# SEAGRASS SYSTEMS

## Stability of seagrass systems against anthropogenic impacts

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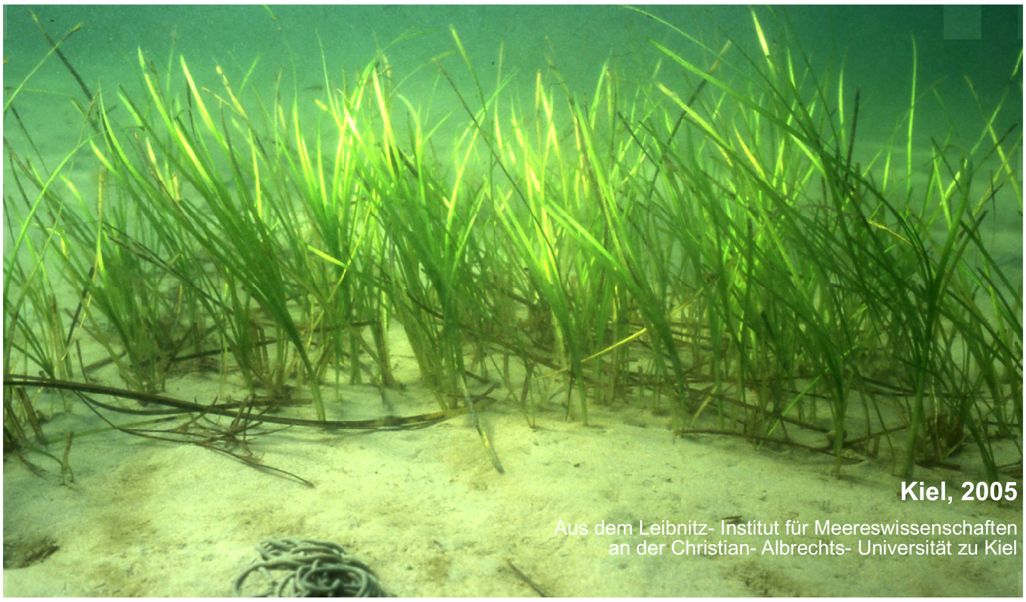

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# Inhaltsverzeichnis

# Summary

The study presented here examines which factors directly or indirectly connected to eutrophication, are relevant to the deterioration of seagrass populations in the Baltic Sea. More particularly it is a study of the interacting effects of seagrass autotrophic competitors (epiphytic algae, drifting macroalgae and phytoplankton) on seagrass. These are interesting yet largely studied and were, in this study, investigated through the field observations and experiments of a seagrass population in the Greifswalder Bodden, Germany.

This shallow water system measures over 500 km$^2$, but is only 5-6 m deep and is a naturally nutrients sink. Over decades, this environment has been enriched with anthropogenic overfertilizing, making it an area of sufficient nutrient concentrations for plant growth year-round, resulting in strong phytoplankton blooms and the presence of floating algal mats. However, the remixing and resuspension of organic material limits light availability and plant growth in these eutrophic waters.

This study reveals that shoot densities and above-ground biomass of *Zostera marina* were very low, in comparison to the values for other sites on the Baltic Sea which were 3 to 4 fold higher (manuscript I).

As an adaptation to the low light supply in the Bodden, seagrass produced relatively long leaves. It is well known, that the most important factor determining the growth of seagrass is light. Also, in this study, the 78% of the variance of the eelgrass biomass and leaf area can be explained by light availability and water temperature.

To determine impact of ephemer epiphytes on the availability of light supply for *Zostera marina*, seasonal development and species diversity of epiphytes (mostly diatoms and filamentous algae) were estimated (manuscript II). It was assumed, that high nutrient concentrations in the Greifswalder Bodden would promote epiphytes growth, resulting in their high biomass. Surprisingly, seagrass shoots showed only low load of epiphytes, despite high nutrient supply. As grazing pressure, due to the very low abundances of herbivores, could be neglected as a determining factor, it appeared that epiphytes were light limited. In contrast to the findings of many other studies of the Baltic Sea and in the world, ephemer epiphytes seem to play just a minor role in the decline of the seagrass populations in the Greifswalder Bodden.

On the basis of enclosure and exclosure field experiments, the impact of floating macroalgal mats, which, accumulate at the bottom of the seagrass meadow, were estimated (manuscript III). The increasing number of reports about the loss of seagrass populations, which are associated with a spread of macroalgal mats, suggest that the decline in seagrass meadows is due to the appearance of macroalgae. The experiments were intended to provide evidence of the suggested negative impacts of the macroalgal mats on *Zostera marina*, and to estimate the strength and the mechanism. The experiments show that macroalgal mats had a strong negative effect on shoot density, biomass and growth of seagrass plants. Contrary to the expectations, no high ammonia concentrations were found during the decay of macroalgae and thus toxic effects on rhizome and eelgrass shoots could be disregarded. The main impact of algal mats on *Zostera marina* was a strong light attenuation and shading of new shoots. During the period of macroalgal mats presence, the development of new shoots was stopped. Depending on its duration and extent drifting algae can prevent the regeneration of seagrass meadows and

consequently result in a loss of seagrass communities.

The previous manuscripts (I-III) showed that light availability is the dominant factor controlling the growth and survival of seagrass populations in the Greifswalder Bodden. Irradiance is especially determined by the high phytoplankton- and resuspended particle concentrations in the Bodden. To get a better understanding of the current state of the seagrass meadows and the light conditions in the Bodden, the historical development of the macrophyte populations under the influence of the eutrophication and the changing light climate were analyzed over the last 25 years (manuscript IV). Due to the high nutrient loading in the sixties, phytoplankton and suspended solids concentrations increased strongly, resulting in a clear decrease in light penetration. The resulting increased light attenuation led to an "ecosystem shift", from a macrophyte dominated system to a phytoplankton dominated system. Within few decades, the predominant part of the macrophyte stock disappeared, promoting further light attenuation. Despite strong reduction in nutrient loading after 1985, water quality did not improve significantly and macrophytes stock were not able to recover (until this day). The resilience of the Greifswalder Bodden as a system dominated by phytoplankton was explained by the "ecosystem shift" Model. Restoration measures to improve the current state of the Bodden and to turn it back into a system dominated by macrophytes, is not realistic due to the large size of the Bodden.

This work shows the extensive impact of eutrophication on the ecosystem. It clarifies strongly, that anthropogenic interferences could only be reversed over a long period of time or, in extreme cases, may never be reversible. Therefore, it is especially important to provide ecological precaution, to conserve clear-water-systems and therewith economically valuable habitats.

Another coauthored study dealt with the impact of predatory fishes on herbivorous grazers in the eelgrass community (manuscript V). Abundance and diversity of fishes were estimated by a newly developed catch cage developed with the intention of avoiding the usual damage on seagrass shoots. Ten fish species were found, which showed a characteristically seasonal distribution. Biomass and abundance of small fishes were correlated to water temperature and seagrass biomass. Stomach analyses of fishes showed, that invertebrate herbivores that graze on seagrass play only a minor role in the diet of small fishes in the seagrass ecosystem in comparison to phytoplankton. These results show the observations made in the other manuscripts, that this benthic ecosystem is strongly determined and modified by pelagic impacts.

In conclusion, seagrass meadows in the Greifswalder Bodden are strongly controlled by abiotic factors ("bottom-up"), especially light, temperature and nutrient supply. Biological factors like grazing by herbivores or predation ("top-down" control) just play a minor role in this eutrophic system. A possible recovery of the seagrass meadows may result in a higher abundance and diversity of herbivorous invertebrates and fishes in the seagrass meadows. This would most likely result in an increase in the importance of the biological over the abiotic control as found in most Baltic systems.

# Zusammenfassung

Die vorliegende Arbeit untersucht, welche mit Eutrophierung direkt oder indirekt verknüpfte Faktoren für die Schädigung der Seegrasbestände in der Ostsee maßgeblich sind. Hierbei interessieren insbesondere die bislang wenig untersuchten Wechselwirkungen zwischen den autotrophen Konkurrenten der Seegräser, die im Rahmen von taucherischen Freilandbeobachtungen und Feldexperimenten an Seegraswiesen im Greifswalder Bodden untersucht wurden. Dieses über 500 km$^2$ große, aber nur 5-6 m tiefe Flachwasser-Ökosystem ist als Sedimentfalle ein natürlicher Nährstoffspeicher, der über Jahrzehnte anthropogener Überdüngung so weit angereichert wurde, dass ganzjährig hohe Nährstoffkonzentrationen vorliegen. Starke Planktonblüten und Driftalgenmatten sind die Folge. Durchmischung und Resuspension von Trübstoffen begrenzen Lichtangebot und Pflanzenwachstum in diesem eutrophen Gewässer.

Entsprechend gering waren Sproßdichten und Biomassen von *Zostera marina* im Vergleich zu drei- bis vierfach höheren Werten an Standorten in der westlichen Ostsee (Manuskript I). Überraschenderweise waren die maximalen Blattwachstumsraten der Seegrassprosse, vergleichbar mit denen von Seegrasbeständen an Standorten mit guten Lichtbedingungen.
Als Anpassung an das geringe Lichtangebot im Bodden, bildeten die Seegräser relativ lange Blätter aus. Es ist allgemein anerkannt, dass das Lichtangebot der bestimmende Faktor für das Wachstum von Seegräsern ist. Auch in dieser Untersuchung lassen sich 78% der saisonalen Variation in der Seegrasbiomasse und Blattfläche durch Lichtverfügbarkeit und Wassertemperatur erklären.

Um den Einfluss von ephemeren Aufwuchsalgen auf das Lichtangebot für *Zostera marina* zu bestimmen, wurde über 2 Jahre die saisonale Entwicklung und Artenzusammensetzung der Epiphyten (meist Diatomeen und filamentöse Algen) auf den Seegrasblättern bestimmt (Manuskript II). Es wurde vermutet, dass das hohe Nährstoffangebot im Greifswalder Bodden das Wachstum der Epiphyten fördert und es so zu hohen Biomassen von Aufwuchsalgen kommen würde. Überraschend zeigten die Seegrassprosse im Bodden trotz des hohen Nährstoffangebots einen nur geringen Aufwuchs von Epiphyten. Da Fraßdruck hierbei aufgrund der nur geringen Dichte von Weidegängern keine nennenswerte Rolle spielte, waren die Epiphyten offenbar Licht-limitiert. Im Gegensatz zu anderen Standorten spielen ephemere Aufwuchsalgen offenbar eine sehr untergeordnete Rolle für den Rückgang der Seegrasbestände im Bodden.

Anhand von Einschluss- und Ausschluss-Freilandexperimenten sollte der Einfluss von driftenden Makroalgen, die sich am Boden von Seegraswiesen zu Matten verdichten können, bestimmt werden (Manuskript III). Zunehmende Meldungen über Verluste von Seegrasbeständen, die mit einer Ausbreitung von Makroalgenmatten einhergehen, legen nahe, den Rückgang von Seegraswiesen auf dieses saisonale Phänomen zurückzuführen. Die Experimente sollten dazu dienen, den Einfluss von Makroalgenmatten auf *Zostera marina* zu belegen und die Stärke und den Mechanismus zu bestimmen. In den Versuchen übten Makroalgen einen deutlichen negativen Einfluss auf die Sprossdichte, die Biomasse und das Wachstum der Seegräser aus. Entgegen den Erwartungen wurden keine hohen Ammoniumkonzentrationen beim Abbau der Makroalgen gefunden, so dass toxische Effekte auf die Rhizome ausgeschlossen

werden können. Der wichtigste Einfluss der Makroalgenmatten auf *Zostera marina* lag in der starken Beschattung, die die Ausbildung neuer Seegrassprosse zeitweilig verhinderte. In Abhängigkeit von der Dauer und dem Ausmaß der Makroalgenmatten können die Driftalgen die Erneuerung von Seegraswiesen verhindern und damit zu einem Rückgang der Seegrasbestände führen.

In den vorangegangenen Untersuchungen wurde das Lichtangebot als der dominierende Faktor für das Wachstum und Überleben der Seegraswiesen im Greifswalder Bodden beobachtet. Das Lichtklima im Bodden wird vor allem durch die hohen Phytoplankton- und Trübstoffkonzentrationen bestimmt. Um den aktuellen Zustand der Seegraswiesen im Bodden und das Lichtklima verstehen zu können, wurde die historische Entwicklung der Makrophytenbestände im Greifswalder Bodden unter dem Einfluss von Eutrophierung und Lichtklima über die letzten 25 Jahre untersucht (Manuskript IV). Durch die hohen Nährstoffeinträge stiegen die Phytoplanktonkonzentrationen und Trübstoffe stark an, was zu einer deutlichen Reduzierung der Lichtdurchdringung führte. Die Lichtschwächung führte zu einem Wechsel des Ökosystems von einem von Makrophyten dominierten System hin zu einem von Phytoplankton dominierten System. Innerhalb weniger Jahrzehnte verschwand der überwiegende Teil der Makrophytenbestände, wodurch sich das Lichtklima noch weiter verschlechterte. Trotz der deutlichen Reduzierung der Nährstoffeinträge nach 1985 blieb die Wasserqualität mangelhaft, so dass sich die Makrophytenbestände nicht erholen konnten. Das Verharren des Greifswalder Boddens in einem von Phytoplankton dominierten System konnte anhand des “ecosystem shift” Modells erklärt werden. Renaturierungsmaßnahmen, um den aktuellen Zustand des Greifswalder Boddens zu verbessern und ihn in Richtung eines von Makrophyten dominierten Zustandes zurückzuversetzen, sind aufgrund der Größe des Boddens nicht anwendbar. Diese Arbeit zeigt die enormen Auswirkungen der Eutrophierung auf das Ökosystem. Und sie verdeutlicht, dass anthropogen zugefügte Schäden oftmals nur stark verzögert oder in Extremfällen gar nicht rückgängig gemacht werden können. Es ist daher wichtig, ökologisch vorzusorgen, um Klarwassersysteme zu erhalten und damit ökonomisch wertvolle Habitate zu schützen.

In einer weiteren Studie mit mir als Co-Autorin wurde der Einfluss von räuberischen Kleinfischen auf die Weidegänger innerhalb der Seegraswiese bestimmt (Manuskript V). Die Abundanz und Diversität der Kleinfische wurde mit Hilfe eines neu entwickelten Fangkäfigs ermittelt, der die sonst übliche Schädigung der Seegräser verhindert. Es wurden 10 Fischarten gefunden, die eine charakteristische saisonale Verteilung besaßen. Die Biomasse und Abundanzen der Kleinfische korrelierten mit der Wassertemperatur und der Seegrasbiomasse. Magenanalysen der Fische zeigten, dass Weidegänger gegenüber Plankton eine nur untergeordnete Rolle in der Ernährung der Fische im Seegrasökosystem spielen. Diese Ergebnisse belegen die in den übrigen Manuskripten gemachten Beobachtungen, dass diese benthischen Ökosysteme stark pelagischen Einflüssen unterworfen sind.

Insgesamt lässt sich feststellen, dass die Seegraswiesen im Greifswalder Bodden stark von abiotischen Faktoren (“bottom-up”), vor allem Licht-, Temperatur- und Nährstoffangebot kontrolliert werden, während biologische Faktoren wie Wegfraß durch Weidegänger oder Räuber (“top-down” control) eine nur untergeordnete Rolle in diesen eutrophierten Systemen spielen. Es ist zu erwarten, dass nach Erholung der

Seegraswiesen entsprechend des "ecosystem shift" Modells, biologische Kontrollmechanismen im Zuge einer größeren Abundanz und Vielfalt von Wirbellosen und Fischen in den Seegraswiesen stärker greifen.

## Publikationsliste

Die Dissertation beruht auf folgenden Veröffentlichungen, die in der Arbeit durch römische Ziffern markiert sind. Zwei Studien sind in einer nationalen und einer internationalen Zeitschrift und ein Vortrag ist als abstract im Konferenzband des internationalen Seegrassymposiums 2004 bereits erschienen. Die übrigen drei Manuskripte sind bei internationalen Zeitschriften eingereicht worden. Die experimentellen und beobachtenden Untersuchungen sind von mir initiiert und durchgeführt worden. Ulrich Sommer unterstützte mich während meiner Arbeit und leistete editorische Hilfe. Claudio Richter war maßgeblich beim Schreiben des dritten Manuskriptes beteiligt. Für das fünfte Manuskript führten Ivo Bobsien und ich gemeinsam die Felduntersuchungen durch. Ivo Bobsien war für die Bereitstellung und Analyse der Fischdaten und ich für die Seegrasdaten zuständig und das Manuskript schrieben wir gemeinsam.

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|---|---|
| Manuskript I | Eelgrass population: growth and productivity<br>eingereicht bei: Aquatic Botany<br>Britta Munkes, Ulrich Sommer |
| Manuskript II | Eelgrass - epiphyte dynamics: nutrient enrichment and grazing in an eutrophic estuary<br>eingereicht bei: Aquatic Botany<br>Britta Munkes, Ulrich Sommer |
| Manuskript III | Impact of macroalgae canopies on growth and survival of seagrass in an eutrophic estuary<br>eingereicht bei: Marine Ecology Progress Series<br>Britta Munkes, Claudio Richter and Ulrich Sommer |
| Manuskript IV | Eutrophication, phase shift and delayed return in the Greifswalder Bodden, Baltic Sea<br>Aquatic Science, published online: 30. August 2005<br>Britta Munkes |
| Manuskript V | Seasonal variation of fish community and habitat structure in an eelgrass bed (*Zostera marina* L.) in the southern Baltic Sea<br>Rostocker Meeresbiologische Beiträge; Bd. 12 (2004), S. 39-59<br>Ivo Bobsien, Britta Munkes |
| Manuskript VI | Impact of macroalgae canopies on growth and survival of eelgrass in an eutrophic estuary<br>Abstract of oral presentation, International Seagrass Symposium, Townsville 2004. Britta Munkes |

# Begriffserläuterung: Definitionen und Abkürzungen

| | |
|---|---|
| AGB | (above-ground biomass) Oberflächenbiomasse |
| ANOVA | Varianzanalyse |
| DIN | (Dissolved inorganic nitrogen) gelöster, anorganischer Stickstoff (Ammonium + Nitrat + Nitrit) |
| DIP | (Dissolved inorganic phosphorus) gelöster, anorganischer Phosphor |
| DM | (Dry mass) Trockengewicht |
| eutrophication | Eutrophierung: Erhöhter Eintrag von Nährstoffen & organischem Material |
| epibiota | Autotrophe und heterotrophe Organismen, die auf Seegrasblättern siedeln |
| epiphyte | Mikro- und Makroalgen, die auf Seegrasblättern siedeln |
| epizoa | Tiere, die auf anderen Organismen (hier gemeint Seegrasblätter) siedeln |
| grazer | Herbivore Invertebraten, Weidegänger |
| macrophytes | Makroskopische Pflanzen |
| macroalgae mats | Akkumulationen von herumdriftenden Makroalgen |
| SE | (Standard error) Standardfehler |
| TP | (Total phosphorus) Gesamtphosphor (gelöster + partikulärer Phosphor) |

# Übersicht

## Das Ökosystem: Seegraswiese

Wenngleich Seegraswiesen heute in der Öffentlichkeit kaum mehr ein Begriff sind, so waren sie früher wohl bekannt und wurden vielfach für verschiedene Bedürfnisse der Gemeinden an den Küsten verwendet (Borum et al., 2004). So wurden Seegrasblätter traditionell zum Verpacken von fragilen Gegenständen (Töpfereiartikel) im Mittelmeerraum benutzt, wie auch für den Transport von Fischen von den Küstengebieten ins Landesinnere. Seegras wurde an Schweine und Kleintiere verfüttert und in manchen Regionen als Streu für Rinderställe verwendet. Bis in die 50er Jahre nutzte man Seegräser für Matratzenfüllungen. Ebenso wurden sie im Deichbau, zur Hausisolierung und als Dachmaterial eingesetzt. Auch heutzutage hat man die günstigen Eigenschaften von Seegräsern wieder entdeckt und nutzt angeschwemmtes Seegras als Isoliermaterial im Hausbau und in der privaten Kleintierhaltung.

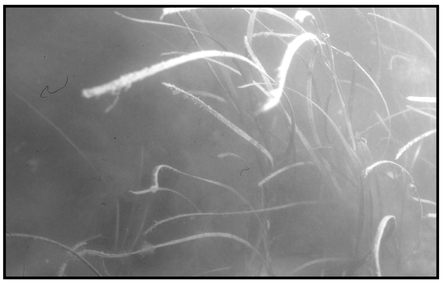
Das in den letzten 40 Jahren angesammelte Wissen über die Biologie und Ökologie von Seegräsern hat das Bewusstsein über den ökonomischen Wert von Seegräsern geschärft. Zusammen mit Makroalgen werden die durch Seegräser zur Verfügung gestellten biologischen Ressourcen und ökologischen Leistungen auf 3,8 Milliarden US $ pro Jahr geschätzt (Fischerei, Küstenschutz, Nährstoffrecycling, Rohstoffe) (Costanza et al., 1997). Somit stellen sie einen vergleichbaren Wert wie tropische Regenwälder dar (3,81 Milliarden US $).

Intakte Seegraswiesen gehören mit ihren schnellen Wachstums- und Produktionsraten von 190-900 g Kohlenstoff pro Quadratmeter und Jahr zu den produktivsten Meeres- und Ökosystemen der Welt (McRoy and Helfferich, 1977; Duarte and Chiscano, 1999). Makrophyten bilden ca. 20% der globalen Primärproduktion der Meere (Duarte, 1995). Global betrachtet bilden Seegraswiesen einen signifikanten Speicher für Kohlenstoff, der nach Schätzungen 12-15% des gesamten Kohlenstoffspeichers der marinen Ökosysteme ausmacht (Duarte and Chiscano, 1999; Green and Short, 2003). Zusammen mit Makroalgen haben Seegräser eine strukturell und funktionell große Bedeutung in Küstenökosytemen (Jackson et al., 2001). Ihre hohe pflanzliche Produktion ermöglicht die extrem hohen Biomassen von Fischen und Invertebraten der Küstenmeere. So stammen fast 20% der weltweiten Fischereierträge aus Küstengebieten (Smith, 1981; Charpy-Roubaud and A., 1990; Duarte, 1995).

Von den Polargebieten abgesehen, kommen Seegräser an sämtlichen tropischen, gemäßigten und subarktischen Küsten der Welt vor (den Hartog, 1970; Duarte et al., 2002). Ihre weltweite Verbreitung wird auf eine Fläche von ca. 500000 km$^2$ geschätzt (Green and Short, 2003). Sie wachsen in Weich- und Sandböden, wobei sie besonders an den deutschen Küsten, denen es oft an Hartsubstrat fehlt, ein wichtiges strukturgebendes Habitat darstellen.

Seegraswiesen ermöglichen eine vielseitige Fisch- und Invertebratenfauna, mit Abundanzen und Biomassen, die die von Sandböden um bis zu zwei Größenordnungen übertreffen (Boström and Bonsdorff, 1997). Für eine Vielzahl von Tieren bieten sie Schutz und Zufluchtstätte vor Räubern und Verdriftung. Sie fungieren für eine beträchtliche Anzahl von zum Teil kommerziell genutzten Organismen als Kinderstube und dienen als Nahrungsgrundlage in Form von Blättern, Epiphyten oder Detritus.

Seegraswiesen verhindern durch Konsolidierung des Sedimentes die Erosion des Untergrundes und haben somit eine wichtige Bedeutung für den Küstenschutz (Christiansen et al., 1981). Der dichte Blätterwald von Seegräsern verringert die Wasserbewegung und fördert das Rückhalten von suspendierten Partikeln, so dass sie wie ein Filter für die Küstengewässer wirken. Als Folge davon können Seegräser bis zu einem bestimmten Grad die Transparenz des Wasser aufrechterhalten. Eine weitere wichtige Ökosystemfunktion von Seegräsern besteht darin, dass sie wie andere mehrjährige Makrophyten, Nährstoffe langfristig in ihrer Biomasse binden, die sie dem freien Wasser entziehen. Somit können sie Eutrophierungseffekte abmildern (Scheffer et al., 1993; Winfried and Nienhuis, 1996).



Seegräser sind an oligotrophe (nährstoffarme) Ökosysteme angepasst. Sie besitzen geringe Nährstoffansprüche und speichern Nährstoffe längerfristig, zeigen jedoch ein langsames Wachstum und benötigen hohe Lichtintensitäten zur Photosynthese (Duarte, 1995; Hemminga and Duarte, 2000). Dieses bereitet ihnen Konkurrenznachteile unter eutrophen Bedingungen gegenüber opportunistischen, schnellwachsenden Mikro- und Makroalgen. So ist der Rückgang von Seegrasbeständen aufgrund von steigenden Nährstoffbelastungen in einer Vielzahl von Studien beschrieben worden (Baden et al., 2003; Plus et al., 2003; Cardoso et al., 2004)

Viele küstennahe marine Ökosysteme stehen unter einem großen Druck durch die Menschen. Etwa 70% der Weltbevölkerung leben in Küstennähe; ihre nährstoffreichen Abwässer gelangen meist unbehandelt in die Küstengewässer oder sie erreichen die Küsten über Flüsse und die Atmosphäre. Der menschliche Einfluss auf das Nährstoffangebot in aquatischen Ökosystemen ist so weit reichend, dass man eine direkte lineare Korrelation zwischen der Populationsdichte der Menschen und den Nitratkonzentrationen der größten Flusssysteme der Welt nachweisen kann (Peierls et al., 1991). Dieser zunehmende Eintrag von Nährstoffen und organischem Material (Eutrophierung) verändert die Flachwasser-Ökosysteme nachhaltig.

Eutrophierungsfolgen lassen sich deutlich in der stark belasteten Ostsee erkennen. Da sie von neun Industriestaaten umgeben wird, die zum Teil dicht besiedelt sind, gelangen jedes Jahr große Mengen an Schad- und Nährstoffen anthropogenen Ursprungs in die Ostsee (Schramm and Nienhuis, 1996; Elmgren, 2001). Insbesondere die Bodden- und Haffgewässer leiden unter der hohen Fracht von Nährstoffen und organischem Material (Birr, 1997; Flindt et al., 1999).

Unabhängige Beobachtungen aus verschiedenen Regionen der Ostsee deuten auf einen alarmierenden Rückgang von perennialen Makrophyten (Spermathophyten, Characeen) und Makroalgen hin (Breuer, 1988). Für nahezu alle Küsten der Ostsee wurden eutrophierungsbedingte Veränderungen z.B. in der Tiefenverbreitung, der Artenzusammensetzung, den Abundanzen und der Primärproduktion von Pflanzengemeinschaften dokumentiert (Cederwall and Elmgren, 1990; Rumohr, 1993; Boström et al., 2002). Infolge des erhöhten Nährstoffangebots vermehrt auftretende und länger andauernde Phytoplanktonblüten führen zu einer starken Beeinträchtigung des Lichtangebots für Makrophyten und damit zum Rückgang von tiefer gelegenen Makrophytenbeständen (Bianchi et al., 2000; Blümel and Schubert, 2002; Baden et al., 2003), bis hin zur einer völligen Verdrängung der mehrjährigen Pflanzen durch heterotrophe Raumkonkurrenten, v. a. Muscheln (Reusch et al., 1994; Bologna et al., 2005). Die verbliebenen Makrophyten zeigen einen verstärkten epiphytischen Aufwuchs von ephemeren Fadenalgen und werden oftmals von Massenansammlungen herumtreibender Makroalgen bedeckt. Exemplarisch für diese Veränderungen in den Seegrasbeständen der Ostsee ist die Kieler Bucht, in der die zuvor dominierenden Zostera- und Fucus-Bestände durch Rotalgen und ephemeren Fadenalgen verdrängt wurden (Breuer, 1988; Vogt and Schramm, 1991). Auch in den dänischen Inselgewässern nahm die Dichte von Seegraswiesen (Zostera marina) von den 30er bis zu den 80er Jahren um 50% ab (Giesen et al., 1990; Council, 1991; Frederiksen et al., 2004). Heute sind im Bereich der Danziger Bucht (Polen) die in den 50er Jahren noch reichen Bestände an Zostera marina wie auch andere Makrophyten fast völlig verschwunden (Kruk-Dowgiallo, 1991). Betroffen sind auch die pommerschen Boddengewässer. Im Greifswalder Bodden gab es in den 30er Jahren ausgedehnte Zostera-Wiesen, deren Verbreitung deutlich zurückgegangen ist.

## Zielsetzung und Gliederung der Arbeit

Diese Arbeit beschäftigt sich mit den Folgen von Eutrophierung auf Seegraspopulationen in Brackwasser-Ökosystemen, wie dem Greifswalder Bodden. Die wesentlichen Ziele waren hierbei herauszuarbeiten, welche der durch Eutrophierung veränderten Faktoren für die Beeinträchtigung der Seegraswiesen maßgeblich sind und wie sie zusammenwirken. Aus den gewonnenen Rückschlüssen sollten Vorhersagen für die weitere Entwicklung und mögliche Wege zu einer Renaturierung getroffen werden. Hierbei wurden insbesondere die Auswirkungen dreier Schlüsselgruppen (ephemere Aufwuchsalgen, Makroalgenmatten und Phytoplanktonblüten) auf das Seegras-Ökosystem hin untersucht.

Eine wesentliche Ursache für die Schädigung von Seegraswiesen liegt im massiven Wachstum von Epiphyten (meist Diatomeen und filamentöse Algen), die bei einem hohen Nährstoffangebot (“bottom-up”) die Blattoberfläche der Seegräser besiedeln (Frankovich and Fourqurean, 1997; Gross et al., 2003). Dieses führt zu einer starken Beeinträchtigung des Wachstums der Seegräser, da die Epiphyten sie sowohl beschatten als auch Nährstoffe abfangen (Orth et al., 1984; Harrison and Durance, 1985). Somit lässt sich erwarten, dass Epiphyten eine Schlüsselrolle bei der Modifizierung des Lichtangebotes für Seegräser im Greifswalder Bodden haben und eine wesentliche Ursache für den Rückgang der Seegrasbestände sind.

