold.

Data set	Source	df	Perennials	Annuals	Filter feeder	Grazer	Predators
			P	P	P	P	P
A. Baltic	Region	3	0.0001	0.0001	0.0001	0.0003	nd
	Error	36					
B. NW Atlantic	Season	1	0.0765	0.5520	0.1212	0.6145	0.9471
Spring.	Trophic Status	1	0.2703	0.9507	0.1130	0.6559	0.1881
Summer	Region	3	0.5215	0.5632	0.2426	0.2883	0.8691
	S x T	1	0.1252	0.0679	0.1737	0.0987	0.8395
	S x R	2	0.4638	0.3571	0.3294	0.6048	0.0563
	T x R	3	0.0011	0.0155	0.1371	0.1460	0.4139
	S x T x R	2	0.7765	0.0161	0.0007	0.0290	0.7931
Error		51					
C. NW Atlantic	Trophic Status	1	0.0518	0.9525	0.3579	0.6680	0.6785
Point source	Region	3	0.7993	0.7828	0.7249	0.8839	0.7483
	T x R	3	0.0001	0.0001	0.0001	0.0001	0.0644
	Error		72				

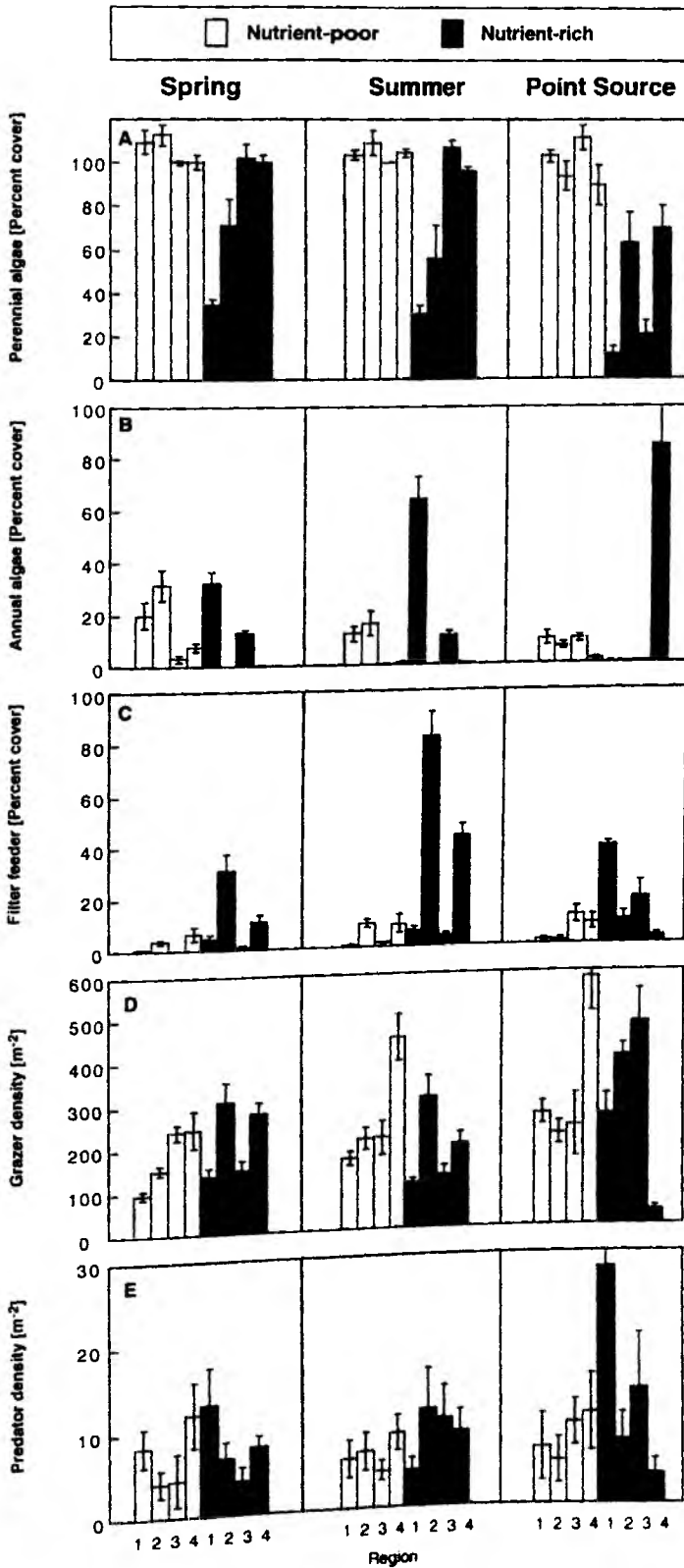


Fig. 8.6. Community structure at nutrient-poor and nutrient-rich sites in the 4 NW Atlantic experimental regions in spring and summer. Community structure at an independent set of sites close (nutrient-rich) and 4 sites distant (nutrient-poor) to a nutrient point source is also shown. Data are means ± 1 SE ($n=10$).

Near nutrient point sources, perennial cover was strongly reduced compared with nutrient-poor control sites (Fig. 8.6, Table 8.3 C). Cover of annual algae was very high near point sources in region 4, but low in region 1 - 3. In contrast, abundance of filter feeders and grazers were high in region 1 and 3 and lower in region 2 and 4. Grazers density was high at all sites, except near point sources in region 4. Predators had high abundance at sites with high cover of filter feeders (region 1 and 3). In summary, the changes between nutrient-poor sites and nutrient-rich sites near point sources depended on the region (Table 8.3 C, T x R, $P < 0.0001$), except for predators which did not show significant changes in abundance.

When I surveyed 25 sites in the Baltic Sea I found that *Fucus vesiculosus* was the only perennial species in the shallow subtidal zone except for one site in Sweden (Figeholm, 57°21.8' N, 16°37.4' E), where *Furcellaria lumbricalis* occurred at low densities. Coverage of *Fucus* was negatively correlated with cover of filamentous or foliose annual algae such as *Enteromorpha intestinalis*, *Ceramium nodulosum*, *Cladophora glomerata* or *Pilayella littoralis* (Fig. 8.7 A). Similarly, *Fucus* recruit densities across the Baltic declined with increasing annual algal cover during the period of *Fucus* reproduction and settlement (Fig. 8.7 B). Recruit densities in Germany were consistently higher than in the other regions (Fig. 8.7 B). Further analysis showed that *Fucus* cover was strongly positively correlated with the density of gastropod grazers (Fig. 8.7 C) and cover of annual algae was negatively correlated with gastropod densities (Fig. 8.7 D). In a multiple regression model predicting *Fucus* cover at a given site, the effects of annual algae cover ($P < 0.0001$) and gastropod grazers ($P = 0.0009$) were significant, but the effect of crustacean grazers was insignificant ($P = 0.52$). This model explained >76% of variation in *Fucus* cover (overall $r^2 = 0.76$, $n = 25$, $P < 0.0001$). Filter feeders were mostly rare and did not explain a significant part of the variance in *Fucus* cover ($P > 0.2$).

