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Population dynamics an species interactions in macroalgal blooms: abiotic versus biotic control at different life-cycle stages

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The rates, scales, kinds, and combinations of changes occurring now are fundamentally different from those at any other time in history; we are changing Earth more rapidly than we can understand it. [...] In a very real sense, the world is in our hands - and how we handle it will determine its composition and dynamics, and our fate.

P.M. Vitousek, H.A. Mooney, J. Lubchenco, J.M. Melillo (1997)

Contents

Glossary

A	Appendix, used in table and figure numerations (e.g. Tab. A5.1, Fig. A7.1) indicating that this table or figure can be found in the Appendix
α	Initial slope = V_{max}/K_m of nutrient uptake kinetic
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
d	Day(s)
DW	Dry weight
GeO_2	Germanium dioxide
h	Hour(s)
K_m	Half saturation constant of nutrient uptake kinetic
L:D	Light : dark rhythm
min	Minute(s)
PAR	Photosynthetically active radiation (400-700 nm)
PES	Provasoli enriched seawater, a growth medium
RGR	Relative growth rate
SA/V-ratio	Surface area to volume ratio
standard T/L-conditions	Standard temperature and light conditions: 15°C, 100 µmol photons $m^{-2}s^{-1}$, 14:10 L:D
V_{max}	Maximal uptake rate of nutrient uptake kinetic
wk	Week(s)
WW	Wet weight

Abstract

The structure and diversity of marine benthic communities has changed over the last decades in the course of increasing eutrophication. Most visibly, mass blooms of opportunistic fast-growing macroalgae now occur frequently in eutrophicated coastal waters worldwide. These blooms clearly threaten biodiversity and functioning of nearshore ecosystems by harming or destroying the perennial vegetation and epi- and endobenthic fauna. Despite numerous reports on the occurrence and consequences of macroalgal blooms, a causal understanding of this phenomenon is still fragmentary. Although the view of a broad positive correlation between macroalgal blooms and nutrient loads is generally accepted, the great variability in extent, distribution and composition of these blooms can not be explained or predicted with the existing knowledge. The main objective of my study was to provide a mechanistic understanding of interacting abiotic and biotic factors that control population development and species dominance patterns within macroalgal blooms.

Most previous studies have focused only on the ecophysiological traits of adult algae in relation to increased nutrient loading. In this study, I provide tests of the hypotheses that (I) factors controlling early life-cycle stages may be of equal or greater importance than factors affecting adult organisms and (II) competition and herbivory, in addition to abiotic conditions, are predominant factors controlling the initiation, development, extent, and species composition of macroalgal blooms. I focused on two common cosmopolitan macroalgae which co-occur in the Baltic Sea (the study area), *Pilayella littoralis* (Phaeophyceae) and *Enteromorpha* spp. (Chlorophyceae). I studied (1) the phenology of propagules, germlings and adults, (2) the initiation of blooms by overwintering and germination of early life stages, (3) growth and nutrient kinetics of adult stages, (4) the relative effects of four herbivore species on early life stages and adult algae. Finally, to provide a conceptual synthesis, I studied (5) the combined effects of recruitment, nutrient enrichment, and herbivory on population development and competitive interactions in *Pilayella* and *Enteromorpha*.

In field observations from 1995-1998, I found a sharp difference between *Enteromorpha* spp. and *Pilayella littoralis* populations. *Enteromorpha* showed a very long and intense reproductive period over 7 months with peak densities of 60 million settling propagules $m^{-2}d^{-1}$ and continual supply with germlings covering 20-40% of hard substratum from April to September. However, adult *Enteromorpha* achieved only a minor amount of biomass.

Pilayella achieved a 10- to 30-fold higher biomass during blooms (up to 15 g DW m^{-2}) despite a shorter (only 2-3 months) and less intense reproductive period (only 25% peak propagule density) than *Enteromorpha*. In both species, population development originated from overwintering microscopic forms in a propagule bank comparable to a terrestrial seed bank. Within this propagule bank, *Enteromorpha* was 10- to 50-fold more abundant (up to 330 individuals germinating cm^{-2}) than *Pilayella*. However, germlings and adults of *P. littoralis* appeared one month before *Enteromorpha* spp. in the field. I showed experimentally that this difference in timing of population development can be explained by the species-specific ecophysiological constraints of early life stages. *P. littoralis* germinated at 5°C whereas *Enteromorpha* spp. required 10° or 15°C for germination. Temperature was the most important factor controlling germination in early spring, followed by light intensity and day length. In addition, nutrient supply influenced germination rate. Single and combined enrichment with nitrate and phosphate increased germination rate in both species, changing from P-limitation in early spring to N-limitation in summer.

Significant differences in the ecophysiology of early life stages of *Enteromorpha* and *Pilayella* were not observed in adults of the two species. In growth experiments with similar designs to germination tests, adult stages of the two species performed very similarly in relation to temperature, light, and nutrient enrichment. In addition, no differences in nutrient uptake kinetics were observed despite obvious morphological differences. The finely branched thallus of *Pilayella littoralis* has a 10-fold surface area to volume ratio and thus a greater metabolically active area compared to the foliose thallus of *Enteromorpha intestinalis*. In both species, uptake of nitrate, ammonium, and phosphate was strongly time dependent with highest uptake rates in the first 15-30 min indicating the ability of fast responses to nutrient pulses in the environment.

Taken together, timing and rate of germination and not productivity of adults appeared to be the ecophysiological bottleneck for the initiation of macroalgal mass development in spring. However, further discrepancies in population development of *Enteromorpha* and *Pilayella* in the field can not be explained through ecophysiological properties alone.

Feeding experiments in the laboratory as well as in the field showed that crustacean and gastropod mesoherbivores (*Idotea chelipes*, *Gammarus locusta*, *Littorina saxatilis*, *L. littorea*) strongly consumed *Enteromorpha* and *Pilayella* as germlings (64-86% reduction of germling density cm^{-2} within 14 d in the field) and adults (8-12% thallus loss d^{-1} in the field).

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Enteromorpha was the preferred food source over *Pilayella* at all life stages. Interestingly, the relative effects of individual herbivore species varied with algal life stage indicating the importance of a diverse herbivore guild for an effective control of bloom-forming algae. Thus, in addition to ecophysiological constraints, herbivores, if present, play a decisive role in controlling macroalgal mass developments.

As a synthesis, I performed a factorial field experiment from February to December 1997 where I studied the combined effects of recruitment from a propagule bank (dormancy) versus recruitment from newly generated propagules (dispersal), herbivory, and nutrient enrichment on population development of bloom-forming macroalgae. Complex interactions among the treatment factors occurred and clearly determined the outcome of space competition between *Enteromorpha*, *Pilayella* and other macroalgal species. In early spring, initiation of population development was controlled by abiotic factors which determined timing and rate of germination out of the propagule bank. Despite the advantage of germination at lower temperatures in *Pilayella, Enteromorpha* first dominated all substrata through massive recruitment from the propagule bank. This pattern was drastically altered when herbivores became active in late April, indirectly favoring *Pilayella* and other macroalgae by selective consumption of *Enteromorpha.* In herbivore exclusion plots, however, *Enteromorpha* completely dominated the substratum, preventing all other algae from colonizing. When the propagule bank was excluded by sterilization of the substratum, recruitment depended on new reproduction which started in May. At this time, herbivores were already active, preventing *Enteromorpha* from colonizing thereby favoring *Pilayella* dominance. Coexistence of both species and other macroalgae occurred if both propagule bank and herbivory were left unmanipulated, whereas the propagule bank favored *Enteromorpha* and herbivory favored *Pilayella.* Continual low-level nutrient enrichment was introduced as an additional factor from June to September when ambient nutrient pools were largely depleted. Enrichment had minor effects on adult populations. However, new recruitment of *Enteromorpha* and *Pilayella* in summer was strongly enhanced by nutrient enrichment and even overcompensated massive losses by herbivory. Both relative effects of nutrients and herbivory on recruitment were more pronounced in *Enteromorpha.* I conclude that herbivores may effectively control mass-blooming macroalgae but that nutrient enrichment can override this control mechanism. In summary, abiotic control in early spring

shifted to a combined biotic and abiotic control of macroalgal mass blooms in late spring and summer, a pattern which is paralleled in plankton and terrestrial plant assemblages.

In conclusion, the results of my study indicate that the extent of macroalgal blooms and species dominance patterns within blooms depend on interactions of abiotic and biotic factors controlling early life stages at the beginning of the vegetation period. The importance and ecological role of a dormant propagule bank as well as the life-stage specific ecophysiological and ecological traits of mass-occurring algae were established in this study for the first time. My results closely mirror patterns of overwintering of seeds, germination control, seed and seedling predation within terrestrial plant communities. I propose that an understanding of processes that affect early life stages is indispensable in explaining population dynamics, aspects of community structure and important human-induced changes in plant-dominated ecosystems. In addition, my results strongly emphasize the importance of herbivore consumer diversity for an effective control of mass-occurring macroalgae at different life stages. To control macroalgal blooms and related problems it will be necessary to (1) reduce nutrient loads and (2) effectively conserve complete nearshore communities with their native food-web complexity and biodiversity.

Zusammenfassung

Die stetig zunehmende Nährstoffanreicherung (Eutrophierung) der Gewässer hat tiefgreifende Auswirkungen auf die komplexen Lebensgemeinschaften der Küsten und Schelfmeere. So wurden im Laufe der letzten Jahrzehnte weltweit Veränderungen in der Zusammensetzung mariner Benthosgemeinschaften registriert. Das stark vermehrte Auftreten von Massenblüten opportunistischer, schnell wachsender Makroalgen in eutrophierten Küstengewässern ist ein besonders problematisches Symptom. In vielen Meeresgebieten gefährden diese Blüten massiv die Biodiversität und die Funktion küstennaher Ökosysteme, indem sie die mehrjährige Vegetation und die epi- und endobenthische Fauna schädigen oder zerstören. Trotz zahlreicher Berichte über das Auftreten und die Folgen von Makroalgenblüten ist das kausale Verständnis dieser Phänomene gering. Es ist zwar allgemein akzeptiert, daß ein vermehrtes Auftreten von Makroalgenblüten mit den zunehmenden Nährstofffrachten korreliert ist, jedoch kann die große Variabilität im Ausmaß, der räumlichen und zeitlichen Verteilung und der Artenzusammensetzung dieser Blüten bisher nicht erklärt oder zuverlässig vorhergesagt werden. Das Hauptanliegen meiner Arbeit war, ein grundlegendes Verständnis der Populationsentwicklung massenblühender Makroalgen und ihrer Dominanzverhältnisse der Arten zu schaffen. Dabei stand die Frage im Vordergrund, in welcher Weise abiotische und biotische Faktoren bei der Steuerung von Massenblüten zusammenwirken.

Die meisten früheren Studien an massenblühenden Algen befaßten sich allein mit den ökophysiologischen Ansprüchen adulter Pflanzen. In dieser Arbeit habe ich zusätzlich die folgenden, zentralen Hypothesen geprüft: (I) frühe Lebensstadien (Sporen, Keimlinge) und Faktoren, welche die Entwicklung früher Stadien beeinflussen, steuern entscheidend den Verlauf von Massenblüten, und (II) zusätzlich zu den abiotischen Umweltbedingungen spielen biotische Wechselwirkungen wie Konkurrenz und Herbivorie eine zentrale Rolle für die Entwicklung, das Ausmaß und die Artenzusammensetzung von Makroalgenblüten. Ich habe mich dabei auf zwei besonders häufige, weltweit verbreitete Makroalgen konzentriert, *Pilayella littoralis* (Phaeophyceae) und *Enteromorpha* spp. (Chlorophyceae). Diese Arten kommen gemeinsam in der Ostsee (dem Untersuchungsgebiet) vor. Meine Untersuchungen umfaßten (1) eine quantitative Erfassung des jahreszeitlichen Vorkommens von Sporen, Keimlingen und adulten Algen, (2) Experimente zur Entstehung der Algenblüten aus

überwinternden und auskeimenden frühen Lebensstadien, (3) vergleichende Experimente zum Wachstum und zur Nährstoffkinetik adulter Stadien, (4) Studien zur Konsumption von Keimlingen und adulten Algen durch vier häufige Herbivore. Als Synthese führte ich (5) ein 10-monatiges Freilandexperiment durch, in dem ich die relative Bedeutung von Rekrutierungsprozessen, Herbivorie und der Verfügbarkeit von Nährstoffen auf die Populationsentwicklung von *Pilayella* und *Enteromorpha* und die Wechselwirkungen zwischen beiden Arten untersucht habe.

In Freilanduntersuchungen von 1995-1998 konnte ich deutliche Unterschiede in der Populationsentwicklung von *Enteromorpha* spp. und *Pilayella littoralis* feststellen. *Enteromorpha* zeigte eine intensive, 7-monatige Reproduktionsperiode mit maximalen Siedlungsdichten von 60 Millionen Sporen pro m^2 Substrat und Tag und einem daraus resultierenden kontinuierlichen Nachschub von Keimlingen, welche von April bis September 20-40% des verfügbaren Hartsubstrates bedeckten. Adulte Stadien von *Enteromorpha* erreichten jedoch nur eine geringe Biomasse. Im Gegensatz dazu erlangte *Pilayella* eine 10- bis 30-fach höhere Biomasse während der Blüte (bis zu 15 g Trockengewicht pro m^2) trotz einer kürzeren (2-3 Monate) und weniger intensiven Reproduktionsperiode (nur 25% der Sporendichte) im Vergleich zu *Enteromorpha*. Beide Arten waren in ihrer Entwicklung auf eine Sporenbank aus überwinternden, mikroskopischen Stadien angewiesen. In dieser Sporenbank, die funktionell einer terrestrischen Samenbank vergleichbar ist, waren Sporen von *Enteromorpha* 10- bis 50-fach häufiger (bis zu 330 Individuen keimten pro cm^2) als Sporen von *Pilayella*. Keimlinge und Adulte von *P. littoralis* traten im Freiland einen Monat früher auf als *Enteromorpha* spp. In vergleichenden Experimenten konnte ich zeigen, daß dieser Unterschied im zeitlichen Verlauf der Populationsentwicklung mit artspezifischen, ökophysiologischen Ansprüchen der frühen Lebensstadien zu erklären ist. *P. littoralis* keimte bei 5°C aus, während *Enteromorpha* spp. 10° bis 15°C zum Auskeimen benötigte. Wassertemperatur war der wichtigste Steuerfaktor für die Auskeimung zu Beginn des Frühjahrs, gefolgt von Lichtintensität und Tageslänge. Zusätzlich wurde die Auskeimrate von der Nährstoffverfügbarkeit beeinflußt. Eine alleinige oder kombinierte Anreicherung mit Nitrat und Phosphat steigerte die Auskeimrate beider Arten, wobei eine P-Limitation zu Beginn des Frühjahrs zu einer N-Limitation im Sommer wechselte.

Interessanterweise konnte ich die deutlichen ökophysiologischen Unterschiede zwischen frühen Lebensstadien von *Enteromorpha* und *Pilayella* nicht zwischen den adulten Stadien

beider Arten beobachten. In Wachstumsexperimenten mit analogem Versuchsaufbau zu den Keimungsexperimenten verhielten sich die adulten Stadien der beiden Arten sehr ähnlich in Bezug auf Temperatur, Licht und Nährstoffanreicherung. Trotz sehr unterschiedlicher Morphologie der Adulten zeigten sich auch beim Vergleich der Nährstoffkinetiken keine Unterschiede. Der feinverzweigte Thallus von *Pilayella littoralis* hat ein 10-fach größeres Oberflächen : Volumenverhältnis und damit eine größere metabolisch aktive Oberfläche verglichen mit dem flächigen Thallus von *Enteromorpha intestinalis*. Bei beiden Arten war die Aufnahme von Nitrat, Ammonium und Phosphat gleichermaßen zeitabhängig mit höchsten Aufnahmeraten in den ersten 15-30 Minuten. Dies ermöglicht beiden Arten eine schnelle Reaktion auf kurze Nährstoffpulse in der Umgebung.

Zusammenfassend scheinen der saisonale Zeitpunkt der Keimung und die Keimungsrate der ökophysiologische Engpaß für die Entstehung einer Massenblüte im Frühjahr zu sein und nicht die Produktivität der adulten Stadien. Die weitere, große Diskrepanz in der Populationsentwicklung von *Enteromorpha* und *Pilayella* im Freiland konnte jedoch nicht allein mit ökophysiologischen Eigenschaften der Arten erklärt werden.

Fraßexperimente im Labor und im Freiland zeigten, daß herbivore Asseln, Flohkrebse und Schnecken (*Idotea chelipes, Gammarus locusta, Littorina saxatilis, L. littorea*) in starkem Maße Keimlinge von *Enteromorpha* und *Pilayella* (64-86% Reduktion der Keimlingsdichte pro cm^2 innerhalb von 14 Tagen im Freiland) und Adulte (8-12% Thallusverlust pro Tag im Freiland) konsumierten. *Enteromorpha* wurde stets bevorzugt gefressen. Dabei wurden die verschiedenen Lebensstadien der beiden Algen in unterschiedlichem Ausmaß von den verschiedenen herbivoren Arten kontrolliert. Aufgrund solcher komplementären Effekte mag eine artenreiche Gilde von Herbivoren eine effektive Kontrolle von massenblühenden Algen erzielen. Somit können herbivore Konsumenten, zusätzlich zu abiotischen Umweltfaktoren eine entscheidende Rolle in der Kontrolle von Massenentwicklungen von Makroalgen spielen.

Als Synthese führte ich ein mehrfaktorielles Freilandexperiment durch, in dem ich die relative Bedeutung der Sporenbank ("dormancy") versus dem Anteil neu produzierter Sporen ("dispersal"), sowie die Bedeutung von Herbivorie und Nährstoffanreicherung auf die Populationsentwicklung massenblühender Algen untersuchte. Hierbei traten komplexe Wechselwirkungen zwischen den experimentellen Faktoren auf. Diese Wechselwirkungen zeigten deutliche Auswirkungen auf das Ergebnis der Konkurrenz zwischen *Pilayella*, *Enteromorpha* und weiteren Algenarten um das nur limitiert zur Verfügung stehende Substrat.

Im zeitigen Frühjahr wurde der Beginn der Populationsentwicklung von abiotischen Faktoren kontrolliert, welche den Zeitpunkt und die Rate der Auskeimung aus der Sporenbank bestimmten. Trotz des Auskeimvorteils von *Pilayella* bei tieferen Temperaturen dominierte zunächst *Enteromorpha* aufgrund der hohen Abundanz in der Sporenbank das verfügbare Substrat. Dieses Muster wurde Ende April durch die zunehmende Aktivität der Herbivoren drastisch verändert. Durch selektiven Wegfraß von *Enteromorpha* wurde *Pilayella* indirekt gefördert. Waren Herbivore experimentell ausgeschlossen, dominierte *Enteromorpha* das gesamte Substrat, was die Ansiedlung anderer Algen verhinderte. Wurde die Sporenbank durch Sterilisation eliminiert, hing die Entwicklung der Algen von der neuen Reproduktion ab, welche im Mai begann. Zu diesem Zeitpunkt waren die Herbivoren bereits aktiv, was die Ansiedlung von *Enteromorpha* unterdrückte und dadurch die Dominanz von *Pilayella* förderte. Eine Koexistenz der beiden Arten und weiterer Makroalgen war möglich, wenn sowohl die Sporenbank als auch Herbivore unmanipuliert blieben, wobei die Sporenbank *Enteromorpha* und die Herbivoren *Pilayella* begünstigten. Als zusätzlicher Faktor wurden von Juni bis September kontinuierlich Nährstoffe auf niedrigem Niveau angereichert. In dieser Zeit sind die Nährstoffvorräte in der freien Wassersäule weitgehend aufgezehrt. Auf die adulten Populationen hatte diese Anreicherung nur geringe Auswirkungen. Die Auskeimung neu angesiedelter Sporen von *Enteromorpha* und *Pilayella* wurde jedoch durch die Nährstoffanreicherung deutlich gesteigert, so daß massive Verluste durch Wegfraß kompensiert werden konnten. Dabei zeigten die Nährstoffanreicherung und Herbivore deutlich stärkere Effekte auf *Enteromorpha*. Aus diesen Ergebnissen schließe ich, daß herbivore Konsumenten massenblühende Makroalgen effektiv kontrollieren können, daß jedoch eine Erhöhung der Nährstofffrachten diesem Kontrollmechanismus entgegenwirkt. Zusammenfassend wurde deutlich, daß die abiotische Kontrolle von Makroalgenblüten zu Beginn des Frühjahrs zu einer kombinierten abiotischen und biotischen Kontrolle im späten Frühjahr und im Sommer wechselt, ein Muster, das auch in planktischen und terrestrischen Gemeinschaften zu finden ist.

Die Ergebnisse meiner Arbeit zeigen, daß das Ausmaß von Makroalgenblüten und die Dominanzverhältnisse der Arten innerhalb einer Blüte entscheidend von Wechselwirkungen zwischen abiotischen und biotischen Faktoren abhängen, welche die Verbreitung früher Lebensstadien zu Beginn der Vegetationsperiode kontrollieren. Die Bedeutung und

ökologische Rolle einer Sporenbank sowie die spezifischen, ökophysiologischen und ökologischen Ansprüche einzelner Lebensstadien von massenblühenden Algen wurden in dieser Studie erstmalig beschrieben. Diese Ergebnisse zeigen gute Übereinstimmungen mit analogen Prozessen in terrestrischen Pflanzengemeinschaften (Bedeutung der Samenbank, Steuerung der Auskeimung, Fraß an Samen und Keimlingen). Dies unterstreicht, daß ein solides Verständnis von Prozessen, die auf die frühen Lebensstadien von Pflanzen einwirken, unentbehrlich ist, um wichtige Aspekte der Populationsdynamik und Struktur von Pflanzengemeinschaften unter dem Einfluß anthropogener Störungen zu erklären und vorherzusagen. Außerdem weisen meine Ergebnisse darauf hin, wie wichtig die Diversität herbivorer Konsumenten für eine effektive Kontrolle von massenblühender Makroalgen auf der Ebene verschiedener Lebensstadien ist. Um Makroalgenblüten und damit verbundene Probleme zu kontrollieren, ist es nötig (1) die Nährstofffrachten zu reduzieren und (2) komplette, küstennahe Lebensgemeinschaften in ihrer natürlichen Komplexität und Biodiversität zu erhalten.

Chapter 1

General introduction

PROBLEM

Although change in community configuration has always been the norm through the history of the planet's ecosystems, anthropogenic influences have enormously increased the rates and scales of change (Vitousek 1994). In fact, today, most ecosystems of the world are human dominated (Vitousek et al. 1997). Global alterations of biogeochemical cycles such as those of carbon dioxide and bioavailable nitrogen compounds are widely recognized as critical aspects of global change. Today, human activity adds at least as much fixed nitrogen to terrestrial ecosystems as do all natural sources combined (Vitousek et al. 1997). Cultural eutrophication of aquatic systems, mainly caused by wastewater disposal, atmospheric fallout, and fertilizer use (Nixon & Pilson 1983, Larsson et al. 1985, Valiela et al. 1997) has severe impacts on marine and freshwater communities worldwide. In coastal regions, the increase of nitrogen loads has caused coastal waters to be among the most highly fertilized ecosystems on earth (Nixon 1986, Kelly & Levin 1986).

Coastal marine ecosystems that are dominated and structured by macrophytes with an associated high diversity fauna and flora belong to the most productive systems on earth comparable to tropical rain forests (Mann 1973). Within the oceans, coastal macrophyte communities have key functions in nutrient cycling, erosion control, and habitat building providing essential ecosystem services to humanity (Costanza et al. 1997). However, in the course of eutrophication, structure and function of coastal communities have changed world-wide (Ryther & Dunstan 1971, Rosenberg 1985, Raffaelli et al. 1989, Cederwall & Elmgren 1990, Nixon 1990, Munda 1993, Duarte 1995, Schramm & Nienhuis 1996, Schories et al. 1997). As a prominent example, in the Baltic Sea, the distributions of large macrophytes such as *Fucus vesiculosus, Furcellaria lumbricalis* and *Zostera marina* are much more restricted than several decades ago (Plinski & Florczyk 1984, Kautsky et al. 1986, Schramm & Nienhuis 1996), observations which have been attributed to the effects of light limitation and increased sedimentation through enhanced phytoplankton blooms (Kautsky et al. 1986, Cederwall & Elmgren 1990, Duarte 1995). Concomitantly, there have been marked increases in abundance of annual filamentous and foliose macroalgae which have reached alarming proportions (Rosenberg 1985, Cederwall & Elmgren 1990, Bonsdorff 1992, Kiirikki & Lehvo 1997). Spring blooms of such opportunistic species often develop rapidly into unusual "mass

blooms" or "green tides", which in some cases persist over the summer. Thick drifting mats of detached algae can cause oxygen deficiency upon decomposition which leads to increasing mortality of epi- and endobenthic fauna and perennial flora (Rosenberg 1985, Hull 1987, Norkko & Bonsdorff 1996).

Despite numerous reports and observations of these phenomena around the world (Ryther & Dunstan 1971, Rosenberg 1985, Nixon 1990, Schramm & Nienhuis 1996) an understanding of the controlling mechanisms of macroalgal blooms is fragmentary (Nixon 1990). The main objective of this study was to provide such mechanistic understanding for two of the most common mass-occurring genera *Enteromorpha* (Chlorophyceae) and *Pilayella* (Phaeophyceae).

PREVIOUS WORK AND FURTHER RESEARCH NEEDS

Macroalgal blooms are generally explained by increased nutrient loads which may selectively favor filamentous and foliose macroalgae because of their physiological traits (Larsson et al. 1985, Wallentinus 1984, Cederwall & Elmgren 1990, Duarte 1995). These opportunistic species are characterized by high rates of nutrient uptake, photosynthesis and growth compared to the perennial, late-successional vegetation (Wallentinus 1978, 1984, Sand-Jensen & Borum 1991, Duarte 1995). Upon nutrient enrichment, bloom-forming macroalgae may gain competitive advantage and overgrow or replace slow-growing macrophytes which may suffer from decreased light levels, increased sedimentation of organic matter, and oxygen deficiency upon decomposition of macroalgal mats.

The existing literature on macroalgal blooms is surprisingly uniform in regard to the approaches adopted to support this view (overview in Fletcher 1996, Schramm & Nienhuis 1996). There is a wealth of information on the distribution and abundance of bloom-forming algae. Interpretations of these phenomena are predominantly based on observations, descriptive data on species abundance and chemical water parameters, and measurements of selected physiological traits. Repeatedly, it has been noted that experimental evidence for the mechanisms proposed is often lacking and the predictive power of current concepts on various effects of eutrophication is often low (Nixon 1990).

The overall assumption of a positive correlation between macroalgal blooms and eutrophication is generally accepted and substantiated by a still increasing number of records of these phenomena around the world. However, the great variability in extent, distribution and composition of macroalgal blooms within and between systems can not be explained and

thus, based on the existing knowledge reliable predictions on mass occurrences can hardly be made (Schories et al. 1997). For example, mass blooms of macroalgae do not occur in all eutrophicated areas, implying that some systems are more vulnerable to change than others. Also, there is considerable variability within systems. Even when nutrient status remains relatively constant over time, the extent of blooms can vary 2-20 fold among years and areas in any given system (e.g. North Sea: Schories 1995a, Baltic Sea: Bonsdorff 1992, Schramm et al. 1996). Moreover, species dominance pattern can not be explained solely by analysing abiotic water parameters and ecophysiological traits of species. Numerous co-occurring species often show similar high productivity levels under current abiotic conditions (Wallentinus 1978, 1984) and do not explain observed dominance of few or single species out of a larger species pool.

Physiological traits such as nutrient uptake rates, photosynthetic and growth rates have been investigated mostly in laboratory experiments using adult plants only. Requirements and characteristics of other life-cycle stages are likely to be important in explaining observed distribution patterns (reviewed in Santelices 1990, Vadas et al. 1992) but studies regarding this topic are largely lacking for bloom-forming macroalgae. For five species of *Enteromorpha* in the North Sea, growth rates of germlings in relation to seasonal change of temperature and light explained species dominance patterns in spring but not in summer (Lotze 1994). Until now, little knowledge has been gained on the role of species interactions in determining composition, timing and distribution of macroalgal blooms. Locally, herbivory (Geertz-Hansen et al. 1993), competition (Fong et al. 1993, 1996), and substratum availability (Schories & Reise 1993) have been shown to affect macroalgal mass development.

In many coastal areas, macroalgal blooms are dominated by one or two green algal species of the genera *Enteromorpha*, *Ulva* or *Cladophora* (Warwick et al. 1982, Reise 1983, Piriou & Menesguen 1992, Lotze 1994, Fong. et al. 1996, Schramm & Nienhuis 1996). In contrast to most of the Atlantic and Mediterranean, in many parts of the Baltic Sea the filamentous brown alga *Pilayella littoralis* dominates mass blooms (Plinski & Florczyk 1984, Kruk-Dowgiallo 1991, Norkko & Bonsdorff 1996, Kiirikki & Lehvo 1997, this study). In addition to *P. littoralis,* several species of *Enteromorpha* co-occur in the Baltic (Kautsky 1982, Wallentinus 1984, Kiirikki & Lehvo 1997) but rarely become dominant. Despite its cosmopolitan occurrence (South & Tittley 1986, Clayton 1994), blooms dominated by *Pilayella* have been reported rarely from other parts of the world (but see Wilce et al. 1982).

To explain the dominance of *Pilayella littoralis* over *Enteromorpha* spp. in the Baltic is a further goal of this study.

Taken together, the above observations imply temporal and spatial variability of some factors other than nutrient input that may control the extent and composition of macroalgal blooms. To enhance our understanding of macroalgal blooms as well as our ability to predict the consequences of nutrient input in a variable world Nixon (1990) - among others - called for an expansion and improvement of experimental work on eutrophication-related phenomena, including experimental manipulations in the field.

QUESTIONS

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

- Which mechanisms control the initiation, development, extent, and species composition of macroalgal blooms?
- What is the relative importance of abiotic factors (predominantly nutrients, temperature and light) versus species interactions such as competition and herbivory?
- Do early life stages show responses similar to adult algae in relation to abiotic factors and herbivory?
- How is it possible to restrict or reduce mass occurrences and their related problems?

APPROACH

To answer these questions I chose an approach integrating the study of physiological traits, population processes and species interactions.

Patterns of species distribution and abundance were first predominantly explained by correlation with abiotic parameters and resource availability in the environment in conjunction with physiological traits of species (Lewis 1964, Stephenson & Stephenson 1972). When the field of community ecology emerged in the 1960s, strong evidence was obtained for the importance of species interactions such as competition and predation (Connell 1961, Paine 1966, Dayton 1971, overview in Diamond & Case 1986). Today, it is accepted that physical and biological factors interact in determining population and community structure (Lubchenco 1980, Keddy 1989, Carpenter 1990, Krebs 1994, Sommer 1994).

However, in the majority of studies in community ecology, knowledge has been gained through investigations of adult organisms only. The importance of factors affecting propagule

supply, germination, growth, and survival of early life stages has been often overlooked (Reed et al. 1988, Roughgarden et al. 1988, Reed 1990, Fenner 1992, Vadas et al. 1992). In this study, I will argue that a knowledge of biotic and abiotic constraints on propagules, germlings and adults is required to gain a comprehensive understanding of the ecological control of macroalgal blooms.

OUTLINE OF THESIS

First, I will describe the phenology of different developmental stages in the life cycle of the two mass-occurring macroalgae, *Enteromorpha* and *Pilayella* (Chapter 3). In a next step, I will provide an understanding of the origin and initiation of macroalgal blooms discussing factors that affect overwintering of propagules and their germination in spring (Chapter 4). Growth rates, uptake kinetics and species productivity in relation to temperature, light and nutrients are treated in Chapter 5. Taken together, Chapter 4 and 5 provide a comparative analysis of ecophysiological demands of different life stages in *Pilayella* and *Enteromorpha*. The response of different life stages to herbivory is compared in Chapter 6. Finally, factorial field experiments (Chapter 7) give an overall synthesis including the interactive effects of propagule supply, nutrient availability, competition, and herbivory on population development of *Pilayella* and *Enteromorpha* in the field. General conclusions integrating the results of this and other studies and an outlook on further directions are provided in Chapter 8.

Chapter 2

Study site and description of species

The study was carried out in the outer Schlei (54°41' N, 10°0' E), western Baltic Sea, Germany (Fig. 2.1). The Schlei is a tideless, 40 km long fjord-like inshore water system of glacial origin with an average depth of 2.4 m. The maximum depth of 15 m is reached within a deeper central channel. Maasholm Bay, the study site, is the outermost of several shallow bays which extend towards both sides of the channel. In this area, wind induced water exchanges occur with nutrient rich water from the inner, highly eutrophicated fjord and comparatively nutrient poor water from the adjacent Kiel Bight.

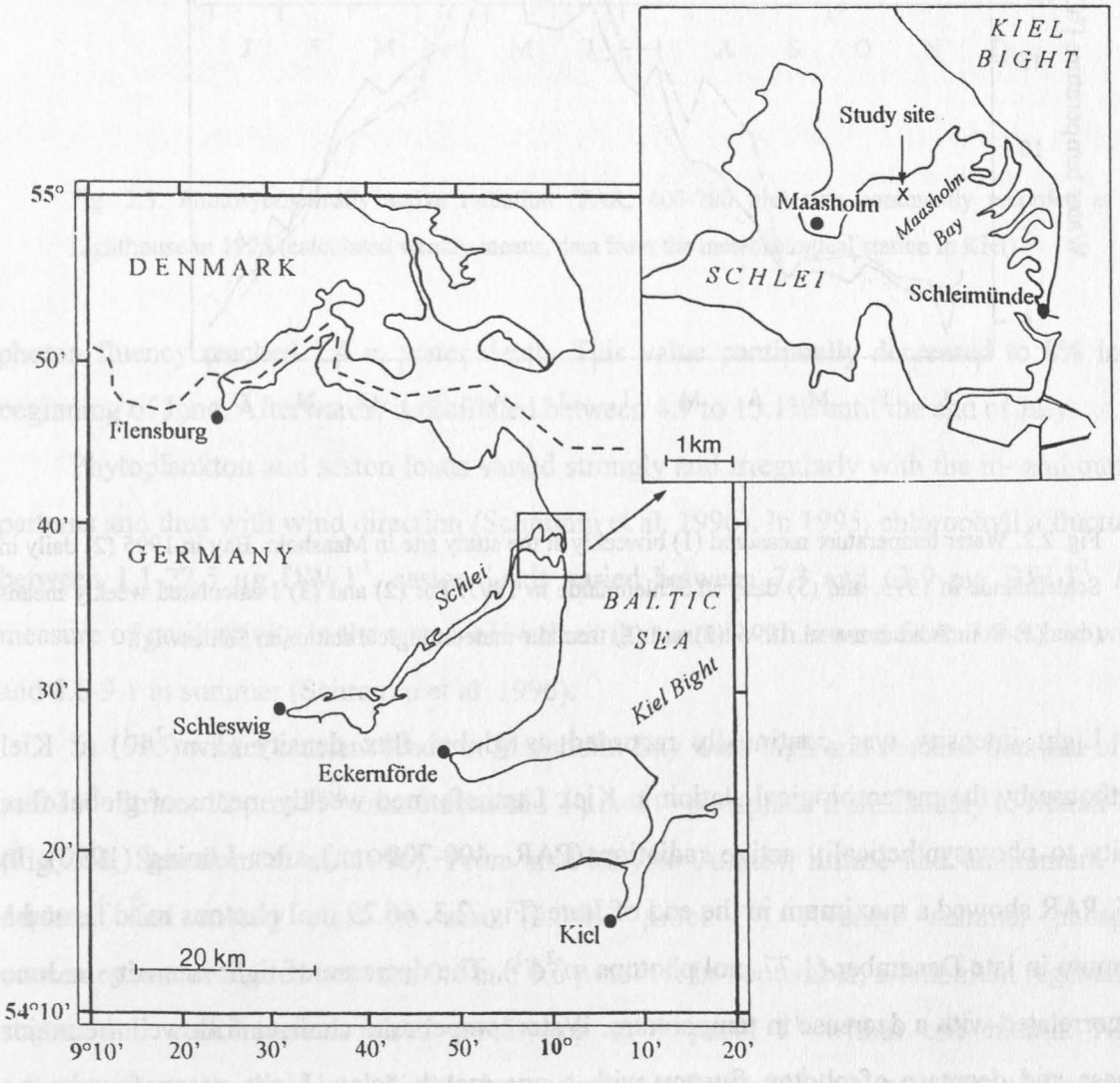

Fig. 2.1. Map of the study site Maasholm Bay located in the outer Schlei, western Baltic Sea.