Andererseits kann das Wachstum der Epiphyten in mäßig eutrophen, marinen Systemen durch herbivore Epifauna kontrolliert werden (“top-down”) (Williams and Ruckelshaus, 1993; Hughes et al., 2004; Hays, 2005) und somit einen übermäßig starken Aufwuchs verhindern (Abbildung 1, A) (Orth et al., 1984; Wetzel and Neckles, 1986). Es wurde gezeigt, dass Invertebraten (Amphipoda, Gastropoda, Isopoda) durch das Abweiden von Epiphyten das Wachstum von Makrophyten fördert (Howard and Short, 1986).

Bei einem zu hohen Nährstoffeintrag oder bei einer Dezimierung der Herbivoren aufgrund von ungünstigen Umweltbedingungen (Strömung, Sauerstoffmangel, Umweltgifte) können herbivore Weidegänger nicht vollständig gegen den Anstieg der Epiphyten wirken (Abbildung 1, B). Folglich kann es wiederum zu einer Beeinträchtigung des Seegrases durch epiphytischen Aufwuchs kommen.

Inwieweit dieses “top-down - bottom-up” Modell eine Bedeutung für die Seegraswiesen eutropher Brackwasser-Ökosysteme besitzt, sollte im Greifswalder Bodden untersucht werden. Ausgangshypothese war, dass durch das hohe Nährstoffangebot im Bodden das Wachstum der Epiphyten auf den Seegräsern stark gefördert würde und somit hohe Abundanzen von Weidegängern ermöglicht, die als Antagonisten zu dem Aufwuchs wirken.

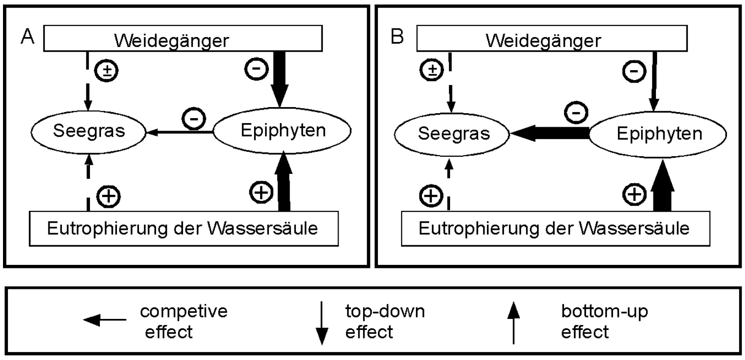


Abbildung 1: Darstellung des “top-down - bottom-up” Modells anhand eines von Weidegängern (A) kontrollierten und eines von Epiphyten (B) dominierten Systems.

Ein weiterer Schlüsselfaktor, der für den Rückgang von Seegrasbeständen verantwortlich gemacht wird, sind driftende Algenmatten (Hauxwell et al., 2001; McGlathery, 2001; Cummins et al., 2004). Makroalgenmatten werden hauptsächlich durch schnellwachsende, ephemere Algen wie Chaetomorpha, Chladophora, Enteromorpha, Polysiphonia und Pilayella gebildet. Das hohe Nährstoffangebot der Küstengewässer fördert das Wachstum dieser opportunistischen Makroalgen und es wurde in den letzten Jahrzehnten beobachtet, dass die Abundanzen und das Ausmaß von Makroalgen-Akkumulationen deutlich zunimmt (Raffaelli et al., 1998). Untersuchungen an Makroalgenmatten zeigen, dass in der untersten Algenschicht Sauerstoffmangel, extrem hohe Ammoniumkonzentrationen und völlige Lichtbeschattung auftreten können (Krause-Jensen et al., 1999). Zunehmende Meldungen über Verluste von Seegrasbeständen, die mit einer Ausbreitung von Makroalgenmatten einhergehen, legen nahe, die Rückgänge von Seegraswiesen auf das Erscheinen der Makroalgen zurückzuführen. Allerdings gibt es nur wenige Studien über den Einfluss von Makroalgenmatten auf Seegräser. Unklar war bislang, durch welche Faktoren Makroalgenmatten sich negativ auf Seegräser auswirken und wie stark die Schädigung durch die Algen ist. Ausgehend von Untersuchungen, die an Makroalgen durchgeführt wurden (ohne Seegräser zu berücksichtigen), blieb zu klären, ob Makroalgenmatten zu toxischen Ammoniumkonzentrationen in Seegraswiesen führen können, in wieweit Makroalgenmatten das Wachstums von Seegräsern durch die Bildung von anoxischen Zonen beeinträchtigen und welche Bedeutung Makroalgenmatten bei der Beschattung von Seegräsern haben.

Ein vielfach diskutierter Ansatz, der den Rückgang von Makrophyten in graduell eutrophierten Gewässern beschreibt, ist das „ecosystem shift“ Modell von Scheffer (Scheffer et al., 1993; Scheffer and Carpenter, 2003). Darin wird der plötzliche Wechsel eines Ökosystems zu einem alternativen stabilen Zustand aufgrund einer graduellen Eutrophierung beschrieben. Dieses Modell illustriert die katastrophalen Effekte eines schleichenden Nährstoffeintrags, der zu einem starken Anstieg der

Biomasse des Phytoplanktons sowie opportunistischer Makroalgen führt, wodurch das Licht für am Boden wachsende Makrophyten reduziert wird. Oberhalb eines kritischen Schwellenwertes führt die Lichtattenuation zu einer drastischen Mortalität der Makrophyten und es kommt zu einer Verschiebung von einem Makrophyten-dominierten zu einem Phytoplankton-dominierten System. Der neue Zustand des Ökosystems erzeugt sich selbst verstärkende Prozesse (verstärkte Resuspension, verstärktes Wachstum des Phytoplanktons, Zunahme der Lichtattenuation), die zu einer Konsolidierung des neuen Zustandes führen. Dieses Modell wurde vor allem für Süßwassersysteme angewendet und bislang gibt es nur vereinzelte Vergleiche aus marinen oder brackigen Ökosystemen. Somit stellt sich die Frage, ob das „ecosystem shift“ Modell auf den Greifswalder Bodden übertragen werden kann. Unbekannt ist, ob der starke Rückgang der Makrophytenbestände in den 60er Jahren als plötzlicher „ecosystem shift“ stattgefunden hat und ob die aktuelle „Resilience“ des Boddens in einem Phytoplankton-dominierten Zustand trotz deutlicher Reduzierung des Nährstoffeintrags anhand des Modells erklärt werden kann.

Die Arbeit ist in 6 Manuskripte unterteilt, die die Auswirkungen der 3 Schlüsselgruppen auf das Seegrassystem verdeutlichen sollen. Nach einer generellen Einleitung, stelle ich das Hauptuntersuchungsgebiet vor.

In Manuskript I werden die Ergebnisse der Monitoring-Untersuchungen über den aktuellen Zustand von Seegraswiesen im Greifswalder Bodden und deren saisonaler Verlauf präsentiert.

Die Wechselbeziehungen zwischen der Nährstoffbelastung, dem epiphytischen Aufwuchs, sowie den Weidegängen in den Seegraswiesen des Boddens werden in Manuskript II analysiert und mit dem “top-down - bottom-up” Modell diskutiert.

In Manuskript III werden die Stärke und der Mechanismus des Einflusses von Makroalgenmatten auf *Zostera marina* quantifiziert. Um den aktuellen Zustand der Seegraswiesen im Bodden besser beurteilen zu können, wurde in Manuskript IV die historische Entwicklung der zunehmenden Eutrophierung des Greifswalder Boddens und deren Einfluss auf die Makrophytenbestände anhand der abiotischen Faktoren zusammen mit der Entwicklung des Phytoplanktons über die letzten 25 Jahre untersucht. Die Veränderungen der Makrophytenbestände im Bodden wurde in Beziehung zum “ecosystem shift” Modell diskutiert (Scheffer, 1990). Es wurde versucht Methoden aufzuzeigen, die zu einer Verbesserung des Lichtklimas führen können und somit die Lebensbedingungen für Seegräser im Bodden verbessern würden.

Abschließend folgt die Gesamtdiskussion, die eine Synthese der Ergebnisse der einzelnen Manuskripte und die Schlussfolgerung der Arbeit gibt.

Im Appendix wird die Fischgemeinschaft einer Seegraswiese im Greifswalder Bodden beschrieben (Manuskript V), die in Zusammenarbeit mit Ivo Bobsien (Erstautor) erfolgte (Bobsien and Munkes, 2004). Mit Hilfe einer neu entwickelten Fangtechnik wurden die Diversität und Abundanzen der Kleinfische einer Seegraswiese im Jahresgang ermittelt. Anhand der Artenlisten und Häufigkeitsverteilungen wurde der Einfluss der Kleinfische auf die Weidegänger und somit die Bedeutung der Fischgemeinschaft für die Seegraswiese abgeschätzt.

Zuletzt ist die Zusammenfassung meines Vortrags beim Internationalen Seegras Symposium aufgelistet (Manuskript VI), den ich im Oktober 2004 in Townsville, Australien vorgetragen habe.

## Das Untersuchungsgebiet

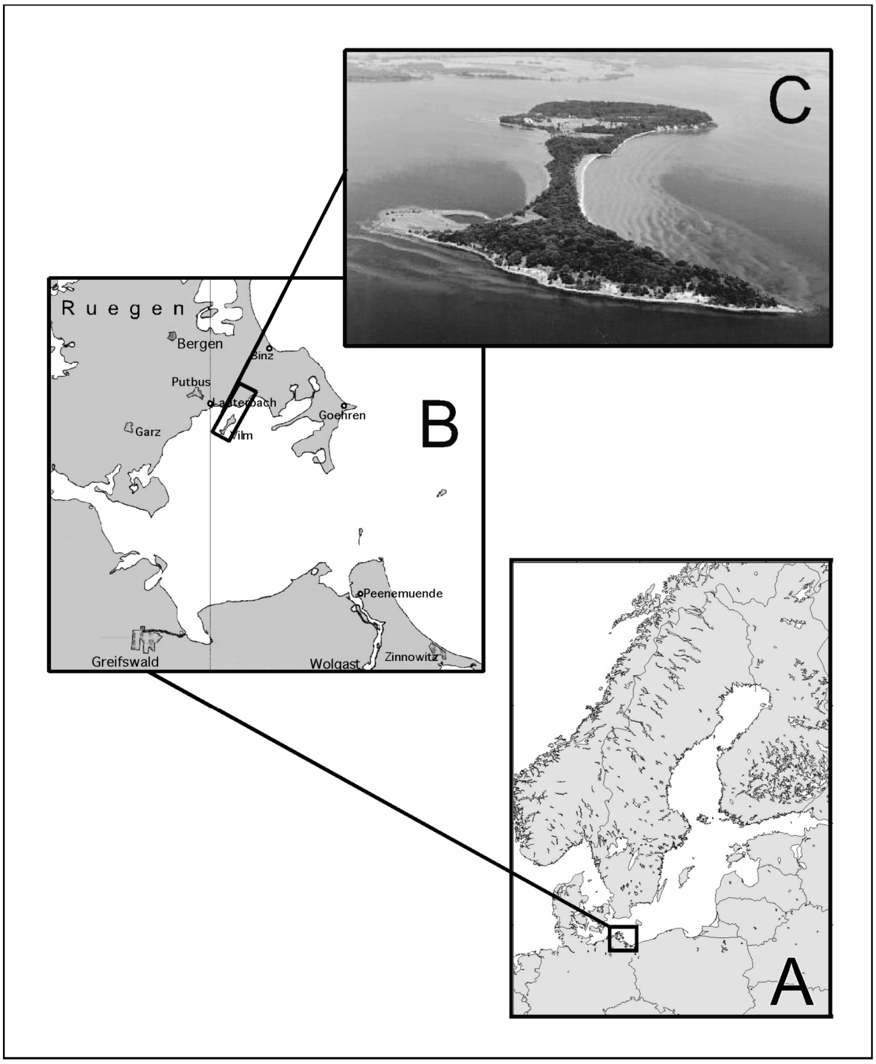


Abbildung 2: Das Untersuchungsgebiet Vilm (C), im Greifswalder Bodden (B) und eine Übersicht über die Lage des Bodden in der Ostsee (A).

Während meiner Promotion habe ich vergleichende Felduntersuchungen in der Ostsee durchgeführt. Der Schwerpunkt der Untersuchungen fand im Sublitoral bei der Insel Vilm im Greifswalder Bodden statt (Abbildung 2).

## Der Greifswalder Bodden

Der Greifswalder Bodden ist das größte, der als Boddengewässer bezeichneten flachen Randgewässer an der Küste der südlichen Ostsee. Mit einer Fläche von 514 km$^2$ entspricht seine Größe etwa dem Oderhaff. Er hat sowohl im Norden (zwischen der Insel Ruden (sic! nicht auf der Karte eingezeichnet) und dem Thiessower Harken) als auch im Süden (zwischen der Insel Ruden und dem Peenemünder Harken) eine flache Verbindungen zur Ostsee (7 und 2 km Breite). In ihn münden die zwei Flüsse Peene und Strelasund ein (Abbildung 2B). Die mittlere Wassertiefe beträgt 5,8 m. Während der Westteil eine relativ einheitliche flache Mulde mit Wassertiefen von 6-8 m aufzeigt, gibt es im Norden und Osten ein starkes Relief von Bodenschwellen (2-3 m) und Senken mit einer maximalen Tiefe von 13.5 m (Lampe and Meyer, 1995). Da lunare Gezeiten fehlen, übt das wechselnde Steigen und Fallen des Wasserspiegels den größten Einfluss auf die Hydrodynamik des Greifswalder Boddens aus. So strömen bei Hochwasser frische Wassermassen aus der Ostsee in den Bodden. Bei einer angenommenen vollständigen Durchmischung des Wasserkörpers wird somit eine Erneuerung des Boddenwassers erreicht. Nach Schätzungen wird das gesamte Volumen des Greifswalder Boddens im Jahr durchschnittlich acht Mal ausgetauscht (Stigge, 1989). Prozesse wie Niederschlag, Verdunstung, Flusswassereinstrom, Ein- und Ausstrom des Strelasund spielen im Vergleich dazu eine wesentlich geringere Rolle.

Tabelle 1: Morphometrische and hydrologische Charakteristika des Greifswalder Boddens.

| Parameter | |
|---|---|
| Oberfläche (km$^2$) | 510 |
| Volumen (m$^3$) | $2.96 \times 10^9$ |
| Mittlere Tiefe (m) | 5.8 |
| Salinität (PSU) | 5-8 |
| Temperatur (°C) | -0.5 – 24 |

Anhand der Temperaturen lässt sich der Binnenseecharakter des Boddens erkennen. Im Gegensatz zu den Wassertemperaturen der Ostsee steigen die Temperaturen im Greifswalder Bodden im Frühjahr schneller an und fallen im Herbst schneller ab (Hubert et al., 1997). Zusammen mit den geringen Tiefen des Boddens kommt es im Winter häufig zu Eisbedeckung, die in den Flachwasserbereichen bis zum Grund reichen kann.

Der mittlere Salzgehalt liegt bei 5-8. Als typisches Brackgewässer ist sein Artenspektrum stark reduziert (Hubert et al., 1995). Dafür kommen einige Meerwasser-, wenige Süßwasser- und Brackwasser-Arten zusammen vor. So wächst z.B. im Flachwasser bis zu einer Tiefe von ca. 2 m *Potamogeton pectinatus*, eine Süßwasserpflanze, und in tieferen Bereichen das marine Seegras *Zostera marina*.

Der Greifswalder Bodden gehört zu den mesoeutrophen Gewässern. Während des gesamten Jahres kommt es zu keiner vollständigen Nährstoffaufzehrung, so dass das Pflanzenwachstum vor allem durch das Lichtangebot begrenzt wird.

Die Verbreitung und Ökologie der Seegrasbestände im Greifswalder Bodden ist kaum bekannt. Meist wird das Vorkommen von *Zostera marina* im Zusammenhang von Makrophyten-Kartierungen erwähnt. In einer der ersten Pflanzen-Kartierungen wurden bereits 1899 (Reinke, 1901) Seegrasbestände nahe der Insel Vilm dokumentiert. Somit gibt es an dem Hauptuntersuchungsstandort, sowie einigen weiteren Bereichen im Greifswalder Bodden Seegrasbestände, die schon seit 100 Jahren existieren. Da es für diesen Zeitraum jedoch nur wenig detaillierte Untersuchungen gibt, lassen sich keine Aussagen über die Verbreitung und Veränderungen der Seegraspopulationen treffen.

# Manuskript I

# *Zostera marina* in the Greifswalder Bodden, Baltic Sea: eelgrass growth and productivity near the limit

## Abstract

Seasonal variation in biomass, reproduction and morphometric parameters (shoot density, leaf length, leaf area and daily leaf growth) of *Zostera marina* (L.) were studied from July 2001 to December 2003 in the Greifswalder Bodden, a eutrophic estuary on the German Baltic Sea. Eelgrass population showed one of the lowest shoot density (136 ± 3.8 $m^{-2}$) and above-ground biomass (about 31.9 ± 3.2 g DM $m^{-2}$) reported for *Zostera marina* in the Baltic Sea. Individual shoots featured low biomass (0.2 ± 0.01 g DM $shoot^{-1}$) but annual mean leaf length (55.5 ± 0.5 cm) and leaf growth (2.4 – 5.9 cm $day^{-1}$) were high. Frequency of flowering shoots was low (3%-10% of total shoot density) resulting in low seed production (99 – 224 seeds $m^{-2}$). Water temperature and light availability (Secchi depth) were the best predictors of eelgrass biomass and leaf area. In the Greifswalder Bodden eelgrass populations are subjected to a stressful environment, particularly in terms of low irradiance and low salinity, and strong competition with phytoplankton and drifting macroalgal mats. Overall, eelgrass appears to live near its growth limits in the estuary.

Keywords

biomass, growth, eelgrass, leaf production, *Zostera marina*

## Introduction

*Zostera marina* (L.), popularly referred to as eelgrass, is the most common seagrass in the northern temperate coastal waters (Kentula and McIntire, 1986; Thom, 1990) and is found along the coast of the Atlantic, Pacific and Baltic Sea (Boström et al., 2004).
Compared to the large literature on the ecology of eelgrass communities of the American coasts, only few investigations are available on the distribution and importance of *Zostera marina* in the Baltic Sea, mostly along the Danish and Swedish coasts. Only few investigations have been carried out in the German part of the Baltic Sea. In the largest German estuary of the Baltic Sea, the Greifswalder Bodden, there is a dearth of information on the occurrence and the production of *Zostera marina*. Current international political agreements (e.g. the European Water Framework Directive) require a better knowledge of the seagrass distribution and growth dynamics in the Baltic Sea to assess human induced impacts on these ecosystems.

In the Baltic Sea *Zostera marina* forms dense meadows, extending from mean low-water level down to depths between 2 to 14 m (Bobsien and Brendelberger, ; Sand-Jensen, 1975; Wium-Andersen and Borum, 1984; Borum et al., 2004). Flourishing seagrass meadows belong to the most productive marine ecosystems featuring high growth rates and primary productivities of 190 – 900 g carbon $m^{-2}$ $y^{-1}$ (McRoy and Helfferich, 1977; Duarte and Chiscano, 1999). They provide a diverse and abundant fish- and invertebrate community (Boström and Bonsdorff, 1997). Although the general importance of seagrass systems to nearshore food webs in coastal waters is well known (den Hartog, 1970; Borum et al., 2004), the role of *Zostera marina* in sustaining the production in the eutrophic Greifswalder Bodden estuary needs to be ascertained.
The Greifswalder Bodden differs from the open Baltic Sea in its high nutrient concentrations. Given the low salinities in the estuary the eelgrass lives in an environment, which is more similar to eutrophic lakes than to the open Baltic Sea. Therefore, eelgrass communities have to cope with problems of eutrophication, phytoplankton blooms and shading of the rooted macrophytes.
The aim of this study was to investigate the adaptation mechanisms and the role of *Zostera marina* in this special environment. Specific objectives were to describe the autecology of the eelgrass, to study seasonal variation of the biomass, reproduction and the main morphometric parameters (shoot density, leaf length, leaf area, daily leaf growth).

## Study area

The study was carried out in an eelgrass meadow in the Greifswalder Bodden, next to the island Vilm (Figure 1) from June 2001 to December 2004. It is a semi-enclosed eutrophic estuary, next to the island Rügen, characterized by its shallow depths (mean depth = 6 m) and high nutrient concentrations. During the growing season (March to October), incident light is strongly reduced by phytoplankton blooms. Plant and animal biodiversity is low in brackish waters featuring salinities around 7. Sediment consists of mud and to a smaller extent of sand and a clay-gravel-mixture. Hydrodynamics are governed mainly by wind, which results in a well-oxygenated water column down to the seabed. The study was performed on a large *Zostera marina* (L.) meadow on the eastern coast of the island Vilm in the Greifswalder Bodden. Near the island Vilm *Zostera marina* is distributed from 2.2 m down to a depth of 3.4 m sea level. In the estuary a mixture of marine-, brackish- and freshwater species occur, like *Zostera marina*, *Potamogeton pectinatus*, *Ruppia maritima*, *Myriophyllum spicatum* and *Ranunculus baudotii*. The studied eelgrass meadow was dominated by *Zostera marina*, only interspersed with a few *Potamogeton pectinatus*.

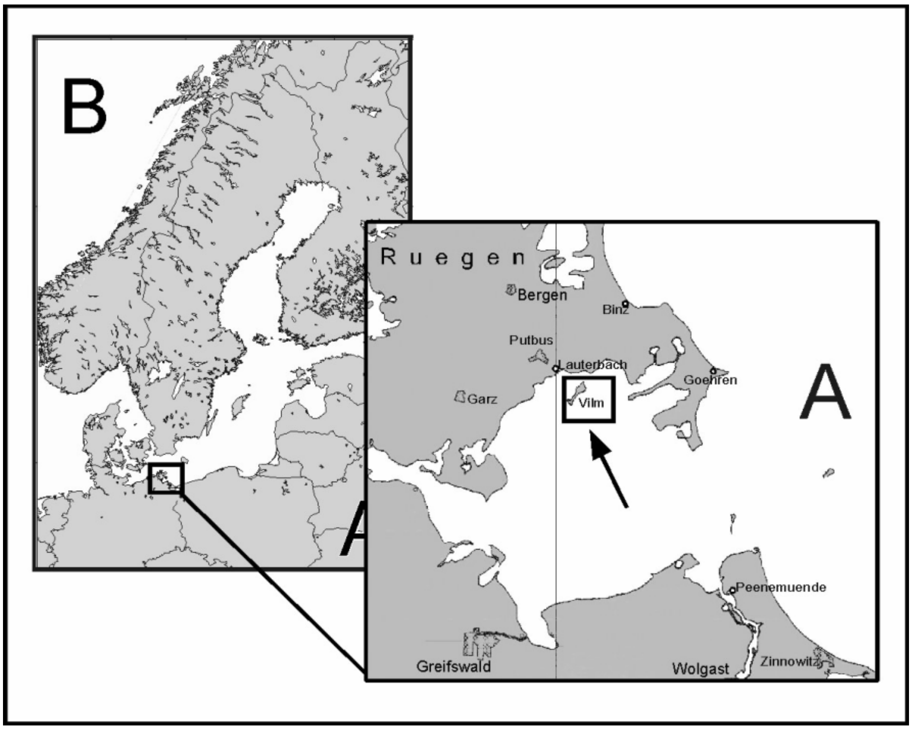


Figure 1: Overview over the Island Vilm (arrow) and the Greifswalder Bodden (A) in the Baltic Sea (B).

# Materials and Methods

## Abiotic environment

Surface irradiance and air temperature were measured continuously every hour with a meteorological station (F&C Forschungstechnik). Photon flux density within the photosynthetically active wavelength spectrum (PAR; µmol photons $m^{-2}$ $s^{-1}$) was calculated from irradiance data (E; W $m^{-2}$) according to the equation

$$PAR = E * 685 * V(\lambda_{555}) * 0.0185$$

where $V(\lambda_{555})$ is the luminous efficiency at 555 nm (for sunlight) = 0.9733. PAR values were transformed to daily values $PAR_d$ (mol photons $m^{-2}$ $day^{-1}$).

Underwater visibilities were taken with a Secchi disc once a week in front of the island Vilm, concomitant with salinity, water temperature and oxygen concentrations measured with a multi-sensor (OXI 197; Cellox 325).

## Eelgrass parameters

Every four weeks the eelgrass meadow was monitored by scuba diving or snorkeling. Density and size distribution of shoots was quantified in a randomly distributed frame (size = 0.25 $m^2$ ; n=12). During summer fertile eelgrass shoots were counted in 3 fixed 1 $m^2$ size squares. During study period 28 fertile shoots were sampled and seed coats abundance per shoot were estimated.

Eelgrass shoots samples were taken, by cutting of 20 eelgrass shoots with leaf blades next to the ground. Samples were washed with 100 µm-filtered seawater to remove sediment. For each shoot leaf length, leaf width and numbers of leaves were estimated. For dry mass (DM) eelgrass shoots were dried to constant weight at 60 °C for 24 hours (Duarte and Kirkmann, 2001). Eelgrass shoots, which could not be analyzed immediately were separated and frozen at –25°C until further analysis.

Eelgrass leaf growth was estimated by leaf marking method (Short and Coles, 2001). Twenty-four randomly chosen shoots were marked *in situ* with a pinhole through the leaf sheath. Tent rakes pushed into the sediment and flagged with plastic bands were used to re-locate marked shoots. After 12 to 17 days, marked shoots were sampled and growth of the first youngest leaf, second youngest leaf and third youngest leaf per shoot were measured to the nearest mm (Figure 2).

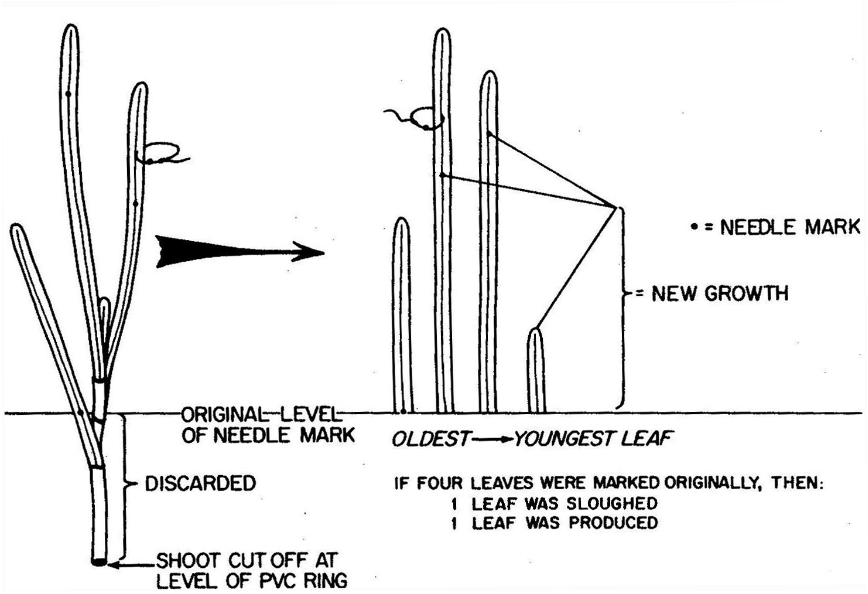


Figure 2: Procedure of leaf marking technique to estimate the new growth of seagrass leaves (Figure from Kentula, (2003).

# Results

## Abiotic environment

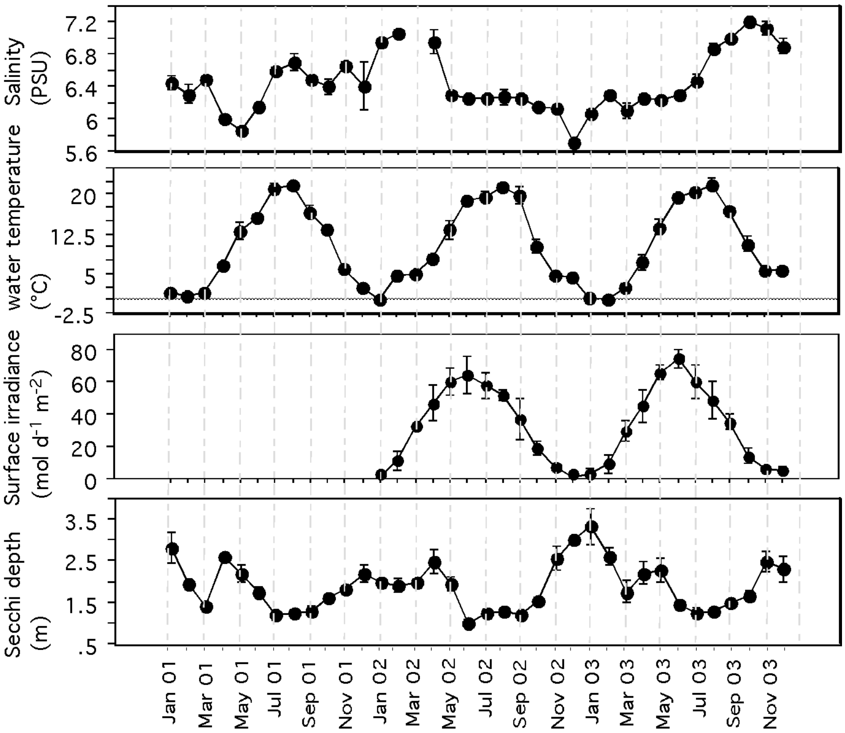


Figure 3: Abiotic environment: Seasonal variability (mean+ SE) in salinity, water temperature, surface irradiance and Secchi depth in 2001 to 2003.

Salinity ranged from 5.7 to 7.3, with a mean of 6.5 ± 0.04 and no distinct seasonal trend (Figure 3). Between May 2002 and May 2003 salinity remained at a nearly constant by 6.3, except in November 2002.

Water temperature varied between -0.2 °C and 24 °C during the study and peaked in August in all 3 years, reaching on average 22 °C ± 0.2. In January and February the shallow areas of the Greifswalder Bodden were covered with ice.

Surface irradiance showed a regular pattern, with low values in December to February (2.5 – 9.9 mol $d^{-1}$ $m^{-2}$) a continuous increase in irradiance and peaked in June (87.4 mol $d^{-1}$ $m^{-2}$). In 2003 irradiance reached slightly higher values (37.1 ± 4.3 mol $d^{-1}$ $m^{-2}$) than in 2002 (34.2 ± 4.0 mol $d^{-1}$ $m^{2}$ ).