Comparing all 16 sites in the NW Atlantic, I found that the abundance of annual algae and filter feeders combined correlated negatively with the abundance of perennial algae (Fig. 8.8 A). Interestingly, filter feeder abundance was positively correlated with predator abundance (Fig. 8.8 B). In contrast, grazer abundance was not significantly correlated with predator abundance ($P > 0.2$). Cover of annual algal declined strongly with increasing grazer density (Fig. 8.8. D). In contrast to the Baltic, perennial algal abundance is not correlated with grazer density (Fig. 8.8 C).

8.4. Discussion

Field experiments

I performed comparative grazer experiments in the Baltic and NW Atlantic in order to test predictions regarding the impact of grazers on annual algae at sites of different productivity (prediction 1 - 3, see introduction). All 3 predictions were sustained by the experiments. The results showed that grazers represent a dominant force that limits colonization by fast growing

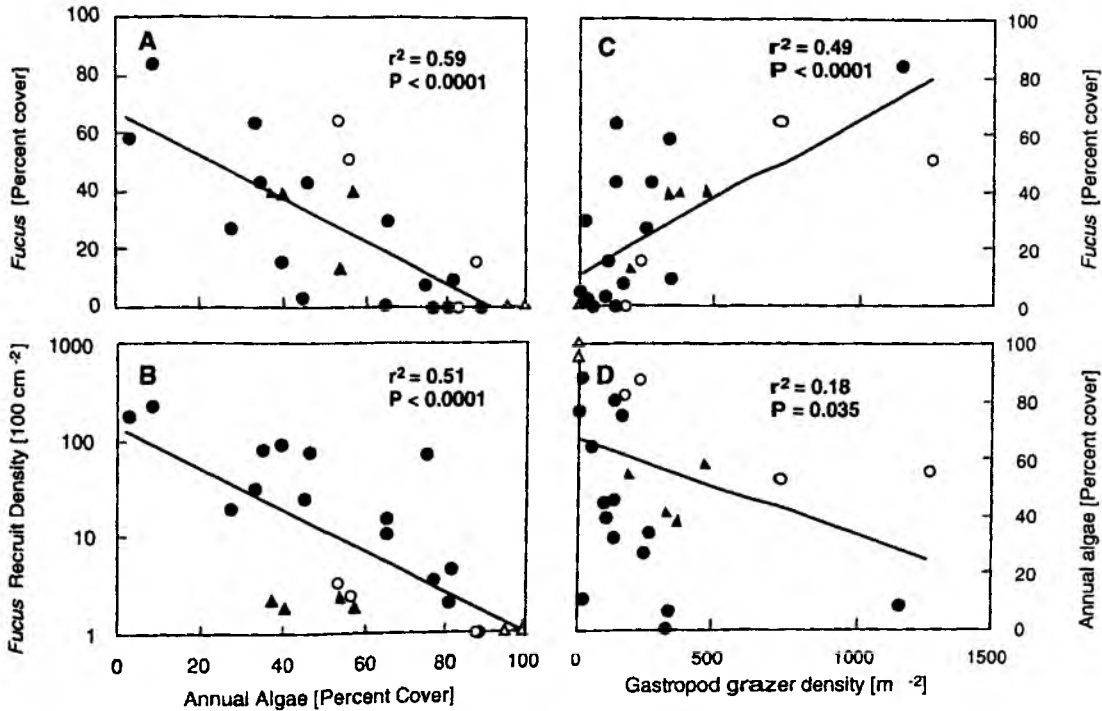


Fig. 8.7. Baltic Sea. Large-scale relationships among perennial *Fucus vesiculosus*, annual algae and gastropod grazers. The survey covered 25 sites in Germany (●), Sweden (○), Finland (▲) and Lithuania (△). (A) *Fucus* cover was predicted from the abundance of annual algae ($y=68.057-0.738x$). (B) Relationship between the cover of annual algae during the period of *Fucus* settlement and *Fucus* recruit densities ($\log[y+1]=2.16-0.022x$). (C) Positive correlation between gastropod grazer densities (western Baltic: *Littorina* spp., eastern and northern Baltic *Theodoxus fluviatilis*) and *Fucus* cover ($y=11.091+0.054x$). (D) Negative relationship between gastropod grazer densities and the cover of annual algae ($y=66.37-0.034x$).

annual macroalgae (prediction 1). This was proposed by Lotze et al. (1999, 2000) as an important mechanism that may prevent destructive macroalgal mass blooms. Indeed, I found that massive blooms of fast-growing annual algae (>50% cover) only occurred at nutrient-rich sites with reduced grazer densities (<500 m^{-2} in the Baltic, <100 m^{-2} in the NW Atlantic). This indicates that increased nutrient loading and reduced grazer densities are both conditions that favor intense macroalgal blooms (Geertz-Hansen et al. 1993, Hauxwell et al. 1998, Lotze et al. 2000).

In the Baltic experiments, grazer effects were strong in spring but weakened in summer, while grazer effects were similar in spring and summer in the NW Atlantic (prediction 2). In contrast, germling productivity in the absence of grazing was higher in spring than in summer in both experiments. This probably indicates increasing nutrient limitation of bloom-forming green algae in summer (Pedersen & Borum 1996, Lotze 1998, Lotze et al. 2000). These broad patterns of (1) increasing nutrient limitation and decreasing algal biomass from spring to summer, (2) high grazing pressure in spring but lower grazing pressure in summer in eutrophic