Abiotic environment and water parameters

In Maasholm Bay, salinity fluctuates with season between 12-18 PSU in summer and 15-20 PSU in winter. In 1995, biweekly measurements of water temperature at the study site showed a maximum of 23.9°C in August and a minimum of -0.7°C in January (Fig. 2.2). In 1997, sea ice covered the Schlei until the end of January. Measurements from Schleimünde show a more rapid increase of water temperature in early spring of the 1997 season (5 °C reached in March) compared to 1995 when 5 °C were reached in April.

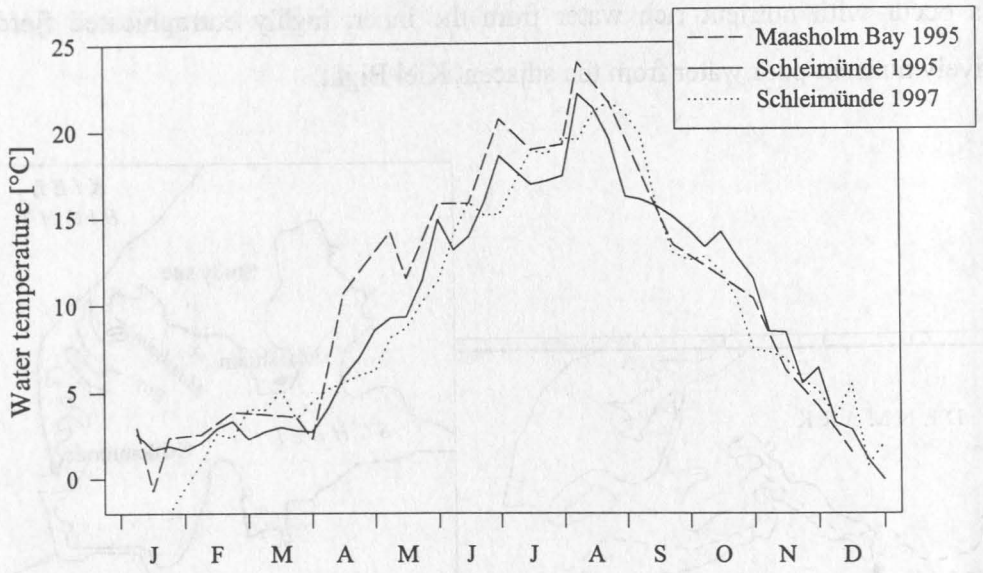

Fig. 2.2. Water temperature measured (1) biweekly at the study site in Maasholm Bay in 1995 (2) daily in Schleimünde in 1995, and (3) daily in Schleimünde in 1997. For (2) and (3) I calculated weekly means (data (1) from Schramm et al. 1996, (2) and (3) from the meteorological station in Schleswig).

Light intensity was continually recorded as global flux density (J $m^{-2}d^{-1}$) at Kiel Lighthouse by the meteorological station in Kiel. I transformed weekly means of global flux density to photosynthetically active radiation (PAR, 400-700 nm) after Lüning (1990). In 1995, PAR showed a maximum in the end of June (Fig. 2.3, 66.29 mol photons $m^{-2}d^{-1}$), and a minimum in late December (1.77 mol photons $m^{-2}d^{-1}$). The decrease of light intensity in June was correlated with a decrease in temperature. Water temperature changes followed the major increase and decrease of photon fluency with a one-month delay. Light attenuation in the water column was recorded in 1995 (Schramm et al. 1996). In mid-May, 21% of surface

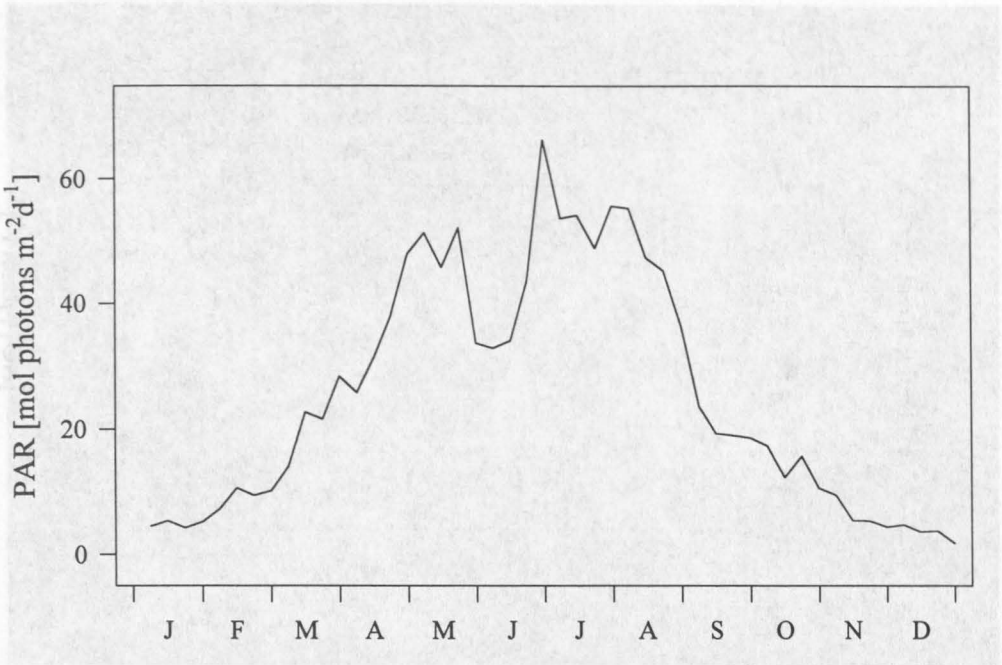

Fig. 2.3. Photosynthetically active radiation (PAR, 400-700 nm) was continually recorded at Kiel Lighthouse in 1995 (calculated weekly means, data from the meteorological station in Kiel).

photon fluency reached 1.4 m water depth. This value continually decreased to 8% in the beginning of June. Afterwards, it oscillated between 4.9 to 15.1% until the end of July.

Phytoplankton and seston loads varied strongly and irregularly with the in- and outflow patterns and thus with wind direction (Schramm et al. 1996). In 1995, chlorophyll a fluctuated between 1.1-22.5 µg DW l^{-1}, seston loads varied between 7.3 and 62.9 mg DW l^{-1}. As a measure of productivity in the water, pH-values fluctuated with season from 7.8-8.1 in winter and 8.6-9.1 in summer (Schramm et al. 1996).

In 1995, winter nutrient loads in Maasholm Bay were high and reached maxima of 160 µmol l^{-1} nitrate, 12 µmol l^{-1} ammonium and 2 µmol l^{-1} phosphate from January to March 1995 (Fig. 2.4, Schramm et al. 1996). From mid-May to August, nitrate and ammonium were depleted and mostly close to zero (0.0-0.3 µmol l^{-1}). Average summer phosphate concentrations remained between 0.1 and 0.6 µmol l^{-1}. In September, ammonium regeneration started and concentrations rised rapidly up to 9 µmol l^{-1} within one month. Nitrate concentrations remained low, slightly increasing up to 7 µmol l^{-1} in November and December.

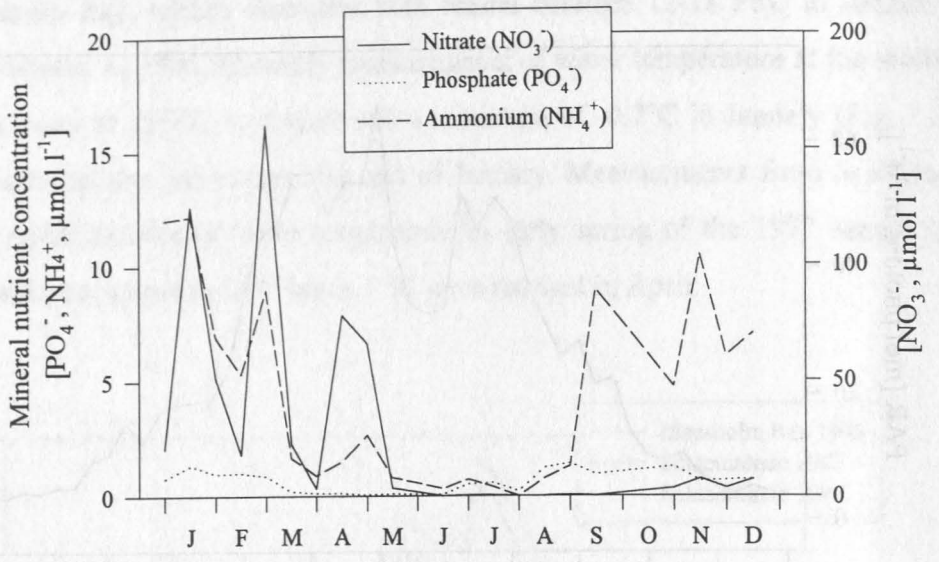

Fig. 2.4. Nutrient concentrations in Maasholm Bay in 1995. Calculated means (n=3) of biweekly measurements are shown (data from Schramm et al. 1996).

Biotic environment

The bottom at the study site was dominated by sand with scattered rocks and boulders. The dominant benthic macrophytes in the study area were *Fucus vesiculosus* (L.) and *Potamogeton pectinatus* (L.) from 0-1.5 m water depth, and *Zostera marina* (L.) below 1.2 m water depth. In spring and early summer, these macrophytes were overgrown by epiphytic *Pilayella littoralis* ([L.] Kjellm.) (Fig. 2.5, 2.6) and *Enteromorpha* (L.) spp., which also occurred on rocks, boulders and mussel shells. In late spring and summer, mesoherbivores were abundant at the site reaching peak densities of a few hundred to thousand individuals m^{-2} in the *Fucus/Potamogeton* zone (Chapter 6, Schramm et al. 1996). The main species were isopods: *Idotea chelipes* (Pallas), *I. baltica* (Pallas), amphipods: *Gammarus* spp., mainly *G. locusta* (L.), and periwinkles: *Littorina saxatilis* (Olivi) and *L. littorea* (L.).

Fig. 2.5. Mass bloom of *Pilayella littoralis* overgrowing *Fucus vesiculosus* plants and partly drifting in a free-floating stage.

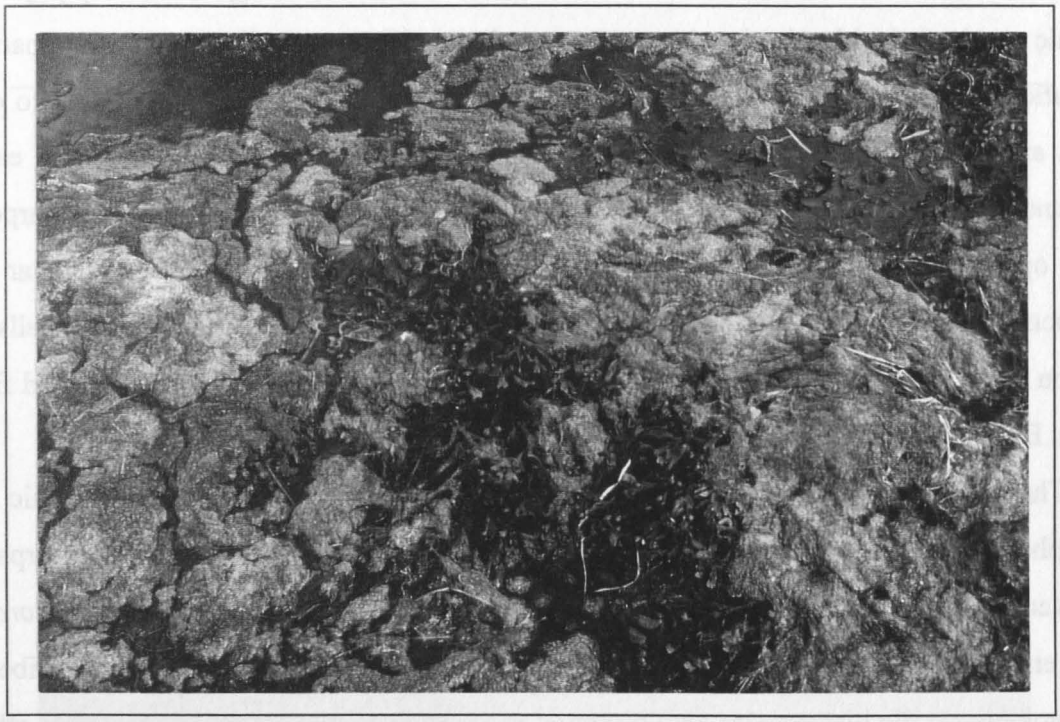

Fig. 2.6. Mass bloom of *Pilayella littoralis* drifting and decomposing at the water surface.

Species description of Pilayella and Enteromorpha

In this study, I chose to focus on the two common bloom-forming macroalgae *Pilayella littoralis* and *Enteromorpha* spp. (Fig. 2.7, 2.8). *Enteromorpha* and *Pilayella* are truly cosmopolitan genera which can be found abundantly in temperate to polar seas in both hemispheres (South & Tittley 1986, Clayton 1994, Clayton et al. 1997). According to the functional-form model of Steneck & Dethier (1994), *Pilayella* belongs to the filamentous category and *Enteromorpha* to the foliose category. Both algae are regarded as opportunistic (Littler & Littler 1980) and fast-colonizing forms ("ruderal strategy", Grime 1979). In the Baltic Sea, *Pilayella littoralis* is found in abundance and thrives even under the lowest salinities (<5 PSU) in the Bothnian Bay. *E. intestinalis* among other species of *Enteromorpha* co-occurs with *Pilayella* throughout the Baltic Sea up to the Bothnian Bay (Nielsen et al. 1995).

Pilayella littoralis (L.) Kjellm. is traditionally placed in the Ectocarpales (Phaeophyceae), but some authors have affiliated it with the Dictyosiphonales or Tilopteridales because of the occasional occurrence of longitudinal divisions (Müller & Stache 1989 and references therein). Estuarine populations of *P. littoralis* and populations in the brackish Baltic are extremely euryhaline compared to plants from fully marine environments (Bolton 1979a, Reed & Barron 1983). The morphology of this epiphytic or epilithic species is highly plastic with strong variation among seasonally or spatially separated populations (Bolton 1979b). The filamentous thallus is mostly highly branched, light to dark brown and achieves up to 40 cm height (Fig. 2.7). The morphology of *Pilayella* is easily confounded with that of *Ectocarpus*. *P. littoralis* can be distinguished from other ectocarpoids by the opposite branching pattern of the central axes, the intercalary rows of unilocular and plurilocular sporangia, and the occurrence of several discoid plastids in vegetative cells. In addition to the most typical attached form, a free-living ball-shaped form was described from Nahant Bay, Massachusetts (Wilce et al. 1982).

The life history of *P. littoralis* is not completely clarified. Usually, an isomorphic and heterophasic alternation of a sporophyte and a gametophyte is found in the Ectocarpales. However, several deviations from this pattern can occur (Strasburger 1991). In *P. littoralis*, both generations were found to reproduce asexually, and some authors have described a diplohaplophasic life history with an alternation of sporophyte and gametophyte, while others reported an apomeiotic development (Nygren 1975 and references therein). It is not clear,

whether gametophytes are monoecious or dioecious (Kylin 1933). Müller & Stache (1989) found no evidence for sexual fusion of zoids released by unilocular and plurilocular sporangia, and zoids germinated and developed into plants of the parent type.

Fig. 2.7. Adult *Pilayella littoralis* from the study site (size of the bar = 1 cm).

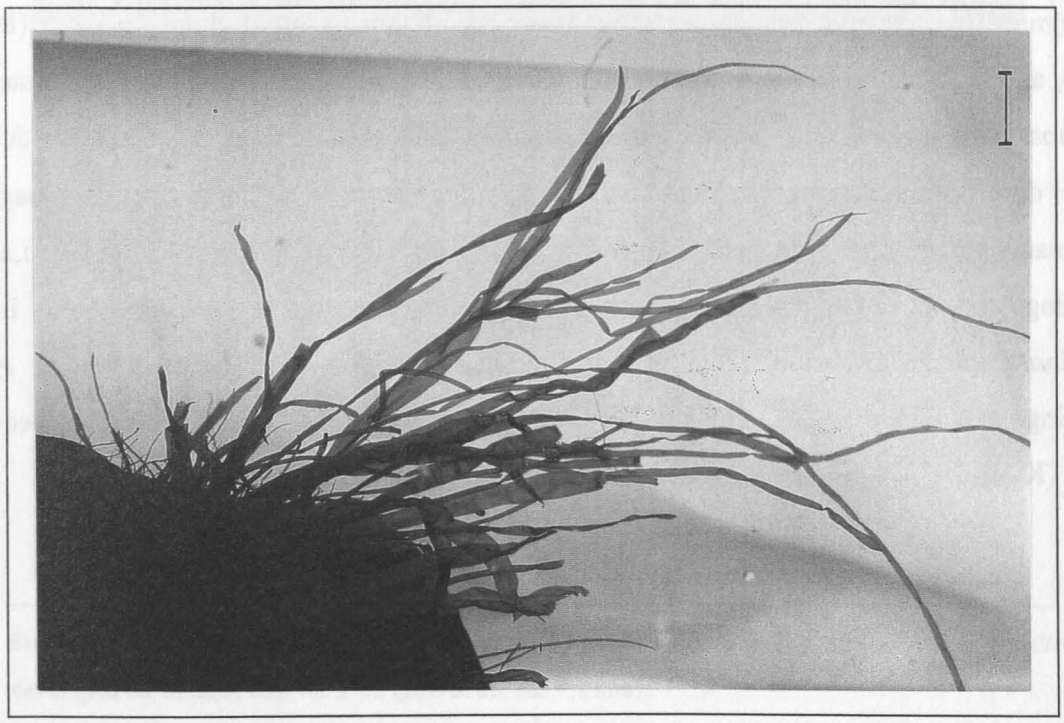

Fig. 2.8. Adult *Enteromorpha intestinalis* from the study site (size of the bar = 1 cm).

In the outer Schlei, I identified three co-occurring *Enteromorpha* species (Ulvales, Chlorophyceae) during 1995-1998. In all years, *E. intestinalis* (L.) Link clearly dominated adult biomass (>90%) compared with *E. prolifera* (O.F. Muell.) J. Agardh and *E. clathrata* (Roth) Grev. Also within the stage of propagules and germlings, *E. intestinalis* was most abundant. However, germlings of *E. intestinalis* and *E. prolifera* can only be distinguished microscopically on an individual basis. Counting hundreds to thousands of germlings per experiment, I usually had to treat these two species together, assuming that they may behave similarly during early life stages. Thus, in this thesis, early life stages are not separated into species and are treated as *Enteromorpha* spp.

The thallus of *Enteromorpha intestinalis* (Fig. 2.8) is a hollow tube which is composed of one cell layer. In *E. intestinalis*, the thallus is unbranched, tubular and inflated, up to 80 cm long and 4 cm wide with a short stipe. Cells are not arranged in rows and contain cap-like chloroplasts (Koeman 1985, Lotze 1994). *Enteromorpha* species generally show an isomorphic and diplohaplophasic life history, but both generations are also able to reproduce asexually, and gametophytes are dioecious (Koeman 1985).

Terminology of life-cycle stages

In this thesis, I use the following terminology (in italics) for different life-cycle stages (Fig. 2.9). All unicellular reproductive units (e.g. sexual or asexual zoids) are called *propagules*. In *Pilayella*, propagules show a size of 5-6 µm in longitudinal diameter (Kylin 1933), and 6-10 µm in *Enteromorpha* (Koeman 1985). Dispersed propagules which attach to the substratum are generally called settlers (Connell 1985). As long as these settlers do not further develop into an erect filament I call them *settled propagules*. These settled propagules germinate into rhizoids and erect filaments which are called *germlings* (Fig. 2.10). Larger germlings (>5 mm length) start branching in *P. littoralis* and *E. prolifera*, and in *E. intestinalis* the hollow tubular thallus starts to inflate (Kylin 1933, Koeman 1985). After germlings exceed a size of 2 cm in *Pilayella* and 4 cm in *Enteromorpha* they can become fertile (Kylin 1933, Koeman 1985) and thus, they are then called *adults*.

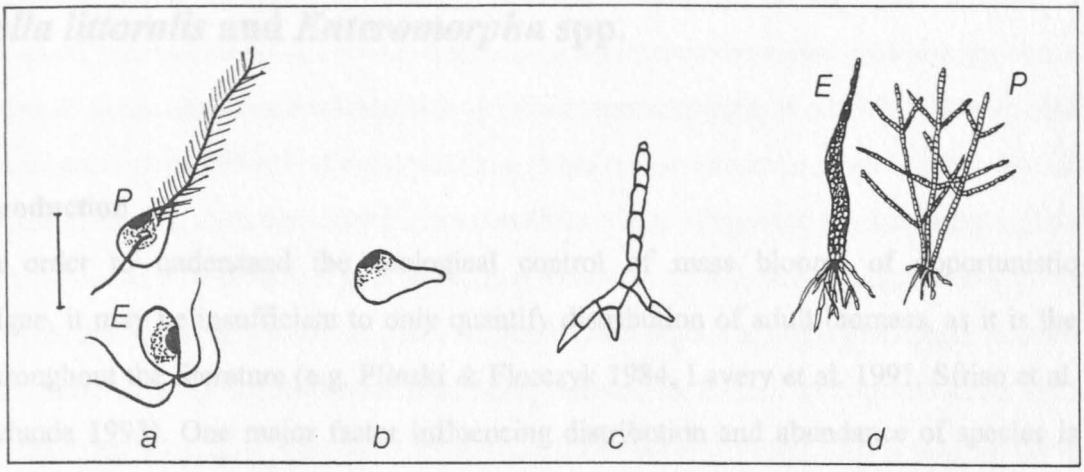

Fig. 2.9. Morphology of different life-cycle stages in *Pilayella littoralis* (P) and *Enteromorpha intestinalis* (E): (a) propagules, (b) settled propagule, (c) one wk old germling with rhizoids and erect filament (b and c are similar for both species), (d) 3 wk old germlings (altered after Kylin 1933, Koeman 1985, Müller & Stache 1989). For adults see Fig. 2.7 and 2.8. Size of bar = 10 µm in a and b, 100 µm in c, and 1 mm in d.

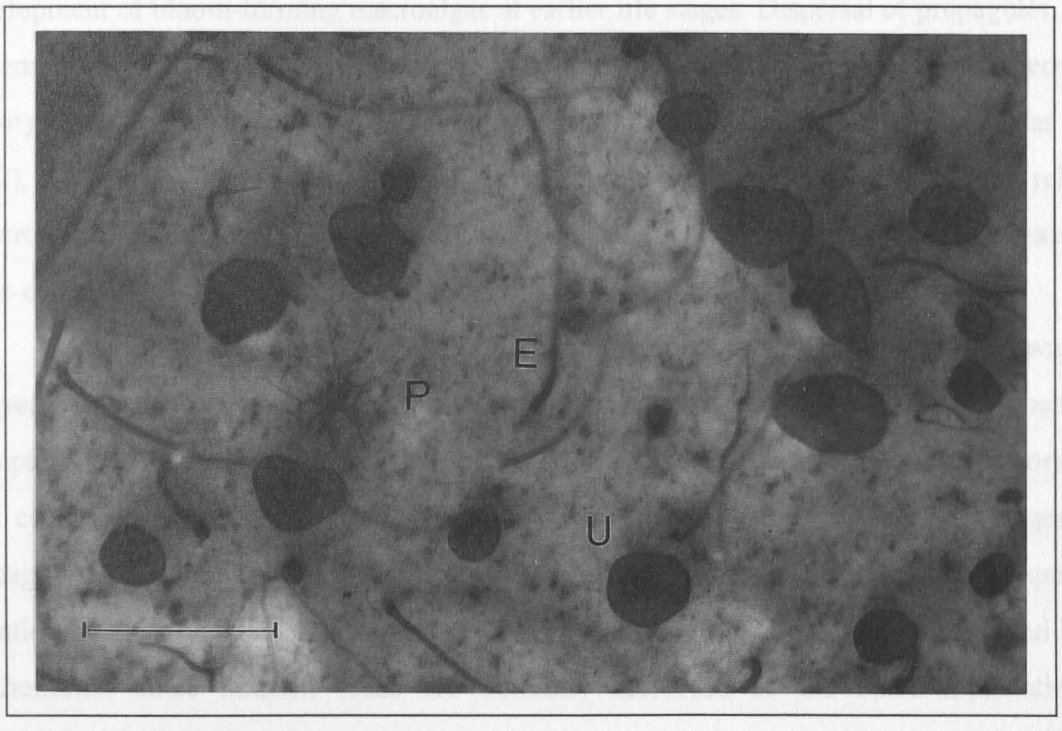

Fig. 2.10. Germlings of *Enteromorpha* spp. (E), *Pilayella littoralis* (P), and *Ulvopsis grevillei* (U) developed on ceramic tiles for 2 wk (size of the bar = 1 mm).

Chapter 3

Phenology of different life stages: *Pilayella littoralis* and *Enteromorpha* spp.

3.1. Introduction

In order to understand the ecological control of mass blooms of opportunistic macroalgae, it may be insufficient to only quantify distribution of adult biomass, as it is the norm throughout the literature (e.g. Plinski & Florczyk 1984, Lavery et al. 1991, Sfriso et al. 1992, Munda 1993). One major factor influencing distribution and abundance of species is variation in processes that affect recruitment such as propagule supply, settlement, germination and survival to the adult stage (Dean et al. 1989, Reed 1990). Many earlier studies on community structure have been criticized for not incorporating recruitment variability (Underwood & Denley 1984) and a field termed "supply-side ecology" has emerged (Underwood & Fairweather 1989).

In this study, I hypothesized that controlling mechanisms may influence population development of bloom-forming macroalgae at earlier life stages. Dispersal of propagules, their settlement and survival may be critical processes that potentially reduce actual germling density as suggested for some perennial macroalgae (reviewed in Santelices 1990, Vadas et al. 1992). Quantitative knowledge on propagule supply, germling density and their relative importance in population development of annual macroalgae is rare, but first studies exist for mass-occurring *Enteromorpha* in the North Sea (Lotze 1994, Schories 1995a).

In the Baltic Sea, macroalgal blooms are dominated by the filamentous brown alga *Pilayella littoralis* while green algae such as *Enteromorpha* seem to be of minor importance (Chapter 1). In my examination of this unusual dominance of *Pilayella* over *Enteromorpha,* I first compared the seasonal distribution and abundance of three different life stages: (1) propagules, (2) germlings, and (3) adults of both genera at the experimental site. To quantify variation between years, I compared the phenology of two vegetation periods, 1995 and 1997. Furthermore, since nutrient loads are currently discussed as the main explanation of macroalgal blooms, I compared seasonal tissue nutrient concentration in adult *Pilayella* and *Enteromorpha* to analyze possible differences in nutrient limitation.

3.2. Material & methods

Propagule supply

To obtain a relative measure of the amount of viable macroalgal propagules in the water column, I sampled propagule settlement on ceramic tiles at 2-4 wk intervals. I used ceramic tiles because of their surface structure which is suitable for algal settlement. Settlement on tiles may be not the same as on natural rock surfaces, but my objective was to make a relative comparison between propagule supply of *Enteromorpha* and *Pilayella* and not a demographic budget. Six ceramic tiles (10x10 cm) were vertically hung in the water column 50 cm above the sediment surface (water depth was 70 cm) for 4 h (10.00-14.00, after Schories 1995a). This method allows settlement of positive phototactic zoids and gametes on their way to the water surface and of negative phototactic zygotes on their way back from the water surface. After transportation to the laboratory in a cooler, tiles were maintained in 500 ml PES (Starr & Zeikus 1987) at constant temperature of 15°C and constant light intensity of 100 µmol photons $m^{-2}s^{-1}$ in 14:10 h L:D. Here, I define these temperature and light conditions as "standard T/L-conditions", a term which will be used throughout this thesis. Germanium dioxide (GeO_2) was added to the medium to suppress growth of diatoms in a concentration of 0.5 mg l^{-1} which is the standard concentration used throughout the study. This GeO_2-concentration was rather low but effective within the short cultivation times I used, and was sufficiently low to avoid inhibitory effects on *Pilayella* (Wang 1993). After 7 d of cultivation, germlings (>200 µm length) were counted using a dissecting microscope with an integrated grid (mean of 10 randomly chosen subsamples of 4x4 mm per tile). This method provides only a minimum estimate of propagule supply because of potential mortality during dispersal, settlement, and early recruitment.

Because no propagules of *Pilayella littoralis* were detected using this method, I slightly modified the sampling procedure in 1997. First, assuming that propagule release may vary with daytime, I increased the incubation period to 24 h. Second, after germination experiments in 1995 I considered the preference of *Pilayella* for lower germination temperatures. Thus, I cultivated tiles at 10°C in 1997.

Germling density

In 1995, I determined germling density every 4 wk on 30 randomly collected rocks (ca. 5 cm in diameter) from 30 to 70 cm water depth along a 200 m transect at the study site. In

contrast to germlings developed from propagules on tiles (method above), germlings on rocks were mostly growing too densely to give good estimates of individual numbers. Instead, I estimated percent cover of germlings using a dissecting microscope with an integrated grid in 5 randomly chosen subsamples (10x10 mm) per rock. Since larger sand grains represent a second important substratum for germination of some macroalgae (Schories 1995a) I also quantified germling density on sand grains every 4 wk. Therefore, I sampled 10 sediment cores (3 cm in diameter) of the upper 5 mm of sediment with a modified plastic syringe. Then I spread out these sediment samples in petri dishes (9 cm in diameter) and counted all germlings using a dissecting microscope. After May, I had to cease sampling sand grains since the sediment surface was covered with thick mats of organic matter.

Adult biomass and C/N/P-content

Adult algal biomass (mg DW m^{-2}) was determined monthly at the study site in 1995. Within the zone dominated by *Fucus vesiculosus* and *Potamogeton pectinatus* (30-150 cm water depth), I placed 6 quadrats (25x25 cm) randomly along a 100 m transect line (vertical to the coast line) and sampled them with a framed sampling net. I detached all epiphytic and epilithic macroalgae from their substratum (most biomass referred to epiphytes on *Fucus*), sorted them by species which were then dried for 48 h at 70°C for dry weight determination. Afterwards, C/N-content of dried *Enteromorpha* and *Pilayella* was determined in 3 replicates using a C/N-Analyzer (Fisons Instruments, NA 1500 N). For the analysis of P-content dried algal material was combusted (550°C for 2 h), eluted with 5 ml H_2O and 0.1 ml H_2SO_4 (4.5 n) and then PO_4-P was photometrically analyzed with a continuous flow analyzer using the methods of Grasshoff et al. (1986).

In early spring, I observed high loads of epiphytic diatoms on *Pilayella*. To quantify epiphytic diatom biomass I detached them from their host algae using filtered kiwi (*Actinidia chinensis*) fruit extract (3:1 vol. extract:H_2O), which dissolves the stalks of settled diatoms (Booth 1981). I determined DW of the host *Pilayella* and their epiphytic diatoms separately as described above. This was carried out in February, May and June 1995 with 5 replicates respectively.

For comparison of the extent of macroalgal blooms in different years, I determined adult algal biomass in 1997 but on *Fucus* only. I used the same method but samples were taken along a 300 m transect line parallel to the coast line at about 50 to 70 cm water depth.

3.3. Results

Propagule supply

Over the entire vegetation period from March to October 1995, viable propagules of *Enteromorpha* spp. occurred abundantly in the water column (Fig. 3.1a). Peak densities were found in April at 1.2 million settling propagules $m^{-2}h^{-1}$. In 1995, I did not detect propagules of *Pilayella littoralis* in any month, sampling between 10.00-14.00. In 1997, with a 24-h sampling procedure, propagules of both, *Enteromorpha* spp. and *Pilayella littoralis*, settled on the tiles (Fig. 3.2a). This may indicate that *Pilayella* released spores into the water column significantly earlier than 10.00 or later than 14.00. Both species initiated reproduction in May 1997 which was one month later than in 1995 for *Enteromorpha*. The reproductive period of *Pilayella* was short and had ended already in July whereas *Enteromorpha* propagules were present until the end of October. In *Pilayella*, there was a maximum of 15 million settling propagules $m^{-2}d^{-1}$, which was only a quarter of the maximal amount in *Enteromorpha* (60 million $m^{-2}d^{-1}$) in July. Assuming that *Enteromorpha* propagules settle around the day with equal density, peak values of 1995 reached 28.8 million settling propagules $m^{-2}d^{-1}$ (this corresponds to 1.2 million $m^{-2}h^{-1}$) which is in accordance with values found in June 1997.

Germling density

At the beginning of the vegetation period in March and April 1995, *Pilayella* germlings occurred earlier at the study site than *Enteromorpha* germlings (Fig. 3.1b). On hard substratum (rocks), *Pilayella* covered up to 80% of space in March but declined rapidly towards zero cover in June. In contrast, *Enteromorpha* germlings appeared in April and persisted with 20 to 40% cover on rocks over the entire summer until October. On sand grains, density of *Enteromorpha* germlings (93750 m^{-2}) was 3 times higher than in *Pilayella* (37500 m^{-2}) in April (Table 3.1) but, amounts decreased in both species towards June when sediment became increasingly covered with organic matter.

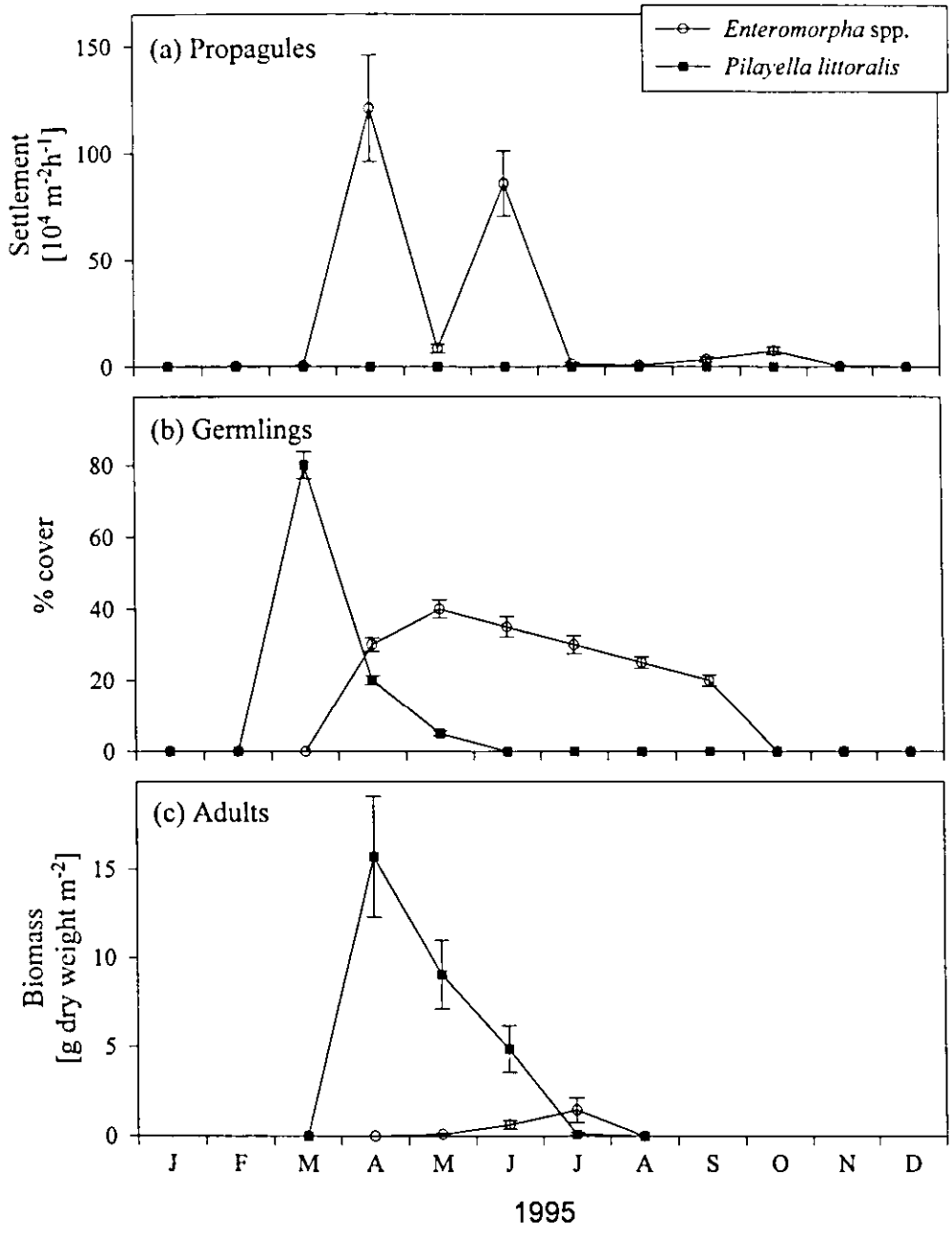

Fig. 3.1. Occurrence of 3 life stages of *Enteromorpha* spp. and *Pilayella littoralis* at the study site in 1995: (a) Density of viable propagules settling per h from the water column onto ceramic tiles exposed for 4 h from 10.00-14.00. No propagules of *P. littoralis* were detected using this method. (b) Percent cover of germlings on rocks. (c) Biomass of adults, mainly epiphytically growing on *Fucus vesiculosus*. Data are means ± 1SE (n=6 in a, c and n=30 in b).