The water was extremely turbid in summer and fall (Secchi depths not exceeding 1.4 m). In the rest of the year average Secchi depth ranged from 0.8 to 4.2 m depth, showing a seasonal pattern.

## Eelgrass parameters

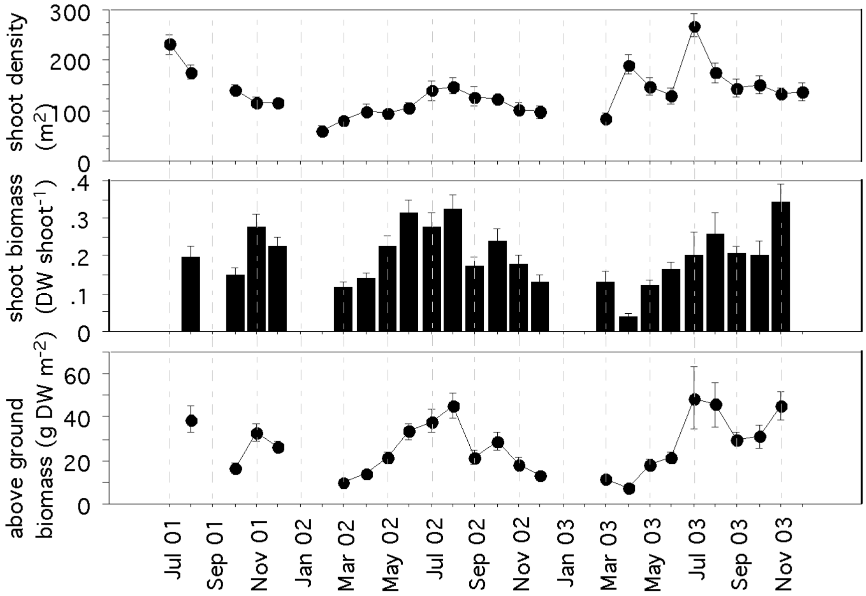


Figure 4: Variation (mean+ SE) in eelgrass shoot density, shoot dry mass and above ground biomass throughout July 2001 to December 2003.

*Zostera marina* shoot density showed clear seasonal changes and ranged between 32 and 384 shoots m$^{-2}$, with an average shoot density of 136 ± 3.8. In 2002 the eelgrass meadow consisted of large shoots (0.22 ± 0.01 g DW shoot$^{-1}$, Figure 4) with a medium density of 106 ± 4.1 shoots m$^{-2}$. The following spring shoot density was lower (84 ± 10.1 shoots m$^{-2}$) with only small individual shoots (0.18 ± 0.01 g DW shoot$^{-1}$). During 2003 shoots never attained a size comparable to that of the previous year, but the shoot density was higher (157 ± 7.2 m$^{2}$), so that the Leaf Area (LA) (Figure 4) was similar in 2002 and 2003. In 2002 shoot density collapsed in May and June and recovered in July. The year 2001 showed high shoot density, comparable to 2003 (162 ± 8.2 m$^{2}$) but shoot size was smaller than in 2003.

The maximum above-ground biomass was attained between July and August, the minimum biomass of 10.19 ± 0.02 g DM m$^{-2}$ was found in March, after the ice melt. The maximum above-ground biomass in 2002 and 2003 did not differ markedly (42.3 vs. 47.9 g DM m$^{-2}$). In 2002 biomass increased continuously from spring to August, while in 2003 growth of eelgrass delayed in April and June and started to catch up in late summer.

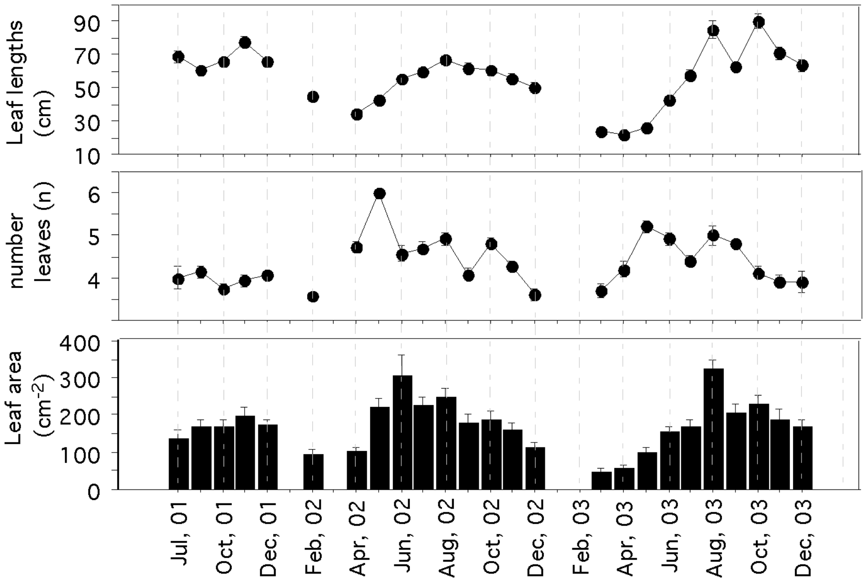


Figure 5: Seasonal variability (mean+ SE) in eelgrass leaf length, number of leaves per shoot and leaf area from July 2001 to December 2003. Missing winter values are due to ice cover.

Eelgrass leaves showed a continuous leaf growth from spring until August, and in 2001 and 2003 there was a second peak in leaf length between October and November (Figure 5). Therefore maximal monthly averaged leaf length was found in July/August and October/November with 66 ± 1.8 and 65.7 ± 2.2 cm, respectively. In this study mean leaf length was 55.5 ± 0.5 cm with a maximal leaf length of 178 cm.

Number of leaves per eelgrass shoot (without fertile shoots) vary between 1 and 7 leaves per shoot, with low leaf numbers in winter and highest numbers of leaves in Mai and summer.

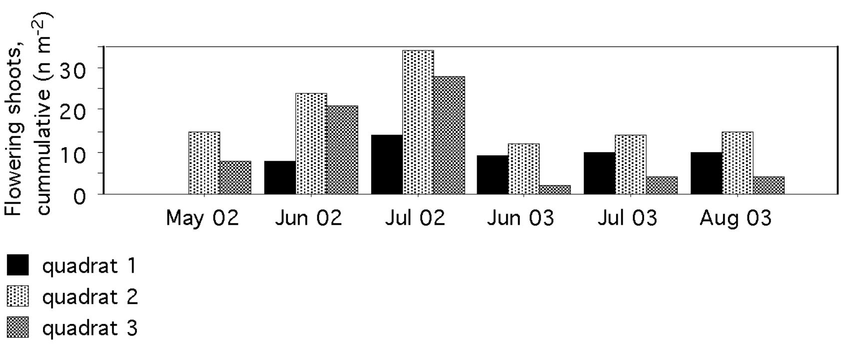


Figure 6: Flowering eelgrass shoots in three 1 m$^{-2}$ quadrates in the growing season 2002 and 2003. Shown is the cumulative abundance of fertile eelgrass shoots in 2002 and 2003.

Flowering of fertile eelgrass shoots started in the middle of May and continued until the end of July in 2002. In August no fertile shoots were found. The highest increase in flowers took place between mid of May until mid of June (Figure 6). In 2003 flowering of shoots started one month later and extended until August. Eelgrass plants developed more fertile shoots (34) in 2002, than in 2003 (15). Frequency of flowering shoots was 10% in 2002 and 3% in 2003 of total shoot density. Mean seed coat density in flowering eelgrass shoots (n = 28) was 6.6 seed coats per shoot. Assuming a mean density of 8 seeds coat$^{-1}$ (Olesen, 1999), mean production of 224.4 and 99 seeds m$^{-2}$ a$^{-1}$ were found in 2002 and 2003, respectively.

Table 1: Growth rate of eelgrass leaves of different ages.

| leaf age (days) | growth rate (cm day$^{-1}$)+ SE |
|---|---|
| 0 - 17 | 2.44 ± 0.81 |
| 17 - 46 | 0.91 ± 0.38 |

Mean leave growth was 1.72 ± 0.36 (SE) cm day$^{-1}$ in summer 2003. New developing leaves showed higher growth rates than older leaves (Table 1). Maximum leave growth rate was 5.86 cm per day.

## Discussion

Eelgrass beds in the Greifswalder Bodden are subjected to stressful environmental conditions. Nutrient-enhanced phytoplankton growth and resuspended organic material determine the availability of light to the benthos, so that eelgrass growth mirrors the productivity of the water column aloft: during the phytoplankton bloom eelgrass growth is at its minimum, while eelgrass growth is at its maximum spring and fall, when the water is more transparent. In winter, by contrast, eelgrass growth appears to be limited by the low temperatures.

Table 2: Range of shoot density (shoots $m^{-2}$) and above-ground biomass (g DM $m^{-2}$) for *Zostera marina* (vegetative shoots) throughout its geographical distribution range in the Baltic Sea.

| Location | Shoot density (shoot $m^{-2}$) | Biomass (g DM $m^{-2}$) | Reference |
|---|---|---|---|
| Eckernförder Bight (Germany) | | 15-307 | (Gründel, 1982) |
| Kiel Bight (Germany) | 400-1600 | 200-800 | (Feldner, 1976) |
| Oresund ( Denmark) | 550-3500 | 12-280 | (Wium-Andersen & Borum, 1984) |
| Tvärminne (Finland) | 115-170 | | (Boström et al., 2002) |
| Åland Islands (Finland) | 96-264 | 4-33 | (Boström et al., 2004) |
| Kiel Bight (Germany) | 880-1200 | | (Reusch et al., 1994) |
| Denmark | 596-1054 | | (Olesen, 1999) |
| Hopavågen (Norway) | 2730-4270 | 142-150 | (Duarte and al., 2002) |
| Isefjord ( Denmark) | 1055-1810 | 58-226 | (Sand-Jensen, 1975) |
| Review of 49 studies | | 298 | (Duarte, 1999) |
| Denmark | | 272-960 | (Petersen, 1913) |
| Kiel Bay (Germany) | 381±95 | 109 ± 69 | (Bobsien, pers. communication) |
| Greifswalder Bodden (Germany) | 32-384 | 10-93 | this study |

The limiting light availability is reflected in the very low shoot densities and standing crop of the eelgrass population at Vilm. In a broader comparison, light attenuation values were at the very low end of the range reported from other areas of the Baltic Sea (Table 2). Only Boström et al. (2004) reported lower values for eelgrass throughout the species' geographical range.

The seasonal pattern of eelgrass biomass followed the usual pattern of Northern temperate eelgrass communities: shoot density and leaf length were at their maximum in late summer and at their minimum in winter (Wium-Andersen and Borum, 1984). In 2002, the highest increase in biomass, leaf length and leaf area was recorded at the time of maximum surface irradiance in May-June. A similar periodicity was reported from Vellerup, Denmark (Sand-Jensen, 1975).

The increase in eelgrass above-ground biomass, shoot density, leaf length and leaf area at Vilm were compared with the seasonal development of surface irradiance, Secchi depth, water temperature and salinity using multiple regression analysis. About 80% of the seasonal variation in above-ground biomass and 78% of variation in leaf lengths could be explained by variations in Secchi depth and temperature. Salinity did not contribute significantly, due to the low fluctuations in 2002. However, it can be assumed that the low salinity has a negative impact on eelgrass growth, because salinities at Vilm were near the lower tolerance limit reported for eelgrass (3-7, den Hartog, 1970).

Leaf growth of *Zostera marina* is continuous throughout the year, but it shows a seasonal pattern with maximal growth in summer and minimal growth in winter (Wium-Andersen and Borum, 1984). Also, leaf age determines the growth of eelgrass. This study showed that the youngest leaves in a given shoot grew fastest, while leaf growth decreased with age and stopped altogether in the older leaves of shoots exceeding 4 leaves. These findings agree with the results of previous investigations. Sand-Jensen (1975) showed that leaf growth decreases with age and that only the three youngest leaves on eelgrass shoots showed significant growth. Unexpectedly, maximal growth of eelgrass leaves at Vilm (1.7 - 5.9 cm $day^{-1}$) was in the same range as growth of other reported eelgrass (1.6 – 5.7 cm $day^{-1}$) sites despite low light supply in the estuary (Sand-Jensen, 1975; Kobarg, 1993; Sfriso and Francesco Ghetti, 1998). Eelgrass in the Bodden seems to be able to have high growth rates during periods of sufficient light supply. This might be important for this species to withstand periods low light conditions.

Leaves at Vilm were rather long, with mean lengths of 66 ± 1.8 cm and maximum values of 178 cm. In Kiel Bay in September 2002, eelgrass leaves were found to be shorter (49 ± 12.2 cm; Bobsien, pers. communication). Both, this study and Jacobs (1979) reporting similar findings in deeper albeit clearer waters (Roscoff), suggest that light is positively related to shoot density and negatively related to leaf length. Much eelgrass leaf material was lost in the form of whole senescent leaves through leaf replacement, especially from June to October. One of the reasons for this was the loss of whole shoots by detachment of flowering stems during seed spreading, a common phenomenon in temperate eelgrass meadows (den Hartog, 1970; Wium-Andersen and Borum, 1984). A second substantial biomass loss occurred in early spring through wave action and shading due to ice cover, when eelgrass lost most of its long leaves.

Like biomass and shoot density, seed production was very low in the Vilm eelgrass (99-225 seeds per $m^2$), compared to perennial populations of *Zostera marina* in the literature (392-78224 seeds per $m^2$) (Olesen, 1999). In general perennial eelgrass communities invest less energy in sexual reproduction and show lower seed production than those of annual populations (Hemminga and Duarte, 2000). In the Greifswalder Bodden eelgrass meadows even seem to have lower capabilities for growth and therefore, less reserves for producing fertile shoots and seeds.

In the estuary, accumulations of drifting macroalgae are a widespread problem (manuscript III). In 2003, especially, dense macroalgae mats were observed on the eelgrass meadows and superposed other regulating factors. Algal mats hampered shoot growth and promoted eelgrass leaf senescence by shading. The delayed growth and low above-ground biomass of *Zostera marina* shoots in early summer in 2003 can be related to the occurrence of macroalgal mats in the eelgrass area.

In conclusion eelgrass stands in the Greifswalder Bodden are subjected to stressful conditions of irradiance and salinity, of which low irradiance is the most important abiotic factor limiting eelgrass growth. Together with the occasional occurrence of algae mats, eelgrass lives near its growing limits. The extremely low biomass and shoot densities of eelgrass in the Bodden in comparison to studies in the Baltic Sea and other areas in the geographical range of eelgrass, show the strongly deleterious effects of eutrophication on the growth of this species.

## Acknowledgements

Special thanks to Dr. Knapp, Dr. von Nordheim, Peter Hübner and the staff of the Federal Office for Nature Conservation (BfN) on Vilm and to the director and staff of the Center for Tropical Marine Ecology (ZMT) for their warm support and hospitality. I am especially grateful to the shipping authorities and the national park authority for granting the permission to work in the national park area. Many thanks to C. Richter for valuable comments and improving this manuscript. This study was founded by a scholarship program of the German Federal Environmental Foundation (DBU).

# Manuskript II

# Eelgrass - epiphyte dynamics: nutrient enrichment and grazing in an eutrophic estuary

## Abstract

In an eelgrass community the relevance of “top-down” grazer effects and “bottom-up” nutrients effects on epiphyte biomass (diatoms and filamentous algae) and Zostera marina growth were examined by following the seasonal development of epiphytes, eelgrass (Zostera marina), herbivore grazers and the main abiotic factors in an eutrophic, oligohaline estuary of the German Baltic Sea between 2001 and 2003. It was hypothesized that epiphytes would respond positively to high nutrient concentrations in the water column, and sustain high abundances of herbivorous grazers, mitigating negative effects of the epiphyton on eelgrass. It was surprising that (I) grazing pressure was negligible in the system and (II) in spite of high nutrient concentrations epiphyte biomass was very low. Despite the lack of grazing pressure, epiphytes did not overgrow eelgrass leaves. Grazers seem to be rare due to low salinity and a low and unpalatable food supply. While the shading effects of epiphyton were minimal light conditions for eelgrass were determined by strong attenuation due to high concentrations of phytoplankton and suspended solids. It can be concluded that, contrary to well-known examples from other sites, epiphytes were not “top-down” controlled but rather limited by light.

Keywords
“top-down - bottom-up”; grazing; epiphytes; seagrass; nutrient enrichment

## Introduction

There has been an increasing number of reports during the last years that anthropogenic nutrient enrichment in coastal marine areas contributes to seagrass decline by promoting epiphytic overgrowth (Hemminga and Duarte, 2000; Hughes et al., 2004). The stimulating effect of nutrient enrichment on epiphyte development has been experimentally demonstrated in several investigations (Phillips et al., 1978; Kemp et al., 1983; Silberstein et al., 1986). Colonization of epiphytes (mainly diatoms and filamentous algae) on seagrass leaf surface led to a modification in microhabitat due to shading as well as intercepting nutrients, which contributes in turn to a strong impairment of seagrass growth (Orth et al., 1984; Harrison and Durance, 1985).

Small invertebrate grazer (amphipoda, isopoda, gastropoda) play an important role in controlling epiphytic algal abundance in marine systems (Howard, 1982; Orth and Van Montfrans, 1984; Wetzel and Neckles, 1986; Heck et al., 2000). The effect of epiphytic grazers can be stronger than the effect of nutrient enrichment and therefore can mitigate or mask eutrophication effects (van Montfrans et al., 1984, Williams & Ruckelshaus, 1993; Howard and Short, 1986). Epiphyte removal by grazers has been shown to enhance macrophyte growth and survival rate (Hootsmans and Vermaat, 1985; Schanz et al., 2002). Also grazing by small invertebrates can modify epiphytic algal composition by reducing the outer, loosely adhering epiphytes, or by avoidance of inedible or unpalatable groups like cyanobacteria (Neckles et al., 1994).

It is assumed that a strong reduction of grazer abundance by strong currents, oxygen depletion, toxic pollution or other environmental extreme can release epiphytic algae from grazing pressure and lead to an uninhibited growth of epiphytes. Therefore, there is a multitude of effects, which affect and modify the grazer - epiphyte - seagrass relationship. While there are many studies working experimentally on grazer - epiphytes - seagrass or nutrient enrichment - epiphyte - seagrass interactions, only very few field investigations focus on the relationships of these main players with other potential controlling factors like phytoplankton, salinity or predator pressure.

Here, I studied the interactive effects of nutrient concentration, epiphyte growth and grazing on epiphytes and eelgrass health in situ in a eutrophic estuary. The purpose of this study was to test the prevailing ideas concerning the effects of resources and consumers on a seagrass meadow under the influence of high nutrient enrichment, low salinity and algal competitors. The initial hypothesis was that high nutrient supply would lead to high growth rates of epiphytes and would sustain high abundances of herbivorous grazers, which would act antagonistically to the epiphyton.

## Study Area and Methods

This field study was carried out in the Greifswalder Bodden in 2001 to 2003. With its 510 km$^2$ it is the largest estuary along the German Baltic Coast. The Bodden is a semi-enclosed eutrophic estuary, with a narrow opening to the Baltic Sea and two tributaries, the Peene river and the Strelasund river (Figure 1).

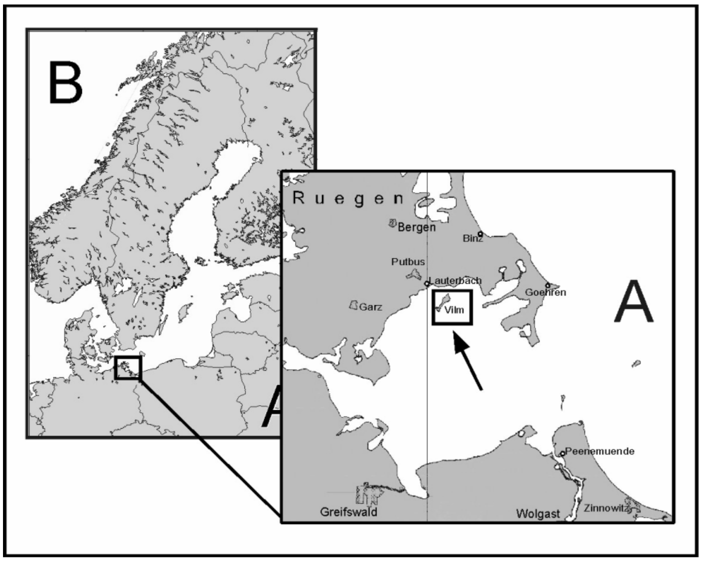


Figure 1: The island Vilm (arrow) in the Greifswalder Bodden (A) and its position in the Baltic Sea.

The Bodden is characterized by shallow waters (mean depth = 5.8 m) and high nutrient concentrations, which promote the dominance of phytoplankton as primary producer in the system. During the growing season (March to October), incident light is strongly reduced through phytoplankton blooms. Plant and animal biodiversity is reduced because salinity levels fluctuate around ca. 7 PSU, which indicates the biodiversity minimum reported by Kinne (1971). Hydrodynamics are governed mainly by wind, which results in a well-oxygenated water column down to the seabed. In this study, I investigated the epibiota on an extensive sub-littoral seagrass meadow on the eastern coast of the small island Vilm in the Greifswalder Bodden. Near Vilm *Zostera marina* is distributed from 2.20 m down to a depth of 3.40 m sea level. The meadow consisted *of Zostera marina* interspersed with a few *Potamogeton pectinatus*. The present investigation was carried out from June 2001 through December 2004.

## Abiotic environment

Surface irradiance was measured continuously every hour with a meteorological station (F&C Forschungstechnik). Photon flux density within the photosynthetically active wavelength spectrum (PAR; µmol photons $m^{-2}$ $s^{-1}$) was calculated from irradiance data (E; W $m^{-2}$) according to the equation:

$$PAR = E * 685 * V(\lambda_{555}) * 0.0185$$

where $V(\lambda_{555})$ is the luminous efficiency at 555 nm (for sunlight) = 0.9733. PAR was transformed to daily values $PAR_d$ (mol photons $m^{-2}$ $day^{-1}$).

Weekly temperature and salinity data, measured with a multi-sensor (OXI 196+96 type EOT 196-4; OXI 197; Cellox 325) near the island Vilm, were provided by courtesy of the Federal Office for Nature Conservation (BfN) on Vilm.

The light attenuation coefficient of the photosynthetic active radiation (PAR; 400 to 700 nm) (light reflection on the water surface and total water column light attenuation down to the bottom) were estimated on six sunny days throughout the growing season, using a calibrated 0.5 cm diameter 4π microquantum sensor in combination with a LI-193SA data-logger.

Nutrient and chlorophyll concentration were kindly provided by the State Agency for the Environment, Nature Conservation and Geology of Mecklenburg-Western Pommerania (LUNG, 1998), Germany. Nutrients data as well as Chlorophyll a (Chl *a*) concentrations were taken 2 to 5 times a month. For methodological details see LUNG (1998).

## Epibiota

Samples were taken once a month by scuba diving or snorkeling, by cutting off 12 eelgrass shoots with leaf blades next to the ground in a randomly distributed frame (size = 0.25 $m^2$ ; n = 12). Samples were washed with 100 µm-filtered seawater to remove the sediment. For each shoot, epibiota groups were counted, after which the abundance of epibiota groups were categorized to: 0 = non-existent; 1 = rare; 2 = abundant; 3 = very abundant.

Epiphytes comprise as both the microalgae and macroalgae colonizing the external surface of seagrass. Epibiota included autotrophic and heterotrophic organism. Microalgae included all algae, which were not visible with the naked eye, like blue-green algae, diatoms as well as small green-, brown- or red algae. Macroalgae were defined as all algae visible with the naked eye.

For studying the epibiota species diversity 3 to 5 additional shoots were examined and species were determined on the oldest leaf of the shoots, where highest species richness was found.

For dry mass (DM) and chlorophyll a (Chl *a*) analysis, epibiotic material was gently scraped of all leaves of each shoot with a razor blade and washed with filtered seawater onto pre-dried, pre-weighed GFF-filters. Half of the samples were taken for determination of epibiota DM, the other half was used for analysis of epiphyte pigment concentrations. DM was determined by drying epiphyte samples at 60°C for 48 hours; (Kendrick and Lavery, 2001). Epiphyte Chl *a* were analyzed by macerating the other half of epiphyte samples with a cell mill and analyzed photometrical according to Jeffrey & Humphrey (Jeffrey and Humphrey, 1975).

The light attenuation ($I_{epis}$) due to epiphytes was calculated according to Silberstein et al. (Silberstein et al., 1986),

$$(I_{epis}) = 100\ (1 - e\ (-0.3\ \mathrm{Chl}\ a^{\ epis)})$$

where Chl *a* epis is the content of Chl *a* epis (in µg $cm^{-2}$) within the epiphytes covering a unit area of leaves (in $cm^{-2}$).

In order to estimate the importance of autotrophic to heterotrophic organisms on seagrass leaves, an autotrophic index (AI = µg Chl *a*: mg DM epiphyte) according to Frankovich & Fourqurean (1997) was determined.

## Epiphyte host

Seasonal changes in seagrass production were quantified every four weeks by counting density of shoots in a randomly distributed frame (size = 0.25 $m^2$; n = 12). For estimating DM of seagrass shoots, 20 eelgrass shoots were sampled and leaf length and width were measured to the nearest mm. Epiphytes were scraped of all leaves and epiphyte-free seagrass shoots were dried individually at 60°C for 24 hours to constant weight (Duarte and Kirkmann, 2001).

## Epiphyte grazers

For estimating the abundance and number of species on seagrass leaves, grazers were caught with gauze nets, which were put over single shoots. Species and abundance of grazer were determined and individuals of *Idothea chelipes* were categorized to 3 size classes (0-6 mm; 6-10 mm; >10 mm). Additionally direct census by scuba diving were conducted to control the results of the net catches.

## Results

## Abiotic environment and phytoplankton

Surface irradiance varied from a minimum of 2.56 ± 1.48 standard error mol quanta $m^{-2}$ $day^{-1}$ in January to a maximum of 69.69 ± 6.3 mol quanta $m^{-2}$ $day^{-1}$ SE in June (Figure 2). The light attenuation coefficient ranged from $k^{-1}$ = 0.7 to 1.4 $m^{-1}$ during the growing season. Water temperature varied between -1° and 21 °C, exceeding 10°C between mid-April and October. In January to February the study area was frequently ice-covered. In 2001 to 2003 salinity ranged from 5.7 to 8.0 with a mean value of 6.7 and showed no distinct seasonal trend.

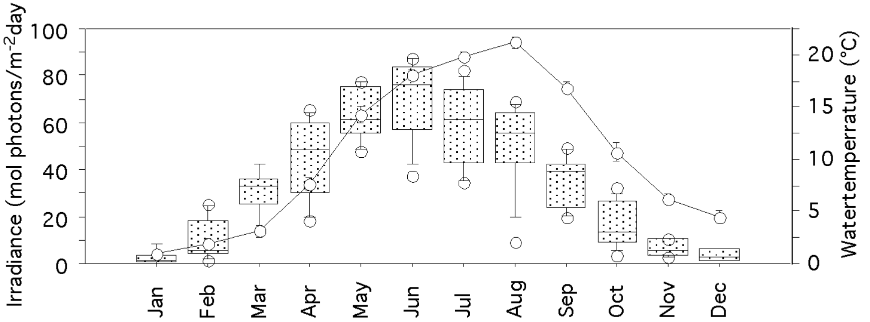


Figure 2: Seasonal changes in surface irradiance (box plots) and water temperature (dots) in the years 2001-2003.

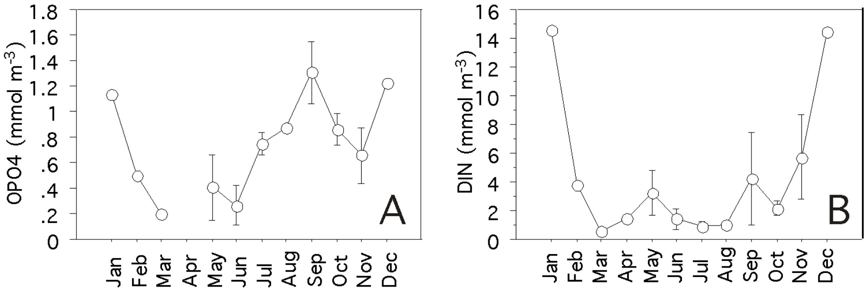


Figure 3: Seasonal changes of orthophosphate concentration and dissolved nitrogen concentration in 2001-2003.

Nutrient concentrations in the estuary were usually high. Orthophosphate reached maximal values of 1.87 mmol $OPO_4$ $m^{-3}$ (Figure 3A). Values were high and variable throughout most of the year except during spring (March to May) when concentrations of orthophosphate were lower, but still sufficient to sustain strong algal growth in the estuary (> 0.21 ± 0.18 mmol $m^{-3}$) (Figure 4). This persistence of high phosphate concentrations during the phytoplankton growth period can be explained by internal loading caused by the release of ironbound phosphorus from the sediment.

The nitrogen in the Greifswalder Bodden originates primarily from agricultural drainage water, which is highest during winter and early spring. With the begin of the phytoplankton bloom in spring 2001-2003, concentrations of nitrogen decreased strongly and during summer months nitrogen became the limiting factor (Figure 3B). Dissolved nitrogen (DIN) remained below 1 mmol $m^{-3}$ in the Bodden waters from July to August and rose again in late autumn and winter due to wind mixing. The low DIN:DIP ratio during summer (<2) coincided with the appearance of diazotrophic cyanobacteria sustaining high chlorophyll a levels through summer in spite of low N levels (Figure 4). Highest concentrations of phytoplankton were found in February and April with 18.6 ± 6.5 mg Chl *a* $m^{-3}$. During the growing season of eelgrass (April to October) phytoplankton chlorophyll concentrations did not fall below 11.83 mg $m^{-3}$ ± 1.7.

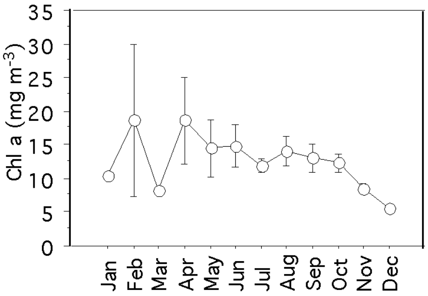


Figure 4: Seasonal phytoplankton chlorophyll a concentration in 2001 to 2003.