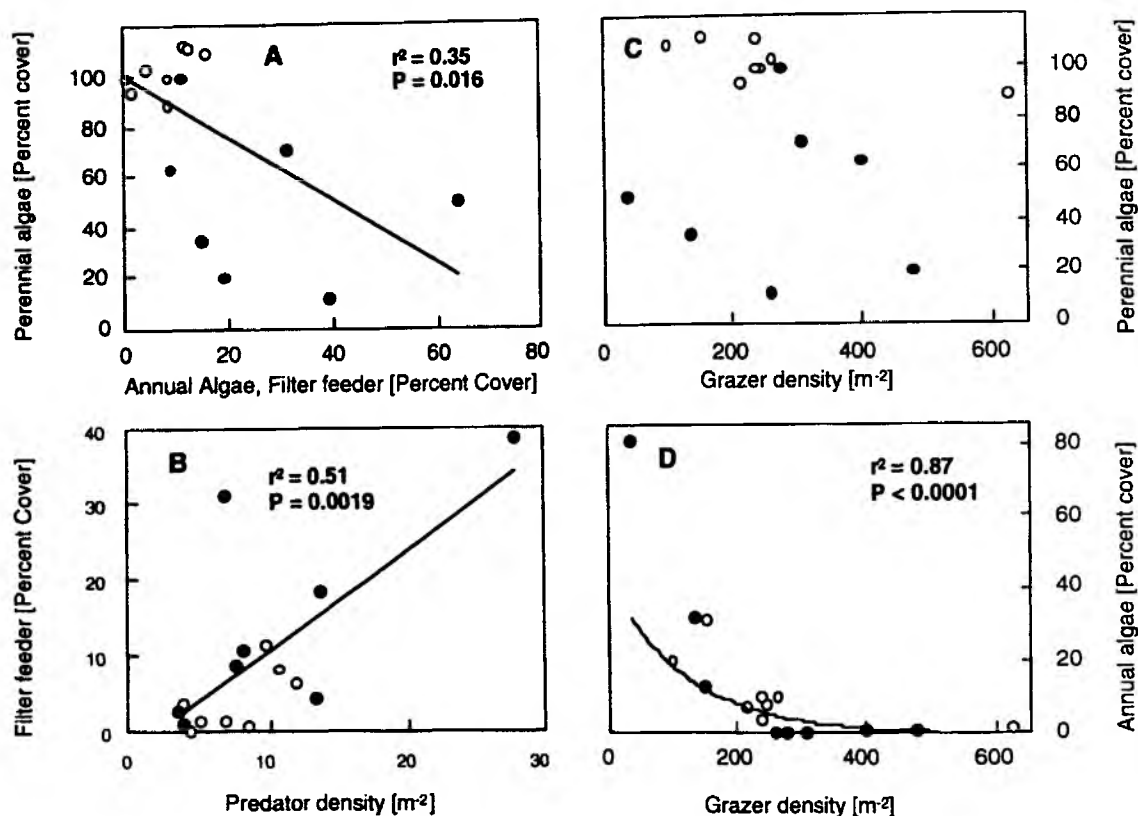


Fig. 8.8. NW Atlantic. Large-scale relationships among perennial algae (>95% fucoids), annual algae, filter feeders (*Mytilus edulis*, *Balanus* sp.), grazers (>90% gastropods) and predators (mostly crabs, starfish, whelks) at nutrient-poor (○), and nutrient-rich sites (●). (A) Fucoid cover declines with increasing cover of annual algae and filter feeders ($y=99.853-1.254x$). (B) Cover of filter feeders is positively correlated with predator densities ($y=-2.879+1.331x$). (C) No significant relationship between perennial algae and grazer densities. (D) Exponential decline of annual algal cover with increasing grazer density ($y=42.36 * e^{-0.0083x}$).

systems, and (3) high grazing pressure in spring and summer in oligotrophic systems are also predicted by a model of seasonal succession in phytoplankton communities (Sommer et al. 1986).

Weak grazer effects in summer in Maasholm (Baltic Sea) may be linked to increased predator densities and strong declines of all herbivores in summer (Chapter 6). Whether similar processes were operating at the other Baltic sites, where grazer impact weakened in summer is unclear, because I have no reliable estimates of predator densities or predation intensity at these sites. At 16 sites in the NW Atlantic, there was no clear evidence for seasonally declining grazer effects (Fig. 8.3 B) or grazer densities (Fig. 8.6 D). Also, predator densities were not increased in summer (Fig. 8.6 E) and there was no significant correlation between grazer and predator densities in the NW Atlantic. These limited data do not suggest that trophic cascades from predators to mesograzers (snails and crustaceans) and macroalgae are common in the studied rocky shore food webs (but see Duffy & Hay 2000). In contrast, trophic cascades appear to be

common in rocky shore food webs dominated by macrograzers (mostly sea urchins, Wootton 1995, Estes & Duggins 1995, Estes et al. 1998, Sala et al. 1998). It is important, however, to realize that the Canadian NW Atlantic is severely overfished and the abundance of vertebrate predators greatly reduced (Myers et al. 1997). Work in marine protected areas, where fishing pressure was reduced showed that predatory fish were more abundant and had cascading effects on grazer and algae (Sala et al. 1998, Steneck 1998)

In the NW Atlantic, nutrient-rich sites had on average 9-fold increased germling densities in both grazed and ungrazed plots compared with nutrient-poor sites. Thus nutrient enrichment can override grazer control of annual algal growth (prediction 3). Grazers removed a relatively constant portion of germlings, independent of total germling densities. The regression line in Fig. 8.4 indicates that ca. 80% of germlings were consumed across 3 orders of magnitude in productivity. This means when germling productivity at nutrient-poor versus nutrient-rich sites is 10 versus 1000 germlings cm^{-2} , grazers reduce these to 2 and 200 germlings cm^{-2} , respectively. Sommer (1999) found that for *Littorina littorea* ingestion rates for benthic microalgal films increased with microalgal biomass in a saturating function. At subsaturating food levels, *Littorina* increased the area grazed per time but not grazing intensity in that area. This may also apply for my study, where *Littorina* spp. was the most abundant grazer species and grazing intensity on the tiles was independent of total food abundance.

Field surveys

Survey results indicated that under nutrient-rich conditions, perennial algae were replaced by annual algae or filter feeders (predictions 4 and 5, see introduction). Perennial algae had low cover at 3 out of 4 experimental sites in the Baltic and at 6 out of 8 nutrient-rich sites in the NW Atlantic (prediction 5). In contrast, the cover of perennial algae was close to 100% at all nutrient-poor sites in the NW Atlantic. Furthermore, *Fucus* cover at 25 sites in the Baltic was a negative function of annual algal cover (Fig. 8.7 A, prediction 4). Gastropod grazer seemed to counteract this, as indicated by a significant negative correlation between annual algae and snail densities and a resulting positive correlation between snail densities and cover of *Fucus* in the Baltic (prediction 6, Fig. 8.7 C, D). However, no such relationship was found in the NW Atlantic. Although grazers limit colonization by annual algae (Fig. 8.8 D) there was no positive correlation between grazer densities and cover of perennial algae.

Based on my field experiments at Maasholm (Chapter 5, 6), I had hypothesized that blocking of *Fucus* zygote settlement in spring by a turf of annual algae is an important mechanism that drives the observed decline of *Fucus* in the Baltic (Chapter 5, 6). These small-scale experimental results were strongly supported by the large-scale evidence. The relationship between *Enteromorpha* canopy cover and *Fucus* recruitment in my experiment ($\log[y+1]=2.436-0.021x$, see Fig. 5.5 B, Chapter 5) was paralleled when I correlated the cover of annual algae at 25 sites with *Fucus* recruitment ($\log[y+1]=2.16-0.022x$, Fig. 8.7 B). Recruit densities at sites in the eastern Baltic were consistently lower compared with sites in the western

Baltic (Fig. 8.7 B). This may indicate that an additional factor constrained *Fucus* settlement in the eastern Baltic. Probably this factor was the reduced salinity. Low salinity in the eastern Baltic (<6 PSU) interferes with the fertilization process in *Fucus*, which reduces the overall recruitment success of this species (Serrao et al. 1996). Because of these additional constraints, *Fucus* in the eastern Baltic may be even more susceptible to increased competition from annual algae.

In the NW Atlantic, perennial algal cover declined with increasing cover of annual algae and filter feeders (mainly mussels, *Mytilus edulis*) at nutrient-rich sites. Interestingly, annual algae and filter feeders were never both abundant but appeared to be alternative community states at nutrient rich sites (compare regions 1 and 3 versus 2 and 4, Fig. 8.6 B, C). Grazer were abundant at sites dominated by filter feeders but rare at sites dominated by annual algae (Fig 8.6 D). Thus grazer (and also predator) density did not increase with nutrient enrichment in a consistent fashion which refutes prediction 7 (transmission to higher trophic levels). It remains an open question why the effects of nutrient enrichment transmitted to higher trophic levels in several of my experiments (Chapter 3, 6, 7), whereas I found no consistent patterns in my surveys. Increased grazer and predator densities in nutrient-enriched experimental plots were most likely not caused by an increase in birth rates but by increased immigration from a source pool of grazers and predators around the experiment. An increase in birth and population growth rates at larger scales may be regulated by additional variables such as habitat availability (Salemaa 1987, Gosselin & Chia 1995, Boström & Mattila 1999) which was not a factor in my small-scale manipulations.