Table 3.1. Density of germlings of *Enteromorpha* spp. and *Pilayella littoralis* on sand grains (0-5 mm sediment depth) in 1995 in Maasholm Bay (n=10).

	Density of germlings [$*10^3$ m^{-2}]			
	Enteromorpha spp.		*Pilayella littoralis*	
Month	Mean	SE	Mean	SE
March	0.00	0.00	12.50	8.33
April	93.75	36.38	37.50	21.25
May	43.75	16.27	31.25	25.09
June	0.00	0.00	0.00	0.00

Adult biomass and C/N/P-content

In 1995, *P. littoralis* formed a maximal biomass of 15.7 g DW m^{-2} in April (Fig. 3.1c) mainly epiphytically on *Fucus vesiculosus*. Later in the year, adult biomass declined steadily, and *Pilayella* disappeared in July. Maximum biomass of *Enteromorpha* spp. was only 1.4 g DW m^{-2} in July and this species disappeared as an epiphyte on *Fucus* in August. In February and June, almost no epiphytic diatoms grew on *Pilayella*. Biomass ratio of diatom : *Pilayella* g DW was 0.0:1 in February and 0.09(±0.02):1 in June. In May, high loads of epiphytic diatoms with a biomass ratio of 3.17(±0.74):1 occurred indicating the spring diatom bloom. Hence, *Pilayella* biomass is compounded with diatoms in spring. In contrast, very few epiphytic diatoms were observed on *Enteromorpha*.

C/N/P-content of adult tissues in *Enteromorpha* and *Pilayella* was highly fluctuating in summer 1995 (Table 3.2). N-content varied in a similar fashion in both species, ranging from 1.6 to 3.3% of DW in *Pilayella* and 1.4 to 3.1% of DW in *Enteromorpha*. P-content fluctuated greater in *Pilayella* (0.09-0.87% of DW) than in *Enteromorpha* (0.15-0.28% of DW). Overall, a trend of decreasing C:N- and N:P-ratios was observed with time.

In 1997, macroalgal biomass was lower than in 1995 (Fig. 3.2b). *Pilayella* first appeared in March 1997 with minor amounts of 0.3 g DW m^{-2} and achieved a maximum biomass in June with 6 g DW m^{-2}. Adult *Enteromorpha* only appeared in July with a biomass of 0.2 g DW m^{-2}.

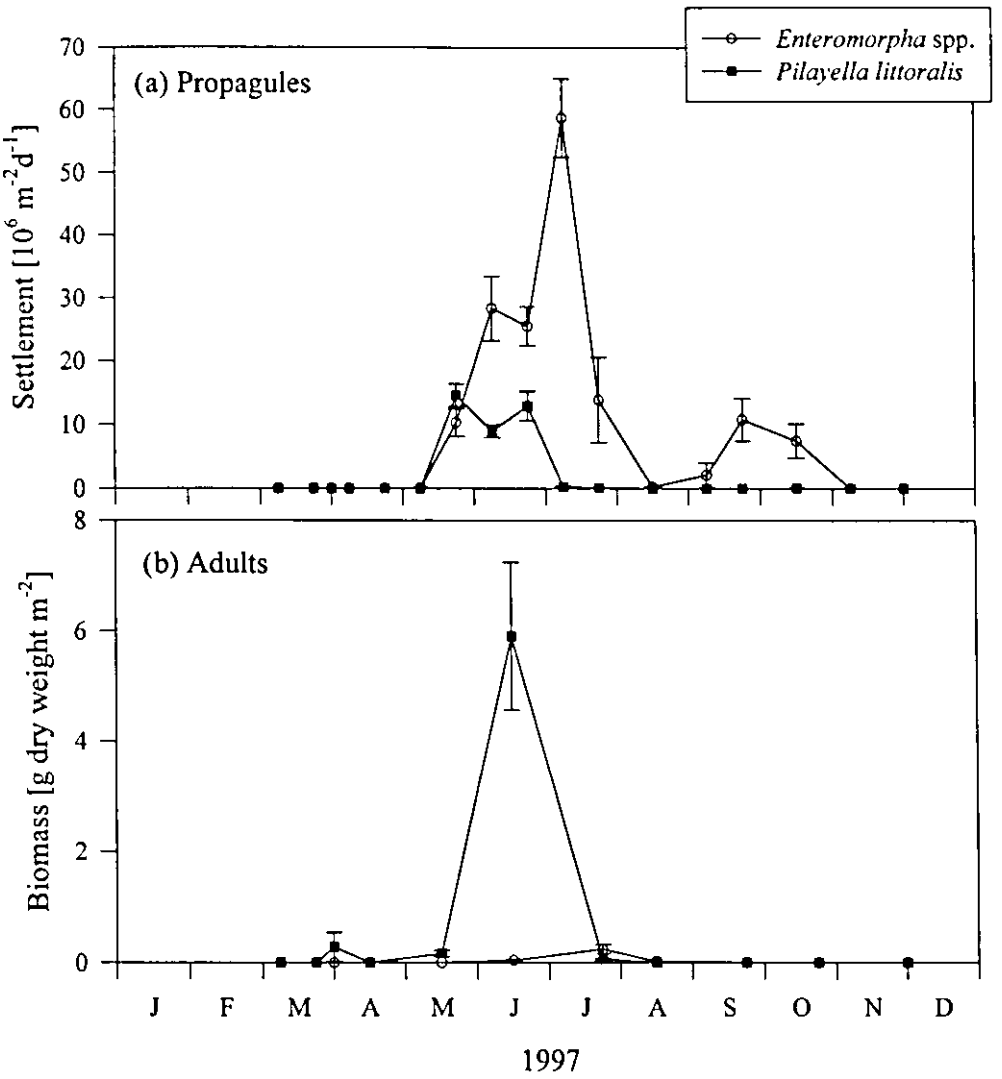

Fig. 3.2. Occurrence of propagules and adults of *Enteromorpha* spp. and *Pilayella littoralis* in 1997: (a) Densities of viable propagules settling per d from the water column onto ceramic tiles exposed for 24 h at the study site. (b) Biomass of adults growing epiphytically on *Fucus vesiculosus*. Data are means ± 1SE (n=6).

Table 3.2. Tissue content of C, N, and P of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* sampled at Maasholm Bay in 1995 (n=3) and calculated atomic ratios of C:N and N:P (data compiled from Schramm et al. 1996).

Date	Tissue content [% of DW]						Atomic ratios	
	C	SE	N	SE	P	SE	C:N	N:P
	Pilayella littoralis							
10.04.95	22.940	*0.310*	2.757	*0.020*	0.219	*0.001*	270	28
10.05.95	17.720	*0.559*	1.557	*0.050*	0.086	*0.000*	535	40
24.05.95	24.290	*0.773*	2.810	*0.145*	0.264	*0.001*	237	24
07.06.95	17.250	*0.923*	1.750	*0.082*	0.136	*0.001*	327	28
14.06.95	32.702	*1.129*	3.309	*0.212*	0.368	*0.012*	230	20
22.06.95	21.080	*0.258*	2.217	*0.029*	0.253	*0.001*	215	19
06.07.95	14.583	*1.184*	1.653	*0.149*	0.869	*0.000*	43	4
	Enteromorpha intestinalis							
24.05.95	35.547	*0.460*	3.067	*0.041*	0.160	*0.000*	574	42
14.06.95	28.514	*1.059*	2.143	*0.073*	0.198	*0.014*	373	24
22.06.95	30.613	*0.330*	1.440	*0.030*	0.151	*0.009*	524	21
19.07.95	33.487	*0.243*	1.730	*0.010*	0.149	*0.000*	580	26
15.08.95	27.126	*1.372*	1.588	*0.077*	0.281	*0.051*	250	13

3.4. Discussion

Observations on the phenology of mass-occurring macroalgae showed that there is a consistent discrepancy in the seasonal distribution and abundance of propagules, germlings and adults of *Pilayella littoralis* (relatively low propagule supply and high adult biomass) and *Enteromorpha* spp. (high propagule supply and low adult biomass).

Enteromorpha produced huge volumes of propagules over 7 month with extremely high peak densities of 60 million settling propagules $m^{-2}d^{-1}$. Similar seasonal occurrence and densities of settling *Enteromorpha* propagules in the range of 10^5 to 10^7 $m^{-2}d^{-1}$ were reported from the Wadden Sea (Schories 1995a). This classifies *Enteromorpha* as an opportunistic macroalgae with a high reproductive output reflected in high abundance of propagules in the water column (Littler & Littler 1980, Hoffmann & Ugarte 1985). *Pilayella* was characterized by a smaller supply of propagules (25% peak density of settling propagules) and a shorter reproductive period (March to May) compared to *Enteromorpha*.

Enteromorpha propagules developed into a dense population of germlings covering 20-40% of hard substratum from April to September. Surprisingly, these germlings did not

develop into a corresponding adult biomass. In *Pilayella* however, the germling peak in March 1995 was followed by a corresponding adult peak one month later with a 10-fold higher peak biomass (up to 15 g DW m^{-2}) than *Enteromorpha*. Thus, propagule and germling supply were not directly coupled with the occurrence of adults in *Enteromorpha*. Similarly, in the German Wadden Sea, the extent of green algal mats was not correlated with the amount of viable propagules (Schories 1995a). Obviously, additional factors may affect bloom-forming macroalgae before they reach the adult stage which will be explored in the next chapters.

Adult biomass varied between years with a peak biomass in *Pilayella* of 15 g DW m^{-2} in 1995 and 6 g DW m^{-2} in 1997. In both years, *Pilayella* dominated with a 10- to 30-fold higher biomass than *Enteromorpha*. This dominance pattern appears to be typical for most of the Baltic Sea (Kruk-Dowgiallo 1991, Norkko & Bonsdorff 1996, Schramm et al. 1996). Strong and mostly unexplained variation in the extent of macroalgal blooms between years and areas is common in eutrophicated coastal waters, e.g. 10-800 g DW m^{-2} in the Baltic (Bonsdorff 1992, this study), 20-600 g DW m^{-2} in the Wadden Sea (Lotze 1994, Reise & Siebert 1994, Schories 1995a), 0.2-400 g DW m^{-2} in coastal waters around Europe (Charlier & Lonhienne 1996).

Tissue nutrient concentrations of adult *Enteromorpha* and *Pilayella* showed a broad trend of increasing N-limitation (N:P < 30:1, Atkinson & Smith 1983) towards late spring and summer when ambient nitrogen pools were largely depleted (Chapter 2, Fig. 2.4). However, during summer, C/N/P-ratios strongly fluctuated indicating the availability of nutrient pulses which may be quickly utilized by the algae (Pickering et al. 1993). From this I raise the following questions: (1) Would further nutrient enrichment enhance macroalgal productivity? (2) Do *Pilayella* and *Enteromorpha* differ in their ability to use short term nutrient pulses versus long term nutrient enrichment? (3) Do nutrient concentrations and other potential control mechanisms show different effects on various life stages?

Chapter 4

Early life stages: overwintering and germination

4.1. Introduction

Population development of annual plants in temperate ecosystems strongly depends on the availability of a recruitment source in spring and further, on survival and growth of germlings into the adult stage. In contrast to terrestrial plant communities for which there is a large body of empirical work on seed banks, germination control, and seedling ecology (Fenner 1992), similar topics have received little or no attention in marine macroalgae. Only recently have banks of microscopic macroalgal propagules been identified (Chapman 1986, Santelices et al. 1995) and compared with terrestrial seed banks (Hoffmann & Santelices 1991). However, knowledge on the functioning of marine propagule banks and their role in community recovery and regulation is lacking so far (Hoffmann & Santelices 1991). For some selected perennial species, it has been suggested that factors affecting early life stages may be of equal or greater importance than factors affecting adult thalli (reviewed in Santelices 1990, Vadas et al. 1992). This has been quantified through matrix modeling for a *Fucus distichus* population in western Canada indicating that the absence of a germling bank can reduce yearly population growth rate by 83% (Ang & De Wreede 1993). Early life stages such as propagules and germlings are very delicate structures, lacking some of the resistance mechanisms (e.g. structural defenses against desiccation or herbivory) found in adult individuals (Lubchenco 1983, Brawley & Johnson 1991). Therefore, they are likely to represent critical phases in the life cycle of macroalgae and other organisms (Vadas et al. 1992).

In this chapter, I address differences in the overwintering and germination of early life stages of *Enteromorpha* spp. and *Pilayella littoralis* in the Baltic. I asked whether species-specific differences occur already at the initiation of algal population development in spring. As a first step, I quantified pools of overwintering propagules as sources for the initiation of population development of *Enteromorpha* and *Pilayella*. I hypothesized that differences in seasonal timing of germination may be an important variable controlling species composition in macroalgal blooms. Here, I define germination as development of a settled propagule into a macroscopic, erect germling. As possible cues for germling development I studied isolated

and combined effects of (1) temperature, (2) light intensity, (3) day length, and (4) nutrient enrichment on germination of *Enteromorpha* spp. and *Pilayella littoralis*.

4.2. Material & methods

Overwintering

In winter 1994-95, I did not observe any overwintering adult thalli of *Enteromorpha* spp. and *Pilayella littoralis*. Therefore, I assumed that overwintering occurred in the stage of microscopic forms on various substrata. Five different types of substrata were sampled in the field in December 1994: (1) dead shells of *Mytilus edulis*, (2) sand grains from the sediment surface to 5 mm sediment depth, (3) small rocks, (4) thalli of *Fucus vesiculosus*, and (5) leaves of *Zostera marina*. Because no germlings or other microscopic forms were visible with a dissecting microscope (40x) prior to cultivation in the laboratory, I assumed that propagules did not germinate in winter or that they overwintered in the stage of settled propagules or small germlings composed only of a few cells. All 5 substrata were cultivated with 6 replicates in 500 ml PES with GeO_2 added at standard T/L-conditions. After 2 wk all germlings (>200 µm length) per cm^2 area of substratum were counted and germling density was determined.

Germination in relation to temperature and light intensity

To explain the different temporal pattern of distribution and abundance of *Enteromorpha* spp. and *P. littoralis* in the field (Chapter 3), I tested whether germination rates of the species differ as a function of temperature or light intensity, or a combination of these factors. In February 1995, I collected shells of *Mytilus edulis* with attached overwintering propagules in the field and cultivated them in the laboratory in 500 ml PES with GeO_2 added at three temperatures (5, 10, 15°C) combined with three light intensities (50, 100, 200 µmol photons $m^{-2}s^{-1}$ in a 14:10 h L:D) in a completely crossed design (n=5 for each treatment combination). The chosen light intensities correspond to daily sums of 2.52, 5.04 and 10.08 mol photons m^2 respectively. After 12 d of cultivation, I counted developed germlings (mean of 3 subsamples of 4x4 mm per shell) with a dissecting microscope and an integrated grid. Two-way ANOVAs (factors: light, temperature, 3x3) on germling densities were performed for each species separately. Post-hoc comparisons were done according to Tukey-Kramer

procedure. Data were log-transformed to achieve homogeneity of variances. Throughout the study, homogeneity of variances was checked by Cochran's test, and the relative effect size of the experimental factors was calculated as omega-squared (ω^2) for a fixed-factor model and transformed to the percentage of explained variance (Howell 1992).

Germination in relation to day length and light intensity

The life cycles of many algal species are controlled by photoperiod (Lüning 1990). Hence, I asked whether light intensity or day length is the key variable that may control timing and extent of germination in spring in *Enteromorpha* spp. and *Pilayella littoralis*. In the end of April 1995, 6 ceramic tiles were incubated for 4 h in the field to allow settlement of propagules. I cultivated these tiles at 15°C in 500 ml PES with GeO_2 added at three day lengths (8:16, 12:12, 16:8 L:D) combined with three light intensities (50, 100, 200 µmol photons $m^{-2}s^{-1}$) in a completely crossed design (n=5 for each treatment combination). Corresponding daily sums of photon fluency are shown in Table 4.1.

Table 4.1. Daily sums of photon fluency in mol photons $m^{-2}d^{-1}$ resulting from the combined manipulation of day lengths and light intensities.

	Light intensity (µmol photons $m^{-2}s^{-1}$)		
Day length (h L:D)	50	100	200
8:16	1.44	2.88	5.67
12:12	2.16	4.32	8.64
16:8	2.88	5.76	11.52

After 10 d of cultivation, I counted developed germlings (mean of 6 subsamples of 4x4 mm per tile) with a dissecting microscope and an integrated grid and mean germling density per cm^2 was calculated. Since only *Enteromorpha* germlings occurred in sufficient amounts to allow for statistical analysis, a two-way ANOVA (factors: day length, light intensity, 3x3) was performed on germling density for this species only. Data were log-transformed to achieve homogeneity of variances. Post- hoc comparisons were done according to Tukey-Kramer and with planned mean comparisons (t-Test).

Germination in relation to nutrient enrichment

Ambient nutrient concentrations in the water column decline in spring through consumption by phytoplankton spring blooms and annual macroalgal development. I was interested to know (1) whether germination rates of *Enteromorpha* spp. and *Pilayella littoralis*

in early spring and summer could be enhanced by nutrient enrichment, (2) whether enhancement differs between the two species, and (3) whether enhancement differs among months. Because nutrient levels in the Schlei are highly variable (Chapter 2, Fig. 2.4) and characterized by wind driven pulses of high nitrogen concentrations from inside the Schlei, I only focused on effects of short-time pulse concentrations in the laboratory in 1995. Effects of long-time, low-level enrichment were studied as a part of a factorial field experiment in 1997 (Chapter 7).

In February 1995, I collected shells of *Mytilus edulis* with attached overwintering propagules from the field and used them as a source for germination. In April and July, when new reproduction had started, I used ceramic tiles which were incubated in the Schlei for 4 h. These substrata were then cultivated in the laboratory in 500 ml freshly collected and 0.2 µm filtered seawater from the study site at standard T/L-conditions. Background seawater nutrient levels were determined with an autoanalyzer using the methods of Grasshoff et al. (1986). Nutrient pulses were simulated with single enrichments at the beginning of the experiment with nitrate/phosphate 0/0, 0/30, 500/0, 500/30 µmol l^{-1}. The levels of 500 µmol l^{-1} nitrate and 30 µmol l^{-1} phosphate represent high but realistic pulse concentrations which can be found in the hypertrophic waters of the inner Schlei fjord (Schramm et al. 1996). Besides, they correspond to levels used in the standard PES, which is assumed to provide optimal concentrations for macroalgal growth. After 10 d of cultivation, I counted developed germlings (mean of 3 subsamples of 4x4 mm per shell, and of 6 subsamples per tile, n=5) with a dissecting microscope. Germling density cm^{-2} and the relative increase in germling density caused by different nutrient enrichment treatments was calculated. Two-way ANOVAs (factors: phosphate, nitrate, 2x2) were performed on germling density for each species separately in February because species did not develop independently on shells. In April and July, only *Enteromorpha* germlings developed in sufficient amounts on experimental tiles. Data were log- or sqrt(log)-transformed to achieve homogeneity of variances.

4.3. Results

Overwintering

In December 1994, both species overwintered in the form of settled propagules on all substrata tested, but *Enteromorpha* propagules consistently exceeded *Pilayella* propagule

densities by 10- to 50-fold (Fig. 4.1). I found maximum densities of germlings developing from overwintering propagules on rocks, which seemed by far the most suitable substratum for settling or overwintering (with up to 330 propagules cm^{-2} for *Enteromorpha*, and only up to 6.7 propagules cm^{-2} for *Pilayella*). Since *Fucus vesiculosus* has been growing during autumn and winter, germlings developed on older thallus parts only. Propagules of *Petalonia fascia*, *Ectocarpus* sp., *Ulothrix* sp., and *Ulvopsis grevillei* occurred in minor amounts on the substrata tested.

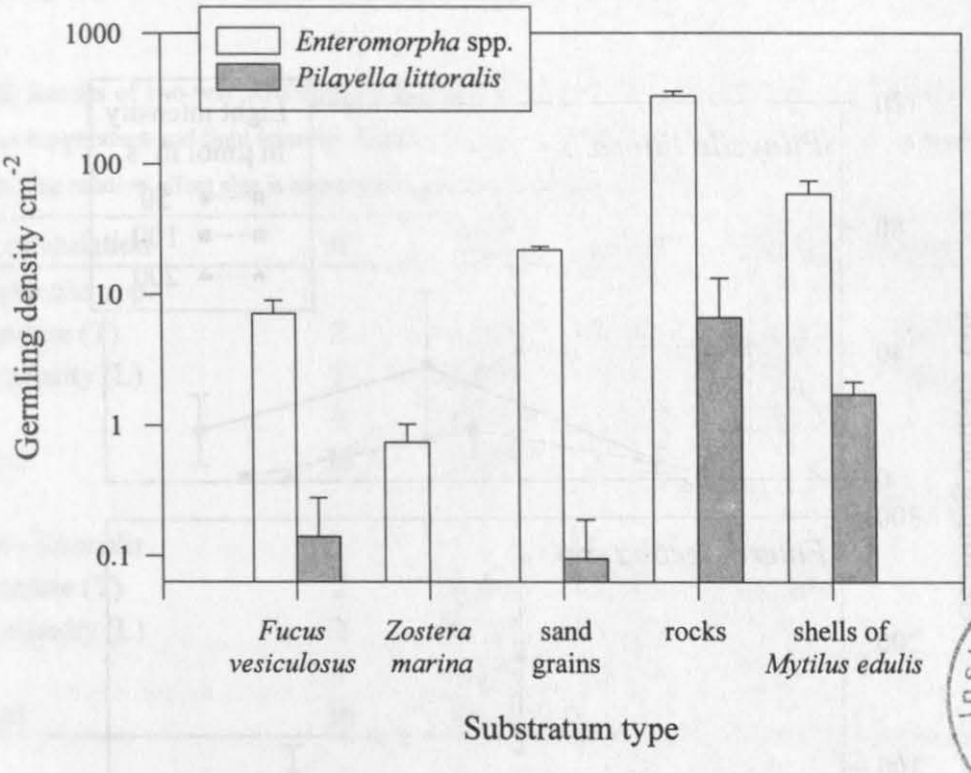

Fig. 4.1. Overwintering of settled propagules of *Enteromorpha* spp. and *Pilayella littoralis* on different substrata collected in the field in December 1994. Densities were determined as developed germlings per cm^2 after 2 wk cultivation in the laboratory and plotted on a log-scale (means ± 1SE, n=6).

Germination in relation to temperature and light intensity

In February 1995, germination rate of *P. littoralis* in relation to the combined effects of temperature and light intensity showed no significant differences among treatments (Fig. 4.2,

Table 4.2). Mean germling density averaged over all treatments was 2.91 (±0.85) cm^{-2} (n=45). In contrast, germination rate of *Enteromorpha* spp. was significantly affected by temperature and light intensity (Fig. 4.2, Table 4.2). A maximum germling density of 190.0 (±76.31) cm^{-2} occurred at 10°C in combination with 200 µmol photons $m^{-2}s^{-1}$. In *Enteromorpha* spp., post-hoc comparisons among temperature treatments showed significantly higher ($p<0.01$) germination rates at 10 and 15°C compared to 5°C. Light intensity positively influenced germination rates which were significantly higher ($p<0.01$) at 200 µmol photons $m^{-2}s^{-1}$ compared to 50 µmol photons $m^{-2}s^{-1}$.

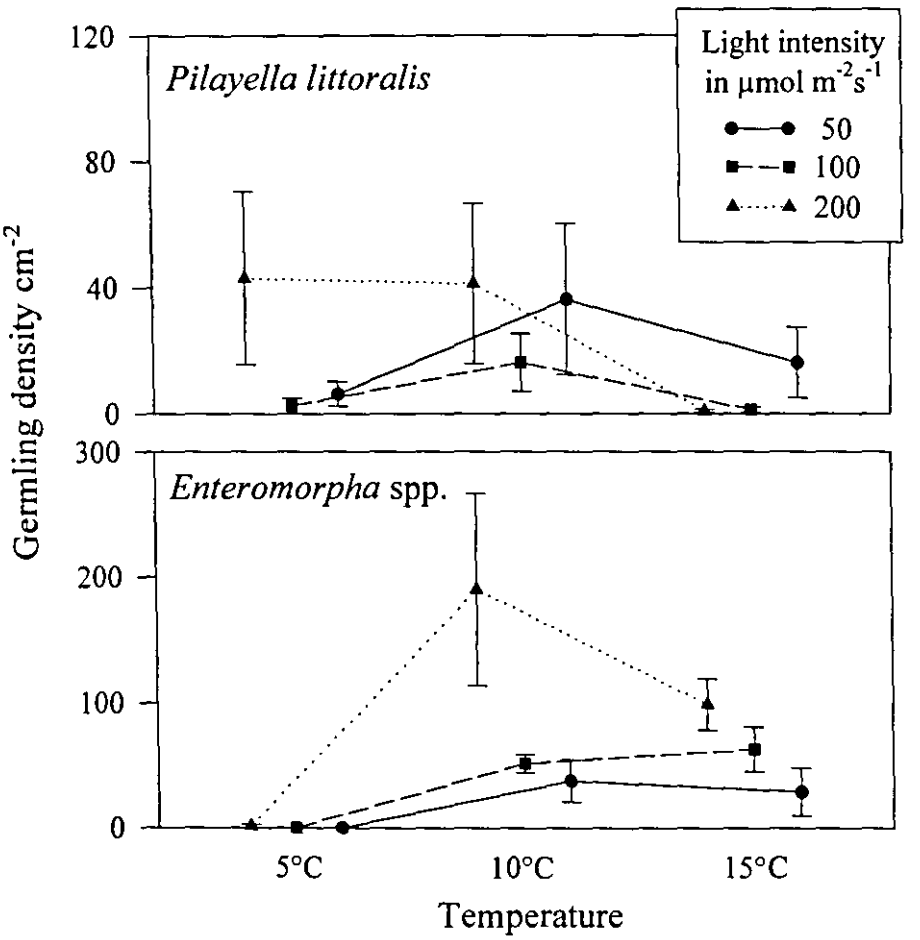

Fig. 4.2. Germination of *Enteromorpha* spp. and *Pilayella littoralis* at 3 temperatures fully crossed with 3 light intensities in February 1995. Shells of *Mytilus edulis* with attached overwintering propagules were used as a source for germination. Density of developed germlings was determined after 10 d of cultivation (mean ± 1SE, n=5). Refer to Table 4.2 for statistical analysis.

Since both species germinated together on the tiles their development may be not independent of each other. As far as comparison is possible, marked differences occurred between species. *Enteromorpha* spp. showed distinctly higher germination rates at 10 and 15°C combined with 100 and 200 µmol photons $m^{-2}s^{-1}$ than *P. littoralis*. In contrast, at 5°C, *P. littoralis* showed distinctly higher germination rates than *Enteromorpha* at all light intensities with a maximum of 42.92 (±27.35) germlings cm^{-2} at 200 µmol photons $m^{-2}s^{-1}$. *Enteromorpha* spp. reached only 1.25 (±1.25) germlings cm^{-2} at 5°C. In *Enteromorpha*, temperature was the factor with the greatest effect size (Table 4.2). The results from this laboratory experiment are in close agreement with my findings from the field where germlings of *P. littoralis* appeared earlier in spring than those of *Enteromorpha* spp. (Chapter 3, Fig. 3.1b).

Table 4.2. Results of two-way ANOVAs on germination rate of *Enteromorpha* spp. and *Pilayella littoralis* in relation to temperature and light intensity. Data were log-transformed to meet the assumption of homogeneity of variances. The relative effect size is expressed as per cent variance explained.

Source of variation	df	MS	F-ratio	P-value	Variance (%)
Enteromorpha spp.					
Temperature (T)	2	4.181	41.737	0.0001	56.7
Light intensity (L)	2	0.827	8.260	0.0011	10.1
T x L	4	0.166	1.655	0.1819	
Residual	36	0.100			
Pilayella littoralis					
Temperature (T)	2	0.363	1.851	0.1718	
Light intensity (L)	2	0.146	0.744	0.4822	
T x L	4	0.136	0.694	0.6012	
Residual	36	0.196			

Germination in relation to day length and light intensity

In *Enteromorpha* spp., day length and light intensity significantly interacted ($p=0.0075$) on germination rate (Fig. 4.3, Table 4.3), whereas in *Pilayella* germling densities were too low to be statistically analyzed. Post-hoc comparisons indicated that germination rate was significantly lower ($p<0.01$) at short days (8:16 h L:D) than at 12:12 h and 16:8 h L:D. Similarly, germination rate was significantly lower ($p<0.01$) at 50 µmol photons $m^{-2}s^{-1}$ than at 100 and 200 µmol photons $m^{-2}s^{-1}$. Comparing the main factors, light intensity was more important explaining 52.8% of total variance than day length (25.6%).

Planned mean comparison between treatment combinations with identical daily sums of 2.88 mol photons $m^{-2}d^{-1}$ (Table 4.1) showed no differences in germination rates, but at daily sums of 5.76 mol photons $m^{-2}d^{-1}$ germination rate was significantly lower ($p=0.0105$) at 8:16/200 than at 16:8/100 (L:D/µmol photons $m^{-2}s^{-1}$ respectively).

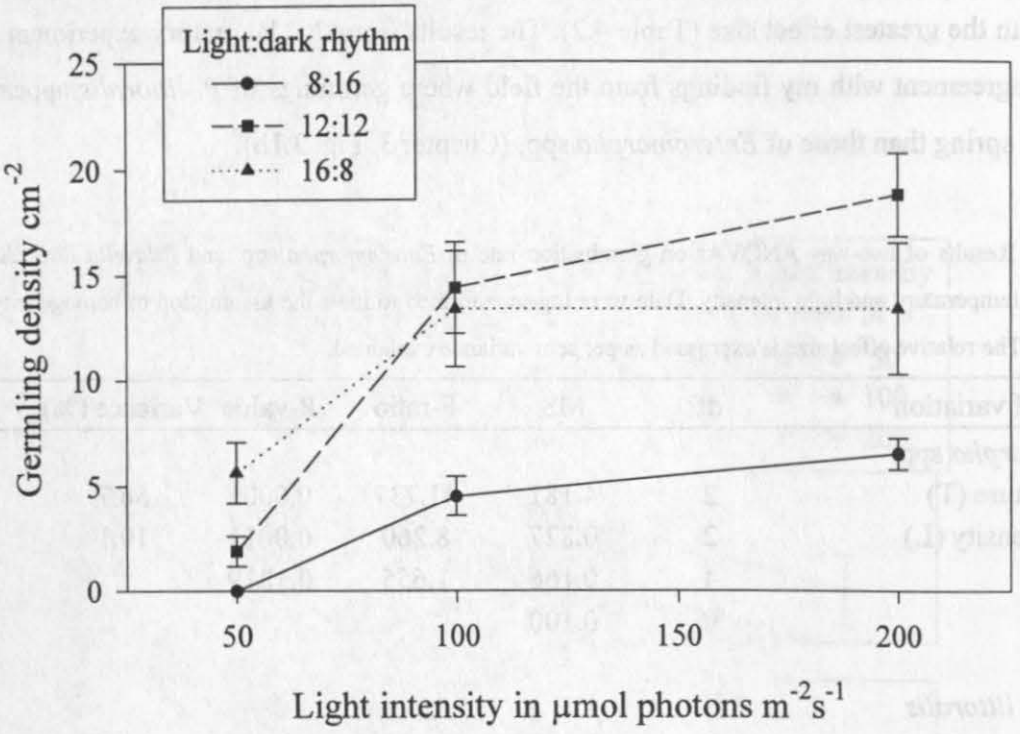

Fig. 4.3. Germination of *Enteromorpha* spp. at three day lengths fully crossed with three light intensities in April 1995. Ceramic tiles with settled propagules were used as a source for germination. Density of developed germlings was determined after 10 d of cultivation (mean ± 1SE, n=5). One extreme outlier was deleted from the data set. Refer to Table 4.3 for statistical analysis.

Table 4.3. Results of a two-way ANOVA on germination rate of *Enteromorpha* spp. in relation to day length and light intensity. Data were log-transformed to meet the assumption of homogeneity of variances. The relative effect size is expressed as per cent variance explained. I deleted one extreme outlier from the data set.

Source of variation	df	MS	F-ratio	P-value	Variance (%)
Day length (D)	2	1.046	34.408	0.0001	25.6
Light intensity (L)	2	2.129	69.997	0.0001	52.8
D x L	4	0.126	4.144	0.0075	4.8
Residual	35	0.030			

Germination in relation to nutrient enrichment

In February 1995, germination of *Enteromorpha* spp. and *Pilayella littoralis* from dormant propagules on mussel shells was significantly enhanced by nutrient enrichment (Fig. 4.4, Table 4.4). In both species, phosphate enrichment showed a greater effect on germination rate than nitrate enrichment and explained 72% and 83% of total variance in *P. littoralis* and *Enteromorpha* spp. respectively. While phosphate enrichment resulted in an 8-fold increase of germling density in *Pilayella* and an 11-fold increase in *Enteromorpha*, nitrate enrichment increased germling densities only 2-fold in both species. Combined enrichment with both nutrients caused a 15-fold increase in *Pilayella* and a 20-fold increase in *Enteromorpha*. Since background nitrogen levels were rather high in February (50 µmol l^{-1} nitrate, 7 µmol l^{-1} ammonium), germination occurred without any nutrient enrichment.

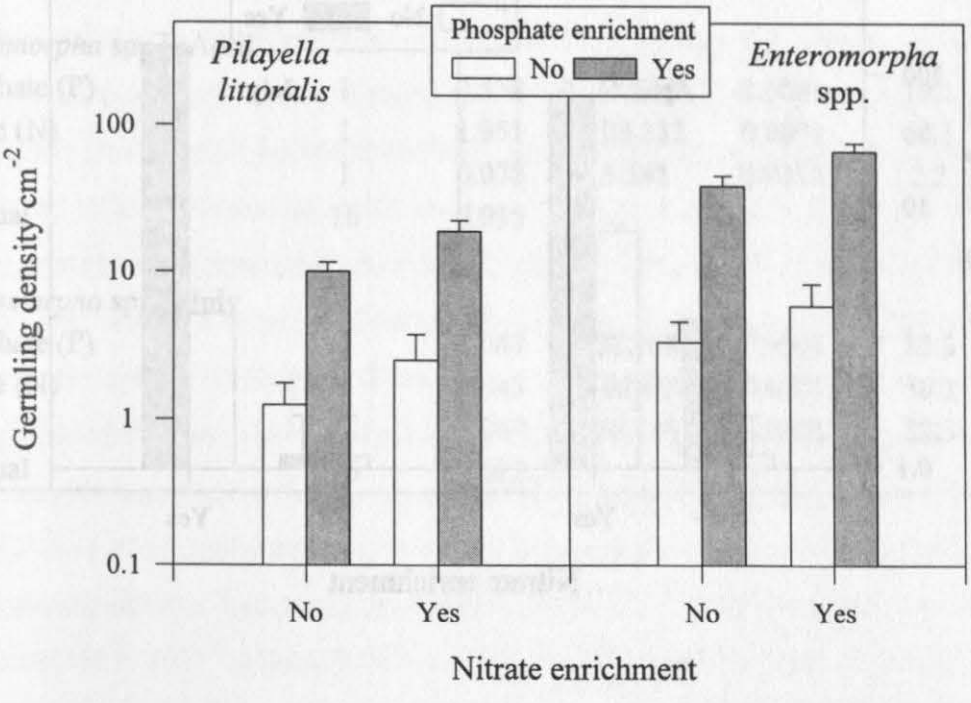

Fig. 4.4. Germination of *Enteromorpha* spp. and *Pilayella littoralis* in relation to a single pulse enrichment of phosphate (30 µmol l^{-1}) and nitrate (500 µmol l^{-1}) in February 1995. Shells of *Mytilus edulis* with attached overwintering propagules were used as a source for germination. Density of developed germlings was determined after 10 d of cultivation and plotted on a log-scale (mean ± 1SE, n=5). Background seawater nutrient levels correspond to 50 µmol l^{-1} nitrate, 7 µmol l^{-1} ammonium, 1 µmol l^{-1} phosphate. Refer to Table 4.4 for statistical analysis.

