

THE MICROBIAL FOOD WEB OF THE COASTAL SOUTHERN
BALTIC SEA AS INFLUENCED BY WIND-INDUCED
SEDIMENT RESUSPENSION

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TOBIAS GARSTECKI
aus Magdeburg

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Berichterstatter: Prof. Dr. STEPHEN A. WICKHAM

Prof. Dr. HARTMUT ARNDT

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Inhaltsverzeichnis

Angabe von verwendeten Fremddaten	5
Abkürzungsverzeichnis	6
1. Einleitung	7
1.1. Begründung der Fragestellung	7
1.2. Herangehensweise	11
2. A comparison of benthic and planktonic heterotrophic protistan community structure in shallow inlets of the Southern Baltic Sea	13
2.1. Summary	13
2.2. Introduction	14
2.3. Materials and Methods	15
2.3.1. Study sites	15
2.3.2. Sampling design	17
2.3.3. Sampling procedure	18
2.3.4. Identification and enumeration of protists	19
2.3.5. Statistical analysis	20
2.4. Results	20
2.4.1. General trends	20
2.4.2. Distribution and taxonomic composition of ciliates	24
2.4.3. Distribution and taxonomic composition of rhizopods	30
2.4.4. Distribution and taxonomic composition of flagellates	30
2.4.5. Relationships between layers and between pelagic protists, seston, and chlorophyll a concentrations	31
2.5. Discussion	32
2.5.1. Quantitative importance of heterotrophic protists	32
2.5.2. General trends of heterotrophic protistan community structure	33
2.5.3. Contribution of taxonomic groups	34
2.5.4. Methodology	37
2.5.5. Significance of benthic-pelagic coupling	37

3. Seasonal abundances and community structure of benthic rhizopods in a shallow lagoon of the Southern Baltic Sea	39
3.1. Summary	39
3.2. Introduction	39
3.3. Materials and Methods	41
3.3.1. Study area	41
3.3.2. Sampling	42
3.3.3. Determination of the taxonomic composition of the rhizopod community	42
3.3.4. Enumeration of rhizopods	43
3.3.5. Methodological investigations	44
3.4. Results	45
3.4.1. Abundance and biovolume totals at station Bäk	45
3.4.2. Taxonomic composition of the rhizopod fauna	46
3.4.3. Contribution of taxonomic groups	46
3.4.4. Applicability of the liquid aliquot method	50
3.5. Discussion	52
3.5.1. Quantitative importance and distribution of rhizopods	52
3.5.2. Rhizopod community structure	53
3.5.3. Methodology	56
4. Effects of experimental sediment resuspension on a coastal planktonic microbial food web	58
4.1. Summary	58
4.2. Introduction	58
4.3. Materials and Methods	60
4.3.1. Study site	60
4.3.2. Experimental design	60
4.3.3. Abiotic parameters and chlorophyll <i>a</i>	61
4.3.4. Microbial community structure	62
4.3.5. Statistical analysis	62
4.4. Results	63
4.4.1. Abiotic parameters	63
4.4.2. Autotrophs	65
4.4.3. Bacteria and heterotrophic protists	68
4.4.4. Microbial food web interactions	71

4.5. Discussion	72
4.5.1. Effectiveness of experimental design	72
4.5.2. Direct transport effects of resuspension	72
4.5.3. Indirect effects of resuspension on autotrophic organisms ..	74
4.5.4. Indirect effects of resuspension on heterotrophic organisms	76
4.5.5. Significance of resuspension for the microbial food web	
of the study area	77
5. The response of a benthic rhizopod community to experimental	
sediment disturbance does not support the intermediate disturbance	
hypothesis	79
5.1. Summary	79
5.2. Introduction	79
5.3. Materials and Methods	81
5.3.1. Reference site	81
5.3.2. Experimental design	82
5.3.3. Sampling and sample analysis	83
5.4. Results	84
5.4.1. Intensity experiment	84
5.4.2. Frequency experiment	88
5.5. Discussion	88
6. Effects of resuspension and mixing on population dynamics	
and trophic interactions in a model benthic microbial food web	92
6.1. Summary	92
6.2. Introduction	93
6.3. Materials and Methods	93
6.3.1. Model community	93
6.3.2. Experimental design	95
6.3.3. Inoculation and incubation	96
6.3.4. Sampling and sample analysis	97
6.3.5. Statistical analysis	98

6.4. Results	98
6.4.1. Whole-community experiment	98
6.4.2. Community subset experiment	100
6.4.3. Particulate enrichment experiment	103
6.5. Discussion	107
6.5.1. Food web structure	107
6.5.2. Resuspension effects on <i>Amphora coffeaeformis</i> and bacteria	108
6.5.3. Resuspension effects on protistan population dynamics ...	109
6.5.4. Significance under field conditions and possible mechanisms	111
7. Zusammenfassung	113
7.1. Vergleich des benthischen und des planktischen mikrobiellen Nahrungsgewebes der Boddengewässer unter besonderer Berücksichtigung der benthisch-pelagischen Kopplung durch Sedimentresuspension	113
7.2. Die besondere Bedeutung der Rhizopoden im benthischen mikrobiellen Nahrungsgewebe	115
7.3. Auswirkungen der Sedimentresuspension auf das mikrobielle Nahrungsgewebe in der Wassersäule	116
7.4. Die Bedeutung der Sedimentresuspension für die Erhaltung der Diversität der benthischen Protistengemeinschaft am Beispiel der Rhizopoden	118
7.5. Populationsdynamik und trophische Interaktionen in resuspendierten benthischen Nahrungsgeweben – Untersuchungen an Modellgemeinschaften	120
7.6. Schlußbetrachtung	122
8. Literaturverzeichnis	124
9. Kurzzusammenfassung	144
10. Abstract	145

Verwendete Daten anderer Personen

Die folgenden Daten wurden nicht vom Autor, sondern von anderen Personen erhoben und dem Autor als Rohdaten zur weiteren Analyse überlassen:

Kapitel 2

- Abundanz und taxonomische Zusammensetzung der heterotrophen Flagellaten (H. Arndt, D. Dietrich),
- Abundanz und taxonomische Zusammensetzung der Ciliaten bei den Meßkampagnen April/Mai 1996 bis Januar 1997 (R. Verhoeven)
- Abundanz und Biomasse der Meiofauna (G. Arlt und F. Georgi)
- Abundanz und Biomasse des Metazooplanktons (R. Heerkloss, R. Burckhardt, A. Hammer)

Kapitel 4

- Abundanz der Bakterien, Nanoheterotrophen, Picoautotrophen und Nanoautotrophen (A. Scherwass)
- Taxonomische Zusammensetzung der heterotrophen Flagellaten (H. Arndt)
- Nitrat- und Nitritkonzentrationen, Chlorophyll *a* - Konzentrationen (S. Dahlke)

Zusätzlich lediglich zu Vergleichszwecken herangezogene Einzelinformationen von anderen Personen sind im Text als persönliche Mitteilung oder mit Quellenangabe gekennzeichnet.

Abkürzungsverzeichnis

ANOVA ...	Analysis of variance (Varianzanalyse)
ASW ...	Artificial Seawater (künstliches Seewassermedium, CARON 1993)
BMERC ...	Baltic Marine Environment Protection Commission
DAPI ...	4',6'Diamidino-2-phenylindol (Fluoreszenzfarbstoff)
DOC ...	Dissolved organic carbon (gelöster organischer Kohlenstoff)
DOM ...	Dissolved organic matter (gelöstes organisches Material)
HF ...	Heterotrophic flagellates (heterotrophe Flagellaten)
HNaN ...	Heterotrophic nanoplankton (heterotrophes Nanoplankton)
HNF ...	Heterotrophic nanoflagellates (heterotrophe Nanoflagellaten)
IDH ...	Intermediate disturbance hypothesis (Connell 1978)
KB ...	Kirrbucht
LAM ...	Liquid aliquot method (Flüssigkulturmethode)
MERD ...	Modified Føyns-Erdschreiber medium (modifiziertes Føyns-Erdschreiber Medium, PAGE 1983)
MPN ...	Most probable number method (SINGH 1946)
OC ...	Organic carbon (organischer Kohlenstoff)
POC ...	Particulate organic carbon (partikulärer organischer Kohlenstoff)
POM ...	Particulate organic matter (partikuläres organisches Material)
PSU ...	Practical salinity units
RM-ANOVA	Repeated measures – analysis of variance (Varianzanalyse mit Meßwiederholungen)
RS ...	Rassower Strom

1. Einleitung

1.1. Begründung der Fragestellung

Die Entdeckung des „microbial loop“ im Nahrungsgewebe des marinen Pelagials hat der Erforschung mikrobieller Lebensgemeinschaften und ihrer Bedeutung für den Stoffhaushalt von aquatischen Ökosystemen starken Auftrieb gegeben (SOROKIN 1977, AZAM ET AL. 1983). Während das ursprüngliche Konzept des „microbial loop“ sich noch speziell auf den Kohlenstoff-Fluß vom Phytoplankton über Exsudate zum Bakterioplankton und weiter zu heterotrophen Nanoflagellaten (nachfolgend HNF) als Hauptbakterivoren bezog (AZAM ET AL. 1983), wurde der Blickwinkel inzwischen auf das gesamte mikrobielle Nahrungsgewebe – die Gesamtheit der prokaryotischen und eukaryotischen Mikrobengemeinschaft einschließlich ihrer trophischen Wechselwirkungen – erweitert (PORTER ET AL. 1988, LAYBOURN-PARRY 1992, CARON & FINLAY 1994). Es hat sich gezeigt, daß das mikrobielle Nahrungsgewebe einen hohen Anteil zum Stoffumsatz im Pelagial verschiedenster Ökosysteme beiträgt (LAYBOURN-PARRY 1992, ARNDT 1994, PORTER ET AL. 1985). Außerdem wurde deutlich, daß auch in benthischen Sedimenten ein mikrobielles Nahrungsgewebe existiert, das durch sedimentierenden Detritus und teilweise durch benthische Primärproduktion mit Energie und organischem Kohlenstoff versorgt wird (ALONGI & HANSON 1985, EPSTEIN 1997 A, B, DANOVARO ET AL. 1998, DIETRICH & ARNDT 2000). Dies bestätigte frühere Ergebnisse über die Bedeutung von Protozoen in benthischen Sedimenten (z. B. MARE 1942, FENCHEL 1967, 1969).

Auch in vielen Küstengewässern wird der Stoff- und Energiefluß in hohem Maße durch das mikrobielle Nahrungsgewebe mitgetragen (BAIRD & ULANOWICZ 1989, ARNDT ET AL. 1990, UITTO ET AL. 1997). Dieses weist gegenüber dem mikrobiellen Nahrungsgewebe des offenen Meeres einige Besonderheiten auf: infolge der meist geringen Tiefe kann Licht bis ins Benthon dringen und dort ein Wachstum von Mikrophytobenthos ermöglichen (MACINTYRE ET AL. 1996, MEYERCORDT & MEYER-REIL 1999). Zusätzlich können absinkende Planktonorganismen und Detritus die Sedimentoberfläche erreichen, bevor der in ihnen gebundene organische Kohlenstoff und die in ihnen gebundenen Nährstoffe remineralisiert sind, und sich dort anreichern (OLESEN & LUNDGAARD 1995, LUNDGAARD & OLESEN 1997, HEISKANEN & TALLBERG 1999). Die Anreicherung von autochthon produziertem und importiertem organischen Material macht die Sedimentoberfläche zu einem Zentrum der mikrobiellen Aktivität der Küstengewässer (GRAF ET AL. 1982, 1983, MEYER-REIL 1983, NOVITSKY & KARL 1986), und bietet eine reiche Nahrungsgrundlage für detritivore,

bakterivore und herbivore Protisten (z.B. BAK ET AL. 1991, 1995). Daraus läßt sich die Hypothese ableiten, daß dem benthischen mikrobiellen Nahrungsgewebe in Küstengewässern im Vergleich zum mikrobiellen Nahrungsgewebe in der Wassersäule eine besondere Rolle zukommt. Komponenten des benthischen mikrobiellen Nahrungsgewebes sind in der Vergangenheit in einer Reihe von Küstengewässern quantitativ untersucht worden (z. B. MARE 1942, FENCHEL 1967, 1969, SCHARF 1979, BAK & NIEUWLAND 1989, ALONGI 1990, AL-RASHEID & SLEIGH 1995, BUTLER & ROGERSON 1995, DIETRICH & ARNDT 1999). Da sich die meisten dieser Untersuchungen auf eine oder wenige taxonomische Gruppen (Ciliaten, heterotrophe Flagellaten oder Rhizopoden) konzentrierten, ist über die relative Bedeutung der einzelnen Taxa jedoch noch wenig bekannt (MARE 1942, FERNANDEZ-LEBORANS & NOVILLO 1993). Umfassende qualitative und quantitative Vergleiche zum mikrobiellen Nahrungsgewebe in der Wassersäule fehlen bisher.

Eine weitere Besonderheit des mikrobiellen Nahrungsgewebes von flachen Küstengewässern besteht darin, daß das Benthos und das Pelagial dort enger aneinander gekoppelt sind als in tieferen Gewässern. Abgesehen vom größeren Verhältnis zwischen Sedimentoberfläche und überstehendem Wasservolumen, das allein schon eine stärkere Wechselwirkung zwischen Pelagial und Wassersäule ermöglicht, sind dafür vor allem wellen- und strömungsinduzierte Resuspensionsprozesse verantwortlich. Resuspension durch Strömungen tritt vor allem infolge der Gezeiten auf, während die welleninduzierte Resuspension auch ohne Gezeitenwirkung durch Windeinwirkung hervorgerufen werden kann. Die Bedeutung von Resuspensionsprozessen für die Struktur und die Funktion von Küstengewässern ist in der Vergangenheit unter verschiedensten Gesichtspunkten untersucht worden: die Resuspension wurde als physikalischer Prozeß beschrieben (GEORGI ET AL. 1980, GABRIELSON & LUKATELICH 1985, DEMERS ET AL. 1987, PEDERSEN ET AL. 1995, BOOTH ET AL. 2000), und es wurden mathematische Beziehungen zwischen Einflußgrößen wie Windstärke, Strömungsgeschwindigkeit, Dauer der Wind- oder Strömungseinwirkung, Gewässertiefe und –größe auf der einen Seite und der Quantität, Qualität und Dynamik des resuspendierten Materials auf der anderen Seite aufgestellt (LESHT ET AL. 1980, ARFI ET AL. 1993, BERNAT ET AL. 1994, ARFI & BOUVY 1995, CLARKE & ELLIOT 1998, HANLON ET AL. 1998, TROUW ET AL. 2000). Des Weiteren wurden Auswirkungen der Resuspension auf das DOC- und Nährstoffangebot in der Wassersäule entdeckt (FANNING ET AL. 1982, ULLMAN & SANDSTROM 1987, FLODERUS & HAKANSON 1989, BALLS ET AL. 1994, MORTIMER ET AL. 1998, FURNAS & MITCHELL 1999). Ähnliche Erkenntnisse wurden parallel dazu an Flachseen gewonnen (DEGROOT 1981, KRISTENSEN ET AL. 1992, EVANS 1994, BLOESCH 1995, HAMILTON & MITCHELL 1996, 1997, NOGES ET AL. 1999).

Die weitreichenden physikalischen und chemischen Effekte der Sedimentresuspension legen die Vermutung nahe, daß die Resuspension ähnlich weitreichende Auswirkungen auf die

Struktur der mikrobiellen Lebensgemeinschaft und die Funktion des mikrobiellen Nahrungsgewebes in Küstengewässern hat. Tatsächlich kann beispielsweise resuspendiertes Mikrophytobenthos einen großen Anteil an der autotrophen Biomasse und an der Primärproduktion in der Wassersäule erlangen (SHAFFER & SULLIVAN 1988, DE JONGE & VAN BEUSEKOM 1992, MACINTYRE & CULLEN 1996). Ähnliches gilt für resuspendierte Picoautotrophe (ARFI & BOUVY 1995). Bakterien können indirekt durch den Import von besiedlungsfähigen Oberflächen – und wohl auch durch den Import von DOC – in ihrem Wachstum gefördert werden (WAINRIGHT 1987, 1990, RITZRAU & GRAF 1992).

Über Auswirkungen der Resuspension auf heterotrophe Protisten ist dagegen relativ wenig bekannt: obwohl typisch benthische Protisten immer wieder in der Wassersäule von Küstengewässern gefunden wurden (ROGERSON & LAYBOURN-PARRY 1992, A, B, ANDERSON & ROGERSON 1995, MURZOV & CARON 1996, ZIMMERMANN & KAUSCH 1996, ZIMMERMANN-TIMM ET AL. 1998, SHIMETA & SISSON 1999), ist ihr Anteil an der Gesamtbio­masse und am Gesamtstoffumsatz des Protozooplanktons noch nicht systematisch untersucht worden. Hinweise auf eine indirekte Förderung des Populationswachstums von HNF durch resuspendiertes Material und darauf wachsende Bakterien wurden in Mikrokosmosexperimenten gefunden (WAINRIGHT 1987). Darüber hinaus ist über indirekte Resuspensionswirkungen auf das Protozooplankton, also solche, die nicht allein durch einen Vertikaltransport von Zellen aus dem Benthos in das Überstandswasser hervorgerufen werden, aber noch nichts bekannt. Grundsätzlich sind sowohl positive als auch negative Resuspensionswirkungen auf die heterotrophe Protistengemeinschaft in der Wassersäule denkbar: Planktische Protozoen könnten resuspendiertes POM – und gegebenenfalls auch DOM (SHERR 1988) – aufnehmen und so von der Resuspension profitieren (WAINRIGHT 1987), sie könnten aber auch durch resuspendiertes mineralisches Seston bei ihrer Nahrungsaufnahme behindert und so in ihrem Populationswachstum gebremst werden. Negative Auswirkungen mineralischer Schwebstoffe sind von filtrierenden Planktonciliaten des Süßwassers berichtet worden (JACK ET AL. 1993, JACK & GILBERT 1993).

Auf der anderen Seite sind indirekte Resuspensionswirkungen auch im Mikro- und Nanozoobenthos zu erwarten: Es stellt sich die Frage, wie sich das Populationswachstum und trophische Interaktionen in resuspendierten benthischen mikrobiellen Nahrungsgeweben gegenüber dem sedimentierten Zustand verändern, und welche Konsequenzen dies für den Stoffumsatz im benthischen mikrobiellen Nahrungsgewebe in flachen Küstengewässern hat. Weiterhin ist zu fragen, welche Bedeutung Resuspensionsereignisse generell als Störungen der benthischen mikrobiellen Lebensgemeinschaft haben. Der Störungsaspekt ist von besonderem Interesse, weil in benthischen heterotrophe Protistengemeinschaften häufig sehr viele Arten miteinander koexistieren (z.B. FERNANDEZ-LEBORANS & NOVILLO 1993, FENCHEL ET AL. 1997, BUTLER & ROGERSON 2000). Diese Arten konkurrieren um ein

begrenztes Nahrungsangebot in Form von Bakterien und anderem organischen Kohlenstoff. Da die Konkurrenz um Ressourcen zum lokalen Aussterben von Arten unter konstanten Bedingungen führen kann (GAUSE 1935, VANDERMEER 1969, TILMAN 1982), müssen in artenreichen natürlichen Protistengemeinschaften Mechanismen existieren, die diesem Ausschluß entgegenwirken. Störungen könnten – ähnlich wie beim Phytoplankton (GAEDEKE & SOMMER 1986, REYNOLDS ET AL. 1993, SOMMER 1995) – eine Rolle bei der Erhaltung der Artenvielfalt benthischer Protistengemeinschaften spielen, indem sie dem Konkurrenzausschluß einzelner Arten durch eine Neuschaffung von besiedelbarem Substrat und durch eine Veränderung der Konkurrenzbedingungen entgegenwirken. Dieser Zusammenhang ist generell in der „intermediate disturbance hypothesis“ formuliert worden. Die „intermediate disturbance hypothesis“ ist eine grundlegende Hypothese der modernen Ökologie, die weiterhin besagt, daß die Wirksamkeit von Störungen für die Diversitätserhaltung bei mittleren Störungshäufigkeiten bzw. –intensitäten am höchsten ist (CONNELL 1978). Ein experimenteller Beweis dieser Hypothese anhand von heterotrophen Protistengemeinschaften ist jedoch noch nicht gelungen (siehe MCGRADY-STEED & MORIN 1996).

Aus dem dargestellten Wissensstand über das mikrobielle Nahrungsgewebe und die Bedeutung der Resuspension in flachen Küstengewässern ergeben sich eine Reihe von Fragen, deren - teilweise beispielhafte - Beantwortung Ziel der vorliegenden Arbeit war:

1. Strukturorientierte Fragen (Kapitel 2 und 3): Welchen Anteil hat das Mikro- und Nanozoobenthos an der Gesamtbiomasse der heterotrophen Protistengemeinschaft in flachen Küstengewässern? Welches sind die grundlegenden Unterschiede zwischen der taxonomischen Zusammensetzung der benthischen heterotrophen Protistengemeinschaft und der der Wassersäule? Wie groß ist der Anteil resuspendierter benthischer Protozoen am Protozooplankton?

2. Prozeßorientierte Fragen (Kapitel 4 – 6): Wirkt sich die Resuspension über einen direkten Vertikaltransport von benthischen Protisten hinaus auf das mikrobielle Nahrungsgewebe in der Wassersäule aus? Wie verändern sich die Populationsdynamik und die trophischen Interaktionen in resuspendierten benthischen Protistengemeinschaften im Vergleich zum sedimentierten Zustand? Wirken Störungen durch Resuspensionsereignisse diversitätserhaltend - im Sinne der „intermediate disturbance hypothesis“ – auf das Mikro- und Nanozoobenthos?

1.2. Herangehensweise

Die Resuspension ist ein komplexer Prozeß, der sich grundsätzlich über verschiedenste Mechanismen auf das mikrobielle Nahrungsgewebe auswirken kann. Für die Untersuchung der Resuspension ergibt sich daraus das Problem, daß eine realistische Erfassung ihrer Gesamtauswirkungen im Freiland (bzw. eine entsprechende Laborsimulation) und eine gleichzeitige Analyse aller zugrundeliegenden Mechanismen nicht möglich sind. Um der Komplexität der mit der Resuspension verbundenen Teilprozesse gerecht zu werden, mußte ich in der vorliegenden Arbeit Untersuchungen an unterschiedlichen Teilen des mikrobiellen Nahrungsgewebes (Benthos und Plankton), und auf unterschiedlichen räumlichen und zeitlichen Skalen sowie auf unterschiedlichem Komplexitätsniveau miteinander kombinieren. Zunächst habe ich beschreibende und vergleichende Freilanduntersuchungen (Kapitel 2 und 3) in den Mecklenburg-Vorpommerschen Boddengewässern durchgeführt, um die genannten strukturorientierten Fragen zu beantworten. Die Boddengewässer sind flache, brackige Küstengewässer der südlichen Ostsee. Sie sind - einschließlich ihres mikrobiellen Nahrungsgewebes - unter verschiedensten Blickwinkeln untersucht worden (Übersichtsartikel: ARNDT 1988, 1994, ARNDT 1991, SCHIEWER & JOST 1991, SCHIEWER ET AL. 1992, SCHLUNGBAUM ET AL. 1994, SCHIEWER 1998). Obwohl die Bodden kaum von Gezeiten beeinflußt werden, kommt es wegen ihrer geringen Tiefe häufig zu windinduzierten Resuspensionsereignissen (GEORGI ET AL. 1980, SCHIEWER 1994). Damit bieten sich die Boddengewässer für eine beispielhafte Untersuchung der beschriebenen Besonderheiten des mikrobiellen Nahrungsgewebes in flachen Küstengewässern an.

Die Freilanduntersuchungen wurden in einem (zweiwöchigen bis dreimonatigen) Beprobungsrhythmus durchgeführt, der weit über der Dauer von einzelnen Resuspensionsereignissen in den Boddengewässern lag. Deshalb wurden zur Untersuchung der Dynamik des mikrobiellen Nahrungsgewebes während Resuspensionsereignissen Resuspensionsexperimente mit natürlichen Sedimentkernen durchgeführt (Kapitel 4 und 5). Die Dauer und der Beprobungsrhythmus dieser Experimente wurden der Dauer natürlicher Resuspensionsereignisse (Stunden bis Tage) angepaßt. Dabei lag die Betonung auf einer möglichst realistischen Simulation der Resuspension unter Freilandbedingungen, und die Fragestellung zielte auf Nettoeffekte der Resuspension auf das mikrobielle Nahrungsgewebe der Wassersäule (Kapitel 4) bzw. einen Teil des mikrobiellen Nahrungsgewebes im Sediment (Kapitel 5). Gleichzeitig wurden neben dem mikrobiellen Nahrungsgewebe eine Vielzahl von abiotischen und biotischen Rahmenparametern erfaßt, um im Nachhinein eine Rekonstruktion zugrundeliegender Mechanismen zu ermöglichen. Bei den im Kapitel 6 dargestellten Planktonradexperimenten setzte ich – bei ähnlicher zeitlicher Skalierung - schließlich ein gegenüber dem Freiland vereinfachtes und besser manipulierbares System

ein, um einen genauen Einblick in Mechanismen der Resuspensionswirkung auf resuspendierte benthische Protistengemeinschaften zu erlangen.

Die in den Kapiteln 2-6 dargestellten Ergebnisse sollen somit in ihrer Gesamtheit, und über die Aussagekraft hinsichtlich ihrer speziellen Fragestellungen hinaus, einen Beitrag zum Verständnis der Funktion des mikrobiellen Nahrungsgewebes in flachen Küstengewässern leisten. Dieser Aspekt wird am Ende der Zusammenfassung (Kapitel 7) herausgearbeitet.

2. A comparison of benthic and planktonic heterotrophic protistan community structure in shallow inlets of the Southern Baltic Sea

2. 1. Summary

The taxonomic composition, abundance, and biomass of heterotrophic protists (ciliates, heterotrophic flagellates, rhizopods, and actinopods) in the sediment and in the water column of shallow inlets of the Southern Baltic was studied under a variety of environmental conditions during 1996 - 1997. A shallow, highly eutrophic station and a deeper, less eutrophic station were compared. Community biomass ranged from 0.12 – 0.34 $\mu\text{g C cm}^{-3}$ in the water column and from 1.5 – 105 $\mu\text{g C cm}^{-3}$ in the sediment. Heterotrophic protists dominated zooplankton biomass at both stations (73 % and 84 % mean contribution), while they were of minor importance within the zoobenthos. Expressed per unit area, benthic biomass contributed a significant part (44 % and 49 %) to the total heterotrophic protistan community, which indicates a potentially strong impact of resuspended benthic protists on protozooplankton community structure.

Although the methodology for ciliate and heterotrophic flagellate enumeration was focussed on a high taxonomic resolution, the results reveal some general trends of heterotrophic protistan distribution: protozooplankton biomass was dominated by flagellates (80 % mean biomass contribution) at the shallow station and by ciliates (73 % mean biomass contribution) at the deep station. In the benthos of both stations, ciliates were the dominant protozoans, followed by the hitherto little-studied rhizopods (25 % and 35 % mean biomass contribution) and flagellates.

The degree of benthic-pelagic coupling differed between taxonomic groups. Benthic and pelagic communities of ciliates showed little taxonomic overlap. In contrast, many heterotrophic flagellate species were found both in the benthal and in the pelagial. These benthic-pelagic species contributed significantly to the biomass of heterotrophic flagellates in the water column. The planktonic rhizopod community contributed little to protozooplankton community biomass and consisted of a subset of those species found in the benthal. Benthic and pelagic protist abundances were positively correlated at the shallow station, but taxonomic data indicate that the direct exchange between benthic and pelagic communities was only partly responsible.

2. 2. Introduction

An assessment of the importance of heterotrophic protistan communities in aquatic ecosystems is still difficult because most quantitative accounts have focussed on individual protistan groups, and either on benthic or on pelagic habitats. Within the protozooplankton, ciliates have received most attention in broad surveys (e. g. BEAVER & CRISMAN 1989, LEAKEY ET AL. 1998, WITEK 1998), followed by heterotrophic flagellates (e. g. BERNINGER ET AL. 1991, ARNDT ET AL. 2000). Planktonic rhizopods and actinopods have only occasionally been studied because they are difficult to identify and early data suggested that they are less important (e.g. CARON & SWANBERG 1990, ARNDT 1993). Although MARE'S (1942) and FENCHEL'S (1967, 1969) classic studies of the micro- and nanozoobenthos were wider in scope, most of the recent literature on benthic protistan community structure is also split along taxonomic borders. Again, ciliates have been studied most completely (e.g. AL-RASHEID & SLEIGH 1995, BERNINGER & EPSTEIN 1995), followed by flagellates (e.g. BAK & NIEUWLAND 1989, STARINK ET AL. 1996). The possible importance of benthic rhizopods has only recently been addressed (BUTLER & ROGERSON 1995, ANDERSON 1998, DECAMP ET AL. 1999).

Ecological interpretation of abundances or biomasses of individual groups is compromised if it is not clear how large a part of the heterotrophic protistan community they represent, and how they interact with other parts. A number of studies were aimed at the overall structure of either the protozooplankton or the micro- and nanozoobenthos, usually identifying either ciliates or flagellates as the dominant groups (e.g. SMETACEK 1981, FERNANDEZ-LEBORANS & NOVILLO 1993, MATHES & ARNDT 1994, EPSTEIN 1997A, B). Comparisons between protozooplankton and benthic protistan communities were rarely presented (BARK 1981, FINLAY ET AL. 1988, ARNDT ET AL. 2000). Therefore, little information is available on the distribution of protistan communities between water column and sediment, and on the influence of exchange processes between both habitats.

Apart from providing information on the vertical and taxonomical partitioning of community biomass, benthic-pelagic comparisons including all protistan groups are interesting with regard to benthic-pelagic coupling (BOERO ET AL. 1996). Data about autotrophic protists suggest some possibly important mechanisms and consequences of benthic-pelagic coupling: benthic and pelagic populations of autotrophic protists can be coupled by active vertical migration (HANSSON 1996), or passively by sedimentation and sediment resuspension. Wind- or tide-induced resuspension of autotrophic protists may have profound effects on autotrophic biomass, taxonomic composition, and primary production in the water column of shallow lakes and coastal waters (e.g. PADIŠAK ET AL. 1990, DE JONGE & VAN BEUSEKOM 1995). Field data from the coastal North Atlantic suggest

that similar mechanisms may connect benthic and pelagic communities of heterotrophic protists (SHIMETA & SISSON 1999).

The aim of this study was to provide a comprehensive account of heterotrophic protistan community structure (including ciliates, rhizopods and heterotrophic flagellates) in different sediment layers and in the water column of shallow brackish inlets which are subject to frequent wind-induced resuspension events. In order to minimise methodological ambiguities and to achieve a high taxonomic resolution, the same methods were used for the analysis of plankton and sediment samples: live-counting for the ciliates and flagellates, and the liquid aliquot method, the only well-established method for the rhizopods and actinopods. Based on results of this comparison obtained under a variety of environmental conditions, I wanted to assess the degree of taxonomic overlap between benthic and pelagic heterotrophic protistan communities and the significance of coupling between them. The study was also intended to elucidate the relative importance of protistan groups, and of the entire protistan fauna, within the shallow coastal waters of the study area.

2.3. Material and Methods

2.3.1. Study sites

The study was carried out in shallow (mean depth 1 - 2 m), brackish, non-tidal inlets of the Southern Baltic (Fig. 2.1). Salinity decreases from about 10 PSU at the outlet to the Baltic to about 0.5 PSU in the innermost inlets. Dissolved nutrient and water column chlorophyll *a* concentrations show the opposite trend, increasing towards the inner inlets. The study area including its microbial food web have been the subject of numerous studies (reviewed in SCHIEWER, 1998).

Two sampling stations with contrasting environmental conditions were chosen as part of the interdisciplinary "Oekobod" project (Table 2.1). Station Rassower Strom (RS) was situated close to the outlet in a relatively deep basin characterised by frequent sedimentation and resuspension events: during a total of 142 d between 15 May and 1 December 1996, turbidity and wind data have indicated 66 wind-induced resuspension events at this station (situations with < 10 % light transmission and > 5 m s⁻¹ wind speed at station Arkona, about 15 km distant from station RS, data from S. DAHLKE, pers. comm., and Deutscher Wetterdienst). Station Klosterloch was sampled instead of station RS in January 1997 because station RS could not be reached due to poor ice conditions. Station Klosterloch was situated about 3 km from station RS. It had a similar water depth and similar general characteristics as station RS. Station Kirrbucht (KB) was located at a shallow, wind-exposed

site in the inner part of the estuarine system, close to the Zingster Strom. Although no turbidity measurements are available from station KB, data of other workers suggest that sediments were resuspended even more frequently there than at station RS (GEORGI ET AL. 1980).

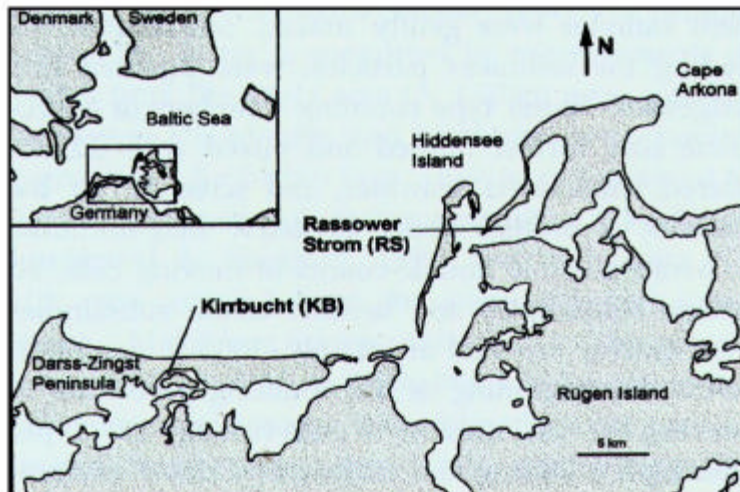


Figure 2.1. Location of sampling sites.

Table 2.1. General characterization of the sampling sites. Ranges are given in parentheses (OC: organic carbon content).

	Rüssow Strom	Kirtzbucht
Water depth [m]	3.8	0.7
Salinity [PSU]	9 (8-12)	5 (2-10)
Trophic status	mesotrophic	polytrophic
Sediment type	sandy mud	muddy sand
Sediment OC [%]	4	1
Thickness of flocculent surface layer [mm]	2-8	2-4

Table 2.2. Environmental conditions during the sampling campaigns. Wind data by courtesy of Deutscher Wetterdienst, other data by courtesy of S. DAHLKE, pers. comm. (seston, temperature), S. Gerbersdorf & J. MEYERCORDT, pers. comm. (Chl **a**). (¹) station Klosterloch; surface: 0.3 m, KB; 1 m, RS; above bottom: 0.5 m above the sediment, only RS; n. det.: not determined).

Station	Date	Seston (surface) [mg l ⁻¹]	Seston (bottom) [mg l ⁻¹]	Wind speed [m s ⁻¹]	Water temperature [° C]	Water column chlorophyll <i>a</i> [µg l ⁻¹]
RS	29. 04. 1996	4.5	5.2	5.9	11.4	1.5
	08. 07. 1996	6.2	39	2.9	16.9	4.5
	30. 09. 1996	9.3	10.5	11.1	12.2	4.2
	19. 01. 1997 ¹⁾	3.1	3.8	6.2	-0.3	2.0
	14. 04. 1997	10.9	8.3	15.8	5.8	1.3
KB	01. 05. 1996	52.7	n. det.	5.2	n. det.	32.9
	01. 07. 1996	71.4	n. det.	2.8	14.1	32.9
	07. 10. 1996	60.6	n. det.	1.2	12.9	29.6
	27. 01. 1997	17.2	n. det.	6.0	1.2	12.1
	07. 04. 1997	100.5	n. det.	4.4	5.9	13.3

2.3.2. Sampling design

At both stations, five sampling campaigns were carried out between April 1996 and April 1997. This schedule was chosen in order to study benthic and pelagic community structure under a variety of environmental conditions, rather than to address seasonal succession (Table 2.2). Wind data from stations Arkona (about 15 km from station RS) and Barth (about 5 km from station KB) were provided by the Deutscher Wetterdienst. The wind velocities given in Table 2.2 are averages over 4 h prior to each sampling. According to a comparison of wind and turbidity data (data not shown), this timespan was sufficient to allow wind-driven waves and suspended matter concentrations in the water column to reach equilibrium.

2.3.3. Sampling procedure

At each sampling campaign, triplicate water samples, samples of the flocculent surface layer (a layer of recently settled organic material, devoid of sand grains and usually about 2 mm thick) and sediment samples (0 - 5 and 5 - 10 mm sediment horizons) were taken. According to studies with oxygen microelectrodes of sediments from the study area (GERBERSDORF ET AL. 2001), the 0 - 5 mm horizon represented the oxic sediment layer and the 5 - 10 mm represented the anoxic layer.

Pelagic samples were taken with a 5 l vertical sampler from 1/2 water depth (1.9 m at station RS and 0.3 m at station KB). The other samples were taken from triplicate sediment cores (10 cm diameter) with overlying water. These cores were obtained in plexiglass tubes by a ship-operated multicorer at station RS and by a boat-operated manual corer at station KB. During the winter campaigns, sampling was carried out from the ice. In order to exclude artifacts in water column data due to resuspension during the sampling procedure, water samples were always taken prior to sediment samples, and the sampling stations were approached at minimal speed.

Subsamples of the flocculent surface layer were taken according to the following procedure: after most of the overlying water had been siphoned off the cores, the entire flocculent surface layer was siphoned off the sediment surface with 4 mm internal diameter tubing. During this procedure, the lower part of the tubing was fixed in an upright position and suction was kept at a level that was just sufficient to remove the flocculent material from the surface of the core, without removing underlying sediment grains. The success of this sampling procedure was checked microscopically.

Subsequently, plexiglass tubes (25 mm internal diameter) were gently pushed into the sediment surface and covered with rubber stoppers. After extraction, the subcores were cut into the 0 - 5 mm and 5 - 10 mm layers, "0" referring to the sediment surface after removal of the flocculent layer. No ciliate or rhizopod samples from the 5 - 10 mm layer were taken during the first sampling campaign. The resulting sediment and flocculent surface layer subsamples were diluted with defined volumes of 0.2 µm-filtered, autoclaved seawater and stored at *in situ*-temperatures in the dark until further processing. The remainder of the flocculent surface layer slurry was kept in a measuring cylinder at 20 °C for 24 h. From the compaction of the particulate matter in this slurry, correction factors for the dilution of the flocculent surface layer during sampling were calculated.

2.3.4. Identification and enumeration of protists

Flagellates, ciliates, and rhizopods were identified in fresh samples or in qualitative enrichment cultures (rice/wheat grain cultures or Føyns-Erdschreiber medium, PAGE 1983) under a Zeiss Axioplan microscope with 40 - 1000x magnification, equipped with phase contrast and interference contrast optics. When necessary, ciliate species were identified in quantitative protargol stain preparations (SKIBBE, 1994).

Ciliates and heterotrophic flagellates were enumerated by light-microscopical live-counting within 3 - 8 h after sampling (GASOL 1993, see ARNDT ET AL. 2000). Prior to enumeration, diluted sediment samples were gently shaken. Subsamples including the sediment particles were pipetted into Sedgewick-Rafter type counting chambers of appropriate size, further diluted and mixed with 0.2 µl-filtered, autoclaved seawater, and screened for the presence of protists under 40x - 400x magnification. To avoid possible double-counts of moving cells, all pelagic subsamples and benthic ciliate subsamples were quickly scanned at low (40 - 100x) magnification at the beginning of the counting procedure to establish the total number of cells (usually 10 - 20 per subsample). During the subsequent closer examination, only those cells crossing the equator of the microscopic field in the direction of stage movement were counted, and those crossing it opposite this direction were subtracted from the resulting number (GASOL 1993). This precaution was relevant only occasionally in sediment HF samples, however, because the stage movement was generally much faster than the movement of benthic HF. The ciliates and flagellates were detected by their movement and assigned to species or genera. This procedure usually lasted 20 min per subsample. It was repeated with new subsamples until about 50 protists had been counted. Although triplicate samples were taken for the enumeration of protists, only one to two sediment samples could be analysed for ciliates and heterotrophic flagellates.

Rhizopods were enumerated by the liquid aliquot method because they are usually not recognizable in fresh samples due to their slow locomotion and close surface association. The liquid aliquot method is described in more detail elsewhere (ANDERSON & ROGERSON 1995, BUTLER & ROGERSON 1995, Chapter 3). Briefly, small (10 - 50 µl) aliquots of the diluted subsamples were pipetted into wells of tissue-culture plates (Falcon) each containing 2 ml of Føyns-Erdschreiber medium. After 12 and 24 days incubation the wells were screened for the presence of rhizopod morphospecies. From the frequency of occurrence of individual species (number of wells in which a species was found), subsample abundance estimates were calculated assuming a Poisson distribution.

