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NUISANCE BROWN MACROALGA *PILAYELLA LITTORALIS*: PRIMARY PRODUCTION, DECOMPOSITION AND FORMATION OF DRIFTING ALGAL MATS

Abstract

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CONTENTS

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III. Paalme, T. & Kukk, H. 2003. Comparison of net primary production rates of *Pilayella littoralis* (L.) Kjelm. And other dominating macroalgal species in Kõiguste Bay, northeastern Baltic Sea. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **52**, 125-133.

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V. Kotta, J., Paalme, T., Martin, G. & Mäkinen, A. 2000. Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica*. *Internat. Rev. Hydrobiol.*, **85**, 697-705.

The author`s involment in papers II, III and IV was substantial including the generation of hypotheses, fieldwork and writing process. As for publications I and V the responsibility was shared with other coauthors and my main activities were participation in the experimental design, fieldwork, and laboratory analysis and in writing process related to the specific field of this thesis.

PREFACE

During the past decades the mass blooms of filamentous brown algae *Pilayella littoralis,* accompanied by formation of drifting algal mats has become an annually repeated phenomenon in the Baltic Sea. Hence, it becomes essential to know which environmental variables control the primary production and decomposition rates of *P. littoralis,* formation and dynamics of drifting macroalgal mats.

Several *in situ* primary production experiments of *P. littoralis* were carried out in the Archipelago Sea, SW Finland (1996–1997) and in Kõiguste Bay, Gulf of Riga (1997–2001) to study seasonal variation in primary production rates and to validate the role of abiothic (nutrients, light, temperature) and biothic (grazing pressure) factors in this process. (**III, V**).

In paper **II** the data on the distribution of drift alga and associated invertebrates in the Estonian coastal sea were summarized. The formation and dynamics of *P. littoralis* dominated drifting algal mats were followed in two selected sites in the Gulf of Finland and Kõiguste Bays. The physiological state of the algal material as well the share of invertebrate feeding groups during different developmental stages of these driting algal mats was estimated during one season in 2002/2003.

The decomposition of *P. littoralis* and *Cladophora glomerata* was studied in laboratory and field conditions. The objective of the experiments was to determine decomposition rates of the macroalgae, follow the changes in tissue nutrient content and validate the role of benthic invertebrates in this process. (**IV**).

1. INTRODUCTION

Within the past few decades the extensive supply of nutrients into coastal ecosystems has resulted in the luxurious growth of opportunistic filamentous macroalgal species in many regions of the world (Cederwall & Elmgren, 1990; Bonsdorff, 1992; Fletcher, 1996; Schramm & Nienhuis, 1996; Valiela et al., 1997; Raffaelli et al., 1998). Characterized by high rates of nutrient uptake, photosynthesis, and growth, these opportunistic species gain competitive advantage over the perennial, late-successional vegetation in shallow water phytobenthic communities (Wallentinus, 1978, 1984; Harlin & Thorne-Miller, 1981; Breuer & Schramm, 1988; Raffaelli et al., 1989; Reise et al., 1989; Sand-Jensen & Borum, 1991; Vogt & Schramm, 1991; Hardy et al., 1993; Munda, 1993; Duarte, 1995; Pedersen, 1995). Moreover, opportunistic macroalgal species are characterized by the high tolerance to highly fluctuating abiotic conditions, i.e. changes in temperature, light, salinity, and dissolved oxygen levels, which in turn enhances the success of these algae in eutrophic coastal areas (Peckol et al., 1994; Peckol & Rivers, 1995; Fong et al., 1996; Raffaelli et al., 1998). First of all distribution area and biomass of *Fucus*-belts, *Zostera*- and *Chara*-meadows, are significantly reduced due to increased competition with fast-growing filamentous algae (Wallentinus, 1981; Schramm, 1996; Valiela et al., 1997; Snoeijs, 1999; Schubert & Yousef, 2001).

As a consequence of large macroalgal "blooms", the mass drift of algae is increasingly observed. This is due to the detachment of sessile filamentous algae at the end of their lifecycles and/or disturbances, caused by heavy wave actions or currents. The floating algae are either washed up on the shore or they sink down and form drifting algal mats on the sea bottom. (Morand & Briand, 1996; Schramm, 1996; Paerl, 1997; Valiela et al., 1997; Lotze & Schramm, 2000).