In April and July, *Pilayella* only germinated in minor amounts on tiles and data were insufficient for analysis. In both months, *Enteromorpha* showed only small germination rates without nutrient enrichment (Fig. 4.5). While phosphate enrichment alone enhanced germination rate 11-fold in April, this had no effect at all in July. Nitrate enrichment alone resulted in a 50-fold increase in germination rate in April and a 12-fold increase in July. Combined enrichment of both nutrients showed an enhancement of germination rate by a factor of 556 in April and 1324 in July. Thus, the significant interactions between the two nutrient treatments (Table 4.4) became more pronounced in July (p=0.0001) than in April (p=0.0373).

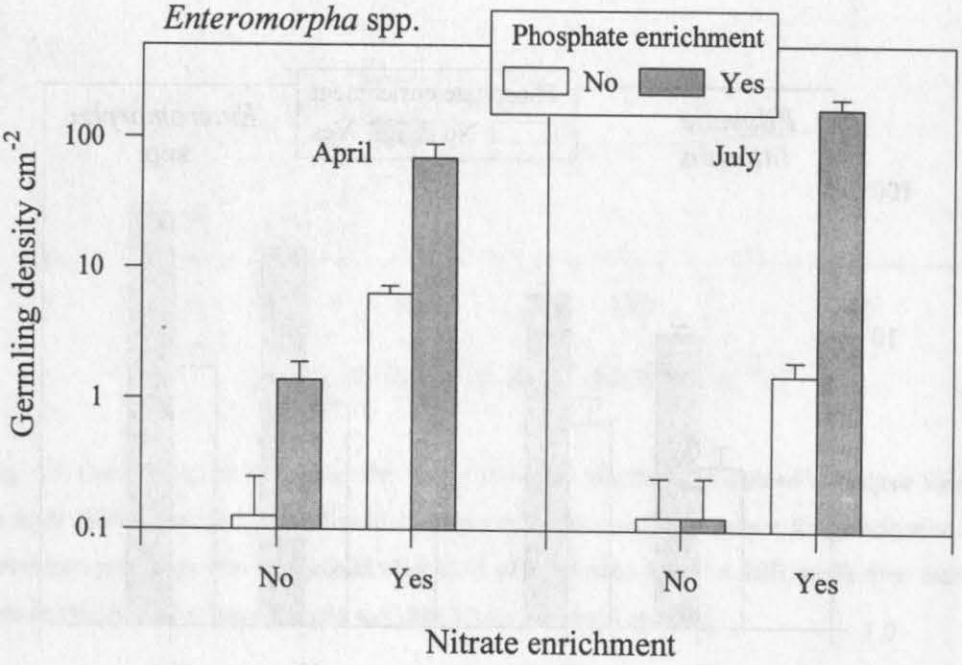

Fig. 4.5. Germination of *Enteromorpha* spp. in relation to a single pulse enrichment of phosphate (30 µmol l^{-1}) and nitrate (500 µmol l^{-1}) in April and July 1995. Ceramic tiles with newly settled propagules were used as a source for germination. Density of developed germlings was determined after 10 d of cultivation and plotted on a log-scale (mean ± 1SE, n=5). Background seawater nutrient levels correspond to 3.3 µmol l^{-1} nitrate, 0.9 µmol l^{-1} ammonium, 0.1 µmol l^{-1} phosphate in April and 0.5, 0.4, 0.5 in July respectively. Refer to Table 4.4 for statistical analysis.

Table 4.4. Results of two-way ANOVAs on germination rate of *Enteromorpha* spp. and *Pilayella littoralis* in relation to nutrient enrichment in February, April, and July 1995. Nutrient treatments were unenriched or enriched with either 30 µmol l^{-1} phosphate or 500 µmol l^{-1} nitrate or both. Data were log-transformed in February, and sqrt(log)-transformed in April and July to meet the assumption of homogeneity of variances. The relative effect size is expressed as per cent variance explained.

Source of variation	df	MS	F-ratio	P-value	Variance (%)
Pilayella littoralis - February					
Phosphate (P)	1	0.779	66.138	0.0001	71.8
Nitrate (N)	1	0.069	5.870	0.0276	5.3
P x N	1	0.020	1.684	0.2127	
Residual	16	0.012			
Enteromorpha spp. - February					
Phosphate (P)	1	2.663	118.192	0.0001	83.0
Nitrate (N)	1	0.113	5.032	0.0394	2.8
P x N	1	0.023	1.010	0.3298	
Residual	16	0.023			
Enteromorpha spp. - April					
Phosphate (P)	1	0.558	36.955	0.0001	19.1
Nitrate (N)	1	1.951	129.232	0.0001	68.1
P x N	1	0.078	5.161	0.0373	2.2
Residual	16	0.015			
Enteromorpha spp. - July					
Phosphate (P)	1	1.047	88.748	0.0001	22.3
Nitrate (N)	1	2.343	198.697	0.0001	50.3
P x N	1	1.047	88.748	0.0001	22.3
Residual	16	0.012			

4.4. Discussion

My observations and experiments suggest that early life stages may be of critical importance for population dynamics of opportunistic macroalgae in the Baltic Sea. Based on my results, I propose that overwintering in a propagule bank and the timing of germination out of this bank in early spring may be important processes controlling the initiation of macroalgal blooms and species dominance patterns within these blooms.

Overwintering of propagules (or seeds) is a strategy of surviving unfavorable conditions in an environment with pronounced seasonality. In so-called aseasonal annuals (Sears & Wilce 1975), adult thalli survive in the deeper subtidal zone and act as a source for a new generation. In seasonal annuals, recruitment in spring occurs from overwintering adult thalli or thallus fragments which persist buried in the sediment of soft bottoms (Fletcher & Callow 1992, Schories 1995b), from surviving crustose life phases (Lüning 1990), or from overwintering cryptic microscopic forms which may have analogous functions to terrestrial seed banks (Chapman 1986, Hoffmann & Santelices 1991). Investigations of these "banks of microscopic forms" are rare. A detailed characterization of such an assemblage of microscopic forms, their species composition and turnover, was done for tide pools on a Chilean shoreline (Santelices et al. 1995). In these tide pools, both perennial and ephemeral species (a total of 25 taxa) were present as microscopic forms. The authors suggested that the bank seemed to be more important for the survival of perennial species because of their low-colonizing capacity. At my study site, both *P. littoralis* and *Enteromorpha* spp. were absent as macroscopic thalli in winter. I showed that both species overwinter abundantly in the form of cryptic microscopic forms (Fig. 4.1). These forms, which were not visible under a dissecting microscope, may be settled but not germinated propagules, or propagules which have developed into microscopic thalli which suspend growth while environmental conditions are unfavorable. Propagules of *Enteromorpha* have been found to build up a solid cell wall immediately after attachment to a substratum, and this may provide physical protection (Fletcher & Callow 1992). In the majority of macroalgae investigated, germination proceeds within 24 h after attachment with no obvious resting stages (Santelices 1990, Fletcher & Callow 1992). However, dormancy has been reported in the genus *Dictyota* after initial establishment of propagules (Richardson 1979). In the Wadden Sea, large quantities of *Enteromorpha* propagules have been found to overwinter in sediments (Schories 1995b). Other dormancy strategies involve gametophytes, germlings and algal embryos (reviewed by Hoffmann & Santelices 1991). Some of these forms may persist for extended periods of time. Settled propagules of *Enteromorpha* spp. have been reported to survive >10 months in darkness at 5°C and 15°C but survival rates decreased with time and increasing temperature (Schories 1995a). Beside their dark resistance, *Enteromorpha* propagules were able to tolerate low temperatures and even frost (Kylin 1947, Schories 1995a).

Various substrata can be used for overwintering. I found that rocks supported 50- to 250-fold higher densities of overwintering propagules than macrophyte substrata (*Fucus vesiculosus* and *Zostera marina*) and appeared to be the most important substratum for overwintering at my study site. On soft bottoms, the shells of the mud snail *Hydrobia ulvae* have been reported to be the most suitable substratum for overwintering of *Enteromorpha* spp. (Schories 1995b).

On five substrata, I found 10- to 50-fold higher overwintering propagule densities for *Enteromorpha* compared to *Pilayella*. These high densities may be due to the massive reproductive output of *Enteromorpha* during summer (Chapter 3) which was several times higher and lasted longer than in *Pilayella*. Given the relatively low densities of overwintering propagules and the high cover of germlings observed in early spring, it is likely that *Pilayella* initiates reproduction shortly after germination. Indeed, laboratory cultures reproduced within <1 month after germination (Müller & Stache 1989). In addition, other overwintering strategies may occur in *Pilayella*. In Newfoundland, *P. littoralis* has been found year-round in the subtidal, but as a distinct summer annual in the intertidal zone (Steele & Whittick 1991). Similar distribution patterns, along with a reproductive period in winter has been reported for *P. littoralis* in Finland (Kiirikki & Lehvo 1997). In this study, I found no evidence for recruitment from overwintering thalli.

In spring, the timing of germination may be important since the environmental conditions become less favorable later in the year. As a regular pattern in the Baltic (and many temperate aquatic systems), high winter nutrient concentrations decline steeply in late spring, when the phytoplankton bloom begins (Lüning 1990). Subsequently, high phytoplankton densities attenuate incoming light and light limitation may occur, depending on water depth. Moreover, in late spring, mesoherbivores increase in abundance and activity (Chapter 6, Schramm et al. 1996). With rising temperature, light intensity and daylength, development of spring annuals is initiated, whereas the limiting factor is probably species specific. Favorable abiotic and biotic conditions may define a "recruitment window" of optimal germination and growth conditions (Deysher & Dean 1986). At my study site, *Pilayella* occurred earlier in the germling stage than *Enteromorpha* (Chapter 3, Fig. 3.1b). This pattern can be explained by an earlier "recruitment window" of *Pilayella*, which germinated abundantly at 5°C (Fig. 4.2), a temperature which was not exceeded in the field until the end of March (Chapter 2, Fig. 2.2). Germination of *Enteromorpha* was largely inhibited at this temperature. In my laboratory

experiments, *Enteromorpha* germinated massively only at 10 and 15°C. This pattern was paralleled in the field, when 10°C was exceeded in the end of April. Thus, *Pilayella* germlings had a time advantage of at least one month before *Enteromorpha* appeared. Pre-emptive space competition may occur among developing *Pilayella* and *Enteromorpha* (see Chapter 7). Similarly, space pre-emption has been found among other competing macroalgae (Hruby & Norton 1979, Sousa 1979, Reed 1990).

Germination of *Enteromorpha* spp. and *Pilayella littoralis* in spring seems to be controlled by abiotic factors, among which temperature rather than light tends to be the limiting factor. This is in concordance with terrestrial communities where predominantly temperature and to some extent light intensity triggers germination of seeds in spring (Fenner 1992). Within the factor light, light intensity was more important than day length in affecting germination of *Enteromorpha*. Germination seemed not to be triggered by photoperiod since it occurred independently of short or long day conditions. In other algae such as *Spyridia filamentosa*, germination may be suppressed in short day conditions (Provasoli 1965). In my study, light intensity and day length showed interacting effects on germination. At low light levels (daily sum of 2.88 mol photons $m^{-2}d^{-1}$), additive effects of day length and light intensity occurred and thus only total amount of photon fluency was important for germination of *Enteromorpha* spp. In contrast, at higher light levels (daily sums of 5.76 mol photons $m^{-2}d^{-1}$), long days (16:8 L:D) combined with 100 µmol photons $m^{-2}s^{-1}$ were more advantageous than short days (8:16 L:D) combined with 200 µmol photons $m^{-2}s^{-1}$. Thus, I conclude that germling development is light saturated above 100 µmol photons $m^{-2}s^{-1}$ and further increase in germination rate only occurs by an elongation of day length and not by increasing light intensity. Since germination rates were similar at 12:12 and 16:8 L:D combined with 100 or 200 µmol $m^{-2}s^{-1}$, I assume that light saturation can occur quite early in the year in March, depending on the water depth (Chapter 2, Fig. 2.3). Light saturation at 80 to 120 µmol photons $m^{-2}s^{-1}$ at a temperature of 15°C has also been reported for germlings of several *Enteromorpha* species in the North Sea (Lotze 1994). However, light saturation of germination is species dependent and in some algae germination is not affected by the light level at all (reviewed in Santelices 1990).

As soon as temperature and light conditions become favorable in early spring and thus open the recruitment window, nutrient concentrations in the water decline (Chapter 2, Fig. 2.4). In 1995, phosphate concentrations were close to zero from mid March until mid June,

nitrate and ammonium were depleted from mid May to the end of July. Germination of *Pilayella* and *Enteromorpha* occurred under field nutrient concentrations in February, but germination rate could potentially be enhanced by further enrichment with phosphate (8- and 11-fold), nitrate (2-fold) or both (15- and 20-fold) in *Pilayella* and *Enteromorpha* respectively. Thus, increasing eutrophication with resulting enhanced winter nutrient concentrations may cause a further increase in spring recruitment of annual algae if temperature and light conditions are favorable. Nitrogen limitation was evident for development of early stages in *Enteromorpha* in the North Sea (Lotze 1994, Schories 1995a), and for the productivity of adult algae in many coastal marine ecosystems (e.g. Ryther & Dunstan 1971, Chapman & Craigie 1977, Howarth 1988, Fong et al. 1993). However, Hoffmann et al. (1984) described only minor effects of nutrient concentrations on germination of *Lessonia nigrescens* and discussed the use of internal nutrient reserves for germination. In my study, the potential P-limitation in February shifted to strong N-limitation in spring and summer. Seasonal variation of nutrient limitation caused by seasonal variability of several environmental factors has been suggested from physiological experiments (e.g. Duke et al. 1986, 1989, Fong et al. 1993). In April and July, germination of *Enteromorpha* did not occur in batch culture with unenriched seawater from the study site. However, in the field, germlings of *Enteromorpha* occurred continually, covering 20-40% of hard substratum. Water motion has been shown to enhance nutrient availability (Parker 1981). Moreover, irregular nutrient pulses may be used for algal germination in the field. Such pulses can be caused by nutrient recycling through the detritus food chain (Pregnall & Miller 1988, Lavery & McComb 1991, Hanisak 1993), herbivore excretion (Williams & Carpenter 1988), nutrient flux out of the sediment (Christiansen et al. 1992, Brennan & Wilson 1993), wind-driven upwelling (Kiirikki & Blomster 1996), or wind-driven nutrient outflow from the inner Schlei fjord (Chapter 2).

The amount of overwintering propagules as well as high germination rates suggest that *Enteromorpha* has a good potential to form a mass bloom in spring. However, after successful germination *Enteromorpha* still remained largely inhibited at the germling stage, which seemed to be a bottleneck in the development of this species. This is in contrast to *Pilayella*, where the germling peak was followed by a large corresponding adult biomass (Chapter 3, Fig. 3.1c). I hypothesize that intense consumption of *Enteromorpha* germlings by abundant mesoherbivores may suppress the development of adult *Enteromorpha*. This is tested in Chapter 6.

In other areas, temperatures exceeding 24°C were found to inhibit germination in *Enteromorpha* (Schories 1995a) and temperature from 28-31°C were reported to be the upper survival level of this cosmopolitan species (Bischoff & Wiencke 1993). In comparison, summer die back of *Ulva lactuca* has been explained by reduced productivity at 25°C (Rivers & Peckol 1995). However, these temperatures were never reached at my study site and thus, summer temperature may not limit *Enteromorpha* development. In contrast, *Pilayella* appeared to be less resistant towards higher temperatures. At my study site in 1995-1998, adults of this species regularly disappeared in July when temperature exceeded 20°C and in 1995, germination rate decreased already in May and June. Strong reduction of growth at 20°C compared with 5-15°C and an upper survival limit between 21-25°C was reported for this species by Bischoff & Wiencke (1993). Field experiments in 1997 and 1998 showed that herbivores and nutrient enrichment had no effect on the sudden disintegration and disappearance of *Pilayella* in July suggesting that temperatures above 20°C are most likely the limiting factor for further development of this species (Chapter 7, Worm & Lotze unpublished). An additional limiting factor could be elevated irradiance or direct exposure to sunlight which was reported to be damaging or lethal to germlings of some macroalgal species (Santelices 1990), but may occur rarely in the tideless Baltic Sea. Another possibility causing the summer die back of *Pilayella* may be an epidemic infection by marine fungi or viruses (Wilce et al. 1982, Maier et al. in press).

Overall, the recruitment window of *Enteromorpha* and *Pilayella* is limited by abiotic (temperature > light) control of macroalgal development in early spring which may shift to a combined abiotic (resource control, high temperature) and biotic (herbivory, competition) control in late spring and summer. Within this pattern significant differences between early life stages of *Enteromorpha* and *Pilayella* occurred and are hypothesized to be important for competitive abilities and species dominance pattern.

Chapter 5

Comparative ecophysiology of adult stages: growth response and nutrient kinetics

5.1. Introduction

Ecophysiological traits of species in conjunction with abiotic parameters in the environment define their potential distribution in space and time (fundamental niche, Keddy 1989). However, their actual distribution and abundance in the environment (realized niche) is modified by ecological traits such as competitive abilities and susceptibility to herbivores (Lubchenco 1980, Keddy 1989, Carpenter 1990, Krebs 1994). In this chapter, I analyze selected ecophysiological traits of co-occurring *Enteromorpha* and *Pilayella* to test whether differences in physiology can explain the observed dominance of *Pilayella* over *Enteromorpha* in the Baltic Sea. The most obvious difference comparing the brackish Baltic Sea with fully marine areas where macroalgal blooms occur is the low salinity in the former. It has been demonstrated however, that productivity levels of *Pilayella* and *Enteromorpha* are not reduced under brackish salinity conditions in comparison with fully marine sites (Bolton 1979a, Reed & Russell 1979). Thus, the unusual dominance of *Pilayella* can not be explained by better adaptation to reduced salinity.

Some important physiological properties in algae are thought to be coupled to morphological attributes such as thallus differentiation and structure (Littler & Littler 1980, Steneck & Dethier 1994), SA/V-ratio (Rosenberg & Ramus 1984, Nielsen & Sand-Jensen 1990), and size class (Hein et al. 1995). The results of former studies were synthesized in functional-group classifications which have the capacity to explain some aspects in species distribution patterns such as zonation or succession (Littler & Littler 1980, Steneck & Dethier 1994, Hein et al. 1995). On the other hand, there is evidence that species with similar morphology can perform very differently. As an example, several *Enteromorpha* species occurring in a seasonal succession within green algal mats in the North Sea had different temperature and light optima for growth (Lotze 1994). In addition to such interspecific differences, intraspecific differences in productivity levels have been described, mainly in algae with a heteromorphic life cycle (Littler & Littler 1980). As a major hypothesis of my study, I propose further intraspecific differences on the ecophysiological and ecological level

among different life stages of the same species. Here, I test whether interspecific differences in ecophysiological demands of *Enteromorpha* and *Pilayella* germlings (Chapter 4) are also found in adult stages.

Pilayella with its filamentous, highly branched thalli has a SA/V-ratio more than 10-fold higher than that of the foliose thalli of *Enteromorpha intestinalis* (Nielsen & Sand-Jensen 1990, own measurements). Hence, *Pilayella* has a greater metabolically active surface area than *Enteromorpha* which is generally thought to translate into higher nutrient uptake and possibly growth rates (Rosenberg & Ramus 1984, Carpenter 1990). Comparison of literature data on nutrient uptake or growth rates for both genera is not possible since productivity studies on *Pilayella* are rare and have not been performed under experimental conditions comparable to those used for *Enteromorpha*. The only comparative nutrient uptake study available showed similar uptake rates of nitrogen and phosphorus in *Enteromorpha ahlneriana* and *Pilayella littoralis* (Wallentinus 1984). However, uptake kinetics of *E. ahlneriana* with its highly branched thallus may not be similar to *E. intestinalis*, which is the most abundant *Enteromorpha* species at my study site. Moreover, temperature varied among the experiments performed by Wallentinus (1984) and time dependency of nutrient uptake rates was not considered (Pedersen 1994).

In this chapter, I asked whether the dominance of *Pilayella* over *Enteromorpha* may be explained by differences in growth rates or nutrient kinetics. Within this framework, I compared the ecophysiological demands of adult stages with those of early developmental stages (Chapter 4). Towards this goal, I designed tests very similar to the germination experiments (Chapter 4) and checked growth rates of adult thalli of *E. intestinalis* and *P. littoralis* in relation to (1) temperature and light intensity, and (2) nutrient enrichment. Nutrient uptake rates were determined at several incubation times. In this way, I searched for species-specific differences in fast responses towards short nutrient pulses which are common in eutrophic fjords and estuaries such as the study site.

5.2. Material & methods

All studies were conducted in June 1995 when both species were abundant in the field and the high epiphytic diatom load on *Pilayella* had disappeared (Chapter 3). Thus, a possible confounding with physiological properties of the epiphytic diatoms was avoided.

Growth rate in relation to temperature and light intensity

In the beginning of June, I determined growth rates of *Pilayella littoralis* and *Enteromorpha intestinalis* at three temperatures (5, 10, 15°C) fully crossed with three light intensities (50, 100, 200 µmol photons $m^{-2}s^{-1}$ in a 14:10 h L:D). Algal material without macroscopic epiphytes was freshly collected in the field. Treatments (n=5 for each treatment combination) started with a standard algal biomass of 0.1 g WW in 750 ml PES with GeO_2 added. I determined algal wet weight (WW) in a standardized manner with a specially constructed centrifuge, operating as a spin drier, removing adherent water for 30 s with constant r.p.m. Media were changed every 2 d. After 10 d, algal material was reweighed and relative growth rates ($RGR = (\ln w_1 - \ln w_2) / (t_2 - t_1)$, with w = wet weight, t = time) were calculated. Statistical analysis was performed by 3-way ANOVA (factors: light, temperature, species, 3x3x2) on the dependent variable RGR. Data were log-transformed to achieve homogeneity of variances. Post- hoc comparisons were done according to Tukey-Kramer procedure.

Growth rate in relation to nutrient enrichment

Growth experiments testing nutrient effects on *E. intestinalis* and *P. littoralis* were designed closely to resemble the experiment described above. Levels of nutrient enrichment were chosen as high, short-time pulse concentrations which were about 5 times higher than maximum concentrations measured in the outer Schlei (Chapter 2). Effects of long-time, low-level enrichment were studied as a part of a factorial field experiment in 1997 (Chapter 7).

In a first trial, thalli of *Enteromorpha* and *Pilayella* were exposed to 500 µmol l^{-1} nitrate (as $NaNO_3$), 50 µmol l^{-1} ammonium (as NH_4Cl), and 5 µmol l^{-1} urea ($CO(NH_2)_2$) separately. Treatments with no nitrogen enrichment were run as controls. To prevent P-limitation 30 µmol l^{-1} phosphate (as KH_2PO_4) was added to all treatments. In a further trial, combined enrichments with 30 µmol l^{-1} phosphate and 500 µmol l^{-1} nitrate were performed. Each treatment (n=5) was started with a standard weight (described above) of 0.1 g algal WW in 750 ml freshly collected, 0.2 µm filtered seawater with nutrients with GeO_2 added. Background seawater levels were 0.09 µmol l^{-1} phosphate, 3.49 µmol l^{-1} nitrate, 0.80 µmol l^{-1} ammonium, and 0.61 µmol l^{-1} urea. Media were replaced every 2 d. All tests were run at standard T/L-conditions. After 10 d, algal material was reweighed and RGR was calculated.

Statistical analysis was performed by 3-way ANOVA (factors: species, nitrate, phosphate, 2x2x2) and 2-way ANOVA (factors: species, nitrogen 2x2) on the dependent variable RGR. Untransformed data met the assumption of homogeneity of variances.

Nutrient uptake

In the end of June, I determined uptake rates of nitrate, ammonium and phosphate of *Enteromorpha intestinalis* and *Pilayella littoralis* by using a combination of the perturbation and the multiple flask method as recommended by Pedersen (1994). While the multiple flask incubation with different substrate concentrations and short incubation time is the best method for estimation of kinetic parameters in nutrient-limited algae, the combination with the perturbation methods provides important information on the time dependency of nutrient uptake (Harrison et al. 1989, Pedersen 1994). Time intervals and concentrations used in the following experiments were chosen according to the results of a pilot study (unpublished data).

Uptake experiments with nitrate ($NaNO_3$) and ammonium (NH_4Cl) were started with initial nutrient concentrations of 0, 5, 10, 20, 50, 100, 200, 500 µmol l^{-1}. Although I found no evidence for potential phosphorus limitation of nitrogen uptake in the literature all experiments received a precautionary moderate phosphate (KH_2PO_4) addition of 3 µmol l^{-1} to avoid P-shortage. Uptake rate was followed by analysing nitrate concentrations in the media at 0, 30, 60, 120, 180 min in the nitrate experiment and ammonium at 0, 15, 30, 45, 60, 120 min in the ammonium experiment. The phosphate uptake experiment was started with initial concentrations of 0, 3, 6, 12, 18, 30 µmol l^{-1} phosphate and an additional 50 µmol l^{-1} nitrate and 50 µmol l^{-1} ammonium and was sampled at 0, 60, 120, 240 min. Uptake rates measured with this experimental design represent transient responses to nutrient pulses (surge uptake) and should be distinguished from acclimated (steady state) uptake rates measured in continuous culture.

Fresh algal material was collected at the study site and stored in filtered seawater from the site for 1 d at standard T/L-conditions until initiation of the experiment. C/N/P analysis indicated N-limitation of algal tissue (N:P=19 in *Pilayella* and 21 in *Enteromorpha*, Chapter 3, Table 3.2, 22.06.95). For all uptake experiments, I used freshly collected and 0.2 µm filtered seawater from the study site with corresponding background nutrient levels of 0.54 µmol l^{-1} phosphate, 0.41 µmol l^{-1} nitrate, 0.56 µmol l^{-1} ammonium. All uptake tests were run

at 15°C and 200 µmol $m^{-2}s^{-1}$ light intensity from 12.00-14.00 or 15.00. Nitrate and ammonium uptake rates were determined in 1 L sterilized glass bottles, phosphate uptake was determined in 1L sterilized PETG (polyethylene terephthalate copolyester, Nalgene) bottles because of phosphate absorption by glass. For adaptation of algae to experimental conditions, I filled beakers with 1 L of 0.2 µm filtered seawater and added 1 g of algal WW (entire thalli) 2 h in advance. Aeration provided continual mixing of the medium. After this adaptive period, I removed the algae carefully with a sieve, added nutrients from a concentrated stock solution, mixed carefully, took the first nutrient sample (1 ml) with an Eppendorf pipette (using 1 tip per sample), and put the algae back into the beaker. The nutrient samples were diluted and analyzed immediately with an autoanalyzer using the methods of Grasshoff et al. (1986). After the last sampling, algae were dried for 48 h at 70°C for DW determination. In each uptake experiment a control without algal material and with addition of 100 µmol l^{-1} nitrate, ammonium or 12 µmol l^{-1} phosphate was run. No autogenic changes in substrate concentrations were detected over the experimental period.

Uptake rates (V) were calculated from changes in substrate concentrations during each sampling interval as µmol $h^{-1}g^{-1}$ DW: $V = ((S_0 \cdot vol_0) - (S_t \cdot vol_t)) / (t \cdot W)$, where S_0 is the actual substrate concentration at the beginning and S_t at the end of a sampling interval, vol_0 is the water volume at the beginning and vol_t at the end of a sampling interval, t is the time of the sampling interval and W is the algal biomass as g DW. Uptake rates were plotted against S_0 for each time interval separately and fitted to the Michaelis-Menten equation, $V = (V_{max} \cdot S_0) / (K_m + S_0)$, using nonlinear least-squares regression. This provided estimates of V_{max} (maximum uptake rate), K_m (half-saturation constant), and α (initial slope = V_{max} / K_m).

For statistical analysis of differences between uptake rates of *Pilayella* and *Enteromorpha* I performed ANCOVA (analysis of covariance) on V_{max} and K_m with "species" as the main factor and "time interval" as a covariate for each nutrient tested. Homogeneity of slopes was tested by analysing the interaction "species x time interval" which was not significant ($p>0.05$) for all three nutrients and thus met the assumptions for ANCOVA.

Estimated kinetic parameters V_{max}, K_m, and α given in the literature were mostly gained by lineralization of the Michaelis-Menten equation. For data comparison, I also calculated V_{max} and K_m by linear regression using DeBoer plot (S/V vs. S) and Eadie-Hofstee plot (V vs. V/S) which may be the most reliable lineralizations for parameter estimation (Dowd & Riggs 1965). However, the variables plotted against each other in these linear transformations are

not independent which creates a severe artifact. Spurious correlations result because the dependent variable in these plots is calculated by incorporating the independent variable (i.e. S/V contains S). Thus, nonlinear least-squares regression analysis should be preferred (I used Marquardt-Levenberg algorithm, the process is iterative).

5.3. Results

Growth rate in relation to temperature and light intensity

Temperature and light intensity significantly (p=0.0141) interacted on growth rate of *Enteromorpha intestinalis* and *Pilayella littoralis* (Fig. 5.1, Table 5.1).

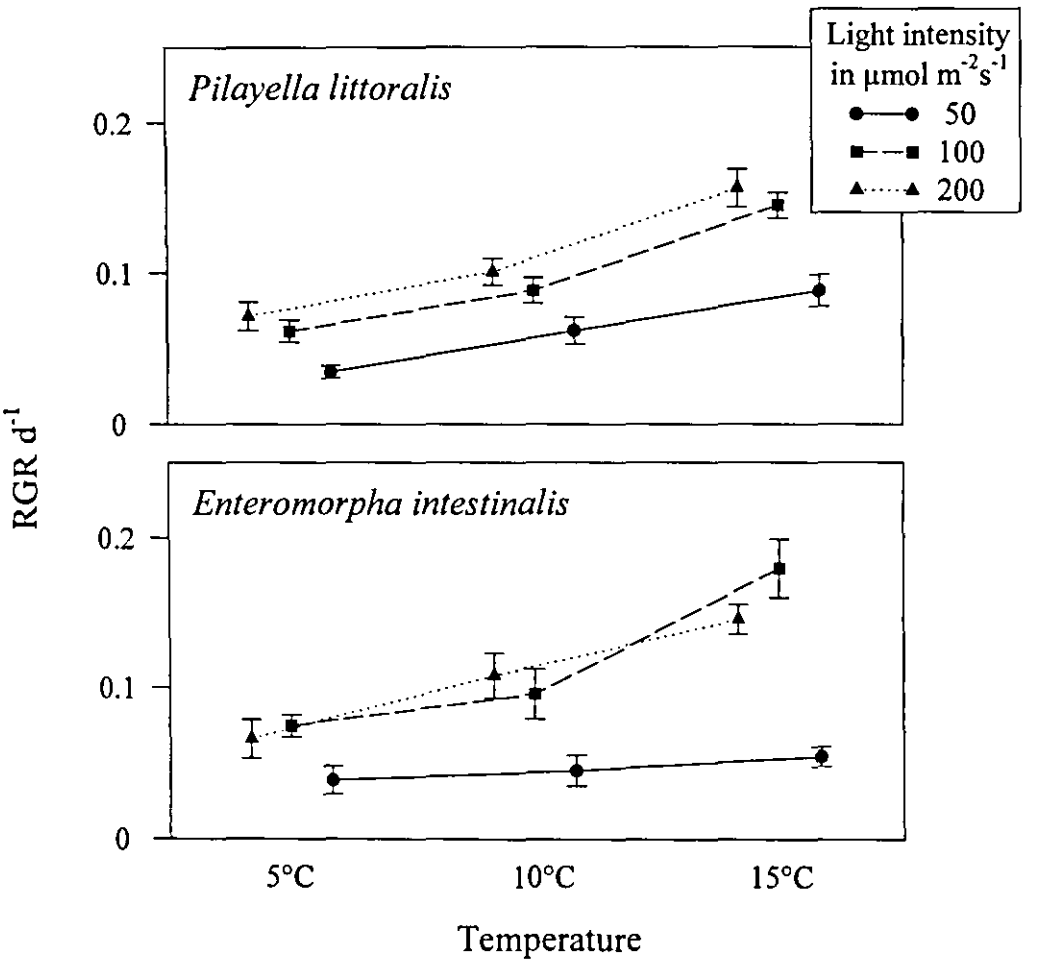

Fig. 5.1. Growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* at 3 temperatures fully crossed with 3 light intensities. Relative growth rate (RGR) d^{-1} was determined by measuring the relative increase in WW (means ± 1SE, n=5). Refer to Table 5.1 for statistical analysis.

Table 5.1. Results of three-way ANOVA on the effects of temperature and light intensity on growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* (factor "species"). Relative effect size is shown as explained variance in %.

Source of variation	df	MS*10^3	F-ratio	P-value	Variance (%)
Species (S)	1	1.038	1.296	0.2587	
Temperature (T)	2	29.679	37.054	0.0001	27.9
Light intensity (L)	2	31.576	39.422	0.0001	29.7
S x T	2	1.661	2.074	0.1331	
S x L	2	2.698	3.369	0.0399	1.8
T x L	4	2.690	3.358	0.0141	3.7
S x T x L	4	1.396	1.743	0.1500	
Residual	72	0.800			

However, the explained variance of this interaction was low (3.7%) and mainly caused by the high enhancement of growth rate in *Enteromorpha* treatments at 15°C and 100 µmol $m^{-2}s^{-1}$. The two species tested only showed a minor difference indicated by a slight species x light intensity interaction (p=0.0399) which explained 1.8% of the total variance. This interaction was caused by higher growth rates of *Pilayella* compared to *Enteromorpha* at 50 µmol photons $m^{-2}s^{-1}$ averaged over all temperatures, whereas at 100 and 200 µmol $m^{-2}s^{-1}$ no differences between species occurred. Compared to the variance explained by the main factors temperature (27.9%) and light intensity (29.7%) the interactions may be less important.

Growth rate in relation to nutrient enrichment

In June 1995, ambient nutrient concentrations in the outer Schlei were almost depleted (Chapter 2) except for short-time wind-driven pulses of nutrient-rich water out of the inner Schlei. In growth experiments, all treatments with nitrogen enrichment significantly increased the growth rate of *E. intestinalis* and *P. littoralis* but no significant differences between the two species were detected (Table 5.2 and A5.1). Nitrate enrichment (500 µmol l^{-1}) more than doubled growth rate in *Enteromorpha* (2.1-fold) and *Pilayella* (2.4-fold). Ammonium enrichment (50 µmol l^{-1}) resulted in a 1.7- and 1.4-fold increase, urea enrichment (5 µmol l^{-1}) in a 1.6- and 1.3-fold increase in growth rate of *Enteromorpha* and *Pilayella* respectively.

No interaction between nitrate and phosphate enrichment was detected in a combined enrichment experiment (Fig. 5.2, Table 5.3). Nitrate enrichment had the main effect on growth rate explaining 45% of variance without a significant difference between species.

Table 5.2. Effects of different nitrogen treatments on relative growth rates of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* (means ± 1SE, n=5). Phosphate enrichment was 30 µmol l^{-1} in all treatments. All nitrogen treatments showed significant effects on growth of both species. No significant differences between species were found (for complete ANOVA tables see Table A5.1).