In order to estimate heterotrophic protist biomass, specific individual biovolumes were calculated from the average cell dimensions of at least 20 individuals of each species by analogy to geometrical models. These biovolumes were converted to individual biomass

assuming a carbon conversion factor of $0.2 \text{ pg C } \mu\text{m}^{-3}$ (OHMAN & SNYDER 1991). For benthic ciliates, this factor is supported by measurements of species from the study area (A. GÜBER, pers. comm.). Population abundances and biomasses were pooled to give totals for higher taxa. They were compared to biomass estimates of metazooplankton (HEERKLOSS ET AL. 1999) and meiofauna (G. ARLT, pers. comm.) from the same sampling campaigns. Meiofauna were assigned to taxonomic groups and enumerated in formaldehyde-fixed samples with a stereomicroscope. Meiofauna biomass was estimated from species abundances, standard species biovolumes and biomass conversion factors (G. ARLT, pers. comm.).

2.3.5. Statistical analysis

Pelagic biomass totals and abundances of ciliates, rhizopods, and flagellates were correlated to those of the flocculent surface layer and of the sediment, and to seston and chlorophyll *a* concentrations. Since the pelagic abundance contribution of seston-associated protists was assumed to be proportional to seston concentration, Pearson's correlation coefficient was used to analyse this relationship. The non-parametric Spearman's rank correlation coefficient was employed for correlations between layers and between pelagic abundances and chlorophyll *a*, because I did not assume that the variables had linear relationships to one another. The hypothesis that pelagic protistan abundances may be influenced by resuspension of sediments containing benthic protists was tested using multiple linear regression analysis with seston concentration and benthic abundance as independent variables and water column abundance as dependent variable. All statistical procedures were carried out using SPSS.

2.4. Results

2.4.1. General trends

During the whole investigation, heterotrophic protistan biomass estimates ranged from $0.12 - 0.34 \text{ } \mu\text{g C cm}^{-3}$ in the water column and from $1.5 - 105 \text{ } \mu\text{g C cm}^{-3}$ in the sediment and flocculent surface layer (Fig. 2.2). Thus, protistan biomass was about two orders of magnitude higher in the sediment than in the overlying water. However, due to the height of the water column at the stations, a similar protozoan biomass per square meter was contained in the pelagial and in the benthic. The relative importance of pelagic and benthic communities differed between taxonomic groups and stations (Fig. 2.3): protozooplankton

tended to be quantitatively more important than benthic forms at station RS, mainly due to the distribution of ciliates. Rhizopod biomass per area was dominated by the benthic community. In contrast, planktonic flagellates were always more important within the total biomass of flagellates at station KB, and mostly at station RS.

Protozooplankton biomass at station KB was on average four times higher than at station RS (Fig. 2.2), and was dominated by flagellates. Ciliates were the dominant group at station RS except in July 1996. Rhizopods never contributed significantly to planktonic biomass (Table 2.3). Pelagic protistan biomass maxima were reached in July 1996 at both stations.

During the spring and summer sampling campaigns, the flocculent surface layer at station KB contained higher biomasses of heterotrophic protists than that at station RS (Fig. 2.2). The reverse relationship was found during the campaigns in January 1997 and especially in September/October 1996 when exceptionally high biomass values of all groups were found at station RS. Ciliates tended to dominate protozoan biomass in this layer, but biomass contributions of flagellates and particularly rhizopods were conspicuously high during spring (Table 2.3).

At station RS, benthic biomass was similarly distributed between layers throughout the study. The maxima of the vertical biomass distribution of station KB shifted from the flocculent surface layer in April and July 1996 to the 5 - 10 mm sediment layer in October 1996 and January 1997 (Fig. 2.2). This shift was reversed again in April 1997. It was mainly due to the ciliates which dominated protozoan biomass in the sediment, (Table 2.3).

Heterotrophic protists dominated the standing stock of the combined proto- and metazooplankton in all samples from station KB and in all but one sample from station RS. In contrast, they usually contributed moderately to the combined biomass with meiofauna (Fig. 2.4). While contributions of heterotrophic protists to the biomass of pelagic phagotrophs were minimal during the spring samplings, no such pattern was found in the meiofauna comparisons. For the comparison shown in Figure 2.4, only data from the flocculent surface layer and the 0 - 10 mm layer were considered since the deeper sediment layers contained only a very low biomass of meiofauna and heterotrophic protists.

Since the abundance and taxonomic composition of most protistan groups showed no systematic differences between the 0 - 5 mm and 5 - 10 mm sediment layers, the respective figures of both layers were pooled for further analysis.

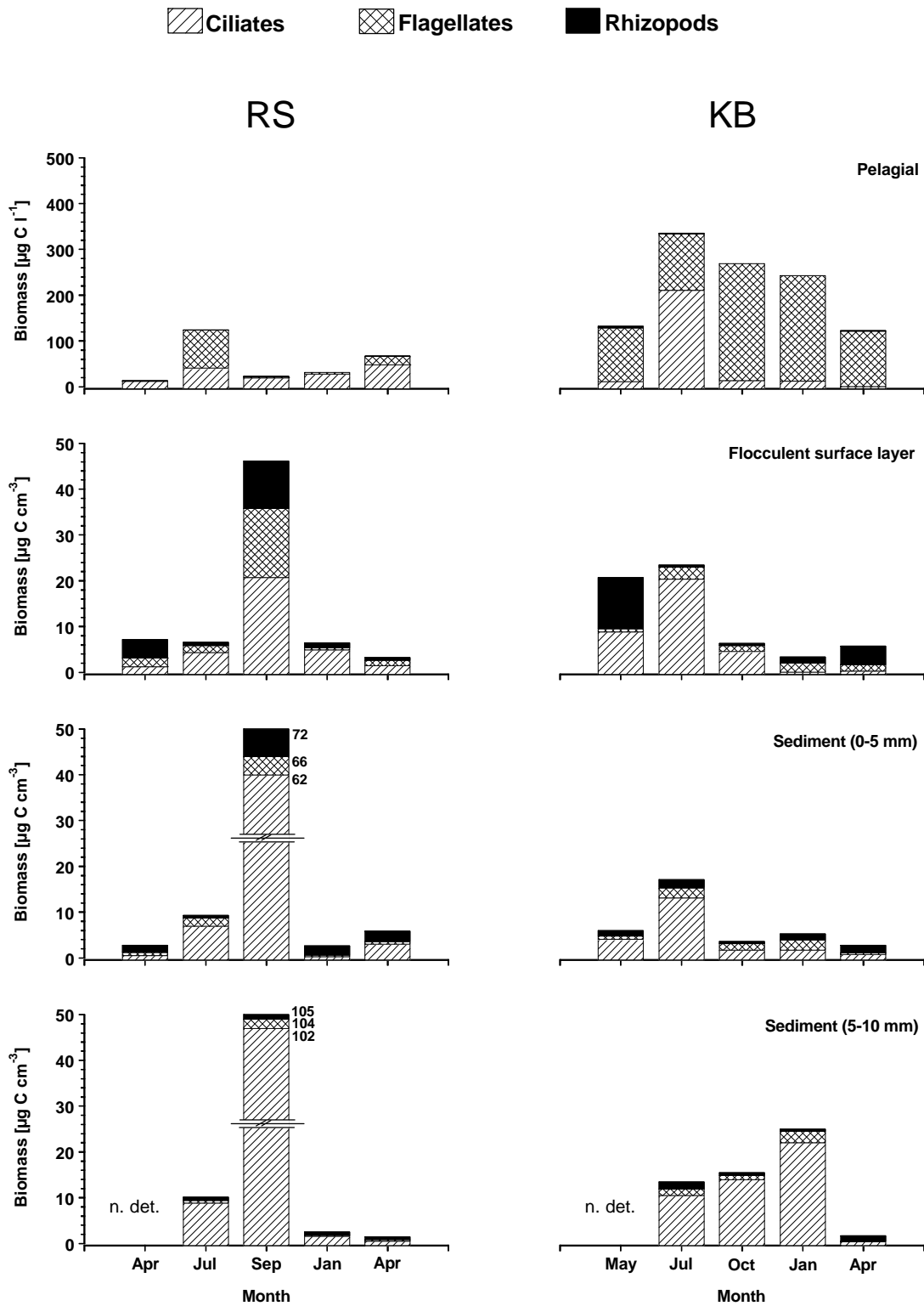


Figure 2.2. Biomass distribution of heterotrophic protists (ciliates, heterotrophic flagellates, and rhizopods) between layers and stations. The 5-10 mm sediment layer was not sampled during the spring campaign in 1996.

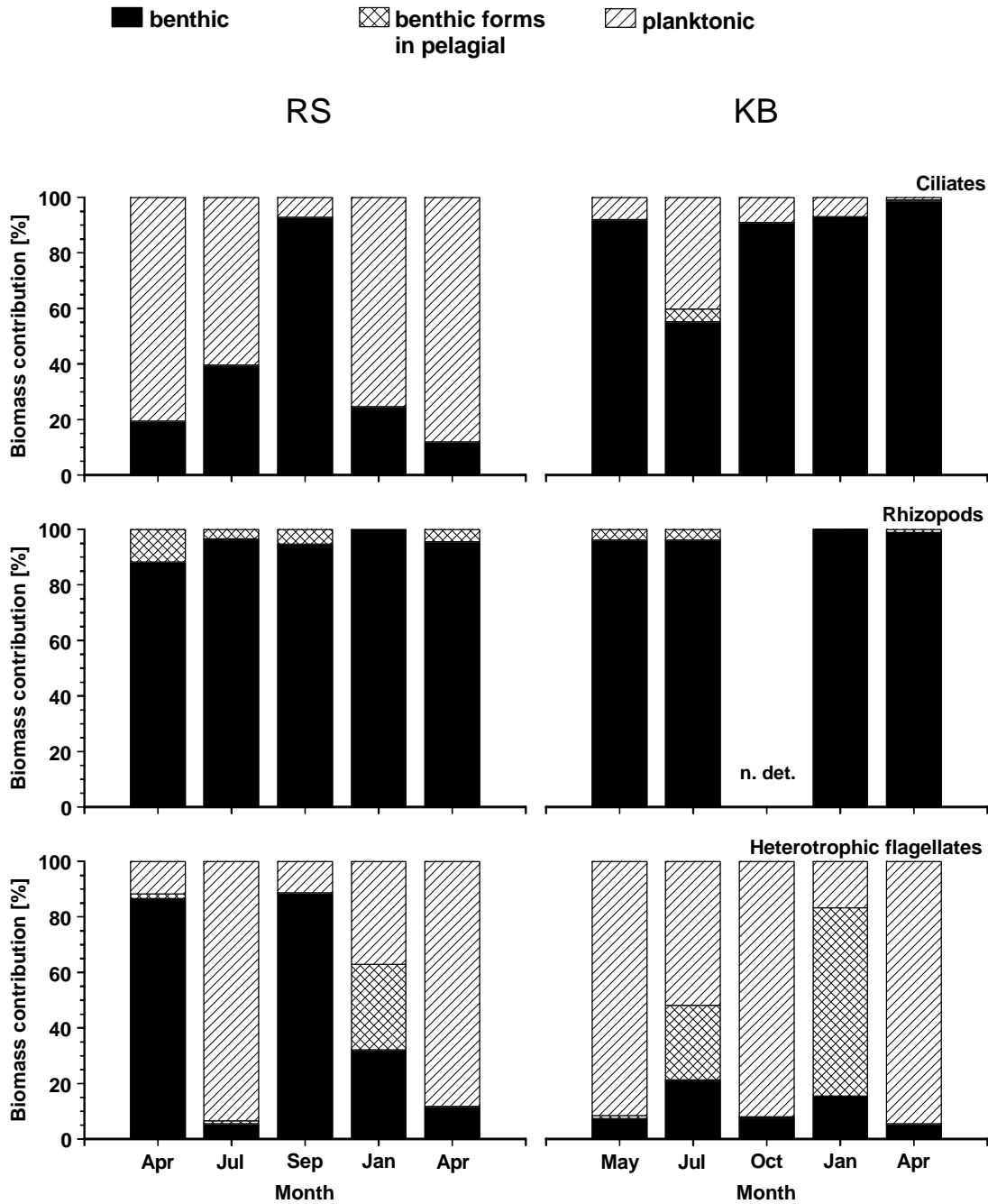


Figure 2.3. Contribution of benthic, planktonic, and suspended benthic protists (benthic forms in the water column) to the biomass per unit area of protistan groups.

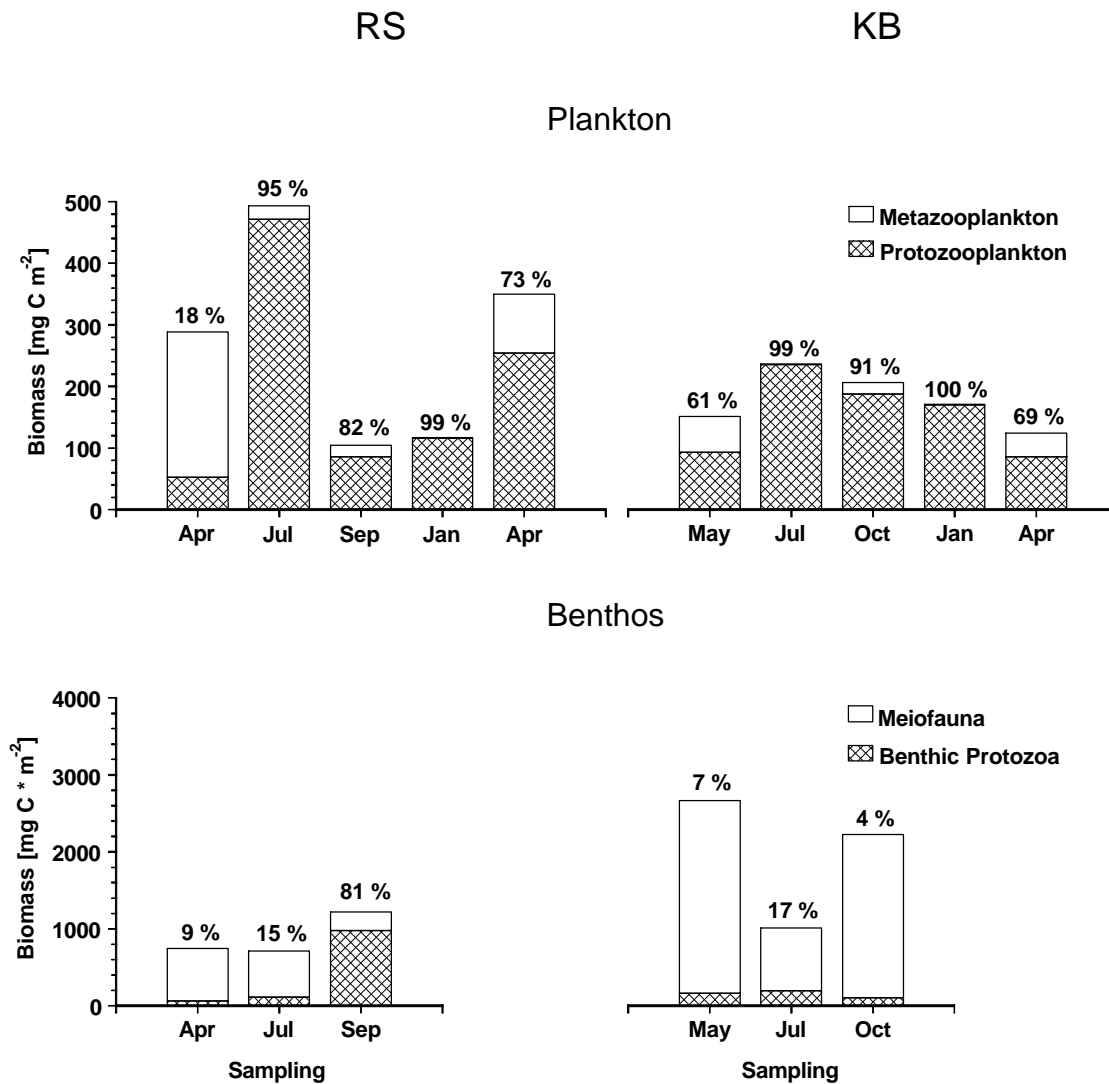


Figure 2.4. Biomass contribution of heterotrophic protists to total zooplankton biomass and to the combined biomass with meiofauna. The percentages on top of the bars are relative biomass contributions of heterotrophic protists. No meiofauna data were available for the 1997 sampling campaigns.

2.4.2. Distribution and taxonomic composition of ciliates

Ciliate abundances showed a high degree of temporal variability, and the between-replicate variance in plankton and flocculent surface layer samples was high whenever estimated. However, some general trends could be detected: abundance totals of 0.17 - 88 ind. cm⁻³ in the water column, 70 - 2,300 ind. cm⁻³ in the flocculent surface layer and 40 - 3,000 ind. cm⁻³ in the sediment were found (Fig. 2.5). Apart from exceptionally high values in the water column of station KB (July 1996) and in the benthos of station RS (September

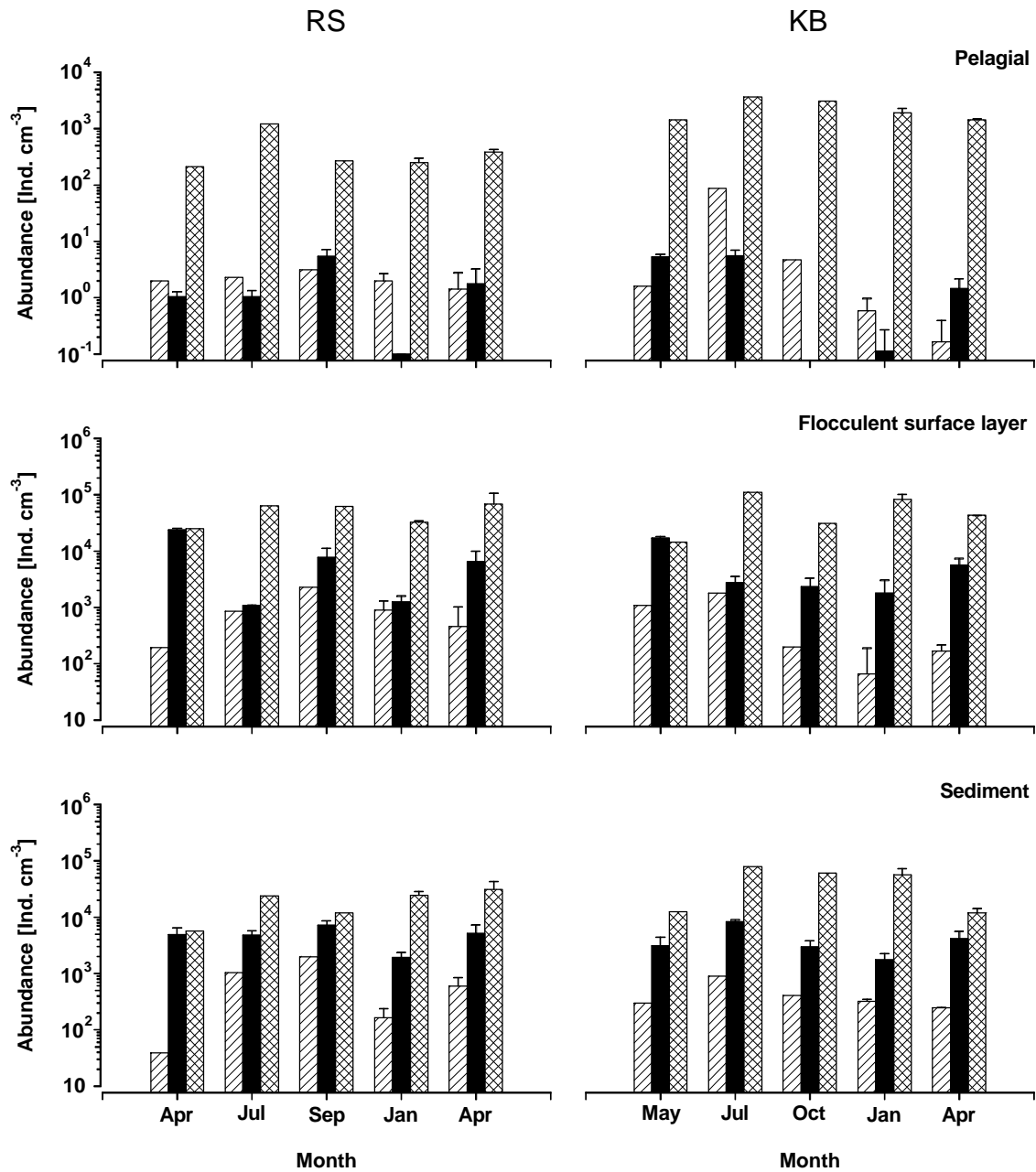


Figure 2.5. Abundances of ciliates, rhizopods and heterotrophic flagellates. Sediment figures refer to the 0-5 mm layer (ciliate and rhizopod 1996 spring samples), or to the 0-10 mm layer (all other samples). Note the different scale of the pelagial graph. Error bars: S.D., N = 3 (rhizopod samples, ciliate and flagellate plankton samples), N = 2 (ciliate and flagellate flocculent surface layer and sediment samples). No variance estimates are available for ciliates and heterotrophic flagellates from the 1996 campaigns.

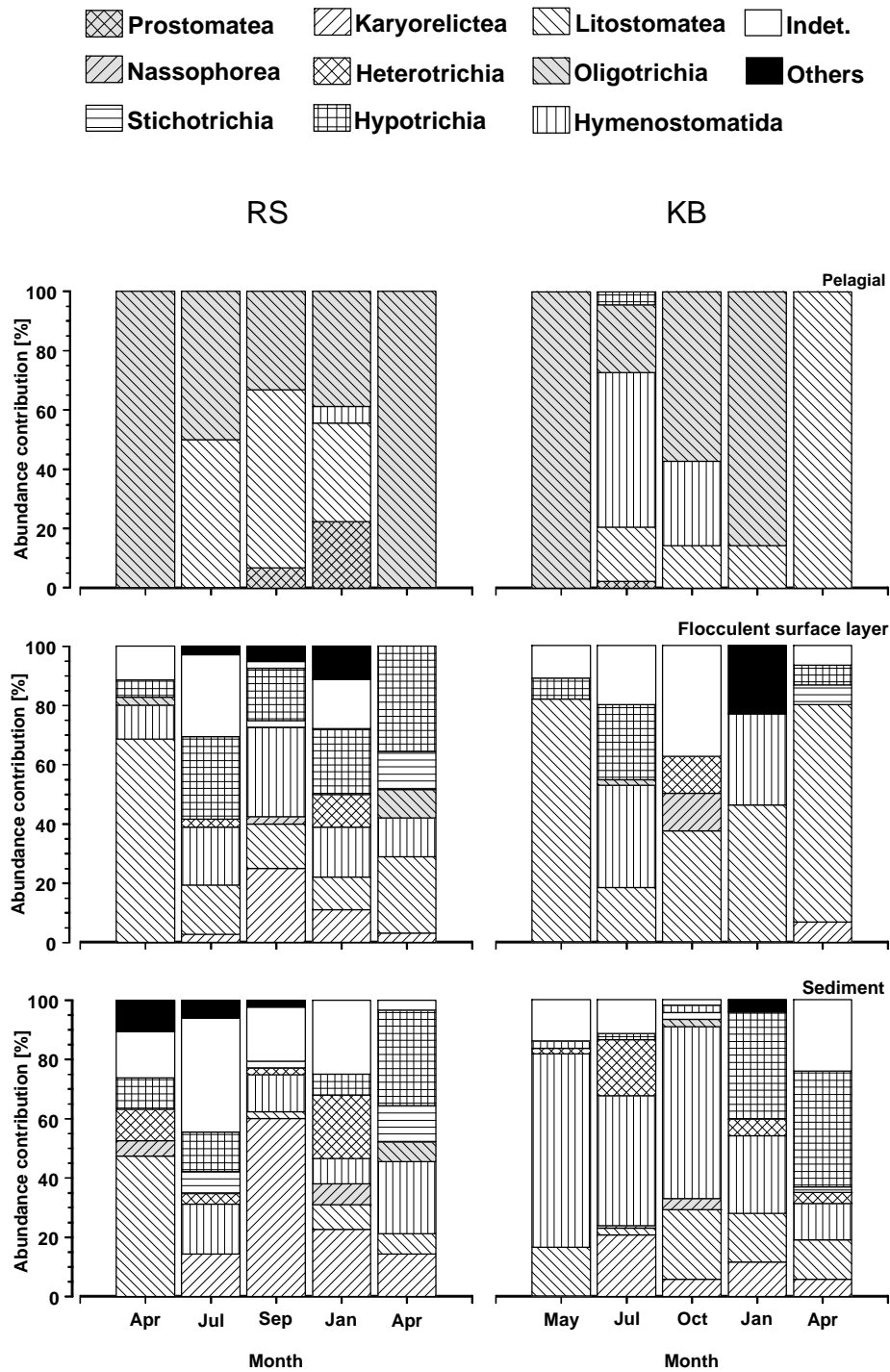


Figure 2.6. Taxonomic composition of ciliates (means of 2-3 replicates). Sediment figures refer to the 0-5 mm layer (1996 spring samples), or to the 0-10 mm layer (all other samples).

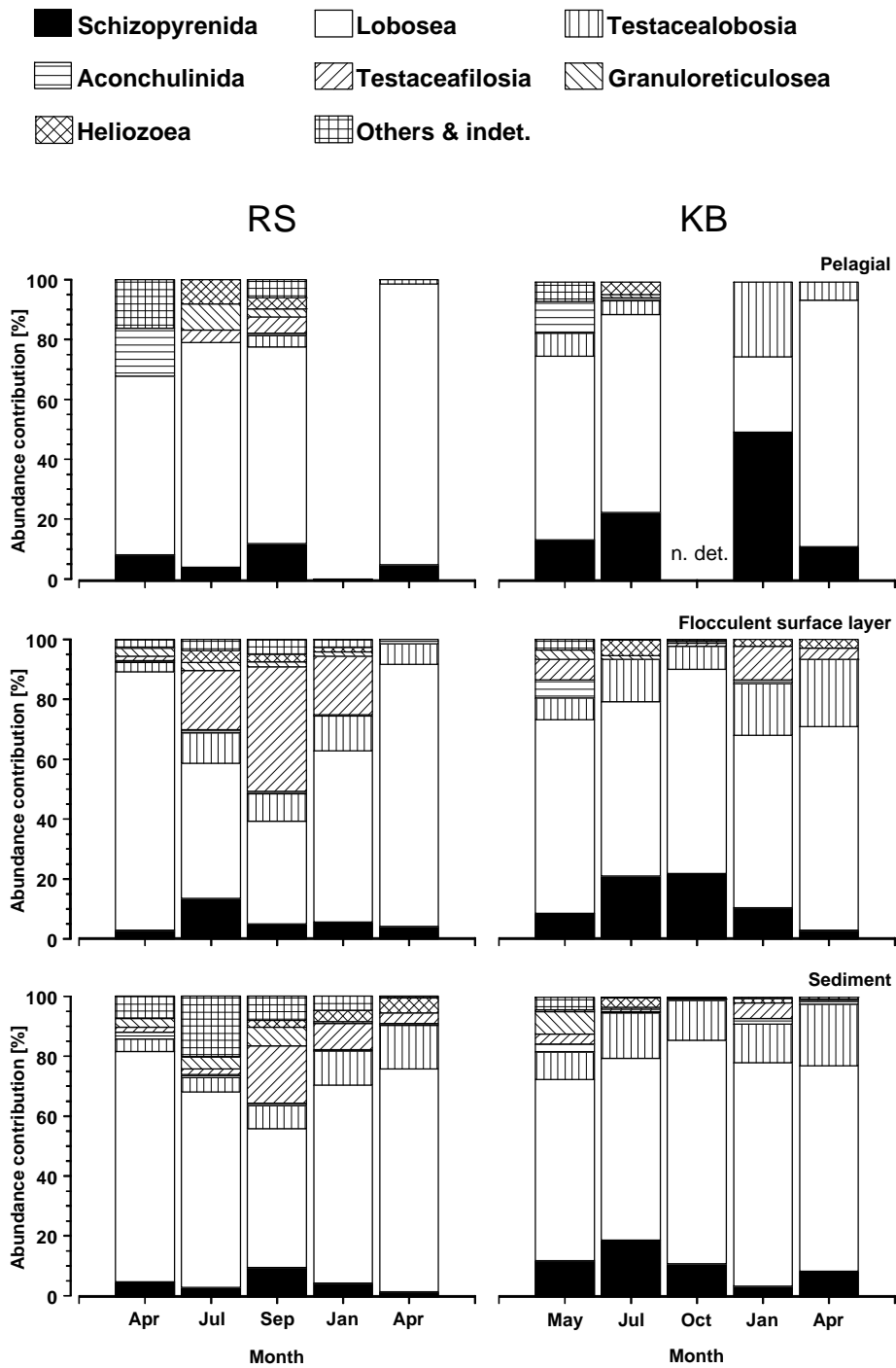


Figure 2.7. Taxonomic composition of sarcodines (rhizopods and heliozoans, means of 3 replicates). Sediment figures refer to the 0-5 mm layer (1996 spring samples), or to the 0-10 mm layer (all other samples).

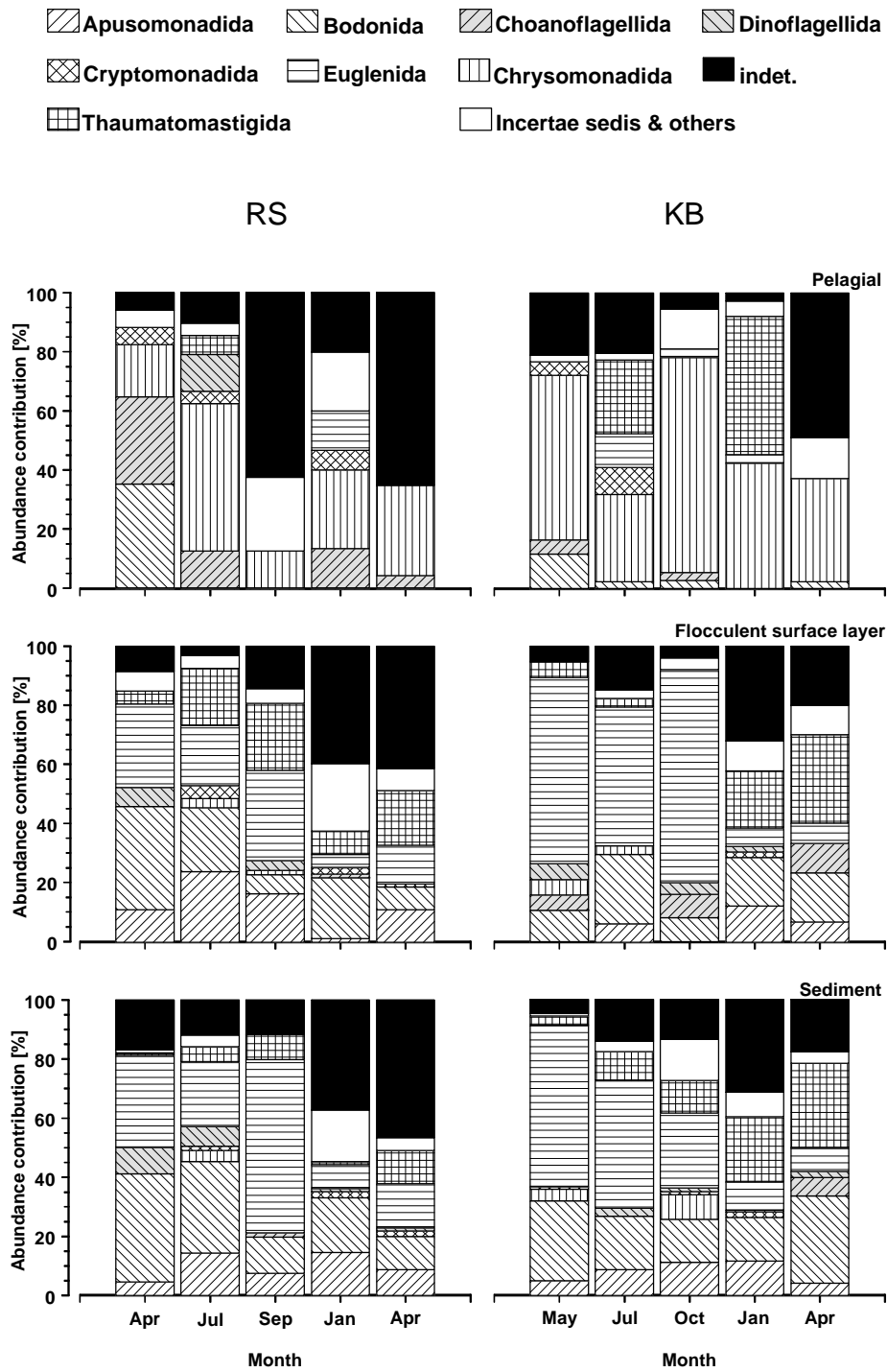


Figure 2.8. Taxonomic composition of heterotrophic flagellates (means of 2-3 replicates).

Table 2.3. Mean contributions (average of five sampling campaigns) of ciliates, rhizopods and heterotrophic flagellates to the combined biomass of heterotrophic protists (¹ April / May campaign 1996 excluded; ² October campaign 1996 excluded; Fsl ... flocculent surface layer).

Station	Layer	Ciliates [%]	Rhizopods [%]	Flagellates [%]
RS	Plankton	73	3	24
	Fsl	50	25	25
	Sediment (0-5 mm)	48	37	15
	Sediment (5-10 mm) ¹	70	19	11
KB	Plankton ²	19	1	80
	Fsl	41	35	24
	Sediment (0-5 mm)	50	26	24
	Sediment (5-10 mm) ¹	69	22	9

1996), ciliate abundances were within the same range at both stations. The abundance peak in July 1996 at station KB was due to a mass development of small scuticociliates and oligotrichs.

Observations ² on the ciliate fauna yielded about 60 species. Clear differences were found between pelagic and benthic ciliate communities. Small aloricate Oligotrichida and Litostomatea (mainly *Mesodinium pulex* and *Didinium nasutum*) dominated water column abundances at station RS. Although this was generally true for station KB as well, Hymenostomatida (mainly small scuticociliates) were abundant at two occasions, and Hypotrichia at one occasion (Fig. 2.6).

The taxonomic composition of the benthic ciliate fauna varied between stations and sampling campaigns (Fig. 2.6). On average, Karyorelictea (mainly *Cryptopharynx spp.*, *Kentrophorus spp.*, and Trachelocercida) were the most abundant group at station RS (22% mean abundance contribution). Their average contribution doubled from the 0 - 5 mm to the 5 - 10 mm layer (data not shown). Hymenostomatea (mainly *Pleuronema coronatum* and other, smaller scuticociliates) dominated sediment abundance at station KB (41 % mean contribution). The ciliate community of the flocculent surface layer at station KB was dominated by small Litostomatida (mainly *Mesodinium pulex*) at most occasions.

2.4.3. Distribution and taxonomic composition of rhizopods

Although rhizopods ranked above flagellates in terms of benthic biomass, their abundances were usually lower than those of flagellates (Fig. 2.5). In the flocculent surface layer, they ranged from 1,100 – 24,000 ind. cm⁻³, and in the sediment from 1,800 - 8,400 ind. cm⁻³. Flocculent surface layer abundances showed the highest temporal variability, whereas sediment abundances fluctuated less. Minimal benthic abundances were generally found in the January samples. Water column abundances of rhizopods were low (< 0.08 – 5.5 ind. cm⁻³) and highly variable.

Benthic rhizopod abundance was dominated by members of the Gymnamoebia (64 % and 66 % abundance contribution at stations RS and KB, respectively, Fig. 2.7). Due to their greater body size, Testaceafilosia contributed up to 76 % to the biomass of benthic rhizopods (September 1996, station RS, data not shown). The rhizopod community in the water column consisted of a subset of the species found in the benthos, mainly of small Vannellidae and Vexilliferidae. Larger Testaceafilosia (e. g. *Cyphoderia ampulla*) or Aconchulinida (e. g. *Lithocolla globosa*) only significantly contributed to pelagic rhizopod biomass when their benthic abundances were high and wind speed exceeded 5 m s⁻¹. Heliozoa were of minor importance within the protistan community sampled. Rhizopods and heliozoans together comprised about 50 morphospecies.

2.4.4. Distribution and taxonomic composition of flagellates

Total flagellate abundances ranged from 210 – 3700 ind. cm⁻³ in the water column, from 14 - 111 * 10³ ind. cm⁻³ in the flocculent surface layer and from 6 - 80 * 10³ ind. cm⁻³ in the sediment (Fig. 2.5). Planktonic flagellate abundances at station KB exceeded those at station RS by a factor of five on average. A similar - though less pronounced - trend prevailed in the sediment. Within the benthos, flocculent surface layer abundances were usually higher and more variable than sediment abundances.

More than 100 species of heterotrophic flagellates have been identified in the study area, most of them in the benthos (A.P. MYLNIKOV & H. ARNDT, pers. comm.). Chrysomonadida and Choanoflagellida tended to dominate pelagic abundances, whereas Euglenida (mainly *Petalomonas spp.*), Bodonida (*Bodo spp.* and *Rhynchomonas nasuta*), Thaumatomastigida (mainly *Protaspis spp.*), Apusomonadida (mainly *Amastigomonas spp.*) and Dinoflagellida usually were the dominant groups in the benthos (Fig. 2.8). This pattern was altered at several occasions when representatives of the latter groups attained high relative abundances in the pelagial.

Table 2.4. Correlations (Spearman's rank correlation coefficient) of pelagic abundances of ciliates, rhizopods, and heterotrophic flagellates (HF) to their benthic (sediment and flocculent surface layer) abundances, and to water column chlorophyll **a**. (one-tailed significance: * $p < 0.05$; ** $p < 0.01$).

Station	Water column abundance of	Chl <i>a</i>	Flocculent layer abundance	Sediment abundance
RS	Ciliates	0.872*	0.667	0.667
	Rhizopods	-0.051	0.410	0.975**
	HF	0.400	0.900*	0.500
KB	Ciliates	0.718	0.800	0.900*
	Rhizopods	0.949*	0.400	1.000**
	HF	0.237	0.616	1.000**

2.4.5. Relationships between layers and between pelagic protists, seston, and chlorophyll **a** concentrations

The water column abundances of all protistan groups at station KB were positively correlated to those of the sediment (Table 2.4). They resulted in a significant positive correlation between water column and sediment biomass of protists at this station (Spearman's $r = 0.900$, $p = 0.037$). Correlations were mostly non-significant at station RS and between water column and flocculent surface layer abundances at both stations. Water column ciliate abundance was positively correlated to chlorophyll **a** at both stations (station RS: $p = 0.027$, station KB: $p = 0.086$). In contrast, flagellates showed only weak, non-significant correlations to chlorophyll **a**. Rhizopods were the only group showing different trends at both stations, with a strongly positive correlation to chlorophyll **a** at station KB, but no correlation at station RS.

At station RS, total protistan biomass and the abundance of flagellates in the water column were significantly positively correlated to seston concentrations measured directly above the sediment (protistan biomass: Pearson's $r = 0.899$, $p = 0.038$, flagellate abundance: Pearson's $r = 0.985$, $p = 0.002$). Except for rhizopod abundance at station RS, positive but non-significant correlations to seston concentration were found for all protistan groups. Significant multiple linear regressions with seston concentration and sediment abundance as independent variables and water column abundance as the dependent variable were found for the flagellates at station RS and for the ciliates at station KB (Table 2.5). However, when

the R^2 was corrected for the number of variables in the model, the multiple regression explained less of the variance of ciliate abundance than a linear regression on sediment abundance alone. In the case of the flagellates, only slightly more of the variance was explained by the multiple regression than by the simple linear regression on seston concentration. Thus, pelagic flagellate abundance at station RS was closely related to seston concentration, whereas the other pelagic abundances were closer related to the abundances of the respective groups in the sediment.

Table 2.5. Parameters of multiple linear regressions with water column abundance as dependend variable and seston concentration (station RS: above bottom seston concentration) and sediment abundance as independend variables. (HF: heterotrophic flagellates).

	Constant	Non-standardized regression coefficient		Partial correlation coefficient		Adjusted R^2	Significance
		Seston conc. [mg l ⁻¹]	Sediment abund. [Ind. cm ⁻³]	Seston conc. [mg l ⁻¹]	Sediment abund. [Ind. cm ⁻³]		
HF (RS)	-8.97	27.23	5.57	0.985	0.369	0.975	0.013
Ciliates (KB)	-49341	123.03	140.00	0.199	0.984	0.955	0.022

2.5. Discussion

2.5.1. Quantitative importance of heterotrophic protists

According to my data, the quantitative importance of heterotrophic protists differs between pelagial and benthal. Heterotrophic protists usually dominated the standing stock of the combined proto- and metazooplankton, but played a relatively minor role in the benthos (Fig. 2.4). Their estimated biomass contributions of 73 % (station RS) and 84 % (station KB) were higher than those previously reported from lakes and coastal waters (e. g. SMETACEK 1981, MATHES & ARNDT 1994). Resuspension of benthic protists into the water column alone does not explain these contributions because they were also found when protozooplankton biomass consisted exclusively of true planktonic species. Instead, the high protozooplankton

contributions reflect the decline in metazooplankton biomass in response to eutrophication and the particular importance of the microbial food web in the system under study (SCHIEWER 1998). Biomass contributions of protozooplankton were minimal in spring when copepods (mainly *Acartia* spp. at station RS and *Eurytemora* spp. at station KB) feeding on particles within the protozooplankton size range reached peak abundances (HEERKLOSS ET AL. 1999).