The occurrence of drifting algal mats has become a widespread phenomenon also in shallow coastal waters of the Baltic Sea (Bäck et al., 1996, 2000; Kiirikki & Blomster, 1996; Norkko & Bonsdorff, 1996 a,b; Pihl et al., 1999; Vahteri et al., 2000; Lehvo & Bäck, 2001; Rönnberg, 2004). The proliferation of annual filamentous algae and the formation of drifting algal mats have been observed in the whole Estonian coastal range (Trei, 1983, 1991; Martin et al., 2003; **II**). It is suggested that the occurrence of drifting algal mats reflects the shift in macroalgal communities from the perennial macrophytes to fast growing filamentous macroalgae, caused by increasing eutrophication of coastal waters in the Baltic Sea during the past decades (Nehring & Matthäus, 1987; Rosenberg et al., 1990; Bäck et al, 1993; Mäkinen et al, 1994; Bonsdorff et al., 1997). Naturally Baltic filamentous algae grow on different hard substrates and exhibit strong seasonality (Kiirikki, 1996a; Kiirikki & Lehvo, 1997). However, after detachment and formation of loose lying algal mats, they may extend their growing area to a completely new niche, to soft bottoms. Occupying a unique habitat of higher aquatic plant and macrozoobenthos communities, the drifting algal mats represent a serious threat to the biodiversity of coastal areas (Pihl et al., 1999; Lehvo & Bäck, 2001; Berglund et al, 2003). The accumulation and decomposition of these algal mats can modify nutrient dynamics both in a water column and sediment (Lavery & McComb, 1991; Peckol & Rivers, 1996; **IV**), affect negatively the underwater light climate, result in widespread hypoxic and anoxic conditions among the algae and in the sediment, and hence destabilize the whole shallow-water ecosystem (Norkko & Bonsdorff, 1996 a,b; Hansen & Kristensen, 1997; Snoeijs, 1999). First of all in shallow coastal areas with limited water exchange, organic matter from decomposed algae can accumulate to the sediment. During mineralization processes inorganic carbon and nutrients will be released to the water. Hence, rapid decomposition of opportunistic fast-growing algae during the summer results in a continuous input of the organic matter from the water column to the sediment and could constitute the basic pool for future algal blooms (Sfriso et al., 1987; Lavery & McComb, 1991; Kautsky, 1995; Norkko & Bonsdorff, 1996 a,b; Pihl et al, 1996, 1999).

In many coastal areas of the world, macroalgal blooms are dominated by green, algal species of the genera *Enteromorpha*, *Ulva*, *Cladophora*, or *Chaetomorpha* (Reise 1983; Kautsky et al., 1986; Lundalv et al., 1986; Wennberg, 1987; Fletcher, 1996; Schramm & Nienhuis, 1996; Raffaelli et al., 1998). In contrast to the common dominance of green tides, in various parts of the Baltic Sea the mass spring blooms are dominated by the filamentous brown alga *Pilayella littoralis* (Wallentinus, 1984; Kruk-Dowgiallo, 1991; Norkko & Bonsdorff, 1996a,b; Kiirikki & Lehvo, 1997, Lotze et al., 1999).

Pilayella littoralis (L) Kjellmann (PHAEOPHYTA) is a cosmopolitan macroalgal species of ephemeral habits, i. e. alga which completes its life cycle in less than one year (Taylor et al., 2001). *P. littoralis* is very common in the whole coastal zone of the Baltic Sea (Nielsen et al., 1995). The finely branched thallus of *P. littoralis* has high surface area to volume ratio (Nielsen & Sand-Jensen, 1990) resulting in high rates of photosynthesis, growth and nutrient uptake (King & Schramm, 1976; Ramus, 1978; Wallentinus, 1984; Leskinen et al., 1992). *P. littoralis* as facultative epiphyte is very common on various perennial algal species. In addition to being affected by direct shading, *P. littoralis* may compete with perennial species for free substrata (Kiirikki & Ruuskanen, 1996). The reduction of abundances and biomasses or disappearance of *Fucus vesiculosus* and *Furcellaria lumbricalis* observed at many localities in the Baltic Sea has been considered to be connected with the mass occurrence of filamentous brown algae *P. littoralis* (Rönnberg et al., 1985; Mäkinen et al., 1988; Kruk-Dowgiallo, 1991, 1996; Ciszewski et al., 1992; Haroon et al., 2000; Eriksson, 2002; Andrulewicz et al., 2004; **V**).

This thesis was compiled to provide data on primary production and decomposition rates of *P. littoralis* – the prevailing filamentous macroalgal species in mass blooms and in drifting macroalgal mats in the northern Baltic Sea. Besides, records about the occurrence of drifting macroalgal mats in Estonian coastal area in the last decades were summarized.

2. OBJECTIVES

The objectives of this thesis are:

- to study the seasonal variation in primary production rates of the brown macroalga *Pilayella littoralis*; to validate the importance of abiothic (nutrients, light, temperature) and biothic (herbivores) factors in formation and control of mass blooms of *P. littoralis*
- to summarize the data about the occurrence of drifting macroalgal mats in Estonian coastal area in last decade; study the formation and dynamics of *P. littoralis* dominated drifting macroalgal mats and the share of invertebrate feeding groups in these mats
- to estimate the decomposition rate of the prevalent mat-forming filamentous macroalga *P. littoralis* and *Cladophora glomerata*; to investigate the effect of temperature, algal species and benthic invertebrates (herbivores, detrivores and filter-feeders) on rate of decomposition and release of nutrients

3. MATERIAL AND METHODS

3.1. *IN SITU* PRIMARY PRODUCTION EXPERIMENTS

Diurnal primary production measurements of *Pilayella littoralis* (L.) Kjellm., *Fucus vesiculosus* (L.) and *Furcellaria lumbricalis* (Huds.) Lamour were carried out in the Seili area (60º14´N, 21º58´E), in the Archipelago Sea, SW Finland, from July 1996 until May 1997. In 1997–2001, within the framework of different projects, several *in situ* primary production experiments of *P. littoralis* were carried out in Kõiguste Bay (58º22´N, 22º59´E), Gulf of Riga (**III; V**). The studied two areas were similar in terms of salinity, temperature, nutrient concentrations and light regime. The algal vegetation in the Archipelago Sea area is described in detail by Ravanko (1968, 1972), Mäkinen et al. (1984), and Rönnberg et al. (1985). *F. vesiculosus* and *F. lumbricalis* prevailed in the benthic vegetation of Kõiguste Bay up to 1995, while *P. littoralis* dominated along most studied depth range (0.1 to 6 metres). The species occurred as epiphyte or epilithic at lower depths and freefloating at higher depths (**V**).