## Seasonal changes in epibiota and seagrass biomass and shoot density.

For most of the year epibiota dry mass (DM) was in the range from 0.8 g up to 7 g DM $m^{-2}$ bottom area (Figure 5). In July and

November average epibiota biomass reached up to 13.76 ± 6.46 (SE) g DM m$^{-2}$ and 22.57 ± 9.12 (SE) g DM m$^{-2}$ and contributed with 41% to the overall above ground biomass. On average epibiota dry mass was 20% of overall above ground biomass in 2001 to 2003.

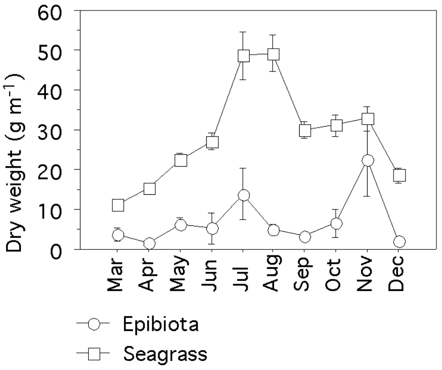


Figure 5: Seasonal course of epibiota and eelgrass dry mass.

An epibiota load of 0.50 ± 0.19 mg DM cm$^{-2}$ leaf area was measured on older seagrass leaves from March to July (Figure 6). Calculated light attenuation by epibiota shading on older shoots averaged 5.2% of the incoming light of $I_0$ during the year, with a minimum of 1.2% in October and a maximum of 18.6% in November. The epibiotic load and hence light attenuation on young shoots was negligible.

The annual mean shoot density of *Zostera marina* was rather low with 136.2 ± 3.86 shoots per m$^{-2}$ (Figure 7). In February shoot density was minimal (60.3 ± 10.74 shoots per m$^{-2}$) and increased subsequently to a density in July of 221.8 ± 14.8 shoots per m$^{-2}$ and decreased again to low shoot densities in winter.

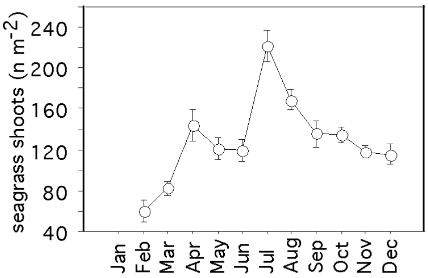


Figure 7: Seasonal changes in Zostera marina shoot density in the years 2001-2003.

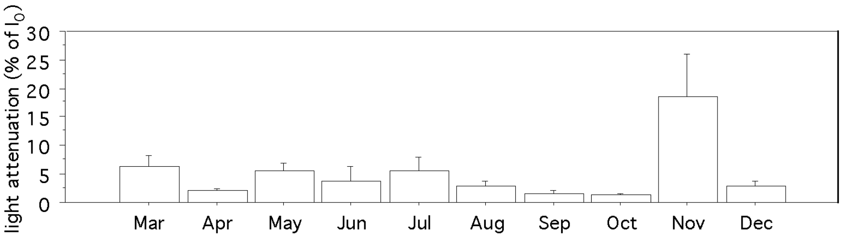


Figure 6: Epibiotic light attenuation in percent of incoming irradiance on seagrass leaves throughout the year.

## Seasonal changes in epibiota biomass and Chl a concentration

The biomass of epibiota followed a trimodal seasonal pattern (Figure 8A) with peaks in March, early summer and fall. The first minor peak in March (0.34 ± 0.10 mg DM cm$^{-2}$ of leaf area) was mainly due to microalgae like diatoms, blue-green algae and to protozoa.

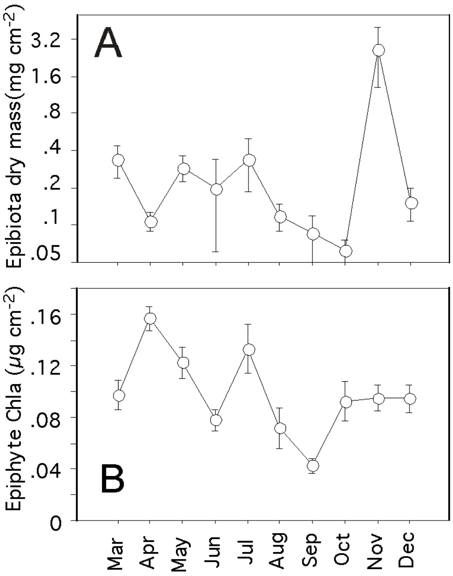


Figure 8: Epibiota biomass (A) and epiphyte Chl *a* (B) per square centimeter seagrass leaf throughout the years 2001-2003. Data are means ± 1 SE (n=12; 8).

The second minor peak in epibiota biomass was observed during July (0.34 ± 0.15 mg DM cm$^{-2}$) consisted mostly of bryozoa and some hydrozoa. In November biomass reached up to a distinct maximum of 2.62 ± 1.32 mg DM cm$^{-2}$. This can be explained by a strong hydrozoa bloom in November 2001 and 2003 with biomass concentrations up to 13.02 mg DM cm$^{-2}$. Excluding the exceptional high biomass in November, on average epibiota DM was 0.19 ± 0.12 mg DM cm$^{-2}$.

Epiphyte chlorophyll a concentration per square centimeter leaf area (µg cm$^{-2}$), are shown in Figure 8B. The highest chlorophyll a concentrations were found in April (0.166 ± 0.04 µg Chl *a* cm$^{-2}$ of leaf), high values were found again in July (up to 0.145 ± 0.01 µg Chl *a* cm$^{-2}$). The lowest concentrations were found in August and September, moderate chlorophyll a concentration during the last quarter (October-December).

The autotrophic index (AI) ranged from 0.15 to 9.42 µg mg$^{-1}$ (Figure 9). Autotrophic epiphytes were highest in spring and early summer with a high AI about 6.16 ± 1.15 (SE) µg mg$^{-1}$, while from July to December epibiota were dominated by heterotrophic organisms and AI were on average 0.69 ± 0.172 µg mg$^{-1}$.

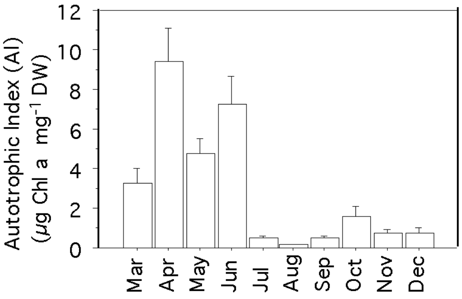


Figure 9: Autotrophic index (epiphytes Chl : DW per square centimeter seagrass leaf area) throughout the years 2001-2003. Data are means ± 1 SE.

## Seasonal changes in species composition and frequency of epibiota on eelgrass leaves

Autotrophic and heterotrophic organisms occurred on eelgrass leaves throughout the year, but species composition and frequency varied considerably with season (Figure 10). Epiphytes ranged from microscopic forms such as diatoms, to larger algae of which the most common genera were *Ectocarpus sp., Pilayella sp.* (phaeophyta); *Polysiphonia sp.*, *Furcellaria sp.* (rhodophyta); *Enteromorpha sp.* and *Chladophora sp.* (chlorophyta). The epizoa were represented by *Balanus improvisus* (balanidae) and *Laomedea flexuosa*, *Electra crustulenta* (bryozoa), as well as *Cordylophora caspia* (hydrozoa) and protozoa. In early spring, green macroalgae and diverse microalgae, particularly diatoms, dominated the epiphytic community (Figure 10). In May and early June, the macroalgae *Ectocarpus sp.* and *Pilayella litoralis* dominated the epiphyte community. Only a few heterotrophic organisms were recorded, predominantly small crusts of bryozoa and some hydrozoa. Scattered young *Balanus improvisus* settled in July in high numbers and were found with lower frequency during the later part of the year.

In late summer until winter, bryozoa became more abundant, with *Electra crustulenta* forming dense, brown crusts on older eelgrass leaves.

In autumn there was a second maximum of attached macroalgae, and diatoms showed high densities. The hydrozoa had their maximum frequency in October until December. During winter, epizoa like hydrozoa and bryozoa dominated, whereas the flora was only poorly developed.

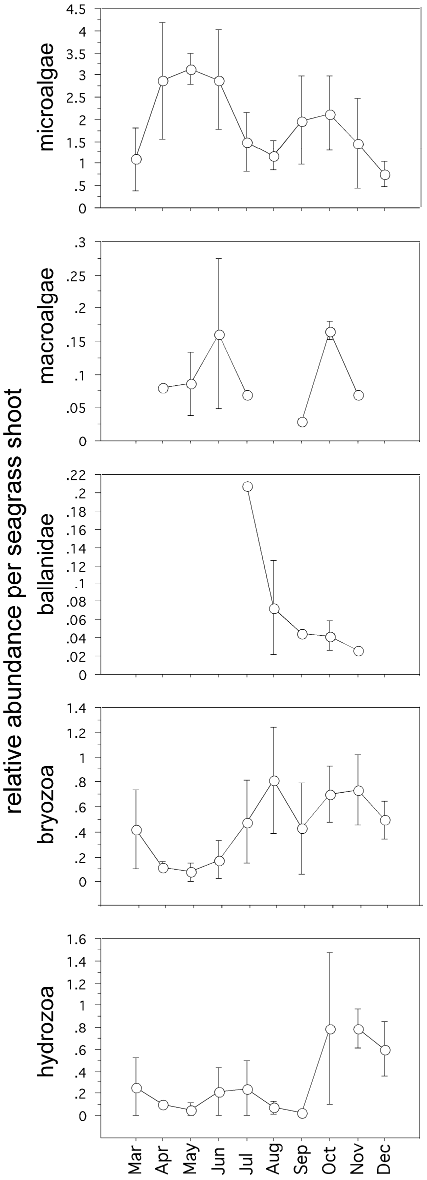


Figure 10: Seasonal abundance of epiphytes and epizoa per seagrass shoot during the years 2001-2003. Relative abundances were estimated by counting epiphytic groups for each shoot and categorizing to: 0 = non-existent; 1 = rare; 2 = abundant; 3 = very abundant.

## Grazer density

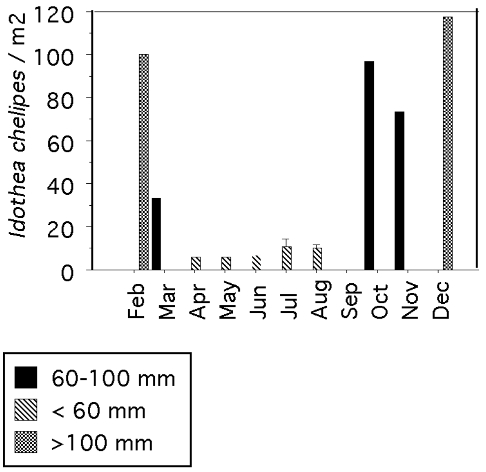


Figure 11: Abundance of *Idothea chelipes* throughout the season. Abundance of *Idothea chelipes* was categorized to 3 size classes (0-6 mm; 6-10 mm; >10 mm).

Idothea chelipes, Jaera albifrons and Sphaeroma hookeri, Gammarus zaddachi, Gammarus oceanicus and Corophium lacustre are known to graze on eelgrass epiphytes in the Baltic Sea. However, except for Idothea chelipes (0.4 ± 0.12 (SE) ind. shoot$^{-1}$), we found only extremely low densities of those species in the seagrass meadow during our study. Gastropoda (Hydrobia ulvae) were found only once in June 2002. Therefore it can be assumed that grazing pressure on eelgrass epiphytes was negligible. Idothea chelipes showed highest densities during autumn and winter (Figure 11). In spring and summer only juvenile isopoda were observed, while adults were absent.

## Discussion and Conclusion

Epibiota biomass is typically 30-60% of total seagrass above ground biomass (seagrass+ epibiota biomass) and may reach 50 to 100 mg DM cm-2 (Penhale, 1977; Borum and Wium-Andersen, 1980; Hemminga and Duarte, 2000). In this study epibiota load were on average 7.22 ± 1.4 g DM m-2, which accounts for 20% of total seagrass above ground biomass, due to the overall low seagrass biomass. While in other regions the biomass and primary production of the epiphyte component in seagrass meadows is vitally important and even can exceed seagrass biomass, in the Greifswalder Bodden the contribution of epiphytic biomass to total seagrass biomass is quite low.

In this study a large proportion in epibiota community was made by heterotrophs, notably hydrozoa and bryozoa, which showed high densities, while the epiphyte load on seagrass leaves (0.05 - 0.16 µg Chl a cm-2) was close to the low end of the range reported in other studies (0.03 – 6.57 µg Chl a cm-2) (Borum and Wium-Andersen, 1980; Borum, 1985; Silberstein et al., 1986; Lin et al., 1996). Gross et al. (Gross et al., 2003) found that eutrophic lakes also showed a high ratio of heterotrophic to autotrophic biomass in the epibiota. The ratio of heterotrophic to autotrophic epibiota might reflect the high nutrient condition of the Greifswalder Bodden.

While in many seagrass systems herbivore grazers play a central role in controlling epiphyton and are an important pathway in the food web by utilizing energy from epiphyte resources to higher consumer levels (Hootsmans and Vermaat, 1985; Mazzella and Alberte, 1986; Borum, 1987; Jernakoff et al., 1996), the importance of grazers in the Greifswalder Bodden is negligible and can not explain the low epiphytic load. In contrast to our study (40,2 ± 12.6 (SE) ind. $m^{-2}$ bottom area) in other regions of the Baltic Sea densities of *Idothea* sp. were found to be in the range of 280 to 2100 ind. $m^{-2}$ (Gründel, 1982; Wolken, 1994; Boström and Mattila, 1999; Bobsien and Munkes, 2004). Due to their very low abundance the grazers cannot exert a significant "top-down" control on the epiphyte community or support a high biomass of predators.

Epiphyte grazers appear to be food limited, because of low growth of epiphytes and due to the unpalatable food source (blue-green algae). Nutrient enrichment can lead to a stimulation of small diatoms and blue-green algal epiphytes (Coleman and Burkholder, 1994). In summer the phytoplankton in the Bodden is dominated by blue-green algae (Schmidt, 1990a) and blue-green algae are abundant on seagrass leaves, too. Coleman (1994) showed, that small pennate diatoms could be missed by herbivores, that consume larger, loosely attached species and that only few herbivores, including isopods would feed on blue-green algal epiphytes (Neckles et al., 1993). As a consequence the high nutrient supply in the Bodden could lead to negative effects on higher food web components, by promoting growth of unpalatable algae.

Another reason for the low grazer density in the Bodden might be related to the sparsely vegetated seagrass meadow. The generally poor light conditions in the Greifswalder Bodden cause relatively low shoot density at all sites compared to other reported seagrass densities on the coasts of the Baltic Sea (manuscript I; table 2). Studies showed that low seagrass biomass is unlikely to provide sufficient protection for high densities of mesograzers (Heck et al., 2000).

The present results suggest strong "bottom-up" and negligible "top-down" control of eelgrass epibiota in the Bodden. As nutrient supplies by advection and release from sediments always exceed demand, nutrients are never exhausted (Schlungbaum, 1982). Instead light appears to be limiting photo-autotrophic growth, both in the plankton and in the benthos.

This assumption is supported by the work of Munkes (2005), who showed that the Chl *a* concentration of the phytoplankton in the Greifswalder Bodden steadily increased with increasing temperature and a similar progression to the daily insolation and showed no sign of nutrient limitation. Instead epiphytic algae seem to be outcompeted by phytoplankton shading. In combination with the high concentration of resuspended organic matter and sediment, epiphytic growth is most probably suppressed by light limitation.

We found that phytoplankton and non-living particle (tripton) were responsible for a light attenuation of up to more than 90% of surface light until reaching the seagrass shoots. Epibiotic light attenuation was rather low compared to that by phytoplankton and tripton and had a minor impact on seagrass light conditions. On average epibiota load caused a light attenuation of 5% and a maximum of 19% of the light reaching the seagrass. Glazer (in Brush (2002) found that the attenuation due to an epibiota community primarily composed of bryozoan colonies had markedly greater PAR transmission compared to the attenuation due to a carpet of mixed green-red algae dominated epibiota. But even with a higher attenuation coefficient it is clear that, epibiota load is too low to have a strong effect on seagrass light conditions in the Greifswalder Bodden.

This study indicates that the biomass of epibiota can be controlled by "bottom-up" effects, like light limitation and nutrient concentration. Generalizations regarding the relative importance of grazing and nutrient enrichment on macrophyte survival must be considered with caution. The results show that epiphyte response to grazing and nutrient enrichment must be studied at the system level because of the complexity of seagrass ecosystems that interact with epiphytes.

## Acknowledgements and grants

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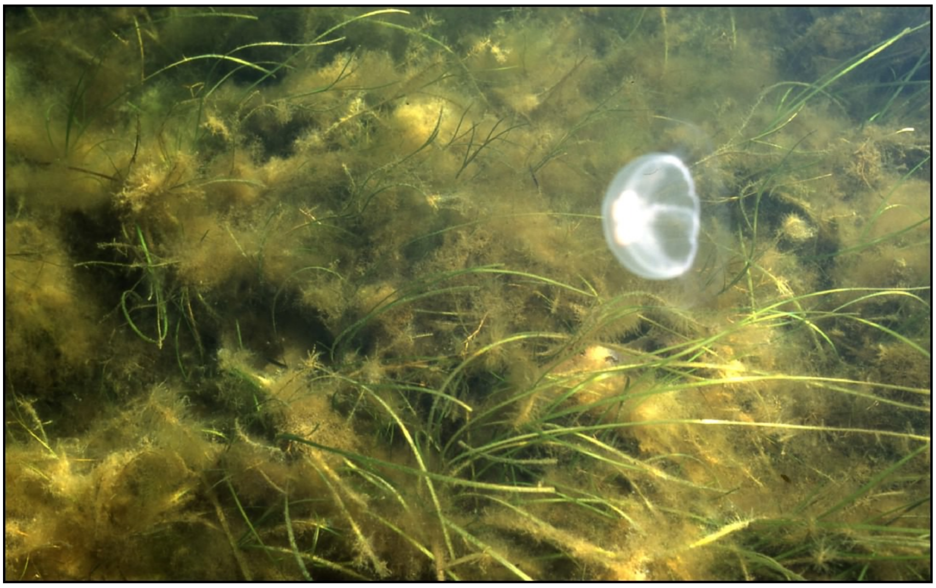
# Manuskript III



# Impact of macroalgae canopies on growth and survival of seagrass in an eutrophic estuary of the Baltic Sea.

## Abstract

The proliferation of ephemeral floating macroalgae is a common phenomenon of eutrophic estuaries. In the Greifswalder Bodden estuary, Germany, the accumulation of drift algae is usually restricted to calm areas. However in 2003, red algal mats covered the entire area reaching as far as the seagrass meadows on the current-exposed East side of the island.

We tested the effect of dense macroalgal canopies on shoot density, biomass, leaf C:N content and survival of the seagrass *Zostera marina*, employing macroalgae enclosure-exclosure experiments in the Bodden from May to July 2003. In enclosures with natural concentrations (1750 g WW $m^{-2}$) of brown and red algae, above-ground biomass and shoot density of *Zostera* decreased by 22%, relative to control plots without algae. The decrease in seagrass biomass was due to a decrease in both, shoot density and leaf growth. In the presence of algae, leaf growth was reduced by 19%. The main impact of macroalgal canopy on seagrass was a strong reduction in incoming irradiance for new shoots and resulted in a hindrance of the development of new shoots. Our experimental results support the hypothesis that nutrient-enhanced blooms of macroalgae may have contributed significantly to the demise of seagrass meadows in the Greifswalder Bodden.

Keywords

seagrass, estuary, macroalgae, eutrophication, light, *Zostera marina*, epiphytes

## Introduction

The proliferation of fast-growing ephemeral floating macroalgae is a growing concern for shallow coastal ecosystems worldwide as an obvious symptom of coastal eutrophication (Sundbäck et al., 2003). In estuaries macroalgal blooms occur naturally, however, there seems to be an increase in their frequency and magnitude in many areas of the world, resulting from enhanced delivery of anthropogenic nitrogen (Duarte, 1995; Raffaelli and Hawkins, ; Raffaelli et al., 1998; Cummins et al., 2004). Over the past years the smothering effect of algal mats on the underlying macrophytes (Valiela et al., 1997) thus altering the ecology and productivity of coastal waters has raised much interest (Cummins et al., 2004). A particular problem is the effect of macroalgal blooms on seagrass meadow structure and function, notably their high plant and animal diversity (Cummins et al., 2004), and their role as sediment and nutrient trap.

The loss of seagrass (*Zostera marina*) meadows from temperate estuaries worldwide often coincides with increased accumulations of filamentous macroalgae (den Hartog and Polderman, 1975; Reise et al., 1989; Shepherd et al., 1989; Messner and von Oertzen, 1990; den Hartog, 1994; Raffaelli et al., 1998; Hauxwell et al., 2001; Cummins et al., 2004). Dense macroalgal mats are able to destroy entire seagrass beds and are responsible for the general decline of seagrass (Shepherd et al., 1989; Holmquist, 1997). However, there are only few studies (Hauxwell et al., 2001; Cummins et al., 2004) focusing on the underlying mechanisms of this process.

Macroalgal canopy may alter water and sediment redox conditions (Bierzychudek and Valiela, 1993; Krause-Jensen et al., 1996; McGlathery et al., 1997; Hauxwell et al., 2001). Oxygen concentrations in macroalgal mats are reduced at night and the lower layers of the mats often become anoxic (Krause-Jensen et al., 1999). The formation of hydrogen sulfide during the decay of macroalgae mats was even reported. This leads to an increase in energy requirements and a decrease in maximum photosynthetic rates of seagrasses (Hauxwell et al., 2001). The macroalgal canopy may also modify available nutrient concentrations by exploiting nutrient resources during their growth or by raising ammonia concentrations during their decay to levels toxic for seagrass (Holmquist, 1997; van Katwijk et al., 1997; van Katwijk et al., 1999). Additionally, seagrass suffer through shading caused by the proliferation of fast growing perennial macroalgae. Seagrass, like other macrophytes featuring both photosynthetic and structural tissues, have a much lower light absorption per unit plant weight than fleshy macroalgae (Duarte, 1995) and a higher light compensation point (Ic) (Brun et al., 2003). Seagrass responds to shading with reduced growth, fewer new shoots, flowering inhibition and a decrease in biomass (Backman and Barilotti, 1976; Short and Burdick, 1995; Onuf, 1996).

Consequently, a vast number of possible effects of macroalgae mats on seagrass systems can be assumed. As the number of reports increase about the loss of seagrass meadows due to the expansion of opportunistic macroalgae (Raffaelli et al., 1998), a link may reasonably be established between seagrass decline and the appearance of macroalgae mats. However, there are hardly any studies using controlled manipulative field experiments to verify the effects of macroalgal canopy on seagrass.

In the present study, we endeavour to fill this gap and carried out field experiments to test the presumed strong negative impact of macroalgal canopy on *Zostera marina*. We examined the effects of macroalgal mats on:

- growth and survival of seagrass shoots.
- oxygen, nutrient and sulphide concentrations in and near the sediment.
- the light climate for *Zostera marina*.

## Study site

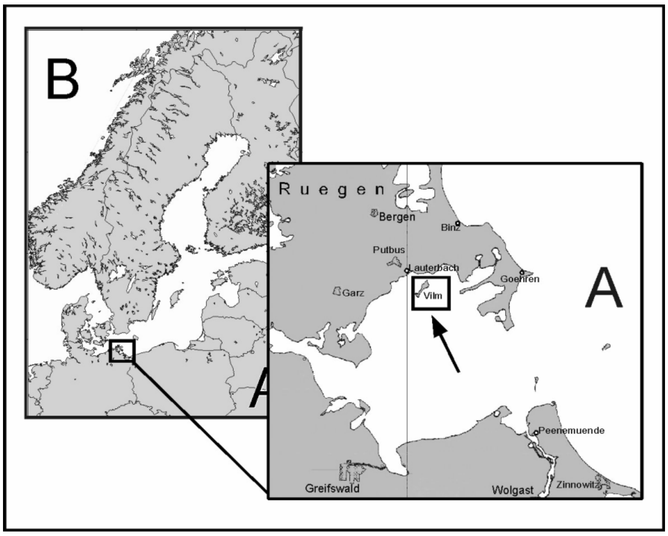


Figure 1: The Greifswalder Bodden (A), inside the island Vilm and the position in the Baltic Sea.

The study was carried out in a seagrass meadow in the Greifswalder Bodden, which is the largest estuary on the northeast coast of Germany (Figure 1). Shallow-water systems are locally called “boddens” or “haffs”. The study was performed on a large *Zostera marina* meadow of about 0.40 km$^2$ on the eastern coast of a small island Vilm in the Greifswalder Bodden.

The Greifswalder Bodden is a semi-enclosed eutrophic estuary, characterised by its shallow depth (mean depth = 6 m). The estuary has a surface area of 510 km$^2$ and is open to the Baltic Sea via a narrow and shallow sill which allows a limited water exchange. Two rivers flow into the Bodden and play an important role for the nutrient and phytoplankton input in the estuary. Due to its shallow depth, the water column is well mixed by wind. Wind-driven advection leads to the exchange of water masses between the Bodden and the Baltic proper. There are no perceivable lunar tides (Stigge, 1989; Hubert et al., 1995; Lampe and Meyer, 1995). Salinity is around 7. Sediment consists of mud and to a smaller extent of sand and a clay-gravel-mixture. Large phytoplankton blooms dominate primary production in the estuary. Dense blooms of drift macroalgae, usually of the genera *Enteromorpha intestinalis*, *Furcellaria lumbricalis*, *Polysiphonia urceolata*, and *Chladophora* spp. are common in spring and early summer. Normally they are restricted to shallow and calm areas of the estuary, where the macroalgae accumulate. At the beginning of May 2003, however, an exceptionally strong growth of macroalgae was observed. Even in the more exposed parts of the estuary, macroalgal mats covered the entire ground surface including the seagrass meadow surveyed in this study that consisted of *Zostera marina* interspersed with a few *Potamogeton pectinatus*.

## Materials and Methods

### Experimental design

To test the hypothesis that macroalgal mats affect seagrass biomass and abundance, macroalgal enclosure-exclosure experiments were conducted during spring and early summer 2003 at a depth of 2.80 m. Macroalgal presence/absence was manipulated in a factorial design with six replicates per experimental unit.

The experimental units were 0.8 $m^2$ plots, fenced by a 0.40 m high plastic netting to prevent unintended import and export of macroalgae. The 2.0 x 2.0 cm mesh-size of the plastic netting was small enough to retain the macroalgae, and large enough to allow sufficient water circulation and cause none obstruction of light. Half of the plots were cleaned of algae, the other half of the plots received 1750 g WW (wet weight) of macroalgae corresponding to natural background level. Macroalgae used in the addition treatments were collected from within the seagrass meadow, and consisted of a mix of *Cladophora* spp., *Furcellaria lumbricalis*, and *Polysiphonia urceolata*. One experimental unit with algae and one without algae were grouped and six replicates were randomly distributed. To test for cage effects, the seagrass meadow with macroalgae in natural densities outside the cages was monitored alongside with the regular monthly sampling at the height of the growth season, spring through summer (14 May, 19 June, 14 July and 25 July) of 2003.

To evaluate how macroalgal mats affect seagrass, we performed the following measurements in the presence or absence of macroalgae as well as in the controls: *Zostera marina* above-ground biomass, shoot density, leaf growth, recruitment, root lengths, C-N content of leaves and roots .

Density and size distribution of shoots was quantified every four weeks by counting and measuring the shoots in the 0.8 $m^2$ quadrat plots. Preliminary data revealed (Figure 2) that the maximum leaf length of a shoot ($L_{max}$, in cm) was a reasonable proxy for its biomass (in g dry mass).

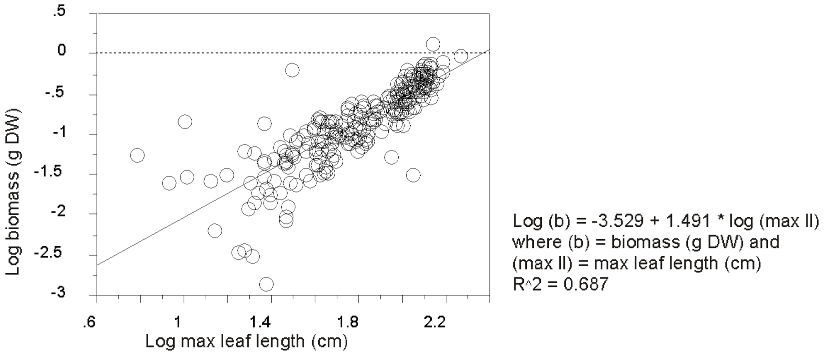


Figure 2: Regressions analysis between the logarithm of maximal leaf length (cm) and the logarithm of eelgrass shoot biomass (g dry mass).

This method of measuring total plant biomass has the advantage to be non-destructive. We estimated the leaf growth rate per shoot by measuring the $L_{max}$ from all shoots in treatments and controls on every sampling date. In each experimental area an additional three shoots were sampled in May and June for further investigations, such as root lengths, C-N content, dry mass and leaf length. In July, at the end of the experiment we sampled 12 plants of each area. Shoots were brought to the laboratory and leaf length and width as well as root lengths were measured to the nearest mm. Subsequently, the samples were dried at 60°C for 24 hours (Duarte and Kirkmann, 2001) to constant weight.

The C-N analysis was performed by cleaning 10 to 20 shoots of epiphytes and adherent sediment, split in leaves and rhizome+ roots, then dried at 60°C to constant weight (Duarte and Kirkmann, 2001). The dried material was stored in polyethylene vials for subsequent C-N analysis. Dried samples were ground and homogenized with a mortar and pestle after shock freezing in liquid nitrogen. The leaves from one shoot were pooled. Carbon and nitrogen content of the ground plant material (leaves and root tissue) was measured using a CHN-Analyser (NA 1500N Fisons Instruments). Carbon and nitrogen content was determined in duplicate for all samples.