In contrast to their high contribution to zooplankton biomass, heterotrophic protist biomass was much lower than that of meiofauna in the sediment. This finding is in agreement with earlier data (ARNDT ET AL. 1990, FENCHEL 1967). If macrofauna would have been included in the benthic biomass comparison, the contribution of heterotrophic protists would have been even lower. Macrozoobenthos biomasses in the order of 4.8 – 11.5 g C m⁻² and 0.6 – 6.1 g C m⁻² have been found at stations close to station RS and KB, respectively (ARNDT 1988).

2.5.2. General trends of heterotrophic protistan community structure

Protozooplankton biomass was within the same order of magnitude as at comparable inshore sites (SMETACEK 1981, GAST 1985, WITEK 1998). The fact that it was on average five times higher at the shallow and highly eutrophic station KB than at station RS is in agreement with data from varying environments: similar trends were found during other studies of Baltic protozooplankton (GAST 1985, ARNDT 1991), and in cross-lake comparisons (BEAVER & CRISMAN 1982, MATHES & ARNDT 1994).

The benthic heterotrophic protistan communities contributed approximately the same biomass per area as the protozooplankton (44 % at station RS and 49 % at station KB). There are only a few studies with which to compare these benthic biomasses. FENCHEL (1967) found ciliate biomasses of 0.03 – 2.3 g m⁻² (fresh weight) in Danish coastal sediments. Converted to organic carbon units, this would be within the range found during my study. FENCHEL (1967) concluded that heterotrophic flagellates and amoebae were much less important than ciliates but was aware that his methodology was most suitable for the enumeration of ciliates. FERNANDEZ-LEBORANS & NOVILLO (1993) found that in sandy sediments of the Bay of Biscay, biomass was dominated by ciliates at two of the three stations investigated, and by amoebae at the third station. FINLAY ET AL. (1988) estimated biomasses of benthic and pelagic heterotrophic protists in a hypertrophic freshwater pond. Expressed per unit of area, biomass of ciliates in the water column exceeded that of the aerobic and anaerobic sediments by factors of six and 41, respectively, making the benthic biomass contribution of ciliates relatively low in this freshwater system. In contrast, the large anaerobic archamoeba *Pelomyxa palustris* reached a high benthic biomass. BARK (1981)

found a numerical dominance of heterotrophic flagellates in the top centimeter of a freshwater sediment that was subjected to summer bottom anoxia. Benthic protistan contributions to the combined biomass with protozooplankton were also lower than in my study. The occurrence of an anoxic hypolimnion and sediment surface in stratified lakes and ponds appears to be responsible for part of the difference of their heterotrophic protistan vertical distribution to shallow coastal waters.

2.5.3. Contribution of taxonomic groups

Although total protistan biomass was similar in the benthos and in the pelagial, it was represented by different taxonomic groups. The main difference between benthic and planktonic community structure was the high benthic biomass contribution of naked and testate rhizopods, making rhizopods more important than flagellates in the benthos (Table 2.3). Rhizopods also contributed a significant portion (about 50 morphospecies as compared to about 100 species of heterotrophic flagellates and 60 species of ciliates) to the species richness of the heterotrophic protistan community of the study area. These comparative data support the idea of rhizopods as a prominent part of the nano- and microzoobenthos. BUTLER & ROGERSON (1995, 2000) found 70 species and mean annual abundances of 870 and 2,200 rhizopods cm^{-3} in sandy and silty sediments, respectively, of the Clyde Sea area (Scotland). Abundances of gymnamoebae of 17,600 - 40,600 cells g^{-1} sediment were found in inshore marine and brackish habitats at Bermuda (ANDERSON 1998), similar to my findings.

The structure of the rhizopod community of my study area showed some peculiarities that reflected its relatively low salinity: in addition to Gymnamoebia, Schizopyrenida and Testaceafilosia, members of the Aconchulinida and Testacealobosia (mainly *Cochliopodium* spp.) were frequently observed. These organisms are typical of brackish and freshwaters. Foraminiferans were only occasionally found in enrichment cultures or in meiofauna samples from the study area (DIETRICH, pers. comm.).

The low abundance of rhizopods in the water column as compared to the benthos, the strong correlation between benthic and pelagic rhizopod abundance and the absence of exclusively planktonic rhizopod morphospecies from my samples suggest that there is no autochthonous pelagic community of rhizopods in my study area. This may be due to the strong benthic influence in these exceptionally shallow waters, but a comparison of benthic and pelagic data from the deeper Clyde Sea shows a similar trend (ANDERSON & ROGERSON 1995, BUTLER & ROGERSON 1995). Therefore, a close coupling of pelagic to benthic rhizopod communities may be a general feature of coastal waters. This notion is further supported by increased pelagic rhizopod abundances in the vicinity of shallow shelf areas of the Black Sea that was attributed to sediment resuspension (MURZOV & CARON 1996). Pelagic ciliate

communities were generally comprised of different taxa than those in the benthal. This finding is in agreement with an earlier benthic-pelagic comparison of ciliate community structure (FINLAY ET AL. 1988), and with studies focusing on either benthic or pelagic ciliate communities (e.g. FENCHEL 1967, LEAKEY ET AL. 1993, WITEK 1998). The taxonomic composition of the pelagic ciliate fauna, with aloricate Oligotrichida as the dominant group and fluctuating contributions of Tintinnida, Litostomatida, Prostomatida, and Hymenostomatida, was similar to those reported previously from the Baltic and other coastal waters (SMETACEK 1981, LEAKEY et al. 1993, WITEK 1998).

The taxonomic composition of benthic ciliates resembled the ciliate fauna of other coastal sediments (reviewed by PATTERSON ET AL. 1989). However, the abundance contributions of scuticociliates and *Mesodinium spp.* at station KB are conspicuously high in comparison to station RS. Increased planktonic abundance contributions of small scuticociliates like *Cyclidium spp.* have been reported from eutrophic waters (BEAVER & CRISMAN 1982, SHERR ET AL. 1986). My data are consistent with a similar trend in the sediment.

The benthic ciliate abundances found during this study and during other studies in the same area (DIETRICH & ARNDT 2000) occupy the same range as those found in a British estuary and in a tidal flat in Massachussets Bay (AL-RASHEID & SLEIGH 1995, EPSTEIN 1997A). Lower mean annual abundances of 533 – 729 ind. cm⁻³ were found in sandy coastal sediments of the Bay of Biscay (FERNANDEZ-LEBORANS & NOVILLO 1993), likely due to the coarser sediments and lower organic input.

In contrast to the ciliates, benthic and pelagic communities of heterotrophic flagellates showed a high degree of taxonomic overlap at some occasions. Numerous species of bodonids, thaumatomastigids, apusomonadids and Protista incertae sedis were found both in the benthos and in the pelagial where they were probably associated to suspended particles (Fig. 2.3). These species should be considered benthic-pelagic, rather than benthic or pelagic (see ARNDT ET AL. 2000). The taxonomic composition of the flagellate communities is reflected by significant correlations of pelagic flagellate abundances to those in the sediment or in the flocculent surface layer (Table 2.3). Surface-associated flagellates of benthic and pelagic origin (e.g. chryomonads) formed the major part of flagellates in the water column (Fig. 2.6, 9), comparable to other estuarine ecosystems (e. g. ROGERSON & LAYBOURN-PARRY 1992 A).

Total pelagic flagellate abundances were within the lower part of the range reported from comparable coastal ecosystems (FENCHEL 1982, SANDERS ET AL. 1992). The trend towards higher flagellate biomass at station KB compared to station RS may reflect differences in food supply: bacterial abundances at station RS ranged from 4.8 – 10.1 * 10⁶ ind. cm⁻³ (with the exception of a September peak of 20.5 * 10⁶ ind. cm⁻³), whereas at station

KB higher abundances of $16.7 - 38.4 \cdot 10^6 \text{ ind. cm}^{-3}$ were recorded (R. SCHUMANN, pers. comm.). The taxonomic composition of planktonic flagellate communities has only occasionally been addressed. The dominance of chrysomonads and the occurrence of other surface-associated flagellates from different taxonomic groups (Fig. 2.9) resembles the general structure of pelagic flagellate communities from lakes, rivers and estuaries (for review see ARNDT ET AL. 2000).

The benthic flagellate abundances found during this study are at the lower end of the range published from comparable habitats (e. g. BAK & NIEUWLAND 1989, STARINK ET AL. 1996). However, up to now most studies used epifluorescence microscopy, which gives only little information on the taxonomic composition of the communities studied. Within the benthic flagellate community of my study area, relatively large, herbivorous or omnivorous groups contributed a significant part to abundance and biomass. The predominance of bodonids and euglenids and the regular appearance of thaumatomastigids, apusomonads and cercomonads agree with the few available data from marine, brackish and limnetic sites (ARNDT ET AL. 2000).

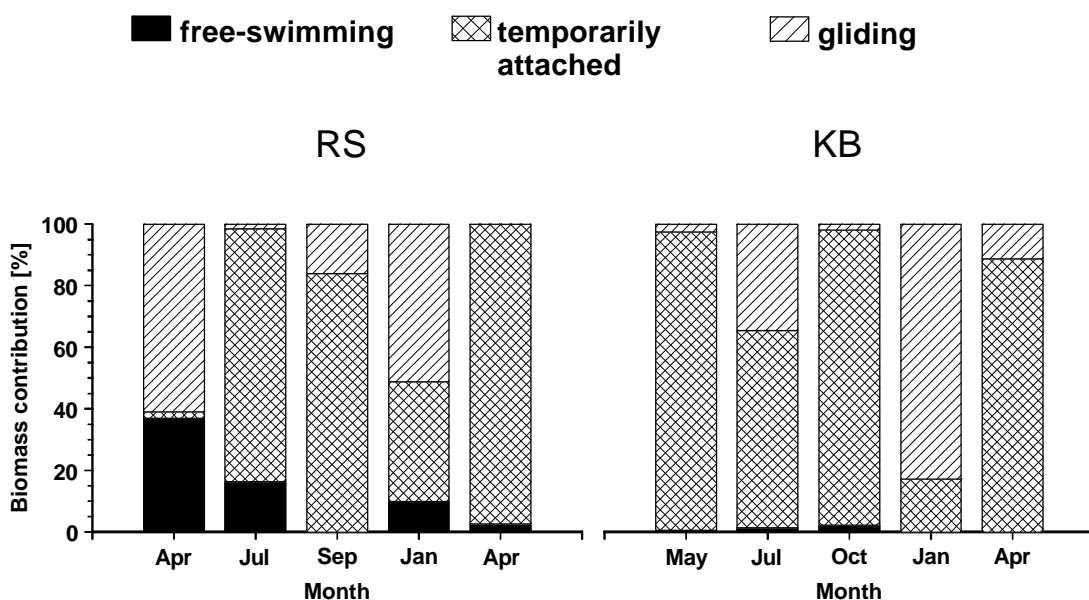


Figure 2.9. Contribution of free-swimming (Choanoflagellida, Dinoflagellida, *Katablepharis spp.*), gliding (Bodonida, Thaumatomastigida, Cercomonadida), and temporarily-attached forms (Chrysomonadida) to the biomass of heterotrophic flagellates in the water column.

2.5.4. Methodology

Part of the difference between my study and other published accounts of heterotrophic protistan community structure may be due to differing methodologies. The live-counting method was chosen because differences in community structure between benthic and pelagic heterotrophic protists were a main focus of this study. Although there are other methods for the analysis of pelagic ciliate community structure (e. g. SKIBBE, 1994), pelagic ciliates were also counted in fresh samples in order to improve the comparability of benthic and pelagic data. Since sample size and number are limited with live-counting methods, rare species may have been overlooked during my study, and only one to two sediment samples could be analysed with respect to the ciliates and heterotrophic flagellates. This limitation was due to the specific conditions of the sediment which renders the use of fixed samples for protist identification and enumeration difficult. As a consequence, the variance of ciliate and heterotrophic flagellate abundances could only be assessed at two of the five sampling campaigns, which makes conclusive comparisons of protistan abundances between layers, campaigns, and taxonomic groups problematic. However, the data are sufficient to correlate them between layers and to environmental variables, and to show general trends of heterotrophic protistan distribution in my study area. The detection limits were low enough that only species making up less than 5 % of the total abundance were likely to be missed. Recent methodological developments will help to solve the problem of benthic ciliate community analysis in the future (WICKHAM ET AL. 2000).

For the analysis of rhizopod community structure, the liquid aliquot method is the only well-established method. The abundance data obtained with this method are likely to be minimum estimates of actual abundances because culture conditions or competition within the cultures may exclude some of the rhizopod species, and any clumping of sediment aggregates during inoculation results in underestimates of actual abundance (see BUTLER & ROGERSON 1995 and Chapter 3 for a detailed discussion of this method).

2.5.5. Significance of benthic-pelagic coupling

Although pelagic abundances of all groups were closely coupled to sediment abundances at the shallow station KB, this may reflect seasonal effects on both benthic and pelagic communities, rather than direct transport effects. Significant exchange of species between benthic and pelagic communities was only found in the flagellates. The resuspension of benthic rhizopods was insignificant at the level of the whole protozooplankton community. Turbidity usually decreases quickly with decreasing wind

speed in my study area, as indicated by stronger correlations with decreasing than with increasing wind speed. Thus, the direct effects of wind-induced sediment resuspension on the vertical distribution of heterotrophic protists are probably restricted to short intervals. A limited duration of wind-induced turbidity effects was also detected in other estuarine systems and in a variety of shallow lakes (WARD ET AL. 1984, OGILVIE & MITCHELL 1998).

This finding does not exclude a trophic coupling between the benthic and pelagic microbial food web, however. The positive correlation of pelagic ciliate abundances to both chlorophyll *a* concentrations and benthic abundances suggest that both benthic and pelagic ciliates responded to water column chlorophyll *a*. The same appears to be true for the benthic rhizopods at station KB. Sedimentation of phytodetritus also enhanced population growth of heterotrophic flagellates in sediments of the coastal North Sea (BAK ET AL. 1991, 1995). On the other hand, experimentally induced resuspension of particulate matter increased heterotrophic protistan population growth in the overlying seawater (WAINRIGHT 1987). According to these findings and to my data, there may be a close coupling between benthic and pelagic food webs which is governed largely by trophic mechanisms, such as the exchange of edible organic matter by wind-driven resuspension and deposition. This aspect of the benthic-planktonic coupling of coastal microbial food webs requires experimental study (Chapter 4).

3. Seasonal abundances and community structure of benthic rhizopods in a shallow lagoon of the Southern Baltic Sea

3.1. Summary

In order to assess the quantitative importance and community structure of benthic rhizopods in brackish lagoons of the Southern Baltic Sea, their abundance, biovolume, and taxonomic composition were studied with a liquid cultivation method. Seasonal dynamics in the superficial sediment of station Bäk (Hiddensee Island) were investigated during eleven sampling campaigns between March and November 1996.

Rhizopod abundances at station Bäk ranged from 2,800 – 10,900 cells cm⁻³. A seasonal trend with a summer maximum and minima in early spring and late autumn was observed. 46 morphotypes of rhizopods were found, 27 of which were identified to species. *Gymnamoebia* and *Schizopyrenida* always dominated the rhizopod community numerically, whereas testate and naked filose rhizopods sometimes contributed the major part to community biovolume. Typical marine and freshwater rhizopods coexisted in the study area. In addition to bacterivorous forms, high contributions of herbivores and omnivores were found.

My results suggest that the hitherto little-studied rhizopods are a major component of benthic protistan communities of shallow coastal waters. The high contributions of herbivorous and omnivorous forms to the rhizopod community indicate a complex trophic role of rhizopods within the benthic microbial food web.

3.2. Introduction

The functional importance of the microbial food web for the carbon and nutrient turnover of pelagic ecosystems is now firmly established (e. g. AZAM ET AL. 1983, FENCHEL 1987). Recent findings show that a similar food web exists in coastal sediments, fuelled by sedimenting detritus and microphytobenthos primary production (FENCHEL 1967, BAK ET AL. 1995, EPSTEIN 1997A). Similar to the water column, heterotrophic protists act as bacterivores, herbivores, and omnivores within the benthic microbial food web. While rhizopods other than foraminiferans generally play a minor role within the protozooplankton (CARON & SWANBERG 1990, ARNDT 1993), their importance in the benthos is still unclear.

Studies focussing on rhizopod abundance and distribution in marine sediments have only recently been published (BUTLER & ROGERSON 1995, ANDERSON 1998, DECAMP ET AL. 1999). Abundances in the order of $10^3 - 10^4$ ind. cm^{-3} which were found during these studies support the hypothesis that - in contrast to the water column - rhizopods are an important component of the benthic microbial food web. However, conclusive statements about the quantitative importance of rhizopods within a given ecosystem require comparative data on other protistan groups, which have only rarely been presented (e. g. FERNANDEZ-LEBORANS & NOVILLO 1993).

Micro- and nanozoobenthic rhizopods are a polyphyletic and heterogeneous group. They include Schizopyrenida, Gymnamoebia, Testacealobosia, Aconchulinida, Testacea-filosia, Granuloreticulosea, and amoeboid Protista incertae sedis. The few quantitative accounts published have focussed on naked lobose rhizopods belonging to the Gymnamoebia and Schizopyrenida. The taxonomic resolution of these studies was restricted to a distinction between broad morphological categories (ANDERSON 1998, DECAMP ET AL. 1999). In contrast, faunistic studies have shown that rhizopod communities may comprise a considerable species richness (SAWYER 1974, 1975 A, B, VØRS 1992, GOLEMANSKY 1998 A, B). The trophic roles of natural rhizopod communities are likely to vary with their taxonomic composition because bakterivory, herbivory, and omnivory have been experimentally demonstrated in a variety of rhizopod species (BOVEE 1960, BUTLER & ROGERSON 1997, LAYBOURN-PARRY ET AL. 1987). A high taxonomic resolution of quantitative field data is necessary to derive hypotheses about the role of rhizopods within the benthic microbial food web using functional group approaches (e. g. PRATT & CAIRNS 1985).

This study was carried out in order to provide new information about the ecological role of rhizopods within the benthic microbial food web. I have assessed the quantitative importance (absolutely and in comparison to other protistan groups), seasonal distribution and taxonomic composition of a micro- and nanozoobenthic rhizopod community in a shallow lagoon of the Southern Baltic. In order to quantify the relative importance of rhizopods, their community biovolumes were compared to those of ciliates and heterotrophic flagellates which were enumerated in the same samples by cooperating colleagues (DIETRICH & ARNDT 2000). Based on the taxonomic composition of the community, I have estimated the relative importance of different functional groups, and of marine versus freshwater species, within the benthic rhizopod community.

3.3. Materials and Methods

3.3.1. Study area

The study was carried out in shallow, non-tidal, brackish lagoons at the German coast of the Baltic Sea (Figure 3.1). Rhizopod community structure and seasonal dynamics in the superficial sediment were investigated at station Bäk throughout 1996. Additional samples from three sediment layers and from the water column were taken during five sampling campaigns in 1996 and 1997 at stations Rassower Strom and Kirrbucht. In this article, abundance and biomass totals from station Bäk and data about the community structure of all three stations are presented. The stations varied in salinity, depth, trophic status and sediment type (Table 3.1, Figure 3.2).

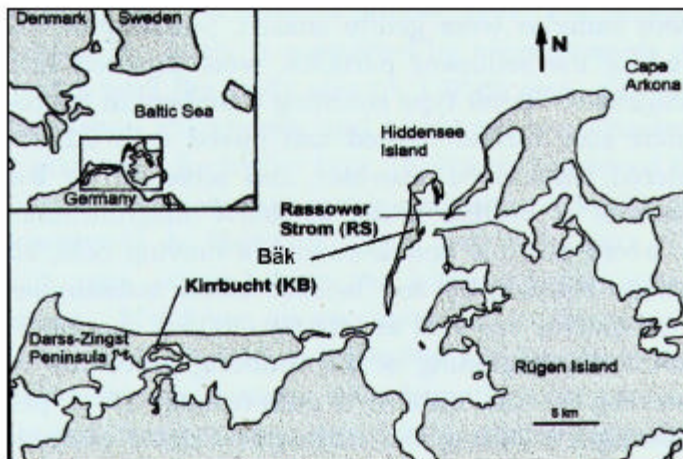


Figure 3.1. Location of sampling sites.

Table 3.1. Characterization of sampling sites. Ranges are given in parentheses (n. det.: not determined; OC: organic carbon content)

	Bäk	Rassower Strom	Kirrbucht
Water depth [m]	0.5	3.8	0.7
Salinity [PSU]	8 (6-10)	9 (8-12)	5 (2-10)
Trophic status	mesotrophic	mesotrophic	polytrophic
Water column chl a [$\mu\text{g l}^{-1}$]	n. det.	2.7 (1.3-4.5)	24 (12-33)
Seston [mg l^{-1}]	n. det.	7 (4.5-11)	60 (20-100)
Sediment type	muddy sand	sandy mud	muddy sand
Sediment OC [%]	4	4	1

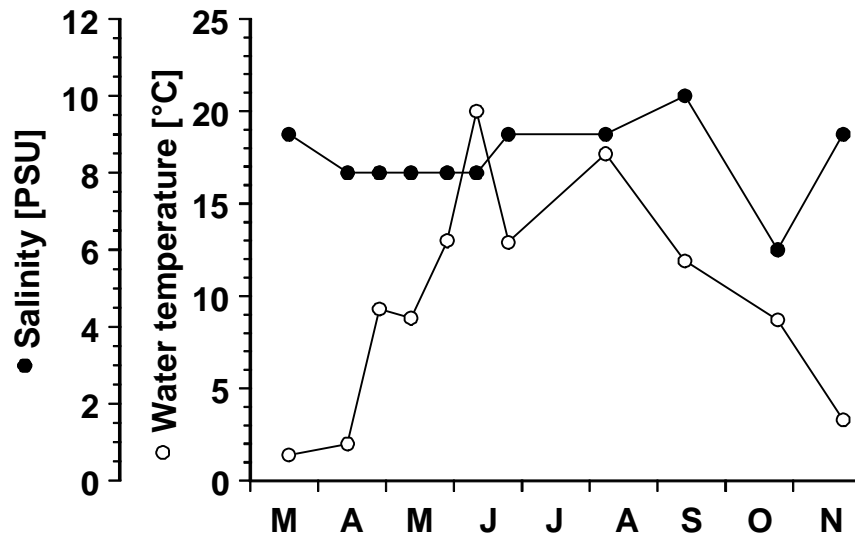


Figure 3.2. Water temperature and salinity at station Bäk.

3.3.2. Sampling

At each sampling, duplicate sediment cores (100 mm internal diameter) with approximately 10 cm overlying water were obtained with a manual corer. From these cores, subsamples were taken for sediment characteristics, direct microscopical observation, enrichment cultures, and for the enumeration of amoebae, respectively. The subsamples (0 - 3 mm depth) were taken with a cut off plastic-syringe with an 11 mm internal diameter. Three subsamples were taken from each core and pooled to reduce the small-scale spatial heterogeneity within individual cores.

Since the aerobic sediment layer usually extended down to a depth of 3 - 5 mm (GERBERSDORF ET AL. 2001), the 0 - 3 mm subsamples from station Bäk represented the oxic sediment stratum. Additional sediment layers were sampled during another sampling campaign at two other stations. Data from these stations are reported elsewhere (Chapter 2).

3.3.3. Determination of the taxonomic composition of the rhizopod community

The morphotype composition of the sediments was determined in fresh samples and in enrichment cultures under a Zeiss Axioplan microscope with phase contrast and interference contrast optics. Enrichment cultures from approximately 1 ml of the diluted subsamples were incubated at 18 °C in 7.5 ml modified Føyns-Erdschreiber-medium (MErd,

(PAGE 1983)) for 10 - 20 d. Cell dimensions (length and breadth of cells, diameter of nucleus and nucleolus, proportion of hyaloplasm and granuloplasm) were measured with an ocular micrometer under 400x magnification. The thickness of attached rhizopods was measured with a calibrated stage drive (interval 1 μm). 20 - 50 cells of each species were measured, depending on their frequency of occurrence. Specific individual biovolumes were estimated from cell dimensions (without subpseudopodia) applied to geometric models (Table 3.2). In addition to these parameters, the speed and locomotive behaviour of moving cells and the morphology of floating forms were recorded. Whenever possible, modern identification keys or original descriptions were used for the identification of rhizopods (HIBBERD 1971, SAWYER 1975 B, 1980, PAGE 1977, 1983, 1988, PAGE & WILLUMSEN 1983, DYKSTRA & PORTER 1984, PATTERSON & FENCHEL 1990, PAGE & SIEMENSMA 1991, MIKRJUKOV & MYLNIKOV 1998). Some species identifications were based on older identification literature, however (GROSPIETSCH 1972, BOVEE 1985A-C).

Table 3.2. Geometric models and formulas for biovolume calculations from cell dimensions of rhizopods. Subpseudopodia were not considered for biovolume calculations. d... diameter of cell; d_{gp} ... diameter of the granuloplasmatic hump; h... height of cell; h_c ... height of cylinder; h_s ... height of spherical segment; l... length of cell; l_c ... length of semi-cylinder; V... volume of cell; w... width of cell.

Rhizopod group	Shape	Remarks	Formula
Limax amoebae, <i>Stygamoeba</i>	Semi-cylinder	$l_c = 0.8 * l$	$V = 0.5 \pi * h^2 * l_c$
Thecamoebidae, <i>Paraflabellula</i>	Spherical segment		$V = \pi / 6 * h * (0.75 * l^2 + h^2)$
Paramoebidae, Vexilliferidae Chrysamoeba, Massisteria	Flat cylinder with ovoid cross-section		$V = 0.25 \pi * l * w * h$
Vannellidae, Cochliopodidae,	Flat cylinder with ovoid cross section + spherical segment	Flat ellipse: $h_c = 0.5 * h$ Spherical segment: $h_s = 0.5 * h$ and $d = d_{gp}$	$V = 0.25 \pi * l * w * h_c + \pi / 6 * h_s * (0.75 * d_{gp}^2 + h_s^2)$
Aconchulinida, <i>Diplophrys</i>	Sphere	Cytoplasm only	$V = \pi / 6 * d^3$
Phryganella	Hemisphere	Cytoplasm only	$V = \pi / 12 * d^3$
Testaceafilosia, Granuloreticulosea	Rotation ellipsoid	Cytoplasm only	$V = \pi / 6 * l * h * w$

3.3.4. Enumeration of rhizopods

For the enumeration of amoebae, a modified version of the liquid aliquot method (BUTLER & ROGERSON 1995, SMIRNOV ET AL. 1998) was employed. 36 aliquots (10 μl) from the enumeration subsample of each core were inoculated into the wells of tissue culture

plates (Falcon) containing 2 ml of MErd-medium. The plates were incubated in the dark at 18 °C and screened for the presence of rhizopod morphotypes after 12 and 24 days under an inverted microscope (Nikon Diaphot) at 200x magnification. The abundance of rhizopods of each morphotype in the subsamples was estimated from their frequency of occurrence in the wells assuming a Poisson distribution:

$$P(k) = \lambda^k / k! * e^{-\lambda}$$

with $\lambda = N / T$

where $P(k)$ is the probability of a culture to originate from k cells in the inoculum, λ is the parameter of the Poisson distribution, N is the actual number of cells in the inoculum, and T is the number of cultures. Although not tested explicitly, the Poisson distribution is the most conservative assumption if on average there are only few cells per well (SOKAL & ROHLF 1995). Based on this distribution, expected frequencies of cultures originating from one, two, and more inoculated cells were calculated for different cell abundances in the inoculum. From the proportion of cultures originating from one, two or more cells, it was possible to calculate a calibration curve relating the number of cultures in which a species was found to the number of cells of this species in the inoculum. Cell abundance (N) for each sample was calculated from the number of cells in the inoculum according to the following formula:

$$N [\text{Ind. cm}^{-3}] = (N_i * f_d * 1000) / (36 * V_a [\mu\text{I}])$$

where N_i is the number of cells in the inoculum, f_d is the factor of sample dilution, and V_a is the inoculum volume pipetted into each of the 36 wells.

3.3.5. Methodological investigations

The potential problem of an overestimation of vegetative cell abundance due to excystment during incubation was addressed in three ways: 1) The taxonomic resolution of the analysis allowed a discrimination between cyst-forming species and others without a documented ability to form cysts. 2) At one sampling occasion (station Bäk, 12 September 1996), parts of each subsample were kept in seawater-HCl (2 % final concentration) for 12 h to kill vegetative cells. This procedure is commonly used in studies of soil protozoa (SINGH 1946, BERTHOLD & PALZENBERGER 1995). After neutralization, the pre-treated subsamples were incubated and scored as usual. All cells found in these cultures were attributed to

excystment. 3) From the crude enrichment cultures described in the previous section, strains of the common potentially cyst-forming species were isolated. These cultures were subjected to a variety of adverse conditions: gradual heating to 35 °C and subsequent desiccation, gradual cooling to 5 °C and starving conditions, gradual (within 14 d) decrease of salinity to < 2 PSU, and gradual (within 3 d) decrease of pH to < 3. They were regularly screened for the presence of cysts during the following 21 d. Subsequently, standard conditions were restored and those cultures where no vegetative cells had been found after 21 d were checked for their reappearance after another 7 d.

3.4. Results

3.4.1. Abundance and biovolume totals at station Bäk

In the superficial sediment layer of station Bäk, total rhizopod abundances ranged from 2,800 – 10,900 cells cm⁻³ (Fig. 3.3). The corresponding biovolume estimate ranged from 5.1 – 28.5 * 10⁶ µm³ cm⁻³. Maximal abundances were found in late summer. Rhizopod biovolumes peaked in spring and summer.

Apart from a relative decrease between April and July 1996 that was caused by a shift of biovolume dominance from cells > 40 µm to cells < 30 µm equal spherical diameter (data not shown), biovolume estimates generally showed similar trends as rhizopod abundance.

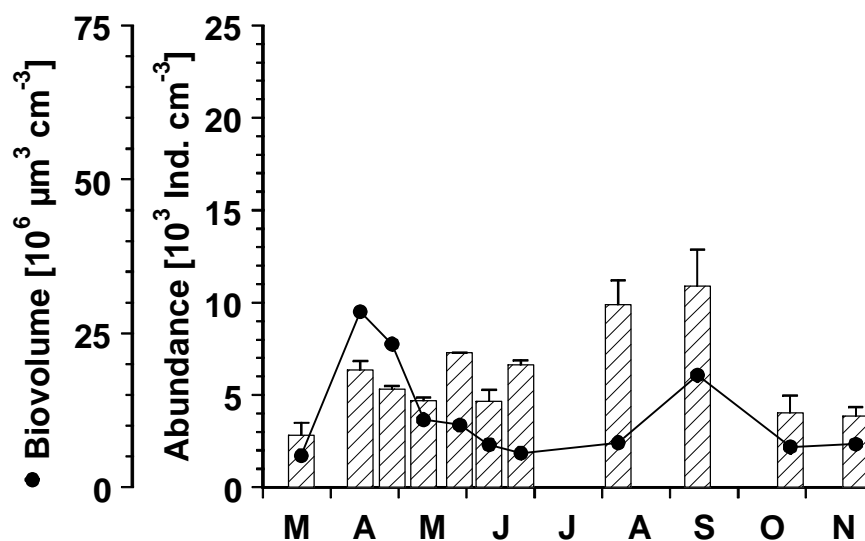


Figure 3.3. Abundance and biovolume of rhizopods in sediment samples (0-3 mm) at station Bäk (Error bars: ½ range, N=2).

3.4.2. Taxonomic composition of the rhizopod fauna

During the whole investigation, 46 amoeboid morphotypes were found, 27 of which could be attributed to described species (Table 3.3). These organisms represented a variety of taxonomic groups including the Schizopyrenida (2 morphotypes), the Gymnamoebia (19), the Testacealobosia (6), the Aconchulinida (4), the Testaceafilosia (4), the Granuloreticulosea (2), and the Protista incertae sedis (4). Accordingly, the rhizopod fauna consisted of several feeding types (PRATT & CAIRNS 1985) and occupied a broad size range. Individual biovolumes ranged from 20 – 45.000 μm^3 . Expressed as equivalent spherical diameter, most of the rhizopods were in the range of 10 - 20 μm . Both marine and typical freshwater rhizopods occurred in the study area, but no shift towards dominance of the latter was found at station Bäk when salinity was low (see Fig. 3.2). Apart from a few rare species, most rhizopods were found at all sampling stations. While only a small minority of the species identified are known to encyst, some of the forms that could not be identified to species belong to genera which include at least some cyst-forming species (e.g. *Vahlkampfia*, *Hartmannella*, *Cochliopodium*, and members of the Testaceafilosia).

In addition to the species listed in Table 3.3, a number of unidentified limax amoebae (amoebae with an elongate, semi-cylindrical cell shape), Vannellidae, Paramoebidae, Granuloreticulosea, and small (< 5 μm) or non-motile, naked rhizopods were found. Among the testate rhizopods, empty tests of a number of marine interstitial forms (e. g. *Pseudocorythion* sp., *Micropsammella* sp.) were recorded.

3.4.3. Contribution of taxonomic groups

The main taxonomic groups contributed differently to the combined abundance and biovolume of the rhizopod community, and they showed different seasonal trends. Gymnamoebia and Schizopyrenida dominated abundances (49 and 22 % mean abundance contribution, respectively), whereas larger Testaceafilosia (mainly *Cyphoderia ampulla* and *Trinema lineare*), Testacealobosia (mainly *Phryganella spec.*), and Aconchulinida (mainly *Lithocolla globosa*) dominated biovolume totals during the first part of the sampling programme (Fig. 3.4). During late spring and summer, biovolume dominance shifted towards the Gymnamoebia and Schizopyrenida. Granuloreticulosea were generally of minor importance (< 1 % mean biovolume contribution). *Stygamoeba polymorpha* (Protista incertae sedis) reached abundances of up to 1030 cells cm^{-3} and thus was the only rhizopod of uncertain taxonomic position which contributed significantly to the rhizopod community.

Table 3.3. Commented list of those morphotypes identified to species or genus. Occ. ... occurrence; n. det. ... not determined; F... freshwater; M...marine; C ... common (present in most samples); R ... regularly (present in > 10 % of samples); O ... rare (present in < 10 % of samples).

Species	Biovol. [µm ³]	Typical Habitat	Cysts	Occ.	Previous Baltic records
Limax amoebae					
<i>Vahlkampfia damariscottae</i>	150	M		C	-
<i>Vahlkampfia spec.</i>	1,100	F/M	X	R	
<i>Hartmannella vermiformis</i>	120	F	X	R	-
<i>Cashia limacoides</i>	n. det.	F		O	-
<i>Saccamoeba spec.</i>	13,400	F/M	?	O	
<i>Rhizamoeba spec.</i>	n. det.	M		O	-
Thecamoebidae & Vannellidae					
<i>Thecamoeba orbis</i>	480	M		C	VØRS 1992
<i>Thecamoeba hilla</i>	1,300	M		R	-
<i>Vannella aberdonica</i>	150	M		C	VØRS 1992
<i>Vannella simplex</i>	4,200	F		R	VØRS 1992
<i>Vannella platypodia</i>	980	F		R	VØRS 1992
<i>Vannella spec.</i>	1,300	F/M		R	
<i>Platyamoeba langae</i>	110	M		C	-
<i>Platyamoeba spec.</i>	210	F/M	?	O	
Paramoebidae & Vexilliferidae					
<i>Mayorella smalli</i>	720	M		R	-
<i>Mayorella gemmifera</i>	5,600	M		C	-
<i>Mayorella (Dactylamoeba ?)</i> <i>spec.</i>	670	F/M		R	
<i>Vexillifera minutissima</i>	110	M		R	-
<i>Vexillifera spec.</i>	300	F/M		O	
Other naked lobose amoebae					
<i>Paraflabellula reniformis</i>	600	M		O	e. g. SCHMOLLER 1964
<i>Stygamoeba polymorpha</i>	120	M	?	C	-
<i>Acanthamoeba spec.</i>	n. det.	F	X	O	

Table 3.3. (continued) Commented list of those morphotypes identified to species or genus. Occ. ... occurrence; n. det. ... not determined; F... freshwater; M...marine; C ... common (present in most samples); R ... regularly (present in > 10 % of samples); O ... rare (present in < 10 % of samples).

Species	Biovol. [µm ³]	Typical Habitat	Cysts	Occ.	Previous	Baltic records
Testacealobosia						
<i>Cochliopodium bilimbosum</i>	970	F		O	e. g. VØRS	1992
<i>Cochliopodium minus</i>	480	F	X	C		-
<i>Cochliopodium spec.</i>	90	F	?	R		
<i>Gocevia spec. ?</i>	1,100	F	?	O		
<i>Arcella vulgaris</i>	n. det.	F	X	O	e. g. GOLEMANSKY	1998A
<i>Phryganella spec. ?</i>	33,000	F		R		-
Aconchulinida						
<i>Nuclearia spec.</i>	n. det.	F	X	O		
<i>Pinaciophora rubicunda</i>	n. det.	F/M		O	ROIJACKERS & SIEMENSMA	1988
<i>Lithocolla globosa</i>	11,000	F/M		R	SCHULZE	1874
<i>Arachnula spec.</i>	n. det.	F	X	O		
Testaceafilosia						
<i>Lecythium spec. ?</i>	310	F	X	R		
<i>Trinema lineare</i>	3,500	F/M	?	R	e. g. GOLEMANSKY	1998A
<i>Cyphoderia ampulla</i>	45,000	F/M	?	R	e. g. GOLEMANSKY	1998A
<i>Paulinella chromatophora</i>	n. det.	F/M	?	O	PANKOW	1982
Granuloreticulosea						
<i>Gymnophrys cometa</i>	80	F		R		-
<i>Apogromia spec.</i>	240	F/M		R		
Other amoeboid protists						
<i>Diplophrys marina</i>	n. det.	M		O		-
<i>Chrysamoeba radians</i>	70	F		R		-
<i>Massisteria marina</i>	20	M		O	LARSEN & PATTERSON	1990

Gymnamoebia were the most important group in terms of species richness and abundance. Vannellidae and Paramoebidae were the dominant gymnamoebian families (Fig. 3.5). They reached mean abundance contributions of 47 % and 36 %, respectively. The Thecamoebidae were present in all samples at low abundance (6 % mean contribution), whereas abundance contributions of Vexilliferidae and Flabellulidae (the latter represented by *Paraflabellula reniformis* only) were low during spring and summer and increased in autumn (4 % and 1 % mean contribution).

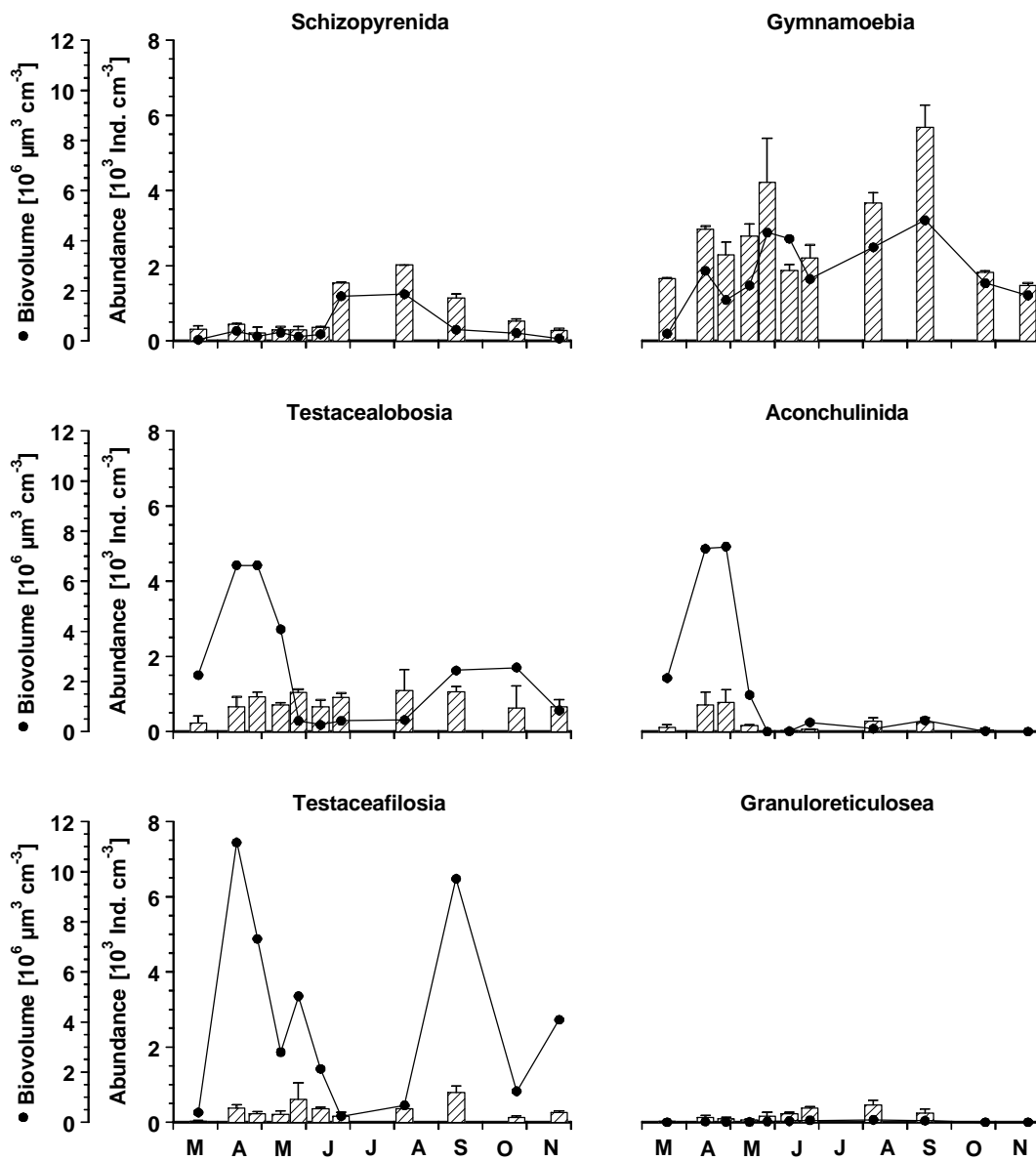


Figure 3.4. Abundance and biovolume of major taxonomic groups of rhizopods in sediment samples (0-3 mm) from station Bäk (Error bars: $\frac{1}{2}$ range, N=2).