N-enrichment	RGR - *E. intestinalis*		RGR - *P. littoralis*		P-value
[µmol l^{-1}]	mean	SE	mean	SE	N-enrichment
0	0.049	0.012	0.052	0.007	
NO_3^- (500)	0.103	0.008	0.123	0.005	0.0001
NH_4^+ (50)	0.087	0.014	0.074	0.010	0.0148
Urea (5)	0.079	0.012	0.065	0.003	0.0319

While growth of *Enteromorpha* was not affected by phosphate enrichment, phosphate significantly increased growth of *Pilayella*, indicated by a species x phosphate interaction (p=0.0148). Combined enrichment of nitrate and phosphate resulted in an increase of growth rate by 3.5-times in *Pilayella* and 1.6-times in *Enteromorpha*.

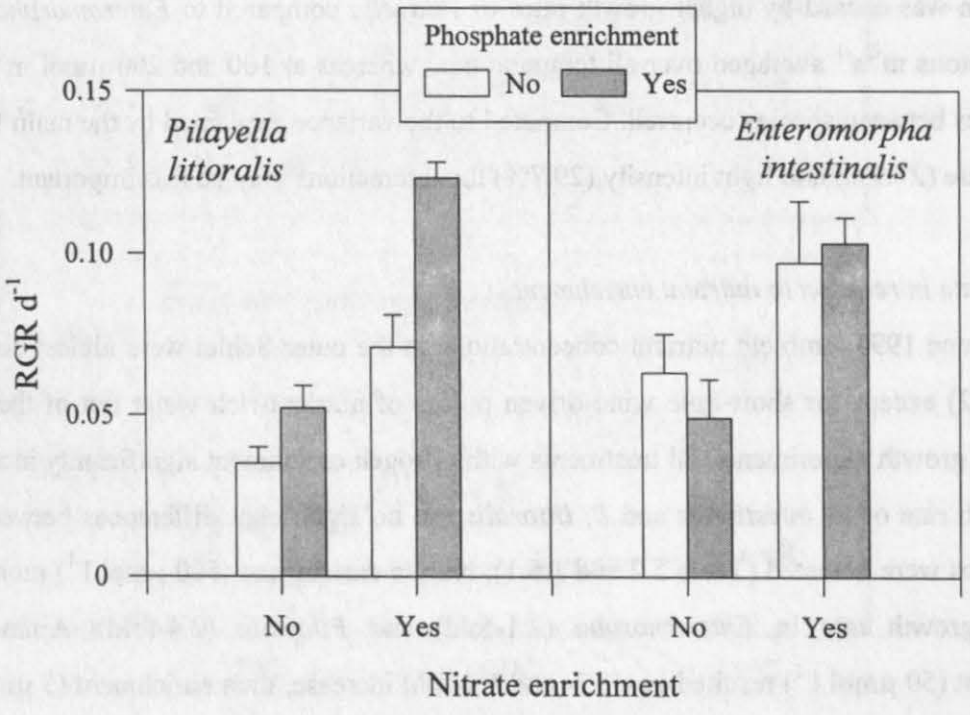

Fig. 5.2. Growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* in relation to phosphate (30 µmol l^{-1}) and nitrate enrichment (500 µmol l^{-1}). RGR d^{-1} was determined by measuring increase of WW (means ± 1SE, n=5). Refer to Table 5.2 for statistical analysis.

Table 5.3. Results of three-way ANOVA on single and combined effects of phosphate (30 µmol l^{-1}) and nitrate (500 µmol l^{-1}) enrichment on growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* (factor "species"). Relative effect size is shown as explained variance in %.

Source of variation	df	MS*10^3	F-ratio	P-value	Variance (%)
Species (S)	1	0.562	0.984	0.3287	
Nitrate (N)	1	23.771	41.623	0.0001	45.0
Phosphate (P)	1	2.243	3.927	0.0562	
S x N	1	0.235	0.411	0.5260	
S x P	1	3.789	6.634	0.0148	6.3
N x P	1	1.920	3.361	0.0761	
S x N x P	1	0.143	0.251	0.6199	
Residual	32	0.571			

Nutrient uptake

Responses of *Enteromorpha intestinalis* and *Pilayella littoralis* to short-term pulses of nitrate, ammonium, and phosphate over several time intervals were investigated at the end of June 1995. No significant differences between the two species were detected in uptake rates of any nutrient tested. However, uptake rates significantly decreased with time (Fig. 5.3, Table A5.3) causing strong declines of lower maximum uptake rates (V_{max}) and lower values of the half-saturation constant (K_m) with time in all three nutrients. Highest uptake rates were achieved during the first 15 min of ammonium uptake with V_{max} of 439 and 467 µmol $h^{-1}g^{-1}$ DW and K_m of 66 and 67 µmol l^{-1} in *Enteromorpha* and *Pilayella* respectively (Table A5.2). Lowest uptake rates were found in phosphate uptake during the last time interval (120-240 min) reaching V_{max} of 14 and 8 µmol $h^{-1}g^{-1}$ DW and K_m of 8 and 4 µmol l^{-1} in *Enteromorpha* and *Pilayella*. The initial slope of uptake curves (α) did not show a significant trend with time in ammonium and nitrate, reaching higher values in ammonium (Table A5.2). In phosphate uptake, statistical analysis revealed significantly higher α-values in *Pilayella* compared to *Enteromorpha* (Table A5.3) and a significant decrease with time was detected. However, this analysis was based on 3 values per species only and should be interpreted with caution.

Parameter estimations via linear transformation by DeBoer and Eadie-Hofstee consistently underestimated V_{max} and K_m values (Table A5.4) compared to results of nonlinear regression analyses.

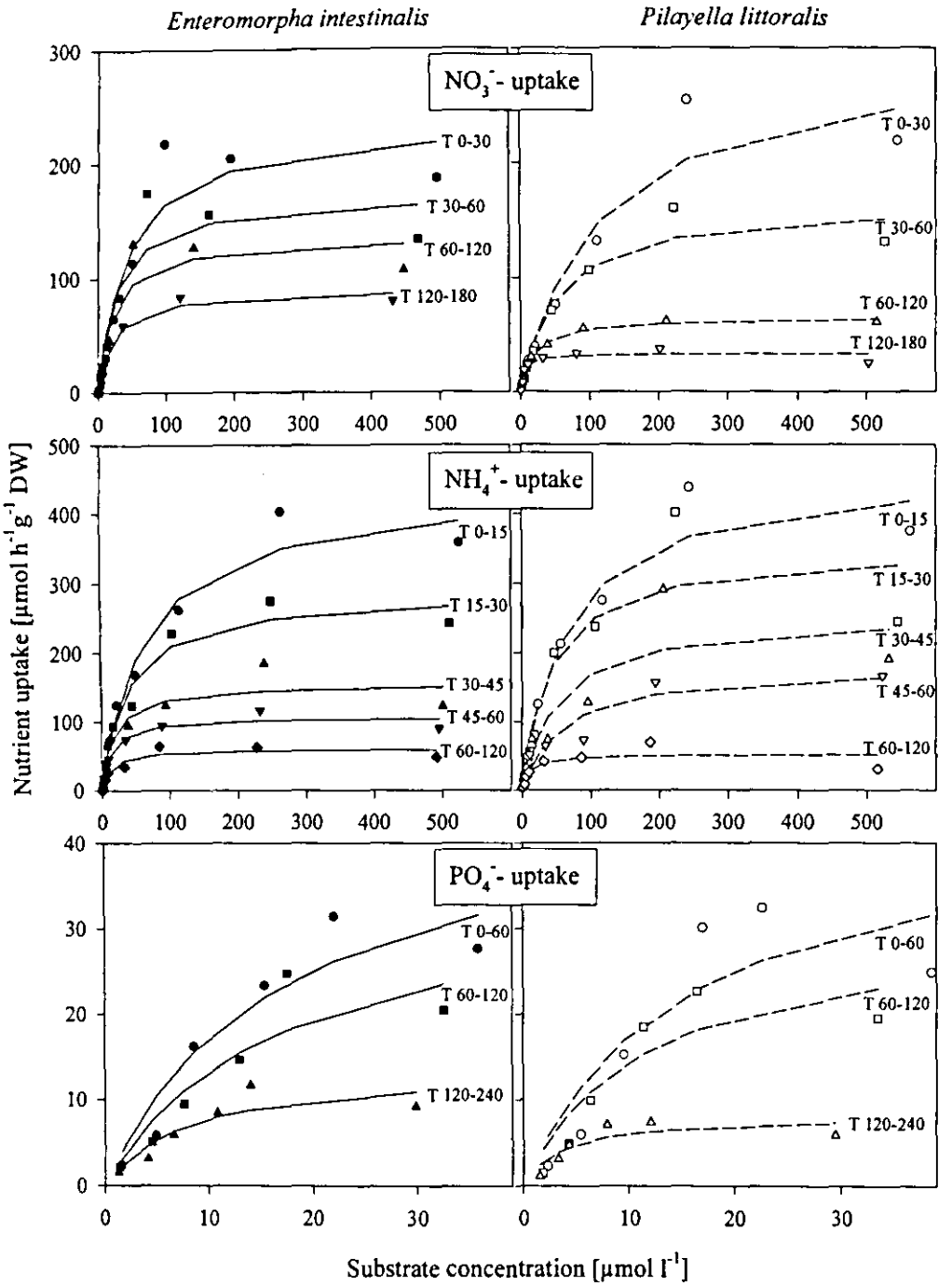

Fig. 5.3. Nutrient uptake of *Pilayella littoralis* and *Enteromorpha intestinalis* in relation to substrate concentration at different time intervals (symbols are following increasing time interval in the order: O, □, Δ, ∇, ◊). Regression lines at different time intervals (T) were calculated by nonlinear regression analyses. For parameter estimation (V_{max}, K_m, α) see Table A5.2, for statistical analyses of species differences see Table A5.3.

5.4. Discussion

Attributes of opportunistic life style (e.g. high rates of nutrient uptake, photosynthesis, growth) are generally accepted to favor filamentous and foliose species so equipped over perennial species with increasing eutrophication (Harlin & Thorne-Miller 1981, Wallentinus 1984, Larsson et al. 1985, Cederwall & Elmgren 1990, Duarte 1995). However, only a few studies have compared the physiology of different opportunistic species in order to explain dominance patterns within macroalgal blooms. In this chapter, I asked whether the observed dominance of *Pilayella* over *Enteromorpha* in the Baltic may be explained by differences in growth rates or nutrient kinetics between the two species. Unexpectedly, adult stages of both algae performed very similarly at various abiotic conditions. Therefore, their ecophysiological properties are of no use in predicting the observed dominance pattern in the field. As a surprise, marked interspecific differences among germlings of *Pilayella* and *Enteromorpha* (Chapter 4) are not paralleled in adults. This indicates that some basic ecophysiological properties of early life stages can not be predicted from measurements on adult algae.

Growth of adult *Pilayella* and *Enteromorpha* increased with rising temperature (5<10<15°C) and light intensity (50<100<200 µmol photons $m^{-2}s^{-1}$) with no major differences between species. Only at 50 µmol photons $m^{-2}s^{-1}$ there was a slight advantage for *Pilayella*, but this light intensity may be only relevant from November to January (Chapter 2, Fig. 2.3). Most importantly, no species x temperature interaction was detected, which demonstrates that differences in responses to temperature found in germlings (Chapter 4) are not found in adults. Thus, the advantage of *Pilayella* of germinating at lower temperature is not paralleled in adult growth. Moreover, *Enteromorpha* is not able to compensate for the time advantage attained by germlings of *Pilayella* by an increased growth rate during the adult stage.

Growth rate of *Enteromorpha* and *Pilayella* did not increase with light intensity from 100 to 200 µmol photons $m^{-2}s^{-1}$. This may indicate light saturation, as already discussed for germination in Chapter 4. This is in concordance with other studies, where light saturation at 15°C was found above levels of 80-125 µmol $m^{-2}s^{-1}$ (Kim et al. 1991, Lotze 1994). Light saturation at levels of 240 and 559 µmol $m^{-2}s^{-1}$ at 20 and 28°C respectively has been reported for *Enteromorpha clathrata* (Shellem & Josselyn 1982, Fitzgerald 1978). This can be explained by a positive relationship between levels of light saturation and temperature (Geertz-Hansen & Sand-Jensen 1992).

Similar to the effects of temperature and light, nitrogen enrichment did not affect growth of adult *Enteromorpha* and *Pilayella* differently. In both algae, growth rates were significantly enhanced by nitrate, ammonium and urea in June when nitrogen concentrations were almost depleted in the field (Chapter 2). Only phosphate enrichment resulted in a selective fertilization of *Pilayella* whereas *Enteromorpha* remained unaffected by this treatment. However, this effect can be regarded as less important because it only explained 6.3% of the variance in growth rates. In contrast, nitrate enrichment explained 45% of the variance (Table 5.3) indicating pronounced N-limitation of both species in summer, similar to the effects on germination (cf. Chapter 4). Compared with the dramatic effects of simultaneous nitrogen and phosphorus enrichment on germination rate of both species (15- to 20-fold increase in February up to 500- to 1000-fold in summer, Chapter 4) the effects of identical treatments on growth of adult *Enteromorpha* and *Pilayella* (1.6- and 3.5-fold increase) seem weak. Thus, in accordance with my initial hypothesis, there is evidence that processes affecting early life stages can be of overriding importance for population dynamics in bloom-forming algae.

Similar growth responses of *Enteromorpha intestinalis* and *Pilayella littoralis* in relation to nutrient enrichment are corroborated by the results of nutrient uptake studies. No major differences in uptake rates of nitrate, ammonium, and phosphate were detected although the two species differ markedly in their morphology and show a more than 10-fold difference in SA/V-ratio. For *Pilayella littoralis* the SA/V-ratio is 1694 (Nielsen & Sand-Jensen 1990) for *Enteromorpha intestinalis* I determined a SA/V-ratio of 140 (20 individuals measured). Higher uptake rates have been shown to be associated with higher SA/V-ratios when comparing algal functional groups (Rosenberg & Ramus 1984). For example, microalgae have higher uptake rates than macroalgae (Hein et al. 1995), and filamentous and sheet-like annuals perform better than perennials (Wallentinus 1984). However, comparing two annual algae, I did not detect differences between the foliose, unbranched *Enteromorpha intestinalis* and the filamentous, finely branched *Pilayella littoralis*, indicating limitations in the use of SA/V-ratios for predicting algal nutrient-uptake capabilities and limited predictive power of the functional-form model on physiological traits.

Species with low K_m and high α may have a competitive advantage under nutrient-poor conditions due to efficient uptake at low ambient concentrations (Wallentinus 1984, Fujita 1985). In estuaries and other habitats where frequent nutrient pulses occur, species with high V_{max} may be favored particularly if nutrients can be stored to promote growth when ambient

concentrations have declined again (Carpenter 1990). Comparatively low K_m and high V_{max} values favor opportunistic annuals such as *Enteromorpha* or *Pilayella* over perennial species in spring and summer (Wallentinus 1984). However, perennials such as kelps gain advantage due to their ability to grow and take up excess nutrients in winter and store them for later use in summer (Chapman & Craigie 1977). Uptake kinetics vary with the nutritional history, physiological status, and age of the plants and it has been argued that there is no straightforward extrapolation from nutrient uptake kinetics to the relative competitive abilities among algal species (Carpenter 1990). For example, Fong et al. (1996) showed in laboratory experiments that *Enteromorpha intestinalis* and *Ulva expansa* directly competed for nutrients when starved of nitrogen. In single cultures, both algae showed similar nitrogen uptake and growth rates. Yet, in mixed cultures, *E. intestinalis* was the superior competitor over *U. expansa*. As a further complication to comparative physiological approaches, the available data are based on very different experimental designs and conditions. Uptake kinetics depend on time course (Thomas & Harrison 1987, Pedersen 1994), abiotic background parameters (Duke et al. 1989), water motion (Parker 1981), season (Hurd & Dring 1990), method of uptake measurement (Rosenberg et al. 1984, Harrison et al. 1989, Pedersen 1994), and on methods used for calculation of uptake parameters (Dowd & Riggs 1965, Wallentinus 1984). As far as comparison is possible at all, my data fit into the wide range of levels reported in the literature (Table 5.4) but seem to be fairly high. This may be partly explained by my method of parameter estimation. Parameter estimation through linear transformation according to DeBoer (S/V vs. S) and Eadie-Hofstee (V vs. V/S) mostly underestimated values of V_{max} and K_m (Table A5.4) and this must be taken into account in comparison with other data. Moreover, increasing starvation, rising temperature and decreasing incubation time are all known to enhance V_{max} and K_m (Wallentinus 1984, Fujita 1985, O'Brian & Wheeler 1987, this study). Since the algal material I used was starved at least for nitrogen and chosen incubation times for the first uptake period were very short, high maximal uptake rates and high saturation constants can be expected.

In my experiments, half-saturation constants (K_m) and maximum uptake rates (V_{max}) declined with increasing incubation time. Time-dependent uptake may occur because intracellular pools become filled and uptake rates become increasingly dependent on internal (cell) rather than external (water column) nutrient concentrations (Fujita et al. 1988, Pedersen 1994).

Table 5.4. Comparison of kinetic parameters V_{max} (µmol $h^{-1}g^{-1}$ DW) and K_m (µmol l^{-1}) resulting from different nutrient uptake studies with *Enteromorpha* species and *Pilayella littoralis* using different experimental designs and parameter estimation methods.

Species	V_{max}	K_m	°C	Time	Treatment	Estimation	Reference
NH_4^+-uptake							
E. prolifera	188	9	-	1-2h	low tissue N	nonlinear	O'Brian&Wheeler 1987
E. prolifera	188	13	-	1-2h	med.tissue N	nonlinear	O'Brian&Wheeler 1987
E. prolifera	39	3	-	1-2h	high tissue N	nonlinear	O'Brian&Wheeler 1987
E. ahlneriana	409	17	13	1-4h	in situ	S/V vs. S	Wallentinus 1984
E. compressa	37	24	14	4d	in situ	S vs. S/V	Kautsky 1982
E. sp.	996	25	20	1-2h	starved	V vs. V/S	Fujita 1985
E. sp.	120	4	20	1-2h	not starved	V vs. V/S	Fujita 1985
E. intestinalis	439	66	15		T 0-15 min.	nonlinear	this study*
E. intestinalis	61	13	15		T 60-120 min.	nonlinear	this study*
P. littoralis	32	2	8	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	39	5	1	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	467	67	15		T 0-15 min.	nonlinear	this study*
P. littoralis	53	10	15		T 60-120 min.	nonlinear	this study*
NO_3^--uptake							
E. sp.	129	17	15	20min	----	V vs. V/S	Harlin 1978
E. prolifera	169	13	-	1-2h	low tissue N	nonlinear	O'Brian&Wheeler 1987
E. prolifera	75	2	-	1-2h	med.tissue N	nonlinear	O'Brian&Wheeler 1987
E. ahlneriana	28	2	9	1-4h	in situ	S/V vs. S	Wallentinus 1984
E. intestinalis	237	44	15		T 0-30 min.	nonlinear	this study*
E. intestinalis	90	20	15		T 120-180 min.	nonlinear	this study*
P. littoralis	33	4	6	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	70	14	1	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	300	116	15		T 0-30 min.	nonlinear	this study*
P. littoralis	34	5	15		T 120-180 min.	nonlinear	this study*
PO_4^--uptake							
E. ahlneriana	1	0.2	2	1-4h	in situ	S/V vs. S	Wallentinus 1984
E. ahlneriana	8	3	12	1-4h	in situ	S/V vs. S	Wallentinus 1984
E. compressa	2	1	14	4d	in situ	S vs. S/V	Kautsky 1982
E. intestinalis	47	17	15		T 0-60 min.	nonlinear	this study*
E. intestinalis	14	8	15		T 120-240 min.	nonlinear	this study*
P. littoralis	6	4	8	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	4	2	1	1-4h	in situ	S/V vs. S	Wallentinus 1984
P. littoralis	44	15	15		T 0-60 min.	nonlinear	this study*
P. littoralis	8	4	15		T 120-240 min.	nonlinear	this study*

*) for uptake parameters of further time intervals see Table A5.2.

Both species seemed to be starved in summer (cf. C/N/P-ratios, Chapter 3), and thus respond quickly to short-term nutrient pulses. Nutrient pulsing may enable growth under low ambient nutrient levels. Such pulses may be created by benthic regeneration, herbivore excretion and nutrient flux from sediment (discussed in Chapter 4). Frequency of nutrient pulses was shown to be more important than pulse concentration in favoring *Enteromorpha* and *Ectocarpus* because of limits to nutrient storage capacity (Pickering et al. 1993). The nitrogen storage time of *Enteromorpha* was only between 8-10 d (Fujita 1985). Hence, in environments with episodic N-supply, species specific N-storage capacities may be an important trait affecting algal competitive abilities. This may be a possible but untested difference in *Enteromorpha* and *Pilayella*.

In summary, results of growth experiments and nutrient uptake rates of adults do not explain the dominance of *Pilayella* over *Enteromorpha* in the field. However, taking together all results of nutrient enrichment experiments, I can answer the questions I raised in Chapter 3: (1) Further nutrient enrichment in the course of increasing eutrophication will further enhance macroalgal productivity with much stronger effects on early life stages than on adults. (2) In the adult stage, *Pilayella* and *Enteromorpha* do not differ in their ability to use short-term nutrient pulses (uptake rates) versus long-term nutrient enrichment (growth rates). (3) Nutrient enrichment and other abiotic control mechanisms (temperature, light) showed different effects on various life stages.

Chapter 6

Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae

6.1. Introduction

As I concluded in Chapter 4 and 5, differences in ecophysiological traits of early life stages and of adults are insufficient to explain observed dominance patterns of *Pilayella littoralis* over *Enteromorpha* spp. in the Baltic Sea. This led me to the hypothesis that, in addition to abiotic factors, species interactions such as competition and herbivory must be considered as factors controlling species composition, timing and extent of macroalgal blooms.

Variable herbivore pressure has been shown to affect plant species composition, distribution and diversity in a wide range of ecosystems and abiotic conditions (Lubchenco & Gaines 1981, Davidson 1993, McNaughton et al. 1997). The most detailed and comparative evidence comes from macroalgal communities on rocky shores (Underwood 1980, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Chapman 1995). However, most studies have focused on the effects of herbivory on the perennial vegetation. According to the functional-form model (Littler & Littler 1980, Steneck & Dethier 1994), opportunistic, fast-growing filamentous and foliose algae are more vulnerable to herbivory than perennial species because of their reduced investment into structural or chemical defense (Gaines 1985, Hay & Fenical 1988). On rocky shores, strong herbivore pressure may typically prevent dominance of filamentous and foliose algae (Lubchenco 1986). Limited evidence suggests that herbivore control may be less effective in soft-bottom habitats (Wilhelmsen & Reise 1994). Studies analysing the effects of herbivores on bloom-forming macroalgae are conspicuously rare. Biomass accumulation of mass-blooming *Ulva lactuca* was reduced in the presence of invertebrate herbivores in an eutrophic Danish estuary (Geertz-Hansen et al. 1993). Variable abundance of crustacean herbivores caused by fish predation was proposed as an explanation of irregular development of *Enteromorpha* blooms on estuarine mud-flats in Southern England (Warwick et al. 1982). These isolated studies suggested that effects of herbivores on bloom-forming macroalgae have to be considered. However, both studies only consider a consumption of adult biomass. I propose that herbivore control of early life stages such as

macroalgal propagules and germlings may be equally or more effective than consumption of adult biomass.

It has been suggested that, following the secure attachment of propagules, foraging activities by herbivores may constitute the greatest source of mortality to early post-settlement stages of macroalgae (Vadas et al. 1992). This has been demonstrated in studies of perennial brown algae such as fucoids (e.g. Brawley & Johnson 1991, Worm & Chapman 1996, 1998) or kelps (e.g. Chapman 1984, Reed 1990). Strong herbivore effects on early life stages of filamentous or foliose algae such as *Enteromorpha* have been discussed (Lubchenco 1980, Hawkins 1981) because intense development of annual algae was commonly observed upon herbivore exclusion. However, I know of no previous study that quantified these effects.

In this chapter, I will present data on the effects of herbivores on different life stages of *Enteromorpha* spp. and *Pilayella littoralis*. First, I will describe seasonal abundance of herbivores at the study site. In laboratory and field tests, herbivore effects are quantified as (1) loss of settled propagules, (2) loss of germlings, and (3) loss of adult biomass. To analyze the importance of herbivore diversity for the control of blooming macroalgae, I performed feeding choice experiments on germlings and adults of *Pilayella* and *Enteromorpha* using four abundant herbivore species.

6.2. Material & methods

Seasonal occurrence of herbivores in the field

In 1997, together with sampling of adult algal biomass, abundance of herbivores was estimated at the study site. The sampling method is described in Chapter 3.

Effects of herbivores on settled propagules

In June 1995, I investigated the effects of herbivores on settled propagules in a simple laboratory experiment. I exposed 18 ceramic tiles to the natural propagule rain in the water column at the study site for 4 h from 10.00 to 14.00 to allow propagule settlement. Individuals of the two most abundant crustacean herbivores, *Idotea chelipes* and *Gammarus locusta* were collected at the same time. Each tile was cultivated in 500 ml of PES with GeO_2 added at standard T/L-conditions. One *Idotea* or 2 *Gammarus,* respectively, were added to the tiles. A treatment without herbivores served as a control for autogenic changes. Each treatment was run with 6 replicates. After 7 d of cultivation, germlings (>200 µm length) were counted

(mean of 10 subsamples of 4x4 mm) on each tile using a dissecting microscope with an integrated grid. To determine whether herbivores removed the settled propagules completely or only suppressed their germination and growth, all tiles were cultivated for another 7 d in new medium without herbivores. Germling density was determined again after this second cultivation period.

Effects of herbivores on new recruitment

From May to June 1997, I investigated the effects of herbivores on new recruitment (settlement, germination and subsequent growth) of propagules in the field. At 70 cm depth, 48 ceramic tiles were exposed as colonization substratum (5x10 cm). Tiles were hung up within closed cages (1-mm mesh size, exclusion of herbivores >1 mm), open cages (free access for herbivores), and without cages (cage artifact control). For this experiment, cages from a larger experiment were used. Details of the design are described in Chapter 7. Also, data on herbivore densities within treatments can be found in Chapter 7. These data, together with evidence from this chapter, indicate that open cages had about 40% lower snail densities compared to control treatments without a cage (Table 7.2). This was due to the weekly brushing of cages to prevent fouling and consequent light limitation. After 14 d of exposure, settled and germinated propagules were counted on the tiles using a dissecting microscope (25x, mean of 6 subsamples of 4x4 mm). Only germlings of *Enteromorpha* and *Pilayella* were found. Herbivore effects were analyzed with a paired t-test as recommended in Peterson & Renaud (1989) for feeding preference experiments, in which $t = (m_T - m_C) / \sqrt{(s^2/n_T + s^2/n_C)}$, with m_T= mean of differences between treatments, and m_C= mean of differences between the controls, s^2=variance, n=number of replicates. This analysis tests the null-hypothesis that the difference between germling density of *Pilayella* and *Enteromorpha* in herbivory treatments (open cages) is equal to the difference in germling density of the two algae in control treatments (closed cages). This eliminates the problem of independence. As a cage-artifact control, I further analyzed whether the difference in species germling density on open plots is similar to that of open cages. Data were log transformed to achieve homogeneity of variances.

Effects of herbivores on adults

In May 1997, effects of herbivores on growth of adults were tested in a field assay. In a first trial, 48 pieces of *Enteromorpha intestinalis* thalli of standard width (0.5 cm) and length

(6.0 cm) were cut from the middle part of freshly collected thalli and fixed with plastic clothes pins. Each piece was then exposed at 15 cm above the substratum in an open cage, closed cage or open plot (n=16) of the larger field experiment (see above, Chapter 7). After 8 d, thallus length was measured with a ruler and daily RGR was calculated ($RGR = (\ln l_1 - \ln l_2) / (t_2 - t_1)$, with l = length, t = time). In a following independent assay, bundles of adult *Pilayella littoralis* thalli with standard width (0.5 cm) and length (6.0 cm) were used. Statistical analysis on the dependent variable RGR was performed with a 2-way ANOVA (factors: herbivory, species, 2x2). Untransformed data achieved homogeneity of variances.

Feeding choice on germlings

In June 1997, I performed a feeding preference experiment in the laboratory in which I compared the effects of the 4 most abundant herbivores at my site (*Idotea chelipes*, *Gammarus locusta*, *Littorina littorea*, *L. saxatilis*) on germling density in *Enteromorpha* spp. and *Pilayella littoralis*. Six ceramic tiles (10x10 cm) were exposed in the water column at the study site for 24 h. Subsequently, tiles were cultivated separately for 12 d at standard T/L-conditions in 500 ml PES with GeO_2 added. After cultivation, germlings were counted in 10 subsamples (4x4 mm) with a dissecting microscope (25x). Tiles were broken into 4 pieces and each piece was offered to a different herbivore species (1 individual per piece) for 48 h in a 1 L glass beaker, filled with 300 ml freshly collected seawater. Herbivores were collected 1 d prior to the experiment. After the feeding trial, germling density was determined as described above and % reduction of germling density within 48 h was calculated.

I analyzed differences in germling consumption between *Enteromorpha* and *Pilayella* within single herbivore species. I did not compare consumption rates between different herbivores because of large differences in individual biomass among species. Autogenic changes in germling size and density were assumed to be negligible within the experimental period of 48 h. Germlings were 100-400 µm long in the beginning and did not exceed 600 µm after 48 h (growth rate of ca. 20% d^{-1}). Several earlier experiments revealed that distinct changes in germling density only occur every 3-4 wk in the course of new reproduction, germination, and mortality. Thus, statistical analysis was performed by a paired t-test, two-tailed (Peterson & Renaud 1989, Howell 1992) which tests the null-hypothesis that consumption rate is equal between *Enteromorpha* and *Pilayella*. The dependent variable, % reduction of germling density, was arcsin (x) transformed for this analysis. There was homogeneity of variances in transformed data.

These laboratory experiments give insight in differences between *Pilayella* and *Enteromorpha* resistance to herbivory, but they do not allow an estimation of true herbivore pressure in the field.

Feeding choice on adults

In June 1997, I tested feeding preference on adult *Enteromorpha intestinalis* and *Pilayella littoralis* using those 4 herbivore species tested in the germling preference experiment. Petri dishes (9 cm in diameter) were rinsed with freshly collected seawater several times and filled with 80 ml seawater. Algal pieces of a standard size (0.2x3.0 cm) were from freshly collected material. I used middle parts of 8-10 cm long *Enteromorpha intestinalis* thalli, and similar sized thalli of *Pilayella littoralis*. One piece of each algal species was placed at 6 cm distance within a petri dish. After 30 min, allowing for development of a possible chemical gradient, one herbivore individual was added per treatment, each species in 20 replicates. Within the feeding trial, I counted completely (100%) consumed thalli after 5, 19, 27, 42, 48 h.

6.3. Results

Seasonal occurrence of herbivores in the field

In 1997, main herbivores associated with the *Fucus vesiculosus* community in the field were amphipods, isopods, and littorinid snails. *Idotea* spp. (>95% *I. chelipes*, <5% *I. balthica*) and *Littorina saxatilis* showed strong seasonal trends with a marked increase in abundance in late spring reaching up to 120 and 200 individuals m^{-2} respectively. *Gammarus* spp. (mainly *G. locusta*) and *Littorina littorea* were less abundant (0 to 20 individuals m^{-2}) throughout the vegetation period (Fig. 6.1).

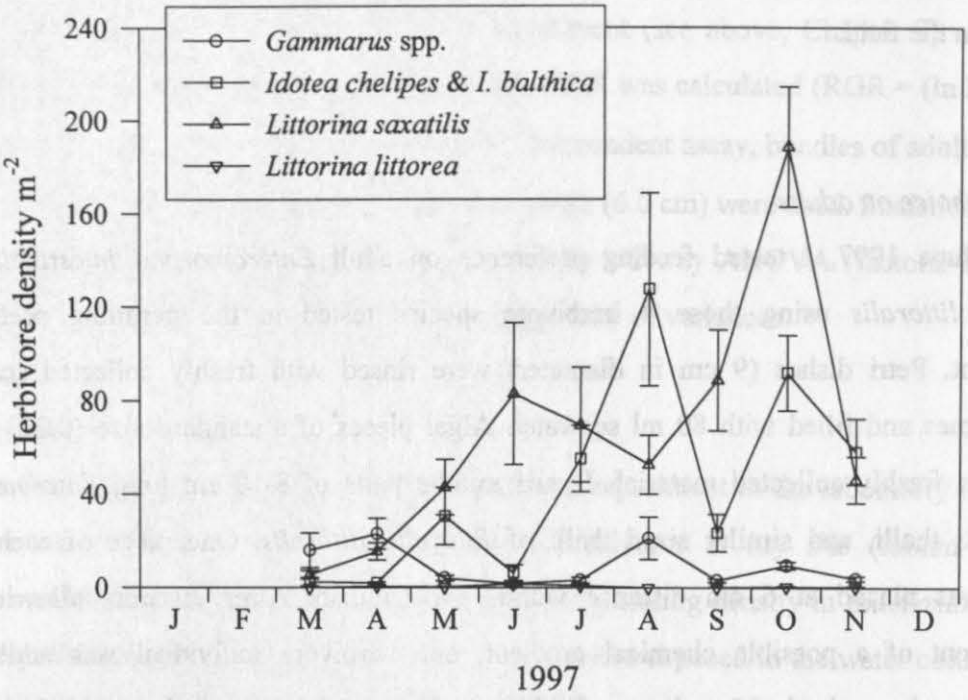

Fig. 6.1. Seasonal occurrence of main herbivore species associated with the *Fucus vesiculosus* community at the study site in 1997 (mean ± 1SE, n=6).

Effects of herbivores on settled propagules

In simple laboratory experiment, *Idotea chelipes* and *Gammarus locusta* had distinct effects on the density of germlings developing out of settled propagules (Fig. 6.2). Only in *Enteromorpha* spp., there developed sufficient amounts of germlings. In the presence of *Idotea,* only 4.4% (*Gammarus* 6.9%) of propagules developed into visible germlings compared to the control treatment (day 1-7). After subsequent cultivation without herbivores (day 7-14), the amount of germinated propagules in the control treatment increased 6-fold. This may be caused by germination of further settled but not yet germinated propagules on the tile (new reproduction occurs after 3 wk at the earliest). Density of germlings in treatments with *Gammarus* increased 8-fold in the second cultivation period, similar to the control. In contrast, germling density in treatments with *Idotea* increased 30-fold. This second part of the experiment suggests that feeding modes may differ among *Idotea* and *Gammarus*. *Gammarus* seemed to be effective in reducing germlings or propagules completely by removing them

from their substratum and, after removal of *Gammarus,* only new germination of later germinating propagules occurred at a rate comparable to the control. *Idotea* seemed to suppress growth of germlings by consuming the emerging erect filaments but not the basal parts. After removal of *Idotea,* both existing germlings and newly germinating ones grew to visible size.

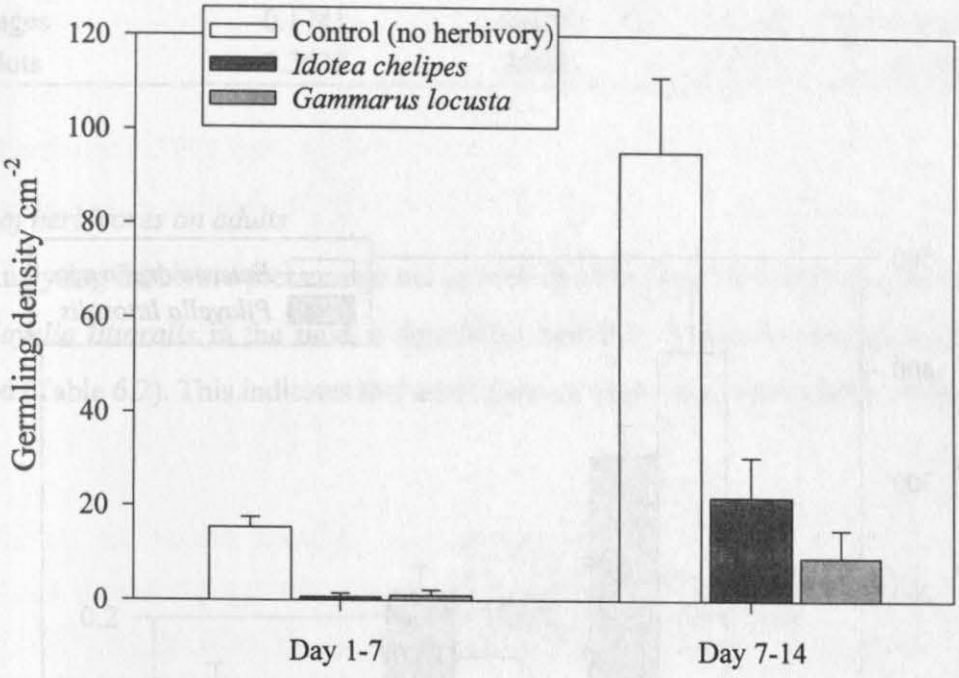

Fig. 6.2. Laboratory experiment on herbivore effects of *Idotea chelipes* and *Gammarus locusta* on settled propagules and their germination. In a first period (day 1-7) tiles with settled propagules were cultivated in the presence of *Idotea*, *Gammarus*, or no herbivores (control), in a second period (day 7-14) cultivation occurred without herbivores in order to distinguish whether herbivores removed germlings or suppressed their growth. After each period germling density was determined (means ± 1SE, n=6).