Concentrations of ammonia ($NH_4^+$), nitrate and nitrite ($NO_3^-$+ $NO_2^+$) and orthophosphate ($OPO_4^-$) were measured in pore water, 2 to 4 cm above ground and in the water column 80 cm (maximum seagrass leaf length) above ground. Samples (50 ml, 4 replicates each) were taken with 60 ml PE syringes, stored in the dark and cold, and fixed with 200 µl $HgCl_2$ (0.1 g $HgCl_2$ $l^{-1}$). Nutrient analyses were conducted using the method of (Strickland and Parsons, 1972) on a SanPlus (SKALAR) autoanalyser.

Oxygen concentrations were measured in July (12 and 14 July 2003) at 3, 20 and 80 cm above ground using a handheld oxygen meter. Additionally, one sediment core (i.d. = 8 cm, height = 25 cm) was taken from the center (to avoid possible edge effects) of each of the replicate treatment plots to determine the height of oxygenated sediment layer.

Photosynthetic active radiation (PAR; 400 to 700 nm), light reflection on the water surface and total water column light attenuation down to a depth of 2.20 m, resp. 2.80 m were measured as incident flux density in µmol quanta $m^{-2}$ $s^{-1}$ on three sunny days throughout the experiment, using a calibrated 0.5 cm diameter 4π microquantum sensor in combination with a LI-193SA data-logger.

Water chlorophyll a (Chl *a*) concentration data were kindly provided by the regional authorities of the environment, the nature conservation and geology (LUNG). Measurements were taken on average once a week (for more details see (LUNG, 1998). Estimates of phytoplankton attenuation was calculated according to (Kirk, 2000), by multiplying the Chl *a* concentration by the chlorophyll-specific light attenuation coefficient $k_c = 0.016\ m^2\ mg^{-1}$ Chl *a*.

Epiphyte biomass of shoots was estimated by gently scraping the epiphytic material of all leaves with a razor blade onto a pre-dried, pre-weighed GFF-filter. Half of them were dried for 24 h to 48 by 60°C for the dry mass while the other half of samples were analysed for the Chl *a* content according to (Kendrick and Lavery, 2001). For each sampling date and treatment, a total of 10 samples were processed. The corresponding light attenuation due to epiphytes was calculated according to Silberstein,

$$f(x) = 100\ (1-e^{(-0.5x)})$$

where x is represented in µg Chl *a* $cm^{-2}$ leaf area (Silberstein et al., 1986).

Before the start of the experiment, the average biomass of macroalgal mats was estimated by snorkeling. Samples were taken in 16 randomly chosen areas of 25 $cm^2$. We found an average macroalgal biomass of 1750g WW/$m^2$ in the studied seagrass meadow. Algal mats consisted mainly of the two red algae *Furcellaria lumbricalis* and *Polysiphonia urceolata* and one green algae *Cladophora* sp. The height of the algal canopy varied between 2 and 7 cm. In the first six weeks the macroalgae were in a good condition, afterwards they started to decompose and at the end of the experiment there were only a few algae left.

## Data analysis

Data (except shoot density) were log-transformed to achieve homogeneity of variances (Cochran's test) and analysed by one-way ANOVA. Fisher's PLSD procedure was used for post-hoc comparisons. Regression analysis was used to analyse the relationship between $L_{max}$ and biomass of the seagrass shoots.

## Results

## Responses of seagrass to macroalgae treatment

Growth, survival, productivity and C:N tissue ratios of *Zostera marina* were significantly different between the treatments and the controls. There was a continuous rise in leaf length from 30.8 to 54.18 cm in macroalgae-free enclosures (Figure 3 A), while seagrass leaves in macroalgal treatments showed a more pronounced growth in average leaf lengths during the first months. Followed by a phase of stagnation and a decrease in leaf lengths at the end of the experiment. Overall, leaf length growth in macroalgae-free enclosures was 19% higher than in the macroalgal treatments. Seagrass leaves growth in enclosure-free controls was similar to macroalgae enclosures, except of a strong increase in leaf length at the last measurement.

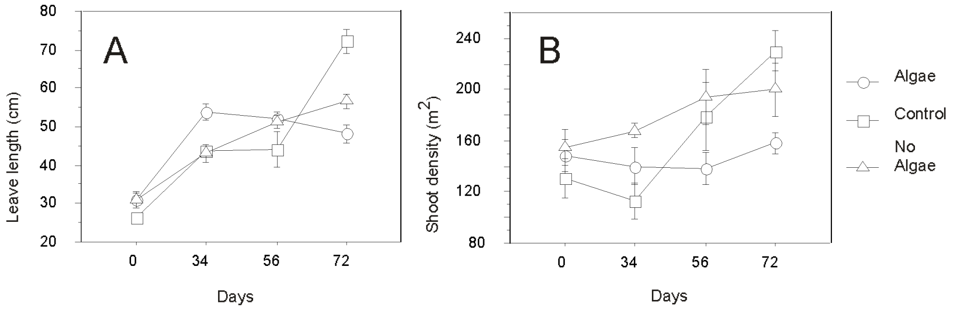


Figure 3: Growth and survival of *Zostera marina* in macroalgal enclosures (circles), macroalgae-free enclosures (triangles) and enclosure-free controls with natural densities of macroalgae (squares). (A) Mean length and (B) mean shoot density of seagrass (*Zostera marina*) in the course of the experiment. Data are means ± 1 standard error, n = 6.

Seagrass shoot density increased by 29% from 155 shoots $m^{-2}$ to 200 shoots $m^{-2}$ in the algae-free enclosures, whereas it decreased in response to algal cover from 148 shoots $m^{-2}$ to 138 shoots $m^{-2}$ and recovered to 158 shoots $m^{-2}$ in response to algal decomposition in the latter part of the experiment (Figure 3 B). Overall, shoot density in the macroalgal treatments was 22% lower than in the macroalgae-free treatments. Initial shoot density was the same at all sites (one way ANOVA; df = 2, F = 1.01, P = 0.379) whereas shoot densities were significantly different between macroalgae-, macroalgae-free treatments and controls (one way ANOVA; df = 2, F = 4.79, P = 0.035). The macroalgal canopy prevented an increase in shoot density. Seagrass shoots at the enclosure-free controls showed a distinct decrease in shoot density after the first 34 days (14%) and a strong increase in the second part of the experiment to a shoot density of 227 shoots $m^{-2}$. The aboveground biomass of seagrass showed a similar trend (Figure 4).

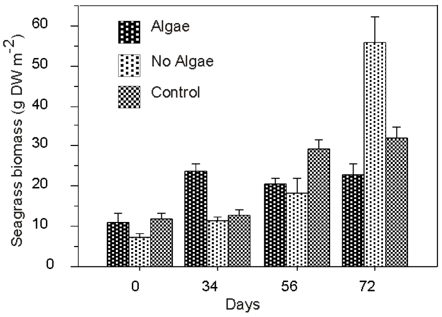


Figure 4: Net seagrass growth in the course of the experiment. Macroalgae treatments (dark bars), algae-free treatments (middle bars) and enclosure-free controls (light bars). Data are means ± 1 (n = 6).

At the beginning of the experiment, differences between macroalgae treatments and macroalgae-free treatments were insignificant (one way ANOVA; df = 2, F = 3.53, P algae/no algae = 0.977). At the end of the experiment the aboveground biomass was 22% higher in the macroalgae-free treatments compared to the plots with algae (one way ANOVA; df = 2, F = 22.39, P algae/no algae = 0.0051).

Furthermore, the macroalgal canopy negatively affected seagrass shoot size. Shoot size was similar in all plots in May (0.063 ± 0.005 g dry mass per shoot; one way ANOVA; df = 2, F = 1.54, P = 0.2235) but significantly different in June (one way ANOVA; df = 2, F = 5.84, P = 0.004, Fischer's : treatment algae/no algae = 0.016). Plots with no algae and control plots showed an increase in shoot size and a strong development of new shoots. Similarly, the plots with algal canopy featured an increase in shoot size but a lack of new shoots, shown clearly by the gap between 0 and 0.5 g dry mass per shoot (Figure 5 A). The algal mats have a strong negative impact on the production of new shoots.

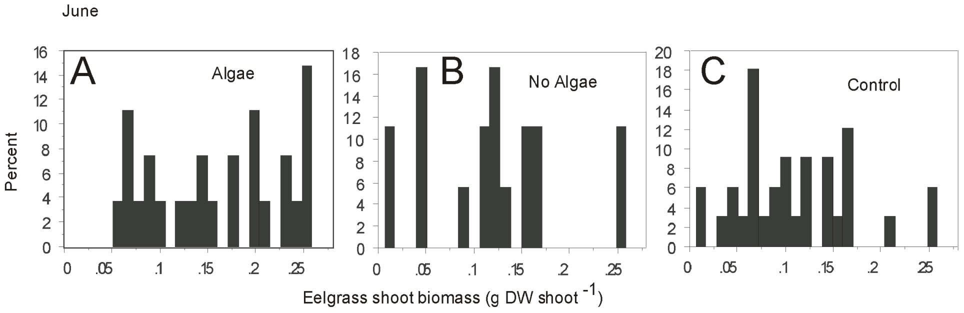


Figure 5: Eelgrass shoot biomass in treatments with algae (A), without algae (B) and control sites (C) in June 2005.

At the end of the experiment shoot size was largest in the enclosure-free control sites, followed by the algae-free treatment and macroalgae treatment showing the lowest shoot weight (Figure 6).

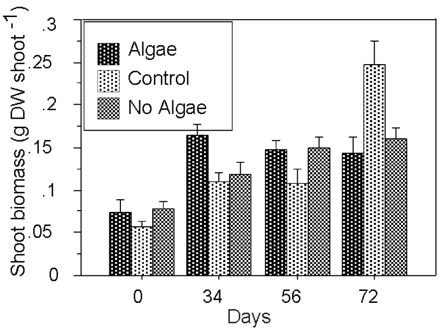


Figure 6: Seagrass shoot size (g DM shoot$^{-1}$) throughout the experiment.

Macroalgae treatments showed higher POC concentrations in seagrass leaves (but not in rhizome tissue) than macroalgae-free treatments (ANOVA, F = 4.06, P = 0.0491; Figure 7). No effect on nitrogen concentration in either leaves or rhizome tissue was found. Carbon : nitrogen tissue ratios increased from March (13.4 ± 0.27% of DM) to July (17.8 ± 0.99% of DM) in all plots.

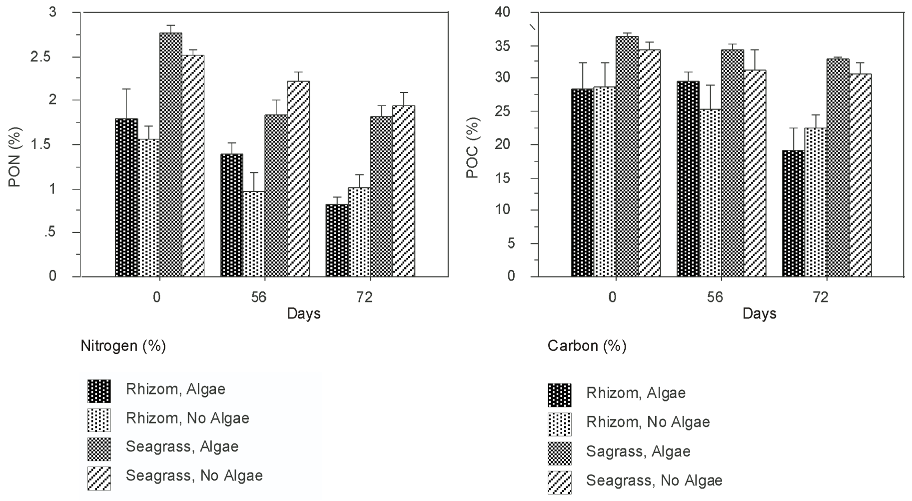


Figure 7: (A) Leaf - and (B) rhizome tissue composition of *Zostera marina* with algae (dark bars) and without algae (light bars). Carbon- (POC) (filled bars) and nitrogen concentration of dry mass (PON) (banded bars) in seagrass tissue after 0, 56 and 72 days of the experiment in summer 2003. Data are means ± 1 SE (n = 6).

## Effects of macroalgal canopy on the biogeochemical environment of *Zostera marina*.

Macroalgal canopies affected ammonia levels, but not the concentration of oxygen, nitrate, nitrite or orthophosphate. Oxygen profiles between the sediment and 1 m above ground show well oxygenated conditions within the algal mats with only slightly lower oxygen levels in the immediate vicinity of the sediment-water interface (Table 1). The top layer of all sediment samples remained well oxygenated and no sulphide production was observed. Treatments with macroalgae showed an oxidized sediment layer of 1.80 ± 0.40 cm, and in treatments without algae oxidized sediment layer was 1.93 ± 0.16 cm.

Table 1: Early morning concentrations of oxygen (12+14 July 2003). Measurements between algae canopy and without algae next to it.

| depth over ground (cm) | oxygen concentration (mg $l^{-1}$)+ SE | position |
|---|---|---|
| 5 | 9.12 ± 0.61 | between algae |
| 5 | 8.80 ± 0.64 | without algae |
| 20 | 9.32 ± 0.67 | without algae |
| 100 | 9.45 ± 0.52 | without algae |

The most dramatic increase in nutrients occurred in pore water (PW) samples at the end of the enclosure experiment (Figure 8 A; ANOVA, F = 4.398, P = 0.042, df = 1), particularly in ammonia, which increased up to 400 times to a maximum concentration of 107 µmol $l^{-1}$ in the macroalgal treatments. Initial PW ammonia concentrations were the same in all enclosures (ANOVA, F = 0.018, P = 0.904, df = 1) (Figure 8 C). Final PW concentrations of nitrate and nitrite ($N0_3$-+ $NO_{2+}$) ranged from 0.4 to 4.1 µmol $l^{-1}$ and orthophosphate from 1.9 to 6.3 µmol $l^{-1}$). In bottom waters (BW), we found only moderate increases in ammonia (1.0 to 7.8 µmol $l^{-1}$), and water column concentrations showed only little temporal variation (Figure 8 B).

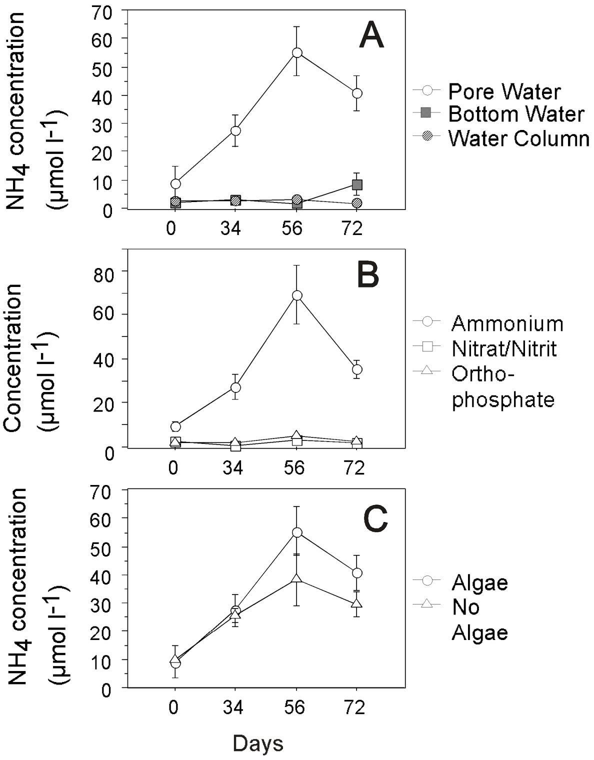


Figure 8: (A) Ammonia concentrations from pore water (PW) (light dots) samples, bottom water samples (BW) (filled quadrates), and water column samples (WC) (filled dots) at day 0, 34, 56 and 72 of the experiment in macroalgal enclosures. Data are means ± 1 SE (n = 12).

(B) Nutrient concentrations from pore water samples throughout the experiment in macroalgal enclosures. Values are means ± 1 SE of ammonia (dots), nitrate plus nitrite (quadrates) and orthophosphate (triangles) (n = 12). (C) Pore water ammonia concentration with treatment: algae (dots) and no algae (triangles) throughout the experiment. Data are means ± 1 SE (n = 12).

Table 2: Primary producers biomass (phytoplankton, epiphytes of seagrass and macroalgae) in May, June and July 2003. Data are means with ± 1 SE (except for the macroalgal canopy). Also shown is the attenuation due to the water column (phytoplankton, tripton, water), phytoplankton alone, epiphytes and macroalgal canopy.

| | | | | Attenuation% of $I_0$ | |
|---|---|---|---|---|---|
| Source | Month | Value | k ($m^{-1}$) | adults (2.20m) | recruits (2.80m) |
| Total water attenuation | May | | -0.7 | 79 | 86 |
| | June | | -0.7 | 79 | 86 |
| | July | | -0.9 | 86 | 92 |
| Phytoplankton biomass (mg Chl a $m^{-3}$) | May | 7.65 ± 0.03 | -0.12 | 24 | 31 |
| | June | 8.27 ± 0.1 | -0.13 | 26 | 33 |
| | July | 15.88 ± 0.3 | -0.25 | 44 | 53 |
| Epiphyte biomass (µg Chl a $cm^{-2}$) | May | 0.104 ± 0.02 | -0.05 | 1.1 | 0 |
| | June | 0.072 ± 0.01 | -0.035 | 0.7 | 0 |
| | July | 0.84 ± 0.27 | -0.42 | 7.1 | 0 |
| Macroalgal canopy height (cm) | May | 2-7 | -1.43 to –2.66 | 0.4 – 1 | 15 - 19 |
| | June | 2-7 | -1.43 to –2.66 | 0.4 – 1 | 15 - 19 |
| | July | 2-7/ 0 | 1.43 to –2.66/0 | 0 – 1 | 0 – 19 |

## Light attenuation due to phytoplankton, epiphytes and macroalgae

Total light attenuation ($K_T$) in the water column (water and suspended solids) was an average 0.8 ± 0.10 $m^{-1}$ at Vilm (Table 2). During summer, $K_p$ (attenuation through phytoplankton) typically comprised a large percentage (20 – 50%) of $K_T$. The largest share of the attenuation in the Greifswalder Bodden can be explained by the water and its nonliving components (tripton).

Summer mean irradiance at the air-water interface, was about 1772.26 µmol photons $m^{-2}$ $s^{-1}$. Correcting for surface reflectance (mean 36%), the incoming irradiance was calculated to be 1134 µmol photons $m^{-2}$ $s^{-1}$. Incoming light covered a distance of 2.20 m to established tall shoots with a mean height of 61 cm, while the distance from the water surface to new recruits of seagrass was 2.80 m. Total water column attenuation between the water surface and the seagrass reached between 81% and 88% for old and new shoots, respectively.

In addition to $K_T$, light was reduced by epiphytic and mat-forming algae. An epiphyte load of 0.30 ± 0.09 µg Chl $cm^2$ was measured on seagrass leaves from May to July. Calculated light attenuation due to epiphyte shading on older shoots ($f(x) = 100\,(1-e^{(-0.5x)})$), (Silberstein et al., 1986) averaged 14% of the incoming light at that depth ($I_z$), resp. 3% of $I_0$ (Table 2), with a minimum of 5% ($I_z$) and a maximum of 34% ($I_z$) during the experiment. The epiphytic load and associated light attenuation on young shoots was negligible.

In May, height of macroalgal canopy was about 2 - 7 cm. Until the end of June, there was no major change in the algal cover, but in early July algae started to decompose and by mid-July no macroalgae were left either in the seagrass meadow or in the enclosures. While healthy, algal canopy intercepted between 76 - 93% of the incoming light ($I_z$), resp. 15 - 19% of $I_0$ for new growing shoots (Table 2). Based on canopy height and shoot size (mean shoot size for established shoots = 61 cm), we estimate that incident light for old shoots was reduced only by 2 - 5% ($I_z$), in contrast to young shoots where macroalgal canopy absorbed about 89% of incoming light ($I_z$).

## Discussion

The decrease and loss of seagrass meadows due to the presence of macroalgal canopies has been observed worldwide (Holmquist, 1997; Valiela et al., 1997; Raffaelli et al., 1998; Hauxwell et al., 2001; McGlathery, 2001; Nelson and Lee, 2001; Cummins et al., 2004).

Our studies in the Greifswalder Bodden have been one of the first experimental confirmations of the negative impact of the macroalgal canopy on seagrass. Surprisingly, our experiment showed, that the most important impact on seagrass attributed to macroalgal canopy was a strong reduction in incoming irradiance for the new shoots. Light availability is one of the most important factors controlling growth and survival of temperate seagrass (Dennison and Alberte, 1982; Duarte, 1991). However, the moderate height of the macroalgal canopy made us expect stronger effects due to toxic nutrient concentration or oxygen depletion caused by the macroalgal cover.

We found that macroalgal cover intercepted nearly all incoming light which had penetrated through the water column (76 to 93% of incoming light in 2.80 m depth (Iz)). Because of the low algal canopy height (2-7 cm) the impact was modest for established shoots (see Table 2), but it had a severe effect on new shoots. Macroalgal canopy reduced the already by phytoplankton strong attenuated incoming light to a maximum of 15 µmol photons m-2s-1 for new growing shoots which is just above the compensation point (for Zostera marina: Icompensation ≈ 10 µmol photons m-2s-1; Isatturation ≈ 120 µmol photons m-2s-1 (Drew, 1979; Dennison and Alberte, 1982, 1985; Marsh et al., 1986; Dennison, 1987; Duarte, 1991; Zimmerman et al., 1991; Olesen and Sand-Jensen, 1993; Short and Burdick, 1995; Koch and Beer, 1996; Moore et al., 1997). As a consequence, the new shoots buried under algal mats did not receive sufficient light to grow and survive. In contrast, leaves of old shoots widely looked out of macroalgal cover and received maximum light intensities of about 170 µmol photons m-2s-1, which is sufficient for seagrass growth. The impact of shading through macroalgal canopy resulted in a reduced shoot density of 22% of the macroalgal-free seagrass enclosures. This was mainly due to reduced sprouting of new shoots in response to shading, whereas mortality of old shoots played only a minor role. These findings suggest that the translocation of photosynthates and the mobilization of stored energies through the

rhizome were not sufficient to allow the sprouting of the shaded shoots.
Our results disagree with the study of Irlandi (Irlandi et al., 2004), who could not find any effect of macroalgal shading on seagrass shoot density. Instead they found a positive impact of the macroalgal cover on the seagrass *Thalassia testudinum*. The cause of this discrepancy between our results and those of Irlandi et al. may have been due to the differences in macroalgae cover on neighbouring shoots. While in our experiment the whole seagrass meadow was covered by a natural macroalgal canopy, most of the seagrass plants in Irlandi's study, except of those in the 0.25 cm$^2$ experimental plots, had no macroalgal cover. The effect of shading through macroalgae might have been masked by translocation of storage products among shaded and unshaded neighbouring shoots in that study, which was not possible for seagrass shoots in this investigation. On the other hand, our results are in close agreement with the work of Hauxwell (2001). They found a similar lethal impact on new *Zostera marina* shoots and a consequential reduction in shoot density caused by light interception by the macroalgae canopy. In contrast to their work, we observed a negative impact with lower algal canopy and a shorter experiment time. This might be the reason for the less pronounced decline in shoot density and above ground biomass in comparison to their study.

The macroalgal enclosures had a marked effect on *Zostera marina*, reducing shoot density and leaf growth compared to algae-free exclosures. The rapid recovery of the seagrass bed in the control sites outside of the enclosures appears to be related to the faster decomposition or physical removal of the macroalgal canopy in response to enhanced circulation and, hence, to improved light conditions. In the first months of the experiment, shoot densities in the unenclosed controls were lower than in the macroalgal enclosures, indicating stronger shading in the former which may be due to continued accumulation of drift algae in the course of the growing season. While this experimental bias in the enclosures results in a conservative estimate of shading effects, the overall course of seagrass growth and density over early summer is similar in enclosures and reference sites, comparable with observations from other temperate estuaries.

In contrast to new shoots, for established seagrass shoots, water column and epiphytes shading were the most important attenuation factors.
Phytoplankton was responsible for a 24-53% of total water column light attenuation ($I_0$) in the estuary during the experiment and together with tripton (non living particles) they caused a light attenuation of up to 92% of incoming light ($I_0$). Epiphyte loads with an average biomass of 0.30 ± 0.09 Chl *a* cm$^{-2}$ per seagrass leave area had a minor impact on seagrass growth. Epiphyte load was rather low compared to other studies in the Baltic Sea. Typically epiphytic loads of 0.62-6.6 Chl *a* cm$^{-2}$, can be found on seagrass leaves in the Baltic Sea (Larkum et al., 1989; Lin et al., 1996), which is much less eutrophicated than the Greifswalder Bodden. In this study, epiphytic algae contributed on average to 3% of the attenuation of $I_0$, resp. 14% of $I_z$ for established shoots. Epiphytes on seagrass leaves contribute to light attenuation at the leaf surface, and inhibit nutrient and gas exchange (Sand-Jensen, 1977; Borum, 1985; Sand-Jensen et al., 1985; Twilley et al., 1985; Short and Burdick, 1995; Brush and Nixon, 2002). Therefore, at high densities epiphytes can be a considerable stress for seagrass.
The study of Irlandi et al. (2004) showed that macroalgae led to a decrease in epiphytic loads on seagrass leaves, which had a

favourable effect on seagrass. In contrast, this positive effect of macroalgae might have no relevance in our investigation. The macroalgal cover had a maximum height of 7 cm, while most of the epiphytes settled on the upper part of seagrass leaves beyond reach of macroalgae. In our investigation, epiphytic cover played just a minor role for seagrass growth.

Furthermore, macroalgal cover affected older shoots by producing unfavourable ammonia concentrations in the water column, that led to a reduction in seagrass above ground biomass, leaf length and a deterioration of seagrass health.

The decline in leaf length in the macroalgal treatments was particularly pronounced during the decay of macroalgae mats in the second half of the experiment. It happened through the degradation of seagrass leaves (brown lesions, necrosis or torn off leaves) which was nearly twice as frequent as in the algal-free exclosures (Figures 9). This might have been due to the nitrogen regeneration by the canopy and underlying sediments. The ground water-ammonia concentrations were 7.5 times higher in treatments with macro-algal canopy. Negative physiological effects of enhanced nutrient concentrations in the water column may become relevant at high levels and affect seagrass growth (Burkholder et al., 1992). Van Katwijk et al. (van Katwijk et al., 1997) measured toxic ammonia levels for *Zostera marina* at about 125 µmol $l^{-1}$ and a growth inhibition starting at a concentration of 7 µmol $l^{-1}$ with an incubation time of 3 to 5 weeks. In this experiment, ammonium nutrient levels (max = 17.8 µmol $l^{-1}$) were too low to have a toxic impact, but the concentration became harmful for seagrass during the three to four weeks experimental duration, which became apparent through the deterioration of *Zostera marina* leaves.

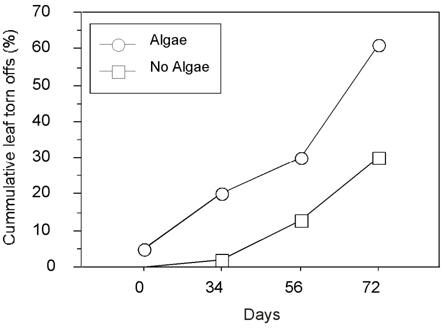


Figure 9: Cumulative eelgrass leaf torn offs throughout the experiment.

It is well known, that in contrast to the nutrient concentrations in the water column, high concentrations in the sediment promote the growth of *Zostera marina*. Even extreme ammonia concentrations (600 µmol $l^{-1}$) show no negative impact on seagrass (Williams and Ruckelshaus, 1993). The ammonia concentrations in this study were quite low in the pore water (max = 100.7 µmol $l^{-1}$, mean = 55.4 ± 8.7 µmol $l^{-1}$). Therefore we can conclude that the macroalgal mats did not cause toxic or even unfavourable nutrient conditions for seagrass within the sediment.

There were no significant differences in PON concentration between seagrass leaves or roots/rhizomes between treatments. Only the POC content was significantly lower in the algae-free treatments than in the algae covered enclosures. This difference was constant over time and can therefore not be attributed to the impact of algal cover, which varied in the course of the experiment. The measured POC (26-39%) and PON (1.2-3.1%) values are in the range of values reported in the literature. Literature values of carbon content of *Zostera marina* range from 29 to 46% of dry mass; nitrogen content ranges from 0.7 to 6.3% (Atkinson and Smith, 1983; Duarte, 1990; Pedersen and Borum, 1993; Abal et al., 1994; Fourqurean et al., 1997). The decrease in PON content in seagrass tissue in our experiment reflects the increased demand of nitrogen during a phase of rapid seagrass growth. The decay of macroalgal mats did not lead to an increase in nitrogen supply for eelgrass as a decrease in PON was seen in the seagrass tissue.

The high oxygen concentrations near the ground (7.8 ± 0.6 $mgl^{-1}$) and between decomposing macroalgae show that mixing by currents provided oxic conditions throughout the experiment. Although sulfide concentrations were not measured in this study, we can safely assume that there was no development of sulfide, due to the fully oxygenated surface layers. As seagrass can grow in oxidized to moderately reduced sediments (Hemminga and Duarte, 2000) negative effects on the experiments can be ruled out.

Without any macroalgae impact, the generally poor light conditions in the Greifswalder Bodden cause relatively low shoot density at all sites (153 ± 6.1 shoots $m^{-2}$) compared to other reported seagrass densities in the Baltic Sea (150-1200 shoots $m^{-2}$) (Grontved, 1958; Feldner, 1976; Gründel, 1982; Olesen and Sand-Jensen, 1994b; Olesen and Sand-Jensen, 1994a; Reusch et al., 1994; Reusch and Williams, 1998; Olesen, 1999; Boström et al., 2002). Low light conditions over longer periods, leads to a decrease in shoot density (Dennison and Alberte, 1982; Duarte, 1991; Hemminga and Duarte, 2000), therefore, repeated loss of new shoots due to macroalgae cover in coming years might result in a complete destruction of the already previously stressed seagrass population in the Bodden.

Our results suggest that growth for young and old seagrass is limited by competition with differing primary producers: benthic macroalgae for young and phytoplankton for mature Zostera marina shoots.