3.4.4. Applicability of the liquid aliquot method

Of the species identified as potential cyst-formers (Table 3.3), only *Vahlkampfia sp.*, *Stygamoeba polymorpha*, *Cochliopodium minus* and the Testaceafilosia contributed more than 5 % to total rhizopod abundance or biovolume in any samples. Their combined contribution to total rhizopod abundance and biomass in samples from station Bäk is shown in Figure 3.6. This contribution was within the same range at stations Rassower Strom and Kirrbucht (data not shown). *Stygamoeba polymorpha* contributed up to 25 % to total rhizopod abundance. The Testaceafilosia dominated the potentially cyst-forming fraction of the rhizopod fauna in terms of biovolume.

In three of the 48 subsamples treated with HCl prior to inoculation on 12 September, 1996, *Acanthamoeba spec.* was found after incubation. No other rhizopod species was found. *Acanthamoeba* was never detected in any of the untreated enumeration cultures. It should be noted that relatively high biovolume contributions of potentially cyst-forming species were found at this sampling occasion (Fig. 3.6).

When cultures of *Acanthamoeba sp.*, *Stygamoeba polymorpha*, *Cochliopodium minus*, and *Vahlkampfia sp.* were subjected to encystment conditions, only *Acanthamoeba spec.* produced clearly distinguishable resting cysts and reappeared in treatments where no vegetative cells were found after 21 d. Cultures of *Cochliopodium minus* always contained a high proportion (average 90 %) of inactive, rounded cells without visible cyst walls or cytoplasmic irregularities, but these cells did not enable the cultures to recolonize those treatments (pH < 3 and heat) where no vegetative cells were found after 21 d. The same was true for inactive, rounded cells of *Vahlkampfia sp.* which were only observed in the acid and heat treatments. These cells did not resemble the typical vahlkampfiid cysts that were regularly found in stock cultures of *Vahlkampfia spec.* Cultures of *Stygamoeba polymorpha* did not form cysts or cyst-like cells and irreversibly disappeared in the acid and heat treatments.

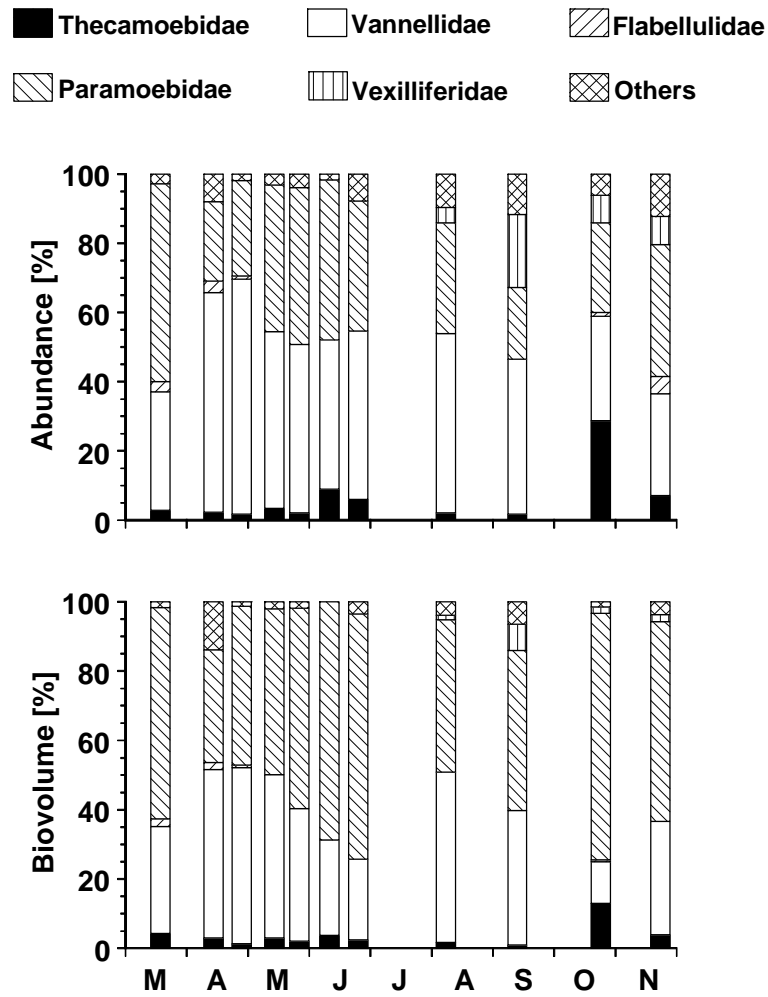


Figure 3.5. Relative contribution of important families to the abundance and biovolume of *Gymnamoebia* in sediment samples (0 - 3 mm) from station Bäk.

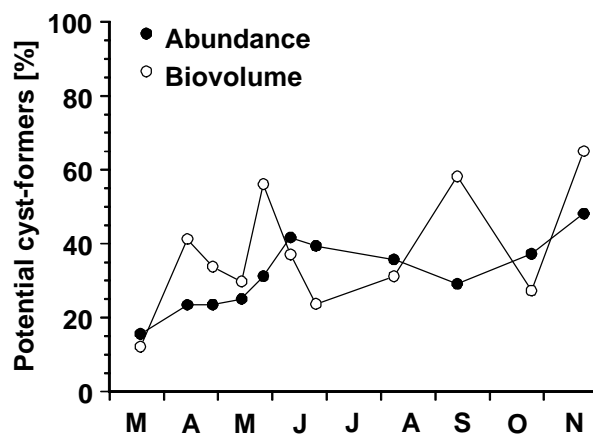


Figure 3.6. Contribution of potentially cyst-forming rhizopod taxa to the abundance and biovolume of rhizopods in sediment samples (0 - 3 mm) from station Bäk.

3.5. Discussion

3.5.1. Quantitative importance and distribution of rhizopods

My results show that rhizopods form a numerically important component of the micro- and nanozoobenthos of the study area, and probably of shallow coastal waters in general. My findings agree with recent data from other coastal waters which were obtained using the same methods: mean annual abundances of 870 and 2,200 cells cm^{-3} (*Gymnamoebia* and *Schizopyrenida* only) were reported from sandy and silty sediments, respectively, of the Scottish Clyde Sea (BUTLER & ROGERSON 1995). Abundances of naked rhizopods of 1,020 - 45,600 and 17,600 - 40,600 cells g^{-1} sediment were found in sediments of Hiroshima Bay and of marine and brackish habitats at Bermuda, respectively (ANDERSON 1998, DECAMP ET AL. 1999). These figures are even higher than mine: expressed on a weight basis, my abundances would have been in the range of 5,600 – 21,800 cells g^{-1} because sediment density at station Bäk was approximately 2 g cm^{-3} .

A comparison of rhizopod biovolume to those of ciliates and heterotrophic flagellates shows the relative importance of rhizopods in the study area (Table 3.4). The latter groups were quantified in the same sediment samples as rhizopods (DIETRICH & ARNDT 2000). On average, rhizopods made up 45 % of the total protistan biovolume in the superficial sediment layer of station Bäk.

The abundance data given in this paper refer to one station and one sediment layer only, and only to a limited part of the seasonal cycle. However, the abundance figures from two other stations in the study area, Rassower Strom and Kirrbucht, generally agree with those of station Bäk (see Chapter 2). In addition, they allow some extrapolations: While similar abundance ranges were found in the superficial sediments, ranges were wider and maximum abundances were higher in the flocculent surface layer. Maxima of 24,000 cells cm^{-3} (Rassower Strom) and 17,000 cells cm^{-3} (Kirrbucht) were found in spring 1996. They may have been a response to phytoplankton sedimentation, as found in earlier studies in the same area (ARNDT ET AL. 1990). The 5 - 10 mm layer abundances at Rassower Strom and Kirrbucht tended to be lower and less variable than those in the superficial sediment layer. In agreement with the low rhizopod densities found at station Bäk in March and November, very low abundances of rhizopods occurred during winter in all sediment samples from Rassower Strom and Kirrbucht. The contribution of taxonomic groups to the rhizopod community at Rassower Strom and Kirrbucht was similar to that of station Bäk except for the fact that *Granuloreticulosea* and *Aconchulinida* were of minor importance.

In conclusion, a tendency towards lower and less variable abundances deeper in the sediment and a seasonal trend with maxima during the warm season emerges from the combined data of all three stations. A similar vertical distribution, but no consistent seasonal

pattern was reported previously from the Clyde Sea, Scotland (BUTLER & ROGERSON 1995). Studies on the seasonality of benthic heterotrophic nanoflagellates have yielded differing patterns as well: While summer maxima and winter minima of benthic flagellate abundances were found in my study area and at the majority of stations investigated during a study of North Sea sediments (HONDEVELD ET AL. 1994, DIETRICH & ARNDT 2000), no such pattern was observed in a freshwater littoral zone (STARINK ET AL. 1996). The seasonal trend of benthic abundances that was found in my study area suggests that the benthic microbial food web in such shallow waters directly responds to seasonal variations of organic input from the water column.

Table 3.4. Contributions [%] of rhizopods, ciliates and heterotrophic flagellates to total heterotrophic protistan biovolume in sediment samples (0 - 3 mm) from station Bäk. Ciliates and heterotrophic flagellates were enumerated by live-counting (DIETRICH & ARNDT 2000).

	17. Mar.	13. Apr.	27. Apr.	13. May	25. May	10. Jun.	24. Jun.
Rhizopods	33	82	64	45	39	27	23
Ciliates	7	8	9	9	29	41	31
Flagellates	60	10	27	46	32	32	46

3.5.2. Rhizopod community structure

The benthic rhizopod community of my study area comprises representatives of all major rhizopod groups and of freshwater as well as marine species. Only 13 of the 27 morphotypes identified to species have been reported from the Baltic before (Table 3.3). Three species (*Hartmannella vermiformis*, *Casbia limacoides*, and *Chrysamoeba radians*) have been found in freshwater habitats only, and three marine species (*Platyamoeba langae*, *Stygamoeba polymorpha*, and *Diplophrys marina*) are new to Europe. The difference in salinity between stations Bäk and Rassower Strom (8 - 10 PSU) and station Kirrbucht (5 PSU) had no influence on the faunal composition of rhizopods. Gymnamoebia were the species-richest group at all stations, followed by Testacealobosia. However, in addition to the two *Vahlkampfia*-species, some of the unidentified limax rhizopods showed eruptive movement and thus may belong to the Schizopyrenida as well. Large testate rhizopods are probably undersampled with the liquid aliquot method, which may explain the low species

yield of this group in my study as compared to other faunistic surveys (e. g. GOLEMANSKY 1998A). The same is true for foraminiferans which were occasionally found in fresh samples.

Although many rhizopod species are easily recognizable under the light microscope, the taxonomic analysis was limited by the methodology to my disposal. The genera *Vannella/Platyamoeba* and *Mayorella/Dactylamoeba* were distinguished based on the morphology of floating and locomotive cells only. Although there are well-established criteria for this kind of distinction, electron-microscopical examination of the cell surface is considered necessary to reach a final conclusion (e. g. PAGE & SIEMENSMA 1991). If these strict criteria would be applied, my species identifications within the above mentioned genera would only be preliminary.

Generally, taxonomy of marine naked rhizopods is still a growing field, and a variety of new species have been described during the last few years (e. g. SMIRNOV 1996, 1999, ANDERSON ET AL. 1997). In the light of this situation it appears likely that some of the morphotypes that could not be identified to species during my study were actually undescribed species. The Cochliopodidae (Testacealobosia), another group that is quantitatively important in the Baltic, have received little attention since the Seventies (BARK 1973, PAGE 1976).

The sometimes high biovolume contributions of filose amoebae and Testacealobosia found during my study indicate that these groups are equally or even more important than naked lobose amoebae in Baltic coastal sediments. Since most of the Testacealobosia and Aconchulinida found were brackish or freshwater species, their high contributions may be a peculiarity of the brackish Baltic community. In contrast, a species-rich fauna of testate rhizopods (excluding foraminiferans) has been reported from the interstitial of other coastal waters as well (e. g. OGDEN & COUTEAUX 1989, GOLEMANSKY 1998 A). Further research into their quantitative importance and functional role appears warranted.

The fact that different taxonomic groups showed different seasonal trends during my study (Fig. 3.4, 3.5) suggests that they respond specifically to environmental conditions such as available food resources. The high biovolumes of Testacealobosia and Aconchulinida in spring were comprised of many large and herbivorous species which may have fed on sedimenting phytoplankton (see PRATT & CAIRNS 1985). They were the main cause of the exceptionally high biovolume contributions of rhizopods to the benthic heterotrophic protistan community in the spring samples.

The taxonomic resolution of earlier quantitative studies on rhizopods has been restricted to the distinction between broad morphological categories. The high contribution of Vannellidae and Paramoebidae to the abundance and biovolume of Gymnamoebia in my samples is in agreement with the dominance of amoebae with subpseudopodia and discoidal or fan-shaped amoebae within the rhizopod communities in sediments of Hiroshima Bay

(Japan) and of some inshore aquatic habitats at Bermuda (ANDERSON 1998, DECAMP ET AL. 1999). Compared to the above mentioned studies, Hartmannellida were conspicuously rare in my samples.

In contrast to earlier findings (BUTLER & ROGERSON 1995, DECAMP ET AL. 1999), *Gymnamoebia* or *Schizopyrenida* smaller than 10 μm contributed little to total rhizopod abundances or biovolume although they were regularly found. However, my sediments were coarser than most of those sampled during the above mentioned studies and the presence of a highly productive microphytobenthos in these shallow waters may have shifted the rhizopod community structure towards larger herbivorous and omnivorous forms (see PRATT & CAIRNS 1985, GERBERSDORF ET AL. 2001). Although the liquid aliquot method selectively favours bacterivorous species, I found high contributions of non-bacterivorous *Gymnamoebia* throughout the study, and especially at the sediment surface (Fig. 3.7). The high contributions of non-bacterivores within the rhizopod community suggest that rhizopods fulfill various trophic roles within the benthic microbial food web, rather than being restricted to bacterivory.

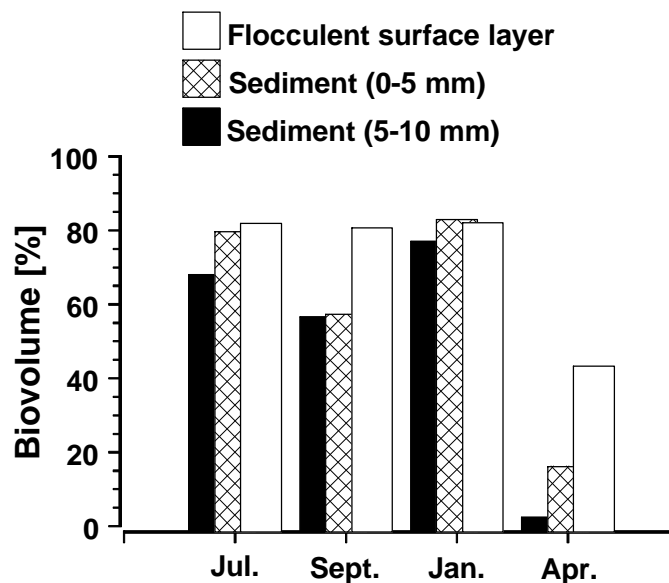


Figure 3.7. Contribution of herbivorous and omnivorous species (according to Pratt & Cairns 1985) to the combined biovolume of *Gymnamoebia* in the flocculent surface layer and in two sediment layers at station Rassower Strom. Data from all campaigns during which all three layers were sampled are included.

3.5.3. Methodology

Rhizopods were also included in earlier quantitative accounts of the marine micro- and nanozoobenthos (e. g. MARE 1942, FENCHEL 1967, BAK & NIEUWLAND 1989, ALONGI 1990, ARNDT ET AL. 1990, FERNANDEZ-LEBORANS & NOVILLO 1993). Except MARE (1942) who used serial dilution cultures and estimated abundances of 2,300 – 6,800 cells g⁻¹ in muddy subtidal sediments of the British Channel, most of these workers reported very low rhizopod densities. This was probably due to the enumeration methods employed: Naked rhizopods are hardly visible in fresh sediment samples because they are often closely surface-associated and move relatively slowly. After fixation, they tend to assume irregular body shapes, or to round up (ROGERSON ET AL. 1994). Therefore, they are easily overlooked or misidentified in live-counted or fixed samples.

Cultivation methods, particularly the liquid aliquot method which yielded higher abundances than the MPN method (SINGH 1946) and plate counting methods in direct comparison (BUTLER & ROGERSON 1995), stand out as the most appropriate enumeration methods for marine naked rhizopods. According to my results, the liquid aliquot method is suitable for sediments from brackish waters as well. Although a number of rhizopods with a potential ability to form cysts were found in my samples, the results of my encystment trials do not indicate that excystation during incubation contributed significantly to the abundances determined by the LAM. The same appears to be true for the larger Testaceafilosia (R. MEISTERFELD, pers. comm.). This is relevant from the methodological point of view because a high rate of excystment would have caused overestimations of vegetative cell abundance in the inoculum.

However, some limitations of the method have to be considered in order to interpret the results properly: my abundance figures are likely to be minimum estimates of the actual abundances because any clumping of sediment and associated rhizopods in the inoculates leads to underestimations of actual abundances under the assumption of a Poisson distribution, and because the culture conditions were certainly not appropriate for all species in the inoculum. For an example, the hartmannellid rhizopod *Cassia limacoides* was frequently observed in fresh samples, but never in LAM cultures. The same may have been true for large herbivorous and omnivorous species although some of them regularly grew in the cultures, possibly feeding on – and controlling - bacterivorous protists. Without these methodological shortcomings, abundance and biovolume contributions of rhizopods to the micro- and nanozoobenthos at station Bäk would have been even higher.

In order to judge the relative importance of taxa of differing size, I calculated biovolumes from live cell dimensions. The accuracy of this approach is limited by the variability of cell morphology and by the accuracy of the cell thickness estimate. Biovolume standard

deviations in the order of 20 - 30 % were frequently observed. However, the range of rhizopod species biovolumes (20 – 45.000 μm^3) found during this study was sufficiently wide in comparison to the errors in biovolume estimation to allow some general comparisons on the basis of life cell dimensions. Alternative methods which use fixed cells (e.g. ROGERSON ET AL. 1994) are prone to cell shrinkage and loss upon fixation, given what is known from ciliates (CHOI & STOECKER 1989). The advance of laser-scanning microscopy may help to solve the problem of rhizopod biovolume estimation in the future.

In spite of the methodological problems involved in the biovolume estimation, quantification, and community analysis of rhizopods, it is obvious that they form a significant component of protistan communities in coastal sediments.

4. Effects of experimental sediment resuspension on a coastal planktonic microbial food web

4.1. Summary

I studied effects of sediment resuspension on microbial food web dynamics in the water column of microcosms consisting of sediment cores with the overlying water. These microcosms were obtained from Rassower Strom, coastal Southern Baltic, and incubated for 108 h under *in-situ* light and temperature conditions. They were resuspended with oscillating grids at intensities that reproduced the range of naturally occurring seston concentrations during resuspension events in these waters.

After 12 h of resuspension, the abundances of pico- and nanoautotrophs, rhizopods (naked and testate amoebae) and heterotrophic nanoplankton had increased and were significantly positively correlated to seston concentration, indicating that resuspension of benthic representatives directly affected their water column abundances. Similar, but non-significant trends were found for benthic diatoms and ciliates. In addition, resuspension enhanced population growth of pico- and nanoautotrophs and resuspended diatoms over the whole course of the experiment. This enhancement was independent of a direct transport of cells from the sediment. According to dissolved nutrient concentrations, it was caused by reduced nitrogen limitation due to resuspension. The abundance of heterotrophic nanoplankton was tightly correlated to those of their main food organisms, pico- and nanoautotrophs and bacteria. It was also significantly increased by resuspension over the whole course of the experiment. This is consistent with a decreased bottom-up control of heterotrophic nanoplankton due to resuspension.

My results indicate that sediment resuspension may strongly affect the planktonic microbial food web of coastal waters, both by a direct transport of cells from the sediment into the water column and by indirect effects mediated by dissolved nutrients and trophic interactions.

4.2. Introduction

Understanding the microbial food web of shallow coastal waters requires knowledge about effects of physical processes which act on these waters. Sediment resuspension by tides or winds is one of these processes. Field data from various coastal waters indicate that sediment resuspension may act as a means of passive dispersal of autotrophic and

heterotrophic protists from the sediment, thereby increasing total abundances and changing the taxonomic composition of the protistan community in the water column (SHAFFER & SULLIVAN 1988, DE JONGE & VAN BEUSEKOM 1992, 1995, ROGERSON & LAYBOURN-PARRY 1992 B, SHIMETA & SISSON 1999). It is also known that the susceptibility of benthic protists to resuspension may vary between species, as found in microphytobenthos and heterotrophic protists (DE JONGE & VAN DEN BERGS 1987, SHIMETA & SISSON 1999).

Parallel to this direct effect, sediment resuspension may enhance remineralization and induce dissolved nutrient and particulate organic matter fluxes into the water column, which can be used by algae and bacteria (WAINRIGHT 1990, ARFI ET AL. 1993, BALLS ET AL. 1994, ARFI & BOUVY 1995, PETERSEN ET AL. 1998). An increase in bacterial abundance and biovolume due to resuspension has been shown both in field and experimental studies. This increase has been attributed to the improved availability of surfaces for colonization in the water column following resuspension (WAINRIGHT 1987, RITZRAU & GRAF 1992). Nutrient-related resuspension effects were found in freshwater phytoplankton (REYNOLDS 1996, OGILVIE & MITCHELL 1998). Although bacterivorous and herbivorous protists should benefit from increased abundances of their prey, the response of higher levels of the microbial food web to the processes described has only occasionally been addressed (WAINRIGHT 1987).

The Boddengewässer are shallow, non-tidal, mesotrophic to eutrophic, brackish lagoons at the north-eastern Baltic coast of Germany. The microbial food web of these waters has been studied extensively (e. g. ARNDT ET AL. 1990, SCHIEWER 1998, DIETRICH & ARNDT 2000). Recent field data indicate that benthic and planktonic protistan communities are closely coupled in the Boddengewässer, and that sediment resuspension is one of the mechanisms responsible (Chapter 2). Based on these field data, I have derived the following hypotheses:

1. Sediment resuspension increases the total abundance and changes the taxonomic composition of the heterotrophic and autotrophic protistan community in the water column by passive transport of protists from the sediment.
2. Resuspension introduces dissolved nutrient and particulate organic matter fluxes into the water column which give rise to growth of autotrophs and heterotrophic bacteria in the water column. The importance of such transport processes depends on the nutrient and organic carbon supply in the water column prior to resuspension.
3. Positive resuspension effects on bacteria and autotrophs are propagated through higher trophic levels of the microbial food web in the water column.

In order to test these hypotheses with a natural microbial community, I have studied the effects of resuspension intensity during an experiment with sediment cores including the overlying water from a station in the Boddengewässer.

4.3. Materials and Methods

4.3.1. Study site

The experiment was carried out with natural sediment cores from station Rassower Strom, Nordrügensche Boddengewässer. Rassower Strom (54° 34' N, 13° 10' O) is characterised as mesotrophic with an average salinity of 9.0 practical salinity units and a mean water depth of 3.8 m. Muddy sediments (4% organic content) prevail. The frequency and duration of naturally occurring resuspension events at Rassower Strom has been estimated from turbidity (S. DAHLKE, personal communication) and wind speed measurements (J. MEYERCORDT, personal communication) in 1996. According to this estimate, 66 wind-induced resuspension events (situations with less than 10 % light transmission 0.5 m above the sediment and more than 5 m s⁻¹ wind speed) occurred during a total of 142 d between May and November 1996.

4.3.2. Experimental design

The experiment was run in June 1997. 20 sediment cores with 2.6 l overlying water were obtained by a ship-operated multicorer from Rassower Strom. The cores were randomised before being assigned to treatments. Four cores were sacrificed and sampled at the start of the experiment. 16 cores were transferred into plastic tubes (length 400 mm, inner diameter 100 mm) and incubated in a water basin at 18 °C under 220 µE m⁻² illumination with a light / dark-cycle of 16 h / 8 h. Light and temperature conditions were chosen to correspond to field conditions. Different resuspension intensities were achieved by oscillating grids (Fig. 4.1a, b; apparatus modified from DAVIS 1993). Experimental groups were treated with piston frequencies of 0.71 s⁻¹, 1.22 s⁻¹, and 1.60 s⁻¹, respectively, for one period of 12 h per day. These frequencies were chosen because they reproduced the range of naturally occurring seston concentrations during resuspension events in preliminary short-term experiments. Another group of four cores was left as control. The experimental microcosms were arranged in a way that allowed three groups of four pistons to be driven by one electric motor each (Fig. 4.1c).

At the beginning of the experiment, water samples were obtained from four reference cores that had been taken together with the 16 experimental cores. Three water samples were taken from each experimental microcosm at regular intervals during the course of the experiment (12, 60 and 108 h). All water samples were analysed for seston parameters,

mineral nutrients, chlorophyll *a* concentration (last sampling only), and microbial community structure.

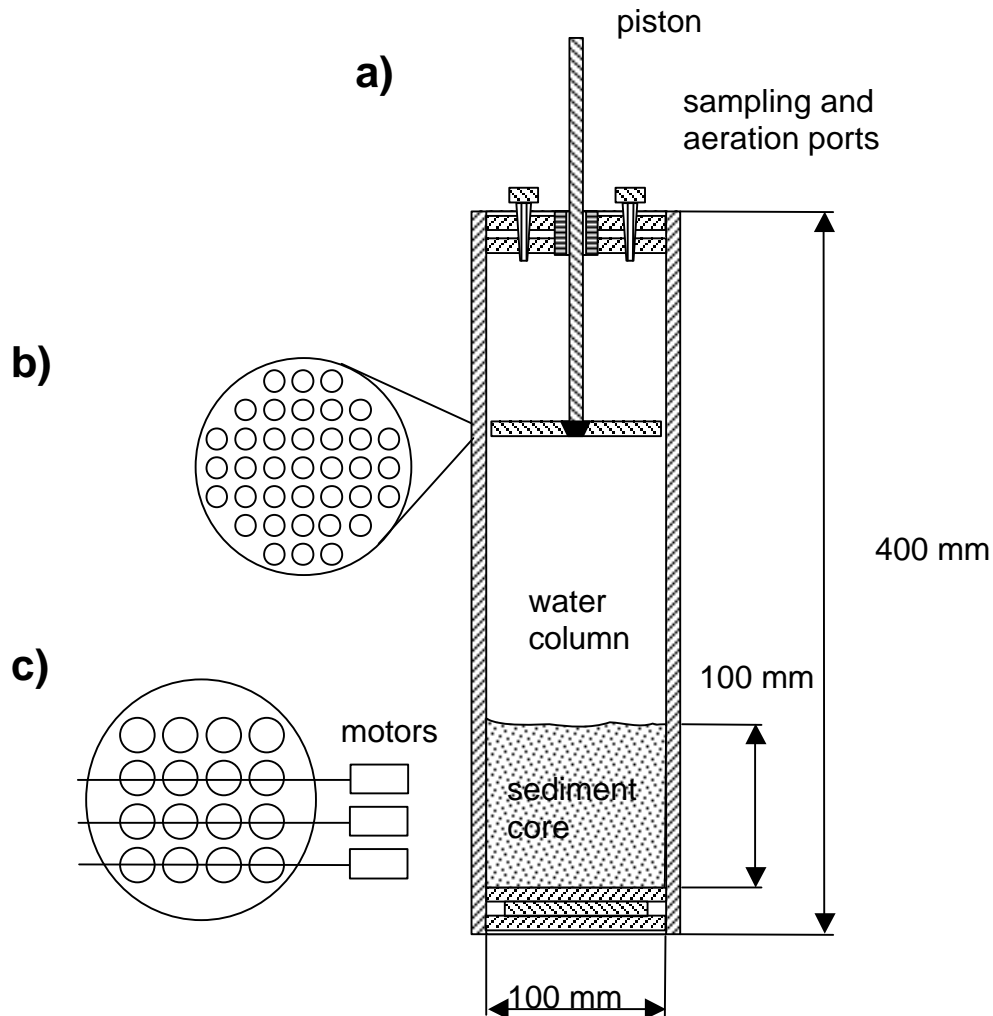


Figure 4.1. Experimental setup: (a) section from top to bottom of an experimental microcosm, (b) schematic view of the oscillating grid, (c) arrangement of experimental microcosms in the water bath.

4.3.3. Abiotic parameters and chlorophyll *a*

Seston dry weight and the concentrations of particulate organic carbon (hereafter POC), dissolved phosphate and dissolved ammonium in the water column were measured according to standard protocols of GRASSHOFF ET AL. (1983). Nitrate and Nitrite concentration was measured with a Sykam 4110 ion chromatographer (S. DAHLKE, personal communication). Measurements of chlorophyll *a* concentration followed the guidelines of the BMERC (1988). Oxygen saturation was measured with an electronic oxygen sensor (WTW, Germany).

4.3.4. Microbial community structure

Water column abundance of bacteria, heterotrophic nanoplankton (hereafter HNAN), picoautotrophs (autotrophs < 2 µm maximum dimension) and nanoautotrophs (autotrophs between 2 and 20 µm maximum dimension), and benthic abundance of bacteria, picoautotrophs, and nanoautotrophs, were counted in samples fixed with 1.5 % (final concentration) glutaraldehyde and stained with DAPI (4',6'diamidino-2-phenylindole) using epifluorescence microscopy (CARON 1983, SHERR ET AL. 1993). Briefly, 0.5 – 2.0 ml subsamples were stained and concentrated on black polycarbonate filters (Millipore) of 0.2 µm pore size. At least 50 pico- and nanoautotrophs, 50 HNAN, and 300 bacteria on a minimum of 50 grids were counted. The abundance of rhizopods was determined with a modified version of the liquid aliquot method (Chapter 3). This method has been optimised for use with samples from the study area and validated by comparison with life counting data. Briefly, 48 subsamples of 100 - 500 µl were inoculated into wells of two tissue culture plates containing 2 ml Føyns-Erdschreiber medium (PAGE & SIEMENSMA 1991). After 14 d incubation at 18 °C in the dark, the wells were screened for the presence of rhizopod species and initial abundance was calculated from the frequency of wells positive for each species assuming a Poisson distribution. Ciliates, diatoms and other large algae were fixed in Bouin's fixative (a mixture of 80 % formaldehyde saturated with picric acid and 20 % acetic acid at 5 % final concentration) and counted after sedimentation of subsamples of 10 - 50 ml according to UTERMÖHL (1958). An overview of the taxonomic composition of algae, HNAN and ciliates at the end of the experiment was obtained by live observation.

4.3.5. Statistical analysis

The significance of short-term, direct transport effects of resuspension on microbial food web components was tested using one-way-ANOVAs based on log-transformed data from the first two sampling occasions ($t = 0$ h, $t = 12$ h). The data were log-transformed for the tests in order to equalise variance between treatments, but untransformed data are given in the figures. Dunnett's post-hoc test was used to test the significance of individual treatment levels, as compared with the control group. Since it was assumed that the susceptibility of individual microcosms to resuspension might differ within experimental treatments, correlations between microbial food web components and seston concentration at the first sampling occasion were analysed in addition to the ANOVAs. Untransformed data and Pearson's correlation coefficients were used for this analysis because it was assumed

that direct transport effects of resuspension would result in linear correlations to seston concentration.

The significance of long-term resuspension effects on microbial food web components over the whole course of the experiment, and of possible interactions with time, were tested using repeated-measures-ANOVAs based on log-transformed data, followed by Dunnett's post-hoc test for individual treatment levels. Spearman's rank correlation coefficients were used to analyse the relationship between seston concentration and microbial food web components over the whole course of the experiment because it was assumed that this relationship would not be mediated by direct transport mechanisms alone, and thus not necessarily be linear. In addition to seston correlations, correlations between microbial abundances were analysed (Spearman's rank correlation coefficient) in order to gauge the degree of trophic coupling within the microbial food web. All statistical procedures were carried out using SPSS.

4.4. Results

4.4.1. Abiotic parameters

Seston concentration increased from an initial value of 17 mg l⁻¹ to a maximum of 425 mg l⁻¹ at the highest resuspension level after 12 h (Fig. 4.2a). It subsequently decreased to final values of 32 - 91 mg l⁻¹ in the resuspended groups, while it remained below 30 mg l⁻¹ in the controls. Seston concentration significantly varied with resuspension intensity after 12 h (one-way-ANOVA, data not shown), and also over the whole course of the experiment (RM-ANOVA, Table 4.3), but due to an interaction between resuspension intensity and sampling occasion, the latter effect was time-dependent. The relative contribution of POC to seston concentration decreased from an initial value of 0.13 % to less than 0.1 % after 12 h (Fig. 4.2b). Thereafter, it tended to increase with time and with resuspension intensity, but this trend was not significant (Fig. 4.2b).

Oxygen saturation increased from values of 68 - 78 % at the 12 h sampling occasion to final values of 101 - 130 % (data not shown). Saturation values were significantly negatively correlated to seston concentration (Table 4.2).

Prior to the experiment, the water column concentrations of dissolved ammonium, nitrate and phosphate were 2.1 µM, 0.22 µM, and 0.94 µM, respectively. No significant effects of resuspension on nutrient concentration, but some trends were found: ammonium concentration increased until 12 h, and this increase tended to be stronger in the resuspended microcosms (Fig. 4.3a). Ammonium concentration subsequently decreased to

less than $1.50 \mu\text{M}$. It was significantly positively correlated to seston concentration (Table 4.2). Nitrate concentration tended to be higher in the resuspended microcosms at the first sampling occasion, but not after 60 h and 108 h (Fig. 4.3b). Phosphate concentration reached maximum values of 1.21 - 1.48 at the lowest resuspension intensity throughout the experiment (Fig. 4.3c).

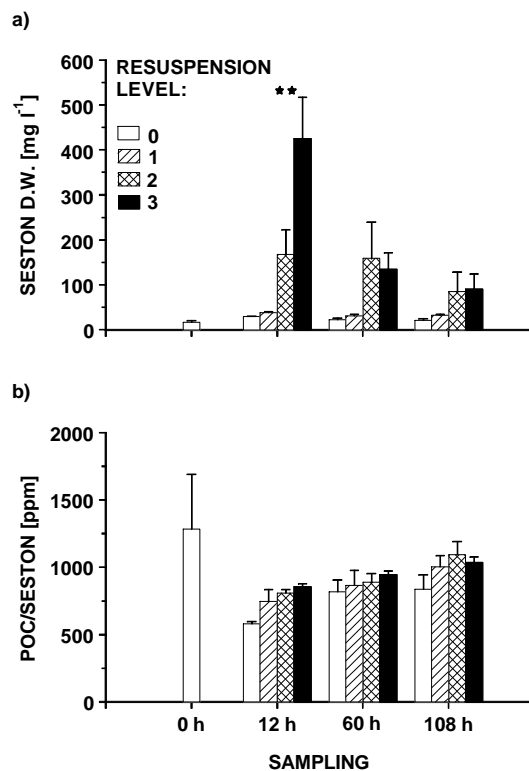


Figure 4.2. Seston concentration (a) and relative contribution of particulate organic carbon to seston (b) (error bars: standard error, $N = 4$; ** $p < 0.01$, one-way-ANOVA).

4.4.2. Autotrophs

The planktonic autotrophic community subjected to the experiment initially consisted of picoautotrophs (260×10^3 Ind. ml⁻¹), nanoautotrophs (92×10^3 Ind. ml⁻¹, mainly *Cryptomonas spp.*, other autotrophic flagellates and coccal chlorophytes), and a relatively low abundance of pigmented dinoflagellates (13 Ind. ml⁻¹, *Gymnodinium spp.*, *Peridinium spp.* and *Dinophysis sp.*) and diatoms (28 Ind. ml⁻¹, mainly benthic *Gyrosigma spp.*, *Amphora spp.* and *Amphiprora spp.*). Initial benthic abundances of pico- and nanoautotrophs were 31×10^6 Ind. cm⁻³ and 33×10^6 Ind. ml⁻¹, respectively.

The autotrophs clearly responded to resuspension (Table 4.1). Compared to the concentration of chlorophyll *a* prior to the experiment (10.2 µg l⁻¹), final concentration was generally higher, and increased with resuspension (23.5 - 82.0 µg l⁻¹, Fig. 4.3d). This finding was reflected in the abundances of picoautotrophs, nanoautotrophs and resuspended benthic diatoms (Fig. 4.4a, b, d), which were significantly positively correlated to seston concentration throughout the experiment (Table 4.2). The picoautotrophs responded very quickly to resuspension and showed a highly significant, positive linear correlation to seston concentration after 12 h (Fig. 4.4a, Table 4.1). However, the effect of resuspension on picoautotrophs was not significant over the whole experiment (Table 4.3), which was partly due to their decline at the highest resuspension level after 108 h (Fig. 4.4a).

Nanoautotrophs also showed a significant linear correlation to seston concentration at the first sampling occasion (Table 4.1). In addition to a moderate increase to up to 120×10^3 Ind. ml⁻¹ during the first 12 h, their abundance multiplied in all resuspended groups and reached 380 - 430 $\times 10^3$ Ind. ml⁻¹ towards the end of the experiment (Fig. 4.4b), which was not accompanied by increasing seston concentration. This resulted in a significant positive effect of resuspension intensity throughout the experiment (Table 4.3).

Compared to initial values, dinoflagellate abundance at $t = 12$ h declined irrespective of resuspension (Fig. 4.4c). They continued to fall to below 2 Ind. ml⁻¹ in the resuspended cores, while growth of a *Peridinium sp.* in two control microcosms led to higher average values of up to 13 Ind. ml⁻¹ in the control group. As a result, dinoflagellates showed a significant negative resuspension effect over the whole course of the experiment (Table 4.3).

Resuspension of benthic diatoms resulted in a moderate increase of their abundance in the water column to a maximum of 92 Ind. ml⁻¹ after 12 h. In spite of decreasing seston concentration in the resuspended microcosms, diatom abundance continued to rise until it reached up to 240 Ind. ml⁻¹ at the second sampling occasion (Fig. 4.4d). The linear correlation to seston concentration after 12 h was not significant (Table 4.1), but according to the RM-ANOVA, benthic diatom abundance in the water column were significantly increased by resuspension during the whole experiment (Table 4.3).