Effects of herbivores on new recruitment

In a field test in May 1997, I studied the effects of the natural herbivore populations on the combined processes of settlement of propagules from the water column, germination and subsequent growth of germlings (Fig. 6.3). Germling density of both algal species, *Enteromorpha* spp. and *Pilayella littoralis*, was effectively reduced by herbivores, but

Enteromorpha was significantly preferred over *Pilayella* ($p<0.001$, Table 6.1) resulting in a reversed pattern of abundance when herbivores were present (Fig. 6.3). Consumption rate and preference for *Enteromorpha* was more pronounced in open plots compared to open cages, resulting in a significant cage artifact ($p<0.05$, Tab 6.1). This was most likely caused by reduced densities of *Littorina saxatilis* (which heavily consumes germlings, see below) in open cages due to weekly brushing (Chapter 7, Table 7.2).

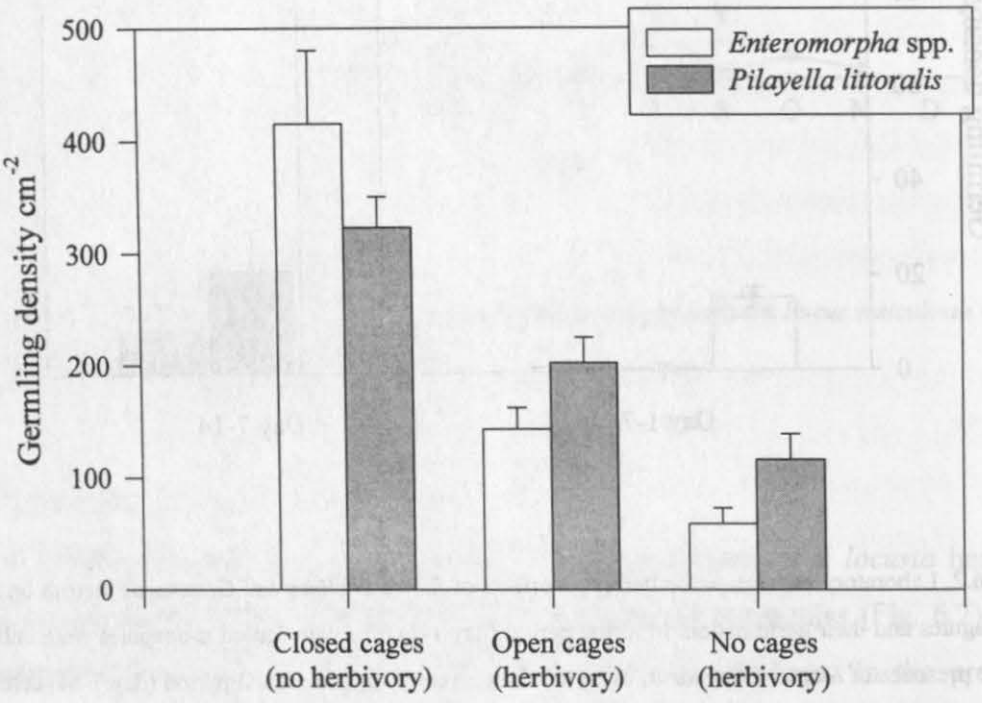

Fig. 6.3. Effects of herbivores on new recruitment (settlement, germination and subsequent growth) of *Enteromorpha* spp. compared with *Pilayella littoralis* in the field. Ceramic tiles as colonization substratum were exposed in closed cages (control, no herbivory), open cages (herbivory), and on open plots (no cages, control for cage artifacts). After 14 d, developed germlings were counted (means ± 1SE, n=16). Herbivore densities within treatments are tabled in Chapter 7, Table 7.2. For statistical analysis see Table 6.1.

Table 6.1. Statistical analysis of herbivore effects on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* in the field. Shown are results of paired t-tests according to Peterson & Renaud (1989) on means of differences between germling density of the two algae (1) between closed and open cages (= herbivory effect), and (2) between open cages and open plots (= cage artifact). Tabled test limits (n=16, k=2) are $t_{crit.}$= 2.04 (p=0.05,*), 2.75 (p=0.01,**), 3.65 (p=0.001,***). Log-transformed data achieved homogeneity of variances.

Treatment	Mean of differences between algal species	Variance s^2	n	t	Conclusion
Closed cages (control)	0.0598	0.0559	16		
Open cages	-0.1741	0.0287	16	-3.2168	** (Herbivory effect)
Open plots	-0.3630	0.0681	16	-2.4276	* (Cage effect)

Effects of herbivores on adults

Analysing herbivore pressure on net growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* in the field, a significant herbivory x species interaction (p=0.0003) occurred (Table 6.2). This indicates that adult *Enteromorpha* was significantly preferred as a

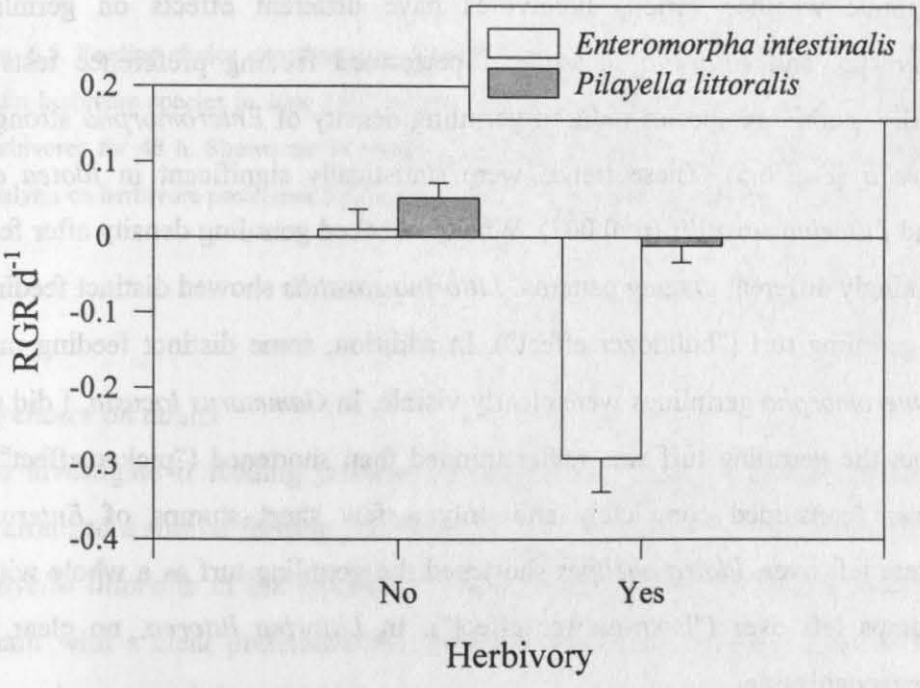

Fig. 6.4. Herbivore effects on growth of adult *Enteromorpha intestinalis* and *Pilayella littoralis* in the field in May 1997. Daily RGR was calculated as the relative increase or decrease of thallus length in the absence or presence of herbivores (means ± 1SE, n=16). For statistical analysis see Table 6.2.

Table 6.2. Results of 2-way ANOVA on effects of herbivores on RGR of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis*. Relative effect size is shown as explained variance in %. There were no cage artifacts (p=0.082) detected in the control experiment.

Source	df	MS	F-ratio	P-value	Variance (%)
Herbivory (H)	1	0.489	35.719	0.0001	23.5
Species (S)	1	0.453	31.457	0.0001	21.7
H x S	1	0.205	14.716	0.0003	9.5
Block	3	0.021			
Residual	57	0.014			

food source over *Pilayella* by herbivores present in the field in May 1997. The overall effects of herbivores were devastating in *Enteromorpha* (Fig. 6.4) with relative daily thallus loss of 29.3%. Despite separate assays for each algal species, herbivores in the field had the choice between *Enteromorpha*, *Pilayella* and further algae present at the study site.

Feeding choice and feeding patterns on germlings

To examine whether various herbivores have different effects on germlings of *Enteromorpha* spp. and *Pilayella littoralis*, I performed feeding preference tests in the laboratory. All 4 herbivore species reduced germling density of *Enteromorpha* stronger than that of *Pilayella* (Fig. 6.5). These trends were statistically significant in *Idotea chelipes* (p=0.012) and *Littorina saxatilis* (p=0.007). When I checked germling density after feeding, I observed strikingly different grazing patterns. *Littorina saxatilis* showed distinct feeding trails through the germling turf ("bulldozer effect"). In addition, some distinct feeding marks on individual *Enteromorpha* germlings were clearly visible. In *Gammarus locusta*, I did not find such trails but the germling turf was rather thinned than shortened ("picker effect"). Most germlings were consumed completely and only a few short stumps of *Enteromorpha* germlings were left over. *Idotea chelipes* shortened the germling turf as a whole with many germling stumps left over ("lawn-mower effect"). In *Littorina littorea,* no clear feeding patterns were recognizable.

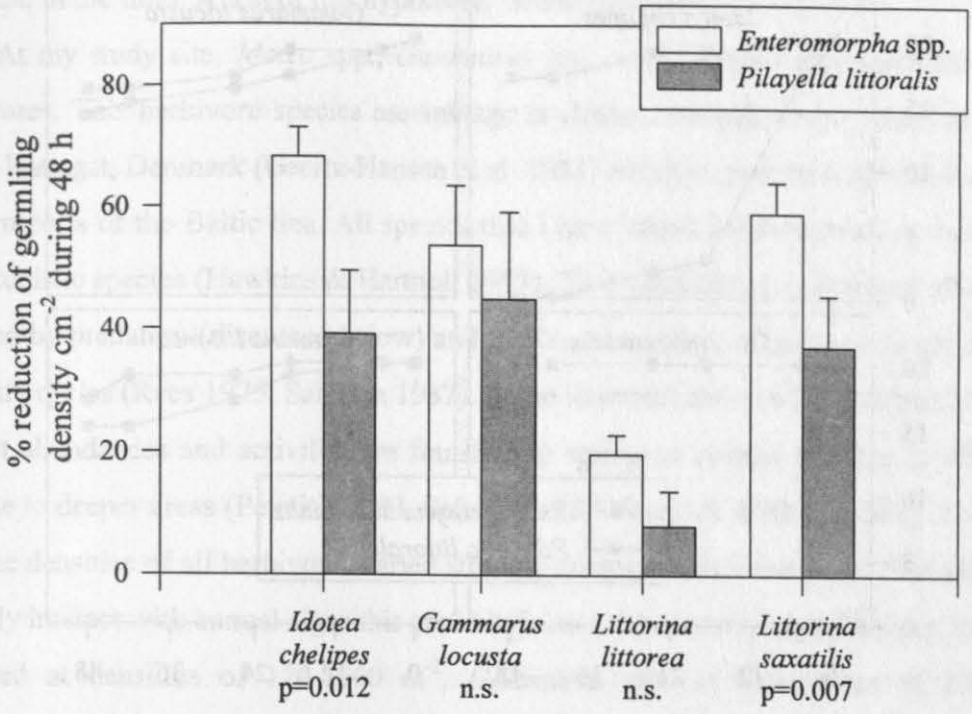

Fig. 6.5. Feeding choice experiment on germlings of *Enteromorpha* spp. and *Pilayella littoralis* with 4 main herbivore species in June 1997. Mixed stands of germlings of both algae were offered to single herbivores for 48 h. Shown are % reduction of germling density cm^{-2} (means ± 1SE, n=6). Statistical analysis on herbivore preference for the two algae was performed by paired t-tests.

Feeding choice on adults

To investigate if feeding patterns of herbivores on germlings are paralleled in adult algae, I arranged a similar feeding preference test for adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* in the laboratory. Only *Idotea chelipes* showed a distinct effect on adult thalli with a clear preference for *Enteromorpha* over *Pilayella* after 19 h (Fig. 6.6). *Gammarus locusta* and *Littorina littorea* had only slight effects with no clear preference for one of the two food sources. *Littorina saxatilis* showed no effect at all, not even feeding marks.

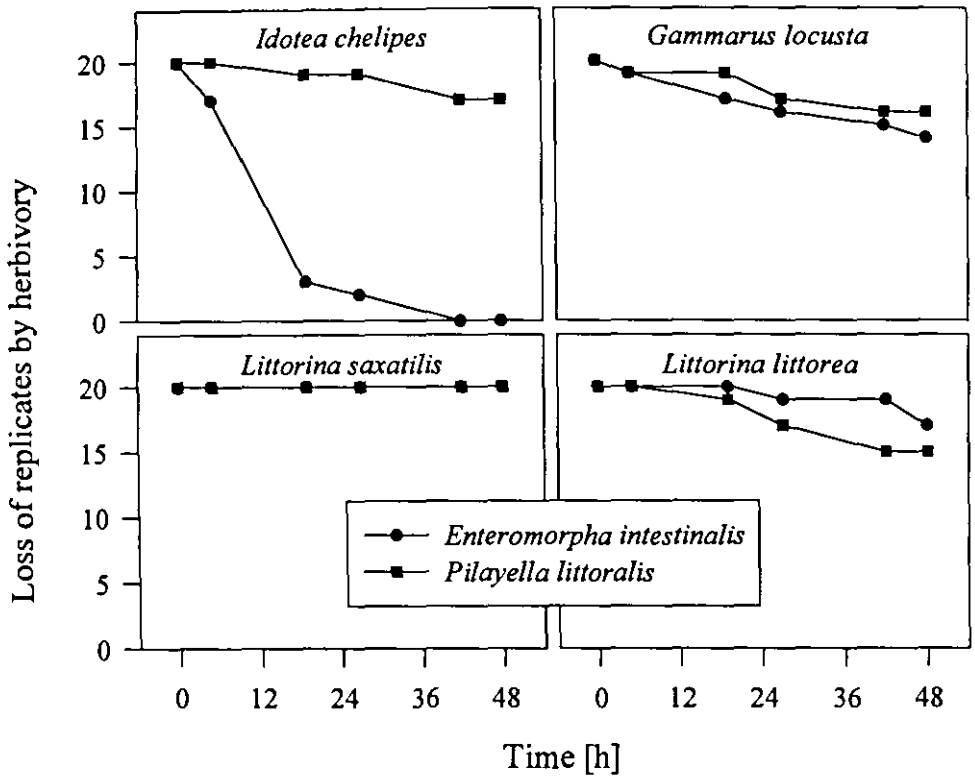

Fig. 6.6. Feeding choice experiment on adult *Enteromorpha intestinalis* and *Pilayella littoralis* with 4 main herbivore species in June 1997. In 20 replicates, individuals of single herbivore species had the choice between thallus pieces of each algae. If one piece was consumed (100%) I terminated the replicate. Graphs show single replicate losses over the experimental period of 48 h.

6.4. Discussion

In communities with a complex assemblage of herbivores, few microhabitats are free from herbivory and most sites harbor numerous herbivore species (Lubchenco & Gaines 1981). Thus, herbivores are likely to have major effects on plant biomass as well as on community structure (Lubchenco & Gaines 1981). My results indicate a strong herbivore control of the two bloom-forming macroalgae *Enteromorpha* spp. and *Pilayella littoralis* in the field. This control was highly effective at several life stages. Interestingly, effects of single herbivore species varied with life stage in a complementary fashion. This indicates the importance of herbivore diversity for the control of annual macroalgae (low redundancy). Because of the greater and selective herbivore pressure on all life stages of *Enteromorpha*

compared to *Pilayella* together with similar productivity rates of the two algae (Chapter 5) I propose effects of herbivores on competitive interactions between *Enteromorpha* and *Pilayella* in the field. A test of this hypothesis will be provided in Chapter 7.

At my study site, *Idotea* spp., *Gammarus* spp., and *Littorina* spp. represent the main herbivores. This herbivore species assemblage is almost identical to that found in Roskilde Fjord, Kattegat, Denmark (Geertz-Hansen et al. 1993) and thus, may be typical at least for the western parts of the Baltic Sea. All species that I have found are recognized as omnivorous, opportunistic species (Hawkins & Hartnoll 1983). Their distribution pattern and abundance is affected by predation (discussed below) and by the seasonality in the environment regulating their life cycles (Rees 1975, Salemaa 1987). In the intertidal and shallow subtidal habitats the highest abundances and activities are found from spring to autumn whereas in winter, they migrate to deeper areas (Petraitis 1983, Salemaa 1987, Steele & Whittick 1991). At my study site, the densities of all herbivores varied strongly among seasons and years. Since herbivores strongly interact with annual algae this could influence the extent of algal biomass. *Idotea* spp. occurred at densities of 120-1200 m^{-2}, *Gammarus* spp. in abundances of 20-340 m^{-2} (Schramm et al. 1996, this study, see also Chapter 7) which is comparable to abundances found in rocky intertidal habitats (Worm & Chapman 1998). *Littorina saxatilis* reached densities of 200-1300 m^{-2} at the study site in 1997, whereas maximum abundances of more than 4000 individuals m^{-2} were observed in 1998 (Worm & Lotze, unpublished). In contrast to many rocky shores where *Littorina littorea* is numerically dominant (218-272 m^{-2}, Lubchenco 1983, Worm & Chapman 1998), this species was rare with 10-12 individuals m^{-2} at my study site in 1995 and 1997.

In various experiments, *Enteromorpha* spp. and *Pilayella littoralis* were heavily consumed in the stage of developing propagules, germlings, and adults. Two patterns emerged: (1) relative effects on early life stages were common and intense and (2) *Enteromorpha* was the preferred food source over *Pilayella* in all life stages. Herbivore food preference of *Enteromorpha* over *Pilayella* may be caused by chemical, structural, morphological, or nutritional differences between the two algae which are untested so far. Chemical and structural defense against herbivores is common in many perennial seaweeds whereas defense mechanisms are low or absent in opportunistic algae (Littler & Littler 1980, Hay & Fenical 1988).

Strong herbivore control of opportunistic, bloom-forming macroalgae was also reported from Roskilde Fjord (Denmark) where herbivores locally prevented macroalgal mass accumulation (Geertz-Hansen et al. 1993). In Southern England, consumption of *Enteromorpha* by crustacean herbivores seems responsible for the breakdown of algal mats that occur on soft bottoms in summer (Warwick et al. 1982). However, *L. littorea* hardly affected development of green algal mats on mud flats in the North Sea (Wilhelmsen & Reise 1994). Field studies of herbivore effects on *Pilayella* are largely lacking. However, this alga is consumed by *L. littorea*, *G. lawrencianus*, and *I. balthica* (Lubchenco 1978, Shacklock & Doyle 1983, Steele & Whittick 1991).

Effects of herbivores on early life stages have been overlooked for a long time. I have quantified such effects for the first time for filamentous and foliose annual algae. Germination of settled propagules in *Enteromorpha* was reduced by 93-95% by *Idotea chelipes* and *Gammarus locusta*. Under natural herbivore pressure in the field, germling density of *Pilayella* and *Enteromorpha* was reduced by 64-86% within 14 days. The paucity or absence of *Enteromorpha* on rocky shores could often be reversed by the removal of herbivores like littorinid snails (Lubchenco & Menge 1978, Lubchenco 1980). After littorinid exclusion, development of *Enteromorpha* germlings has been observed within 2 weeks (Lein 1980). My findings may be further corroborated by indirect evidence from a rocky shore. In New England strong herbivore control appears to be most effective at the germling stage since few snails prevented *Enteromorpha* from colonizing, while high snail densities were required to control an adult *Enteromorpha* canopy (Petraitis 1987).

Relative effects of different herbivore species can vary with algal size and life stage. Whereas germlings of *Enteromorpha* and *Pilayella* were heavily consumed by all main herbivores at my site, *L. saxatilis* and *I. chelipes* had the greatest effects. In contrast, only *I. chelipes* had strong and selective effects on adults of *Enteromorpha*, whereas *L. saxatilis* did not feed on adults at all. Life-stage specific consumption has also been reported in *Fucus vesiculosus* in which young or small plants are more susceptible to consumption by *L. littorea* than are adults or large plants (Lubchenco 1983). However, susceptibility to herbivory may be species specific also on the juvenile level as observed in *Fucus* species. While juveniles of *F. distichus* suffered high mortality from herbivores, these had no effects on juveniles of *F. spiralis* (Chapman 1989, 1990).

Varying preferences for certain algal life stages may be related to differences in feeding modes among herbivore species. Parker et al. (1993) showed that littorinid snails can prevent the establishment of both micro- and macroalgae at the microscopic level whereas gammarid amphipods are ineffective at grazing microalgae and prostrate macroalgae from the substratum, but exert a considerable influence on erect macroalgae. These patterns agree with the large differences I observed in feeding marks left by the various herbivores in the experiments. I characterized *L. saxatilis* as a "bulldozer" which left distinct feeding trails while *G. locusta* appeared to pick single germlings out of the turf. In contrast to Parker et al. (1993), I found *G. locusta* to be an effective herbivore on microscopic *Enteromorpha* and *Pilayella* recruits. *I. chelipes* shortened the germling turf ("lawn-mower effect") but did not remove recruits completely. Both, isopods and amphipods, use their mandibles to bite off small portions of algae, while other mouthparts assist in handling the food items. Littorinids in contrast scrape the substratum with their radula (Hawkins & Hartnoll 1983). Thus, after exclusion of isopods and amphipods, germlings are able to regrow whereas littorinids leave bare substratum. However, even when eaten completely, many algae are able to survive digestion. This has been shown for *Enteromorpha* and *Pilayella* among other opportunistic species consumed by intertidal molluscs (Santelices & Correa 1985) or filter-feeders (Santelices & Martinez 1988). Surprisingly high survival rates of 20-90% were described for *Enteromorpha* and *Ulva* thalli after digestion by different herbivore molluscs (Santelices & Ugarte 1987). Thus, mobile herbivores may even have indirect positive effects by acting as dispersal agents.

Differences in the performance of life-cycle stages may also be important in herbivores, for example when juveniles depend on different food sources compared to adults. This has been discussed for *I. balthica* in the northern Baltic Sea, where adults live within perennial phytobenthic communities (*Fucus*, *Zostera*) but juveniles were found to prefer filamentous algae in the splash zone as a habitat, and possibly as a food source (Salemaa 1987). Further, consumer effects may not only be important among herbivores and algae but also among herbivores and their predators with potential cascading effects on primary producers (Power 1990). Isopods and amphipods are known to be heavily consumed by several fish species present at my site, e.g. *Spinachia spinachia* (fifteen-spined stickleback), *Pomatoschistus minutes* (sand goby), *Gadus morhua* (cod), *Zoarces viviparus* (eelpout) and others (Worthmann 1975, Niemann 1991, H. Thetmeyer pers. com.). Littorinid snails are consumed

by *Carcinus* (M. Wahl pers. com.), seastars and seaurchins (Paine 1966, Lubchenco & Menge 1978). Small littorinids may also be consumed by fish. The balance between crustacean mesoherbivores and their fish predators may be responsible for irregular development of *Enteromorpha* blooms in Southern England (Warwick et al. 1982). Whether true trophic cascades are important in the regulation of benthic macroalgae is currently under investigation (Worm, unpublished data).

Chapter 7

Relative effects of a dormant propagule bank, nutrient enrichment and herbivory on population development in two mass-occurring macroalgae

7.1. Introduction

The actual distribution and abundance of species observed in the field is determined by ecophysiological constraints, resource availability, species interactions, disturbance, and factors affecting propagule supply (Diamond & Case 1986, Roughgarden et al. 1988, Keddy 1989, Krebs 1994, Sommer 1994). This has been demonstrated during the last decades by experimental studies from which a body of important ecological concepts and theories emerged (Paine 1966, Connell 1978, Tilman 1982, Menge & Sutherland 1987, Keddy 1989). Benthic hard-bottom communities thereby often served as an important model system for mechanisms of community regulation with a focus on perennial macroalgae and sessile invertebrates (e.g. Lubchenco & Menge 1978, Menge & Farrell 1989, Paine 1992, Chapman 1995, Karez & Chapman 1998). Within this framework, experimental evaluation of nutrient effects (Menge 1992) and the role of a propagule bank (Santelices et al. 1995) were largely disregarded. Moreover, knowledge on the relative effects of resources (bottom-up) versus consumers (top-down) on benthic communities is rare (but see Williams & Ruckelshaus 1993, Reusch & Chapman 1997).

In the previous chapters, I analyzed effects of temperature, light, nutrients, and herbivory on the performance of early life stages and adults of *Enteromorpha* and *Pilayella.* This provides an understanding of the fundamental niches of the two species. However, taken all results together, the understanding of the dominance of *Pilayella* over *Enteromorpha* is still speculative. In this chapter, I analyze potential interactions among overwintering propagules, herbivory and nutrient enrichment on population development in the field to explain the realized distribution and dominance patterns of *Pilayella* and *Enteromorpha.* I use factorial field experiments in order to generalize upon the importance of selected factors in an actual ecosystem. Moreover, combining the effects of several manipulated factors allows insights in (1) direct effects of single factors, (2) interactions among factors and indirect

effects, and (3) the relative importance of significant single or interacting factors, demonstrated by their relative effect size in the analysis (Underwood 1981).

In terms of adult biomass, *Pilayella* dominates macroalgal blooms (Chapter 3), although it has reduced reproductive output (Chapter 3) and fewer overwintering stages in the propagule bank (Chapter 4) compared to *Enteromorpha*. The ability of *Pilayella* to germinate at lower temperatures than *Enteromorpha* (Chapter 4) may provide a seasonal advantage. This could increase pre-emptive space competition by *Pilayella* and reduce colonization of *Enteromorpha*. Still, *Enteromorpha* is abundant in the germling stage from spring to fall, whereas the *Pilayella* bloom ceases in July. Similar ecophysiological properties of adults (Chapter 5) do not explain this pattern. However, laboratory studies and field experiments equally showed that *Enteromorpha* is heavily consumed by herbivores and preferred over *Pilayella* in the germling and adult stage (Chapter 6). I hypothesize (1) that herbivores may play a decisive role in population development of *Enteromorpha* and to a minor extent of *Pilayella* in the field and (2) that interactions among the two species may be significantly modified by the availability of propagules in spring and seasonal patterns of herbivory and nutrient availability. It was my aim to explain the dominance of *Pilayella* over *Enteromorpha,* and I did not attempt a detailed analysis of competitive mechanisms acting between the two algae which requires experimental manipulation of the abundance of competing species or resources (Olson & Lubchenco 1990).

7.2. Material & methods

Experimental design

From February to December 1997, I performed a 3-factorial field experiment at the study site to analyze the combined effects of herbivory, nutrient enrichment and propagule supply on annual mass-occurring macroalgae. This experiment was carried out in cooperation with B. Worm who investigated the experimental effects on recruitment and growth of *Fucus vesiculosus* (B. Worm, unpublished).

The 3 experimental factors (herbivory, propagule bank, nutrient enrichment) were manipulated in a completely crossed design (2x2x2, Fig. 7.1) with 48 experimental units (plots) and 4 replicates per treatment combination arranged in a "randomized block design" (Hurlbert 1984). The experiment was located at 70 cm water depth in the zone dominated by *Fucus vesiculosus*. The experimental units were flat granite rocks (15-20 cm in diameter)

which were collected in February 1997 at the study site (10-40 cm depth). At that time the rocks had no macroscopic vegetation.

Herbivore presence was manipulated by cages (25x25x25 cm) made of a stainless steel frame covered with 1-mm transparent polyethylene mesh. Herbivores >1mm were excluded from closed cages while open cages with one side cut open allowed free access to herbivores. Plots without cages (open plots) served as controls for cage artifacts. Cages were brushed weekly to prevent fouling. Light measurements (LI-COR underwater quantum sensor LI-192SA) inside and outside the cages revealed that light intensity was reduced by only 8% due to attenuation of the polyethylene mesh which I judged negligible. To determine whether herbivore densities were similar in open cages and uncaged plots, I estimated herbivore densities within a central 10x10 cm area on the experimental rocks in the end of July. Statistical analysis was performed by ANOVAs for each species separately.

For manipulation of the propagule bank, half of the experimental rocks were selected at random and heat sterilized for 48 h at 100°C killing microscopic stages. The other rocks were left untreated.

Nutrient enrichment was performed on one half of the experimental plots from June to September when nutrient pools at the study site were depleted (Chapter 2). Nutrient diffusors were pipes (400x25 mm) of 1-mm polyethylene mesh filled with 160 g N-P-K slow-release fertilizer (Plantacote, Urania Agrochem, Hamburg). Water ammonium and phosphate concentrations were determined on all plots every 3-4 wk after Grasshoff et al. (1986) (Fig. A7.1). Statistical analysis (ANOVA) of these measurements indicated that nitrogen was significantly enriched ($p<0.05$) by the diffusors from late June to the mid of August, and phosphorus ($p<0.01$) from late June to the mid of September. Nutrient enrichment was unaffected by cages and the other treatment factors. Pooled over all treatment combinations, on average, ammonium enrichment did not exceed 4 µmol l^{-1}, and phosphate enrichment did not exceed 1.5 µmol l^{-1} compared to background nutrient concentrations (n=24, Fig. A7.1). In addition, nitrate was released at a fixed molar ratio of 0.69:1 to ammonium (Urania Agrochem, pers. com.) and may have not exceeded 2.5 µmol l^{-1} due to enrichment.

Fucus vesiculosus plants (12-18 cm length) were added to all plots to provide a substratum for epiphyte settlement, habitat for herbivores and a dispersal source for *Fucus* propagules. Performance of these *Fucus* plants was analyzed by B. Worm (unpublished data).

Since only minor epiphyte settlement occurred on these *Fucus* plants they were not important for my study.

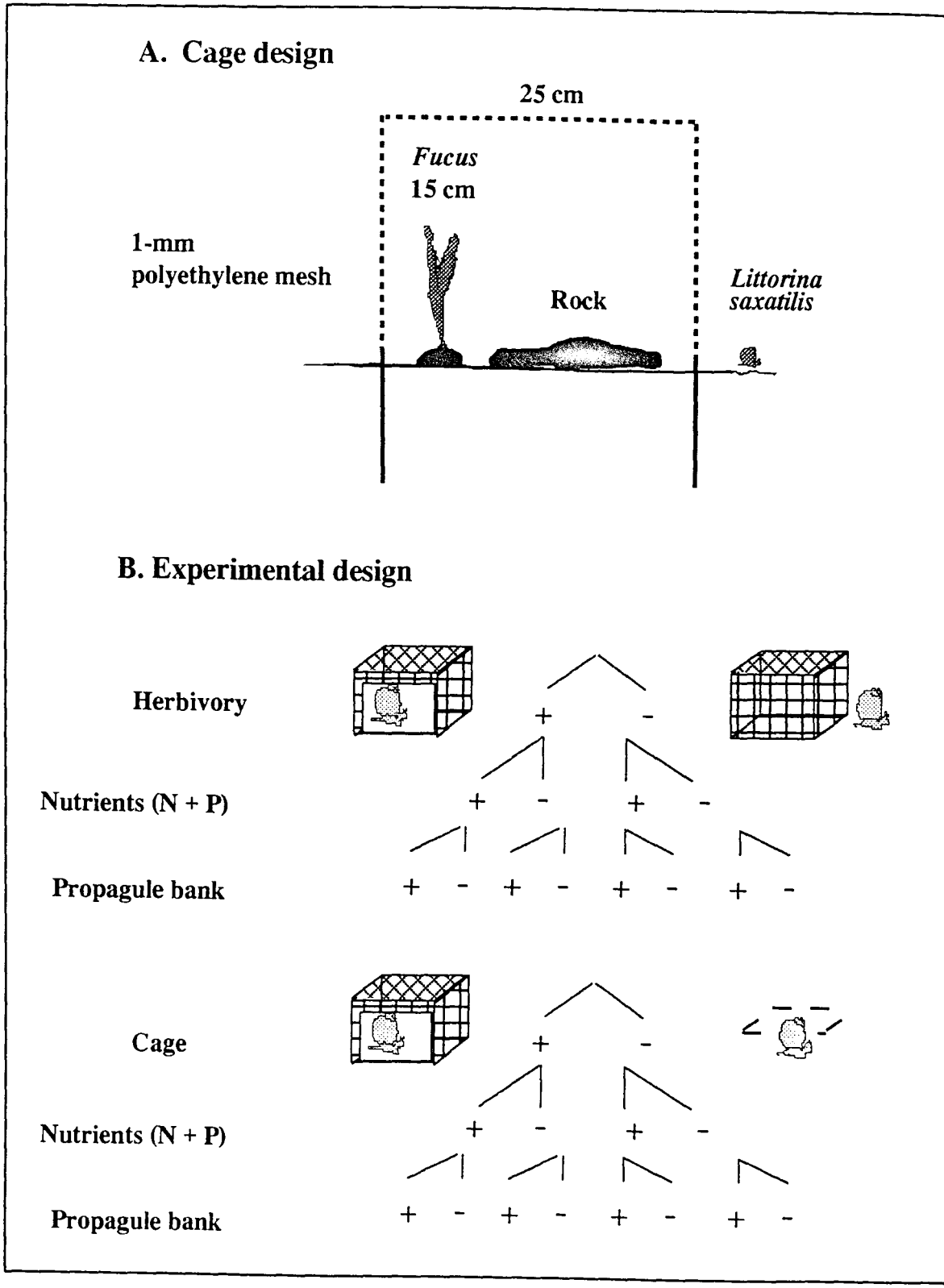

Fig. 7.1. Cage design (A) and experimental design (B) of the factorial field experiment.

Dependent variables and analysis

I determined % cover of all species developing on rocks in monthly intervals, and species canopy height every two months as the dependent variables. For all species, % cover was determined with a 10x10 cm plexiglas sheet with 50 random dots (1 dot = 2% cover). Canopy height of each species was measured with a ruler.

Statistical analyses were performed with 2- and 3-way factorial ANOVAs for randomized block designs on % cover and canopy height of selected months. Homogeneity of variances was checked using Cochran's test. Percent cover data were transformed using the formula arcsin (sqrt (x + 1)) as recommended by Sokal & Rohlf (1981). I checked for correlation among the densities of the main annual species *Pilayella littoralis* and *Enteromorpha* spp. with a regression analysis on % cover data of both species in the end of May.

To analyze the influence of experimental treatments on all macroalgae that occurred in the experiment (>2% cover in any treatment combination) I compared (1) relative experimental effects, (2) microrecruit density in the propagule bank, (3) maximum % species cover, and (4) period of macroscopic occurrence. Since nutrient enrichment had only minor effects on macroscopic algal cover (see results), I only compared treatment effects of the propagule bank and herbivory on all algal species. I calculated a simple index $I = (C_T - C_C)/C_C$, with C_T = % cover in the treatment, C_C = % cover in the control (Paine 1992). The % cover was pooled over all other experimental factors. This index was calculated for herbivore treatments and propagule bank treatments in the one month when the species in question reached its maximum overall density. Positive or negative values identify net positive or negative effects of herbivore presence or the presence of a propagule bank on experimental rocks. Recruit densities of *Enteromorpha* and *Pilayella* were estimated on rocks which were cultivated for 2 wk at standard T/L-conditions to allow germination of settled propagules in the propagule bank (mean, ± 1SE, n=6, 10 pooled subsamples per rock). For *Fucus vesiculosus,* germlings were counted in situ on experimental rocks before new reproduction occurred (n=8).