Consequently, nutrient-stimulated growth and competition of macroalgae and phytoplankton may be key factors governing light-limited growth in seagrass in the Greifswalder Bodden system. Looking at the widespread concurrent changes in opportunistic macroalgae and seagrass beds (Raffaelli et al., 1998) the contribution of macroalgal mats in seagrass loss worldwide is probably quite large and, depending on the system, perhaps of equal importance to that of phytoplankton and epiphytes. Considering the worldwide problem of increasing eutrophication and resulting macroalgal blooms, the effects of macroalgal mats on seagrass growth are a very current issue that needs further attention. Many questions remain unanswered, like the impact of time- and spatial scale of macroalgal cover, the critical macroalgal canopy height/biomass or the importance of influencing environmental conditions. Further controlled manipulative experiments are needed for the thorough examination of these questions.

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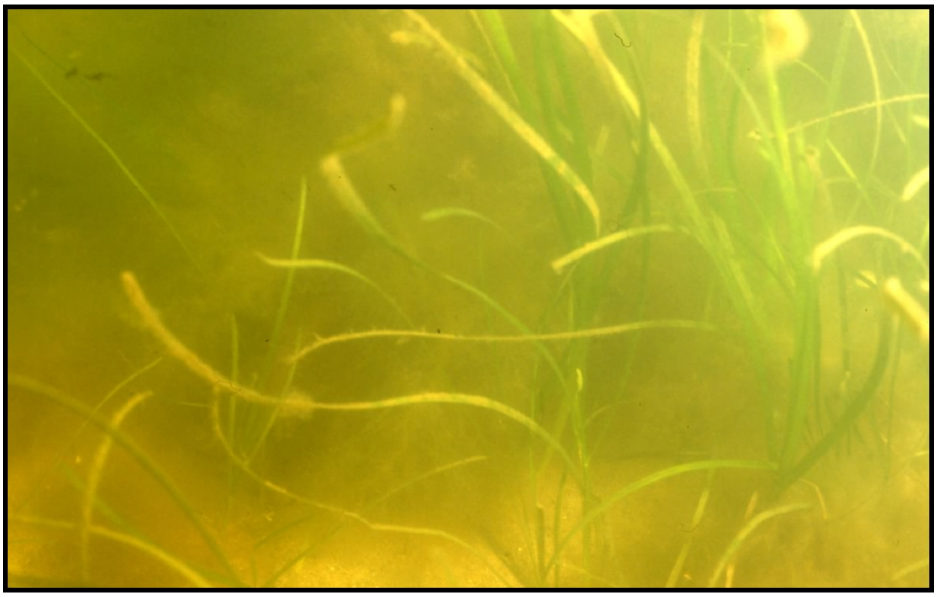
We are especially grateful to the shipping authorities and the national park authority for granting the permission to work in the national park area.

This study was founded by a scholarship program of the German Federal Environmental Foundation (DBU).

## Manuskript IV



# Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea

## Abstract

Between the 1950s and the 1980s concentrations of inorganic nutrients increased in the coastal areas of the Baltic Sea, including the Greifswalder Bodden. As consequence phytoplankton concentration and suspended solids increased strongly and the light penetration decreased substantially. The increased turbidity led to a phase shift from a macrophyte-dominated to a phytoplankton-dominated ecosystem. Within 30 years, macrophyte cover declined from 90% to 15% ground cover. The macrophyte depth limit rose from 14 m to 6 m in the Bodden. After 1985 the nutrient loading declined strongly. Although the nutrient loads in the Greifswalder Bodden were reduced (a 50% decrease in phosphate concentration and a 40% decrease in nitrogen concentration) during the last 15 years, the expected improvement of water quality did not follow. The light conditions improved barely and the macrophytes showed no recovery. Possible reasons for the slow improvement are internal loading and subsequent release of ironbound phosphorus from the sediments. This sustains continuous high nutrient concentrations in the water column facilitating the high growth of phytoplankton and its dominance. During summer, a strong cyanobacteria community fuels the phytoplankton dominance. In addition, the heavy losses of macrophytes cover resulted in an increase of sediment resuspensation, which, furthermore, lead to a strong weakening in light penetration. There is no sign of a rapid change in the current conditions.

Keywords
estuaries, eutrophication, macrophytes, regime shift, resilience

## Introduction

Eutrophication is a major problem of estuarine ecosystems around the world. As a result of increasing urbanisation and agriculture in the river catchment areas , particularly since the middle of the 20th century, estuaries became one of the most nutrient loaded coastal ecosystems (Flindt et al., 1999).

The Greifswalder Bodden, with 510 km$^2$ the largest estuary at the German Baltic coast, represents a natural, shallow basin (average depth = 5.8 m) which filters the nutrients and dissolved organic substances before they enter the Baltic Sea. Nutrient levels in the estuary have increased dramatically between 1950 and 1990, due to urban and agricultural development in the catchment area of the estuary. Higher nutrient supplies have enhanced pelagic productivity and have increased turbidity in the Greifswalder Bodden, deteriorating the light climate and causing high mortalities of macrophytes in the estuary. This has led to a shift from a macrophyte-dominated to a phytoplankton-dominated shallow water ecosystem with high loads of suspended matter. To what extent this shift is reversible, is a matter of debate, as the system has remained in a turbid unvegetated state in spite of marked reductions in nutrient inputs over the last 15 years.

An explanation for this enigma may be sought in Sheffer's model addressing resilience and phase shifts to alternate stable states in freshwater ecosystems subjected to eutrophication (Scheffer, 1990).

Scheffer`s model demonstrates the catastrophic effects of nutrient enrichment on a shallow lake, where the increase in nutrients is followed by a strong increase in the biomass of phytoplankton and opportunistic macroalgae, reducing the light supply for rooted vegetation (Scheffer, 1990). Beyond a critical threshold, light reduction causes a dramatic mortality of macrophytes and a phase shift from a rooted macrophyte-dominated to a phytoplankton-dominated system. The phase shift initiates a self-perpetuating process: The absence of submerged vegetation and concomitant lack of baffling of currents and waves by macrophytes maintains sediments in suspension thus increasing the load in the water column. Increases in both, suspended sediments and phytoplankton, increase the light attenuation in the water column, consolidating the shift of the system to a turbid stage. An important feature of Scheffer's model is the different turbidity response of the vegetated and unvegetated system to changes in nutrient levels: In the vegetated state, turbidity is low and rises monotonously up to a threshold value, beyond which the die-off of the macrophytes triggers a shift to the turbid unvegetated state (Figure 1). Note that the return to the macrophyte-vegetated state follows a different route, where the shift from the turbid to the non-turbid state occurs at a markedly lower nutrient threshold.

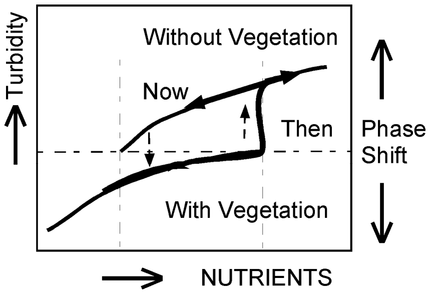


Figure 1: Schematic representation of the effect of vegetation on the nutrient-turbidity relationship and consequences for systems equilibria if vegetation disappears completely (modified from Scheffer, 1990) adapted to the present-day situation in Greifswalder Bodden (see text for details).

This model of “ecosystem shifts” between alternatives states might be also applicable to the brackish Greifswalder Bodden and explain the observation that the reduction in external nutrient loading did not show the expected recovery of the benthos.

This paper aims at presenting an integrated overview of published and unpublished data and an analysis of long-term ecosystem changes in the Greifswalder Bodden due to eutrophication. It shows the historic development and the consequences of eutrophication on the water/habitat quality and on the macrophytes stands and the current environmental conditions for the growth of the remaining macrophytes. Possible reasons for the delayed improvement of the ecosystem after reduction in nutrient loading will be discussed and some perspectives on what might improve the state of the ecosystem will be given.

## Study site

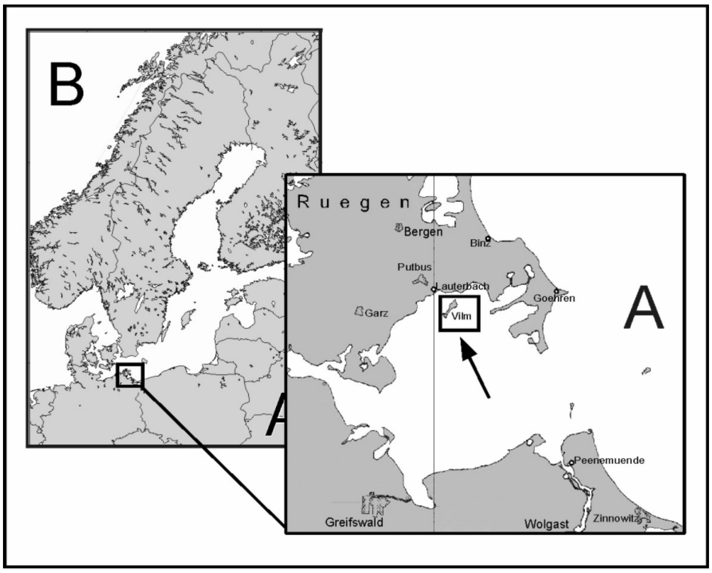


Figure 2: The Greifswalder Bodden (A), insite the island Vilm (arrow) and its position in the Baltic Sea.

The Greifswalder Bodden is the largest shallow bay on the southern coast of the Baltic Sea. Enclosed shallow-water systems are locally called boddens or haffs. The Peene river and the Strelasund river are the two tributaries of the estuary which has a narrow and shallow sill to the Baltic Sea. The sediments consist of mud and to a smaller part of sand and clay-gravel-mixture. Hydrodynamics are governed mainly by the wind. Mixing results in a well-oxygenated water column down to the sea-bed and wind-driven advection exchanging water masses between the Bodden and the Baltic proper generates water level fluctuations of up to 1.5 m near the coast. There are no perceivable lunar tides. During periods of high water, caused by northeasterly winds, water masses flow from the Baltic Sea into the estuary, renewing its waters about 8-12 times per year (Stigge, 1989; Hubert et al., 1995; Lampe and Meyer, 1995) (Figure. 2). Evaporation, precipitation, and river inflow of the Strelasund are of only minor importance for the water balance (Stigge, 1989). However, the inflow of the Strelasund and the Peene play an important role for the nutrient- and phytoplankton budget in the estuary (Hubert et al., 1995; Hubert et al., 1997). Some morphometric and hydrologic characteristics of the Greifswalder Bodden are given in Table 1.

Table 1: Morphometric and hydrologic characteristics of the Greifswalder Bodden.

| Parameter | Value |
|---|---|
| Surface (km$^2$) | 510 |
| Volume (m$^3$) | 2.96 x 10$^9$ |
| Average depth (m) | 5.8 |
| Hydraulic loading (m y$^{-1}$) | 3.44 x 10$^{10}$ |
| Freshwater inflow (m$^3$ y$^{-1}$) | 1.06 x 10$^8$ |
| Water retention time | 4 - 5 weeks |
| Salinity (PSU) | 7 |

## Material and Methods

Data were collected from different sources.

The monitoring data (nutrients, chlorophyll (Chl a), total suspended solids (TSS), temperature) show the average of 2 monitoring stations from LUNG (= by the State Agency for the Environment, Nature Conservation and Geology of Mecklenburg-Western Pommerania (LUNG) / Landesamt für Umwelt, Naturschutz und Geologie), and one station from BfN (= German Federal Agency for Nature Conservation / Bundesamt für Naturschutz ) in the Greifswalder Bodden estuary. The measurements were taken between 2-5 times a months, on average about once a week. Annual or monthly average values and standard errors are shown in the figures. For more details see LUNG, 1998 & unpublished data.

Light penetration are monthly minima, averaged over the growing season (Figure. 3) or monthly averages (Figure. 6) between 1975 and 2003, as measured with a Secchi disc at three monitoring stations in the Greifswalder Bodden. Earlier data were taken from the literature (Reinke, 1901; Seifert, 1938; Subklew, 1955; Scabell, 1988). The depth of the euphotic zone (or phytal, cf. Figures. 3, 4) was estimated from the maximum of occurrence of macrophytes (spermatophytes and charophytes) and macroalgae (rhodophyta).

## Results

Light penetration and vertical range of the euphotic zone decreased markedly in the Greifswalder Bodden over the last century. Whereas macrophytes were reported to occur as deep as 13 m before the Second World War, the maximum depth is now around 6 m and the average less than 4 m (Figure 3; see also Seifert, 1938; Subklew, 1955; LUNG, 1998). The decrease in macrophyte depth coincides with decrease in Secchi readings by 80% (Figure 3) and a marked increase in nutrient concentration between 1950-1980. In spite of recent reductions in nutrient inputs to pre-war levels, turbid waters prevail throughout the restoration period between 1985 and today.

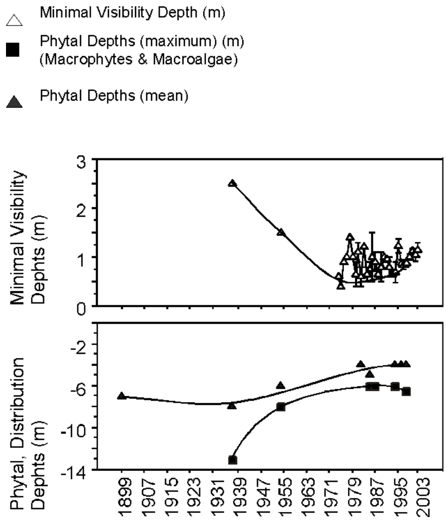
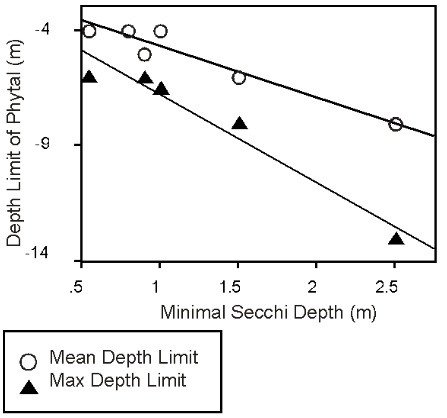


Figure 3: Turbidity and depth of euphotic zone in Greifswalder Bodden over the last century, given by the annual minimal Secchi depths+ SE (n=13-36) and phytal (macrophytes & macroalgae) ranges. Lines fitted by eye. Sources: (BfN, ; Reinke, 1901; Seifert, 1938; Subklew, 1987; Hintze, 1988; Scabell, 1988; Geisel and Messner, 1989; Messner and von Oertzen, 1990; Rambow, 1994; Geisel, 1995; Vietinghoff, 1995; Bartels and Klüber, 1997; Dahlke et al., 1997; Küster, 1997; LUNG, 1998; Böllmann, 2000).

The plants dependency on clear waters is illustrated by the relation between the phytal depth limit in the estuary and the minimal Secchi depth (Figure 4).

Nutrient inputs to the Greifswalder Bodden decreased considerably during the middle of the 1990s. Following the reunion of East- and West- Germany extensive water protection measures were implemented. The use of phosphate-free detergents and the reduction of intensive livestock farming, semi-liquid manure, and fertilizers in agriculture led to a drastic reduction of the nutrient inputs. Further improvements resulted from the construction and upgrading of sewage treatment plants (LUNG, 1998; Behrendt, 1999, 2000; Meyer-Reil and Köster, 2000). This was followed by a decrease of total phosphorus (TP) concentrations (dissolved+ particulate phosphorus) (Figure 5; data by courtesy of (LUNG, 1998). While in the seventies TP concentrations were about 2.5-5.5 mmol m-3, at the end of the nineties the TP concentrations ranged from 1.1-2.4 mmol m-3. During the last few years, the annual average TP concentration reached a level around 1.5 ± 0.03 mmol $m^{-3}$ . Similar to the reduction in TP concentration since 1986, the total nitrogen (TN) concentration also declined (Figure 5). Until 1989, the annual average TN concentrations had a high-level about 63 ± 3.1 mmol $m^{-3}$. After 1989, the TN concentration decreased further, and between 1996 and 2003 an annual average



Mean Depth Limit = -2.45 - 2.22 * SD;
R^2 = 0.93

Max Depth Limit = -2.98 - 3.82 * SD;
R^2 = 0.95

Figure 4: Regression between mean or average depths limit of macrophytes and macroalgae in the Greifswalder Bodden and minimal Secchi depth.

TN concentration about 47 ± 1.05 mmol m$^{-3}$ could be observed.

On the basis of the decrease in nutrient concentrations, the time period from 1975 to 2003 was subdivided into three time periods (Figure 5): 1. from 1975 to 1985: high loading, before phosphate restriction; 2. from 1986-1995: transition, period with first effects of phosphate restriction and time of with water protection measures and 3. from 1996 to 2003: low nutrient loading, after a great reduction of external nutrient loading.

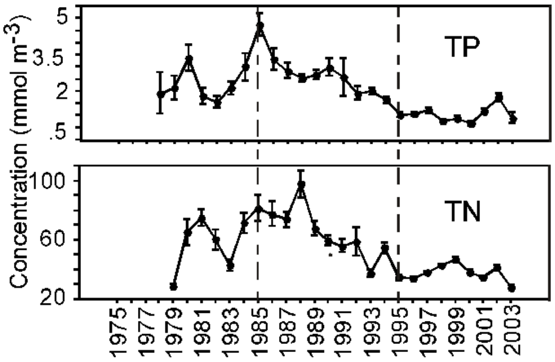


Figure 5: Annual nutrient concentration+ SE (n=3-16) from 1975 to 2003 in the Greifswalder Bodden. Tthe average of three monitoring stations from LUNG and one station from BfN in the Greifswalder Bodden is given (LUNG, unpublished; BfN, unpublished).

When comparing the seasonality of the nutrient concentrations of the three time periods, the strong reduction in nutrient concentration since the end of the 1980s becomes even more evident (Figure 6).

Although the seasonal course of orthophosphate did not change substantially during the last 30 years, the absolute concentration, decreased from 1.07 ± 0.06 mmol m$^{-3}$ to 0.59 ± 0.02 mmol m$^{-3}$ . On the other hand, the dissolved inorganic nitrogen (DIN) showed changes in the absolute and in the seasonal pattern of the concentration. The DIN spring maximum decreased clearly after 1989 and the low-DIN summer period with concentrations below 1 mmol m$^{-3}$ expanded from 1 to 4 months. Low concentrations of DIN (DIN : DIP = 2 : 1 ) are known to limit phytoplankton primary production in summer in the estuary (Schmidt, 1990a).

The response of the phytoplankton to the changing nutrient environment is illustrated by the temporal variations in chlorophyll *a* (Chl *a*) (Figure 6). Dense phytoplankton blooms mark the high load period with mean Chl *a* concentrations of 16.98 ± 2.53 mg m$^{-3}$ and a maximum of 101.6 mg m$^{-3}$ during the 1984 spring bloom. Summer values were generally only half the spring bloom concentrations.

Between 1986 and 1995 (transition) the Chl *a* concentrations dropped to 10.28 ± 0.71 mg m$^{-3}$, as a consequence of the strong reduction in nutrient loading. Also the bloom patterns changed indicating concomitant shifts in the phytoplankton community, so that the Bodden now shows fairly constant

Chl *a* levels over the entire growing season, with a slight excess in summer over the spring Chl *a* values. During low load period the mean Chl *a* concentration remained around 10.2± 0.32 mg $m^{-3}$ .

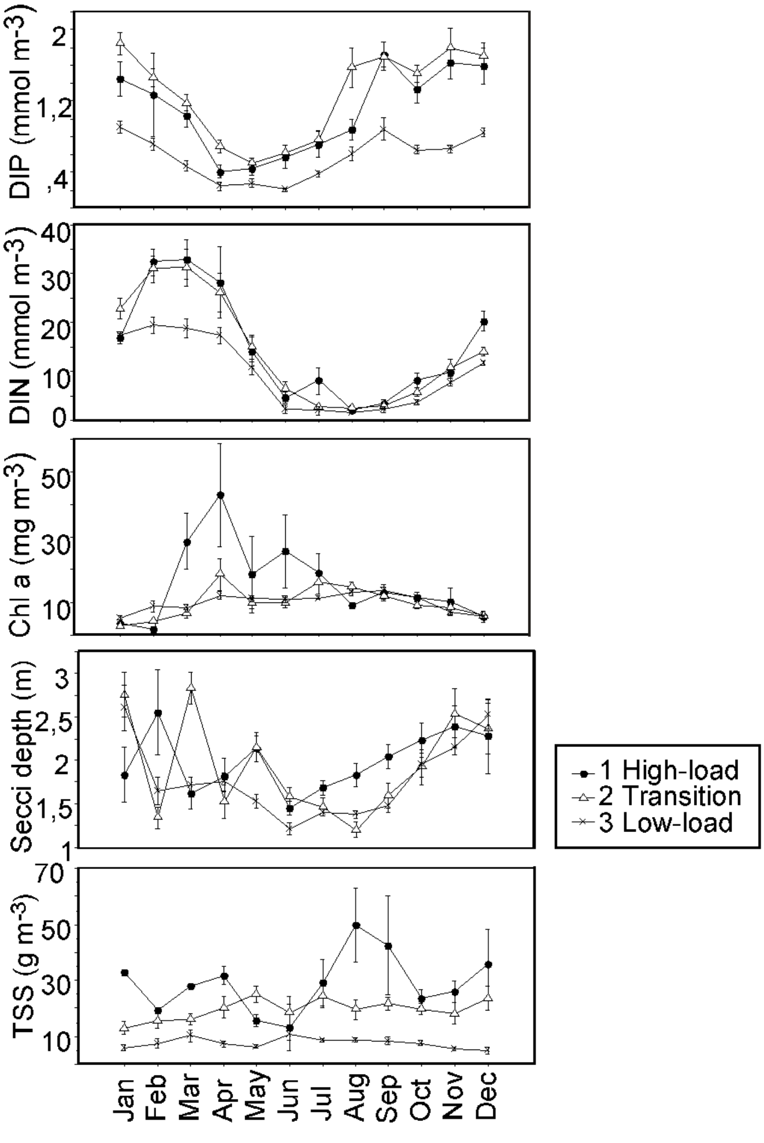


Figure 6: Monthly averaged settings+ SE (n = 6-24) of dissolved inorganic phosphate (DIP), nitrogen (DIN), Chl *a* concentration, the Secchi depths and the total suspended solids (TSS) from 1975 to 1985 (highload), 1991 to 1989 (transition) and 1990 to 2003 (lowloading) in the Greifswalder Bodden.

The average Secchi depth showed changes in the absolute values and in the seasonal pattern (Figure 6). Contrary to expectation, the average Secchi depth decreased from 1.96 ± 0.07 m during the highload period to 1.85 ± 0.05 m during lowloading period, and during the present summer months the turbidity appears to be even higher than during the highload period.

The last graph in figure 6 shows the course of the total suspended solids (TSS). During the time period of 1986 to 1995 there was a strong reduction of the TSS to ca. 46% to a concentration of 23.9 mg $m^{-3}$ ± 1.28 in parallel to the decrease in phytoplankton concentration. There was a further decrease to 7.76 mg $m^{-3}$ ± 0.38 in the low loading period, which still holds today. The strong seasonal peaks during the spring and summer phytoplankton blooms in 1975-1985 became less pronounced until today.

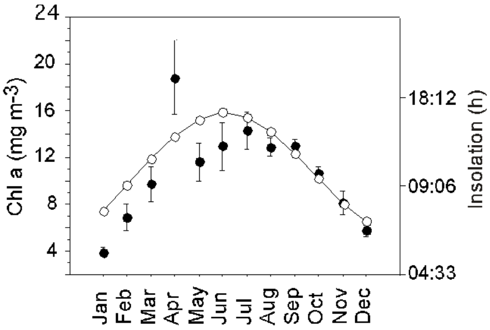
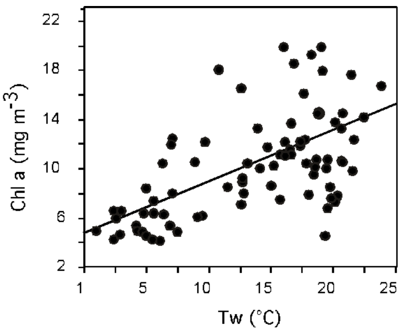


Figure 7: Monthly averaged settings+ SE (n = 38-50) of Chlorophyll a concentration (●) and daily insolation (○) from 1975 to 2003 in the Greifswalder Bodden.

The monthly settings of the chlorophyll a concentration and the daily insolation shows a similar progression (Figure 7). The chlorophyll a concentration follows the insolation curve with a short delay at the beginning of the year. Except for the spring bloom, the phytoplankton in the estuary shows a steady increase in Chl *a* concentration with increasing temperature suggesting that phytoplankton is not limited by nutrients (Figure 8). This is corroborated by the weak relationship between nutrients and chlorophyll ($R^2 < 0.19$; $p \geq 0.01$).



CHLa (mg $m^{-3}$) = 4.83 + 0.42 * Tw (°C);
R^2 = 0.37

Figure 8: Regression of chlorophyll concentrations and water temperature (TW) during low loading period (1990-2003) (spring bloom (Feb - Apr) data were excluded to reduce scatter).

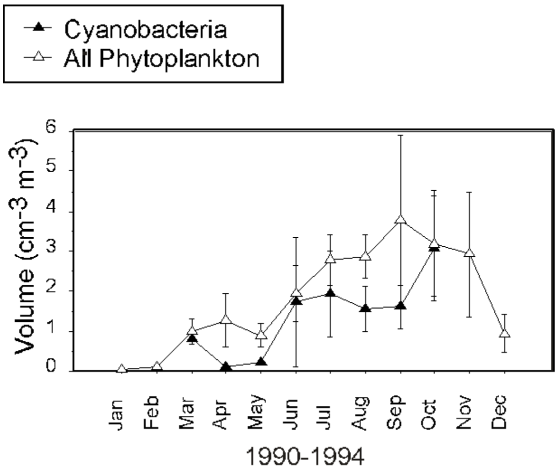


Figure 9: Monthly averaged settings+ SE (n = 5-19) of total phytoplankton and cyanobacteria volumina (source: LUNG, 1998 and unpublished data).

The summer bloom is dominated by cyanobacteria. From 1990 to 1994, the proportion of cyanobacteria made up 34 to 74% of the total phytoplankton biovolume (measurements by (LUNG, 1998) (Figure 9). Phytoplankton blooms triggered a drastic loss of macrophytes in the estuary between 1938 (Figure 10a) when 90% of the estuary were covered with macroalgae and spermatophytes (Seifert, 1938) and 1988 (Figure 10b), when the phytal was reduced to a narrow fringe covering 10-23% of the Bodden (Messner and von Oertzen, 1990).

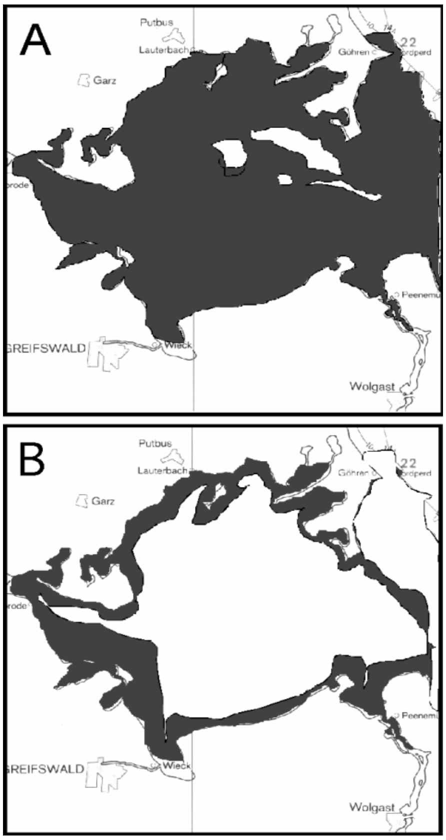


Figure 10: Phytal cover in the Greifswalder Bodden (A) in 1938 and in 1990-1997 (B) (modified after Messner & Oertzen, 1990).

The last extensive monitoring of macrophytes in the Greifswalder Bodden (Bartels and Klüber, 1997) showed no clear increase in macrophytes cover. The depth limit for growing has remained unchanged. In the last 15 years the macrophyte cover of the Greifswalder Bodden was estimated about 10-15% or 51-77 km$^2$ (Messner and von Oertzen, 1990; Vietinghoff, 1995; Bartels and Klüber, 1997; Dahlke et al., 1997).

# Discussion

## The Greifswalder Bodden

In spite of the 70% reduction in external phosphate loading into the Greifswalder Bodden since 1990 (Bachor, 1997), the light conditions barely improved and the phytal did not recover. Obviously, the nutrient concentrations are still sufficient to sustain a strong growth of phytoplankton (Figures 7,8). Part of the remaining high concentrations in the water column can probably be explained by internal loading caused by ironbound phosphorus formation and resultant release of phosphorus from the sediments (Schmidt, 1990a; Hubert et al., 1995). After Schlungbaum (1982) the DIP in the estuary is a reaction of the sorption- desorption equilibrium and doesn’t reflect the internal phosphate loading or the extent of the primary production. Therefore the internal phosphate loads of the sediments that have accumulated over many years remain a serious problem. About 70% of the Greifswalder Bodden is covered by organic-rich mud (Subklew, 1955) and muddy bare bottom have the highest efflux of phosphate compared to bare sandy bottom or vegetated sediments (Flindt et al., 1999). The internal loading of phosphate is well known for lake sediments (Bostrom et al., 1982; Marsden, 1989; Phillips et al., 1994). Especially shallow lakes are more resistant to recovery than deep lakes after the reduction of the external nutrient loading (Phillips et al., 1994). The Greifwalder Bodden estuary seems to have similar stabilizing mechanisms, which maintain the unfavorable state. However, during the summer months nitrogen becomes the limiting factor (Schmidt, 1990a; Hübel et al., 1995; Hubert et al., 1997; LUNG, 1998) (Figures 6). In 1993-1995, nitrate remained below detection in the Bodden waters from June to November (Hübel et al., 1995), coinciding with the appearance of diazotrophic cyanobacteria (Figure 9). Also the decrease in Secchi depth during the summer months indicates the increasing importance of cyanobacteria in the Greifswalder Bodden (Figure 6). The cyanobacteria are favored because of the resulting shift in the ratio of DIN to DIP during summer (Meyer-Reil and Köster, 2000). During summer the ratio of nitrogen to phosphate falls well below the Redfield ratio, with values around 2 indicating strong nitrogen limitation (Schmidt, 1990b, a; LUNG, 1998 and unpublised data). In spite of nitrogen limitation, there is no decline in Chl *a* concentration because N-fixation by cyanobacteria sustains further phytoplankton growth (Figures 7, 8 and Figures. 9). A substantial part of the fixed nitrogen is lost to the environment due to leakage from cells and after decay of the biomass. This leads to local nitrogen fertilization (Hübel and Wolf, 2000).