My survey in the NW Atlantic showed that macroalgae had low abundance at some nutrient-rich sites where filter feeders reached high abundance (Fig. 8.6 A, C). This suggests that interactions among filter feeders and macroalgae can be important at eutrophied sites. This was not predicted by my experiments at Maasholm and Bald Rock because recruitment of filter feeders was very low throughout these experiments. Negative effects of mussels on macroalgae have been described previously, but were mostly related to variations in predation intensity of seastars and whelks on mussels ("top-down", Paine 1966, 1971, Menge 1976, Lubchenco & Menge 1978), not to nutrient enrichment ("bottom-up"). However, several workers have observed an increase in mussel abundance, growth rates and recruitment with increasing primary productivity in Kiel Bight, Western Baltic (Boje 1965), Oregon (Menge et al. 1997) and New Zealand (Menge et al. 1999). Also, predator abundance and predation intensity on mussels increased with increasing primary productivity (Menge et al. 1997). Similarly, I found increased mussel cover at nutrient-rich sites which also had increased chlorophyll a densities (Table 8.1) and productivity (Fig. 8.3). Moreover, mussel cover and predator densities were positively correlated. This evidence may indicate the transmission of bottom-up effects from nutrients to phytoplankton (increased chlorophyll a) to mussels and predators. I conclude that interactions among nutrients, phytoplankton, filter feeders, macrophytes and predators are important in structuring rocky shore food webs (Paine 1966, 1971, Menge 1976, Menge et al.

1997, 1999). Importantly, I would have ignored these interactions if I had relied solely on my experimental results from Maasholm and Bald Rock. I can only speculate on the reasons for low recruitment of filter feeders in my experiments. Adult mussels and barnacles were present both at Maasholm (abundant) and Bald Rock (rare). Larvae of mussels and barnacles spent several days to weeks in the water column (N. Kautsky 1982), in contrast to algal propagules which settle within minutes after fertilization (Santelices 1990). Mesoscale oceanographic conditions play an important role for the transport and settlement of invertebrate larvae, including mussels and barnacles (Roughgarden et al. 1988). Possibly, local conditions at my two main experimental sites prevented abundant settlement of invertebrate larvae in the experiments.

Conclusion

Comparative experiments at 12 sites and large-scale observational evidence support most conclusions derived from small-scale field experiments in the Baltic and NW Atlantic. Competition between annual algae and perennial algae is mediated by grazing pressure ("top-down": controlling annuals) and nutrient supply ("bottom-up": favoring annuals). Grazers cannot overcompensate the effects of enrichment, but loss of grazers can enhance the effects of enrichment. Grazer control of annual algae is stronger in the NW Atlantic than in the Baltic. Unforeseen by my previous experiments, consumer abundance did not increase consistently with nutrient enrichment and increased abundance of filter feeders appears as an important additional variable that limits the success of perennial algae in eutrophied environments.

9. General discussion

The goal of this thesis was to understand how resources and consumers regulate food web structure, species diversity and ecosystem functioning on rocky shores. In this final chapter, I attempt to synthesize this and previous work and provide a conceptual model of species interactions on rocky shores. I will discuss mechanisms that maintain species diversity and ecosystem functioning in littoral systems and give an outlook on what I feel may be promising directions for marine littoral ecology.

Rocky shore food webs

Rocky shores are excellent model systems for the study of food web regulation (Paine 1977, 1994, Menge & Farrell 1989). Traditionally, the focus of study has been on the effects of consumers on lower trophic levels (Fig. 9.1 A, B). Recent work on mussel-dominated sites (Menge et al. 1997, 1999) and my work on sites that are dominated by macroalgae suggest that traditional models should be expanded into a more comprehensive bottom-up versus top-down view of rocky shores (Fig. 9.1 C).

The original experiments by Paine (1966, 1971) in the NE and SW Pacific demonstrated that seastars suppress mussels and prevent competitive exclusion of several species of macroalgae and invertebrates. Thus a single strong interaction was proposed to maintain a species-rich community (Fig. 9.1 A). This model was applied to the NW Atlantic by Menge (1976, 1983, Lubchenco & Menge 1978) who showed that mussels are competitively superior to macroalgae and displace these when they are not controlled by predation (but note criticism by Chapman [1995] who suggested that the experimental design may not allow clear-cut predictions on mussel-fucoid interactions). Further work by Lubchenco (1978, 1982, 1983, 1986, Lubchenco & Menge 1978) suggested that annual algae (e.g. *Enteromorpha* sp., *Ulva* sp.) are next in the competitive hierarchy. They can outcompete perennial algae (*Fucus vesiculosus*, *Chondrus crispus*) at the recruitment stage, but usually do not invade a closed *Fucus* canopy (Lubchenco 1986). If herbivores are removed experimentally, *Fucus* colonization is greatly reduced by competition from annual algae. Thus predators (controlling mussels) and herbivores (controlling annual algae) indirectly maintain successful recruitment of *Fucus* which becomes the dominant species on most rocky shores (Fig. 9.1 B).