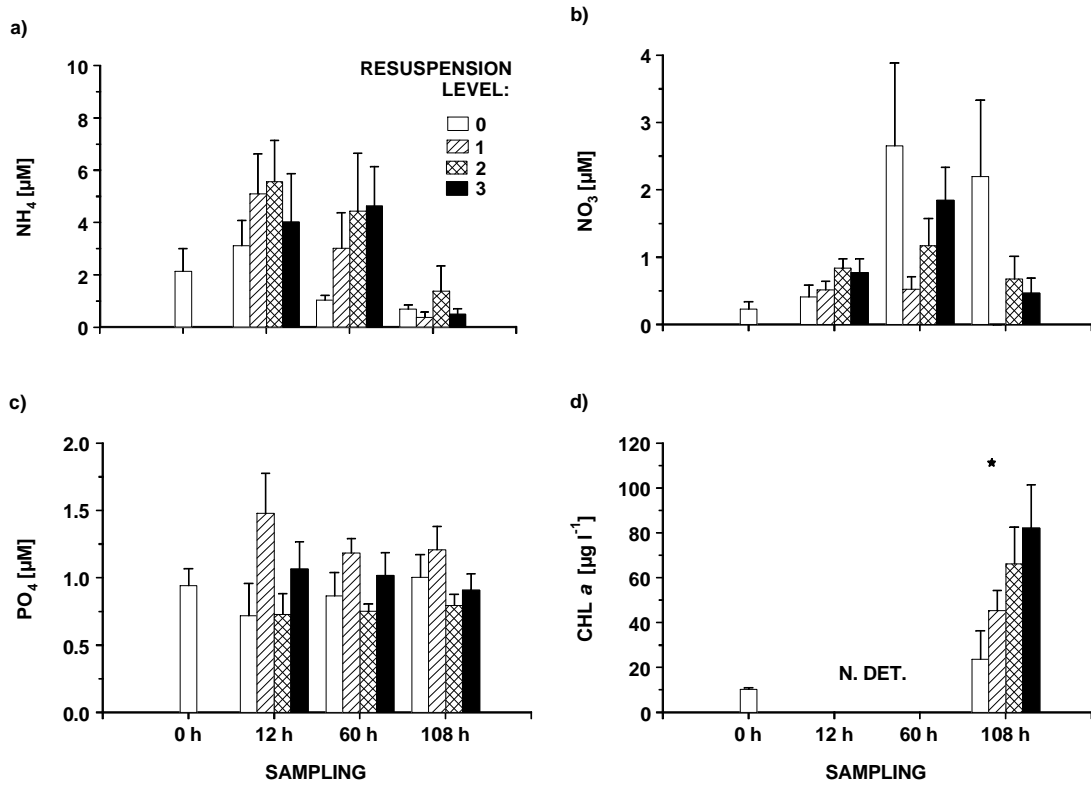


Figure 4.3. Concentrations of dissolved ammonium (a), nitrate (b), phosphate (c) and chlorophyll *a* (d; error bars: standard error, N = 4; * p < 0.05, one-way-ANOVA).

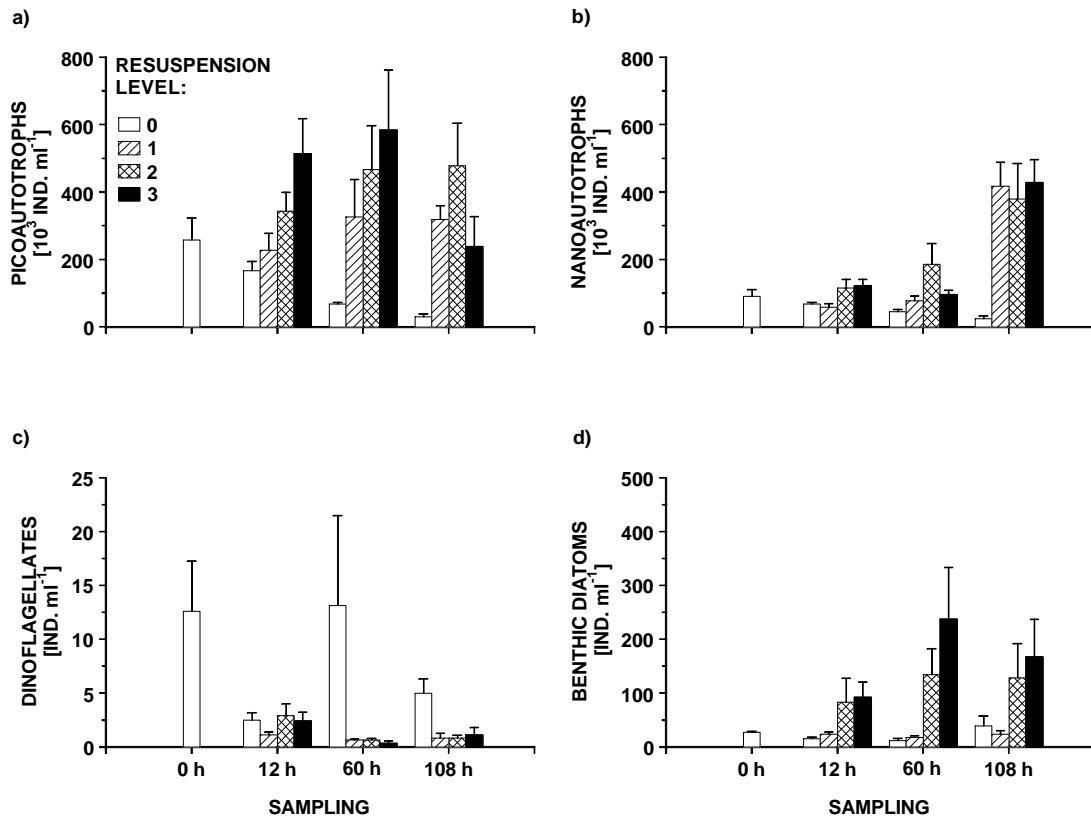


Figure 4.4. Abundances of picoautotrophs (a), nanoautotrophs (b), dinoflagellates (c) and benthic diatoms (d) in the water column of the microcosms (error bars: standard error, N = 4).

Table 4.1. Pearson's correlation coefficients for correlations of microbial and protistan abundances to seston concentrations, first sampling occasion (c.c. correlation coefficient; * $p < 0.05$; ** $p < 0.01$; $N = 16$).

Group	Pearson's c.c., t = 12 h
Picoautotrophs	0.779**
Nanoautotrophs	0.613**
Benthic diatoms	0.397
Dinoflagellates	0.044
Bacteria	0.035
HNAN	0.543*
Rhizopods	0.938**
Benthic ciliates	0.379

Table 4.2. Spearman's correlation coefficients for correlations of oxygen and nutrient concentrations, and microbial abundances to seston concentrations. Data are from all sampling occasions (c.c. correlation coefficient; * $p < 0.05$; ** $p < 0.01$; $N = 52$).

Parameter	Spearman's c.c., all data
O ₂	-0.440**
Ammonium	0.318*
Picoautotrophs	0.649**
Nanoautotrophs	0.371**
Benthic diatoms	0.641**
Dinoflagellates	-0.263
Bacteria	0.231
HNAN	0.514**
Rhizopods	0.840**
Planktonic ciliates	-0.142
Scuticociliates	0.379**
Benthic ciliates	0.231

Table 4.3. P-values of ANOVAs of main effects of resuspension and interactions with time for seston concentrations, microbial and protistan abundances during the experiment (N = 16, repeated measures ANOVA with three sampling occasions, log-transformed data).

Variable	P-values	
	Main effect	Interaction
Seston	0.003	0.015
Picoautotrophs	0.132	0.323
Nanoautotrophs	0.030	< 0.001
Benthic diatoms	0.010	0.627
Dinoflagellates	0.010	0.117
Bacteria	0.947	0.534
HNAN	0.036	0.220
Rhizopods	< 0.001	0.595
Benthic ciliates	0.556	0.190
Planktonic ciliates	0.281	0.452

4.4.3. Bacteria and heterotrophic protists

Prior to the experiment, the heterotrophic part of the microbial food web consisted of bacteria (6.22×10^6 Ind. ml⁻¹), HNAN (21×10^3 Ind. ml⁻¹, among flagellates heterotrophic chryomonads and katablepharids dominated), ciliates (7.3 Ind. ml⁻¹, mainly naked oligotrichs such as *Strobilidium spp.*, and prostomatids such as *Urotricha spp.*) and a very low abundance (< 1 Ind. ml⁻¹) of naked rhizopods. The initial benthic bacterial abundance was 1.4×10^9 Ind. cm⁻³.

Bacterial abundance responded little and transiently to resuspension (Fig. 4.5a). They were positively correlated to seston concentration after 12 h (Table 4.1), but not over all sampling occasions (Table 4.2). Accordingly, no resuspension effect on bacterial abundance was found in the RM-ANOVA (Table 4.3).

In contrast to the bacteria, the abundance of HNAN in the water column was increased by resuspension (Fig. 4.5b). For the first sampling occasion (t = 12 h), this was shown by a significant resuspension effect (one-way-ANOVA, data not shown), and by a significant linear correlation to seston concentration (Table 4.1). The same relationships were found for HNAN abundance of all sampling occasions combined (Tables 4.2, 4.3).

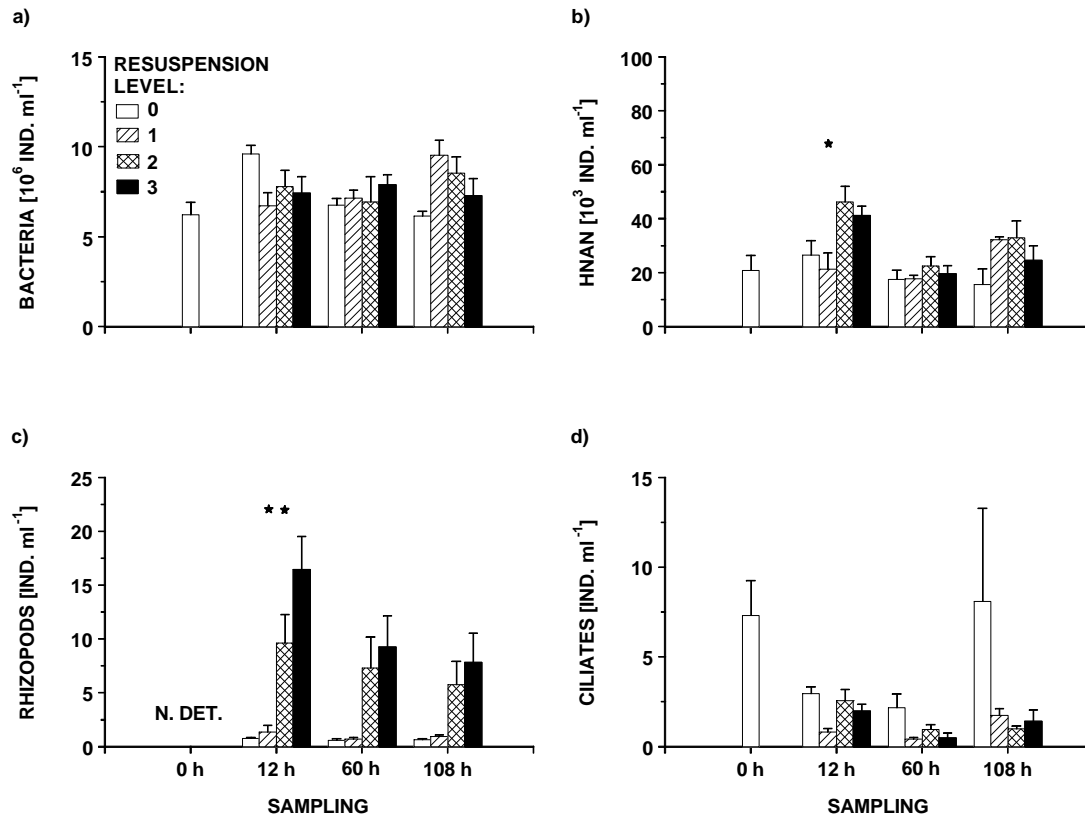


Figure 4.5. Abundances of bacteria (a), HNAN (b), rhizopods (c) and ciliates (d) in the water column of the microcosms (error bars: standard error, N = 4).

While heterotrophic nanoflagellates (hereafter HNF) in the controls and in the cores with the lowest resuspension intensity were comprised of typical planktonic forms (e.g. katablepharids and chrysomonads), some typical benthic forms (e.g. bodonids and euglenids) with a surface-associated mode of living were found in cores of the highest resuspension level.

The positive resuspension effect on water column abundance was even more pronounced in the rhizopods which increased to up to 16.4 Ind. ml⁻¹ in the resuspended microcosms while they remained below 1 Ind. ml⁻¹ in the controls (Fig. 4.5c). The rapid increase of rhizopod abundance at the beginning of the experiment, as well as their subsequent decrease and their highly significant linear correlation to seston concentration after 12 h (Table 4.1), indicate that this increase was mainly due to an import of rhizopods from the sediment. The positive resuspension effect was highly significant both for the first sampling occasion (one-way-ANOVA, data not shown) and for the whole experiment (Table 4.3). Based on biovolume estimates, however, the contribution of rhizopods to the protistan community of the water column was still relatively low even in the most intensely resuspended microcosms (data not shown). The species composition of water column

rhizopods resembled that of the benthic community of the study area (Chapter 3). Small species (biovolume less than $200 \mu\text{m}^3$) of the genera *Vannella* and *Vexillifera* attained a higher relative abundance in the controls than in resuspended groups.

The ciliate community showed an initial decline to below 3.0 Ind. ml^{-1} in all microcosms. Subsequently, ciliate abundance in some of the control microcosms recovered, and growth of *Urotricha spp.* and *Strobilidium spp.* resulted in a relatively high average ciliate abundance of 8.1 Ind. ml^{-1} in the control group at the end of the experiment. Although there was a trend towards increased abundance of benthic ciliates (stichotrichs, hypotrichs, and benthic pleurostomatids) and scuticociliates (a group that comprises both benthic and planktonic species, in this case mainly *Cyclidium spp.* and *Pleuronema sp.*) in the water column of the resuspended microcosms (Fig. 4.6b, c), this trend was not significant (Table 4.3). The increase of benthic ciliate abundance due to resuspension was low (maximum 1.1 Ind. ml^{-1}) compared to the decrease of planktonic ciliate abundance in the resuspended microcosms (Fig. 4.6a). In addition, a relatively high abundance of benthic ciliates and scuticociliates (0.6 and 0.7 Ind. ml^{-1} , respectively) was found in the non-resuspended microcosms after 12 h (Fig. 4.6b, c), and the correlation between benthic ciliate abundance and seston concentration was not significant (Tables 4.1, 4.2).

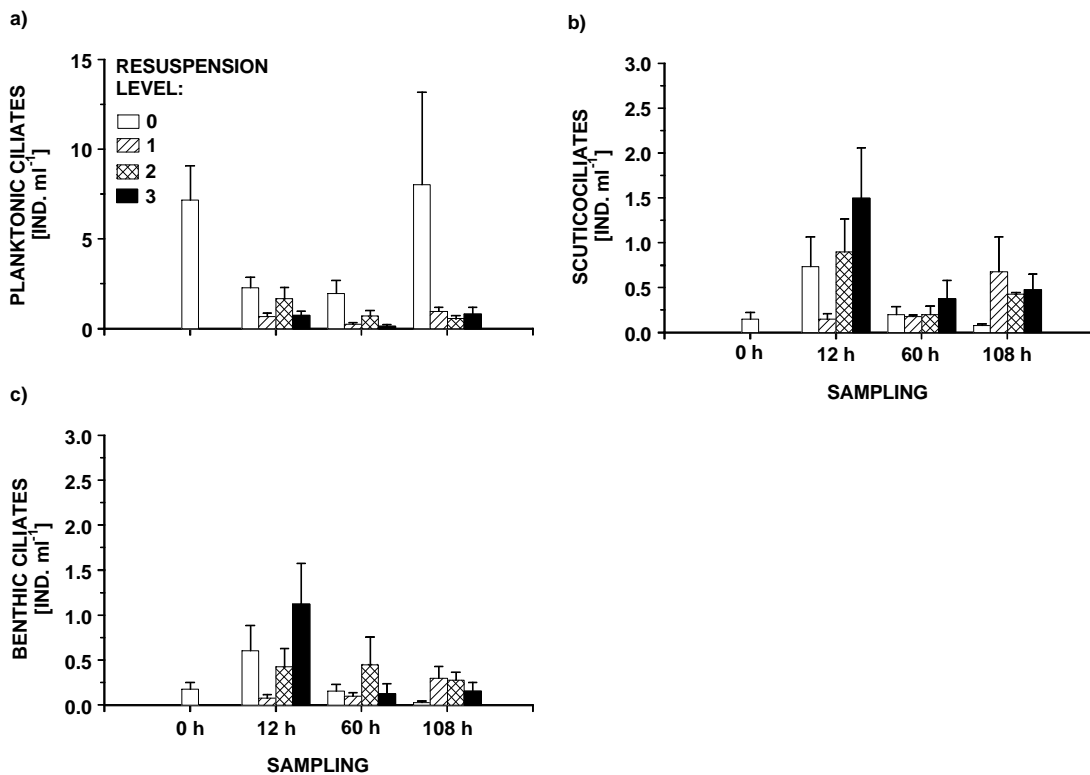


Figure 4.6. Abundances of planktonic ciliates (a), scuticociliates (b) and benthic ciliates (c) in the water column of the microcosms. Note the different scales in a and b-c (error bars: standard error, N = 4).

4.4.4. Microbial food web interactions

The correlations between microbial abundances in the experimental microcosms indicate that the lower levels of the microbial food web were closely coupled to each other (Table 4.4). Bacterial abundance was positively correlated to those of pico- and nanoautotrophs, and the abundance of HNAN was positively correlated to those of bacteria, pico- and nanoautotrophs, their main food organisms. This pattern was reflected by HNAN abundance dynamics: in addition to the initial increase in the resuspended microcosms that could be attributed to an import of HNAN from the sediment, HNAN abundance increased again, and independently of seston concentration, towards the end of the experiment (Fig. 4.5b). In contrast to the HNAN, weak correlations were found between ciliate abundance and those of the other components of the microbial food web (Table 4.4). Diatoms, dinoflagellates and rhizopods were excluded from this analysis. Diatoms and dinoflagellates were excluded because there were no herbivores to feed on them within the microbial food web, and rhizopods were excluded because their contribution to the protistan community in the water column was negligible.

Table 4.4. Spearman's rank correlation coefficients for correlations between microbial abundances (* $p < 0.05$; ** $p < 0.01$, $N = 52$).

	Picoautotrophs	Nanoautotrophs	Bacteria	HNAN
Nanoautotrophs	0.563**			
Bacteria	0.535**	0.500**		
HNAN	0.603**	0.493**	0.574**	
Ciliates	0.151	0.018	0.234	0.250

4.5. Discussion

4.5.1. Effectiveness of experimental design

It was my first hypothesis that resuspension of sediments containing benthic autotrophs, bacteria and heterotrophic protists would affect the structure of the microbial community in the water column. Before these biological resuspension effects can be discussed, however, it needs to be established to what extent my experimental design resulted in realistic physical resuspension effects. An exact simulation of the water movements involved in wave-induced sediment resuspension was not possible as part of my study (see ANDERSON 1972, GABRIELSON & LUKATELICH 1985, HAMILTON & MITCHELL 1997, and BOOTH ET AL. 2000 for a detailed discussion of this subject). However, the range of seston concentrations (32 - 425 mg l⁻¹) produced with my experimental apparatus (Fig. 4.4a) compares well with data from the coastal Southern Baltic and comparable coastal waters: GEORGI ET AL. (1980) found average seston concentrations of 39 mg l⁻¹ and maximum values of 138 mg l⁻¹ during storms in the Darss-Zingster Boddenkette, a system similar and close to the source of the material used in the experiment. Higher values of up to 895 mg l⁻¹ were recorded by autosamplers in Ringkøbing Fjord, Denmark, a system of similar size, depth, wind exposure and salinity as the Boddengewässer (PEDERSEN ET AL. 1995). The decrease of seston concentration in the resuspended microcosms towards the end of the experiment was probably caused by resedimentation of heavier mineral components. This mechanism is consistent with the observed concomitant increase in relative organic carbon content of seston material. A differential resedimentation of organic material and heavier mineral particles has also occurred after natural resuspension events (ARFI & BOUVY 1995).

I conclude that, as far as its effect on seston concentration is concerned, my experimental setup met the assumption of realistic physical resuspension effects.

4.5.2. Direct transport effects of resuspension

Direct transport effects on microbial food web components can be derived from their immediate response to resuspension, as apparent at the 12 h sampling occasion of the experiment. This time point showed significant positive resuspension effects for the HNAN and rhizopods, and non-significant positive trends for all autotrophic groups except dinoflagellates. The failure of pico- and nanoautotroph abundance to show significant resuspension effects was probably due to the high variation in the response of seston concentration to the different resuspension intensities. Pico- and nanoautotroph abundances

were, however, tightly correlated to seston concentration, which is consistent with a transport of cells from the sediment into the water column. The initial benthic abundance of nanoautotrophs (33×10^6 Ind. ml⁻¹) was sufficiently high to account for their observed increase in the water column following resuspension, but the initial benthic abundance of picoautotrophs was only 60 times higher (expressed per cm³ sediment) than their subsequent peak in the water column at the highest resuspension intensity. Given the fact that the superficial sediment was diluted by a factor of 5000 by resuspension of this intensity, and that organisms inhabiting these sediments were certainly diluted by a similar factor, resuspension of benthic picoautotrophs alone cannot account for the observed increase in picoautotrophs during the first 12 h of the experiment. In addition to resuspension of pico- and nanoautotrophs from the sediment into the water column, enhanced growth of picoautotrophs in the water column needs to be considered as a cause of the observed short-term increase in their abundance of up to 100% (see below). A transport of picoautotrophs was also reported from the Ebrie Lagoon, Côte d'Ivoire (ARFI & BOUVY 1995).

The response of benthic diatoms to resuspension intensity varied even more than that of the other autotrophs, but a trend towards increased diatom abundance with increased resuspension intensity was obvious. The variability of diatom abundances in the water column may be due to a variable incorporation of diatoms into EPS matrices. The importance of tide- and wind-induced resuspension for the colonisation of the water column of coastal waters by benthic diatoms has been documented in numerous field studies (SHAFFER & SULLIVAN 1988, DE JONGE & VAN BEUSEKOM 1992, 1995).

Fewer data are available on resuspension effects on HNAN and rhizopod abundance in the water column. The close coupling of water column abundance of rhizopods to suspended sediment concentrations during my experiment supports the idea that rhizopods in coastal waters are essentially benthic and only passively enter the water column during resuspension events (ROGERSON & LAYBOURN-PARRY 1992 B, MURZOV & CARON 1996, Chapter 2). Furthermore, the relatively low rhizopod abundance, compared to that of HNAN, in the resuspended microcosms indicates that rhizopods are not likely to contribute significantly to the coastal protozooplankton even during resuspension events. This is in agreement with biovolume data from the field (Chapter 2).

HNAN counts generally include all kinds of small heterotrophic cells (ARNDT ET AL. 2000). During the present study, about 20% of HNAN were HNF. Within the HNF segment of HNAN, high contributions of typical benthic flagellates have often been found in shallow coastal waters (ROGERSON & LAYBOURN-PARRY 1992A, ZIMMERMANN & KAUSCH 1996, ZIMMERMANN-TIMM ET AL. 1998, Chapter 2). Data on short-term effects of wind-induced resuspension on HNAN abundance have not been presented to my knowledge, but an

increase in water column abundance of HNAN has also been found following tidal resuspension (SHIMETA & SISSON 1999).

Although there was a negative resuspension effect on planktonic, and thus on total ciliate abundance at the first sampling occasion of the experiment, I did observe a non-significant increase in the abundances of scuticociliates and benthic ciliates at the highest resuspension intensity. At the same time, many typical benthic ciliates of the study area, such as karyorelictids, were not found in the water column at all. This pattern agrees with data from Buzzard's Bay, Massachusetts, where a relatively strong tidal resuspension of scuticociliates and hypotrichs such as *Euplotes sp.* was contrasted by little or no resuspension effects on karyorelictids and other benthic taxa (SHIMETA & SISSON 1999). It appears likely that behavioural adaptations which enable these ciliates to withstand resuspension are involved in the limited resuspension effect on benthic ciliates. Similar adaptations have been found in coastal Baltic meiofauna (ARLT 1988).

The negative bottle effects on planktonic ciliate abundance in all microcosms render conclusions about resuspension effects on this group problematic. However, it appears from my data that high seston concentrations and high turbulence do not foster growth of such planktonic ciliates as *Urotricha spp.* and *Strobilidium spp.* This is in agreement with field data from other high-turbidity environments, such as the River Rhine, Germany (A. SCHERWASS, personal communication), and consistent with experimental results about negative clay effects on the population dynamics of small freshwater oligotrichs (JACK & GILBERT 1993, JACK ET AL. 1993).

4.5.3. Indirect effects of resuspension on autotrophic organisms

Although the direct transport of autotrophs and heterotrophic protists into the water column is a major effect of resuspension on the coastal planktonic microbial food web, my experiment reveals indirect resuspension effects of equal importance. The increase in the water column abundance of picoautotrophs at higher resuspension intensities cannot be explained by resuspension of benthic cells alone. In addition, picoautotrophs and resuspended benthic diatoms continued to increase in abundance until the second sampling point, and the abundance of nanoautotrophs rapidly increased in all resuspended groups towards the end of the experiment. Maximum sediment concentrations during the experiment were measured after 12 h, and preliminary short-term experiments with my experimental apparatus indicate that the peak of seston concentration was reached at this sampling occasion or earlier, and not at some time between 12 h and 60 h. Therefore, the increase in autotroph abundance beyond the 12 h sampling occasion, and part of the initial increase in picoautotroph abundance, must be due to growth in the water column. According

to my data, this was mediated by reduced nitrogen limitation: dissolved ammonium and nitrate concentrations at the onset of the experiment were sufficiently low (2.1 μM and 0.2 μM , respectively) to infer nitrogen limitation of autotrophic growth. They tended to increase in the resuspended microcosms until the first sampling at 12 h. It is not surprising that this trend was not proportional to resuspension intensity: nutrient concentrations measured at this time represent net results of release processes from the sediment, enhanced remineralization, desorption from and adsorption to seston (HAMILTON & MITCHELL 1997), and assimilation by organisms which were either resuspended or already present in the water column. Although this means that gross nitrogen transfer into the water column cannot be analysed based on these data, the trend towards increased ammonium and nitrate concentrations was still apparent after 12 h, and dissolved ammonium concentrations were positively correlated to seston concentrations throughout the experiment. A significant increase of dissolved ammonium concentrations due to resuspension was also found in various coastal systems (ULLMAN & SANDSTROM 1987, ARFI ET AL. 1993, BALLS ET AL. 1994, MORTIMER ET AL. 1998).

The decrease of dissolved ammonium and nitrate concentrations towards the end of the experiment is consistent with assimilation by the growing autotrophic community. A rapid growth response of autotrophic picoplankton to dissolved nitrogen import by water column mixing has also been found in the southern Baltic Sea (STAL ET AL. 1999), and resuspended algae have been reported to rapidly reduce water column ammonium concentrations in the Ebrie Lagoon, Côte d'Ivoire (ARFI & BOUVY 1995).

The results of an additional experiment in October 1997 which focussed on effects of resuspension frequency on benthic protists support the role of reduced nitrogen limitation in indirect resuspension effects on the autotrophic community (T. GARSTECKI & S. A. WICKHAM, unpublished data). Although ammonium concentrations were again highly significantly correlated to seston concentrations, the water column of the microcosms was nitrogen-replete at the onset of this experiment. As a consequence of this difference, no nutrient-related resuspension effect on the abundance of autotrophs was found during the additional experiment.

According to several studies from lakes and coastal waters, the increased turbidity during resuspension events prevents resuspended autotrophic organisms from supporting a high primary productivity in the water column (HELLSTRÖM 1991, MACINTYRE ET AL. 1996, MACINTYRE & CULLEN 1996). Although I did not measure primary production, my experimental results do not support these findings: picoautotrophs did grow in the most intensely resuspended microcosms, even at the high turbidity during the first 12 h of the experiment. In addition, the relatively quick resedimentation of mineral particles after the 12 h sampling occasion decreased turbidity when picoautotrophs, nanoautotrophs, and diatoms

were still present in the water column in sufficiently high numbers to benefit from the then improved light and nutrient conditions. Since differential resedimentation also occurs following natural resuspension (ARFI & BOUVY 1995), my data point to a period of improved growth conditions for autotrophs at the end and immediately after resuspension events.

4.5.4. Indirect effects of resuspension on heterotrophic organisms

In contrast to the picoautotrophs, the abundance of heterotrophic bacteria did not respond to resuspension, and was only weakly correlated to seston concentration. Given the only 270-fold difference in abundance between benthic and planktonic bacterial abundance at the onset of the experiment and the dilution of the sediment as it was resuspended, a direct transport effect was not necessarily to be expected. Effects triggered by fluxes of dissolved organic matter from the sediment (see HOPKINSON ET AL. 1998) may have been rendered insignificant by the relatively high concentrations (2 - 8 mg l⁻¹, T. RIELING, personal communication) in the Boddengewässer. However, previous studies have reported positive indirect resuspension effects on bacteria which were independent of such effects: WAINRIGHT (1987) found an increase in the abundance and cell size of planktonic bacteria following the addition of resuspended sediments, and attributed it to the increase in surface area available for bacterial colonization due to resuspension. RITZRAU & GRAF (1992) observed a similar phenomenon after a storm-induced resuspension event in the benthic turbidity zone of the Kiel Bight, southern Baltic. A possible explanation for the failure of bacterial abundance to show a positive resuspension effect is bacterivory by HNF. After 12 h, the abundance ratio of bacteria and HNAN in the resuspended microcosms of the experiment averaged approximately 200, which is less than the ratio of 1000 typical of most freshwater systems (SANDERS ET AL. 1992). Even if only 20% of HNAN consisted of HNF, abundances were certainly abundant enough to exert a strong grazing impact on bacterial abundance in these microcosms.

A nutritive role of resuspended bacteria, algae and other particulate organic matter for zooplankton has been postulated (WAINRIGHT 1987, 1990, ARFI ET AL. 1993, ARFI & BOUVY 1995), but empirical evidence for such a role is scarce (WAINRIGHT 1987). During my experiment, HNAN abundance in the water column was strongly positively correlated to bacterial, pico-, and nanoautotroph abundance which suggests bottom-up control of phagotrophic HNAN by food supply. HNAN abundance was also significantly increased by resuspension. Since this relationship held over the whole course of the experiment, it cannot be explained by transport of cells from the sediment alone. Rather, the increase of HNAN in the resuspended microcosms towards the end of the experiment is consistent with an indirect

positive resuspension effect on phagotrophic HNAN mediated by feeding on bacteria, small autotrophs (see CARON ET AL. 1991, KUUPPO-LEINIKKI ET AL. 1994), and possibly with a similar effect on osmotrophic HNAN, such as yeasts. Although a propagation of resuspension effects through the microbial food web cannot be proven based on correlation data alone, it appears to be the most likely explanation of HNAN abundance dynamics during the experiment. Given the potentially high quantitative importance of mixotrophs within the pigmented flagellate community (SLEIGH 2000), it is even possible that a similar mechanism lead to the final increase in pigmented nanoflagellate (i. e. "nanoautotroph") abundance.

Ciliates were not closely coupled to the other components of the microbial food web during the experiment. This result is in agreement with data from other coastal Baltic waters (KUUPPO-LEINIKKI ET AL. 1994). As a consequence, resuspension effects on the strength of top-down control by ciliates cannot be invoked as an explanation of abundance dynamics at lower trophic levels. In addition, it has to be concluded that ciliates did not benefit from resuspension in a manner similar to HNAN. Although I cannot exclude negative shear effects on ciliate population dynamics as an explanation of the lack of a positive response to resuspension, it is also possible that the increased contribution of unedible mineral particles to the seston during resuspension interferes with the feeding mechanism of planktonic oligotrichs and prostomatids, which are largely filter-feeders. Such a mechanism, and possibly negative effects on feeding of metazooplankton, might lead to a temporal decoupling of the planktonic food web during resuspension events.

4.5.5. Significance of resuspension for the microbial food web of the study area

In most shallow waters, wind-induced resuspension events are limited in duration, and seston concentrations quickly return to background levels when wind speed falls below the resuspension threshold (KRISTENSEN ET AL. 1992, ARFI ET AL. 1993, PEDERSEN ET AL. 1995). Although this is also true for the Boddengewässer, my experiment reveals some mechanisms which may be relevant beyond a short-term effect to the function of this coastal ecosystem. Generalizing my experimental data, the main effect of resuspension appears to be on the autotrophic community. Resuspension of benthic diatoms and other autotrophs should increase water column chlorophyll *a* up to several-fold and alter phytoplankton community structure. After resuspension events, their relatively slow sinking rate should enable resuspended algae to stay in the water column when mineral seston concentrations and turbidity are already decreasing again. Increases in dissolved nitrogen, and possibly phosphorus concentration due to resuspension may enhance growth of these algae, or of phytoplankton already present in the water column. A persistent positive effect of

resuspension on phytoplankton chlorophyll *a* and shifts in phytoplankton community structure towards smaller cell sizes in the wake of resuspension events were also found in shallow lakes (PADIŠAK ET AL. 1988, OGILVIE & MITCHELL 1998).

The difference in initial dissolved nutrient concentrations between the main experiment and the additional frequency experiment, conducted four months apart, is consistent with the seasonality of dissolved nitrogen concentrations in the Boddengewässer (SCHLUNGBAUM ET AL. 1994). From this difference, I generalize that the magnitude of indirect resuspension effects on autotrophs depends on the dissolved nutrient supply in the water column, and therefore will be less pronounced in periods of high dissolved nitrogen supply (generally in autumn and winter) than when dissolved nitrogen is more limiting (generally in summer). This point has been stressed previously (MACINTYRE ET AL. 1996). On the ecosystem level, resuspension accelerates nitrogen recycling within the coastal ecosystem (COOPER 1983), similar to the mechanism found for phosphate recycling in shallow lakes (REYNOLDS 1996). The pulse in nutrients and phytoplankton from a resuspension event has the potential to contribute a substantial proportion to the total water-column productivity of the Boddengewässer. I did not measure primary production, but TENORE (1976) and SHAFFER & SULLIVAN (1988) showed that resuspended benthic diatoms increased water column primary productivity in coastal waters by up to several orders of magnitude.

Apart from transient effects on protozooplankton community structure, my experiment points to the possibility that positive resuspension effects on pico- and nanoautotrophs are propagated through the microbial food web and give rise to enhanced growth of HNAN. The fact that this propagation did not reach to the ciliates poses the question to what extent resuspension interferes with trophic interactions within the planktonic microbial food web. Another unresolved question is how resuspension influences population dynamics and trophic interactions within the benthic microbial food web. In spite of these questions, my results show that resuspension has far-reaching effects on the functioning of the microbial food web of shallow coastal waters.

5. The response of a benthic rhizopod community to experimental sediment disturbance does not support the intermediate disturbance hypothesis

5.1. Summary

Disturbance is one of the mechanisms which counteract competitive exclusion of populations in resource-limited communities, thereby facilitating coexistence and maintaining community species diversity. The intermediate disturbance hypothesis predicts maximum diversity at intermediate disturbance intensities and frequencies. This paper reports results of an experimental test of this hypothesis using a coastal benthic community of rhizopods (Protozoa: Rhizopoda), and experimental sediment resuspension as a simulated natural disturbance. I carried out two experiments of 5 d duration which focussed on the effects of resuspension intensity and frequency, respectively, on the abundance, species richness and on the Shannon-Wiener diversity index of rhizopod communities in surface sediments of natural sediment cores from the coastal Southern Baltic. Care was taken to adjust the experimental treatments to the natural disturbance regime in this area.

24 and 28 rhizopod species were present during the intensity and frequency experiment, respectively. Small bacterivorous rhizopods of the Vannellidae, Cochliopodidae, Paramoebidae and Rhizopoda incertae sedis dominated the communities during both experiments. Rhizopod abundance, species richness and diversity increased towards the end of the intensity experiment, but they did not show effects of disturbance intensity. Similarly, no effects of disturbance frequency were found during the frequency experiment. My results indicate that coexistence and community diversity maintenance in benthic rhizopod communities, and probably in benthic heterotrophic protistan communities in general, may rely on different mechanisms than intermediate disturbance, such as trophic niche separation and high rates of dispersal and colonisation.

5.2. Introduction

The intermediate disturbance hypothesis (hereafter IDH) predicts that disturbance may maintain the diversity of communities because it interferes with competitive exclusion, and that diversity is highest at intermediate intensities and frequencies of disturbance (CONNELL 1978). Concerning aquatic protistan communities, evidence has accumulated for

the applicability of the IDH to phytoplankton (GAEDEKE & SOMMER 1986, REYNOLDS ET AL. 1993, SOMMER 1995, FLODER & SOMMER 1999). Phagotrophic protists differ from phytoplankton in that they assimilate and compete for various types of particulate organic matter, rather than for mineral nutrients, light and carbon dioxide only. Although this difference entails the possibility of stronger resource niche separation in phagotrophic protists, competitive exclusion under constant conditions has been documented for phagotrophic protists as well (GAUSE 1935, VANDERMEER 1969). In aquatic heterotrophic protistan communities, the high proportion of bacterivores and trophic generalists indicates a potentially high degree of trophic niche overlap (FENCHEL 1968, PRATT & CAIRNS 1985, EPSTEIN ET AL. 1992, BUTLER & ROGERSON 1997). As a consequence, many species should depend on a shared pool of bacteria and other particulate organic carbon, resource competition and competitive exclusion should be frequent, and disturbances should be important as they counteract competitive exclusion. Empirical evidence regarding such a relationship is very scarce, however: MCGRADY-STEED & MORIN (1996) found no evidence for a role of desiccation events in maintaining the species richness of rain pool protistan communities. LUCCHESI & SANTANGELO (1997) detected more interstitial ciliate species at a sheltered than at a wave-exposed site on a Mediterranean sandy shore. This difference was probably due to differences in sediment carbon content, continuous wave action and hydrodynamic stress, rather than episodic disturbance.

The micro- and nanozoobenthos of coastal waters is one of the phagotrophic protistan communities that have been studied most intensively (e.g. FENCHEL 1969, PATTERSON ET AL. 1989, DIETRICH & ARNDT 2000). Recent field studies show that rhizopods (naked and testate amoebae) are a major component of this community (BUTLER & ROGERSON 1995, Chapter 2 & 3). Most benthic rhizopod species feed on bacteria (PRATT & CAIRNS 1985, BUTLER & ROGERSON 1997), but herbivory and predation on other protozoa have also been reported (PAGE 1977, LAYBOURN & WHYMANT 1980, YAMAMOTO & SUZUKI 1984, LAYBOURN-PARRY ET AL. 1987). The degree of selectivity between these food sources is largely unknown, which leaves open the possibility of a large degree of generalism and omnivory.

The coastal waters inhabited by benthic rhizopod communities are subject to wind- or tide-induced resuspension events (e.g. ARFI ET AL. 1993, PEDERSEN ET AL. 1995). These events can be regarded as disturbances in the sense of the IDH because erosion of the uppermost sediment layers creates new habitat patches, released nutrients may foster autotrophic and bacterial growth and thus improve food supply, and oxygen may be pumped into superficial sediments (RIEDL ET AL. 1972, WAINRIGHT 1987, ARFI ET AL. 1993).

I have therefore derived the hypothesis that episodic sediment resuspension contributes to the maintenance of the diversity of benthic heterotrophic protists in shallow

coastal waters, and that the response of benthic heterotrophic protists to resuspension should be consistent with the IDH. I experimentally tested this hypothesis using benthic rhizopods in natural sediment cores from the coastal Southern Baltic. Rhizopods were chosen because of their quantitative importance, and because a relatively rapid response to experimental manipulation was expected due to their short generation times (BALDOCK ET AL. 1980). I varied disturbance due to resuspension in two experiments, where in the first, I varied resuspension intensity, and in the second, resuspension frequency.

5.3. Materials and Methods

5.3.1. Reference site

The experiments were carried out with natural sediment cores from a station in the Boddengewässer, shallow, non-tidal, brackish estuaries on the north-eastern Baltic coast of Germany. Rassower Strom (54° 34' N, 13° 10' O) is mesotrophic with an average salinity of 9.0 PSU and a mean water depth of 3.8 m. Muddy sediments (4% organic content) prevail. The frequency and duration of naturally occurring resuspension events at Rassower Strom has been estimated from turbidity (S. DAHLKE, unpublished data) and wind speed measurements (J. MEYERCORDT, unpublished data) between May and November 1996. For the analysis presented in Figure 5.1, resuspension events were defined as situations with less than 10 % light transmission (measured with an MT ecomemory probe) 0.5 m above the sediment and more than 5 m s⁻¹ wind speed at Schwedenhagen, Hiddensee Island, 5 km distant from Rassower Strom.

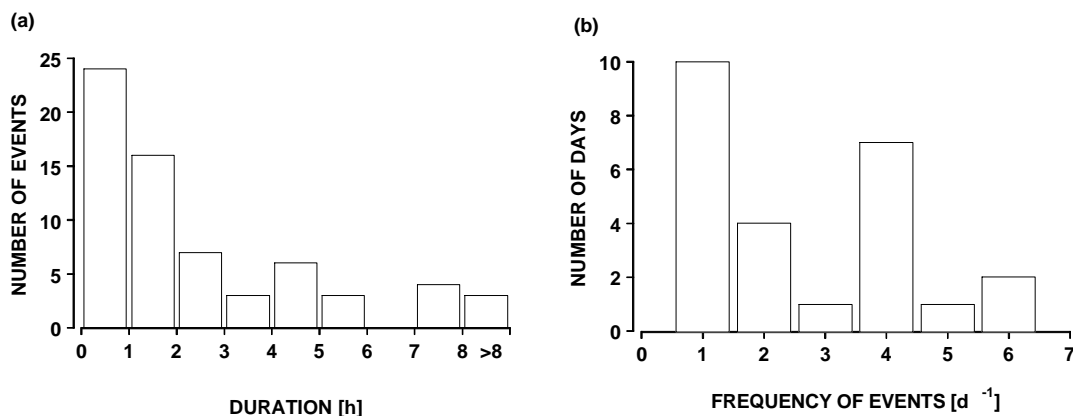


Figure 5.1. Duration (a) and frequency (b) of resuspension events at Rassower Strom in 1996. Turbidity data (48 measurements per day) were available for a total of 142 d between May 15th and November 1st. During this period, 66 resuspension events were recorded. See text for details. Data from Dahlke (unpubl.), Meyercordt (unpubl.).