Macroalgal samples were collected by SCUBA diving at depths between 0.5 and 4 m. Algal material was immediately transported in water tanks to the laboratory nearby where only individuals with no macroepiphytes were chosen for the experiments. In the laboratory also, the *P. littoralis* samples were examined microscopically to check identification. If epiphytically growing algae were observed on algal filaments, the filaments were rinsed well with sea water before incubations.

Small dufts of algae (ca 0.05g of *P. littoralis* and ca 0.5 to 1.0 g DW of *F. lumbricalis* and *F. vesiculosus*) were incubated in glass bottles of 600 ml filled with seawater from the study site. The bottles were incubated *in situ* on special frames hanging horizontally on rope at depths of 0.5 and/or 2.0 and 4.0 m. Bottles that did not include the algae served as controls (**V**). The irradiance at the incubation depths was measured as photosynthetically active radiation (PAR) using a quantum meter Li 188B (Li-Cor Inc.). In case of Kõiguste experiments, the total insolation above the water surface was measured with a pyranometer. Obtained values were converted to μmol m^{-2} s^{-1} (Lüning, 1981) and transformed to PAR by multiplying with factor 0.45 (Bröckel, 1975).

The photosynthetic activity of the algae was studied by measuring the changes in dissolved oxygen concentration in incubation bottles with an oxygen meter (OXI 92, WTW GmbH) (Littler & Murray, 1974; Arnold & Murray, 1980; Köhler, 1998). The hourly net production rates (given as mg O_2 g $_{DW}^{-1}$ h^{-1}) were calculated from the differences in oxygen concentrations, measured over the incubation period (ca 1 - 3 hours). Daily net production rates (NP_{24}) were calculated as the sum of consecutive hourly net production rates and expressed as mg O_2 g $_{DW}^{-1}$ $24h^{-1}$. Dry weight (DW) of the algal material was determined after drying at 60°C for 24 hours (**V**).

Before nutrient analyses the dried algae were homogenized (all three replicate samples were pooled together). Total phosphorus contents were determined from algae by ICP-AES analyzer (Thermo Jarell Ash ICAP 9000) (ISO 5516:1978). Nitrogen and carbon contents of the algae were analyzed at the Department of Limnology, University of Helsinki, using a LECO CHN-900 analyzer. Water quality data, surface water inorganic phosphate phosphorus ($PO_4^{\ 3-}$) and nitrogen ($NO_2^- + NO_3^- + NH_4^+$) in ambient seawater in Seili area were analyzed by the local water authorities (Southwest Finland Regional Environment Center) using standard methods (Koroleff 1976, 1979; National Board of Waters 1981).

During the experiments the sea water temperature (°C) and the transparency as Secchi disc depth (m) were measured.

3.2. DISTRIBUTION AND DEVELOPMENT OF DRIFTING MACROALGAL MATS

Since 1995 quantitative data on the spatial distribution of macroalgal communities have been regularly collected in Estonian coastal waters. During sampling the diver recorded the presence and spatial coverage of different macroalgal communities including the drift algal mats. Most of the studies were performed in late July and August. However, as the drift algae were not specially surveyed no quantitative frame samples from the mat were taken.

In order to collect more quantitative information on the algal mats the development of the drifting algal mats was followed at two selected sites – in Ihasalu (59°84´N, 25°19´E) and Kõiguste (58°22´N, 22°59´E) Bays, in the Gulf of Finland and the Gulf of Riga during the ice-free season in 2002/2003. In addition to plant species the biomass of associated invertebrates was estimated in the samples of the two selected sites. The samples of drifting macroalgal mats were collected by SCUBA diving. A frame sampler (400 cm^2) was used both for plant and animal species. Dry weights were obtained after drying the plant material for 2 weeks and animals for 48 hours at 60°C (**II**).

The physiological state of the algal material during different developmental stages of the drifting algal mat was estimated in the two selected sites. For this purpose the net photosynthetic and dark respiration rates were measured using the oxygen method (**III, V**).

3.3. MACROALGAL DECOMPOSITION EXPERIMENTS

During the laboratory experiments (**IV**) the freshly collected algae (about 20 g wet weight, *i.e.* 3 g dry weight) with no macroepiphytes were placed into nylon mesh bags of 5.5 cm diameter, 20 cm height and 1 mm mesh size. These bags were incubated in 3 l flasks containing natural seawater at 18°C. The water used in the experiment was screened through 55 μm mesh.

The incubation was run in aerobic and anaerobic conditions. In aerobic conditions the oxygen content was kept between 8.1–8.4 mg l^{-1} using aeration (1500 cm^3 min^{-1}). Twice a week the water in the incubation flasks was changed to avoid high nutrient concentrations in water. In the anaerobic conditions the flasks were closed with stopper and water was not changed.

The incubation lasted 35 days. Every 3 to 4 days six bags of decomposing algal material (3 aerobic, 3 anaerobic) were analyzed for dry weight and nutrients. Algal material was dried at 60°C for 24 hours. The content of total nitrogen, total phosphorus and phosphate in remaining algal material was analyzed using standard methods (Grasshoff, 1976; Solorzano & Sharp, 1980; Raimbault & Slawyk, 1991).