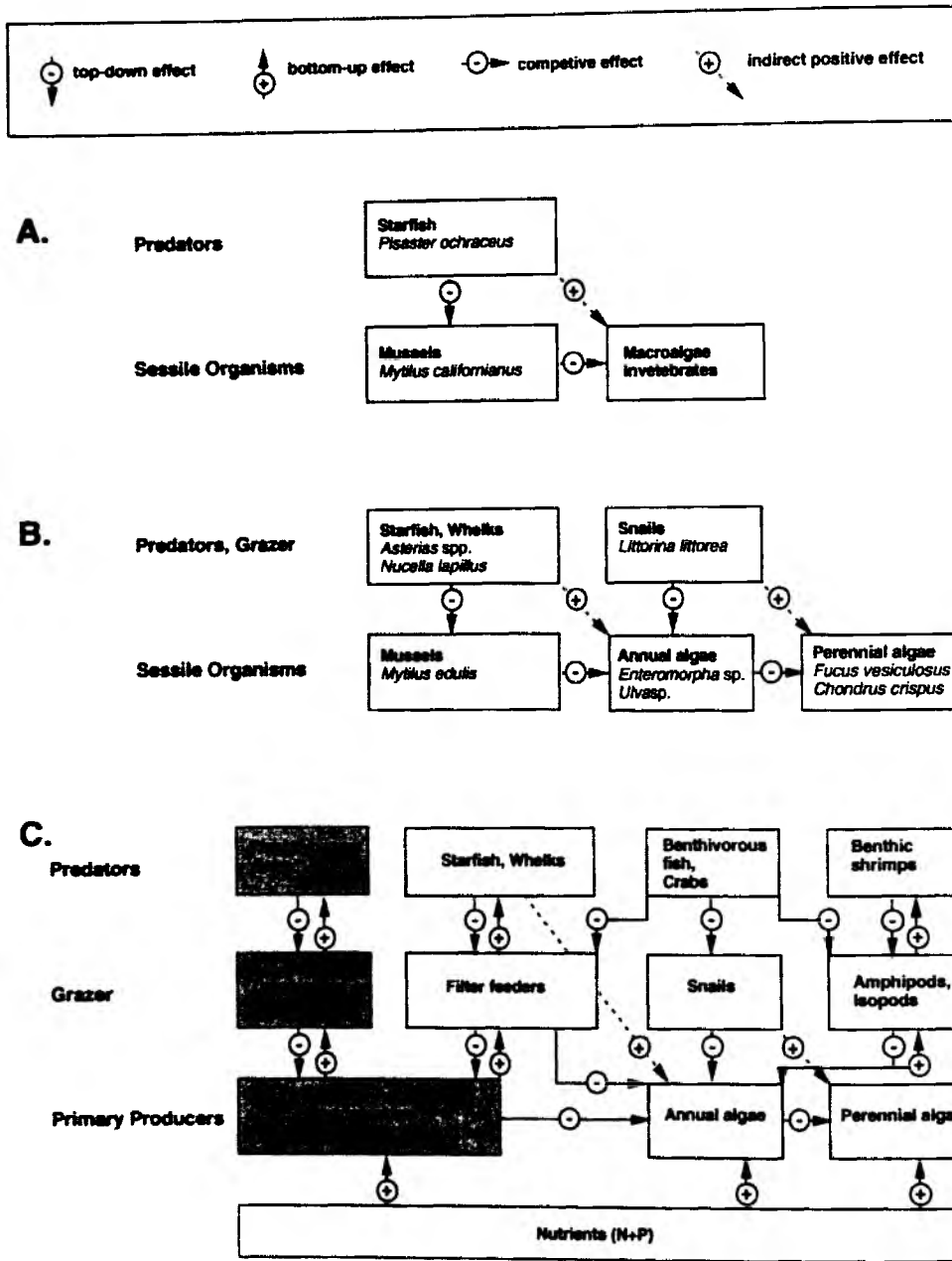


Fig. 9.1. A conceptual model of strong interactions in rocky shore food webs: (A) Paine's original predator model. Seastars control mussels and prevent competitive exclusion of macroalgae and various sessile invertebrates. (B) Menge-Lubchenco model for New England rocky shores. Starfish and whelks control mussels, snails control annual algae and indirectly maintain *Fucus* on the mid shore and *Chondrus* on the low shore level. (C) Integrated model synthesizing results from this and previous studies. Pelagic food-web components (gray boxes) are included to demonstrate benthic-pelagic coupling. This model has 4 new elements: (1) Nutrient enrichment counteracts the effects of grazing on all primary producers. (2) Nutrient effects are transmitted to higher trophic levels. (3) Predators can reduce grazer densities and indirectly favor algae. (4) Benthic-pelagic coupling occurs through interactions between phytoplankton, filter feeders and macroalgae. See text for details and references.

In the Baltic Sea, I found that *Fucus* recruitment could be predicted from the cover of annual algal during the time of *Fucus* reproduction. This relationship seemed quite robust since it was corroborated independently by two small-scale field experiments (Chapter 5, 6) and by large-scale field surveys (Chapter 8). Grazers were important in controlling annual algal cover and exclusion of grazers indirectly reduced *Fucus* recruitment. This model of plant-grazer interactions was corroborated by a positive correlation between the density of gastropod grazers with *Fucus* cover across the Baltic Sea (Chapter 8). These results are completely in line with the Menge-Lubchenco model for New England (Fig. 9.1 B). In addition, I found that bottom-up factors such as nutrient and propagule supply can be equally important as consumer effects for the regulation of perennial-annual algal competition. Similar conclusions were reached for the phytoplankton-mussel-predator food chain (Menge et al. 1997, 1999) and for pelagic food webs in the ocean (Micheli 1999) and in lakes (Sommer 1988, Carpenter et al. 1996, Brett & Goldman 1997). To account for these mechanisms, I expanded the Paine and Menge-Lubchenco models into a conceptual model of nutrient-algae-grazer-predator interactions (Fig. 9.1 C). Three new elements are included in this model:

- (1) Nutrient enrichment counteracts the effects of grazing on primary producers (phytoplankton, annual algae, perennial algae). Among the producers, phytoplankton has the highest nutrient uptake and growth rates but also the highest loss rates to grazing (Duarte 1995). Annual algae have intermediate growth and loss rates, perennial algae have low growth and loss rates (growth versus resistance trade-off, Littler & Littler 1980, Steneck & Dethier 1994). A dynamic balance of nutrient supply and grazing pressure maintains coexistence of these primary producers. Observations and experiments indicate that eutrophication can tilt this balance by favoring fast-growing species (Sand-Jensen & Borum 1991, Neckles et al. 1993, Duarte 1995, Hauxwell et al. 1998, Worm et al. 1999, Lotze et al. 2000). In a predictable sequence, perennial algae are outcompeted by annual algae through recruitment inhibition and epiphyte shading. Attached annual algae become outcompeted by free-floating macroalgae and phytoplankton, which are more efficient competitors for light (Fong et al. 1993). Nutrient limitation thus shifts to light limitation of primary productivity along an eutrophication gradient (Duarte 1995).
- (2) Nutrient effects can be transmitted to higher trophic levels. Thereby, some effects of eutrophication may be delayed or prevented by increases in grazer densities or grazing pressure. In Maasholm for example, phytoplankton, perennial and annual algae coexist under high nutrient loading. In comparison with 24 other sites in the Baltic, Maasholm had the highest cover of perennial algae and the second-highest grazer density. Experiments demonstrated that grazer densities at Maasholm are sufficiently high to control annual algae. Increases in annual algae stimulated by nutrient enrichment were followed by increases in crustacean (but not gastropod) grazers and crustacean predators in the Baltic (Chapter 3, 6) and also in the NW

Atlantic experiment (Chapter 7). Grazers may compensate the effects of eutrophication at some sites but not at others: of 8 nutrient-rich sites in the NW Atlantic, 4 showed increases and 4 showed decreases in grazer densities compared with nutrient-poor sites. The reasons for decreasing grazer densities with increasing nutrient supply and algal biomass are unclear (Hauxwell et al. 1998). Possibly, the foraging efficiency of snails is reduced in dense canopies of filamentous algae. Several crustacean grazers depend on perennial macrophytes as a habitat (Salemaa 1987) and may decline when perennial algae become outcompeted by fast-growing annuals. Finally, grazers are susceptible to low oxygen levels in the vicinity of decomposing macroalgal mats (Valiela et al. 1997).