5.3.2. Experimental design

The effects of resuspension intensity on benthic rhizopod community structure were studied during a first experiment in June 1996. Effects of the frequency of sediment disturbance were studied during another experiment in October 1997. For both experiments, 20 sediment cores with 2.6 l overlying water were obtained by a ship-operated multicorer from Rassower Strom. Four cores were chosen at random and analysed as reference cores at t_0 . The remaining 16 cores were transferred into plastic tubes (length 400 mm, inner diameter 100 mm) and incubated in a water basin at 18 °C under $220 \mu\text{E m}^{-2}$ illumination with a light / dark-cycle of 16 h / 8 h. Light and temperature conditions corresponded to field conditions. Resuspension was achieved by oscillating grids (Fig. 5.2a, b; modified from DAVIS, 1993). The experimental microcosms were randomly assigned to treatments, and arranged in the water bath in a way that allowed three groups of four grids to be driven by one electric motor each (Fig. 5.2c). Another group of four cores was left as control.

During the intensity experiment, experimental groups were treated with grid oscillation frequencies of 0.71 s^{-1} , 1.22 s^{-1} , and 1.60 s^{-1} , respectively, for 12 h per day. These frequencies were found to produce the range of naturally occurring seston concentrations during resuspension events in preliminary short-term experiments. For the frequency experiment, resuspension intensity was kept constant at 1.4 s^{-1} but the frequency of 3 h - resuspension events was 0, 1, 2 or 4 d^{-1} .

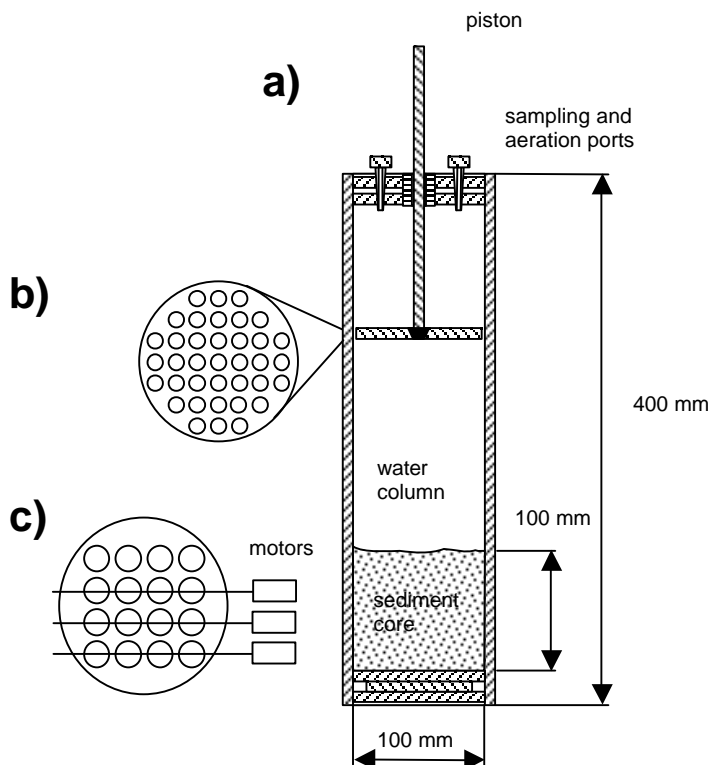


Figure 5.2. Experimental setup: (a) section from top to bottom of an experimental microcosm, (b) schematic view of the oscillating grid, (c) arrangement of experimental microcosms in the water bath.

5.3.3. Sampling and sample analysis

At the beginning of both experiments, I took sediment samples from the reference cores. Immediately after the end of experiments, the experimental cores were also processed for sediment samples. Water samples for the analysis of oxygen saturation and seston concentration were taken from each experimental microcosm after 12, 60 and 108 h (intensity experiment) and 27, 75 and 123 h (frequency experiment). I only report seston concentration as a measure of resuspension intensity, and oxygen concentration in order to exclude possible negative effects of hypoxia on rhizopods. During the frequency experiment, I arranged the sampling schedule in a way that allowed all groups to be sampled immediately after a 3 h - resuspension event.

Seston dry weight was measured according to the standard protocol of GRASSHOFF ET AL. (1983). Oxygen saturation was measured with an oxygen sensor. Prior to sediment sampling for rhizopod community structure, I pipetted the overlying water from the experimental cores. Subsequently, plastic tubes (25 mm internal diameter) were gently pushed into the sediment surface and covered with rubber stoppers. As the subcores were extracted, a slight vacuum was created to prevent sediment-compaction. After extraction, I cut the subcores into the 0 - 5 mm and 5 - 10 mm layers. In the intensity experiment, only the 0 - 5 mm layer was sampled. The resulting sediment subsamples were diluted with defined volumes of 0.2 μm -filtered, autoclaved seawater and stored at *in situ*-temperatures in the dark until further processing. The abundance of rhizopod species was determined with a modified version of the liquid aliquot method (BUTLER & ROGERSON 1995, Chapter 3). This method is suitable for the enumeration of bacterivorous and omnivorous rhizopods, and excystment during incubation has little effect on abundance estimates of rhizopod species from the Boddengewässer (Chapter 3). 48-72 sediment subsamples of 10 μl each were inoculated into wells of two tissue culture plates containing 2 ml Føyns-Erdschreiber medium (PAGE 1983). After 12 and 24 d incubation at 18 °C in the dark, the wells were screened for the presence of rhizopod species and initial abundance was calculated from the frequency of wells positive for each species based on the Poisson distribution. I identified species using original species descriptions or modern identification keys (e.g. PAGE, 1983). I did include into my analysis species that could only be identified to genus, but only provided I could clearly recognise in all samples, and distinguish them from other members of their genus. From the taxonomic analysis and the abundance of individual species, I calculated total rhizopod abundance, the number of morphospecies, and the Shannon-Wiener diversity index (SHANNON & WEAVER 1963). Resuspension effects on seston concentration and oxygen saturation were tested using repeated-measures-ANOVAs, while effects on the abundance of rhizopod species or higher taxonomic groups were tested using one-way ANOVAs.

Datasets were tested for normal distribution and homoscedasticity prior to ANOVAs. Abundances and diversity indices were log-transformed prior to analysis to equalise variance between treatments, but untransformed data are given in the figures. All statistics were calculated using SPSS.

5.4. Results

5.4.1. Intensity experiment

The different resuspension intensities yielded a range of seston concentrations of 20 - 415 mg l⁻¹ (Fig. 5.3a). Seston concentration varied significantly with resuspension intensity, both after 12 h (one-way-ANOVA, $P < 0.001$) and over the whole course of the experiment (repeated-measures-ANOVA, $P = 0.003$). Oxygen saturation increased from 68 - 78 % at the 12 h sampling occasion to final values of 101 - 130 % (data not shown). Saturation values tended to be highest at the lowest resuspension level during the last two sampling occasions, but this trend was not significant. They were significantly negatively correlated to seston concentration (Spearman's $r = -0.440$, $P < 0.01$).

In total, 24 species of rhizopods were found in the intensity experiment (Table 5. 1). 11 - 15 species each were present in the microcosms sampled at t_0 , while at the end of the experiment, 15 - 19 and 13 - 22 species each were present in the individual control and resuspended microcosms, respectively. Small bacterivores such as *Stygamoeba polymorpha* and small *Vannella* spp. dominated rhizopod abundance in all microcosms irrespective of resuspension intensity. *Stygamoeba polymorpha* and the Vannellids reached abundances of 2,400 - 2,800 and 1,200 - 2,300 Ind. cm⁻³, respectively. Thus, they contributed up to 49 % and 25 %, respectively, to the abundance of all rhizopods combined (Fig. 5.4a). They were followed by Paramoebidae (mainly bacterivorous *Mayorella* spp.) and Testaceafilosia (mainly *Trinema lineare* and *Euglypha* spp.). The abundance of these groups also did not show clear resuspension effects. In addition, no resuspension effects were found for the relative abundance contributions within the taxonomic groups which are shown in Figure 5.4. This general pattern was reflected by the failure of any taxonomic group - species or higher taxonomic level - to show resuspension effects in a one-way-ANOVA.

The abundance of benthic rhizopods increased from 5,000 Ind. cm⁻³ at the beginning of the experiment to 7,500 - 9,100 Ind. cm⁻³ at the end of the experiment, but it did not show a resuspension effect (Fig. 5.5a). The same was true for the species number and the Shannon Wiener Diversity Index in the uppermost 5 mm of the sediment which reached values of 19 and 1.08, respectively, towards the end of the experiment (Fig. 5.5c, e).

Table 5.1. Rhizopod species pool of the experimental sediment cores (i... intensity experiment; f... frequency experiment).

Species / Morphospecies		
Paramoebidae &		
Limax amoebae	Vexilliferidae	Testaceafilosia
<i>Vahlkampfia damariscottae</i> (f)	<i>Mayorella smalli</i> (i, f)	<i>Lecythium spec.</i> (f)
<i>Vahlkampfia spec. 2</i> (f)	<i>Mayorella gemmifera</i> (i, f)	<i>Trinema lineare</i> (i, f)
<i>Rhizamoeba spec.</i> (i, f)	<i>Mayorella spec. 3</i> (i, f)	<i>Cyphoderia ampulla</i> (i, f)
<i>Hartmannella vermiformis</i> (i)	<i>Mayorella spec. 4</i> (i, f)	<i>Paulinella chromatophora</i> (i)
<i>Cashia limacoides</i> (f)	<i>Vexillifera minutissima</i> (i, f)	<i>Euglypha spec. 1</i> (i, f)
	<i>Vexillifera spec. (i, f)</i>	<i>Euglypha spec. 2</i> (i, f)
Thecamoebidae &		
Vannellidae	Testacealobosia	Granuloreticulosea
<i>Thecamoeba orbis</i> (i)	<i>Cochliopodium bilimbosum</i> (f)	<i>Apogromia spec.</i> (i)
<i>Thecamoeba hilla</i> (f)	<i>Cochliopodium minus</i> (i, f)	
<i>Vannella aberdonica</i> (i, f)	<i>Cochliopodium spec. 3</i> (i, f)	Aconchulinida
<i>Vannella simplex</i> (i, f)	<i>Gocevia spec.</i> (f)	<i>Nuclearia spec.</i> (i, f)
<i>Vannella platypodia</i> (i, f)	<i>Phryganella spec.</i> (i, f)	<i>Arachnula spec.</i> (i)
<i>Platyamoeba spec.</i> (f)		
		Other amoeboid protists
		<i>Stygamoeba polymorpha</i> (i, f)
		<i>Chrysamoeba radians</i> (f)

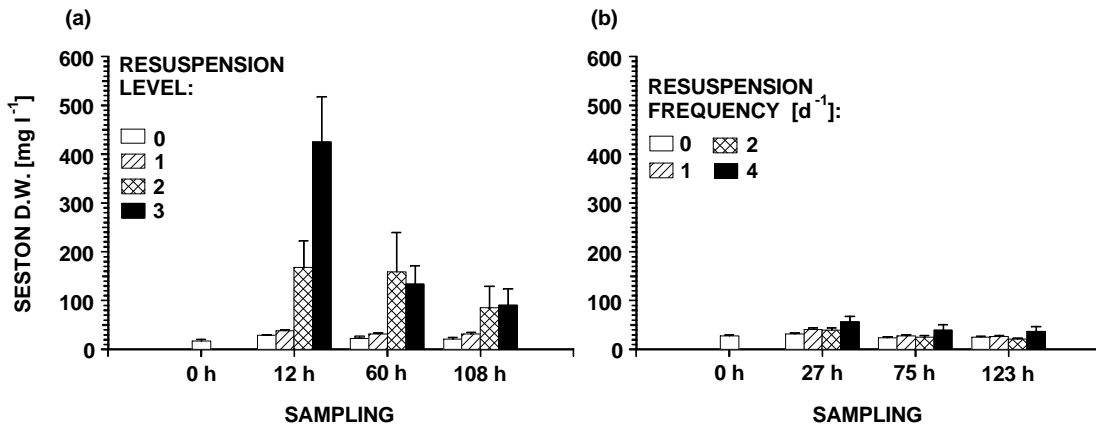


Figure 5.3. Seston concentration in the microcosms during the intensity experiment (a) and during the frequency experiment (b) (error bars: standard error, N = 4).

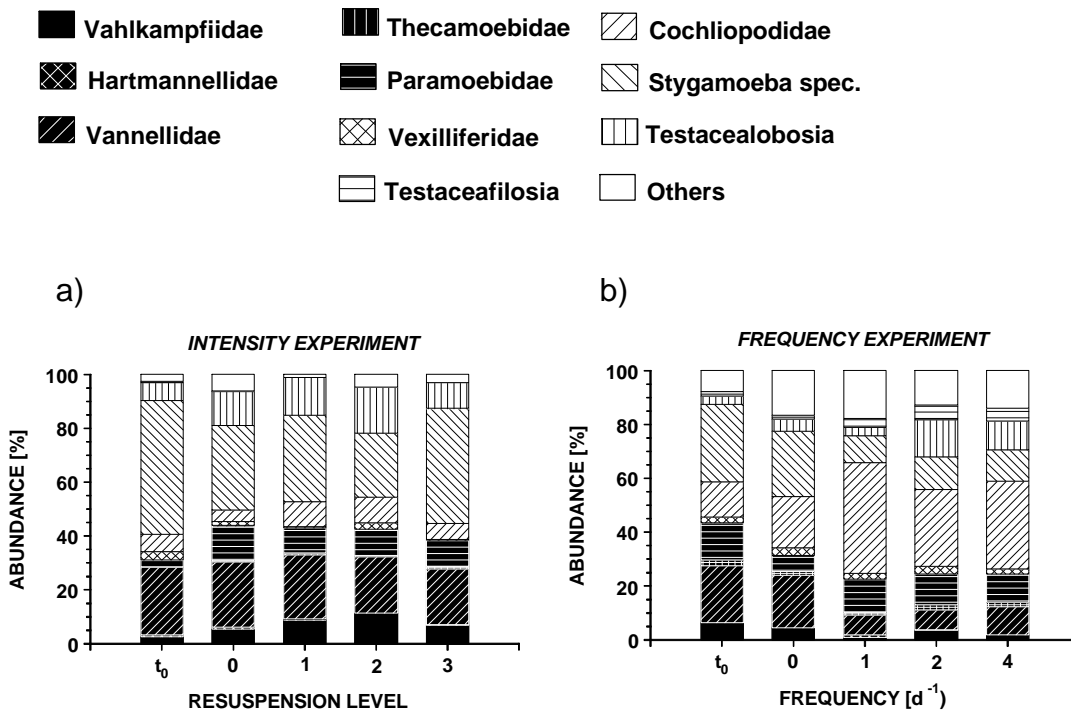


Figure 5.4. Relative contributions of important groups to the rhizopod community in the uppermost 5 mm of the sediment at the beginning (reference cores) and at the end of the intensity experiment (a) and of the frequency experiment (b).

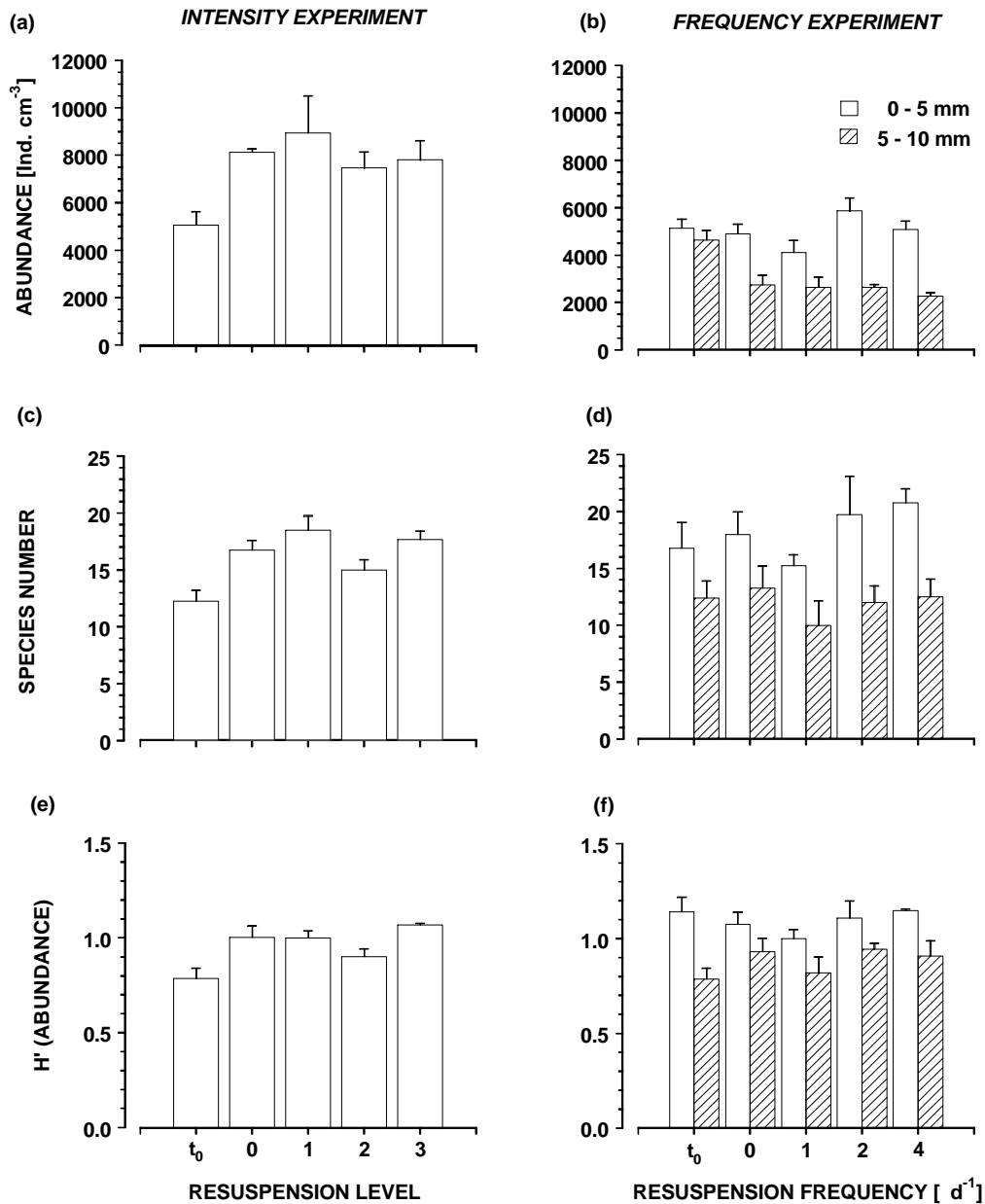


Figure 5.5. Abundance (a, b), species number (c, d), and Shannon Diversity Index (e, f, based on species abundances) of rhizopods at the beginning and at the end of the experiments. Data for the 5-10 mm sediment layer are only available from the frequency experiment (error bars: standard error, N = 4).

5.4.2. Frequency experiment

During the frequency experiment, seston concentrations were lower (21 - 55 mg l⁻¹) because maximum resuspension intensity was lower, and possibly because the sediments were less susceptible to resuspension at this time of the year. Measured directly at the end of resuspension events, differences between experimental treatments were not significant (Fig. 5.3b). Oxygen saturation increased from 56 - 74 % after 27 h to 112 - 126 % after 123 h (data not shown). As in the intensity experiment, saturation values were negatively correlated to seston concentrations over the whole course of the experiment (Spearman's $r = -0.333$ $P < 0.05$). They tended to be highest in microcosms resuspended at 2 d⁻¹, but this trend was not significant.

Similar to the intensity experiment, 28 rhizopod species were found in the 0 - 5 mm layer of the cores of the frequency experiment (Table 5. 1). I found 12 - 23 species each in the microcosms sampled at t_0 , while at the end of the experiment, I found 13 - 22 and 11 - 27 species each in the control and resuspended microcosms, respectively. *Cochliopodium* spp. reached higher abundances of 670 - 1,800 Ind. cm⁻³ in this experiment than in the intensity experiment, and dominated final rhizopod abundance in the resuspended microcosms (28 - 41 % abundance contribution). Contrary to this dominance pattern, *Stygamoeba polymorpha* and small Vannellidae were the most abundant groups at t_0 , and in the control group: in this group, *S. polymorpha* and the Vannellida reached 1,200 and 950 Ind. cm⁻³, respectively, which equalled 24 % and 20 % abundance contribution, respectively (Fig. 5.4b). In the 5 - 10 mm sediment layer, similar dominance patterns as in the 0 - 5 mm layer were found (data not shown). However, these trends towards shifted dominance were not significant, nor were any resuspension effects on individual species or on the groups shown in Figure 5.4b.

The similarity in community structure between resuspended and control groups was reflected by variable, but generally similar total rhizopod abundances (4,100 - 5,800 Ind. cm⁻³, Fig. 5.5b) similar mean species yields (15 - 21 species, Fig. 5.5d) and similar values of the Shannon-Wiener diversity index (1.0 - 1.16, Fig. 5.5f). The corresponding values in the 5 - 10 mm layer were lower (2,400 - 2,700 Ind. cm⁻³, 10 - 13 species and an Shannon-Wiener index of 0.75 - 0.94), but they were also not affected by resuspension (Fig. 5.5b, d, f).

5.5. Discussion

Although a total of 33 rhizopod morphospecies could be distinguished in the sediment samples from the experiments, I did not observe effects of either the intensity or the

frequency of resuspension events on species richness or diversity of the benthic rhizopod community. These results clearly contradict my hypothesis.

The contrary results are not due to an unrealistic range of resuspension intensity and frequency. The frequency experiment covered the whole range of naturally occurring resuspension frequencies, including very high values (Fig. 5.1). According to laboratory experiments, many rhizopod species, including some which were present in my samples, have generation times of only a few hours at 20 °C (BALDOCK ET AL. 1980). Therefore, the frequencies of 1 d⁻¹ and 2 d⁻¹ qualify as intermediate according to the criteria (one disturbance during a period equivalent to approximately two to three generation times) established for autotrophic protists (GAEDEKE & SOMMER 1986, REYNOLDS 1988). The controls can be regarded as treatments with a resuspension frequency of less than 0,2 d⁻¹. Although it is difficult to define an intermediate resuspension intensity, the range of seston concentration during the intensity experiment compares well with the average seston concentration of 39 mg l⁻¹ and maximum values of 138 mg l⁻¹ during storms in the Darss-Zingster Boddenkette, a system similar and close to Rassower Strom (GEORGI ET AL. 1980). Therefore, the seston concentration produced at the lowest resuspension level should reflect an intermediate intensity of resuspension, while those produced at the highest intensity were very high in comparison to concentrations encountered in the field. I conclude that the experimental regimes of the experiments were sufficiently realistic and consistent with theory. Thus, biological explanations for the failure of the rhizopod communities to show the predicted effect need to be considered.

According to the intermediate disturbance hypothesis, disturbances are important for the maintenance of diversity because they set back competitive exclusion in the course of community succession. Therefore, the applicability of the hypothesis to benthic rhizopods and sediment disturbance depends on two criteria: Is competitive exclusion important in natural benthic rhizopod communities, and if so, how does sediment disturbance interfere with it?

Competition effects on rhizopod community structure have been little studied. Experimental results about other heterotrophic protists indicate that competitive exclusion may well happen to populations confined to a limited space, e. g. on a local scale (GAUSE 1935, VANDERMEER 1969). However, it may be rendered insignificant at the metapopulation level – or on a local scale - by the high numbers and dispersal capacity which enable these organisms to recolonize local patches quickly when conditions have changed (FENCHEL 1993, HOLYOAK & LAWLER 1996, FENCHEL ET AL. 1997, WARREN 1996). The size of my experimental cores, and even the size of the subsamples analysed for rhizopod community structure, was rather in the regional than in the local range because a sediment core of several cubic centimeters contains various microzones with varying micro- and nanofauna,

both on the vertical and on the horizontal axis (ARLT 1973, BERNINGER & EPSTEIN 1995, SMIRNOV ET AL. 1998, WICKHAM ET AL. 2000). This small-scale spatial heterogeneity is likely to be relevant for rhizopods as well. It should weaken the strength of competitive interactions and delay competitive exclusion. As a consequence, the effects of sediment disturbance on rhizopod diversity are likely to be complex. If rhizopods coexist by niche separation along gradients in a microheterogeneous environment, the breakdown of spatial structure during resuspension and the mixing of resuspended sediments should actually increase the probability of competitive interactions and competitive exclusion on a regional scale. This should counteract and weaken any positive effect of sediment disturbance on rhizopod diversity.

Another negative effect on the rate of competitive exclusion is expected from the wider range of resource niches of heterotrophic protists, as compared to phytoplankton. Although competition for bacterial prey should influence benthic rhizopod community structure, little is known about the actual width of the trophic niches of individual rhizopod species. A high contribution of food specialists to the rhizopod community should result in decreased resource competition, while a high contribution of trophic generalists should increase the part of the food spectrum that is shared by more than one species, and hence should result in stronger resource competition (TILMAN 1982).

The wider range of resource niches - relative to phytoplankton communities - is a feature not only of benthic rhizopods, but of phagotrophic communities in general. In the light of this difference, it appears only logical that most evidence for the relevance of the IDH in aquatic ecosystems has been found in phytoplankton which compete for a limited number of resources in a relatively homogeneous environment (e. g. REYNOLDS ET AL. 1993, SOMMER 1995, FLODER & SOMMER 1999). As a consequence of both the spatial separation of rhizopod populations, and of trophic niche separation, the effect of competitive exclusion on regional (cm^2 - m^2 scale) rhizopod community structure should be weakened, and so should be the effects of sediment disturbance.

In contrast to dilution and nutrient addition which have been used in experimental tests of the IDH using phytoplankton (GAEDEKE & SOMMER 1986, SOMMER 1995), resuspension simultaneously affects the benthic community in several ways. The net effect on benthic rhizopod community structure and diversity is complex, and may be positive as well as negative. I conclude that wind-induced sediment disturbance plays a complex, but relatively minor role in the maintenance of benthic rhizopod diversity on the time scale of days to weeks. This may partly be due a selective effect of the generally high frequency of resuspension events on the rhizopod community on much larger time scales, which would

allow only those species to survive in the Boddengewässer which are able to cope with frequent resuspension disturbance.

6. Effects of resuspension and mixing on population dynamics and trophic interactions in a model benthic microbial food web

6.1. Summary

The effects of resuspension and mixing on the population dynamics and trophic interactions in a simple benthic microbial food web were studied during three plankton wheel experiments of 9 - 15 d duration. The food web consisted of a mixed bacterial assemblage, the heterotrophic flagellate *Bodo designis*, the ciliate *Euplotes balteatus* and the rhizopod *Vannella platypodia*. The diatom *Amphora coffeaeformis* was included to maintain oxygen concentrations. Population dynamics in 500 ml - microcosms on rotating and non-rotating plankton wheels were compared.

Final abundances of *Amphora* increased in suspension in all experiments. Resuspension increased initial growth rates and final abundances of *Euplotes* and *Vannella* during a whole-community experiment and a community subset experiment during which resuspension effects with and without the top predator *Euplotes* were compared. During the community subset experiment, suspended *Bodo* grew faster and reached higher final abundances than non-resuspended *Bodo* when *Euplotes* was absent, but experienced higher loss to *Euplotes* when the ciliate was present. Individual consumption rates of *Bodo* by *Euplotes* were estimated to be higher in suspension (5.5 versus 3.6 *Bodo Euplotes*⁻¹ h⁻¹), which could not be explained by higher abundance of *Bodo* alone. Similar, but non-significant trends were found for bacteria. During a third experiment, *Euplotes* could not benefit from resuspension at low food concentrations.

My results show that resuspension and mixing can enhance population growth of autotrophic and heterotrophic protists, and that the trophic coupling between flagellates and ciliates, and possibly between other microbial food web components, can become closer in suspension when food supply is sufficient. This suggests that subsidiary energy input by resuspension and mixing may increase the biomass turnover in benthic microbial food webs.

6.2. Introduction

The sediment and the water column of shallow lakes and coastal waters are closely coupled by sedimentation and wind- or tide-induced sediment resuspension. Together with resuspended sediments, bacteria, microphytobenthos, and heterotrophic protists enter the water column during resuspension events (SHAFFER & SULLIVAN 1988, PADIŠAK ET AL 1990, DE JONGE & VAN BEUSEKOM 1992, 1995, ARFI & BOUVY 1995, SHIMETA & SISSON 1999, Chapter 2). Although benthic protists can contribute substantially to water column abundances in the field (SHAFFER & SULLIVAN 1988, DE JONGE & VAN BEUSEKOM 1992, SHIMETA & SISSON 1999, Chapter 2), the effects of resuspension and mixing on resuspended protists and on the benthic microbial food web as a whole have not been studied to date. Instead, experimental studies of microbial responses to resuspension have shown important effects of released nutrients and organic carbon on plankton: phytoplankton can benefit from nutrients imported with resuspended sediments (KRISTENSEN ET AL. 1992, REYNOLDS 1996, OGILVIE & MITCHELL 1998). The same is true for bacterioplankton (WAINRIGHT 1987, JUGNIA ET AL. 1998), and heterotrophic nanoplankton (WAINRIGHT 1987).

The kinetic energy of wind and tides may favour plankton organisms via water column mixing and turbulence (e.g. AGUILERA 1994, PETERS & GROSS 1994, SHIMETA ET AL. 1995). Similarly, sediment resuspension and mixing should not only resuspend buried nutrients, but also increase the total accessible surface area of suspended particulates, and alter encounter rates between predators and prey: dilution of populations inhabiting resuspended sediments should decrease encounter rates, while mixing should increase them. This should result in increased bacterial growth and altered trophic coupling in resuspended benthic microbial food webs. As a first experimental test of this hypothesis, I have studied the effects of resuspension and mixing on a simple, artificially assembled benthic microbial food web. Although the experiments were designed to identify general mechanisms of resuspension on the microbial community, I have chosen benthic organisms that have previously been found in suspension in shallow inlets of the Southern Baltic, and in other shallow coastal waters (ZIMMERMANN-TIMM ET AL. 1998, Chapter 2).

6.3. Materials and Methods

6.3.1. Model community

The model benthic microbial community consisted of a natural mixed bacterial assemblage, the diatom *Amphora coffeaeformis* (length = 25 µm), the bacterivorous

flagellate *Bodo designis* (length = 8 μm), the omnivorous ciliate *Euplotes balteatus* (l = 70 μm), and the presumably bacterivorous rhizopod *Vannella platypodia* (length = 15 μm , experiments 1 and 2 only). The food web structure (Fig. 6.1) was established from direct observation and literature data (PRATT & CAIRNS 1985, PAGE & SIEMENSMA 1991, ZUBKOV & SLEIGH 1996, PREMKE & ARNDT 2000). Representatives of the genera *Bodo*, *Euplotes* and *Vannella* have been found in the water column of coastal waters during resuspension events (Chapter 2, ZIMMERMANN-TIMM ET AL. 1998). The bacterial assemblage and all heterotrophic protists were isolated from sediments of Rassower Strom, coastal Southern Baltic. Sediment aliquots were inoculated into Føyns-Erdschreiber medium (PAGE & SIEMENSMA 1991). Protists were further isolated by dilution until any other eukaryotes were absent. Bacteria were separated from protists by filtration with a 0.8 μm polycarbonate membrane filter. The diatom *Amphora* was too large to be ingested by the other protists. It was included to maintain the oxygen concentration within the experimental bottles, and to foster bacterial growth by exudation.

All stock cultures were kept at 18 °C under 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density (light / dark cycle 15 h / 9 h) in Føyns-Erdschreiber medium, prepared with 10 PSU artificial seawater (hereafter ASW, CARON 1993).

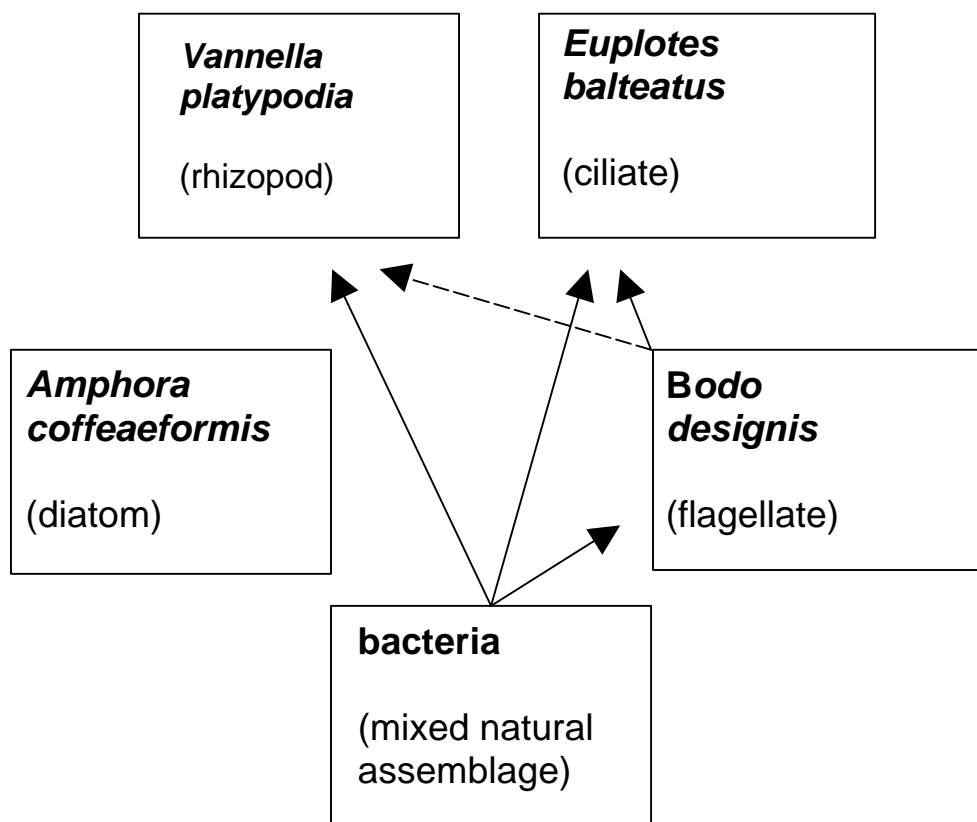


Figure 6.1. Structure of the artificially assembled benthic microbial food web (solid lines: trophic links; dashed line: possible trophic link).

Table 6.1. Inocula, enrichments, initial abundances and sampling schedules. Each group in the community subset experiment and in the particulate enrichment experiment consisted of four resuspended and four control replicate bottles. 12 control, 12 resuspended, and 4 t_0 bottles were used in the whole-community experiment. See text for details.

	Whole community experiment	Community subset experiment			Particulate enrichment experiment	
Inoculum	<i>Amphora</i> bacteria <i>Bodo</i> <i>Vannella</i> <i>Euplotes</i>	Group 1: <i>Amphora</i> bacteria	Group 2: <i>Amphora</i> bacteria <i>Bodo</i> <i>Vannella</i>	Group 3: <i>Amphora</i> bacteria <i>Bodo</i> <i>Vannella</i> <i>Euplotes</i>	<i>Amphora</i> bacteria <i>Bodo</i> <i>Euplotes</i>	
Enrichment	soil extract (5 %)	soil extract (5 %)			Group 1: -	Group 2: <i>Urtica</i> powder (50 mg l ⁻¹)
Initial abundance [ml ⁻¹]						
<i>Amphora</i> bacteria	270 5.2 * 10 ⁶	3200 8.4 * 10 ⁶	4600 11.2 * 10 ⁶	2500 11.0 * 10 ⁶	2500 2.4 * 10 ⁶	2800 3.4 * 10 ⁶
<i>Bodo</i>	660	-	3300	3000	2600	3000
<i>Vannella</i>	43	-	12	19	-	-
<i>Euplotes</i>	3.7	-	-	1.9	0.9	1.2
Sampling points [d]	0, 2, 7, 15	0, 2, 5, 9			0, 2, 5, 9	

6.3.2. Experimental design

The population dynamics of identical communities incubated together with autoclaved surface sediments on rotating and non-rotating plankton wheels were compared during three

plankton-wheel experiments (Table 6.1): a whole-community experiment with liquid enrichment and two semi-continuous experiments, one with liquid enrichment and three different community subsets (hereafter community subset experiment), and one with identical communities, comparing no enrichment with particulate enrichment (hereafter particulate enrichment experiment). The experiments were carried out using plankton wheels (slowly, vertically rotating wheels with 1.2 m diameter). Plankton wheels allow to keep sediment and benthic organisms in suspension without causing turbulence. The whole-community experiment was carried out in order to follow the overall dynamics of the microbial community in a resuspended sediment. The microcosms were enriched once with Føyns-Erdschreiber medium (5%) in order to simulate nutrient and organic carbon pulses during resuspension events. During the community subset experiment I analysed how trophic interactions are affected by resuspension. The population dynamics of bacteria and nanofauna (*Bodo* and *Vannella*) with and without their respective predators (all heterotrophic protists in the case of bacteria and *Euplotes* in the case of *Bodo*) were followed, allowing estimates of loss rates due to predation in resuspended and non-resuspended communities. The particulate enrichment experiment was designed in order to discern resuspension effects mediated by an import of edible organic matter into the water column from resuspension effects without enrichment. *Urtica* powder was used to simulate particulate phytodetritus in this experiment.

6.3.3. Inoculation and incubation

Aliquots of the inocula were inoculated into 24 acid-rinsed 500 ml polycarbonate bottles containing 10 PSU artificial seawater, 0.4 g l⁻¹ double-sterilised, washed surface sediment from Rassower Strom, and enrichment (Table 6.1). Prior to the whole-community experiment, an additional four flasks were prepared in the same way and sampled at t_0 . The individual cultures for the community subset experiment were inoculated separately (Table 6.1). In this experiment, aliquots of 2 μm - filtered cultures of *Vannella*, *Bodo* and *Euplotes* were pipetted into those bottles not receiving the respective inoculates in order to minimise differences in initial bacterial abundance due to bacteria co-inoculated with the protistan cultures. The initial abundances of bacteria, *Bodo*, *Vannella* and *Euplotes* were within the naturally occurring abundance range of the respective groups in the coastal Southern Baltic (see Chapter 2). When closing the incubation bottles after inoculation, care was taken to prevent air bubbles from being trapped inside the bottles.

Eight or twelve bottles each were randomly mounted on two plankton wheels. In the whole-community experiment, all bottles received an identical inoculum. In the community

subset experiment and in the particulate enrichment experiment, each wheel carried two or three groups of four replicate bottles, each group containing different community subsets or different enrichment levels. The plankton wheel carrying the resuspended microcosms rotated at 5 min^{-1} , which was sufficient to keep the included sediments in suspension. The wheel carrying the control microcosms only was turned by 180° once a day to correct for differences in light intensity on its upper and lower sides. The bottles mounted on the plankton wheels were incubated at 18°C and $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ photon flux density (light / dark cycle 15 h / 9 h) for 15 d (whole-community experiment) or 9 d (community subset experiment and particulate enrichment experiment).

6.3.4. Sampling and sample analysis

Prior to each sampling (Table 6.1), the bottles were extensively shaken and oxygen concentrations within the bottles were measured. Samples for the enumeration of bacteria, *Amphora coffeaeformis*, *Bodo designis*, *Vannella platypodia* and *Euplotes balteatus* were taken. During the whole-community experiment, four replicate bottles were removed and sampled from each plankton wheel at each sampling occasion, whereas 100 ml of culture medium were sampled from each bottle at each occasion during both semi-continuous experiments. They were replaced by a cocktail of artificial seawater, sediment and enrichment at concentrations equal to the initial concentrations in the respective bottles.