Field studies (**IV**) were carried out in Kõiguste Bay, northern Baltic Sea on 26.04.–25.05.2000 and 25.07.–24.08.2000. The water temperature ranged between 11 and 16°C during spring and between 16 and 22°C during summer. The algae were handled as described earlier. Nylon mesh bags with algal material were incubated at the depth of 2 m (anchored on a rope about 20 cm from the bottom). Besides algal material, some treatments included benthic invertebrates. We used the prevalent herbivore *Idotea baltica* (Pallas) (5 individuals), the detrivore *Gammarus oceanicus* Segerstårle (5 individuals) and the filter-feeder *Mytilus edulis* L. (10 individuals) in our experiment. The incubation lasted 28 days. Once in a week three replicates of each treatment were collected for determination of algal decomposition rate. For estimating the physiological stage of algal material on different phases of decomposition net photosynthetic rates were measured using oxygen method. Comparative measurements with naturally growing algae in the study site were run parallel.

3.4. *IN SITU* GRAZING EXPERIMENTS

The *in situ* grazing experiments were carried out along a 100 m long transect in Kakumäe Bay, the Gulf of Finland (59°30'N, 24°34'E) monthly from April to October 2002 (**I**). Transect was situated perpendicular to the shore between 0 and 5 m depth. Based on the observations made by a diver the transect was characterised by a mixture of sand, pebbles and boulders above 3 m depth. Deeper down only sandy substrate was found and, hence, the area was devoid of macrovegetation and mesoherbivores. The brown algae *F. vesiculosus* and *P. littoralis* were the prevailing macroalgal species. The coverage of the *F. vesiculosus* varied from 15% in winter to 20% in August. The coverage of *P. littoralis* varied from 0% in winter and late summer to 75% in April-May. The green alga *Cladophora glomerata* (L.) Kütz. occurred only in summer with maximum coverage at 5%. Among mesoherbivores the isopod *I. baltica* and the amphipod *G. oceanicus* prevailed in the study area.

Grazing was studied in 5×5×20 cm nylon netbags of 1 mm mesh size. *F. vesiculosus* and *P. littoralis* were deployed separately and together. About 8 g ww (1 g dw) of *F. vesiculosus* and 2 g ww (0.5 g dw) of *P. littoralis* were added per meshbag. The use of different macroalgal treatments in different seasons depended on the natural occurrence of the algae in the field (**I**).

The mesoherbivores were collected from a shallow (1-3 m) hard bottom area within bushes of *F. vesiculosus* by shaking the algae. Prior to the experiment the test animals were gently placed to the Petri dish filled half with seawater and identified to the species level under a binocular microscope (20–40 × magnification). To each macroalgal treatment either two specimens of adult *I. baltica* (16–21 mm, 0.02 g dw) or two specimens of adult *G. oceanicus* (18–25 mm, 0.02–0.03 g dw) were added. The densities of mesoherbivores in the netbags corresponded to their natural occurrence in the field (i.e. 300 *I. baltica* m^{-2} and 200 *G. oceanicus* m^{-2}). In the grazing experiments, netbags without mesoherbivores served as controls and allowed to estimate production and/or decomposition of the macroalgae. Three replicates of each treatment were used. The netbags were placed at 2 m depth about 0.5 m above the bottom. Each experiment lasted 10 days. Altogether the experiment was carried out at 8 times.

In parallel to the grazing experiments, the *in situ* diurnal primary production of the studied macroalgal species was measured using the oxygen method (**V**).

At the end of the experiment the test animals were counted and the dry weights of invertebrates and macroalgae were determined (60°C during 48 h). The changes in the dry weight of the algae per dry weight of the invertebrates corrected for algal production served as the estimates of invertebrate grazing in the field. Parallel with the grazing experiments water temperature, salinity and concentration of nutrients in water and macroalgae from grazer cages were estimated using standard methods (Grasshoff, 1976; Solorzano & Sharp, 1980; Raimbault & Slawyk, 1991). The water samples were taken daily by a diver at 25 cm distance from the mesocosms (10 sample per experiment × 8 periods).

4. RESULTS AND DISCUSSION

4.1. PRIMARY PRODUCTION

P. littoralis is characterized by the distinct seasonal variation in net primary production rates (**V**). In Archipelago Sea area, SW Finland the net production (NP) rates peaked in early spring (March-April) and in September. The maximum of daily net production (NP_{24}) rates up to 88 mgO_2 gDW^{-1} $24h^{-1}$ (at the depth of 0.5 m) were measured in April. Similar results were obtained in Kõiguste Bay, Gulf of Riga, where the maximum NP rates of *P. littoralis* varied between 5 and 7 mg O_2 DW^{-1} h^{-1}, resulting in daily NP rate up to 66 mgO_2 gDW^{-1} $24h^{-1}$ at the depth of 0.5 m (**III, V**). Compared to perennial algal species *Fucus vesiculosus* and *Furcellaria lumbricalis* was *P. littoralis* responsible for markedly higher net productivity all the year around (**III, V**). Differences in the NP between *P. littoralis* and above-mentioned perennial algal species are most likely determined by the morpho-physiological differences of algal thallus resulting in different growth strategy (Arnold & Murray, 1980; Littler, 1980; Littler & Littler, 1980).