- (3) Predators can reduce grazer densities and indirectly favor the algae. I found evidence for such a trophic cascade during summer in the Baltic where all grazer populations crashed simultaneously when crabs and shrimps became seasonally abundant. As a consequence, annual algae (mainly *Enteromorpha* sp.) increased in abundance. Similarly, Lubchenco (1978) observed that tide pools with crabs (*Carcinus maenas*) present, had high *Enteromorpha* cover and low grazer densities. However, I found no evidence for effects of predators on grazers at various sites in the NW Atlantic. Thus, the generality of this phenomenon is unclear. In contrast, cascading effects of predators are well documented for freshwater pelagic and benthic food webs (Carpenter et al. 1985, Power 1990, Brett & Goldman 1997). Also, predators such as fish, birds, mammals and parasitic amoebas caused trophic cascades on rocky shores where sea urchins were the dominant grazers (Elner & Vadas 1990, Wootton 1995, Estes et al. 1998, Sala et al. 1998). In contrast, in marine pelagic webs nutrients control algal growth and fish can control zooplankton abundance but there is so far little evidence for cascading effects (Micheli 1999).
- (4) Benthic-pelagic coupling occurs through interactions among phytoplankton, filter feeders and macroalgae. Numerous observations suggest that one important mechanism for the decline of macrophytes in eutrophied waters is light competition by phytoplankton (Chapter 3, Kautsky et al. 1986, Sand-Jensen & Borum 1991, Duarte 1995). However, this interaction is probably less important in intertidal compared with subtidal habitats. In addition, there is an indirect effect of phytoplankton on macrophytes through increased abundance of filter feeders. Nutrient-rich sites usually have higher phytoplankton concentrations than nutrient-poor sites (lakes: Vollenweider & Kerekes 1982, ocean: Micheli 1999) High phytoplankton abundance can enhance filter feeder growth, recruitment and density, with negative effects on macroalgal cover (Chapter 8, Menge et al. 1997, 1999). However, these interactions appeared to be of little importance at Maasholm where filter feeder recruitment was generally low, even though adult mussels are common (Reusch 1998) and predators were excluded in the experiments. Possibly, larval supply was intercepted by local hydrographic conditions (Roughgarden et al. 1988). In Kiel Fjord, 60 km S of Maasholm, mussel recruit densities and growth rates are so high that

mussels can outgrow predation by sea stars, which occur at high densities (Reusch & Chapman 1995). Thus a dynamic balance of food-supply, larval supply and predation pressure may regulate filter feeder populations in a similar fashion as nutrient supply, propagule supply and grazing pressure regulate macroalgae (Fig. 9.1 C). Low abundance and recruitment of filter feeders in Bald Rock may be linked to generally low phytoplankton abundance and extremely low growth rates of mussels on the open Atlantic coast of Nova Scotia (Hunt 1997). This fact may explain why mussel-algal competition appears to play a minor role in structuring rocky shore food webs in Nova Scotia (Chapman 1995), in contrast to New England (Menge 1976, Lubchenco & Menge 1978) and the Pacific (Paine 1966, 1971).

In conclusion, the new model (Fig. 9.1 C) predicts that nutrient enrichment has both direct effects on growth rates of primary producers and their interactions as well as indirect effects mediated through increases in phytoplankton density and mussel cover, grazer and predator densities. Grazers have a key role in counteracting nutrient effects on fast-growing plant species. Declines of grazers through disturbance, habitat loss, predation or harvesting will likely exacerbate negative effects of eutrophication on perennial macrophytes (Neckles et al. 1993, Hauxwell et al. 1998, Worm & Lotze 2000).

Species diversity and ecosystem function

This study revealed that nutrient enrichment and eutrophication of nearshore ecosystems has severe impacts on species diversity and ecosystem functioning. In the Baltic Sea, experimental enrichment triggered blooms of annual algae which monopolized space, excluded other macroalgae and caused diversity to decline with enrichment (Fig. 9.2 A, gray bars). The exclusion of perennial fucoids in particular translated into reduced rates of carbon storage and nitrogen retention. In contrast, grazing increased species diversity (Fig. 9.2 B, gray bars), perennial recruitment, carbon storage and nitrogen retention. At a nutrient-poor site in the NW Atlantic, grazers reduced species diversity and nutrient enrichment increased diversity (Fig. 9.2 A, B, white bars). Also, grazer and nutrient effects on *Fucus* recruitment, carbon storage and nitrogen retention were reversed between the Baltic and NW Atlantic. Changing effects of nutrient enrichment on species diversity along productivity gradients were predicted by theory and verified by empirical data (Tilman 1982, Rosenzweig & Abramsky 1993, but see critique by Abrams 1995). Changing effects of grazers on plant species diversity have only recently been linked to nutrient supply and productivity (Proulx & Mazumder 1998). Can these two patterns productivity-diversity and grazer-diversity be merged into a predictive theory of plant species richness? Are productivity and grazing pressure correlated? It appears that these important questions are largely unexplored. One remarkable exception is Huston's (1979) "General hypothesis on species diversity". In order to predict species diversity along environmental gradients, Huston (1979) used traditional Lotka-Volterra competition models and modified these for non-equilibrium conditions.

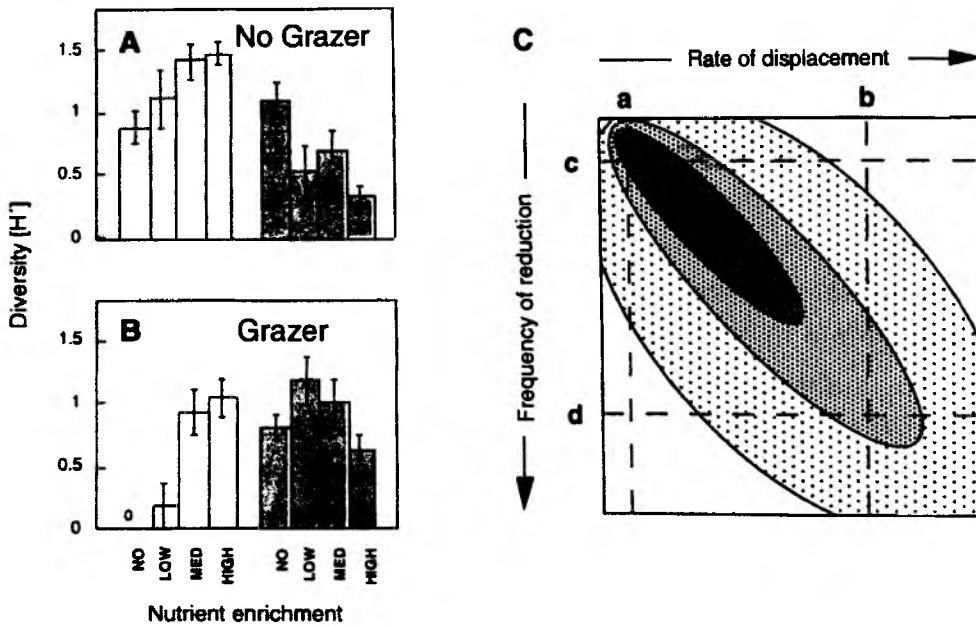


Fig. 9.2. Reversal of grazer and nutrient effects on plant diversity (Shannon-Weaver Index H') in the NW Atlantic (white) and Baltic (gray) experiments. (A) No grazers present. (B) Grazers present. (C) A general model of species diversity (altered, after Huston 1979) qualitatively predicts diversity patterns in the experiments. Increasing darkness indicates increasing species richness. The number of plant species that can coexist is determined by the rate of competitive displacement (which increases with nutrient enrichment) and the frequency of population reduction (which increases with grazing pressure). The hatched line transects (a-d) demonstrate predicted changes in species diversity when one parameter is held constant and the other one varied. See text for details.