Oxygen concentrations were measured with a MTW™ OXI 96 probe. Bacteria and *Bodo* were fixed with glutaraldehyde (1.5 % final concentration) and enumerated in DAPI-stained (4',6'diamidino-2-phenylindole) samples using epifluorescence microscopy (SHERR ET AL. 1993). Briefly, 0.5 ml and 2 ml subsamples were stained ($2.5 \mu\text{g ml}^{-1}$ final DAPI concentration) and concentrated on black polycarbonate filters (Millipore) of $0.2 \mu\text{m}$ and $0.8 \mu\text{m}$ pore size for the enumeration of bacteria and *Bodo*, respectively. At least 50 *Bodo* and 300 bacteria on a minimum of 50 and 15 grids, respectively, were counted. In addition, the presence of picoautotrophs was checked based on chlorophyll autofluorescence at 450 – 490 nm excitation. *Vannella* was enumerated with a modified version of the liquid aliquot method (Chapter 3). Between 24 and 72 subsamples of 1-100 μl were inoculated into wells of tissue culture plates containing Føyns-Erdschreiber medium. After 14 d incubation at 18°C in the dark, the wells were screened for the presence of *Vannella* and initial abundances were calculated from the frequency of positive wells assuming a Poisson distribution. *Euplotes* and *Amphora* were fixed in Bouin's fixative (a mixture of 80 % formaldehyde saturated with picric acid and 20 % acetic acid at 5 % final concentration) and counted after sedimentation of 10 ml-subsamples according to UTERMÖHL (1958). During the community

subset experiment, aliquots of 1 ml from each ciliate-free microcosm were incubated in sterile vials containing ASW enriched with soil extract, and subsequently monitored for contamination with any heterotrophic protists (protist-free group) or *Euplotes* (*Euplotes*-free group).

6.3.5. Statistical analysis

Abundances were corrected for after-sampling replacement dilution in both semi-continuous experiments. Initial exponential growth rates were calculated from mean group abundances at t_0 and $t = 2$ d, the first two sampling points. When appropriate during the community subset experiment, loss rates due to predation were estimated from the difference in growth rate with and without predators present. Individual consumption rates of *Euplotes* were estimated from these loss rates, initial prey abundances and geometric mean predator abundances.

The significance of effects of time, resuspension, predators (community subset experiment only) and enrichment (particulate enrichment experiment only) was tested with log-transformed data using two-way ANOVAs (whole community experiment) or two-way repeated measures ANOVAs (RM-ANOVAs, community subset and particulate enrichment experiment). The data were log-transformed for the tests because the variance differed between treatments, but the untransformed data are given in the figures. The significance of resuspension effects at individual sampling occasions was tested using unpaired t-tests, with Bonferroni corrections for the number of sampling occasions applied to the significance thresholds. Spearman's rank correlation coefficients between microbial abundances at all sampling occasions were calculated in order to gauge the degree of coupling within the microbial communities. All statistical procedures were carried out using SPSS.

6.4. Results

6.4.1. Whole-community experiment

During the whole-community experiment, clear resuspension effects were found on several levels of the model microbial food web (Fig. 6.2). *Euplotes balteatus* showed a dramatic increase in abundance that was even greater in the resuspended bottles, but these effects were only apparent on the last sampling date (68.0 ± 5.1 Ind. ml⁻¹ and 28.1 ± 15.0 Ind. ml⁻¹, resuspended and control microcosms, respectively, $P = 0.016$, Fig. 6.2e). *Vannella platypodia* also showed rapid growth in both the resuspended and the control bottles (Table

6.2, Fig. 6.2d). They exceeded the upper detection limit of the cultivation method (1000 Ind. ml⁻¹) after 5 d. However, their abundances were already significantly higher in the resuspended microcosms than in the controls after 2 d (465 ± 62 Ind. ml⁻¹ and 224 ± 115 Ind. ml⁻¹, P = 0.016). Similar to *Euplotes*, *Amphora coffeaeformis* showed an initial growth lag and was more abundant in the resuspended microcosms at the end of the experiment (10.1 ± 2.2 * 10³ Ind. ml⁻¹ and 6.6 ± 1.7 * 10³ Ind. ml⁻¹, P = 0.025, Fig. 6.2a). Bacteria showed no significant resuspension effect (Fig. 6.2b). *Bodo designis* increased until d 7 (maximum 11.3 * 10³ Ind. ml⁻¹ in the control microcosms) and declined sharply thereafter. Positive resuspension effects on initial growth rates (Table 6.2) did not result in significant differences in abundance at the end of the experiment (Fig. 6.2c).

As shown by Spearman's correlation coefficients, population dynamics within the microbial community were related to each other in a complex manner: the abundances of *Amphora* and *Euplotes* were positively correlated over the whole course of the experiment, while flagellate abundances were negatively correlated to those of the former groups (Table 6.3). Rhizopods were not included in this correlation analysis because they were only counted at the first two sampling occasions.

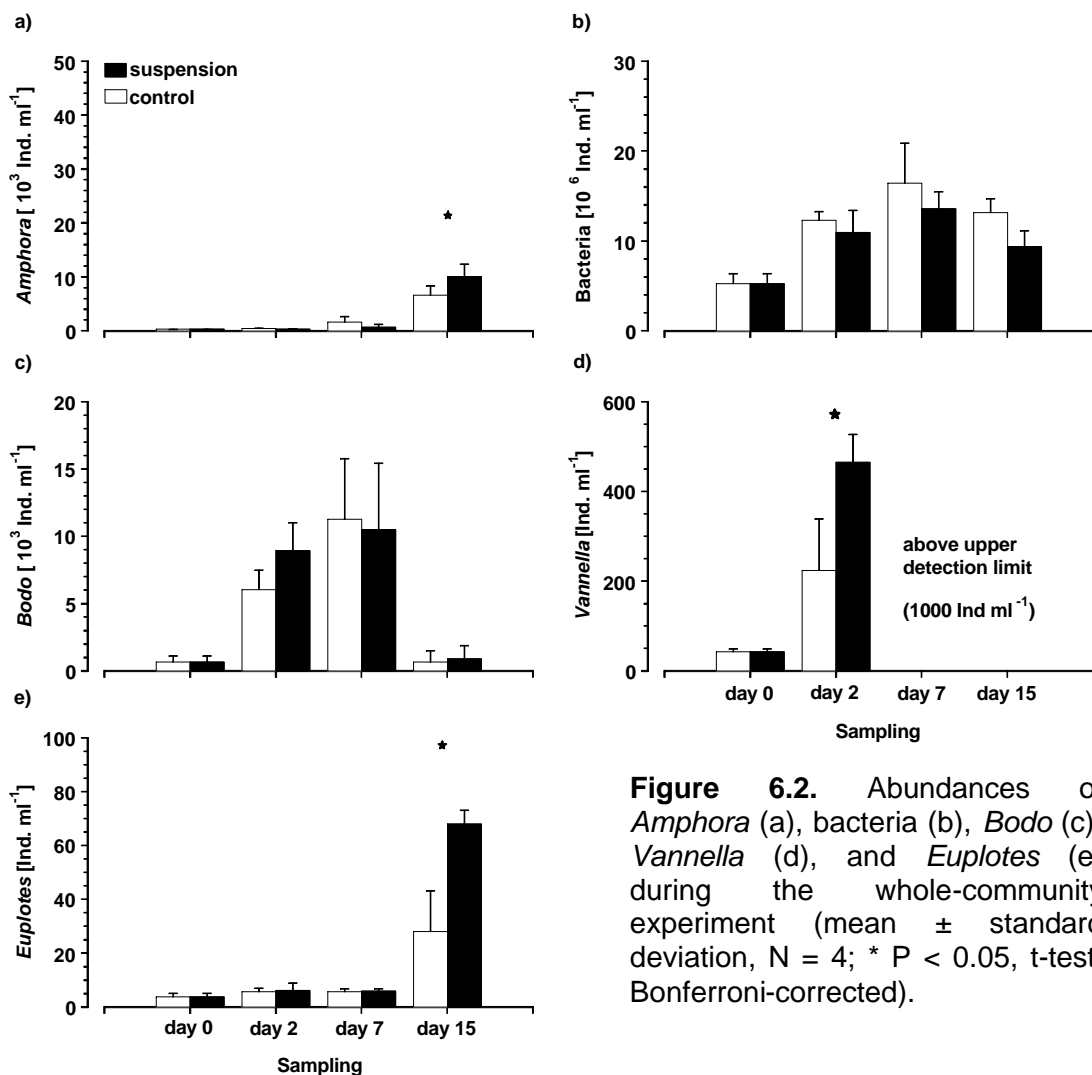


Figure 6.2. Abundances of *Amphora* (a), bacteria (b), *Bodo* (c), *Vannella* (d), and *Euplotes* (e) during the whole-community experiment (mean ± standard deviation, N = 4; * P < 0.05, t-test, Bonferroni-corrected).

6.4.2. Community subset experiment

The general trends of the whole-community experiment were also found in the community subset experiment. Growth of *Amphora coffeaeformis* showed an initial lag and was enhanced in suspension irrespective of microbial community structure (RM-ANOVA, Fig. 6.3, Table 6.4). In contrast, no significant protistan effects on diatom abundance and no interactions were found. Final diatom abundances ranged from $6.7 \pm 2.1 \cdot 10^3$ Ind. ml⁻¹ in the control microcosms with nanofauna only (Fig. 6.3b) to $33,1 \pm 12,8 \cdot 10^3$ Ind. ml⁻¹ in the resuspended whole-community microcosms (Fig. 6.3c).

Similar to the whole-community experiment, *Euplotes balteatus* tended to grow faster in the resuspended microcosms (Fig. 6.4, Table 6.2). The final difference in abundance (75.7 ± 15.8 Ind. ml⁻¹ and 65.1 ± 19.8 Ind. ml⁻¹, resuspended and control microcosms respectively) was not significant in this experiment, however.

In the absence of ciliates, both *Bodo designis* and *Vannella platypodia* tended to grow faster in suspension (Fig. 6.5, Table 6.2). The final difference in abundance was significant for the flagellates ($12.9 \pm 2.6 \cdot 10^3$ Ind. ml⁻¹ and $6.9 \pm 2.6 \cdot 10^3$ Ind. ml⁻¹, resuspended and control microcosms respectively, $P = 0.024$, Fig. 6.5a), but not for the rhizopods (284 ± 70 Ind. ml⁻¹ and 189 ± 83 Ind. ml⁻¹, Fig. 6.5c). In the presence of *Euplotes*, net growth rates of *Bodo* were less, and lower in suspension than in the controls (Table 6.2). The difference in final abundance of *Bodo* in resuspended and control microcosms was less than in the absence of *Euplotes*, and was not significant ($7.5 \pm 1.3 \cdot 10^3$ Ind. ml⁻¹ and $5.8 \pm 2.0 \cdot 10^3$ Ind. ml⁻¹, resuspended and control microcosms respectively, Fig. 6.5b). As a consequence, the RM-ANOVA of flagellate abundance revealed both highly significant main effects of ciliate presence and resuspension and a significant interaction between the two factors (Table 6.4). Estimated individual grazing rates of *Euplotes* on *Bodo* were high during the first 2 d of the experiment (3.6 and 5.5 *Bodo Euplotes*⁻¹ h⁻¹, control and resuspended microcosms, respectively) and declined to < 0.1 *Bodo Euplotes*⁻¹ h⁻¹ towards the end of the experiment when the average ratio of flagellate to ciliate abundance dropped below 10^3 .

In comparison to *Bodo*, *Vannella* growth showed even stronger positive resuspension effects in the presence of *Euplotes*, reaching 459 ± 113 Ind. ml⁻¹ at the end of the experiment, and significantly exceeding the abundances in the non-resuspended microcosms (182 ± 53 Ind. ml⁻¹, $P = 0.012$, Fig. 6.5d). The RM-ANOVA of rhizopod abundances showed a highly significant positive resuspension effect, but no effect of ciliate presence and no interaction (Table 6.4).

In none of the treatment combinations did resuspension affect bacterial abundance (Figure 6.3, Table 6.4). After 2 d, most of the protist-free microcosms were contaminated with *Bodo designis*. Therefore, the initially bacterivore-free group was excluded from further

analysis. With both nanofauna and ciliates present, there was a similar non-significant trend as in the first experiment where resuspension tended to reduce bacterial abundance. In contrast, treatments with ciliates had significantly fewer bacteria than those with only nanofauna, or bacteria alone (Figure 6.3f, Table 6.4). Although no grazing rates of *Euplotes* on bacteria could be calculated from my experiment, mean loss rates to bacterivores were much higher in the presence of all protists including *Euplotes* (-0.26 d^{-1}) than in the presence of *Bodo* and *Vannella* alone (-0.18 d^{-1}), suggesting that *Euplotes* had a strong grazing impact on bacteria.

In those microcosms where all eukaryotes were present, their abundances were significantly positively correlated to each other over the whole course of the experiment. Bacterial abundances were positively correlated to those of *Bodo* only (Table 6.5). Correlations between *Amphora*, *Vannella*, and *Euplotes* were stronger in suspension, while correlations between bacteria on one hand and *Vannella* and *Euplotes* on the other hand were switched from positive to negative (data not shown). In those microcosms where *Euplotes* was absent, all microbial populations were significantly positively correlated to each other (Table 6.5).

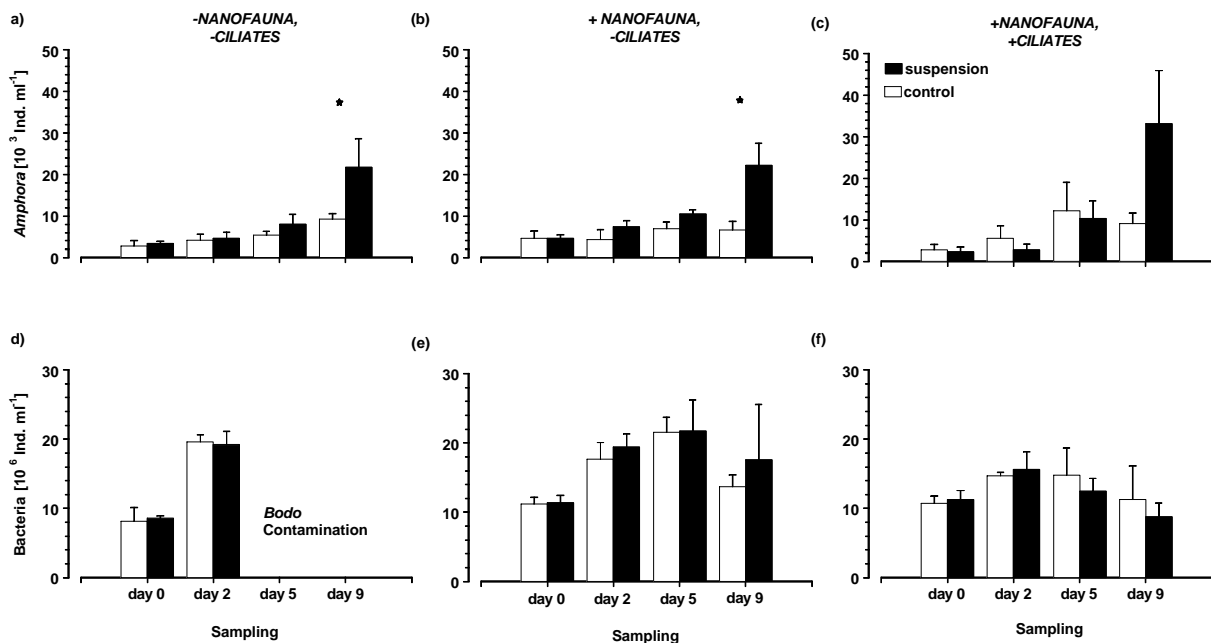


Figure 6.3. Abundances of *Amphora* (a-c) and bacteria (d-f) during the community subset experiment (mean \pm standard deviation, $N = 4$; * $P < 0.05$, t-test, Bonferroni-corrected). The scale for the Y-axis is the same in the three experimental treatments.

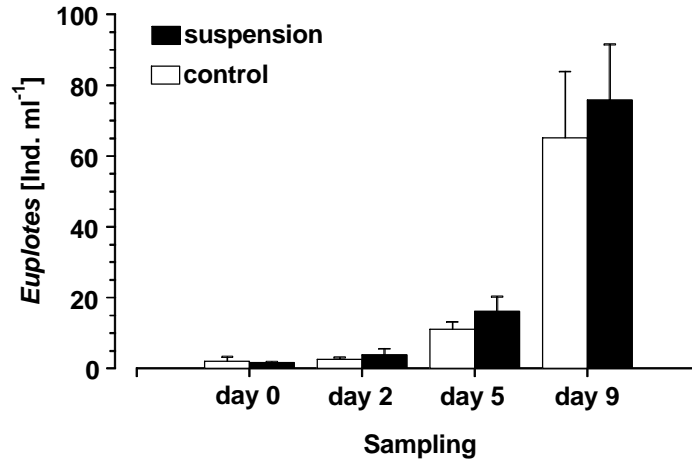


Figure 6.4. Abundance of *Euplotes* during the community subset experiment (mean \pm standard deviation, N = 4).

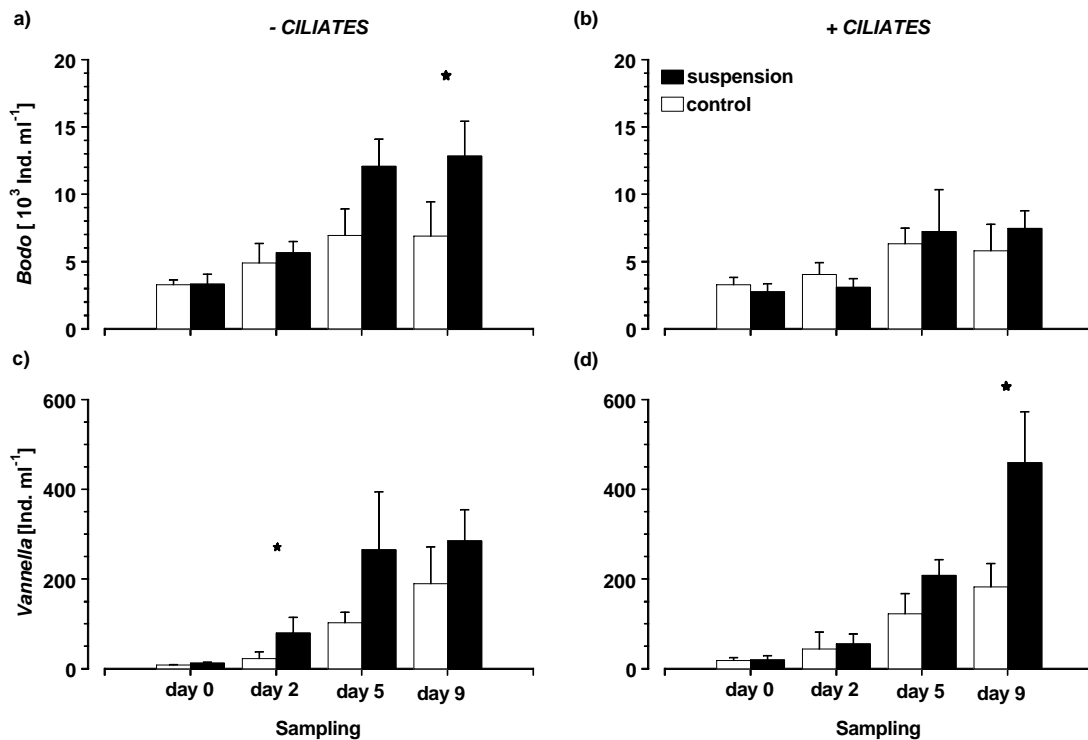


Figure 6.5. Abundances of *Bodo* (a, b) and *Vannella* (c, d) in the presence (+ *Ciliates*) and in the absence of *Euplotes* (- *Ciliates*) during the community subset experiment (mean \pm standard deviation, N = 4; * ... P < 0.05, t-test, Bonferroni-corrected). The scale for the Y-axis is the same in both experimental treatments.

Table 6.2. Mean initial growth rates of microbial populations in the community subset experiment (calculated from abundances on day 0 and day 2).

Experiment	Treatment	Bacteria [d ⁻¹]	<i>Bodo</i> [d ⁻¹]	<i>Vannella</i> [d ⁻¹]	<i>Euplotes</i> [d ⁻¹]
whole	control	0.43	1.11	0.91	0.20
community	suspension	0.37	1.30	1.28	0.30
community subset	control	0.44	-	-	-
	suspension	0.40	-	-	-
	control + nanofauna	0.23	0.20	0.47	-
	suspension + nanofauna	0.27	0.27	0.92	-
	control + all protists	0.16	0.10	0.42	0.12
	suspension + all protists	0.16	0.06	0.53	0.39
particulate enrichment	control	0.24	0.24	-	0.47
	suspension	0.15	0.25	-	0.03
	control + enrichment	0.27	0.46	-	0.25
	suspension + enrichment	0.27	0.53	-	0.43

Table 6.3. Correlations between microbial abundances during the whole-community experiment (Spearman's r; * p < 0.05, ** p < 0.01).

	Amphora	Bacteria	<i>Bodo</i>
Bacteria	-0.099		
<i>Bodo</i>	-0.578**	0.481*	
<i>Euplotes</i>	0.790**	-0.278	-0.629**

6.4.3. Particulate enrichment experiment

The results of the particulate enrichment experiment clarify some of the mechanisms which led to effects in the other experiments. Again, growth of *Amphora coffeaeformis* was fostered by resuspension. *Urtica* powder had a negative growth effect (Fig. 6.6a, b, Table 6.6). Resuspension increased mean final diatom abundance in minimal medium by a factor of three, compared to the final abundance in the controls ($37.9 \pm 5.8 \times 10^3$ Ind. ml⁻¹ and $11.6 \pm 2.9 \times 10^3$ Ind. ml⁻¹, P = 0.004, Fig. 6.6a). Bacterial abundances – and those of *Bodo designis* – were not affected by resuspension (Tables 6.2, 6.6).

Table 6.4. P-values for protistan and suspension effects over time and their interactions within the RM-ANOVA design of the community subset experiment (N = 4; Susp. Suspension; Prot. protist presence).

	<i>Amphora</i>	Bacteria	<i>Bodo</i>	<i>Vannella</i>
Suspension	0.039	0.668	0.073	< 0.001
Protist presence*	0.584	< 0.001	< 0.001	0.312
Time	< 0.001	< 0.001	< 0.001	< 0.001
Susp. x prot.	0.576	0.453	0.015	0.676
Susp. x time	< 0.001	0.850	0.028	< 0.001
Prot. x time	< 0.001	< 0.001	0.189	0.037
Susp. x prot. x time	0.086	0.625	0.841	0.005

* presence of no protists, only *Vannella* and *Bodo*, or all protists in the case of *Amphora* and bacteria (2 x 3 RM-ANOVA), presence or absence of *Euplotes* in the case of *Bodo* and *Vannella* (2 x 2 RM-ANOVA).

Table 6.5. Correlations between microbial abundances during the community subset experiment. Correlation coefficients for the whole community microcosms are given in the lower lefthand corner while those for the ciliate-free microcosms are given in the upper righthand corner (Spearman's r; * p < 0.05, ** p < 0.01).

	<i>Amphora</i>	Bacteria	<i>Bodo</i>	<i>Vannella</i>
<i>Amphora</i>		0.396*	0.575**	0.763**
Bacteria	-0.077		0.915**	0.482**
<i>Bodo</i>	0.362*	0.793**		0.693**
<i>Vannella</i>	0.704**	-0.173	0.405*	
<i>Euplotes</i>	0.783**	-0.103	0.478**	0.893**

Compared to the minimal medium, particulate enrichment increased the final abundance of *Euplotes balteatus* (Fig. 6.6g, h, Table 6.6). Resuspension had a positive, time-dependent effect on ciliate growth and abundance, but only in the enriched microcosms (final abundances of 25.5 ± 1.2 Ind. ml⁻¹ in suspension and 16.0 ± 3.3 Ind. ml⁻¹ in the controls, P = 0.012, Fig. 6.6h). It had a negative effect in minimal medium (final abundances of 6.9 ± 0.9 Ind. ml⁻¹ in suspension and 11.0 ± 1.9 Ind. ml⁻¹ in the controls, P = 0.028, Fig. 6.6g). This resulted in a significant interaction between particulate enrichment and resuspension in the RM-ANOVA (Table 6.6).

Table 6.6. P-values for resuspension and enrichment effects over time and their interactions within the RM-ANOVA design of the particulate enrichment experiment (N = 4; Susp. Suspension; Enr. enrichment).

	<i>Amphora</i>	Bacteria	<i>Bodo</i>	<i>Euplotes</i>
Suspension	0.002	0.082	0.544	0.711
Enrichment	0.018	< 0.001	0.338	< 0.001
Time	< 0.001	< 0.001	< 0.001	< 0.001
Susp. X enr.	0.249	0.830	0.507	< 0.001
Susp. X time	< 0.001	0.434	0.518	0.152
Enr. x time	< 0.001	0.765	0.921	0.001
Susp. X enr. x time	0.184	0.444	0.935	< 0.001

Table 6.7. Correlations between microbial abundances during the particulate enrichment experiment (Spearman's r; * p < 0.05, ** p < 0.01). Correlation coefficients for minimal ASW medium are given in the lower lefthand corner while correlation coefficients for *Urtica* powder are given in the upper righthand corner.

	<i>Amphora</i>	Bacteria	<i>Bodo</i>	<i>Euplotes</i>
<i>Amphora</i>		0.555**	0.042	0.819**
Bacteria	0.632**		0.099	0.771**
<i>Bodo</i>	0.123	0.157		-0.035
<i>Euplotes</i>	0.782**	0.719**	0.097	

The abundances of *Amphora*, bacteria and *Euplotes* were positively correlated over the whole course of the particulate enrichment experiment (Table 6.7), but neither enrichment nor resuspension had effects on these correlations. An exception from this trend was the decoupling of bacteria and *Amphora* in the enriched microcosms by resuspension (Spearman's r without suspension: 0.682, P < 0.004, in suspension: 0.433, P = 0.094).

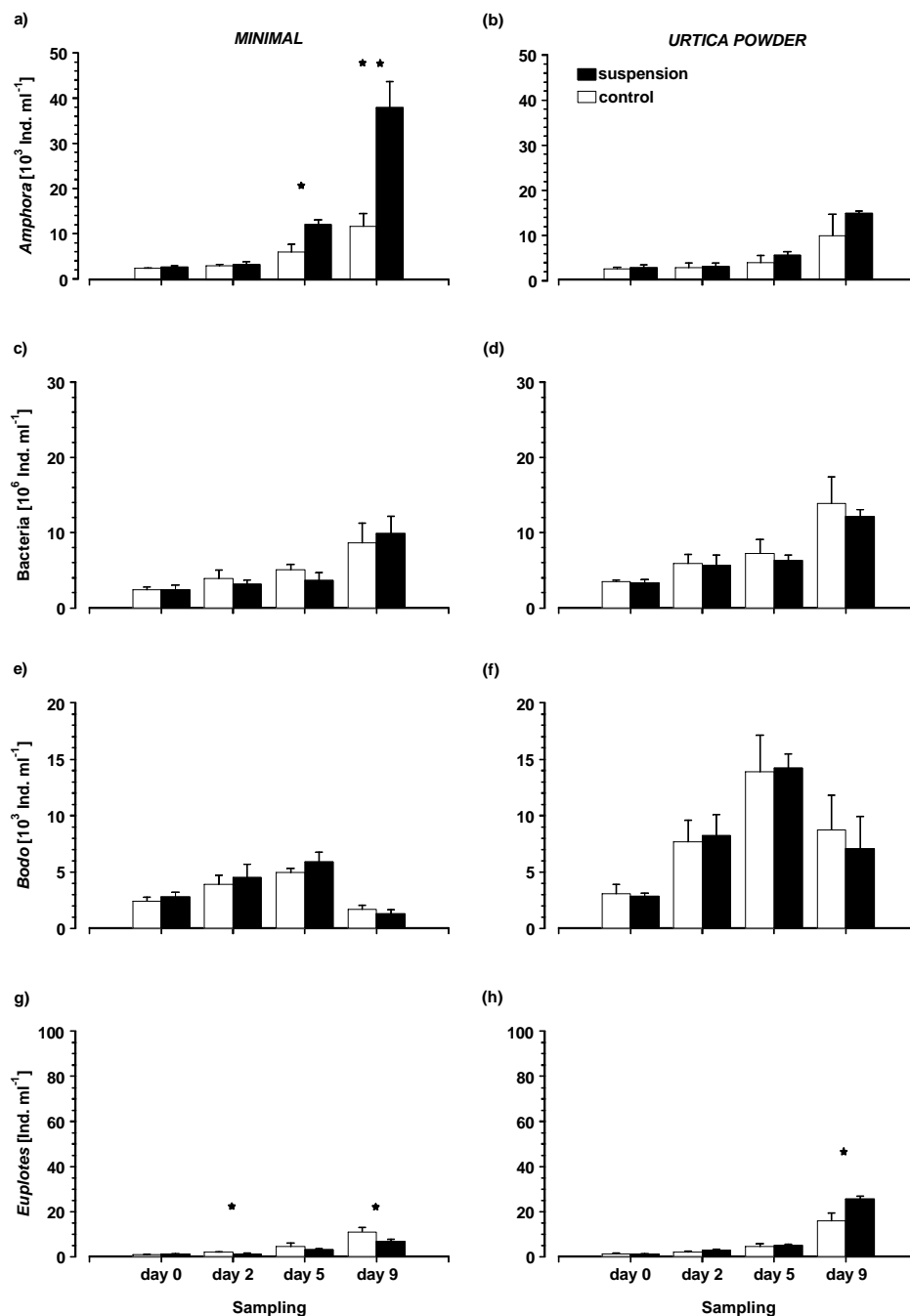


Figure 6.6. Abundances of *Amphora* (a, b), bacteria (c, d), *Bodo* (e, f), and *Euplotes* (g, h) with (*Urtica powder*) and without enrichment (*Minimal*) during the particulate enrichment experiment (mean \pm standard deviation, N = 4; * ... P < 0.05, t-test, Bonferroni-corrected). The scale for the Y-axis is the same in both experimental treatments.

No effects of resuspension, community structure or enrichment on oxygen concentrations in the microcosms or on the size or shape of any organisms were found in any experiment. This was also true for the bacteria which were dominated by rods of 1 - 2 μm length in all treatments. No picoautotrophs were present. Table 6.8 summarizes resuspension effects on the final abundances of microbial food web components.

Table 6.8. Summary of resuspension effects on final microbial abundances. No significant resuspension effects on bacteria were found (+ positive resuspension effect; - negative effect; 0 no significant effect).

Experiment	Group	Amphora	Bodo	Vannella	Euplotes
Whole-community experiment		+	0	+ ¹	+
Community subset experiment	- <i>Euplotes</i>	+	+	0	not present
	+ <i>Euplotes</i>	0	0	+	0
Particulate enrichment experiment	- enrichment	+	0	not present	-
	+ enrichment	0	0	not present	+

1) after 2 d.

6.5. Discussion

6.5.1. Food web structure

The results of my experiments - and especially those of the community subset experiment - support the food web structure shown in Figure 6.1 derived from direct observation and literature data (e. g. PRATT & CAIRNS 1985, PREMKE & ARNDT 2000). The abundances of bacteria and *Bodo designis*, but not those of *Amphora coffeaeformis* and *Vannella platypodia* decreased in the presence of *Euplotes balteatus*. This is consistent with bacterivory and predation on *Bodo* by *Euplotes*, trophic links which are well-known from previous studies. Consumption rates of up to $16 \cdot 10^3$ bacteria $\text{Ind.}^{-1} \text{h}^{-1}$ (*Euplotes mutabilis*) and up to 21 *Bodo sorokini* $\text{Ind.}^{-1} \text{h}^{-1}$ (*Euplotes vannus*) from similar prey concentrations as used in my experiments have been reported (ZUBKOV & SLEIGH 1996, PREMKE & ARNDT 2000).

Bodo designis and *Vannella platypodia* are also bacterivores (PRATT & CAIRNS 1985, PAGE & SIEMENSMA 1991) and should have decreased bacterial abundances in the absence of *Euplotes*, but I did not find evidence for this interaction. A possible explanation is that *Vannella* actually may have fed on *Bodo*, in addition to bacteria. Thus, *Vannella* would have contributed less to bacterivory, while keeping abundances of bacterivorous *Bodo* relatively low. Although predation on *Bodo* by *Vannella* has occasionally been observed in crude cultures, *Vannella* does not appear to be an efficient flagellate grazer (GARSTECKI, personal observations). Nevertheless, the interaction may explain the crash in *Bodo* abundance at the end of the whole community experiment when abundance of *Vannella* was exceptionally high. Predation on heterotrophic protists by *Vannella platypodia* has not been studied yet, but it has been reported from other rhizopods (e.g. BOVEE 1960, PAGE 1977).

In addition to trophic interactions between microbial populations, the links between experimental enrichment and the microbial food web need to be considered. *Amphora coffeaeformis* was not favoured by enrichment. Particulate enrichment with *Urtica* powder, a particulate phytodetritus surrogate, enhanced population growth of all heterotrophic protists (Table 6.6), but it is not clear at which trophic level it was incorporated into the microbial food web. Bacterial utilization after enzymatic breakdown, direct protistan detritovory (POSCH & ARNDT 1996), and a combination of both are possible. The temporal resolution of my data set is not sufficient to discern between them, or between mechanisms of liquid enrichment utilization. Nevertheless, my data confirm the predicted general food web structure. Against the background of this structure, effects of resuspension on individual populations and trophic links can be discussed.

6.5.2. Resuspension effects on *Amphora coffeaeformis* and bacteria

Resuspension increased the abundance of *Amphora coffeaeformis* during all experiments. Since enrichment was identical in resuspended and control microcosms in the first two experiments, and since resuspension tripled final diatom abundances in microcosms without enrichment, it is unlikely that there were insufficient nutrients to support diatom growth in any treatment. Rather, the ability of *Amphora* to utilise the nutrients present in the medium was likely to be higher when they were in suspension, possibly due to increased mean nutrient supply to individual cells in a population dispersed by resuspension (BOTHWELL 1989), or due to reduced transport limitation of nutrient supply to suspended cells. While similar effects of water motion on phytoplankton nutrient uptake and growth are well-established (REYNOLDS 1994, AGUILERA ET AL. 1994, ESTRADA & BERDALET 1997), they have not yet been discussed with respect to resuspension effects on microphytobenthos. DE

JONGE & VAN BEUSEKOM (1995) assumed that suspended microphytobenthos grow as efficiently as sedimented ones. Increased light attenuation after resuspension may decrease microphytobenthos primary production in natural systems (HELLSTRÖM 1991, MACINTYRE & CULLEN 1996). However, the net resuspension effect on water column primary production is also influenced by decreased light attenuation due to reduced self-shading, and nutrient and chlorophyll *a* fluxes from the sediment, and is thus not necessarily negative (GABRIELSON & LUKATELICH 1985, MACINTYRE & CULLEN 1996). Light attenuation by suspended particulates was generally taken into account in my experimental design because sediment was included in the microcosms. Growth of *Amphora* appeared not to be reduced due to insufficient light in suspension. It remains to be seen if enhanced growth due to better nutrient access in suspension is a general phenomenon for resuspended benthic algae, and how different light regimes affect the response of these algae and further effects on the microbial food web.

The failure to detect a positive resuspension effect on bacterial gross growth (Fig. 6.3d) and abundance during my experiments may partly be due to the limited accuracy of my methodology. However, planktonic bacteria did not show direct effects of experimental turbulence and mixing in previous studies, and solitary bacterial cells are considered too small to benefit directly from water motion (MOESENEDER & HERNDL 1995, KARP-BOSS ET AL. 1996, PETERS ET AL. 1998). Therefore, it is unlikely that enhanced bacterial utilization of dissolved organic matter and increased bacterial gross growth rates in suspension contributed to positive resuspension effects which were observed at higher trophic levels in my experimental food web.

6.5.3. Resuspension effects on protistan population dynamics

Resuspension enhanced population growth of *Euplotes balteatus* in all enriched experiments except the minimal ASW medium where there was a significant decline. This pattern is consistent with improved food access or increased growth efficiency of *Euplotes* in suspension when food is generally abundant, and impaired food access or reduced growth efficiency when food is scarce. The results of the community subset experiment support the food accessibility hypothesis: the increase in the abundance of *Bodo designis* in resuspended versus control treatments disappeared when *Euplotes* was present. A similar, but non-significant trend was found for *Euplotes* interactions with bacterial abundance: in the community subset experiment, there was lower abundance in resuspension only when ciliates were present. In the other experiments where ciliates were present in all treatments, there was again the pattern of higher ciliate, but lower bacterial abundance in resuspended microcosms. Only in the unenriched treatments of the particulate enrichment experiment did this pattern not hold. The higher grazing impact of *Euplotes* in suspension was not due to

increased prey abundance and higher functional responses alone because numerical predator/prey ratios were always higher in suspension, and bacterial abundances became lower in suspension than in the controls after 5 d. Suspended, dispersed prey may be more accessible for an average individual in a filter-feeding *Euplotes* population than discrete, surface-associated food patches, and mixing may increase prey encounter rates (SHIMETA ET AL. 1995, PETERS ET AL. 1998).

The data of the particulate enrichment experiment agree with a trophic mechanism mediating resuspension effects on population dynamics of *Euplotes*. The negative resuspension effect on ciliate growth in the minimal ASW group shows that this mechanism operates only above a certain food concentration, and may be non-existent at low food supply in the field. Since abundances of bacteria and *Bodo designis* were low without enrichment, resuspension and dispersal may have decreased prey encounter rates in this group until grazing in suspension was less efficient than grazing from patches of sedimented prey in the non-resuspended treatment. ZUBKOV & SLEIGH (1996) reported a drop of gross growth efficiency from 43% to 20% in *Euplotes mutabilis* as bacterial food concentration was decreased from $30 \times 10^6 \text{ ml}^{-1}$ to $6 \times 10^6 \text{ ml}^{-1}$. The relevance of food supply for ciliate growth during the particulate enrichment experiment is highlighted by positive correlations of bacterial and ciliate abundances which are consistent with bottom-up control of *Euplotes balteatus* by bacterial food supply.

The effects of resuspension on trophic links involving *Euplotes balteatus* cannot be too widely generalised because they partly depend on the feeding ecology of this ciliate. However, another hypotrich ciliate (*Aspidisca* sp.) also responded positively to sediment disturbance in earlier experiments (ALONGI 1985). The rhizopod *Vannella platypodia* and the flagellate *Bodo designis* responded positively to resuspension during my experiments although they have a surface-associated feeding mode. They were probably associated to aggregates in suspension, as has been observed both in the field and in the laboratory (ARTOLOZAGA ET AL. 1997, ZIMMERMANN-TIMM ET AL. 1998). Trophic mechanisms of resuspension effects involving *Vannella* and *Bodo* are difficult to discern because they were always inoculated together, or together with *Euplotes* in the case of *Bodo* in the particulate enrichment experiment. The rhizopods were positively correlated to bacteria and *Bodo* in the community subset experiment when *Euplotes* was absent. This may imply bottom-up control of *Vannella* by bacterial and possibly flagellate food supply, and a similar mechanism as in *Euplotes* leading to improved food access in suspension. Gross growth rates of *Bodo* were much higher in suspension, but most of the surplus biomass in resuspended microcosms was consumed by *Euplotes* when the ciliate was present. Thus, *Bodo* had a higher biomass turnover in suspension, and was a more efficient link in terms of carbon flow. Since *Euplotes* and *Vannella* were the top predators in my food web, and *Amphora* was not consumed,

biomass accumulated in their populations towards the end of the experiments. If higher trophic levels would have been present in the microcosms, biomass turnover of *Amphora*, *Euplotes*, and *Vannella* might have increased in suspension similar to that of *Bodo*. This would have resulted in enhanced carbon flow through the experimental food web.

6.5.4. Significance under field conditions and possible mechanisms

My experimental design was focussed on the effects of resuspension and mixing effects on trophic interactions and population dynamics in a model microbial food web. Different benthic species may react differently to resuspension, but the organisms used are major components of the microbial food web in coastal Baltic sediments (Chapter 2), and have all been found associated with particulates in the water column (ZIMMERMANN-TIMM ET AL. 1998). Sediment concentrations, initial abundances and light availability were set at levels close to field conditions. Although the experimental enrichment levels may have been higher than the organic input to the water column during natural resuspension events, an increase of organic carbon and nutrient concentrations is one of their consequences: substantial stimulations of bacterial population growth by dissolved and particulate carbon inputs from the benthos have been found in various field and laboratory studies (WAINRIGHT 1987, RITZRAU & GRAF 1992, HOPKINSON ET AL. 1998). WAINRIGHT (1987) also reported increased protozoan community biovolume after addition of resuspended material, and OGILVIE & MITCHELL (1998) detected nutrient-mediated positive effects of sediment resuspension on phytoplankton.