The growth strategy of opportunistic species such as *P. littoralis* allows them to exploit a suddenly occurring richness in resource availability, e.g. sea water nutrients (Littler & Littler, 1980; Pedersen & Borum, 1996; Valiela et al., 1997; Lotze, 1998). In the northern Baltic Sea, sea water is rich in nutrients during autumn and winter. Usually nutrients are used up during the phytoplankton bloom in spring and almost disappear through the summer (Haapala, 1994, Hänninen et al., 2000).

Nitrogen supply controls the peak seasonal rates of net primary production and growth in many coastal areas (e.g. Schramm et al., 1988; Peckol et al., 1994; Pedersen & Borum, 1996). The luxurious growth of *P. littoralis* in early spring may be also directly caused by increased nitrogen availability as have been supposed by Kiirikki & Lehvo (1997). Our results support this; the inorganic nitrogen content in the ambient sea water, as well as the total nitrogen content of *P. littoralis*, reached high values in early spring. Moreover, in March before the begin of intense phytoplankton production was *P. littoralis* the dominating ephemeral macroalgal species in the study area. Thus the competition for nutrients among opportunistic species was at its minimum.

The colonization of *P. littoralis* near the surface in very early spring straight after ice break-up indicates that the species may have been favoured by low solar irradiance and low water temperature; e. g. in the Seili area, SW Finland remarkably high NP rates were obtained already at the beginning of March at the water temperature below 1°C and the maximal PAR was less than 100 $\mu mol\ m^{-2}\ s^{-1}$. *Pilayella* showed some photosynthetic activity even in December, despite unfavorable light conditions and low temperature. On the other hand, the reason for the low photosynthetic rates measured at supra-optimal light conditions in late spring could be photo-inhibition (Powles, 1984), as demonstrated for *P. littoralis* by Wallentinus (1978) and Leskinen *et al.* (1992) and/or changes in the physiological state of the alga accompanied with the ageing of algal thallus (incl. degeneration and detachment of filaments) (**III, V**).

Besides abiothic factors (ligh, temperature and nutrients) invertebrate herbivory is considered as a major factor determining the structure and development of macroalgal assemblages (e.g. Paine, 1974; Lubchenco, 1978, 1982; Hawkins & Hartnoll, 1983; Salemaa, 1987; Malm, 1999). Recent studies have demonstrated the preference of grazers to feed on filamentous algae (Cruz-Rivera &

Hay, 2000; Worm & Sommer, 2000). *P. littoralis* was found to be the preferred food for the mesoherbivores *Idotea baltica* (**I**, **V**; Orav-Kotta & Kotta, 2004) and *Gammarus oceanicus* (Orav-Kotta & Kotta, 2003; **I**).

According to paper **I** the physiological state of *P. littoralis* was universal factor that affected the feeding rate and selectivity of benthic mesoherbivores in the northern Baltic Sea. The invertebrate feeding rate was mainly a function of the net photosynthetic activity of *P. littoralis*. Feeding rate increased significantly with decreasing algal photosynthetic activity. When the alga was photosynthetically active its consumption was almost negligible. The grazing increased exponentially prior to the decomposition of *P. littoralis*. The likely mechanism behind the relationship is that the increased photosynthetic activity of macroalgae coincides with their higher unpalatability and/or resistance to herbivory (Birch et al, 1983). During decomposition cell wall break down, concentration of nutrients increases in the decomposing material as a result of increased microbial activity and algae become more attractive for benthic invertebrates (Boyd, 1970; Byren & Davies, 1986; Mann, 1988; Buchsbaum et al., 1991).

The results from papers **I** and **V** indicate that grazers can not control the blooms of annual algae in the northern Baltic Sea. As photosynthetic activity of *Pilayella* decrease with age the invertebrate grazing increases when annual algae have already achieved high densities and start to decompose. In that respect the grazers are not important in buffering eutrophication effects at the earlier stages of the blooms. They may, however, inhibit the recruitment of *P. littoralis* (Lotze & Worm, 2002) and protect perennial macroalgae from excessive epigrowth by *P. littoralis* at the later stages of the blooms (Worm et al., 2002).

4.2. DISTRIBUTION AND DYNAMICS OF DRIFTING MACROALGAL MATS

The occurrence of drifting algal mats has become a widespread phenomenon in shallow coastal waters of the Baltic Sea. The proliferation of annual filamentous algae and the formation of drifting algal mats have been observed in the whole Estonian coastal range (Trei, 1983, 1991; Martin et al., 2003). Since 1995 quantitative data on the spatial distribution of macroalgal communities have been regularly collected in Estonian coastal waters. The drifting macroalgal mats were observed at 18 localities throughout the Estonian coastline. Except for a few locations in the Gulf of Finland the prevailing species in drifting algal mats was *P. littoralis* or *Ectocarpus siliculosus*. The next important species was *C. glomerata*. This pattern reflects the natural occurrence and dominance of species in the area. A similar species composition of drifting algal mats has been described in the Archipelago Sea area, SW Finland (Vahteri et al., 2000; Salovius & Bonsdorff, 2004) and in the northern coast of the Gulf of Finland (Lehvo & Bäck, 2001). Most of drifting algal mats in Estonian coastal zone were observed at very shallow depths and are thus strongly affected by wave action (storms). At the greater depths with the more stable hydrodynamic conditions the drift algae persist longer and may even overwinter (**II**).