New recruitment

In the end of June 1997, I studied the combined effects of herbivory, presence of a propagule bank and nutrient enrichment on new recruitment of *Enteromorpha* and *Pilayella*

propagules out of the water column. One ceramic tile (5x10 cm) per plot was hung up in the factorial field experiment described above (Fig. 7.1). After 14 d, germling abundance was determined with a dissecting microscope (mean of 6 subsamples of 4x4 mm). *Enteromorpha* and *Pilayella* were the main species settling on the tiles. In addition, I detected a few germlings of *Ceramium strictum*.

Statistical analyses were performed by 3-way ANOVA (2x2x2) on germling densities for *Pilayella* and *Enteromorpha* separately, since settlement and germination of the two algae on one tile were not independent. Data were log-transformed to achieve homogeneity of variances. In addition to tests provided in Chapter 6, I analyzed herbivore food preference between the two algae at all treatment combinations in the field. Statistical analysis on food preference of herbivores was performed by t-tests after Peterson & Renaud (1989) as described in Chapter 6. Again, log-transformed data were used.

7.3. Results

Population development of Pilayella littoralis and Enteromorpha spp.

Populations of *Enteromorpha* spp. and *Pilayella littoralis* clearly differed in their response to the combined effects of herbivory and the presence of a propagule bank. Nutrient enrichment from June to September had only minor effects on adult populations compared to the two other factors.

Development of *Enteromorpha* and *Pilayella* began in early March, if the propagule bank was present (Fig. 7.2b). In the absence of this recruitment source, i.e. on sterilized rocks (Fig. 7.2a), population development depended on newly dispersed propagules, which first occurred in May (Chapter 3). Thus, population development of both species was delayed by two month when a propagule bank was absent. This was a major disadvantage considering the seasonal decrease of ambient nutrient concentrations in spring (Chapter 2). However, advantageous effects of the propagule bank were much stronger in *Enteromorpha* which reached around 30% cover until May. In this month, the propagule bank had a significant positive effect (Table 7.1, $p=0.0001$) explaining 45% of total variance in *Enteromorpha* cover. In contrast, only a few thalli of *Pilayella* appeared from the propagule bank and this species started its main development in May, when new reproduction occurred.

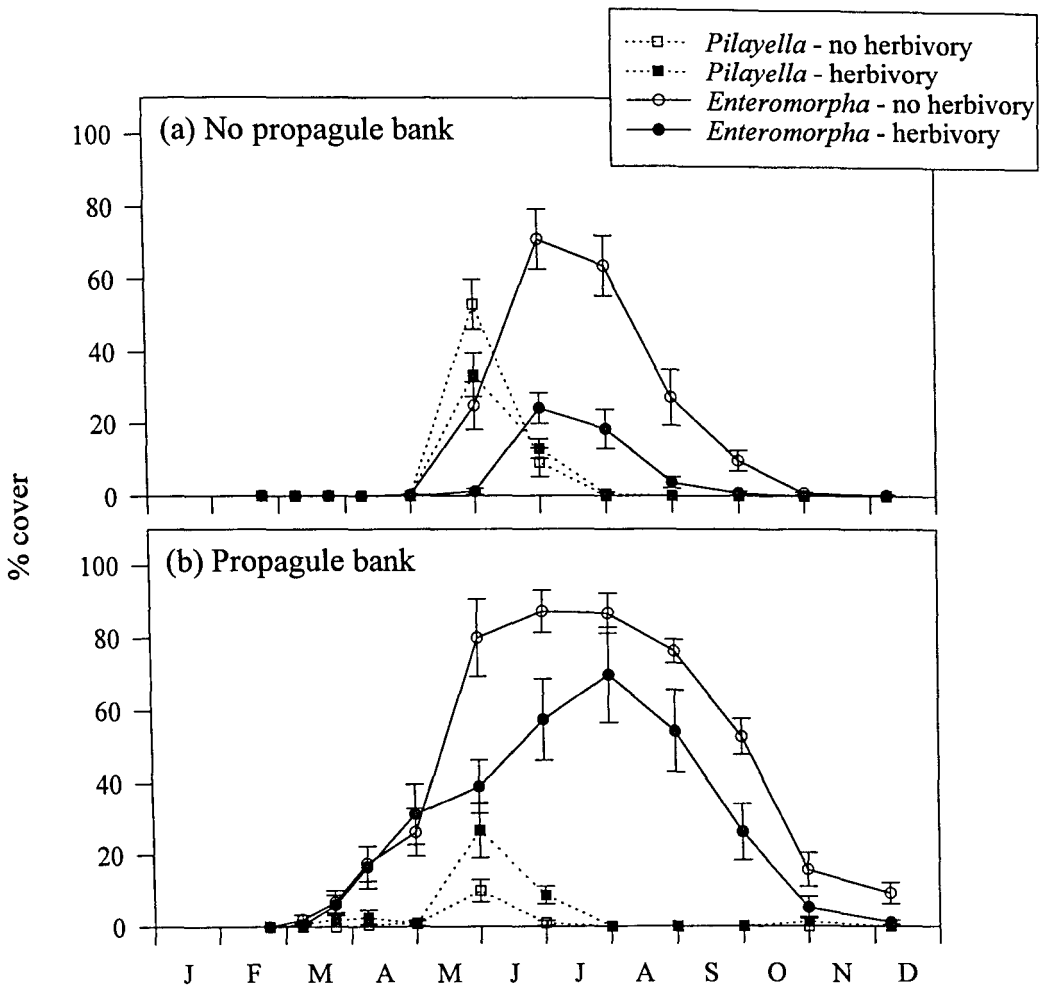

Fig. 7.2. Combined effects of herbivores and propagule bank on population development of *Enteromorpha* spp. and *Pilayella littoralis*. The treatment combinations are indicated as (a) no propagule bank (sterilized rocks), (b) propagule bank (natural rocks), and in the legend: herbivory (open cages), no herbivory (closed cages). Data were analyzed as % cover (mean ± 1SE, n=8).

In May, herbivores, mainly *Idotea* spp., *Gammarus* spp., *Littorina saxatilis* and *L. littorea* (Chapter 6), became active. This was clearly visible in the graph (Fig. 7.2b) by a sudden divergence of the curves with herbivory treatments in May indicating strong herbivore effects. Herbivores significantly reduced (Table 7.1, p=0.0001) *Enteromorpha* cover independent of the presence of a propagule bank (Table 7.1, H x P: p=0.6554). In *Pilayella*,

Table 7.1. Results of 2-way ANOVAs on combined effects of herbivores and propagule bank on % cover of *Enteromorpha* spp. and *Pilayella littoralis* in May. Relative effect size is shown as explained variance in %. Data were arcsin (sqrt (x + 1)) transformed. Significant cage artifacts (p=0.0020 in *Enteromorpha*, p=0.0001 in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots.

Source	df	MS	F-ratio	P-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.875	24.765	0.0001	24.6
Propagule bank (P)	1	3.386	44.711	0.0001	45.3
H x P	1	0.015	0.204	0.6554	
Block	3	0.016			
Residual	25	0.076			
Pilayella littoralis					
Herbivory (H)	1	0.005	0.118	0.7341	
Propagule bank (P)	1	0.599	13.033	0.0013	25.4
H x P	1	0.339	7.379	0.0118	13.5
Block	3	0.013			
Residual	25	0.046			

effects of herbivores varied depending on the propagule bank treatment, shown by a significant herbivore x propagule bank interaction in the analysis (Table 7.1, H x P: p=0.0118). If the propagule bank was present and *Enteromorpha* dominantly covered the substratum *Pilayella* was favored by the presence of herbivores. In contrast, herbivores negatively affected *Pilayella* cover in the absence of the propagule bank. Percent cover of *Pilayella* in May was significantly (p=0.0003, Fig. 7.3) and negatively correlated with % cover of *Enteromorpha*, which in turn depended on the treatment combination (Fig. 7.4). This indicates that direct effects of herbivores and propagule bank on *Enteromorpha* may indirectly control *Pilayella* cover.

In the end of June, the herbivore effect on % cover of *Enteromorpha* became more important (35% of variance explained) compared to May (21%) whereas the propagule bank effect decreased in importance (15% compared to 43% in May, Table 7.1 and Table 7.2). In June, nutrient enrichment was introduced as an additional factor but had no effect on % cover of *Enteromorpha* (Table 7.2). However, nutrient enrichment significantly increased canopy

height of *Enteromorpha* and this effect was stronger in treatments without propagule bank compared to treatments with propagule bank (nutrient enrichment x propagule bank, p=0.0466, Table 7.3). In *Pilayella*, biomass strongly decreased towards the end of June and canopy height could not be analyzed. However, herbivores had significant positive (p=0.0069) and the propagule bank had significant negative (p=0.0086) effects on % cover in all treatments (Table 7.2). Further, nutrient enrichment had significant negative (p=0.0411) effects on % cover of *Pilayella*.

Table 7.2. Results of 3-way ANOVAs on combined effects of herbivory, propagule bank and nutrient enrichment on % cover of *Enteromorpha* spp. and *Pilayella littoralis* in June. Significant cage artifacts (p=0.0001 in *Enteromorpha*, p=0.0503 in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots. Data were arcsin (sqrt (x + 1)) transformed.

Source	df	MS	F-ratio	P-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.849	21.105	0.0002	34.8
Propagule bank (P)	1	0.853	9.739	0.0052	15.2
Nutrient enrichment (N)	1	0.016	0.181	0.6753	
H x P	1	0.014	0.163	0.6906	
H x N	1	0.005	0.052	0.8216	
P x N	1	0.127	1.447	0.2424	
H x P x N	1	0.268	3.059	0.0949	
Block	3	0.001			
Residual	21	0.088			
Pilayella littoralis					
Herbivory (H)	1	0.194	8.969	0.0069	16.0
Propagule bank (P)	1	0.181	8.404	0.0086	14.8
Nutrient enrichment (N)	1	0.102	4.735	0.0411	7.5
H x P	1	0.020	0.938	0.3438	
H x N	1	0.005	0.220	0.6442	
P x N	1	0.006	0.295	0.5928	
H x P x N	1	0.029	1.356	0.2573	
Block	3	0.020			
Residual	21	0.022			

Table 7.3. Results of 3-way ANOVA on combined treatment effects on canopy height of *Enteromorpha* spp. in July. A significant cage artifact (p=0.0001) occurred in the control experiment (explained above). Untransformed data achieved homogeneity of variances.

Source	df	MS	F-ratio	P-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	2178.0	17.879	0.0004	19.8
Propagule bank (P)	1	3321.1	27.262	0.0001	30.8
Nutrient enrichment (N)	1	903.1	7.414	0.0127	7.5
H x P	1	171.1	1.405	0.2492	
H x N	1	231.1	1.897	0.1829	
P x N	1	544.5	4.470	0.0466	4.1
H x P x N	1	144.5	1.186	0.2884	
Block	3	77.3			
Residual	21	121.8			

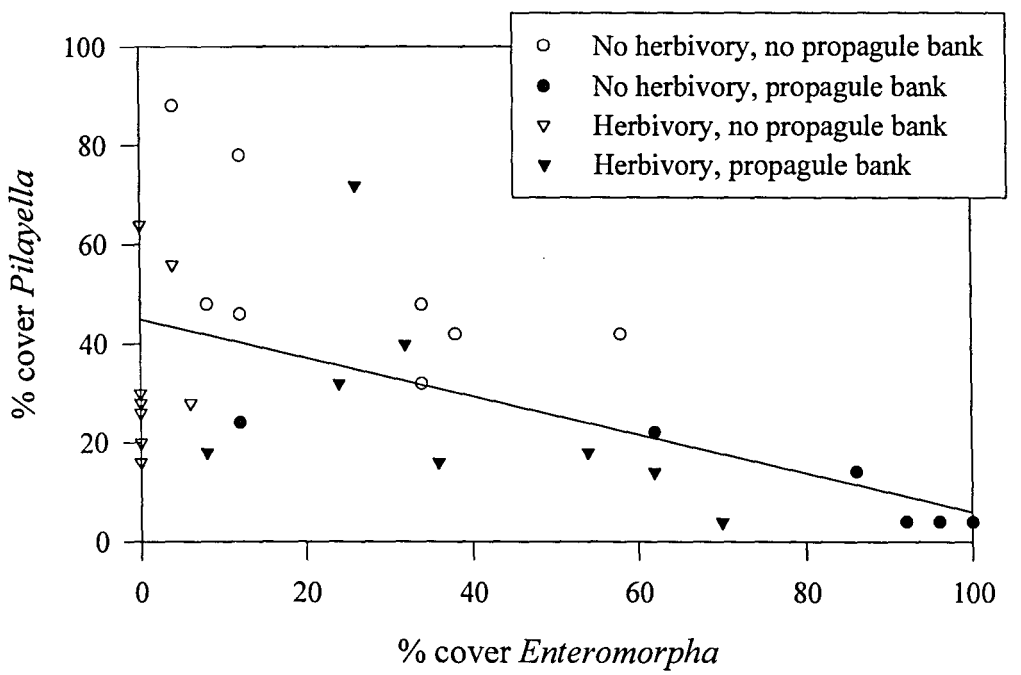

Fig. 7.3. Linear regression of % cover of *Pilayella littoralis* versus % cover of *Enteromorpha* spp. in May. Treatment combinations of herbivory and propagule bank are indicated in the legend. Regression analysis revealed the following equation: $f(x) = -0.390 x + 44.988$; $r^2 = 0.363$; $p = 0.0003$.

Fig. 7.4. Effects of the propagule bank on algal colonization in the absence of herbivory (closed cages) in May. If the propagule bank is absent, *Pilayella* dominates the substratum (left), if the propagule bank is present, *Enteromorpha* is the dominant space occupier (right). The rocks are 15-20 cm in diameter.

In total, *Pilayella* showed a distinctly shorter period of occurrence which ended in late July in comparison with *Enteromorpha* which occurred until December (Fig. 7.2).

Herbivore pressure within open cages was reduced compared to plots without cages (Table 7.4, for complete ANOVA results see Table A7.1). This was most probably caused by the weekly cleaning procedure which was necessary to prevent fouling of cages. This significantly ($p<0.0001$) reduced the density of slow-moving *Littorina saxatilis* which is an important consumer of algal germlings (Chapter 6). A similar but non-significant trend was visible in *L. littorea*, whereas mobile *Idotea* seemed to prefer open cages as a habitat compared to open plots. These differences in herbivore densities between open cages and open plots are assumed to be the main factor causing significant cage artifacts (p-values are noted in the legends of ANOVA tables). All cage artifacts resulted in increased performance of algae in open cages compared to open plots. This was a consistent observation in *Enteromorpha* which is most susceptible to herbivory and thus, corroborates the assumption that cage artifacts are caused by the reduction of herbivore densities. I found no hints for

further cage artifacts such as reduced light level, reduced nutrient supply due to reduced water motion or enhanced sedimentation rate. All these effects would have decreased algal performance within cages in contrast to the observed increase.

Table 7.4. Herbivore density per m^2 of main species in treatment plots of the field experiment in July (means ± 1SE, n=16). Results of statistical analyses of the cage effect on herbivore density are listed below, for complete ANOVA tables see Table A7.1.

Density m^{-2}	*Littorina saxatilis*		*Littorina littorea*		*Idotea* spp.		*Gammarus* spp.	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Open plots	1306.4	226.8	12.7	6.3	211.5	18.0	301.9	89.5
Open cages	446.4	76.8	4.2	4.2	498.6	108.0	338.7	63.2
P-value	0.0001		n.s.		n.s.		n.s.	

Because of the reduction of herbivore pressure in open cages compared to open plots, herbivore effects were conservatively estimated in the experiment. Control treatments without cages may give a more realistic estimate of population development under strong herbivore pressure. On all open plots, *Enteromorpha* and *Pilayella* strongly suffered from the high natural herbivore pressure (Fig. 7.5). Compared to open cages (Fig. 7.2, filled symbols), maximal % cover on open plots was decreased by >60% in both species. If the propagule bank was available, *Enteromorpha* achieved 26% cover until April (Fig. 7.5b) which is almost the same level as in caged plots (Fig. 7.2b). When herbivores became active in May, they reduced *Enteromorpha* cover continuously. *Pilayella* only reached a small peak with 14% cover in the end of May. Without a propagule bank *Enteromorpha* only developed into a minor amount of 1% cover in June and July (Fig. 7.5a). *Pilayella* achieved 7% cover in the end of June. Compared to *Enteromorpha*, this was the only treatment with a clear dominance of *Pilayella*.

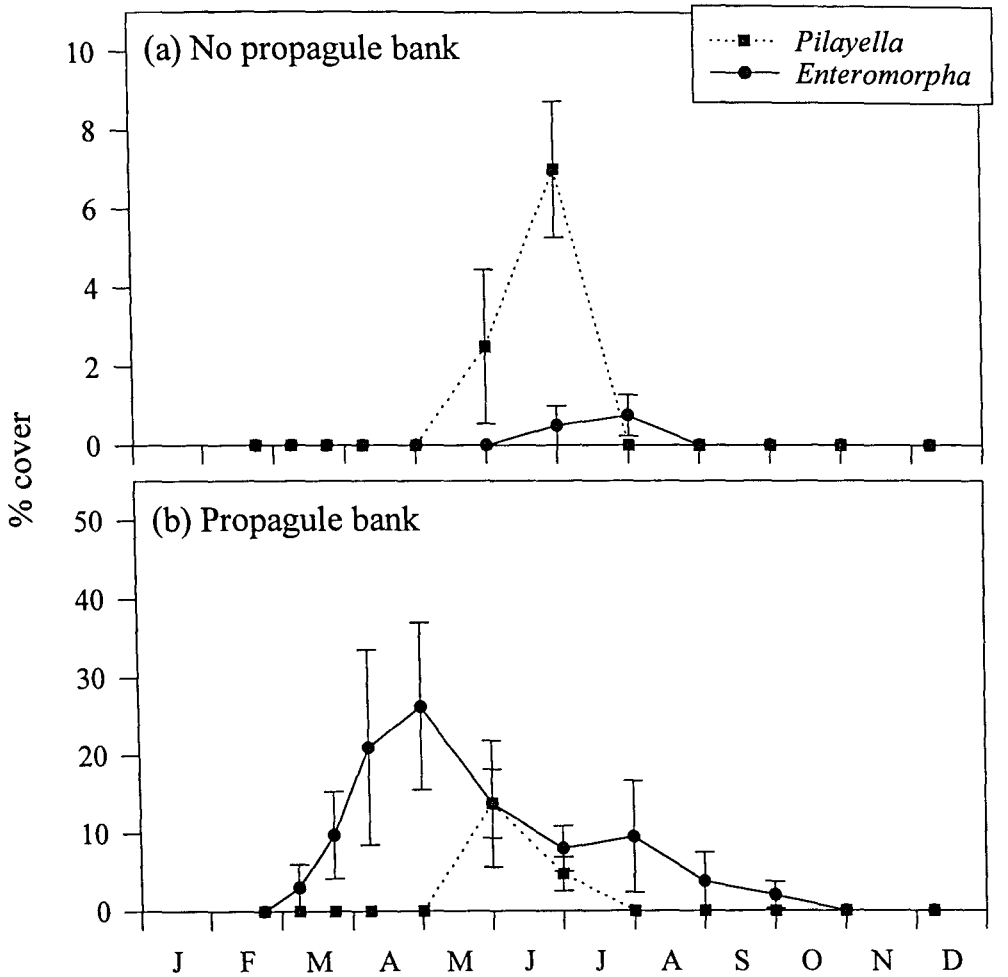

Fig. 7.5. Population development of *Enteromorpha* spp. and *Pilayella littoralis* on open control plots (no cages, full herbivore pressure) without (a) and with (b) propagule bank. Data were analyzed as % cover (mean ± 1SE, n=8).

Comparison of treatment effects for all algae

To determine the importance of the experimental factors for the entire algal community I investigated their impact on all abundant algae (>2% cover). In addition to *Enteromorpha* and *Pilayella,* 5 other macroalgal species occurred over the experimental period but were of minor importance except for the perennial brown alga *Fucus vesiculosus* (Table 7.5). *Fucus* only recruited in small amounts from the propagule bank (7.75 germlings 100 cm^{-2}). This species thus almost completely relied on new recruitment which occurred in April-May. For

most species, opposing effects of the propagule bank and herbivores became visible. Species, which were highly favored by their investment into the propagule bank (e.g. *Enteromorpha*, *Ulvopsis*) were most vulnerable to herbivores. In contrast, herbivores positively affected species which showed a net negative effect of the propagule bank (e.g. *Ceramium*, *Fucus*). The marked effect of the propagule bank on *Ulvopsis* was caused by the fact that dormant propagules were almost the exclusive source of recruitment of this species. Within the three dominant species *Enteromorpha*, *Pilayella* and *Fucus*, a distinct trend towards a trade-off between the investment into a propagule bank and susceptibility to herbivore consumption was visible.

Table 7.5. Experimental effects of herbivores and propagule bank on macroalgae, recruit density of species in the propagule bank, and occurrence period of species during the experiment (see Material & methods for further explanation). Maximum % cover is shown for the most beneficial herbivore x propagule treatment combination (n=8).

Species	Herbivore effect	Propagule effect	Recruit density (100 cm^{-2} ±1SE)	Max. %cover (mean ±1SE)	Occurrence period
Enteromorpha spp.	-0.48	0.52	33000 (±3000)	87.25 (±5.82)	Mar-Dec
Ulvopsis grevillei	-0.23	27.80	no data	20.75 (±9.13)	Mar-Apr
Polysiphonia fibrillosa	-0.21	-0.36	no data	3.50 (±1.92)	Nov-Dec
Pilayella littoralis	-0.04	-0.58	667 (±667)	53.00 (±6.85)	Mar-Jul
Cladophora sp.	0.91	-0.69	no data	9.50 (±5.38)	Jun-Dec
Ceramium strictum	1.03	-0.78	no data	13.25 (±5.10)	Jun-Sep
Fucus vesiculosus	1.55	-0.68	7.75 (±3.04)	69.75 (±4.22)	Jun-Dec

New recruitment

I was interested whether population growth of *Enteromorpha* and *Pilayella* in summer mainly depends on recruitment in spring or if new recruitment during summer provides a significant source of further individuals. New recruitment of algal propagules included settlement from the water column, germination and subsequent growth of germlings. These processes were strongly controlled by the combined effects of herbivory and nutrient enrichment (Fig. 7.6). Nutrient enrichment resulted in a significantly higher abundance of visible germlings in both species, *Enteromorpha* ($p=0.0001$) and *Pilayella* ($p=0.0062$), and

was the factor with the greatest relative effect size of 34% and 16% for the two species respectively (Table 7.6).

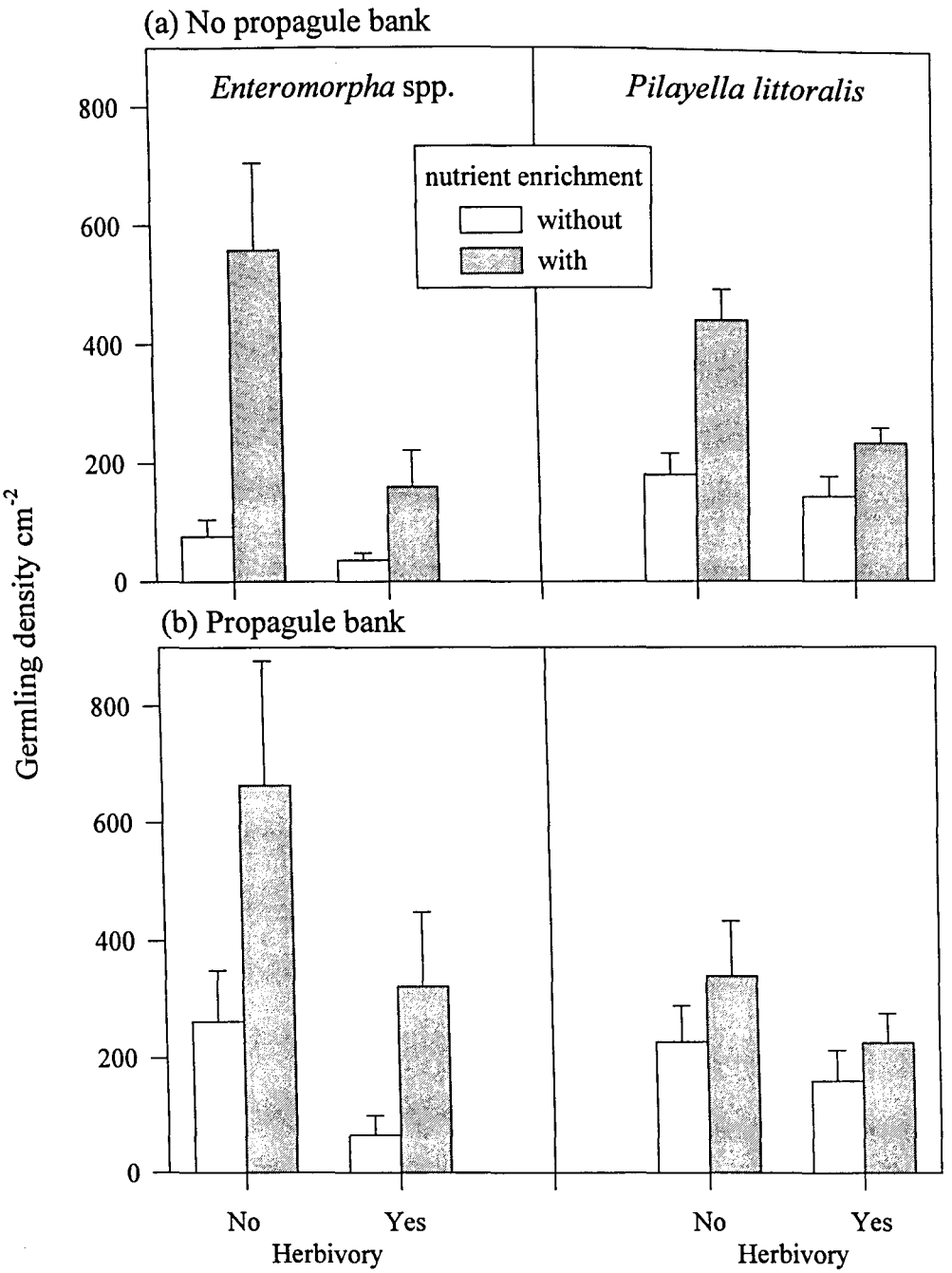

Fig. 7.6. Combined effects of herbivores, propagule bank, and nutrient enrichment on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* in June. Recruitment was examined on ceramic tiles which were exposed to all treatment plots of the main experiment (see Fig. 7.1). Germling density was analyzed after 14 d (means ± 1SE, n=4). For statistical analysis of treatment effects see Table 7.5.

However, herbivore consumption balanced the nutrient effect. Herbivores significantly reduced recruitment of *Enteromorpha* (p=0.0041) and *Pilayella* (p=0.0454) and explained 14% and 8% of the variance respectively (Table 7.6). In *Enteromorpha* spp., there was an additional effect resulting from manipulations of the propagule bank on rocks enclosed in the same cages as the tiles of the recruitment experiment. The propagule bank had a significant positive effect (p=0.0378) on new settlement (Table 7.6). This was an indirect effect most likely caused by a higher density of adult *Enteromorpha* thalli (and thus higher propagule supply) on rocks with a propagule bank (Fig. 7.2b) indicating that the propagule rain is not distributed homogeneously and propagule density can depend on the proximity of the propagule source.

Table 7.6. Results of 3-way ANOVAs on combined effects of herbivory, propagule bank and nutrient enrichment on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* in June. Significant cage artifacts (p=0.0001 in *Enteromorpha*, p=0.0503 in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots. Log-transformed data achieved homogeneity of variances.

Source	df	MS	F-ratio	P-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.684	10.350	0.0041	14.0
Propagule bank (P)	1	0.799	4.914	0.0378	5.8
Nutrient enrichment (N)	1	3.824	23.505	0.0001	33.6
H x P	1	0.030	0.187	0.6699	
H x N	1	0.007	0.041	0.8416	
P x N	1	0.178	1.096	0.3070	
H x P x N	1	0.262	1.612	0.2180	
Block	3	0.179			
Residual	21	0.163			
Pilayella littoralis					
Herbivory (H)	1	0.235	4.525	0.0454	8.5
Propagule bank (P)	1	0.007	0.139	0.7127	
Nutrient enrichment (N)	1	0.482	9.271	0.0062	16.2
H x P	1	0.003	0.056	0.8158	
H x N	1	0.007	0.140	0.7116	
P x N	1	0.062	1.200	0.2857	
H x P x N	1	0.022	0.418	0.5250	
Block	3	0.095			
Residual	21	0.052			

In separate statistical tests, I analyzed if feeding preference of herbivores occurred within the recruitment experiment. Herbivores significantly preferred *Enteromorpha* over *Pilayella* in all treatment combinations (Table A7.2b-d) except when no propagule bank was present and no nutrient enrichment occurred (Table A7.2a) which is the treatment with the lowest *Enteromorpha* density.

7.4. Discussion

Population development and dominance patterns of the two co-occurring opportunistic macroalgae *Pilayella littoralis* and *Enteromorpha* spp. were affected by the combined effects of a dormant propagule bank, herbivore consumption and nutrient enrichment. The magnitude of effects varied with season. As one major result of this study, I could demonstrate the great ecological significance of a macroalgal propagule bank. This marine "seed bank" provides an important mechanism for overwintering and survival of annual and perennial macroalgal populations in the face of environmental variability. Favored by massive recruitment from the propagule bank, *Enteromorpha* spp. was the superior space occupier in spring. Subsequently, recruitment of other colonizing algae was largely inhibited if the propagule bank was present. Secondly, as the main counteracting factor, a diverse herbivore guild prevented single species dominance. By strong and selective consumption of *Enteromorpha* at all life stages herbivores indirectly favored *Pilayella littoralis* and further algae of the community. As a third important result, *Enteromorpha* could overcompensate strong herbivore pressure when I moderately increased nutrient availability in summer. Because of its positive effect on *Enteromorpha* nutrient enrichment negatively affected the performance of *Pilayella*. Finally, both, herbivore and nutrient effects were more pronounced in early life stages compared to adults.

Many species from microbes to trees invest into banks of dormant propagules or seed banks to survive unfavorable conditions and sudden disturbances in a variable environment (Hairston & De Stasio 1988, Leck et al. 1989, Hoffmann & Santelices 1991, Fenchel et al. 1997). With a potential for dormancy periods ranging from weeks to centuries, local recovery and persistence of populations after a disturbance is favored by former investment into a seed bank, depending on timing, frequency and intensity of the disturbance. Different investment into seed banks may be related to species life-history patterns (Grime 1979, Leck et al. 1989). The existence of a macroalgal propagule bank or a "bank of microscopic forms" (sensu

Chapman 1986) has been only recently established (Chapter 4, Hoffmann & Santelices 1991, Santelices et al. 1995). In a first detailed characterization of such a bank of microscopic algal forms on a rocky shore in Chile (Hoffmann & Santelices 1995) the bank was judged to be more important for the survival of perennial species compared to ephemerals. This is in contrast to terrestrial ecosystems, where fast-growing opportunistic annuals invest orders of magnitude more propagules into soil seed banks than slow-growing late successional species (Grime 1979, Leck et al. 1989). My findings are in concordance with the terrestrial systems. Recruitment of annual *Pilayella* and *Enteromorpha* from the propagule bank was increased by two to three orders of magnitude compared with perennial *Fucus vesiculosus* (Table 7.5). I found population development of *Enteromorpha* spp. and *Ulvopsis grevillei* to depend strongly on recruitment from the propagule bank. Since perennials (e.g. *Fucus vesiculosus*) occur year-round, and some annuals (e.g. *Ceramium strictum*) overwinter as adults in the deeper subtidal (discussed in Chapter 4) survival in a propagule bank may not be vital in their life cycles but may act as an insurance against local extinction following disturbance. Furthermore, the propagule bank can provide a storage of genetic diversity (De Stasio 1989). It is unknown so far, if in addition to a transient propagule bank (<1 year old) also a persistent (>1 year old) bank exists for macroalgae as reported for many land plants (Grime 1979, Leck et al. 1989).

Despite their ubiquity the ecological role of a propagule bank or seed bank in modifying mechanisms of community regulation such as competition and herbivory has not yet been examined. My results indicate that the propagule bank (1) provides a 2-month escape from herbivory and (2) enables population growth when nutrient supply is still high. Thus, the propagule bank can act as an adaptation to seasonal variation in herbivore pressure and nutrient availability. This represents a major competitive advantage for opportunistic species that use nutrients very effectively but that are suppressed by herbivores (Lubchenco 1978, Grime 1979, Littler & Littler 1980). However, not all opportunistic species were favored through the propagule bank (Table 7.5). Within dense stands of growing germlings, competition is likely to occur on limiting resources such as space, light and nutrients (Carpenter 1990). Competitive interactions in turn are modified by (1) herbivory (Lubchenco & Gaines 1981, Menge 1995), (2) nutrient availability (Fong et al. 1996), and (3) propagule supply (Roughgarden et al. 1988, Reed 1990).

In spring, alternating dominance patterns occurred depending on the presence or absence of the propagule bank. Among new recruits from the propagule bank, *Enteromorpha* was the

superior space occupier until May. This was in contrast to the previous assumption that *Pilayella* may pre-empt space due to the ability to germinate at lower temperatures. Possibly, this may only be an advantage in years when low water temperatures (<5°C) prevail until late spring as in 1995 (Chapter 2). The much higher investment of *Enteromorpha* into the propagule bank compared to *Pilayella* may explain this dominance. But, it does not explain why recruitment of *Pilayella* from the propagule bank is almost totally suppressed (Fig. 7.2b). Moreover, despite higher propagule supply in *Enteromorpha* (Chapter 3), *Pilayella* dominated space in the course of new recruitment on sterilized substrata from May to June. These different dominance patterns may be caused by shifts in competitive abilities with seasonal nutrient availability. Competitive dominance can be reached by higher rates of resource capture followed by faster growth and subsequent shading or sweeping effects (Carpenter 1990, Santelices 1990, Vadas et al. 1992). In my experiment, new recruitment in *Enteromorpha* was more enhanced by nutrient enrichment (4.4- to 7.3-fold) than in *Pilayella* (1.6- to 2.5-fold, Table 7.6, Fig. 7.6). This is an advantage in nutrient-high conditions as in early spring possibly leading to the observed *Enteromorpha* dominance then. In contrast, in unenriched low-nutrient summer conditions, recruitment in *Enteromorpha* was smaller than in *Pilayella* (Fig. 7.6). *Pilayella* germlings may use nutrients more efficiently at low concentrations outcompeting *Enteromorpha* in the course of new recruitment on sterilized substrata from May to June. Thus, shifting dominance between *Enteromorpha* and *Pilayella* depends on the recruitment source and on seasonal nutrient availability.

Herbivores became abundant and active in May and strongly altered these dominance patterns. Both algal species were heavily consumed yet, effects were stronger on *Enteromorpha* which was the preferred food source in all life stages (this chapter, Chapter 6). Dominance of *Enteromorpha* on rocks with propagule bank was reduced by herbivores resulting in an indirect positive herbivore effect on other species including *Pilayella*. Selective consumption of a superior competitor is known to modify competitive interactions (Menge 1995). However, if *Enteromorpha* was not abundant (as on sterilized plots) herbivores also negatively affected *Pilayella*. Net herbivore effect on *Pilayella* thus depended on the relative abundance of *Enteromorpha* as an alternative food source and thus, on the absence or presence of the propagule bank. Herbivore consumption of both annuals, *Enteromorpha* and *Pilayella*, highly favored further algae and, importantly, enabled recruitment of perennial *Fucus vesiculosus* (Table 7.5, B. Worm, unpublished). Compared to the two annual algae,

Fucus is well-defended against herbivory by polyphenolic feeding deterrents (Hay & Fenical 1988) and structural defenses. But, this species highly suffered from the propagule bank treatment (Table 7.5) because here, an established turf of *Enteromorpha* drastically inhibited new settlement and recruitment of *Fucus vesiculosus* during its reproductive period in May (B. Worm, unpublished). Algal turfs or canopies are well documented to act as a barrier preventing new settlement and recruitment of annual (Hruby & Norton 1979) or perennial propagules (Deysher & Norton 1982, Chapman 1984, Dayton et al. 1984, Worm & Chapman 1998). Mediating effects of herbivores on competition between annuals and perennials have also been described from rocky shores. Among other annuals, *Enteromorpha* inhibited perennial *Fucus vesiculosus* by faster growth when herbivores were rare or inactive but, this pattern was reversed when herbivores were dense and active (Lubchenco 1978, 1983). Clearly, herbivores can play a key role in maintaining species diversity by consuming a dominant space occupier such as *Enteromorpha*. In my experiments however, a diverse herbivore guild rather than a single "keystone species" (Paine 1966, 1995) prevented *Enteromorpha* dominance. Such "diffuse predation" (effect shared by several species of similar potential importance) in contrast to "keystone predation" (large effects of one important predator) is important in some rocky shore communities (Robles & Robb 1993, Menge et al. 1994).