In this model, competition, productivity and disturbance interact in shaping patterns of species diversity. The number of species that can coexist is determined (1) by the rate of competitive displacement (which is thought to be a function of population growth and productivity) and (2) the rate of population reduction through physical and biotic disturbance (Fig. 9.2 C). The model predicts that diversity is highest at low to intermediate productivity (preventing extinction of species which cannot grow at lowest resource levels) and low to intermediate disturbance (preventing competitive exclusion of inferior competitors). Changes in species diversity in my experiments are predicted remarkably well by this model. In the NW Atlantic (low productivity, low rate of displacement), species diversity declined with increasing grazing pressure (Fig. 9.2 A, B, white bars, transect a in Fig. 9.2 C). In the Baltic (high productivity, high rate of displacement) species diversity increased from low to high grazing (Fig. 9.2 A, B, gray bars, transect b in Fig. 9.2 C). At low grazing pressure, the model predicts rapid increases and then gradual decreases in diversity from low to high productivity (transect c), which happened in the experiments (Fig. 9.2 A). At high grazing pressure, the model predicts increases in diversity from low to intermediate

productivity and declines in diversity at highest productivity (transect d). Again this is what I found empirically (Fig. 9.2 B).

Importantly, the model of Huston (1979) states that an increase in productivity and growth rates (e.g. through eutrophication) can have an effect that is very similar to a corresponding decrease in disturbance frequency (e.g. through a decline of grazer populations). If disturbance frequency and productivity increase or decrease together, diversity could remain unchanged. This is exactly what I found when I manipulated productivity (through nutrient enrichment) and disturbance (through grazing) alone and in combination. A terrestrial example comes from the early work of Milton (1940, 1947) who manipulated fertilizer load and the intensity of grazing and mowing on pastures in Wales. In his study, fertilization increased the rate of competitive exclusion while grazing and mowing prevented competitive exclusion and subsequent loss of species.

Outlook

For contemporary ecology, it becomes increasingly important to merge theoretical and applied question in order to provide useful ecological information for management and conservation (Vitousek 1994, Ehrlich 1997, Olson 1998, Lubchenco 1998). My work which had started from a theoretical perspective (regulation of benthic food webs) changed when I realized that humans represent a dominant ecological force in aquatic ecosystems through the influences of eutrophication and harvesting (Vitousek et al. 1997a, b, Pauly et al. 1998, Micheli 1999). My work has led me to believe that a mechanistic understanding of these processes is a prerequisite for successful management of coastal ecosystems. I suggest the following topics for future research:

- (1) **Multiple human influences.** From my work I concluded that harvesting of grazers and perennial algae may exacerbate the effects of eutrophication in coastal ecosystems (Worm & Lotze 2000). Moreover, eutrophication can magnify the effects of certain toxins in littoral food webs (Breitburg et al. 1999). Such synergistic interactions among two or more human influences may occur in the wake of increasing use and alteration of coastal ecosystem (Worm & Lotze 2000). Co-occurring influences in coastal systems include harvesting of multiple trophic levels (Pauly et al. 1998), species introductions (Carlton & Geller 1993, Cohen & Carlton 1998, Reusch & Williams 1998, 1999), habitat fragmentation (Harvey et al. 1998, Reusch & Williams 1999), nutrient and toxic pollution (Carpenter et al. 1998, Breitburg et al. 1999), and climate change (IPCC 1995, Petchey et al. 1999). The frequency of strong interactions among these influences is unknown. Moreover, it is not clear whether the response of a coastal system to a novel influence depends on the history of previous alterations. From the study of ecological invasions it appears that the rate of novel invasions is positively correlated with the number of established invaders ("invasional meltdown hypothesis", Cohen & Carlton 1998, Ricciardi &

MacIsaac 2000). If this is true for other human influences, managers need this information in order to predict impacts of multiple uses of coastal systems.

- (2) Modeling the dynamic behavior of littoral ecosystems. Conceptual models such as those presented in Fig. 9.1 increase our understanding of regulatory mechanisms but allow only limited predictions about the dynamic behavior of a system. Mathematical models can reveal the dynamic behavior of ecological systems but represent only hypotheses that need to be tested with empirical data (van de Koppel 1997). I suggest that increased cooperation between empiricists and ecological modelers is necessary in order to test complex ecological concepts across relevant spatial and temporal scales. The following questions may be of particular interest: Is the behavior of complex food webs predictable? Are there multiple stable states that are stabilized by positive feedbacks? Observations and experiments indicated that a fucoid canopy, an *Enteromorpha* turf and a mussel monoculture are alternative states of rocky shore communities that occur under different nutrient, grazing and predation regimes. It is not clear, whether these states are more stable than mixtures between them and whether there are feedback mechanisms that accelerate or prevent the shift from one state to another. As an overall goal I propose to develop and test a model that reveals changes in rocky shore community structure under different magnitudes and combinations of human influences.
- (3) The relationship between diversity, stability and ecosystem function. Whether there are mechanistic links between species diversity, ecosystem stability and ecosystem functioning (mostly productivity, nutrient cycling) is one of the most fundamental questions in ecology (Darwin 1859, Elton 1958, McNaughton 1977, Schulze & Mooney 1993, Tilman 1999). Evidence from grassland communities and microbial model ecosystems suggests that these links exist (reviewed by Johnson et al. 1996, Tilman 1999), although there is dispute whether a large number of species *per se* or the composition of the community is more important (Hooper & Vitousek 1997, Huston 1997). For hardbottom communities in the Baltic, I found that the loss of diversity always included loss of *Fucus*, which was a key element because it was the only canopy-forming perennial alga. Subsequent declines in ecosystem function could not be clearly related to either changes in diversity or species composition. Explicit tests of the diversity-stability-functioning hypothesis in aquatic ecosystems are lacking and provide an exciting research opportunity for marine ecologists.

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Species list

Alphabetical list all species of algae and animals found associated with rocky substrata at the two main study sites Bald Rock (NW Atlantic=A) and Maasholm (Baltic=B). Relative abundance is indicated by symbols as follows: o= rare, +=common, ++=abundant, +++=dominant. Other species that were mentioned in this thesis but occurred only in the Eastern Baltic (=EB) are listed without reference to their abundance. Algae after South & Tittley (1986) and Nielsen et al. (1995), invertebrates after Hayward & Ryland (1995), Stresemann (1992) and Brinkhurst et al. (1976).