In Estonian coastal waters the drifting macroalgal mats occurred as a rule on sandy-clayey bottoms. Normally filamentous algae do not grow on soft substrates. Hence, the mats represent a serious threat to phanerogams, *Chara* spp., and various animal species characteristic of soft sediments. The negative effects of the drift algae include shading, increase in organic matter as a result of their degradation, and the development of anoxic condition under the mats (Bonsdorff et al., 1997; Bäck et al., 2000; Vahteri et al., 2000; Lehvo & Bäck, 2001).

Drift algae were first observed in late May or early June after detachment of *P. littoralis* from substrate. In June the drifting mats were productive, i.e. the net photosynthetic rates of the dominant species *P. littoralis* measured were relatively high. In July rapid decreased in photosynthetic rates and the increase of oxygen consumption rates was observed (**II**). Depending on the succession of dominant algal species as well as on meteorological conditions, drifting algal mats may occur during quite a short period or persist more than a year. The decomposition rate of drifting algal mat depends on its species composition. The decomposition rate of *P. littoralis* is higher than *C. glomerata*, especially in summer at high water temperatures (**IV**; Salovius & Bonsdorff, 2004).

Vahteri et al. (2000) described and classified drifting algal mass according to the thickness of the mat and occurrence of anoxia. According to their classification the algal mats in the Estonian coastal area may be ranked as “algal cover” i.e. free floating productive algal mass or “mat” with visible oxygen deficiency in the lower layers. The “mattress” i.e. totally anoxic algal mass was observed only at depths below 5 m in Kõiguste Bay (**II**).

The share of invertebrate feeding groups in macroalgal mats is probably dependent on the physiological state of the mat. In the case of productive “algal cover” the prevailing functional group inside the mat was herbivores, whereas detrivores were the most abundant functional group in the partly decomposed “algal mat” (**II**).

4.3. DECOMPOSITION RATE OF THE PREVALENT MAT-FORMING FILAMENTOUS MACROALGAE *P. LITTORALIS* AND *C. GLOMERATA*

Following coastal eutrophication the occurrence of drifting algae is an annually repeated phenomenon in the Baltic Sea (Olafsson, 1988; Bonsdorff, 1992; Norkko, 1997; Norkko et al., 2000). Drifting algal mats have become an ecological and economic problem (Bonsdorff et al., 1997; Bäck et al., 2000; Norkko et al., 2000; Vahteri et al., 2000; Lehvo & Bäck, 2001). The occurrence of the mats significantly affects the structure and function of the benthic community. The algal mats modify the nutrient dynamics (Lavery & McComb, 1991; Pecol & Rivers, 1996) and significantly disturb benthic vegetation and invertebrates (Norkko & Bonsdorff, 1996 a,b,c; Norkko et al., 2000). The decomposition of the algae often results in widespread anoxic conditions, which destroy living organisms in the underlying sediments and destabilize the whole shallow-water ecosystem (Norkko & Bonsdorff, 1996 a,b,c; Hansen & Kristensen, 1997; Thiel et al., 1998; Norkko et al., 2000).

Hence, it becomes essential to know which variables control the decomposition of the drift algae. According to the literature the decomposition rate of the drift algae is highly variable and species specific. The algal mats may already disappear within a month but likewise persist for more than two years (Buchsbaum et al., 1991). The drift algae are often colonised by a dense assemblage of opportunistic macrofaunal species (e.g. Norkko et al., 2000). Being primarily herbivores or detrivores they are likely to be important modifiers of the algal decomposition.

The decomposition of two macroalgal species *Pilayella littoralis* (PHAEOPHYTA) and *Cladophora glomerata* (CHLOROPHYTA) was studied in the laboratory and field conditions (**IV**). These species are known to cause the extensive "macroalgal blooms" in the whole coastal range of the Baltic Sea and are the prevailing species in drifting algal mats in Estonian coastal waters (**II**). Both *in situ* and laboratory experiments were conducted to investigate the effect of temperature, algal species and benthic invertebrates (herbivores, detrivores and filter feeders) on the rate of algal decomposition and release of nitrogen and phosphorus. The field experiments enabled us to estimate the seasonal differences in the decomposition rate of macroalgae and to validate the role of benthic invertebrates in this process (**IV**).

In the laboratory conditions *P. littoralis* and *C. glomerata* had different decomposition rates. However, these values varied highly depending on the conditions of incubation. *P. littoralis* had an extremely rapid decomposition rate in aerobic conditions. If 99% of initial dry weight of *P. littoralis* was lost in aerobic conditions (at a linear rate of 2.8% per day) then only 20% was lost in anaerobic conditions. The weight loss of *C. glomerata* was slightly higher in anaerobic conditions than in aerobic conditions. In aerobic conditions *C. glomerata* lost about 46% of its initial dry weight after five weeks of deployment. The weight loss was linear at 1.4% per day. In anaerobic conditions the weight loss was 56% of initial dry weight with rapid weight loss of about 30% during the first week of decomposition. As a rule, the losses of nitrogen and phosphorus in the decomposing material followed the trend similar to dry weight loss.

The field experiments demonstrated that low temperature strongly inhibited both the decomposition process of studied algae and the activity of benthic invertebrates attached to these algae. Similarly to our findings, earlier studies (e.g. Carpenter & Adams, 1979; Birch et al., 1983) have demonstrated that temperature may be ranked among most crucial factors regulating the decomposition process in field. Beside temperature, the photosynthetic activity of macroalgae was likely as important at the early stages of the decomposition.