Nutrient enrichment during summer had only slight effects on the established algal canopy and did not increase occurrence period or % cover of any species. However, nutrient enrichment significantly increased growth and thus canopy height of *Enteromorpha* which had some negative effect on growth of recruiting *Fucus* germlings (B. Worm, unpublished). Still, the overall nutrient effect on adult populations was small compared to the other treatment effects (herbivory, propagule bank). Greater importance of herbivore effects over nutrient enrichment was also reported for epiphyte growth on seagrass (*Zostera marina*) in experimental mesocosms (Neckles et al. 1993). However, I can only generalize upon processes that occur in response to summer nutrient enrichment. In the course of further eutrophication, nutrients may be enriched during all seasons compared to pristine systems. Effects of nutrients on the community may be much larger when nutrient enrichment occurs during the critical period of algal recruitment in spring. In accordance with this notion, moderate nutrient enrichment had large effects on new recruitment of *Enteromorpha* and *Pilayella* in summer that even exceeded effects of herbivory (Table 7.6). This strong nutrient limitation of recruitment during summer corroborates results from laboratory results (Chapter

4). Furthermore, nutrient enrichment allowed mainly *Enteromorpha* to compensate for losses caused by herbivory. Such a partial compensation of consumer control (*Asterias rubens*) by enhanced productivity under eutrophic conditions was also suggested for the mussel *Mytilus edulis* in Kiel Fjord (Reusch & Chapman 1997). My results again demonstrate the greater sensibility and different reactivity of early life stages towards environmental variability compared to adult stages.

Within my experimental units, no "algal bloom" such as overcrowding or free floating algal masses developed. This led me to propose a possible niche differentiation in *Enteromorpha* and *Pilayella*. While main population growth of *Enteromorpha* occurred on rocks which naturally bear a propagule bank (Fig. 7.5b), population growth of *Pilayella* mainly occurred on bare substrata without a propagule bank (Fig. 7.5a). In the study area, most of the available surface without a dense propagule bank may be provided by *Fucus* plants on which only a few propagules overwintered (Chapter 4, Fig. 4.1). After initial low recruitment from the propagule bank on rocks, *Pilayella* may reproduce quickly and recruit epiphytically on *Fucus* and other bare surfaces. Here, it dominates relative to *Enteromorpha* under natural herbivore pressure. In my experiment, cover of *Pilayella* was rather low and checked by intense herbivory on the sterilized rocks without cages (Fig. 7.5a). However, the distribution pattern of *Pilayella* relative to *Enteromorpha* on these plots closely resembled the seasonal abundance of adult biomass that occurs epiphytically on *Fucus* (Chapter 3, Fig. 3.1c, 3.2b). A further possibility in *Pilayella* to avoid *Enteromorpha* dominance on rocks is to occur as a free-floating stage. I observed that *Pilayella* thalli were usually torn off from the substratum once they exceeded >5 cm length. These unattached filaments became interwoven in dense carpets which drifted around and accumulated in areas of low current velocities. Free-floating life at the water surface is common in bloom-forming macroalgae like *Enteromorpha*, *Ulva* and *Pilayella* (Wilce et al. 1982, Bonsdorff 1992, Fletcher 1996) but was rarely observed in *Enteromorpha intestinalis* at the study site. A drifting adult stage may be generally advantageous for avoiding space competition with other macroalgae and preventing shading by phytoplankton blooms which are common in eutrophicated waters (Sand-Jensen & Borum 1991).

In summary, algal recruitment in spring was the critical period for population development and decisive for the establishment of dominance patterns of the co-occurring macroalgae *Pilayella littoralis* and *Enteromorpha* spp. Under actual environmental conditions in the field,

coexistence of *Enteromorpha* and *Pilayella* and of further algae was possible if both, the propagule bank and herbivores were present. This is the natural situation at my study site. However, the balance between these two counteracting factors may be disturbed by (1) the reduction of herbivory, (2) the enhancement of nutrient availability, (3) the loss of perennial vegetation. These points are all identified as problems that are closely related to eutrophication. Important positive feed-back mechanisms can occur and will be discussed in the following chapter.

Chapter 8

General discussion and conclusions

Changing structure and functioning of coastal ecosystems in the course of increasing eutrophication has been well documented (Chapter 1). Blooms of annual macroalgae as one major problem linked to eutrophication cause severe damage in coastal ecosystems worldwide (reviewed by Fletcher 1996). Despite their increasing importance and impact, a causal understanding of mechanisms controlling macroalgal blooms is fragmentary. In this study, I provide a conceptual model that attempts to synthesize abiotic and biotic factors that control population development and species dominance patterns in macroalgal blooms (Fig. 8.1 and 8.2).

My observations and experiments unequivocally demonstrate that early life stages are of critical importance for population dynamics of bloom-forming macroalgae in the Baltic Sea. This has been proposed before for seaweeds on rocky shores (Hruby & Norton 1979, Lubchenco 1983, Vadas et al. 1992) and on soft bottoms (Lotze 1994, Schories 1995a), but experimental evidence was lacking for bloom-forming algae. The bottleneck character of early life stages may indeed be a very general phenomenon, not only restricted to algae, and has been similarly proposed for marine invertebrates (Roughgarden et al. 1988, Underwood & Fairweather 1989), fish (Fairweather 1991) and terrestrial plants (Leck et al. 1989, Fenner 1992). In this study, early life stages were more sensitive to environmental change than adults. Their overall response to variation of important factors such as nutrient enrichment or herbivory was usually more pronounced compared to adult plants. Moreover, some important differences between the early life stages of different species were not paralleled between the adult stages of the same species (Chapter 4, 5). Taken together, this may indicate that ecophysiological and ecological traits of early life stages can be of greater importance than those of adults in determining population development and species dominance pattern.

A suite of factors controlling the development of early stages in the beginning of the vegetation period define a species-specific recruitment window (sensu Deysher & Dean 1986) of optimal conditions for recruitment of early stages into the macrobenthos (Fig. 8.1). I suggest that the length of this period may be a predominant variable that controls the extent, timing and species dominance patterns of macroalgal blooms. In early spring, rising temperature and light climate (day length and light intensity) opened the recruitment window

for *Enteromorpha* and *Pilayella* among other algae (Fig. 8.1). Potentially, successful recruitment of *Pilayella* in the study area could occur until June or July when temperatures exceeded 20°C, whereas *Enteromorpha* was able to recruit continually until late autumn when decreasing temperature and light climate became inhibitory. I will call this period of potential recruitment which was defined by abiotic environmental conditions the "fundamental recruitment window" (equivalent to a fundamental niche, Keddy 1989). The actual temporal distribution of species, their "realized recruitment window" (realized niche, Keddy 1989) was controlled in late spring and summer by increasing herbivore pressure in combination with increasing nutrient limitation (Fig. 8.1). Finally, recruiting and growing algae competed for space and resources. The dominant space occupier inhibited new recruitment of further algae. The relative importance of these factors was species specific and shifted with time and life stage. Two ecological traits appear to be predominantly important: (1) investment into a overwintering propagule bank and (2) susceptibility to herbivores.

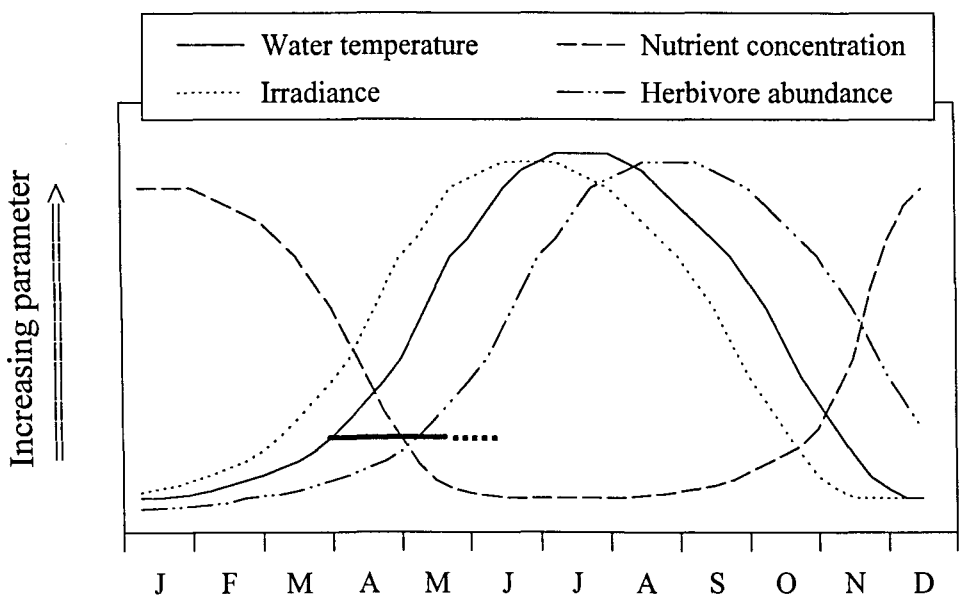

Fig. 8.1. A recruitment window (bold line and dots) of annual, bloom-forming macroalgae. Rising temperature and irradiance open this period of optimal conditions for recruitment in early spring. Towards late spring and summer, increasing herbivore pressure and decreasing nutrient availability control actual species distribution and limit the recruitment window. The actual length of the recruitment window is species specific and may vary among years and regions as a function of climatic variation, changes in herbivore populations and nutrient loading.

The initiation of algal recruitment in early spring originated from overwintering propagules (Fig. 8.2). These propagules were produced in the previous vegetation period, when they settled on various substrata, preferentially on rocks (Chapter 4), but did not recruit into erect germlings. High densities of overwintering propagules were found in opportunistic annuals, whereas perennial *Fucus vesiculosus* was rare in the propagule bank. Abundance in the propagule bank was related to the total reproductive output and was in accordance with the functional-form model of Littler & Littler (1980), that predicts higher rates of propagule production for opportunistic than for late successional perennial forms. After settlement, the propagules or microscopic stages remained in the propagule bank until environmental conditions became favorable for recruitment in next spring. Whereas such an overwintering pattern in the form of seeds or bulbs is the rule for annual land plants (Grime 1979, Leck et al. 1989) its role for annual macroalgae is only emerging (Hoffmann & Santelices 1990, Santelices et al. 1995, Schories 1995b).

Timing and rate of germination appeared to be the ecophysiological bottleneck for the initiation of mass spring development (Fig. 8.2). This step was mainly controlled by temperature and to some extent by light similar to patterns found in terrestrial plants (Fenner 1992). Further population development into adults and the potential for forming a mass bloom depended on the relative impact of nutrients and losses to herbivory in germlings and adults. If nutrients were elevated through experimental enrichment, high capacities of growth and nutrient uptake enabled fast-growing opportunistic annuals to overcompensate high losses to herbivory. Despite nutrient depletion in summer, fast initial responses towards nutrient pulses enabled opportunistic species to use patchily available resources effectively. This is highly advantageous compared to slow responses of perennial species (Wallentinus 1984). Potential P-limitation of germination in early spring shifted to increasing N-limitation of recruitment and growth towards summer. Seasonal variation of nutrient limitation caused by seasonal alteration of environmental conditions has also been proposed in other marine systems (Duke et al. 1989, Fong et al. 1993). The main factor counteracting nutrient enrichment was herbivory (Fig. 8.2). From April onwards, the realized extent of mass blooms was strongly influenced by an abundant and diverse herbivore guild (*Idotea* spp., *Gammarus* spp., *Littorina* spp.). In all life stages, *Enteromorpha* was the preferred food source over *Pilayella*. Yet, effects of individual herbivore species varied with life stage. If *Enteromorpha* was rare, *Pilayella* was heavily consumed as well. "Diffuse consumption" by several herbivore species

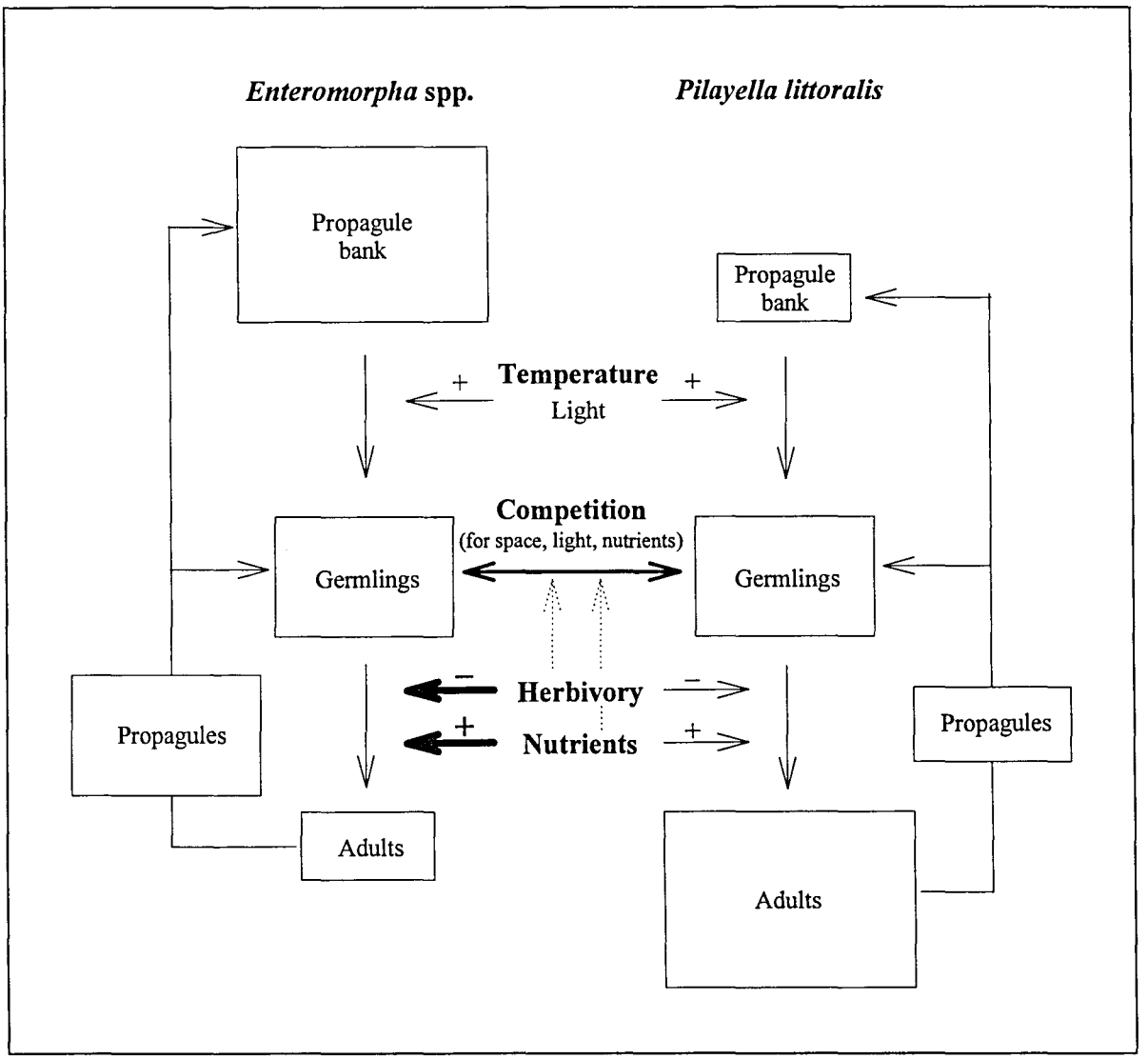

Fig. 8.2. Conceptual model of main mechanisms that control population development and species dominance pattern of *Enteromorpha* spp. and *Pilayella littoralis* in macroalgal blooms at the study site. The box size represents the relative abundance of each life stage. Solid arrows indicate direct effects and transitions from one life stage into another. The thickness of arrows represents the relative importance of effects, +, - the character of direct effects. Dotted arrows indicate modifying indirect effects of herbivory and nutrient concentrations on competitive interactions. Depending on the season, herbivory and nutrients can also have strong effects on the development of propagules into germlings which is not indicated in this figure. For further details refer to the text.

feeding on different algal life stages (Robles & Robb 1993, Menge et al. 1994) in contrast to "keystone consumption" (sensu Paine 1966) appeared important for an effective herbivore control. However, herbivore pressure was more severe on early life stages compared to adults, which again demonstrates the vulnerability of early stages as proposed by Vadas et al. (1992).

Despite herbivore food preferences, species dominance patterns within macroalgal blooms were further controlled by competitive abilities of the algae. The ability to occupy space for recruitment and growth depended on the availability of the propagule bank (dormancy, favoring *Enteromorpha*) or dispersal (favoring *Pilayella*) as a recruitment source. Further, it depended on the effectiveness of resource capture in mixed stands under variable levels of nutrient availability. When *Enteromorpha* and *Pilayella* recruited together, nutrient enrichment favored *Enteromorpha* whereas *Pilayella* seemed to be able to use small resource supply more efficiently. As a consequence, under nutrient enrichment, *Enteromorpha* was able to overcompensate its higher losses through herbivory. Thus, while herbivores can potentially control mass-blooming macroalgae, nutrient enrichment may override this control mechanism. The balance between bottom-up (resource) and top-down (herbivore) control is highly important for the extent of macroalgal blooms.

In conclusion, the relative importance of abiotic factors (predominantly nutrients, temperature and light) versus species interactions such as competition and herbivory varies with season. An abiotic control of the initiation of macroalgal blooms in early spring switches to biotic control in later spring (competition, herbivory), and combined abiotic (nutrient limitation, high temperature) and biotic (herbivory) control in summer. This pattern is paralleled in other food webs, e.g. during plankton succession in temperate lakes and marine systems (Sommer 1989) or in the development of spring annuals in terrestrial ecosystems (Fenner 1992).

One important goal of ecological research is to increase our ability to predict changes in the natural environment upon changes in environmental parameters (Peters 1991). Following my results, prediction of occurrence and extent of macroalgal blooms will have to combine knowledge about the trophic structure of the system, the availability of substratum with a propagule bank, and the combined impact of herbivores. The response of coastal macrophyte communities to variation in these factors should be investigated in further locations to reveal how systems differ in their ability to absorb increased nutrient loading. The goal should be a predictive model that can be translated to other systems for use in coastal management (Valiela et al. 1997).

Predicting species composition and dominance patterns may be more complex than predicting aggregate parameters like total biomass and requires some additional information

on the ecophysiological and ecological traits of species on different life-stage levels. Knowledge on the fundamental recruitment windows (or niches) may be gained by laboratory studies on germination and growth in relation to abiotic parameters. To predict realized occurrence however, field experiments are necessary to determine competitive abilities and susceptibility to herbivory under the actual environmental conditions. In this study, I was able to answer why *Pilayella* dominates macroalgal blooms over *Enteromorpha* in the Baltic Sea. High herbivore pressure, moderately high nutrient concentrations, and the availability of perennial *Fucus* as substratum without a propagule bank favors *Pilayella* over *Enteromorpha*. But, why does *Enteromorpha* (and similar green algae) dominate mass blooms in most other coastal waters around the world? Many coastal lagoons or bays where macroalgal blooms were observed are dominated by soft bottoms and perennial vegetation is rare, e.g. in the Wadden Sea, Germany (Lotze 1994, Schories 1995a), Veerse Meer, Netherlands, Langstone harbor, England, Bay of Lannion, France, Venice lagoon, Italy (Rijstenbil et al. 1996, Schramm & Nienhuis 1996). Sand grains provide substratum for propagule settlement and germination for green algae but probably not for other species. In addition, some typical species of the soft bottom fauna like the mud snail *Hydrobia ulvae*, and tubes of *Lanice conchilega* can serve as substrata (Schories 1995a, b, Schories et al. 1997). On these substrata, herbivore pressure is reduced because littorinid snails can hardly forage on sand or mud (Wilhelmsen & Reise 1994) and foraging time for all mesoherbivores is reduced due to the tides. Moreover, perennial vegetation which is an important habitat for crustacean herbivores (Salemaa 1987) is rare. Thus, several factors favor the green alga *Enteromorpha* and possibly also other common Chlorophyta such as *Ulva*, *Cladophora* and *Chaetomorpha*.

Coexistence of species such as *Enteromorpha* spp., *Pilayella littoralis* and *Fucus vesiculosus* in the Baltic Sea was possible because each algal genus was favored by at least one important environmental variable. An abundant propagule bank favored *Enteromorpha* whereas herbivores favored *Pilayella* and the perennial vegetation. Nutrient supply did usually not allow overcompensation of losses through herbivore consumption. However, this balance between counteracting processes may be disturbed. Increasing loads of nitrogen and phosphorus will continue to favor bloom-forming algae which then threaten biodiversity and sustainability of coastal ecosystems (Vitousek et al. 1997). Despite the necessity and efforts towards stabilizing nutrient loads, no substantial decrease of N- and P-loads have been observed in long-time series of nutrient concentrations in the Baltic (Nehring 1991) and in the

North Sea (Martens 1989, Hickel et al. 1993). The importance of herbivores as a major counteracting factor against macroalgal blooms was not recognized until now. A potential die back or decline of herbivores would release opportunistic, bloom-forming macroalgae from consumption similar to effects in exclusion experiments (Chapter 6, 7). Herbivores may be threatened by several factors, some of which are either eutrophication- or pollution-related problems. For example, enhanced sedimentation as a consequence of increasing phytoplankton blooms may deteriorate the living conditions of snails foraging mainly on hard substratum (Wilhelmsen & Reise 1994). Further threats come from increasing concentrations of synthetic organic chemicals that accumulate in marine organisms from planktonic algae to whales (e.g. insecticides such as DDT, polychlorinated biphenyls (PCBs), Schulz-Bull & Duinker 1996, Vitousek et al. 1997). Some common toxins such as TBT (tributyltin, an antifouling agent) can cause physiological and morphological alterations of invertebrates and can cause the loss of reproductive ability, e.g. in *Hydrobia ulvae* and *Littorina littorea* (Schulte-Oehlmann et al. 1996). Moreover, the decline of the perennial vegetation which is often observed following eutrophication (Chapter 1) leads to a habitat loss for herbivores which are typically closely associated to the perennial canopy (Salemaa 1987). These factors may create positive feed-back mechanisms. Higher nutrient loads favor annual algae (mainly *Enteromorpha, Pilayella*) which massively recruit out of the propagule bank and inhibit perennial recruitment (B. Worm, unpublished). In addition, increasing epiphytic loads enhance the drag on the perennial plants (Lubchenco 1983). The loss of perennial cover will be accompanied by the decline of herbivores which prefer these plants as a habitat (e.g. *Idotea, Gammarus*). Subsequently, herbivore pressure will be reduced resulting in an acceleration of macroalgal blooms. The perennial vegetation will gradually be replaced by monocultures of opportunistic annuals as observed in various parts of the Baltic (Kangas et al. 1982, Vogt & Schramm 1991). This decline of perennial vegetation will consequently lead to a severe loss of biodiversity which is associated to the *Fucus* community (Kautsky et al. 1992). The loss of biodiversity in turn can decrease ecosystem stability (e.g. Tilman 1996, Naeem & Li 1997). Thus, herbivores stabilize the community by favoring the persistence of perennial macrophytes (Lubchenco 1983) whereas nutrient enrichment may destabilize the community by creating positive feed-back mechanisms. Control and reduction of nutrient loads must be a prime goal of coastal and terrestrial management efforts (Valiela et al. 1997). Further, an effective conservation of the perennial vegetation may help to maintain an

abundant and diverse herbivore guild as a natural balancing factor on bloom-forming macroalgae. The recommended establishment of Baltic Sea protected areas (BSPA, HELCOM 1994) on coasts around the Baltic Sea may be a promising first step. Protection of whole ecosystems often represents the most effective way to sustain genetic, population, and species diversity (Vitousek et al. 1997). This is important for the long-term maintenance of critical ecosystem processes which are commonly under biotic control (Chapin et al. 1997).

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Appendix

Chapter 5

Table A5.1. Results of two-way ANOVAs on the effects of different nitrogen enrichments on growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* (factor "species"). Phosphate was enriched with 30 µmol l^{-1} in all treatments.

Source of variation	df	MS*10^3	F-ratio	P-value
Species	1	0.716	2.037	0.1727
Nitrate (500 µmol l^{-1})	1	19.600	55.740	0.0001
Species x nitrate	1	0.372	1.059	0.3187
Residual	16	0.352		
Species	1	0.133	0.223	0.6432
Ammonium (50 µmol l^{-1})	1	4.458	7.463	0.0148
Species x ammonium	1	0.361	0.605	0.4481
Residual	16	0.597		
Species	1	0.145	0.342	0.5671
Urea (5 µmol l^{-1})	1	2.341	5.527	0.0319
Species x urea	1	0.380	0.897	0.3576
Residual	16	0.424		

Table A5.2. Maximum uptake rate (V_{max} in µmol $h^{-1}g^{-1}$ DW), half-saturation constant (K_m in µmol l^{-1}), and initial slope ($\alpha = V_{max} / K_m$) of nutrient uptake of *Pilayella littoralis* and *Enteromorpha intestinalis* at different time intervals. Data were fitted to the Michaelis-Menten equation using nonlinear least-squares regression. Shown are means of estimated kinetic parameters (± 1SE, n=7 for nitrate, ammonium, n=5 for phosphate).

Time	*Enteromorpha intestinalis*					*Pilayella littoralis*				
	V_{max}	*SE*	K_m	*SE*	α	V_{max}	*SE*	K_m	*SE*	α
	NO_3^-- uptake					NO_3^-- uptake				
0-30	237.30	*30.29*	43.71	*18.50*	5.43	300.13	*43.39*	116.43	*45.99*	2.58
30-60	172.76	*24.04*	26.89	*13.44*	6.43	166.51	*16.00*	54.50	*17.14*	3.06
60-120	135.67	*17.56*	21.39	*10.29*	6.34	65.78	*1.49*	19.88	*1.78*	3.31
120-180	90.06	*4.15*	20.35	*3.67*	4.43	33.64	*2.52*	5.18	*1.92*	6.49
	NH_4^+- uptake					NH_4^+- uptake				
0-15	439.13	*33.74*	66.39	*16.25*	6.61	466.68	*43.22*	66.59	*19.12*	7.01
15-30	286.94	*20.08*	37.69	*9.56*	7.61	351.35	*56.17*	42.29	*22.96*	8.31
30-45	156.01	*15.95*	17.67	*7.60*	8.83	257.49	*51.81*	53.07	*34.90*	4.85
45-60	107.45	*6.27*	13.30	*3.47*	8.08	181.62	*27.25*	58.21	*28.51*	3.12
60-120	60.68	*5.53*	12.82	*5.38*	4.73	52.56	*8.08*	10.08	*6.59*	5.21
	PO_4^-- uptake					PO_4^-- uptake				
0-60	46.86	*13.54*	17.33	*10.63*	2.71	44.21	*17.69*	15.44	*13.90*	2.86
60-120	35.93	*14.43*	17.13	*13.84*	2.10	30.97	*9.42*	11.61	*8.00*	2.67
120-240	13.88	*3.92*	8.12	*5.75*	1.71	8.22	*1.78*	3.72	*2.47*	2.21

Table A5.3. Results of one-way ANCOVAs on estimated kinetic parameters (V_{max} , K_m , α) of nutrient uptake of *Pilayella* and *Enteromorpha* (factor "species"). Time interval of nutrient uptake was added as a covariate in these analyses. The assumption of homogeneity of slopes was fulfilled in all analyses.

Source of		V_{max}			K_m			α		
variation	df	MS	F	P	MS	F	P	MS	F	P
NO_3^-- uptake										
Species	1	608	0.29	0.615	875	1.33	0.300	6.46	3.14	0.137
Time	1	44211	20.93	0.006	4415	6.73	0.049	1.85	0.90	0.386
Residual	5	2122			656			2.06		
NH_4^+- uptake										
Species	1	7660	1.35	0.283	716	3.55	0.102	5.26	1.92	0.209
Time	1	154735	27.32	0.012	2623	12.99	0.009	6.95	2.53	0.156
Residual	7	5663			202			2.74		
PO_4^-- uptake										
Species	1	29.3	2.32	0.225	23.2	4.03	0.138	0.25	15.44	0.029
Time	1	1189.5	94.19	0.002	109.6	19.01	0.022	0.68	41.40	0.008
Residual	3	12.6			5.8			0.02		

Table A5.4. Comparison of estimated parameters of Michaelis-Menten kinetic (V_{max} in µmol $h^{-1}g^{-1}$ DW and K_m in µmol l^{-1}) calculated by (1) nonlinear regression analysis and (2) linear regression analysis after plotting according to DeBoer (S/V vs. S) and Eadie-Hofstee (V vs. V/S).

Nutrient and	*Enteromorpha intestinalis*		*Pilayella littoralis*		Parameter estimation
time interval	V_{max}	K_m	V_{max}	K_m	method
NO_3^- (0-30)	237.3	43.7	300.1	116.4	nonlinear regression
	228.2	73.0	270.7	97.7	DeBoer
	187.6	41.7	231.1	72.7	Eadie-Hofstee
NH_4^+ (0-15)	439.1	66.4	466.7	66.6	nonlinear regression
	409.8	53.7	435.7	64.1	DeBoer
	404.5	52.8	482.0	79.7	Eadie-Hofstee
PO_4^- (0-60)	46.9	17.3	44.2	15.4	nonlinear regression
	66.7	37.3	26.5	6.3	DeBoer
	66.7	43.3	5.2	10.6	Eadie-Hofstee

Chapter 7

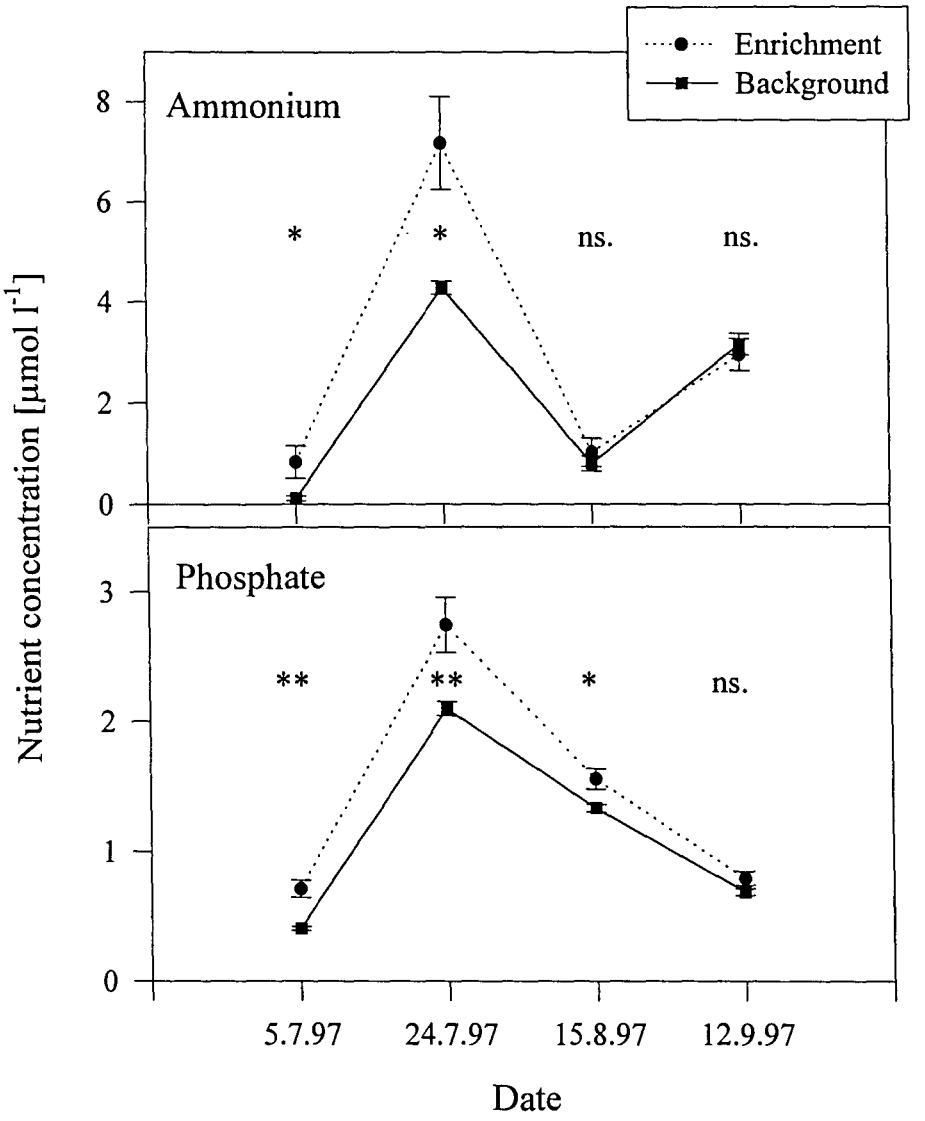

Fig. A7.1. Seawater nutrient concentrations in enriched and unenriched (background) treatments of the factorial field experiment. Water samples were taken 10 cm above the installed nutrient diffusors and experimental rocks. Nutrient enrichment was unaffected by cages and treatment factors (herbivory, propagule bank) and therefore pooled over all treatment combinations (means ± 1SE, n=24). Significant enrichments are indicated as: *=$p<0.05$, **=$p<0.01$, ns.=not significant.

Tab. A7.1. Complete ANOVA tables of cage effects on herbivore density in the main experiment separated by herbivore species. Untransformed data achieved homogeneity of variances.

Source	df	MS	F-ratio	P-value
Littorina saxatilis				
Cage	1	6050.0	23.641	0.0001
Block	3	484.6		
Residual	27	255.9		
Idotea spp.				
Cage	1	63.28	1.714	0.2016
Block	3	19.28		
Residual	27	36.93		
Gammarus spp.				
Cage	1	63.28	1.340	0.2571
Block	3	132.6		
Residual	27	47.2		
Littorina littorea				
Cage	1	0.781	2.039	0.1647
Block	3	0.115		
Residual	27	0.383		

Tab. A7.2. Results of paired t-tests after Peterson & Renaud (1989) on herbivore preference between new recruits of *Enteromorpha* spp. and *Pilayella littoralis* under different treatments of nutrient enrichment and propagule bank. Shown are means of differences between germling densities of the two algae in closed cages (control), open cages, and on open plots. A positive mean indicates that *Pilayella* was more abundant, a negative mean indicates that *Enteromorpha* was more abundant. It was tested (1) whether the mean of differences in open cages was significant different from that in closed cages (= herbivore effect), and (2) whether the mean of differences in open plots differed from that in open cages (= cage effect). Tabled test limits (n=4, k=2) are p=0.001(***): t_{crit}=5.959, p=0.01(**): t_{crit}=3.707, p=0.05(*): t_{crit}=2.447, (ns.): not significant. Data were log transformed to achieve homogeneity of variances.

Treatment	Mean of differences	Variance s^2	n	t		Conclusion
a) No propagule bank, no nutrient enrichment						
Closed cages (control)	0.573	0.0555	4			
Open cages	0.652	0.0049	4	0.6428	ns.	Herbivore effect
Open plots	0.357	0.0104	4	-4.7798	**	Cage effect
b) No propagule bank, nutrient enrichment						
Control	-0.061	0.0055	4			
Open cages	0.273	0.0462	4	2.9380	*	Herbivore effect
Open plots	0.144	0.0088	4	-1.0996	ns.	Cage effect
c) Propagule bank, no nutrient enrichment						
Control	-0.044	0.0132	4			
Open cages	0.455	0.0095	4	6.6191	***	Herbivore effect
Open plots	0.534	0.0070	4	1.2434	ns.	Cage effect
d) Propagule bank, nutrient enrichment						
Control	-0.298	0.0050	4			
Open cages	-0.061	0.0196	4	3.0304	*	Herbivore effect
Open plots	0.227	0.0104	4	3.3210	*	Cage effect