Another reason for the slow improvement of light conditions is the high resuspension of particulate matter caused by wind, boat traffic (Figure 6) and the absence of a rooted vegetation following the macrophyte die-off during the eutrophied period. Dense macrophyte beds normally prevent resuspension of organic matter by reducing turbulent water currents near the sea floor (Fonseca et al., 1982; Madsen et al., 2001). They also serve as effective sediment traps via interception of suspended sediment (Patterson, 1981; Barko and James, 1998). Especially in the Greifswalder Bodden with an average depths of 5.8 m, the resuspension of tripton is one of the major factors causing high attenuation (Figure 6). Therefore, reducing the resuspension would efficiently improve the water clarity.

Furthermore, rooted vegetation enhanced phosphate adsorption capacity in the rhizosphere and also insures low phosphate efflux. This would help to slow down the internal phosphate release into the estuary.

Those stabilizing mechanisms are hampered by the fact, that excessive nutrient loading in the past eliminated the macrophytes community below an effective threshold. The eutrophication hence, led to a dominance of algal competitors (Figure 10ab). Compared to phytoplankton macrophytes have a very high light demand and can not utilize the incident light with the same efficiency (Duarte, 1995). Their need of incoming light is usually about 3 – 20 times higher (Borum, 1983; Duarte, 1991; Sand-Jensen and Borum, 1991; Duarte, 1995; Hill, 1996; Sommer, 1998; Hemminga and Duarte, 2000; Kirk, 2000), the higher light requirements result in lower photosynthetic efficiency in comparison to phytoplankton (Duarte, 1995). The relationship between the light attenuation and the maximum depth distribution of macrophytes, as seen in the Greifswalder Bodden (Figures 3, 4) (Flindt et al., 1999; Cloern, 2001) is therefore typical for eutrophic systems.

Under present-day light conditions, the macrophytes community is unable to remigrate towards the deeper areas of the former extent. Hence, the strong decline in macrophytes support the resilience of the system.

## Some proposals to improve the ecosystem

Restoration of macrophytes in the Greifswalder Bodden should be the main purpose of biomanipulation (Shapiro and Wright, 1984) to shift the system back to its original clearwater, macrophyte dominated state (Comín et al., 1990). The main problem is the insoluble linkage between turbidity and the lack of rooted macrophytes. As long as the waters remain turbid, light is insufficient for the macrophytes to recover; and as long as the rooted macrophytes fail to recover resuspended organic matter and phytoplankton continue to cloud the benthos.

A loophole out of the dilemma is to attempt to directly introduce macrophytes in deeper areas of the Greifswalder Bodden (Comín et al., 1990). But transplants from common macrophytes / macroalgae in the estuary like *Furcellaria fastigiata*, *Potamogeton pectinatus* or *Zostera marina* would not be able to survive at greater depths than they occur today. Data about macrophytes environmental requirements as well as the regression between mean depth limits of macrophytes in the esturay and minimal Secchi disc (Figure 4) indicate that these macrophytes are more likely to survive replantation to pristine depths if turbidity declines by at least one third. The restoration of macrophytes would require a more detailed knowledge of the temporal variability in available irradiance throughout the year and the light demands for the dominant macrophyte groups of the Bodden. On the basis of these data a light requirement model could be used to estimate the average daily period of irradiance-saturated photosynthesis (Hsat) and the variability of the light environment. For example Zimmerman et al. (Zimmerman et al., 1991; Zimmerman et al., 1994) calculated the Hsat hours for the seagrass *Zostera marina* and showed, that survival of seagrass did not only depend on the total length of the Hsat period, but also on the degree of variability in irradiance and the ability to balance out periods with low irradiance through utilisation of carbohydrate stores (sugar and starch) (Zimmerman et al., 1991; Zimmerman et al., 1994; Zimmerman et al., 1995).

Another typical approach out would be to decrease phytoplankton densities in the Greifswalder Bodden, e.g. by reducing planktivorious fish (Comín et al., 1990; Jeppesen et al., 1990). Because planktivorous fish prey on zooplankton which in turn prey on phytoplankton, the resulting cascading effects may help keep phytoplankton in check (Scheffer, 1990; Van Donk et al., 1990a). Reducing fish populations has been successfully used to improve light condition and macrophyte cover in small lakes (Shapiro and Wright, 1984; Jeppesen et al., 1990; Van Donk et al., 1990b), where, the removal of predatory fish promoted the increase in the zooplankton Daphnia, which is a very strong grazer on phytoplankton. But it is doubtful if a comparable biomanipulation would be successful at the Bodden as well. Not only is the 115km$^2$ Bodden much larger, it is essentially open to the adjacent Baltic and river systems, making it difficult, if not impossible, to fence it off against migrating planktivorous fish. Moreover, the trophic cascade is different in the brackish Bodden in comparison to small lakes. The main grazers, copepods and mysids, do not exert the same strong grazing pressure on phytoplankton as Daphnia (Jeppesen et al., 1994). If copepods feed primarily on protozoa (Sommer and Stibor, 2002) even the opposite effect is possible because phytoplankton might be released from protozoan grazing. Therefore, reducing the planktivorous fish community does not seem to be a feasible option for the Greifswalder Bodden.

As the eutrophication of the Greifswalder Bodden was caused by the inflow of agricultural fertilizer remains and wastewater, another frequently cited approach is to minimize the nutrient discharge to restore the ecosystem to its pre-second world war state (Comín et al., 1990; Conley et al., 2000). However, in spite of much effort and money spent after 1985 to reduce phosphorus by 60% and nitrogen by 25% there are no clear signs of recovery. A further reduction of external nutrient loading would be even more difficult, because most of the nutrient discharge is due to diffuse sources, and in spite of all the costs a positive outcome would still not be certain. As Sheffer's model shows, nutrients have to be reduced to very low levels before the system is expected to revert to a low-turbidity state characterized by low phytoplankton concentrations, high biomass of submerged macrophytes and low resuspension of sediments, where the rooted vegetation is able to stabilize its own light climate (Van Dijk and Achterberg, 1992).

An effective way to support the recovery process would be the removal of suspended sediments. This has been successful in shallow lakes (Kleeberg and Kohl, 1999; Phillips et al., 1999) und would probably help to lower the concentration of available phosphate in the Greifswalder Bodden. In studies of (Van der Does et al., 1992; Van Liere and Gulati, 1992) sediment dredging let to a marked reduction of phosphate concentration in the upper sediment accompanied by a reduced phosphorus release into the water column and therefore a decline in phytoplankton concentration. However, lake restoration programs showed that sediment removal alone could not provide long-term changes without additional restoration measures (Ryding, 1982; Boers et al., 1992; Kleeberg and Kohl, 1999; Phillips et al., 1999) and are an expensive restoration tool. Treatment with aluminium-sulfate to bind the phosphorus from the sediment (nutrient inactivating) has been very successful in reducing the concentration of available phosphorus and improving in trophic state (Cooke et al., 1986). Comparing nutrient inactivating to sediment dredging the cost benefit of the latter is much better. No matter which method, it will be challenging to apply it to the huge size of the Greifswalder Bodden.

This work is one of the few studies about brackish ecosystems which demonstrates a phase shift due to eutrophication, it resiliences in a turbid state and the massive loss of macrophytes. The study illustrates occurring problems with internal loading and shows the difficulties for a restoration of the Greifswalder Bodden. It offers a better understanding of the behaviour of shifting shallow brackish systems due to eutrophication and to transfer the experiences to other cases. Further investigations are needed to identify the similarities and differences between brackish and freshwater systems. As the restoration of turbid eutrophied ecosystems is a difficult and long-winded process, prevention measures should be used for preserve clear-water systems.

## Acknowledgements

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# Gesamtdiskussion und Schlussfolgerung

In den letzten 100 Jahren kam es zu einem deutlichen Rückgang der Seegrasbestände im Greifswalder Bodden (Messner and von Oertzen, 1990; Munkes, 2005) und auch heutzutage zeigen die vorhandenen Seegraswiesen eine der geringsten Biomassen und Sprossdichten, die für *Zostera marina* im gesamten Ostseeraum berichtet wurden (Manuskript I). Sie liegen deutlich unter den mittleren Biomassenwerten von *Zostera marina* an Standorten gleicher geographischen Breite (Gründel, 1982; Boström et al., 2004). Dieses läßt auf sehr ungünstige Lebensbedingungen für *Zostera marina* im Greifswalder Bodden schließen.

Eine Reihe von Studien zeigt, dass es durch anthropogene Eutrophierung der Küstengewässer zu einem Rückgang der Seegrasbestände kommt, deren Ursache in der Beschattung der Seegräser durch das Überwachsen mit Epiphyten liegt (Hemminga and Duarte, 2000; Hughes et al., 2004). Der erhöhten Nährstoffeintrag fördert das Wachstum von Epiphyten, was experimentell in zahlreichen Studien belegt worden ist (Phillips et al., 1978; Heck et al., 2000; Hughes et al., 2004). Das hohe Nähstoffangebot führte hingegen im Greifswalder Bodden nicht zu einem starken Algenaufwuchs. Im Vergleich zu anderen *Zostera marina* Beständen wiesen die Epiphyten auf den Seegrasbättern im Greifswalder Bodden eine geringe Biomasse auf (Larkum et al., 1989; Hemminga and Duarte, 2000). Epiphyten bilden typischerweise 30-60% der gesamten Oberflächenbiomasse innerhalb von Seegraswiesen (Borum and Wium-Andersen, 1980; Larkum et al., 1989). In dieser Studie war der epiphytische Aufwuchs jedoch nur für 20% der Gesamtbiomasse der Seegraswiesen verantwortlich. Auffällig war der große Anteil an heterotrophen Organismen innerhalb des Aufwuches. Ein hohes heterotroph / autotroph Verhältnis wurde bereits in anderen eutrophen aquatischen Systemen gefunden (Gross et al., 2003), so dass die Dominanz von heterotrophen über autotrophen Aufwuchsorganismen durch die hohen Nährstoffbedingungen des Boddens verursacht sein könnten.

Ephemere Aufwuchsalgen spielen somit trotz der eutrophen Umweltbedingungen im Greifswalder Bodden eine sehr untergeordnete Rolle. Sie führen nur zu einer geringen Beschattung des Seegrases und können nicht für die geringen Biomassen und Sprossdichten von *Zostera marina* die Ursache sein.

Anzunehmen wäre, dass das Wachstum von Epiphyten durch einen starken Fraßdruck herbivorer Weidegänger eingeschränkt wird. Im Gegensatz zu einer Vielzahl von Studien in anderen Seegrasgebieten, in denen herbivore Weidegänger diese zentrale Kontrollfunktion für den epiphytischen Aufwuchs besitzen (Jernakoff et al., 1996; Jernakoff and Nielsen, 1997) ist es überraschend, dass in den untersuchten Seegrasbeständen herbivore Weidegänger vernachlässigbar sind. Epiphytische Weidegänger scheinen, aufgrund eines geringen Wachstums der Epiphyten und aufgrund ungenießbarer Nahrungressourcen (Blaualgen), nahrungslimitiert zu sein. Coleman (1994) zeigte, dass nur wenige Herbivore epiphytische Blaualgen fressen. Die im Greifswalder Bodden gefundenen Dichten an Weidegängern betrugen nur einen Bruchteil der Weidegängerdichten aus anderen Regionen der Ostsee (Gründel, 1982; Boström and Mattila, 1999; Bobsien and Munkes, 2004). Festzustellen ist, dass herbivore Weidegänger aufgrund ihrer sehr geringen Dichte, keinen signifikanten Fraßdruck und damit keine “top-down”

Kontrolle auf die Epiphyten des Seegrases ausüben.

Eine wichtige Ursache für den spärlichen Seegrasbestand im Greifswalder Bodden ist das Auftreten von Makroalgenmatten. Der Rückgang und die vollständige Zerstörung von Seegrasbeständen aufgrund von Makroalgenmatten sind weltweit beobachtet worden (Holmquist, 1997; McGlathery, 2001; Cummins et al., 2004). Diese Arbeit ist eine der ersten experimentellen Bestätigungen für den negativen Einfluss der Makroalgenmatten auf Seegräser. Überraschenderweise zeigten die Experimente, dass der wichtigste Einfluss der Makroalgen in der Beschattung von neuen Sprossen lag und zu einer vollständigen Unterdrückung der Sprossbildung führte. Lichtverfügbarkeit ist einer der wichtigsten Faktoren, die das Wachstum und das Überleben von Seegräsern in den gemäßigten Breiten bestimmen (Dennison and Alberte, 1982; Duarte, 1991; Duarte et al., 2002). Aufgrund der geringen Höhe der Algenmatte im Vergleich zu adulten Seegraspflanzen war jedoch weniger ein starker Effekt durch Beschattung, als durch die Bildung von toxischen Nährstoffkonzentationen oder Sauerstoffmangelerscheinungen zu erwarten. Durch die in Manuskript III beschriebenen Experimente, wird jedoch belegt, dass Lichtmangel der wichtigste negative Effekt war, der durch die Makroalgenmatten hervorgerufen wurde und das Wachstum neuer Sprosse vollständig unterband. Die Verteilung von gespeicherter Energie von adulten Seegraspflanzen über das Rhizom war nicht ausreichend, um das Überleben der beschatteten jungen Sprosse zu ermöglichen. Ein weiterer negativer Effekt der Makroalgenmatten auf das Seegras lag in einem Anstieg der Ammoniumkonzentration während des Zerfalls der Makroalgenmatten im Sommer. Dieses führte zu einem vorzeitigen Altern und dem Abriss der Blätter von *Zostera marina*. In Abhängigkeit von der Bedeckung durch Makroalgenmatten und ihrem Ausmaß können sie die Erneuerung von Seegraswiesen verhindern und damit zum dauerhaften Rückgang der Seegrasbestände führen.

Berücksichtigt man das weltweite Problem steigender Eutrophierung und den daraus resultierenden Anstieg des Wachstums von Makroalgen (Raffaelli et al., 1998), so ist mit dem Verlust von Seegrasbeständen aufgrund der Ausbreitung von Makroalgenmatten zunehmend zu rechnen.

In den vorangegangenen Untersuchungen (Manuskript I-III) wurde das Lichtangebot als der dominierende Faktor für das Wachstum und das Überleben von *Zostera marina* beobachtet. Im Greifswalder Bodden wird das Lichtklima vor allem durch die Phytoplankton- und Trübstoffkonzentrationen bestimmt. Die über Jahrzehnte andauernde anthropogene Überdüngung des Boddens führte zu einem drastischen Anstieg der Nährstoffkonzentrationen von Mitte bis Ende des 20. Jahrhunderts. Durch die hohen Nährstoffeinträge stiegen die Phytoplanktonkonzentrationen und Trübstoffe im Bodden stark an, was zu einer deutlichen Reduzierung der Lichtdurchdringung führte. Innerhalb weniger Jahrzehnte verschwand der überwiegende Teil der Makrophytenbestände (Messner and von Oertzen, 1990) und es vollzog sich ein “ecosystem-shift” (Scheffer et al., 2001; Scheffer and Carpenter, 2003) von einem Makrophytendominierten System hin zu einem Phytoplankton-dominierten System.

Die Analyse von Literaturdaten der letzten 100 Jahren zeigt, dass die Tiefenverbreitung der Makrophyten sich von 14 m auf 6 m reduzierte und dass für *Zostera marina* das tiefste Vorkommen von 5 m Wassertiefe auf 3-4 m abnahm (Munkes, 2005). Bei der großen Oberfläche und der geringen Tiefe des Boddens ergeben sich daraus mögliche

Verbreitungsabnahmen für *Zostera marina* von fast 40 % des Bestandes.

Seit den letzten 20 Jahren kam es zu einer deutlichen Reduzierung der Nährstoffeinträge in dem Bodden, die erwartete Verbesserung der Wasserqualität blieb jedoch aus, so dass es nicht zu einer Erholung der Makrophytenbestände kam. Anhand von Monitoringsdaten der letzten 25 Jahre, ließ sich eine deutliche Abnahme der Nährstoffkonzentrationen im Bodden feststellen, insbesondere bei der Stickstoffkonzentration. Doch es zeigte sich vor allem, dass die Phosphatkonzentrationen immer noch ganzjährig ausreichend hoch sind, um ein starkes Wachstum des Phytoplanktons über die gesamte Wachstumsperiode zu ermöglichen. Die Analyse von Chlorophyll a Daten ergab, dass das Wachstum des Phytoplanktons im Bodden nicht durch Nährstoffmangel limitiert ist, sondern vor allem durch die Wassertemperatur bestimmt wird. Einen Teil der anhaltend hohen Nährstoffkonzentrationen in der Wassersäule lässt sich durch eine interne Nährstoffbelastungen aus den über Jahrzehnten mit Nährstoffen angereicherten Sedimenten erklären (Schlungbaum, 1982, 1994; Hubert et al., 1995). Vor allem schlammige Sedimente weisen hohe Austrittsraten von Phosphat auf (Flindt et al., 1999), wie sie im Greifswalder Bodden häufig anzutreffen sind (Subklew, 1955).

Ein weiteres Problem stellt das anhaltende Wachstum der Cyanobakterien dar. Durch ihre Fähigkeit atmosphärischen Stickstoff zu binden, sind sie während der Sommermonate nicht Stickstoff limitiert. Darüber hinaus fördern sie das Wachstum anderen Phytoplanktons durch die Freisetzung eines kleinen Teils des von ihnen fixierten Stickstoffs. Monotoringdaten zeigten, dass Cyanobakterien während der Sommermonate bis zu $^2/_3$ des Phytoplanktonbestandes ausmachen.

Erschwerend kommt die ständige Resuspension von organischen Material hinzu, die durch den häufigen Wind und Bootsverkehr und das Fehlen von verwurzelten Makrophyten verursacht wird. Diese Mechanismen (Nährstofffreisetzung aus den Sedimenten, anhaltende Blaualgenblüten, starke Resuspension) führen zu einer Stabilisierung des bestehenden Zustandes (Resilience) und sie Verhindern eine schnelle Verbesserung des Lichtklimas und damit eine Ausdehnung der Makrophytenbestände im Greifswalder Bodden.

Restaurierungsmaßnahmen, die vor allem in Süßwasser-Ökosystemen angewandt werden, um den Erholungsprozess eines eutrophen Ökosystems zu beschleunigen (Kenworthy et al., 2000; Sondergaard et al., 2000; Carpenter, 2003; Lauridsen et al., 2003), sind aufgrund der enormen Größe und einer im Vergleich zu limnischen Ökosystemen stark abweichender trophischer Kaskade (Grazer) nicht durchführbar (Jeppesen et al., 1994).

Insgesamt lässt sich Schlussfolgern, dass im Greifswalder Bodden abiotische Faktoren (bottom-up), vor allem Licht-, Temperatur- und das Nährstoffangebot das Wachstum der Seegraswiesen bestimmen, während biologische Faktoren (top-down) wie Wegfraß durch Weidegänger oder Räuber eine deutlich untergeordnete Rolle spielen. Die Schlüsselfaktoren, die das lichtlimitierte Wachstum von *Zostera marina* bestimmen, sind hierbei die Konkurrenz von Makroalgen und Phytoplankton.

Im Greifswalder Bodden lässt sich daher ein von einer Vielzahl von Seegrasstandorten in der Ostsee abweichendes Beziehungsmuster finden:

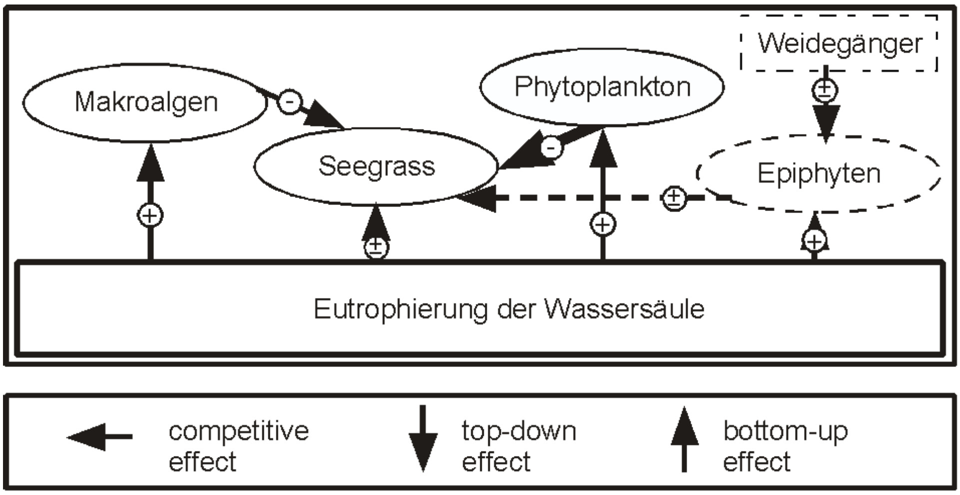


Abbildung 3: Darstellung des “top-down – bottom-up” Modells der Seegraswiesen im Greifswalder Bodden.

Die Arbeit zeigt deutlich die weit reichenden Veränderungen des Ökosystems, die durch anthropogene Eutrophierung hervorgerufen wurden. Eine Restaurierung derartig gestörter Ökosysteme erweist sich als äußerst schwierig. Sie erstrecken sich oftmals über große Zeiträume hinweg und sind nur zum Teil durchführbar. Daher ist es von besonderer Wichtigkeit Vorsichtsmaßnahmen zu ergreifen, um noch bestehende, weitgehend ungestörte Ökosysteme zu erhalten.

# Literaturverzeichnis

Abal, E. G., N. Loneragan, P. Bowen, C. J. Perry, J. W. Udy and W. C. Dennison, 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* (Aschers.) to light intensity. Journal of Experimental Marine Biology and Ecology **178**: 113-129.

Atkinson, M. J. and S. V. Smith, 1983. C:P:N ratios of benthic marine plants. Limnology & Oceanography **28**: 568-574.

Bachor, A., 1997. Nährstoffeinträge in die Vorpommerschen Boddengewässer. Bodden **5**: 25-44.

Backman, T. W. and D. C. Barilotti, 1976. Irradiance reduction: effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. Marine Biology **34**: 33-40.

Baden, S., M. Gullström, B. Lundén, L. Pihl and R. Rosenberg, 2003. Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. Ambio **32**: 374-377.

Barko, J. W. and W. F. James, 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. In: Jeppesen E., Sondergaard M., Sondergaard M. and Christoffersen K. (eds), The structuring role of submerged macrophytes in lakes, Springer, 197-214 pp.

Bartels, S. and U. Klüber, 1997. Die räumliche Verteilung des Makrophytenbenthos und seine Akkumulation von Nährstoffen und Schwermetallen. Teil 1: Erfassung des Bedeckungsgrades des Greifswalder Boddens mit submersen Makrophyten, Greifswald

Behrendt, H., 1999. Nährstoffbilanzierung der Flußgebiete Deutschlands: Forschungsbericht 29625515, Berlin

Behrendt, H., 2000. Nutrient emissions into river basins of Germany: research report 29625515, Institut für Gewässerökologie und Binnenfischerei im Forschungsverbund Berlin e. V., Berlin

BfN, German Federal Agency for Nature Conservation, Bundesamt für Naturschutz, Vilm.

Bianchi, T. S., E. Engelhaupt, P. Westman, T. Andrén, C. Rolff and R. Elmgren, 2000. Cyanobacterial blooms in the Baltic Sea: natural or human-induced? Limnology & Oceanography **45**: 716-726.

Bierzychudek, A. and I. Valiela, 1993. Effects of macroalgae, night and day, on ammonium profiles in Waquoit Bay. Biological Bulletin **185**: 330-331.

Birr, H.-D., 1997. Hydrographische Charakteristik und Umweltprobleme der mecklenburgisch-vorpommerschen Boddengewässer. Greifswalder Geographische Arbeiten **14**: 111-128.

Blümel, C. and M. Schubert, 2002. Entwicklung eines historischen Leitbildes für die submersen Makrophyten der Boddengewässer. Bodden **12**: 71-92.

Bobsien, I. and H. Brendelberger, Comparison of an enclosure drop trap and visual diving census technique to estimate fish populations in eelgrass habitats. Limnology & Oceanography Methods **in press**.

Bobsien, I. and B. Munkes, 2004. Seasonal variation of fish community and habitat structure in an eelgrass bed (*Zostera marina* L.) in the southern Baltic Sea. Rostocker Meeresbiologische Beiträge **12**: 39-59.

Boers, P., J. Van der Does, M. Quaak, J. Van der Vlugt and P. Walker, 1992. Fixation of phosphorus in lake sediments using iron(III)chloride: experiences, expectations. Hydrobiologia **233**: 211-212.

Böllmann, J., 2000. Kartierung der submersen Vegetation der Dänischen Wiek, Diplomarbeit. Biologie, Greifswald

Bologna, P. A. X., M. L. Fetzer, S. McDonnell and E. M. Moody, 2005. Assessing the potential benthic-pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. Journal of Experimental Marine Biology and Ecology **316**.

Borum, J.,1983. The quantitative role of macrophytes, epiphytes, and phytoplankton under different nutrient conditions in Roskilde Fjord, Denmark. Proceedings of the International Symposium on Aquatic Macrophytes, Nijmegen, pp. 35-40

Borum, J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. Marine Biology **87**: 211-218.

Borum, J., 1987. Dynamics of epiphyton on eelgrass (*Zostera marina* L.) leaves: relative roles of algal growth, herbivory, and substratum turnover. Limnology & Oceanography **32**: 986-992.

Borum, J., C. M. Duarte, D. Krause-Jensen and T. M. Greve, 2004. European seagrasses: an introduction to monitoring and management, The EU project: Monitoring and Managing of European Seagrasses (M&MS).

Borum, J. and S. Wium-Andersen, 1980. Biomass and production of epiphytes on eelgrass (*Zostera marina* L.) in the Oresund, Denmark. Ophelia, Supplement **1**: 57-64.

Bostrom, B., M. Jansson and C. Forsberg, 1982. Phosphorus release from lake sediments. Archiv für Hydrobiologie, Beiheft **18**: 5-59.

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

Boström, C., E. Bonsdorff, P. Kangas and A. Norkko, 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. Estuarine, Coastal and Shelf Science **55**: 795-804.

Boström, C. and J. Mattila, 1999. The relative importance of food and shelter for seagrass associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. Oecologia **120**: 162-170.

Boström, C., C. Roos and O. Rönnberg, 2004. Shoot morphometry and production dynamics of eelgrass in the northern Baltic Sea. Aquatic Botany **79**: 145-161.

Breuer, G. S., W., 1988. Changes in macroalgal vegetation of Kiel Bight (Western Baltic Sea) during the past 20 years. Kieler Meeresforschung, Sonderheft **6**: 241-255.

Brun, F. G., J. J. Vergara, G. Navarro, I. Hernández and J. L. Pérez-Lloréns, 2003. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**: 85-96.

Brush, M. J. and S. W. Nixon, 2002. Direct measurements of light attenuation by epiphytes on eelgrass *Zostera marina*. Marine Ecology Progress Series **238**: 73-79.

Burkholder, J. M., K. M. Mason and H. B. Glasgow, 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. Marine Ecology Progress Series **81**: 163-178.

Cardoso, P. G., M. A. Pardal, A. I. Lillebo, S. M. Ferreira, D. Raffaelli and J. C. Marques, 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. Journal of Experimental Marine Biology and Ecology **302**: 233-248.

Carpenter, S. R., 2003. Regime shifts in lake ecosystems: pattern and variation, International Ecology Institute, Oldendorf/Luhe.

Cederwall, H. and R. Elmgren, 1990. Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. Ambio **19**: 109-112.

Charpy-Roubaud, C. and S. A., 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. Marine Microbial Food Webs **4**.

Christiansen, C., H. Christoffersen, J. Dalsgaard and P. Nornberg, 1981. Coastal and near-shore changes correlated with die-back in eelgrass (*Zostera marina*, L.). Sedimentary Geology **28**: 163-173.

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

Coleman, V. and J. M. Burkholder, 1994. Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. Journal of Experimental Marine Biology and Ecology **179**: 29-48.

Comín, F. A., M. Menéndez and J. R. Lucena, 1990. Proposals for macrophyte restoration in eutrophic coastal lagoons. Hydrobiologia **200/201**: 427-436.

Conley, D. J., H. Kaas, F. Mohlenberg, E. Rasmussen and J. Windolf, 2000. Characteristics of Danish Estuaries. Estuaries **23**: 820-837.

Cooke, G. D., E. B. Welch, S. A. Peterson and P. R. Newroth, 1986. Lake and reservoir restoration, Butterworth, Stoneham, 1-392 pp.

Costanza, R., R. d`Arge, R. de Groot, S. Farber, G. M., B. Hannon, K. Limburg, S. Naeem, R. V. O`Neill, J. Paruelo, R. G. Raskin, P. Sutton and M. van den Belt, 1997. The value of the worlds ecosystem services and natural capital. Nature **387**: 253-260.

Council, F. C., 1991. Eutrophication of coastal waters. Coastal water quality management in the County of Funen, Denmark, 1976-1990. Legislation, nutrient loads and eutrophication effects-causes and trends, Funen County Council, Departement of Technology and Environment, Odense

Cummins, S. P., D. E. Roberts and K. D. Zimmermann, 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Marine Ecology Progress Series **266**: 77-87.

Dahlke, S., C. Wolff, L.-A. Meyer-Reil, H. W. Bange and M. O. Andreae, 1997. Mikrobieller N-, S- und C-Umsatz und die Emission von $N_20$ and $CH_4$ im Greifswalder Bodden und im westlichen Teil des Oderästuars., Greifswald

den Hartog, C., 1970. The sea-grasses of the world, 310 pp.

den Hartog, C., 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. Aquatic Botany **47**: 21-28.

den Hartog, C. and P. J. G. Polderman, 1975. Changes in the seagrass populations of the Dutch wadddenzee. Aquatic Botany **1**: 141-147.