In contrast to the focus on transport effects in the above mentioned studies, my experiment focussed on the impact of mixing and suspension at a given nutrient and carbon input. The impact of these processes on resuspended benthic microbial food webs has not yet been studied, but effects of mixing and turbulence on planktonic microbial food web interactions have been addressed (PETERS & GROSS 1994, SHIMETA ET AL. 1995, PETERS ET AL. 1996, 1998). Although turbulence was excluded and laminar shear was not quantified in my experiments, the designs of my experiments and the plankton studies both included mixing and dispersal, and can be compared with respect to their effects: SHIMETA ET AL. (1995) found increased clearance rates in cultures of the choanoflagellate *Monosiga sp.* and the heliozoon *Ciliophrys marina*, but decreased clearance rates in the tintinnid ciliate *Helicostomella sp.* when they were subjected to laminar shear below the turbulence microscale. They hypothesised that non-motile protists and weak swimmers would benefit most from increased turbulence and mixing, which is in agreement with the pronounced growth enhancement of the rhizopod *Vannella* during my experiments. PETERS ET AL. (1998)

reported bacterial net growth enhancement under turbulent conditions due to shifts of food size spectra of planktonic grazers towards larger prey. Consistent with this result, estimated consumption rates of *Bodo designis* by *Euplotes balteatus* were higher in suspension during my community subset experiment, but the negative effect of protistan grazers on bacterial abundance was still stronger in suspension. Although turbulence did not increase individual grazing rates of the heterotrophic flagellate *Paraphysomonas imperforata* during laboratory experiments, enhanced growth rate, decreased mean cell size, and possibly behavioural adaptations resulted in a higher bacterial consumption of the flagellate population under turbulent conditions (PETERS ET AL. 1996). Similar net effects were found in a natural nanoplankton assemblage (PETERS & GROSS 1994).

My results show that mixing during resuspension events may also have profound effects on the dynamics of resuspended benthic microbial food webs. The subsidiary energy input by resuspension and mixing may increase gross growth rates and consumption rates by higher trophic levels. This may result in a higher carbon turnover of benthic microbial food webs in shallow ecosystems.

7. Zusammenfassung

7.1. Vergleich des benthischen und des planktischen mikrobiellen Nahrungsnetzes der Boddengewässer unter besonderer Berücksichtigung der benthisch-pelagischen Kopplung durch Sedimentresuspension

Als Grundlage der vorliegenden Arbeit wurde im Zeitraum zwischen Mai 1996 und Mai 1997 die heterotrophe Protistengemeinschaft im Sediment und in der Wassersäule der Boddengewässer vergleichend erfaßt. Dazu wurden in den Boddengewässern zwei Beprobungsstationen ausgewählt: die sehr flache, eutrophe Station Kirrbucht in der Darß-Zingster Boddenkette und die vergleichsweise tiefe, mesotrophe Station Rassower Strom in den Nordrügensch Boddengewässern. An diesen Stationen wurden zu jeweils fünf Terminen (April/Mai, Juli und September/Oktober 1996, Januar und April 1997) Proben aus zwei Sedimenthorizonten, der Sedimentauflage und der Wassersäule entnommen und hinsichtlich der Besiedlung mit Ciliaten, heterotrophen Flagellaten, Rhizopoden und Heliozoen quantitativ-taxonomisch analysiert. Diese Analyse erfolgte im Rahmen eines umfassenden Meßprogramms innerhalb des interdisziplinären Verbundprojektes "Ökosystem Boddengewässer – Organismen und Stoffhaushalt". Dadurch standen für die Analyse meiner Daten umfassende Vergleichsdaten über abiotische Umweltfaktoren sowie über die Struktur des Zooplanktons, der Meiofauna und der Bakteriengemeinschaft zur Verfügung. Zusätzlich wurden bei der Auswertung Wetterdaten vom Deutschen Wetterdienst herangezogen.

Die Ergebnisse der Freilanduntersuchung unterstreichen den ähnlich bereits in früheren Untersuchungen festgestellten großen Anteil der heterotrophen Protisten (durchschnittlich 78 %) an der Biomasse des Zooplanktons der Boddengewässer (ARNDT ET AL. 1990, ARNDT 1991). Dagegen erreichte das Mikro- und Nanozoobenthos im Vergleich zur Meiofauna nur einen geringen mittleren Biomasseanteil von 22 %. Innerhalb des Protozooplanktons waren in der Kirrbucht die heterotrophen Flagellaten dominierend (80 % mittlerer Biomasseanteil), im Rassower Strom dagegen die Ciliaten (73 % mittlerer Biomasseanteil). Flächenbezogen entfielen etwa gleiche Biomasseanteile auf das Protozooplankton und das Mikro- und Nanozoobenthos, was auf potentiell große Auswirkungen der Resuspension benthischer Protisten auf die Struktur der planktischen Protistengemeinschaft hinweist.

Im Sediment beider Stationen dominierten die Ciliaten (58 % und 59 % mittlerer Biomasseanteil, Kirrbucht und Rassower Strom), gefolgt von den Rhizopoden (24 und 28 % mittlerer Biomasseanteil). Damit rangierten die Rhizopoden hinsichtlich der Biomasse noch vor den heterotrophen Flagellaten. Dies deutet – gemessen am bisherigen Wissensstand über die Struktur benthischer Protistengemeinschaften (z.B. SCHARF 1979, BAK & NIEWLAND 1989, ARNDT ET AL. 1990, FERNANDEZ-LEBORANS & NOVILLO 1993, EPSTEIN 1997A, B, DIETRICH & ARNDT 2000) - auf eine große quantitative Bedeutung dieser nur wenig untersuchten Gruppe hin.

Während sich die taxonomische Zusammensetzung der Ciliaten im Benthos und im Pelagial beider Stationen nur wenig überschneidet, wurden viele typisch benthische heterotrophe Flagellaten (Euglenida, Bodonida, Thaumatomastigida und Apusomonadida) in der Wassersäule gefunden. Angehörige dieser Gruppen erreichten Anteile an der Biomasse der heterotrophen Flagellaten in der Wassersäule von bis zu 67 % (Kirrbucht) bzw. bis zu 31 % (Rassower Strom), was auf einen auch in anderen Küstengewässern angetroffenen hohen Anteil von partikel- und aggregatassoziierten Flagellaten an der Flagellatenfauna der Wassersäule schließen läßt (ROGERSON & LAYBOURN-PARRY 1992 A, ZIMMERMANN-TIMM ET AL. 1998). Der Biomasseanteil der Rhizopoden am Protozooplankton lag stets unter 5 % und bestand ausschließlich aus Arten, die auch im Sediment gefunden wurden.

Positive Korrelationen zwischen den Sediment- und Freiwasserabundanz der Rhizopoden im Rassower Strom, und aller Protistengruppen in der Kirrbucht, weisen auf eine enge Kopplung zwischen der benthischen und der planktischen heterotrophen Protistengemeinschaft vor allem in der flacheren Kirrbucht hin. Die Korrelationen sagen allerdings nichts über die Mechanismen aus, die dieser Kopplung zugrunde liegen. Um die mögliche Rolle eines resuspensionsbedingten Transportes von Zellen für das Zustandekommen der beobachteten Kopplung zu beurteilen, wurde deshalb zusätzlich nach multiplen linearen Regressionen der Protistenabundanz in der Wassersäule gegen die entsprechenden benthischen Abundanz und die Sestonkonzentrationen zum Beprobungszeitpunkt gesucht. Signifikante Regressionen dieser Art wurden lediglich für die heterotrophen Flagellaten des Rassower Stroms und die Ciliaten der Kirrbucht gefunden. Eine parallelverlaufende Saisonalität der Protistenabundanz in beiden Teilsystemen aufgrund einer Kopplung an die saisonal variierende Primärproduktion ist als Alternativhypothese naheliegend. Der zeitliche Rhythmus der Freilanduntersuchungen war jedoch nicht dicht genug, um schlüssige Aussagen über die Saisonalität der benthisch-pelagischen Kopplung des mikrobiellen Nahrungsgewebes in den Boddengewässern zu ermöglichen.

Die Ergebnisse meiner Freilanduntersuchungen deuten darauf hin, daß die heterotrophen Protistengemeinschaften im Sediment und in der Wassersäule der Boddengewässer zwar in ihrer langfristigen Dynamik aneinander gekoppelt sind, daß der direkte Austausch von

Protozoen zwischen beiden Lebensräumen aber nur teilweise für diese Kopplung verantwortlich ist. Die relative Bedeutung von direktem Austausch und weiteren, über trophische Wechselwirkungen oder andere Mechanismen vermittelten kurzfristigen Resuspensionseffekten wurde deshalb im weiteren Verlauf der Arbeit experimentell untersucht.

7.2. Die besondere Bedeutung der Rhizopoden im benthischen mikrobiellen Nahrungsgewebe

Im Rahmen der Freilanduntersuchungen zur benthisch-pelagischen Kopplung der heterotrophen Protistengemeinschaft der Boddengewässer wurde ein Biomasseanteil von Rhizopoden am Mikro- und Nanozoobenthos von etwa 25 % festgestellt. Da sich dieses für das Verständnis der benthischen Protistengemeinschaft wesentliche Ergebnis schon im Vorfeld der Untersuchungen an der Kirrbucht und am Rassower Strom abzeichnete, wurde parallel zu den im Abschnitt 7.2. dargestellten Arbeiten die Abundanz und die taxonomische Zusammensetzung der Rhizopodenfauna an der Station Bäk in den Nordrügensch Boddengewässern in vierzehntägigem bis monatlichem Probenabstand erfaßt. Diese Station wurde wegen ihrer generellen Ähnlichkeit mit dem Rassower Strom, ihrer guten Erreichbarkeit und aufgrund der Tatsache ausgewählt, daß dank einer gleichzeitig stattfindenden Arbeit Vergleichsdaten über abiotische Umweltfaktoren sowie über die Struktur der benthischen Bakteriengemeinschaft, des Mikrophytobenthos, und der benthischen Flagellaten und Ciliaten zur Verfügung standen (DIETRICH & ARNDT 2000).

Die Rhizopodenarten wurden in frischen Sedimentproben oder in Anreicherungskulturen anhand ihrer lichtmikroskopischen Zellmorphologie bestimmt und mit der von BUTLER & ROGERSON (1995) entwickelten Flüssigkulturmethode quantifiziert. Da es grundsätzlich infolge einer Excystierung von Rhizopoden während der Inkubation der Flüssigkulturen zu einer Überschätzung der Abundanz vegetativer Rhizopoden mit dieser Methode kommen kann, wurden zunächst umfangreiche methodologische Untersuchungen zur Bedeutung dieser Fehlerquelle bei der Quantifizierung von Brackwasser -Rhizopoden durchgeführt. Die Ergebnisse dieser Untersuchungen zeigen, daß die Wahrscheinlichkeit von excystierungsbedingten Artefakten bei Proben aus dem Untersuchungsgebiet sehr gering ist, und daß die Ergebnisse der Flüssigkulturmethode als Minimumschätzungen der tatsächlichen Rhizopodenabundanzen anzusehen sind.

Während der Untersuchungen an der Bäk wurden in der Sedimentschicht bis 3 mm Tiefe Rhizopodenabundanzen von 2800-10900 Zellen cm^{-3} festgestellt, wobei saisonale Maxima im Frühjahr (7300 Zellen cm^{-3}) und im Sommer (10900 Zellen cm^{-3}) zu verzeichnen waren.

Im März, Oktober und November erreichten die Abundanzen mit 2800, 4000 und 3900 Zellen cm^{-3} dagegen Minimalwerte. Ein Vergleich der auf der Grundlage der Abundanzen und des individuellen artspezifischen Biovolumens geschätzten Biovolumenanteile der Rhizopoden mit dem der Ciliaten und der heterotrophen Flagellaten (DIETRICH & ARNDT 2000) bestätigt die aufgrund der im Abschnitt 7.1. dargestellten Ergebnisse angenommene besondere Bedeutung der Rhizopoden innerhalb des Mikro- und Nanozoobenthos. Die Anteile der Rhizopoden an der Station Bäk lagen sogar bei durchschnittlich 45% des gesamten benthischen Protozoenbiovolumens. Die hohen Durchschnittswerte sind allerdings vor allem auf die besonders hohen Biovolumenanteile der Rhizopoden - und darunter vor allem der Testacealobosia und Filosea - bei den Aprilbeprobungen zurückzuführen.

Es wurden 46 Morphotypen von Rhizopoden gefunden, von denen 27 beschriebenen Arten und weitere 14 beschriebenen Gattungen zugeordnet werden konnten. Typische Süßwasserarten koexistierten mit marinen Arten. Neben bakterivoren Rhizopoden wurden – vor allem im Frühjahr – herbivore und omnivore Arten nachgewiesen.

Im Gegensatz zum Pelagial stellen die Rhizopoden im Sediment der Boddengewässer – und möglicherweise auch in anderen Küstengewässern – also eine wesentliche Komponente der Mikro- und Nanofauna dar, die bei zukünftigen Untersuchungen dieser Fauna berücksichtigt werden sollte. Der vor allem an der Sedimentoberfläche hohe Anteil von omnivoren und herbivoren Rhizopoden deutet auf eine komplexe Einbindung dieser Gruppe in das benthische mikrobielle Nahrungsgewebe hin.

7.3. Auswirkungen der Sedimentresuspension auf das mikrobielle Nahrungsgewebe in der Wassersäule

Untersuchungen von direkten Auswirkungen der meist nur Stunden oder Tage dauernden Resuspensionsereignisse auf das mikrobielle Nahrungsgewebe sind anhand von Freilanduntersuchungen mit saisonalem Beprobungsrhythmus nicht möglich. Solche Untersuchungen erfordern entweder eine ereignisbezogene Freilandarbeit während Resuspensionsereignissen – und mit entsprechend kurzem Beprobungsabstand – oder eine experimentelle Herangehensweise. Im Rahmen der vorliegenden Arbeit wurde der zweite Weg gewählt: Es wurden natürliche Sedimentkerne mit Überstandswasser vom Rassower Strom gewonnen, unter *in situ* - Licht- und Temperaturbedingungen für fünf Tage inkubiert und mit Resuspensionsaufsätzen resuspendiert. Die Resuspensionsaufsätze nach dem Prinzip des oszillierenden Gitters wurden auf der Grundlage von DAVIS (1993) konstruiert und in Vorversuchen hinsichtlich der zu einer realistischen Resuspensionswirkung - ausgedrückt als Sestonkonzentration - führenden Gitterweite und Hubfrequenz kalibriert. Es wurden im

Juni und Oktober 1997 zwei Resuspensionsexperimente durchgeführt, jeweils eines zur Untersuchung des Effektes der Resuspensionsintensität bzw. -häufigkeit. Mit diesen Experimenten wurden hinsichtlich des planktischen mikrobiellen Nahrungsgewebes die folgenden Hypothesen getestet:

1. Die direkte Resuspension von benthischen Protisten und Prokaryoten verändert die Struktur der mikrobiellen Lebensgemeinschaft in der Wassersäule.
2. Infolge der Resuspension gelangen besiedlungstaugliche Partikel sowie gelöste und partikuläre Nährstoffe in die Wassersäule, die dort von ebenfalls resuspendierten oder bereits in der Wassersäule befindlichen Algen und Bakterien assimiliert werden und so das Populationswachstum dieser Organismen fördern.
3. Positive Resuspensionseffekte auf das Populationswachstum von Bakterien oder Algen wirken über das mikrobielle Nahrungsgewebe weiter auf phagotrophe Protisten.

Hinsichtlich der ersten Hypothese wurde zu Beginn des Intensitätsexperimentes ein von der Resuspensionsintensität abhängiger Transport von Pico- und Nanoautotrophen, benthische Diatomeen, heterotrophen Flagellaten und Rhizopoden in die Wassersäule festgestellt. Benthische Ciliaten wurden tendenziell ebenfalls resuspendiert, aber im Vergleich zu den Ciliatenabundanzen in der Wassersäule zu Beginn des Experimentes fiel dieser Transport kaum ins Gewicht. Neben den genannten positiven Resuspensionseffekten waren tendenziell negative Effekte auf die planktischen Ciliaten und Dinoflagellaten festzustellen, die allerdings durch negative Inkubationseffekte auf die Abundanzen dieser Gruppen überlagert wurden.

Während die Abundanzen der Rhizopoden über die gesamte Dauer der Experimente eng an die Sestonkonzentrationen gekoppelt blieben, konnten bei den genannten Autotrophen im weiteren Verlauf des Experimentes über das aufgrund der Sestonkonzentrationen zu erwartende Maß hinaus erhöhte Abundanzen in den resuspendierten Ansätzen festgestellt werden. Diese erhöhten Abundanzen sind nur durch ein Populationswachstum in der Wassersäule infolge der Resuspension erklärbar. Geringe Stickstoffkonzentrationen ($2.1 \mu\text{M}$ Ammonium und $0.22 \mu\text{M}$ Nitrat) in der Wassersäule zu Beginn des Experimentes und ein resuspensionsbedingter Anstieg der Ammoniumkonzentration legen die Erklärung nahe, daß dieses Wachstum durch eine gelockerte Stickstofflimitation ermöglicht wurde. Diese Erklärung wird durch die Ergebnisse des im Oktober durchgeführten Häufigkeitsexperimentes gestützt: im Oktober waren die Ausgangskonzentrationen von Ammonium und Nitrat infolge der natürlichen Saisonalität in den Boddengewässern relativ

hoch (6.0 μM und 220 μM), und ein transportunabhängiger Effekt der Resuspension auf das Wachstum der Algen und Picoautotrophen trat nicht auf. Die in der Vergangenheit beobachtete Hemmung des Algenwachstums durch eine resuspensionsbedingte Zunahme der Lichtextinktion in der Wassersäule (HELLSTRÖM 1991, MACINTYRE & CULLEN 1996) kam in diesem Fall nicht zum Tragen. Der Grund dafür liegt wohl in einer mit einer schnellen Abnahme der Trübung einhergehenden, differentiell beschleunigten Resedimentation schwerer mineralischer Partikel, die auch durch die Sestonkonzentrationen und den erhöhten Anteil von partikulärem organischen Kohlenstoff an der Sestontrockenmasse gegen Ende des Intensitätsexperimentes widergespiegelt wurde. Ein ähnlicher Effekt tritt auch in natürlichen Systemen auf (ARFI & BOUVY 1995).

Die dritte Hypothese über indirekte Resuspensionseffekte auf phagotrophe Protisten wurde durch die Populationsdynamik der heterotrophen Flagellaten unterstützt, aber nicht bewiesen. Die Abundanzen der heterotrophen Flagellaten wurden über die gesamte Dauer des Intensitätsexperimentes signifikant positiv von der Resuspension beeinflusst und waren gleichzeitig hochsignifikant positiv mit den Abundanzen der Bakterien, Pico- und Nanoautotrophen korreliert. Da eine solche Kopplung der heterotrophen Flagellaten an ihre Hauptbeuteorganismen auf eine Bottom-up-Kontrolle hindeutet, könnte ein verbessertes Nahrungsangebot infolge Resuspension für die beobachteten positiven Effekte auf die Flagellatenabundanzen verantwortlich sein. Dieser Zusammenhang kann ohne eine direkte Analyse der trophischen Interaktionen jedoch nicht bewiesen werden.

Damit wurde für die Abundanzen aller Komponenten des planktischen mikrobiellen Nahrungsgewebes - mit Ausnahme der Ciliaten und Dinoflagellaten - ein positiver Effekt durch direkte Resuspension benthischer Organismen gezeigt. Nährstoffvermittelte Resuspensionseffekte traten - in Abhängigkeit von den Hintergrundkonzentrationen und damit von der Jahreszeit - bei den Autotrophen auf, nicht aber bei den heterotrophen Bakterien. Schließlich deuten die Ergebnisse der Resuspensionsexperimente auf eine über trophische Wechselwirkungen vermittelte Förderung der heterotrophen Flagellaten durch die Resuspension hin.

7.4. Die Bedeutung der Sedimentresuspension für die Erhaltung der Diversität der benthischen Protistengemeinschaft am Beispiel der Rhizopoden

Resuspensionsereignisse beeinflussen nicht nur das mikrobielle Nahrungsgewebe in der Wassersäule, sondern wirken auch als Störungen der Sukzession der benthischen Protistengemeinschaft: benthische Protisten werden durch sie aus ihrem Habitat entfernt, durch die Erosion von Oberflächensedimenten werden Sedimentbereiche zur Neubesiedlung

frei, und durch resuspensionsbedingte Nährstoffflüsse werden autotrophe Organismen potentiell gefördert, was eine Veränderung des Nahrungsangebotes für phagotrophe Protisten zur Folge haben kann. Damit entsprechen Resuspensionsereignisse der Definition von "Störung" im Sinne der "Intermediate disturbance hypothesis" (nachfolgend IDH). Die IDH besagt, daß sich Störungen bis zu einem gewissen Ausmaß und einer gewissen Häufigkeit positiv auf die Diversität einer Lebensgemeinschaft auswirken, weil sie einem Aussterben von Populationen infolge Konkurrenz-Ausschluß im Laufe der Sukzession durch Veränderungen der Konkurrenzbedingungen und Ressourcenfreisetzung entgegenwirken (CONNELL 1978). Die Gültigkeit der IDH für das Phytoplankton wird durch eine Reihe von Freilanduntersuchungen und experimentellen Studien unterstützt (GAEDEKE & SOMMER 1986, REYNOLDS ET AL. 1993, LINDENSCHMIDT & CHORUS 1998, FLODER & SOMMER 1999). Über ihre Anwendbarkeit auf phagotrophe Protistengemeinschaften liegen jedoch noch so gut wie keine Informationen vor, obwohl der große lokale Artenreichtum der Protisten, der hohe Anteil von Generalisten und die seit langem bekannte Möglichkeit eines Konkurrenz-ausschlusses innerhalb dieser Gruppe eine Bedeutung von Störungen im Sinne der IDH nahelegen (GAUSE 1935, PRATT & CAIRNS 1985). Deshalb wurde im Rahmen der im Abschnitt 7.3. vorgestellten Resuspensionsexperimente auch untersucht, ob die Intensität oder die Häufigkeit von Resuspensionsereignissen sich auf die Abundanz, die Artenanzahl oder die Diversität der benthischen Rhizopodengemeinschaft aus dem Untersuchungsgebiet auswirken. Die Rhizopoden wurden ausgewählt, weil sich aufgrund der im Vergleich zu den Ciliaten kurzen Generationszeiten bei dieser Gruppe grundsätzlich eine schnelle Reaktion auf experimentelle Störungen erwarten läßt (BALDOCK ET AL. 1980).

Obwohl in den am Ende der Resuspensionsexperimente gewonnenen Sedimentproben insgesamt 33 Rhizopodenarten bzw. -morphotypen gefunden wurden, hatten weder die Resuspensionsintensität noch die Resuspensionshäufigkeit Einfluß auf die Diversität der benthischen Rhizopodengemeinschaft. Das experimentelle Resuspensionsregime war, soweit sich dies auf Grundlage unserer Informationen beurteilen läßt, realistisch und mit den aus der IDH abgeleiteten Kriterien vereinbar. Deshalb dürften biologische Ursachen für das Nichteintreffen der vorhergesagten Effekte verantwortlich sein: die Sedimente in den experimentellen Mikrokosmen waren nicht homogen, sondern hinsichtlich der Sauerstoffverteilung und anderer Redoxpotential-abhängiger Faktoren vertikal zониert. Hinzu kam möglicherweise eine horizontale Heterogenität hinsichtlich der Porengröße und des Nahrungsangebotes. Die vertikale und horizontale Heterogenität der Umweltbedingungen in den Sedimenten der Kontrollkerne könnte zu einer unterschiedlichen räumlichen Verteilung der einzelnen Rhizopodenpopulationen aufgrund unterschiedlicher Einnischung geführt haben. Eine Separation von potentiell miteinander konkurrierenden Populationen hat grundsätzlich eine Schwächung von Konkurrenzbeziehungen gegenüber der gleichmäßig

durchmischten Situation zur Folge, die in diesem Fall zu einer Verlangsamung von Konkurrenzausschlußprozessen in den Kontrollen geführt haben könnte. Wenn die Experimente also zu kurz waren, um genug Zeit für einen Konkurrenzausschluß in den nicht gestörten Kernen zu lassen, konnte sich in dieser Zeit auch keine relative Diversitätserhöhung in den resuspendierten Kernen einstellen. Deshalb bleibt als Ergebnis der Resuspensionsexperimente festzuhalten, daß die Anwendbarkeit der IDH auf die benthische Rhizopodengemeinschaft durch die Experimente nicht grundsätzlich widerlegt wird, daß bis zur Einstellung der für das jeweilige Störungsregime typischen Diversität aber unter Umständen wesentlich mehr Zeit vergeht als beim Phytoplankton.

7.5. Populationsdynamik und trophische Interaktionen in resuspendierten benthischen Nahrungsgeweben – Untersuchungen an Modellgemeinschaften

Sowohl bei den Resuspensionsexperimenten als auch bei den im Rahmen dieser und früherer Arbeiten durchgeführten Freilanduntersuchungen wurden Komponenten des benthischen mikrobiellen Nahrungsgewebes im Überstandswasser gefunden. Demnach ist eine häufige Resuspension und Resedimentation dieser Organismen eine typische Erscheinung in den Boddengewässern und in anderen flachen Küstengewässern. Daraus ergibt sich die Frage, wie sich die Resuspension und die damit verbundene Durchmischung auf die Populationsdynamik und die trophischen Interaktionen in benthischen mikrobiellen Lebensgemeinschaften auswirken. Um diese Frage beispielhaft für eine einfache benthische Modellgemeinschaft zu beantworten, wurden im Rahmen der vorliegenden Arbeit drei Experimente unter naturnahen Licht- und Temperaturbedingungen und unter Anreicherungsbedingungen durchgeführt, bei denen die Populationsdynamik und die Auswirkungen von Räuber-Beute-Beziehungen auf die Populationsdynamik in Mikrokosmen an rotierenden und stillstehenden Planktonrädern (1,2 m Durchmesser, Drehzahl 5 min^{-1}) miteinander verglichen wurden. Die Modellgemeinschaft bestand aus einer gemischten Bakteriengemeinschaft, der benthischen Diatomee *Amphora coffeaeformis*, dem heterotrophen Flagellaten *Bodo designis*, der Amöbe *Vannella platypodia* und dem benthischen Ciliaten *Euplotes balteatus*. Mit Ausnahme der Diatomee wurden alle Organismen für den Versuch aus den Boddengewässern isoliert.

Die Durchmischung wirkte sich in allen drei Experimenten positiv auf das Populationswachstum der ursprünglich nur zur Aufrechterhaltung der Sauerstoffkonzentration eingesetzten Diatomeen aus. In einem ersten Experiment mit der Gesamtgemeinschaft wurden positive Resuspensionseffekte außer bei den Diatomeen nur bei den Rhizopoden und Ciliaten festgestellt.

Im zweiten Experiment wurden drei unterschiedliche Teilgemeinschaften mit aufsteigendem Komplexitätsgrad (1. nur Bakterien und Diatomeen - 2. Gesamtgemeinschaft, aber ohne Ciliaten - 3. Gesamtgemeinschaft) hinsichtlich der Resuspensionswirkung verglichen. In diesem Experiment wuchsen die Flagellaten schneller in den durchmischten Mikrokosmen, solange ihre Hauptprädatoren, die Ciliaten, nicht anwesend waren. Dieser Effekt war in Anwesenheit der Ciliaten jedoch nicht festzustellen, und die Flagellatenabundanzen waren generell geringer. Die individuellen Flagellaten-Ingestionsraten der Ciliaten lagen bei Durchmischung deutlich höher als ohne Durchmischung (5,5 gegenüber 3,6 *Bodo Euplotes*⁻¹ h⁻¹), und waren nicht allein durch eine beschleunigte Aufnahme aufgrund höherer Flagellatenabundanzen im Rahmen des "Functional Response" der Ciliaten erklärbar.

Die Einbindung der Bakterien in das experimentelle Nahrungsgewebe konnte nur teilweise analysiert werden. Innerhalb der Mikrokosmen, in denen neben den Bakterien auch die bakterivoren Flagellaten, Rhizopoden und Ciliaten anwesend waren, nahmen die Bakterienabundanzen jedoch gegen Ende des Experimentes mit Durchmischung tendenziell schneller ab als ohne Durchmischung. Dies deutet auf eine engere trophische Kopplung in den durchmischten Mikrokosmen, also auf einen ähnlichen Effekt wie bei den Flagellaten hin. Die Ciliatenabundanzen in den resuspendierten Mikrokosmen erhöhten sich in diesem Experiment - ähnlich wie im Experiment mit der Gesamtgesellschaft - tendenziell gegenüber denen der Kontrollmikrokosmen. Eine noch stärkere Förderung des Populationswachstums durch die Resuspension wurde bei den Rhizopoden festgestellt.

Die Bedeutung von trophischen Interaktionen bei der Vermittlung der Resuspensions- und Durchmischungseffekte wird durch die Ergebnisse des dritten Experimentes, bei dem die Resuspensionswirkung mit und ohne eine Anreicherung durch Brennesselextrakt verglichen wurde, unterstrichen. In diesem Experiment konnten die Ciliaten nur dann in ihrem Populationswachstum von der Resuspension profitieren, wenn durch Anreicherung ein ausreichendes Futterangebot gegeben war. Ohne Anreicherung waren die Ciliatenabundanzen nach neun Tagen in den resuspendierten Mikrokosmen sogar niedriger als in den Kontrollen.

Resuspension und Durchmischung förderten also unter Anreicherungsbedingungen das Brutto-Populationswachstum von Diatomeen, Flagellaten, Rhizopoden und Ciliaten und führten zu einer engeren trophischen Interaktion und so zu einer stärkeren Top-down Kontrolle der Flagellaten und unter Umständen auch der Bakterien durch die Ciliaten. Dieses Muster könnte in einer höheren Begegnungswahrscheinlichkeit von Räuber- und Beuteorganismen in den durchmischten Mikrokosmen begründet liegen, die ähnlich auch für planktische Nahrungsgewebe vermutet worden ist (SHIMETA ET AL. 1995). Allerdings setzen Resuspensionsereignisse diese Begegnungswahrscheinlichkeit zugleich durch die Verdünnung der benthischen Lebensgemeinschaft herab. Deshalb sind die in den

vorgestellten Experimenten unter Anreicherungsbedingungen gewonnenen Erkenntnisse wohl nur dann freilandrelevant, wenn das Nahrungsangebot hoch ist oder wenn die resuspendierten Sedimente nicht über die gesamte Höhe der Wassersäule verteilt werden, wie zum Beispiel in der flockigen Sedimentauflage.

7.6. Schlußbetrachtung

Zusammenfassend läßt sich aufgrund meiner Ergebnisse feststellen, daß die windinduzierte Sedimentresuspension die Struktur und die Funktion des mikrobiellen Nahrungsgewebes der untersuchten Küstengewässer im wesentlichen auf drei Ebenen beeinflusst. Erstens werden bei Resuspensionsereignissen Teile des benthischen mikrobiellen Nahrungsgewebes (Diatomeen, Pico- und Nanoautotrophe, Rhizopoden, heterotrophe Flagellaten und in geringerem Ausmaß auch Ciliaten) in die Wassersäule transportiert. Zweitens gelangen durch die Resuspension Nährstoffe (vor allem Ammonium) und organischer Kohlenstoff (in Form von Organismen und Detritus) in die Wassersäule, die dort von autotrophen bzw. heterotrophen Organismen assimiliert werden und das Populationswachstum dieser Organismen fördern können. Drittens können die mit Resuspensionsereignissen assoziierten Durchmischungsprozesse die Nährstoffaufnahme durch resuspendiertes Mikrophytobenthos und trophische Interaktionen in resuspendierten benthischen mikrobiellen Nahrungsgeweben beeinflussen, was ebenfalls Auswirkungen auf die Populationsdynamik der beteiligten Organismen haben kann.

Wie in den Kapiteln 2 und 3 gezeigt, ist das Mikro- und Nanozoobenthos der Bodden- gewässer mit knapp der Hälfte der flächenbezogenen Protozoenbiomasse quantitativ hinreichend bedeutend und hinreichend verschieden vom Protozooplankton, um bei Resuspensionsereignissen einen sowohl quantitativen als auch qualitativen Einfluß auf die heterotrophe Protistengemeinschaft in der Wassersäule zu nehmen. Teilweise starke Überschneidungen in der Zusammensetzung der Rhizopoden- und HNF-Gemeinschaft im Sediment und in der Wassersäule im Freiland, sowie der in den Resuspensionsexperimenten verzeichnete Transport von Angehörigen dieser Gruppen in die Wassersäule zeigen, daß eine solche Einflußnahme tatsächlich erfolgt. Dagegen konnte keine Beeinflussung der Zusammensetzung der benthischen Rhizopodenengemeinschaft durch reuspensionsbedingte Störungen im Sinne der IDH nachgewiesen werden (Kapitel 5). Die Bedeutung der Resuspension als indirekter Förderungsmechanismus für resuspendierte benthische Autotrophe wird durch die Ergebnisse sowohl der Reuspensionsexperimente (Kapitel 4) als auch der Planktonradexperimente (Kapitel 6) unterstrichen. Neben einem verbesserten Nährstoffangebot durch direkten Nährstofftransport oder reuspensionsbedingt verstärkte Remineralisierung scheint hierfür auch eine besserer Nährstoffzugang von

resuspendierten, durchmischten Autotrophen unter Resuspensionsbedingungen mitverantwortlich zu sein. Eine analoge, indirekte Wirkung der Resuspension auf heterotrophes Nanoplankton wird durch meine Ergebnisse unterstützt, aber nicht bewiesen. Auf der anderen Seite scheint die Resuspension sich negativ auf das Wachstum von pigmentierten Dinoflagellaten und filtrierendem Mikrozooplankton auszuwirken.

Benthische Protistenpopulationen können, wie anhand einer Modellgemeinschaft gezeigt, bei ausreichendem Nahrungsangebot mit beschleunigtem Populationswachstum auf die Resuspension reagieren. Weiterhin kann es zu einer engeren trophischen Kopplung in resuspendierten gegenüber sedimentiert vorliegenden benthischen mikrobiellen Nahrungsgewebe, und damit zu einem schnelleren Biomasseumsatz kommen (Kapitel 6).

Insofern sich meine Ergebnisse generalisieren lassen, deuten sie darauf hin, daß die Resuspension in den untersuchten Küstengewässern generell beschleunigend auf den Kohlenstoff- und Nährstofftransfer durch das mikrobielle Nahrungsgewebe wirkt. Dies ist darauf zurückzuführen, daß die Resuspension einer Separation von Ressourcen (Nährstoffe, POM) und Ressourcennutzern (Autotrophe, Phagotrophe) infolge Sedimentation und Ablagerung entgegenwirkt. Darüberhinaus kann die mit Resuspensionsereignissen assoziierte Durchmischung des Wasserkörpers einschließlich resuspendierter Organismen auch in kleinerem räumlichen Maßstab zu einer Erhöhung der Begegnungswahrscheinlichkeit, und damit zu einer engeren Kopplung von Ressourcen und Ressourcennutzern führen.

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9. Kurzzusammenfassung

Das mikrobielle Nahrungsgewebe der küstennahen Ostsee unter besonderer Berücksichtigung der windinduzierten Sedimentresuspension

Anhand von Freilandprobenahmen und Laborexperimenten wurde untersucht, wie sich die in flachen Küstengewässern der Ostsee häufige windinduzierte Sedimentresuspension auf das mikrobielle Nahrungsgewebe an zwei Stationen in den Nordrügenschens Boddengewässern und in der Darß-Zingster Boddenkette (Mecklenburg-Vorpommersche Boddengewässer) auswirkt.

Die flächenbezogene Gesamtbioasse der heterotrophen Protisten (Flagellaten, Rhizopoden, Heliozoen und Ciliaten) in den Bodden entfiel zu etwa gleichen Teilen auf das Sediment und auf die Wassersäule. Die Flagellatengemeinschaft in der Wassersäule wies einen hohen Anteil typisch benthischer Arten auf, während die Ciliatengemeinschaften in beiden Teilsystemen sich deutlich unterschieden. Rhizopoden repräsentierten durchschnittlich 30 % der benthischen Protistenbioasse, während sie im Plankton nur eine untergeordnete Rolle spielten. Ihre taxonomische Zusammensetzung wurde an einer dritten Station ergänzend untersucht. Die Protistenabundanzen im Sediment und in der Wassersäule waren positiv korreliert, was jedoch nicht in erster Linie auf eine direkte Kopplung durch Resuspension zurückzuführen war.

In Resuspensionsexperimenten wirkte die Resuspension als passiver Transportmechanismus von benthischen Protisten in die Wassersäule und hatte darüberhinaus indirekte Auswirkungen auf die Populationsdynamik von resuspendierten Picoautotrophen, Diatomeen und heterotrophen Nanoplankton. Ein Einfluß von Störungen durch Resuspensionsereignisse auf die benthische Rhizopodengemeinschaft im Sinne der „intermediate disturbance hypothesis“ konnte nicht nachgewiesen werden. In einer Reihe von Planktonradexperimenten mit einer Modellgemeinschaft wurde gezeigt, daß resuspendierte benthische Protisten unter bestimmten Voraussetzungen schneller wachsen als im sedimentierten Zustand. Außerdem verstärkten sich im resuspendierten mikrobiellen Nahrungsgewebe trophische Interaktionen zwischen Ciliaten und Flagellaten.

Insgesamt zeigen die Ergebnisse, daß die Sedimentresuspension – abhängig von ihrer Häufigkeit – einen starken Einfluß auf die Vertikalverteilung der heterotrophen Protistengemeinschaft und auf die Funktion des mikrobiellen Nahrungsgewebes von Küstengewässern haben kann.

10. Abstract

The microbial food web of the coastal southern Baltic Sea as influenced by wind-induced sediment resuspension

The relative importance of the benthic microbial food web and the effects of wind-induced sediment resuspension on the benthic and pelagic microbial food web of two stations in the Nordrügensche Boddengewässer and in the Darß-Zinster Boddenkette, southern coastal Baltic, were studied in the field, during resuspension experiments with natural sediment cores and during plankton wheel experiments with an artificially assembled model benthic microbial food web.

Benthic and planktonic heterotrophic protists contributed approximately the same biomass per unit area in the field. The heterotrophic flagellate communities in the sediment and in the water column showed a considerable taxonomic overlap, while the ciliate communities in both habitats were usually comprised of different taxa. Rhizopods contributed 30% to benthic heterotrophic protistan biomass on average, but they were of minor importance within the protozooplankton. Their taxonomic composition and seasonal dynamics were studied in more detail at a third station, revealing a high species richness and a summer abundance maximum. Protistan abundances in the sediment and in the water column of the more shallow station were positively correlated, but taxonomic data indicate that the direct exchange between benthic and planktonic communities was only partly responsible.

Experimental resuspension acted as a passive transport mechanism on benthic heterotrophic protists, diatoms, pico- and nanoautotrophs into the water column. In addition, it fostered growth of resuspended diatoms, other autotrophs and heterotrophic nanoplankton, probably due to released nutrient and food limitation. In contrast, benthic rhizopod community structure responded only marginally to resuspension disturbance, which is not consistent with an applicability of the “intermediate disturbance hypothesis” to benthic rhizopods with this kind of disturbance.

During a series of plankton wheel experiments, resuspended benthic ciliate and rhizopod populations grew quicker than sedimented populations provided food supply was sufficient. The trophic link between ciliates and heterotrophic flagellates, and presumably also other trophic links in the model benthic microbial food web, became closer in suspension.

My results show that resuspension may strongly affect the structure of the heterotrophic protistan community and the functioning of the microbial food web in shallow coastal waters.

LEBENS LAUF

29. 07. 1969 geboren in Magdeburg, DDR

01. 09. 1976 – 31. 8. 1986 Polytechnische Oberschule in Magdeburg und Teltow
(Landkreis Potsdam)

01. 09. 1986 – 01. 07. 1988 Erweiterte Oberschule in Kleinmachnow (Landkreis
Potsdam)

01. 07. 1988 Abitur

01. 11. 1988 – 25. 01. 1990 Wehrdienst als Bausoldat in der NVA der DDR

02. 10. 1990 – 25. 03. 1997 Biologiestudium an der Freien Universität Berlin

18. 01. 1999 Vordiplom in Biologie

26. 09. 1994 – 30. 06. 1995 Erasmus-Studium an der School of Biological Sciences,
University of Wales, Swansea

20. 12. 1995 Abschluss der Diplomprüfungen

01. 03. 1996 – 25. 03. 1997 Externe Diplomarbeit am Institut für Ökologie der Ernst-
Moritz-Arndt-Universität Greifswald: "Qualitative und quantitative
Untersuchungen an Rhizopoden und Heliozoen der Vorpommerschen
Boddengewässer" (Betreuer: Prof. Dr. H. Arndt und Prof. Dr. W. Dohle)

25. 03. 1997 Diplom in Biologie

01. 04. 1997 – 31. 12. 1998 Wissenschaftlicher Mitarbeiter im BMBF-Verbundprojekt
"Ökosystem Boddengewässer – Organismen und Stoffhaushalt",
zunächst am Institut für Ökologie der Ernst-Moritz-Arndt-Universität
Greifswald

10. 12. 1997 Wechsel zum Zoologischen Institut der Universität zu Köln

01. 10. 1998 Immatrikulation zur Promotion an der Universität zu Köln

01. 05. 1999 – 30. 04. 2000 Landesgraduiertenstipendium des Landes Nordrhein-
Westfalen

01. 01. 2001 Higher Scientific Officer, Natural Environment Research Council, British
Antarctic Survey, Cambridge, UK

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GARSTECKI T, ARNDT H 2000. Seasonal abundances and community structure of benthic rhizopods in shallow lagoons of the southern baltic sea. *European Journal of Protistology*, **36**, 103-115.

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(Tobias Garstecki)