The decomposition rate of *P. littoralis* was estimated at 49% of its initial dry weight during spring at water temperatures between 11 and 16°C. The addition of benthic invertebrates had no effect on the decomposition process. In summer, at higher temperatures (16–22°C), the decomposition of macroalgae was notably higher and the contribution of herbivores, detrivores and filter-feeders was significant. The decomposition rates were estimated at 65% for *C. glomerata* and 68% for *P. littoralis* being in the same order of magnitude as observed in laboratory conditions. If the decomposition of *C. glomerata* was faster at the end of the experiment the most significant losses of weight of *P. littoralis* took place during the first two weeks of deployment.

The decomposition rate of *P. littoralis* was reduced by the presence of *Mytilus edulis* and increased by *Gammarus oceanicus*. *Idotea baltica* significantly contributed to the loss of *C. glomerata*. Despite strong preference of *I. baltica* towards *P. littoralis* (**I, V**) the effect of the herbivore on the algae was insignificant. This might be due to the toxicity of the algae (Lawrence et al., 1999) or hypoxic conditions inhibiting the activity of *I. baltica*. *Gammarus salinus*, which tolerate lower oxygen concentrations, significantly contributed to the degradation of *P. littoralis* at the end of the experiment (**IV**).

The results from paper **IV** indicate that despite differences in the decomposition rates of *P. littoralis* and *C. glomerata* a remarkable amount of nitrogen and phosphorus could be released from the decomposing algae already after 5 weeks of decomposition. Hence, the rapid decomposition provides an additional important supply of organic and inorganic compounds to be potentially available for recycling in the water. Released inorganic nutrients are likely to be assimilated by other macrophytes and phytoplankton as the photosynthetic activity of mat-forming macroalgae is generally low. On the other hand, the increase in nitrogen pool in *P. littoralis* (at anaerobic conditions) points to the possibility of immobilization of nutrients at different stages of its decomposition (Buchsbaum et al., 1991). In such conditions the decomposing algal mat could be regarded also as an important sink of nutrients.

5. CONCLUSIONS

Pilayella littoralis is characterized by the distinct seasonal variation in net primary production rates. The net production rate of *P. littoralis* peaks in early spring during a time of high ambient sea water nutrient levels. The second peak in production rates was measured in autumn. *P. littoralis* is responsible of markedly higher net production rates than perennial species *Fucus vesiculosus* and *Furcellaria lumbricalis* all year around. We suppose that the luxurious growth of *P. littoralis* is accomplished first of all due to its efficiency in photosynthesis in cold water and low irradiance. (**III, V**)

As a difference of the previous studies carried out in the southern Baltic Sea it was shown that grazers can not control the blooms of annual algae in the northern Baltic Sea. The invertebrate feeding rate was mainly a function of the net photosynthetic activity of *P. littoralis*. Feeding rate increased significantly with decreasing algal photosynthetic activity. As photosynthetic activity of *P. littoralis* decrease with age the invertebrate grazing increases when annual algae have already achieved high densities and start to decompose. In that respect the grazers are not important in buffering eutrophication effects at the earlier stages of the blooms. They may, however, protect perennial macroalgae from excessive epigrowth by *P. littoralis* at the later stages of the blooms. (**I**, **V**).

The drifting macroalgal mats were observed at 18 localities throughout the Estonian coastline. The prevailing species in drifting algal mats was *P. littoralis.* Most of drifting algal mats in Estonian coastal zone was observed at very shallow depths and as a rule on sandy-clayey bottoms. Hence, the mats represent a serious threat to phanerogams, *Chara* spp., and various animal species characteristic of soft sediments. Drift algae were first observed in late May or early June after detachment of *P. littoralis* from substrate. Due to high decomposition rate of *P. littoralis* as well unfavorable meteorological conditions, drifting algal mats may occur during quite a short period.

The abundance of invertebrate feeding types (herbivores or detrivores) was related to physiological state of the macroalgae in the mat. (**II**).

In the laboratory conditions, the decomposition rates of *P. littoralis* and *C. glomerata* were dependent on oxygen conditions. In general, the loss of phosphorus and nitrogen in algal tissues followed weight loss. The field experiments demonstrated that low temperature strongly inhibited both the decomposition process of studied algae and the activity of benthic invertebrates attached to these algae. At higher temperatures the decomposition of macroalgae was notably higher and the contribution of herbivores, detrivores and filter-feeders was significant. (**IV**).

In this thesis it was demonstrated that a remarkable amount of nitrogen and phosphorus could be released from the decomposing algae already after 5 weeks of decomposition. Hence, the rapid decomposition provides an additional important supply of organic and inorganic compounds to be potentially available for recycling in the water. Released inorganic nutrients are likely to be assimilated by other macrophytes and phytoplankton. On the other hand, the possibility of immobilization of nutrients at different stages of decomposition the decomposing algal mat could be regarded also as an important sink of nutrients. (**IV**).