List A: Algae

Species and Authority	Class	Order	Abundance
<i>Acrothrix gracilis</i> Kylin	Phaeophyceae	Chordariales	A+
<i>Audouinella</i> sp. Bory	Phaeophyceae	Nemaliales	A+
<i>Ascophyllum nodosum</i> (L.) Le Jolis	Phaeophyceae	Fucales	A+++
<i>Berkeleya micans</i> (Lyngbye) Grunow	Bacillariophyceae	Naviculales	A+
<i>Berkeleya rutilans</i> (Trent. ex Roth) Grunow	Bacillariophyceae	Naviculales	A+ B++
<i>Blidingia minima</i> (Naeg. ex Kütz.) Kylin	Chlorophyceae	Ulvaes	B o
<i>Bryopsis plumosa</i> (Hudson) J Agarth	Chlorophyceae	Bryopsidales	A o
<i>Callithamnion tetragonum</i> (With.) SF Gray	Rhodophyceae	Ceramiales	A+
<i>Ceramium nodulosum</i> (Lightf.) Ducluz.	Rhodophyceae	Ceramiales	A+ B o
<i>Ceramium strictum</i> Harvey	Rhodophyceae	Ceramiales	B++
<i>Chaetomorpha linum</i> (OF Müll.) Kuetz.	Chlorophyceae	Cladophorales	A o B+
<i>Chondrus crispus</i> Stackhouse	Rhodophyceae	Gigartinales	A o
<i>Chorda filum</i> (L.) Stackhouse	Phaeophyceae	Laminariales	A o
<i>Cladophora glomerata</i> (L.) Kuetz.	Chlorophyceae	Cladophorales	EB
<i>Cladophora rupestris</i> (L.) Kuetz.	Chlorophyceae	Cladophorales	A+ B+
<i>Corallina officinalis</i> Linnaeus	Rhodophyceae	Corallinales	A+
<i>Dumontia contorta</i> (S Gmelin) Rupr.	Rhodophyceae	Cryptonemial.	A+ B++
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngb.	Phaeophyceae	Ectocarpales	A+ B o
<i>Enteromorpha clathrata</i> (Roth) Grev.	Chlorophyceae	Ulvaes	B+
<i>Enteromorpha intestinalis</i> (L.) Link	Chlorophyceae	Ulvaes	A o B++
<i>Enteromorpha prolifera</i> (OF Müll.) J Agarth	Chlorophyceae	Ulvaes	B+
<i>Elachista fucicola</i> (Vellay) Aresch.	Phaeophyceae	Ectocarpales	A o B o
<i>Eudesme virescens</i> (Carmich.) J Agarth	Phaeophyceae	Chordariales	A+

Species and Authority	Class	Order	Abundance
<i>Furcellaria lumbricalis</i> (Huds.) Lamouroux	Rhodophyceae	Gigartinales	EB
<i>Fucus spiralis</i> Linnaeus	Phaeophyceae	Fucales	A++
<i>Fucus vesiculosus</i> Linnaeus	Phaeophyceae	Fucales	A+++ B+++
<i>Licmophora abbreviata</i> CA Agarth	Bacillariophyceae	Licmophorales	B++
<i>Licmophora paradoxa</i> (Lyngbye) CA Agarth	Bacillarioph.	Licmophorales	A+
<i>Melosira moniliformis</i> (OF Müll.) CA Agarth	Bacillarioph.	Melosirales	B++
<i>Petalonia fascia</i> (OF Müll) O Kuntze	Phaeophyceae	Dictyosiphon.	A+ B++
<i>Pilayella littoralis</i> (L.) Kjellm.	Phaeophyceae	Ectocarpales	A++ B+++
<i>Polysiphonia lanosa</i> (L.) Tandy	Rhodophyceae	Ceramiales	A o
<i>Polysiphonia violacea</i> (Roth) Sprengel	Rhodophyceae	Ceramiales	B+
<i>Rhizoclonium riparium</i> (Roth) Kütz. ex Harvey	Chloroph.	Cladophorales	A+
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Phaeophyceae	Dictyosiphon.	A+ B+
<i>Sphaerotrichia divaricata</i> (Agarth) Kylin	Phaeophyceae	Chordariales	A+
<i>Spongomorpha arcta</i> (Dillwyn) Kütz.	Chlorophyceae	Acrosiphonal.	A o
<i>Ulothrix flacca</i> (Dillwyn) Thuret in Le Jol.	Chlorophyceae	Ulotrichales	A++ B++
<i>Ulva lactuca</i> Linnaeus	Chlorophyceae	Ulvales	A+
<i>Ulvopsis grevillei</i> (Thuret) Gayral	Chlorophyceae	Ulvales	A+ B++

List B: Animals

Species and Authority	Class	Order	Abundance
<i>Asterias vulgaris</i> Linnaeus	Asteroidea	Forcipulata	A o B o
<i>Balanus crenatus</i> Brugière	Crustacea	Thoracica	A+
<i>Balanus improvisus</i> Darwin	Crustacea	Thoracica	B+
<i>Carcinus maenas</i> Linnaeus	Crustacea	Decapoda	A++ B++
<i>Crangon crangon</i> Linnaeus	Crustacea	Decapoda	A o B+
<i>Electra pilosa</i> Linnaeus	Bryozoa	Eurystomata	A o B+
<i>Gammarus locusta</i> Linnaeus	Crustacea	Amphipoda	B+
<i>Gammarus oceanicus</i> Segerstrale	Crustacea	Amphipoda	A+ B+
<i>Gammarus salinus</i> Linnaeus	Crustacea	Amphipoda	B+
<i>Gammarus zaddachi</i> Sexton	Crustacea	Amphipoda	B+
<i>Gobius niger</i> Linnaeus	Actinopterygii	Perciformes	B+
<i>Hydrobia ulvae</i> Pennant	Gastropoda	Monotocardia	B+
<i>Idotea baltica</i> Pallas	Crustacea	Isopoda	A o B+

Species and Authority	Class	Order	Abundance
<i>Idotea chelipes</i> Pallas	Crustacea	Isopoda	B++
<i>Jaera albifrons</i> Leach	Crustacea	Isopoda	B+
<i>Lacuna vincta</i> Montagu	Gastropoda	Monotocardia	A o
<i>Larus argentatus</i> Pont.	Aves	Lariformes	A+ B+++
<i>Larus marinus</i> Linnaeus	Aves	Lariformes	A++ B o
<i>Littorina littorea</i> Linnaeus	Gastropoda	Monotocardia	A+++ B+
<i>Littorina obtusata</i> Linnaeus	Gastropoda	Monotocardia	A+
<i>Littorina saxatilis</i> Linnaeus	Gastropoda	Monotocardia	A+ B+++
<i>Modiolus modiolus</i> Linnaeus	Bivalvia	Filibranchiata	A o
<i>Mysis stenolepis</i> Lilljeborg	Crustacea	Mysidacea	A++
<i>Mytilus edulis</i> Linnaeus	Bivalvia	Filibranchiata	A o B+
<i>Palaemon adspersus</i> Rathke	Crustacea	Decapoda	B++
<i>Phalacrocorax auritus</i> Less.	Aves	Pelecaniformes	A+
<i>Pholis gunnellus</i> Linnaeus	Actinopterygii	Perciformes	A o
<i>Pollachius virens</i> Linnaeus	Actinopterygii	Gadiformes	A o
<i>Pomatoschistus minutus</i> Pallas	Actinopterygii	Perciformes	B+
<i>Tectura testudinalis</i> Müller	Gastropoda	Diotocardia	A+
<i>Theodoxus fluviatilis</i> Linnaeus	Gastropoda	Diotocardia	EB
<i>Semibalanus balanoides</i> Linnaeus	Crustacea	Thoracica	A+
<i>Spinachia spinachia</i> Linnaeus	Actinopterygii	Gasterosteiformes	B o
<i>Zoarces viviparus</i> Linnaeus	Actinopterygii	Perciformes	B o

NOTE: "*Mytilus edulis*" may be *M. edulis* or *M. trossulus* (Gould). These species are not reliably distinguishable using morphological criteria.