Dennison, W. C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany **27**: 15-26.

Dennison, W. C. and R. S. Alberte, 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. Oecologia **55**: 137-144.

Dennison, W. C. and R. S. Alberte, 1985. Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). Marine Ecology Progress Series **25**: 51-61.

Drew, E. A., 1979. Physiological aspects of primary production in seagrasses. Aquatic Botany **7**: 139-150.

Duarte, C. M., 1990. Seagrass nutrient content. Marine Ecology Progress Series **67**: 201-207.

Duarte, C. M., 1991. Seagrass depth limits. Aquatic Botany **40**: 363-377.

Duarte, C. M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia **41**: 87-112.

Duarte, C. M., 1999. Seagrass ecology at the turn of the millennium: challenges for the new century. Aquatic Botany **65**: 7-20.

Duarte, C. M. and e. al., 2002. Analysis of coastal lagoon metabolism as a basis for management. Aquatic Ecology **36**: 3-19.

Duarte, C. M. and C. L. Chiscano, 1999. Seagrass biomass and production: a reassessment. Aquatic Botany **65**: 159-174.

Duarte, C. M. and H. Kirkmann, 2001. Methods for the measurement of seagrass abundance and depth distribution. In: Short F. T., Coles R. G. and Short C. A. (eds), Global seagrass research methods, Elsevier, Amsterdam, 141-154 pp.

Duarte, C. M., R. Martínez and C. Barrón, 2002. Biomass, production and rhizome growth near the northern limit of seagrass (*Zostera marina*) distribution. Aquatic Botany **72**: 183-189.

Elmgren, R., 2001. Understanding human impact on the Baltic ecosystem: changing views in recent decades. Ambio **30**: 222-231.

Feldner, J., 1976. Ökologische und produktionsbiologische Untersuchung am Seegras *Zostera marina* L. in der Kieler Bucht (westliche Ostsee), Dissertation. Institut für Meereskunde, Kiel

Flindt, M. R., M. A. Pardal, A. I. Lillebo, I. Martins and J. C. Marques, 1999. Nutrient cycling and plant dynamics in estuaries: a brief review. Acta Oecologica **20**: 237-248.

Fonseca, M. S., J. S. Fisher, J. C. Zieman and G. W. Thayer, 1982. Influence of the seagrass, *Zostera marina* L., on current flow. Estuarine, Coastal and Shelf Science **15**: 351-364.

Fourqurean, J. W., T. O. Moore, B. Fry and J. T. Hollibaugh, 1997. Spatial and temporal variation in C:N:P ratios, $\partial^{15}$N, and $\partial^{13}$C of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. Marine Ecology Progress Series **157**: 147-157.

Frankovich, T. A. and J. W. Fourqurean, 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. Marine Ecology Progress Series **159**: 37-50.

Frederiksen, M., D. Krause-Jensen, M. Holmer and J. S. Laursen, 2004. Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. Aquatic Botany **78**: 167-181.

Geisel, T., 1995. Pflanzensoziologische Untersuchung am Makrophytobenthos des Greifswalder Boddens, Diplomarbeit. Sektion Biologie, Rostock

Geisel, T. and U. Messner, 1989. Flora & Fauna des Bodens im Greifswalder Bodden, Der Greifswalder Bodden, Schriftenreihe des Meeresmuseums Stralsund, Stralsund, 44-51 pp.

Giesen, W. B. J. T., M. M. van Katwijk and C. den Hartog, 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquatic Botany **37**: 71-85.

Green, E. P. and F. T. Short, 2003. Wold Atlas of Seagrasses, California University Press, Berkeley, 310 pp.

Grontved, L., 1958. Underwater macrovegetation in shallow coastal waters. Journal du Conseil / Conseil Permanent International pour l'Exploration de la Mer **24**: 32-42.

Gross, E. M., C. Feldbaum and A. Graf, 2003. Epiphyte biomass and elemental composition on submersed macrophytes in shallow eutrophic lakes. Hydrobiologia **506-509**: 559-565.

Gründel, R., 1982. Ökosystem Seegraswiese - qualitative und quantitative Untersuchungen über Struktur und Funktion einer Zostera-Wiese vor Surendorf (Kieler Bucht, Westliche Ostsee). Reports Sonderforschungsbereich 95, Wechselwirkungen Meer - Meeresboden. Zoologisches Institut der Christian Albrecht Universität, Kiel

Harrison, P. G. and C. D. Durance, 1985. Reductions in photosynthetic carbon uptake in epiphytic diatoms by water-soluble extracts of leaves of *Zostera marina*. Marine Biology **90**: 117-119.

Hauxwell, J., J. Cebrián, C. Furlong and I. Valiela, 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology **82**: 1007-1022.

Hays, C. G., 2005. Effect of nutrient availability, grazer assemblage and seagrass source population on the interaction between *Thalassia testudinum* (turtle grass) and its algal epiphytes. Journal of Experimental Marine Biology and Ecology **314**: 53-68.

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

Hemminga, M. A. and C. M. Duarte, 2000. Seagrass ecology, Cambridge University Press, Cambridge, 1-298 pp.

Hill, W. R., 1996. Effects of light. In: Stevenson R. J., Bothwell M. L. and Lowe R. L. (eds), Algal Ecology, Academic Press, 121-148 pp.

Hintze, U., 1988. Wasserpflanzengesellschaften im südöstlichen Küstenbereich des Greifswalder Boddens, des Freesendorfer Sees und der Ost- und Südküste der Insel Struck, Diplomarbeit. Sektion Biologie, Greifswald

Holmquist, J. G., 1997. Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. Marine Ecology Progress Series **158**: 121-130.

Hootsmans, M. J. M. and J. E. Vermaat, 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. Aquatic Botany **22**.

Howard, R. K., 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. Aquatic Botany **14**: 91-97.

Howard, R. K. and F. T. Short, 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. Aquatic Botany **24**: 287-302.

Hübel, H. and T. Wolf, 2000. Stickstoff-Fixierung in den Darß-Zingster Boddengewässern, Die Darß-Zingster Bodden, Schriftenreihe des Deutschen Meeresmuseums, Stralsund, 46-52 pp.

Hübel, H.-J., U. Vietinghoff, M.-L. Hubert, S. Rambow-Bartels, H. Westphal and B. Lenk, 1995. Ergebnisse des ökologischen Monitorings Greifswalder Bodden September 1993 bis März 1995. Rostocker Meeresbiologische Beiträge **3**: 5-67.

Hubert, M.-L., A. Kob, P. Eschholz and U. Vietinghoff, 1997. Biomassemodellierung und Wassertransport am Beispiel des Greifswalder Boddens. GOAP: Greifswalder Bodden und Oderästuar - Austauschprozesse, Greifswalder Geographische Arbeiten, Greifswald

Hubert, M.-L., A. Kob and U. Vietinghoff, 1995. Ergebnisse der Modellierung des Ökosystems Greifswalder Bodden. Rostocker Meeresbiologische Beiträge **3**: 123-145.

Hughes, A. R., K. J. Bando, L. F. Rodriguez and S. L. Williams, 2004. Relative effects of grazers and nutrients on seagrasses: A meta-analysis approach. Marine Ecology Progress Series **282**: 87-99.

Irlandi, E. A., B. A. Orlando and P. D. Biber, 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. Marine Ecology Progress Series **279**: 81-91.

Jackson, E. L., A. A. Rowden, M. J. Attrill, S. J. Bossey and M. B. Jones, 2001. The importance of seagrass beds as a habitat for fishery species. Oceanography and Marine Biology: an Annual Review **39**: 269-303.

Jacobs, R. P. W. M., 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquatic Botany **7**: 151-172.

Jeffrey, S. W. and G. F. Humphrey, 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen **167**: 191-194.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Sondergaard, E. Mortensen, O. Sortkjaer and K. Olrik, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia **200/201**: 219-227.

Jeppesen, E., M. Sondergaard, E. Kanstrup, B. Petersen, R. B. Eriksen, M. Hammershoj, E. Mortensen, J. P. Jensen and A. Have, 1994. Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia **275/276**: 15-30.

Jernakoff, P., A. Brearley and J. Nielsen, 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanography and Marine Biology: an Annual Review **24**: 109-162.

Jernakoff, P. and J. Nielsen, 1997. The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aquatic Botany **56**: 183-202.

Kemp, W. M., W. R. Boynton, R. R. Twilley, J. C. Stevenson and J. C. Means, 1983. The decline of submerged vascular plants in Chesapeake Bay: a summary of results concerning possible causes. Marine Technology Society Journal **17**: 78-89.

Kendrick, G. A. and P. Lavery, 2001. Assessing biomass, assemblage structure and productivity of algal epiphytes on seagrasses. In: Short F. T., Coles R. G. and Short C. A. (eds), Global seagrass research methods, Elsevier, Amsterdam, 199-222 pp.

Kentula, M. E. and T. H. DeWitt, 2003. Abundance of seagrass (*Zostera marina* L. ) and macroalgae in relation to the salinity-temperature gradient in Yaquina Bay, Oregon, USA. Estuaries **26**: 1130-1141.

Kentula, M. E. and C. D. McIntire, 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. Estuaries **9**: 188-199.

Kenworthy, W. J., M. S. Fonseca, P. E. Whitfield and H. K., 2000. Experimental manipulation and analysis of recovery dynamics in physically disturbed tropical seagrass communities of North America: implications for restoration and management. Biologia Marina Mediterranea **7**: 385-388.

Kinne, O., 1971. Salinity: Animals - Invertebrates. Marine Ecology **1**: 683-1244.

Kirk, J. T. O., 2000. Light and Photosynthesis in Aquatic Ecosystems, Cambridge University Press, Cambridge, 525 pp.

Kleeberg, A. and J.-G. Kohl, 1999. Assessment of the long-term effectiveness of sediment dredging to reduce benthic phosphorus release in shallow Lake Müggelsee (Germany). Hydrobiologia **394**: 153-161.

Kobarg, N., 1993. Untersuchungen über Faktoren, die die Verbreitung von Seegras (*Zostera marina* L.) kontrollieren, Diplomarbeit. Institut für Meereskunde, Kiel

Koch, E. W. and S. U. Beer, 1996. Tides, light and the distribution of *Zostera marina* in Long Island Sound, USA. Aquatic Botany **53**: 97-107.

Krause-Jensen, D., P. B. Christensen and S. Rysgaard, 1999. Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. Estuaries **22**: 31-38.

Krause-Jensen, D., K. McGlathery, S. Rysgaard and P. B. Christensen, 1996. Production within dense mats of the filamentous macroalgae *Chaetomorpha linum* in relation to light and nutrient availability. Marine Ecology Progress Series **134**: 207-216.

Kruk-Dowgiallo, L., 1991. Long term changes in the structure of underwater meadows of the Puck Lagoon. Acta Ichthyologica et Piscatoria (Suppl.) **22**: 77-84.

Küster, A., 1997. Ökophysiologische Charakterisierung der Characeenbestände an der Küste Mecklenburg Vorpommerns., Diplomarbeit. Mathematisch-Naturwissenschaftliche Fakultät, Rostock

Lampe, R. and H. Meyer, 1995. Sedimentqualität und hydrographische Bedingungen - Ein Vergleich verschiedener Boddengewässer. Bodden **2**: 7-26.

Larkum, A. W. D., A. J. McComb and S. A. Shepherd, 1989. Biology of seagrasses, Elsevier, 842 pp.

Lauridsen, T. L., J. P. Jensen, E. Jeppesen and M. Sondergaard, 2003. Response of submerged macrophytes in Danish lakes to nutrient loading reductions and biomanipulation. Hydrobiologia **506-509**: 641-649.

Lin, H.-J., S. W. Nixon, D. I. Taylor, S. L. Granger and B. A. Buckley, 1996. Responses of epiphytes on eelgrass, Zostera marina L., to separate and combined nitrogen and phosphorus enrichment. Aquatic Botany **52**: 243-258.

LUNG, 1998. Zustand der Gewässergüte von Fließ-, Stand- und Küstengewässern und der Grundwasserbeschaffenheit in Mecklenburg-Vorpommern, State Agency for the Environment, Nature Conservation and Geologie of Mecklenburg-Western Pommerian, Schwerin

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch and D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia **444**: 71-84.

Marsden, M. W., 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshwater Biology **21**: 139-162.

Marsh, J. A., W. C. Dennison and S. A. Randall, 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). Journal of Experimental Marine Biology and Ecology **101**: 257-267.

Mazzella, L. and R. S. Alberte, 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. Journal of Experimental Marine Biology and Ecology **100**: 165-180.

McGlathery, K. J., 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. Journal of Phycology **37**: 453-456.

McGlathery, K. J., D. Krause-Jensen, S. Rysgaard and P. B. Christensen, 1997. Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. Aquatic Botany **59**: 99-115.

McRoy, P. C. and C. Helfferich, 1977. Seagrass ecosystems.

Messner, U. and J.-A. von Oertzen, 1990. Recent changes in the phytal zone of Greifswald Bay. Limnologica **20**: 183-186.

Meyer-Reil, L.-A. and M. Köster, 2000. Eutrophication of marine waters: effects on benthic microbial communities. Marine Pollution Bulletin **41**: 255-263.

Moore, K. A., R. L. Wetzel and R. J. Orth, 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. Journal of Experimental Marine Biology and Ecology **215**: 115-134.

Munkes,2004. Impact of macroalgae canopies on growth and survival of eelgrass in an eutrophic estuary Proceedings of Seagrass. James Cook University, Townsville, Australia, pp. 64

Munkes, B., 2005. Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. Aquatic Science **67**, 3: 372-381.

Neckles, H. A., E. T. Koepfler, L. W. Haas, R. L. Wetzel and R. J. Orth, 1994. Dynamics of epiphytic photoautotrophs and heterotrophs in *Zostera marina* (Eelgrass) microcosms: responses to nutrient enrichment and grazing. Estuaries **17**: 597-605.

Neckles, H. A., R. L. Wetzel and R. J. Orth, 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. Oecologia **93**: 285-295.

Nelson, T. A. and A. Lee, 2001. A manipulative experiment demonstrates that blooms of the macroalgae *Ulvaria obscura* can reduce eelgrass shoot density. Aquatic Botany **71**: 149-154.

Olesen, B., 1999. Reproduction in Danish eelgrass (*Zostera marina* L.) stands: size-dependence and biomass partitioning. Aquatic Botany **65**: 209-219.

Olesen, B. and K. Sand-Jensen, 1993. Seasonal acclimatization of eelgrass *Zostera marina* growth to light. Marine Ecology Progress Series **94**: 91-99.

Olesen, B. and K. Sand-Jensen, 1994a. Biomass-density patterns in the temperate seagrass *Zostera marina*. Marine Ecology Progress Series **109**: 283-291.

Olesen, B. and K. Sand-Jensen, 1994b. Patch dynamics of eelgrass *Zostera marina*. Marine Ecology Progress Series **106**: 147-156.

Onuf, C. P., 1996. Seagrass responses to long-term light reduction by brown tide in upper Laguna Madre, Texas: distribution and biomass patterns. Marine Ecology Progress Series **138**: 219-231.

Orth, R. J., K. L. Heck and J. van Montfrans, 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**: 339-350.

Orth, R. J. and J. Van Montfrans, 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquatic Botany **18**: 43-69.

Patterson, E. M., 1981. Marine macrophytes as a global carbon sink. Science **211**: 838-840.

Pedersen, M. F. and J. Borum, 1993. An annual nitrogen budget for a seagrass *Zostera marina* population. Marine Ecology Progress Series **101**: 169-177.

Peierls, B., N. Caraco, M. Pace and C. J., 1991. Human influence on river nitrogen. Nature **350**: 386-387.

Penhale, P. A., 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. Journal of Experimental Marine Biology and Ecology **26**: 211-224.

Phillips, G., A. Bramwell, J. Pitt, J. Stansfield and M. Perrow, 1999. Practical application of 25 years research into the management of shallow lakes. Hydrobiologia **395/396**: 61-76.

Phillips, G., R. Jackson, C. Bennett and A. Chilvers, 1994. The importance of sediment phosphorus release in the restoration of very shallow lakes (The Norfolk Broads, England) and implications for biomanipulation. Hydrobiologia **275/276**: 445-456.

Phillips, G. L., D. Eminson and B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquatic Botany **4**: 103-126.

Plus, M., J.-M. Deslous-Paoli and F. Dagault, 2003. Seagrass (*Zostera marina* L. ) bed recolonisation after anoxia-induced full mortality. Aquatic Botany **77**: 121-134.

Raffaelli, D. and S. Hawkins, 1996. Intertidal Ecology, Chapman & Hall, London (UK), 372 pp.

Raffaelli, D. G., J. A. Raven and L. J. Poole, 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an Annual Review **36**: 97-125.

Rambow, S., 1994. Untersuchungen zur quantitativen Erfassung des Bedeckungsgrades von submersen Makrophyten im nordöstlichen Greifswalder Bodden mit Hilfe der Unterwasservideographie und der Luftbildauswertung., Diplomarbeit. Mathematisch-Naturwissenschaftliche Fakultät, Rostock

Reinke, J., 1901. Untersuchungen über den Pflanzenbewuchs in der östlichen Ostsee. Wissenschaftliche Meeresuntersuchungen **5**: 1-6.

Reise, K., E. Heere and K. Sturm, 1989. Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. Helgoländer Meeresuntersuchungen **43**: 417-433.

Reusch, T. B. H., A. R. O. Chapman and J. P. Gröger, 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growht through biodeposition. Marine Ecology Progress Series **108**: 265-282.

Reusch, T. B. H. and S. L. Williams, 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**: 428-441.

Rumohr, H., 1993. Erfahrungen und Ergebnisse aus 7 Jahren Benthosmonitoring in der südlichen Ostsee. Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel **240**.

Ryding, S.-O.-. 1982. Lake Trehörningen restoration project. Changes in water quality after sediment dredging. Hydrobiologia **92**: 549-558.

Sand-Jensen, K., 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. Ophelia **14**: 185-201.

Sand-Jensen, K., 1977. Effect of epiphytes on eelgrass photosynthesis. Aquatic Botany **3**: 55-63.

Sand-Jensen, K. and J. Borum, 1991. Interactions among phytoplankton, peripyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany **41**: 137-175.

Sand-Jensen, K., N. P. Revsbech and B. B. Jorgensen, 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. Marine Biology **89**: 55-62.

Scabell, J., 1988. Der Rügensche Frühjahrshering - Das Laichgeschehen. Dissertation, Fakultät für Biologie, Rostock

Schanz, A., P. Polte and H. Asmus, 2002. Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. Marine Biology.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia **200/201**: 475-486.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke and B. Walker, 2001. Catastrophic shifts in ecosystems. Nature **413**: 591-596.

Scheffer, M. and S. R. Carpenter, 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution **18**: 648-656.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss and E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Tree **8**: 275-279.

Schlungbaum, G., 1982. Sedimentchemische Untersuchungen in Küstengewässern der DDR. Teil 11: Phosphatsorptionsgleichgewichte zwischen Sediment und Wasser in flachen eutrophen Küstengewässern. Acta hydrochimica et hydrobiologica **10**: 135-152.

Schlungbaum, G., 1994. Das Eutrophierungsproblem der Bodden und Haffe. Bodden **1**: 13-29.

Schmidt, I., 1990a. Beziehungen zwischen Phytoplankton und Nährstoffverhältnissen im südlichen Greifswalder Bodden. Wissenschaftliche Zeitschrift der Universität Rostock, Mathematisch-Naturwissenschaftliche Reihe **39**: 35-38.

Schmidt, I., 1990b. Beziehungen zwischen Wassertemperatur und Phytoplankton im südlichen Greifswalder Bodden. Acta hydrophysica **34**: 73.

Schramm, W. and P. H. Nienhuis, 1996. Marine benthic vegetation - Recent changes and the effects of eutrophication, Springer, Berlin, 470 pp.

Seifert, R., 1938. Die Bodenfauna des Greifswalder Boddens. Ein Beitrag zur Ökologie der Brackwasserfauna. Zeitschrift für Morphologie und Ökologie der Tiere **34**: 221-271.

Sfriso, A. and P. Francesco Ghetti, 1998. Seasonal variation in biomass, morphometric parameters and production of seagrasses in the lagoon of Venice. Aquatic Botany **61**: 207-223.

Shapiro, J. and D. I. Wright, 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biology **14**: 371-383.

Shepherd, S. A., A. J. McComb, D. A. Bulthuis, V. Neverauskas, D. A. Steffensen and R. West, 1989. Decline of seagrasses. In: Larkum A. W. D., McComb A. J. and Shepherd S. A. (eds), Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, 346-393 pp.

Short, F. T. and D. M. Burdick, 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnology & Oceanography **40**: 740-749.

Short, F. T. and R. G. Coles, 2001. Global seagrass research methods, Elsevier Science, Amsterdam, 1-471 pp.

Silberstein, K., A. W. Chiffings and A. J. McComb, 1986. The loss of seagrass in Cockburn Sound, western Australia. III. The effect of epiphytes on productivity of *Posidonis Australis* Hook. F. Aquatic Botany **24**: 355-371.

Smith, S. V., 1981. Marine macrophytes as a global carbon sink. Science **211**: 838-840.

Sommer, U., 1998. Biologische Meereskunde, Springer, Berlin, 475 pp.

Sommer, U. and H. Stibor, 2002. Copepoda – Cladocera – Tunicata: The role of three major mesozooplankton groups in pelagic food webs. Ecological Research **17**: 161-174.

Sondergaard, M., E. Jeppesen, J. P. Jensen and T. Lauridsen, 2000. Lake restoration in Denmark. Lake & Reservoirs: Research and Management **5**: 151-159.

Stigge, H.-J., 1989. Der Wasserkörper Bodden und seine Hydrodynamik. Der Greifswalder Bodden, Schriftenreihe des Meeresmuseums Stralsund, Stralsund, 10-14 pp.

Strickland, J. D. H. and T. R. Parsons, 1972. A practical handbook of seawater analysis, Bulletin Fisheries Research Board of Canada, Ottawa.

Subklew, H. J., 1955. Der Greifswalder Bodden, fischereibiologisch und fischereiwirtschaftlich betrachtet. Zeitschrift für Fischerei & deren Hilfswissenschaften **4**: 545-588.

Subklew, H. J., 1987. Das Angespül des Greifswalder Boddens. Acta hydrochimica et hydrobiologica **15**: 65-78.

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

Thom, R. M., 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. Botanica Marina **33**: 497-510.

Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson and W. R. Boynton, 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. Marine Ecology Progress Series **23**: 179-191.

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

Van der Does, J., P. Verstraelen, P. Boers, J. Van Roestel, R. Roijackers and G. Moser, 1992. Lake restoration with and without dredging of phosphorus-enriched upper sediment layers. Hydrobiologia **223**: 197-210.

Van Dijk, G. M. and E. P. Achterberg, 1992. Light climate in the water column of a shallow eutrophic lake (Lake Veluwe) in The Netherlands. Archiv für Hydrobiologie, Beiheft **125**: 257-278.

Van Donk, E., M. P. Grimm, R. D. Gulati, P. G. M. Heuts, W. A. de Kloet and L. van Liere, 1990a. First attempt to apply whole-lake food-web manipulation on a large scale in the Netherlands. Hydrobiologia **200/201**: 291-301.

Van Donk, E., M. P. Grimm, R. D. Gulati and J. P. G. Klein Breteler, 1990b. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. Hydrobiologia **200/201**: 275-289.

van Katwijk, M. M., G. H. W. Schmitz, A. P. Gasseling and P. H. van Avesaath, 1999. Efffects of salinity and nutrient load and their interaction on *Zostera marina*. Marine Ecology Progress Series **190**: 155-165.

van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz and J. G. M. Roelofs, 1997. Ammonium toxicity in eelgrass Zostera marina. Marine Ecology Progress Series **157**: 159-173.

Van Liere, L. and R. D. Gulati, 1992. Restoration and recovery of shallow eutrophic lake ecosystems in the Netherlands: epiloque. Hydrobiologia **233**: 283-287.

van Montfrans, J., R. Wetzel, L. and R. Orth, 1984. Epiphyte-grazer relationships in seagrass meadows: consequences for seagrass growth and production. Estuaries **7**: 289-309.

Vietinghoff, U., 1995. Die Forschung begleitendes Monitoring Greifswalder Bodden : Abschlußbericht, Universität Rostock / Fachbereich Biologie, Rostock

Vogt, H. and W. Schramm, 1991. Conspicious decline of *Fucus* in Kiel Bay (Western Baltic): what are the causes? Marine Ecology Progress Series **69**: 189-194.

Wetzel, R. and H. Neckles, 1986. A model of *Zostera marina* L. photosynthesis and growth: Simulated effects of selected physical-chemical variables and biological interactions. Aquatic Botany **26**: 307-323.

Williams, S. L. and M. H. Ruckelshaus, 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology **74**: 904-918.

Winfried, S. and P. H. Nienhuis, 1996. Marine benthic vegetation, Springer, 470 pp.

Wium-Andersen, S. and J. Borum, 1984. Biomass variation and autotrophic production of an epiphyte-macrohyte community in a coastal Danish area: 1. Eelgrass (*Zostera marina* L.) biomass and net production. Ophelia **23**: 33-46.

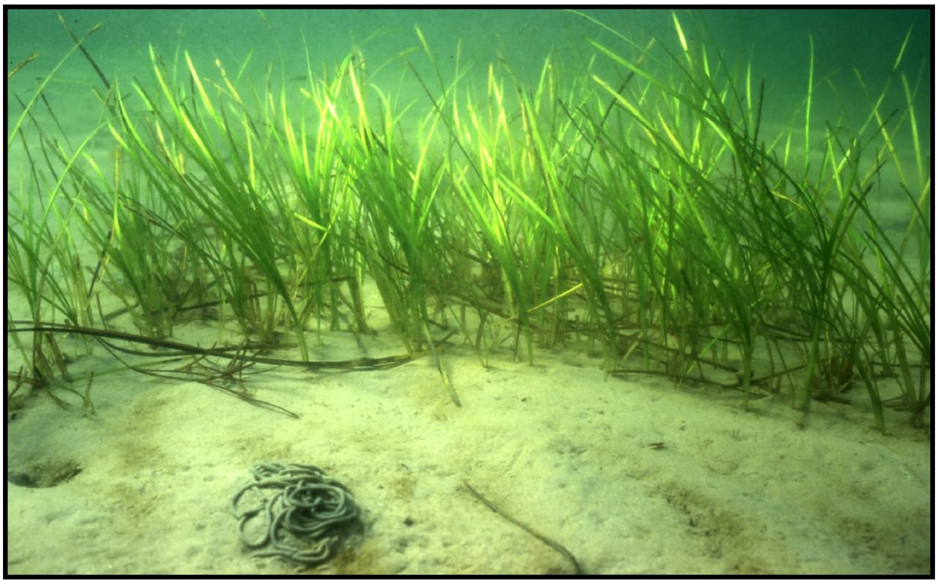
Wolken, K., 1994. Grazing in Seegraswiesen, Diplomarbeit. Institut für Meereskunde, Kiel

Zimmerman, R. C., A. Cabello-Pasini and R. S. Alberte, 1994. Modeling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. Marine

Ecology Progress Series **114**: 185-196.

Zimmerman, R. C., J. L. Reguzzoni and R. S. U. Alberte, 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: Role of light availability on metabolism, growth and survival. Aquatic Botany **51**: 67-86.

Zimmerman, R. C., J. L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn and R. S. Alberte, 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. Aquatic Botany **39**: 353-366.



# Manuskript V

Appendix – zugehörige Veröffentlichungen

## Manuskript V:

# Seasonal variation of fish community and habitat structure in an eelgrass bed (*Zostera marina* L.) in the southern Baltic Sea

Rostocker Meeresbiologische Beiträge, Bd. 12 (2004), S. 39-59

Ivo Bobsien; Britta Munkes

## Abstract

A *Zostera marina* eelgrass bed in Greifswalder Bodden and its associated fish community were quantitatively investigated in monthly intervals from May to December 2002 to determine seasonal aspects of their community structure. 10 fish species were detected, 5 of them were dominant in the catches. Abundances and biomasses of fish and eelgrass indicated strong variations and showed seasonal characteristics with maximum values in spring and summer. Correlations between abundance and biomass of fish and temperature were significant, when the three spined stickleback was not taken into account, which reached highest abundance during spawning season in May. A correlation between eelgrass biomass and water temperature was also found. But there was no evidence of correlation between eelgrass biomass and fish biomass. Water temperature may represent an important factor structuring eelgrass habitat and associated fish community.

# Manuskript VI

# Manuskript VI:

## Impact of macroalgae canopies on growth and survival of eelgrass in an eutrophic estuary

Oral presentation at the International Seagrass Symposium; 24-1. September 2004 in Townsville, Australia, (Munkes, 2004)

## Abstract

The proliferation of ephemeral floating macroalgae is a common phenomenon of eutrophic estuaries. In the Greifswalder Bodden estuary by the island of Vilm, Germany the accumulation of drift algae is usually restricted to calm areas. But in 2003 red algal mat covered the whole area up to the seagrass meadows on the current exposed east-side of the island.

We tested the effect of dense macroalgal canopies on shoot density, biomass, leaf C:N content and survival of *Zostera marina* employing macroalgae enclosure- exclosure experiments in the Bodden from May to July 2003.

Experimental units were 0.8 X 0.8 m plots of eelgrass fenced with 40 cm high plastic netting. Algae were added to the caged plots, equivalent to the naturally occurring bloom (1750 kg wet wt $m^{-2}$). After 7 weeks the stands of brown and red algae started to decompose. The top layer of the sediment remained oxygenated, despite of the macroalgal cover.

Regarding the eelgrass, the above ground biomass and shoot density decreased strongly by 22% respectively in plots with algal cover compared to plots without algal canopies.

We found that the decrease in biomass was caused by a decrease in shoot density and leaf growth. In seagrass shoots, covered with macroalgal canopies leaf growth was reduced by 19%. The ammonia content in the interstitial water increased up to 400%. While the most determining factor was light reduction due to macroalgal cover.

Thus, we conclude that natural blooms of macroalgae observed at the study site are a likely reason for the low biomass and shoot density of seagrass meadows.

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