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PRUUNVETIKAS *PILAYELLA LITTORALIS*: PRIMAARPRODUKTSIOON, LAGUNEMINE JA VETIKAMATTIDE MOODUSTUMINE

Kokkuvõte

Läänemere rannikualade eutrofeerumise tagajärjel on viimastel aastakümnetel toimunud muutused makrovetikate koosluste struktuuris s.o. nihked mitmeaastaste makrovetikate domineerimiselt efemeersete niitjate makrovetikate, s.h. pruunvetika *Pilayella littoralis*, domineerimisele. Kiiresti kasvavad niitjad makrovetikad võivad oma elutsükli lõppedes ja/või tormide või hoovuste poolt oma looduslikult substraadilt lahtirebituna moodustada nn vabalt hõljuvaid vetikamatte ning laiendada nii oma kasvuala ka pehmetele põhjadele. Täiesti uue ökoloogilise nišši s.o. pehmete substraatide hõivamine vetikamattide poolt võib käsitleda kui ohtu rannikumere alade looduslikule mitmekesisusele. Eriti liivastele põhjadele, mis on unikaalseks kasvukohaks erinevatele kõrgemate taimede ja loomakooslustele. Mõistmaks täielikult niitjate makrovetikate massesinemiste potentsiaalset mõju ranniku ökosüsteemidele, on kindlasti vajalikud andmed nii nende kujunemisest ning kui neis toimuvatest bioloogilistest protsessidest.

Doktoritöö põhieesmärgid:

- välja selgitada erinevate keskkonnategurite (valgus, temperatuur, herbivoorid) mõju ja tähtsus pruunvetika *P. littoralis* primaarproduktsioonile erinevatel vegetatsiooniperioodi etappidel;
- uurida nn vabalt hõljuvate vetikamattide levikut, moodustumist ja dünaamikat Eesti rannikumeres; võrrelda selgrootute loomade erinevate toitumistüüpide esinemist vetikamattide kujunemise ja arengu erinevates faasides;
- mõõta ja võrrelda vetikamatte moodustavate niitjate vetikate *P. littoralis* ja *Cladophora glomerata* lagunemiskiirust erinevates katsetingimustes; uurida temperatuuri ja selgrootute loomade (herbivoorid, detrivoorid, filtreerijad) mõju lagunemisprotsesside kiirusele;

Doktoritöö olulisemad tulemused võib kokku võtta järgmiselt:

- Liigi *P. littoralis* primaarproduktsiooni iseloomustab kindel sesoonne muutlikus, kusjuures kõrged primaarproduktsiooni väärtused mõõdeti juba varakevadel suhteliselt madala veetemperatuuri ja valguskiirguse juures.

- Herbivoorid ei kontrolli *P. littoralis* varakevadisi massesinemisi Läänemere põhja osa rannikumeres. Herbivooride toitumisaktiivsus sõltub eelkõige *P. littoralis* fotosünteetilisest aktiivsusest, s. t. fotosünteetilise aktiivsuse vähenedes (enne „vananeva" vetika substraadilt eraldumise ja lagunemisprotsesside intensiivistumise) herbivooride toitumisaktiivsus kasvab märkimisväärselt.

- Eesti rannikumeres esinevad vabalt hõljuvad vetikamatid suhteliselt madalates ja varjulistes lahtedes ning valdavalt liiv-savipõhjadel. Peamiseks vetikamatte moodustavaks liigiks Eesti rannikumeres on *Pilayella littoralis*. Vetikamattide moodustumine algab kevadel pärast *P. littoralise* kevadise põlvkonna substraadilt eraldumise. Suvel võib vetikamattide liigiline koosseis muutuda sinna lisanduvate uute liikide, näit. *C. glomerata* tõttu. Vetikamattide esinemise kestvus sõltub nii vetikamatte moodustavate vetikaliikide füsioloogilisest seisundist, nende lagunemiskiirusest, veetemperatuurist kui ka meteoroloogilistest tingimustest. Herbivooride ja detrivooride arvukus vetikamattides sõltub matis domineerivate vetikaliikide füsioloogilisest seisundist.

- Laboratoorsete katsete tulemusena selgus, et *P. littoralis* ja *C. glomerata* lagunemiskiirused olid erinevad ning sõltusid inkubatsioonitingimustest (s.o. aeroobne või anaeroobne keskkond). Liigile *P. littoralis* oli iseloomulik äärmiselt kiire ning ühtlane lagunemine aeroobsetes tingimustes ~ 3% päevas, mille tulemusena kaotas ta 5 nädalaga 99% oma algsest massist. Seevastu anaeroobsetes tingimustes kaotas *P. littoralis* katseperioodil ainult 20 % oma algsest massist. *C. glomerata* lagunemine anaeroobsetes tingimustes oli veidi kiirem kui aeroobsetes tingimustes.

  Madal veetemperatuur kevadel aeglustas märkimisväärselt lagunemisprotsessi käiku *in situ* katsetes, eriti rohevetikaliigil *C. glomerata.* Suvel kõrgema veetemperatuuri juures oli nii *Cladophora* kui *Pilayella* lagunemine märgatavalt kiirem. Erinevalt kevadel läbiviidud katsetest aitasid mesoherbivoorid oluliselt kaasa vetikate lagunemisele, filtreerijad aga pidurdasid lagunemisprotsessi.

  Reeglina järgisid üldlämmastiku- ja üldfosfori sisalduse muutused lagunevates vetikates muutusi kuivkaalus. Märkimisväärne kogus fosforit ja lämmastikku vabaneb lagunevatest vetikatest juba 5 nädala jooksul. Seega moodustub kiire lagunemisega ökosüsteemi potentsiaalne toitainete lisaallikas, mis kasutatakse koheselt ära teiste makrofüütide ja fütoplanktoni poolt. Lagunemisprotsessi erinevates faasides võib toimuda aga ka toitainete immobiliseerumine, kas mikrobiaalse produktsiooni või siis adsorptsiooni tagajärjel. Seega võib lagunevaid vetikamatte vaadelda ka kui olulist ajutist toitainete „tagavara".