Interactions Between Benthic Macroalgal and Microalgal Mats

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Abstract

Benthic primary producers play a key role in regulating carbon and nutrient turnover in shallow-water coastal areas. Macroalgal (MA) mats, which persist from months to over a year, consist of fast-growing filamentous or sheet-like algae on the sediment or floating at the water surface. Benthic microalgal mats (microphytobenthos, MPB), which occur throughout the year, are mostly dominated by diatoms and confined to the photic zone of the sediment. The two mats interact, directly and indirectly, through their impact on light, oxygen, and nutrient conditions. While shading by dense MA mats decreases MPB production, there are shade-adapted MPB that co-exist with MA. Oxygen deficiency below dense and decomposing MA affects the sediment community and increases nutrient efflux from the sediment, a feedback mechanism that favours MA growth. Both mats are temporary sinks for inorganic nutrients and reduce the efflux of remineralized nutrients from the sediment, thereby decoupling benthic and water-column nutrient turnover. Despite large differences in biomass, the quantitative role of both mats for nitrogen assimilation can be similar, making turnover time of algae-bound nutrients a key factor in nutrient retention. The MA–MPB coupling cannot be described by a single model, but rather by different models describing scenarios of MA occupying the water column or the sediment surface. Support was found for the general eutrophication models, predicting that benthic production will decrease with increasing nutrient levels. The impact on MPB may be slower than for seagrasses, and MPB, resistant to anoxia, may promote benthic recovery by rapidly re-oxygenating the sediment surface.

Introduction

Coastal shallow-water areas are productive and therefore are often considered to be buffer zones that influence the transport of nutrients between land and sea. Because the water column is shallow, benthic processes tend to be more important than pelagic processes in these systems. In areas where the bottom substratum is soft, most important biogeochemical processes take place in the sediments, where the density of microorganisms in the top few millimetres is several orders of magnitude higher than in the water column. Benthic primary producers, such as seagrasses, macroalgal (MA) mats and benthic microalgae
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(microphytobenthos, MPB), play a key role in regulating carbon and nutrient turnover in these shallow-water areas [e.g., Welsh et al., 2000; Dudley et al., 2001; McGlathery et al., 2001; Eyre and Ferguson, 2002; Tyler et al., 2003], whereas phytoplankton often play a minor role, except in highly enriched systems [Valiela et al., 1997]. In this chapter we will consider interactions between two of the benthic primary producers, MA mats and MPB. For interactions between other primary producers, such as seagrasses, the reader is referred to the review by McGlathery et al. [2004] and references therein.

Increased anthropogenic loading of nutrients into the coastal zone is now a worldwide phenomenon. It has been predicted that one of the consequences of this marine eutrophication ultimately will be a shift from benthic to pelagic primary production [Sand-Jensen and Borum, 1991; Duarte, 1995; Valiela et al., 1997], implying an increased turbidity due to increased phytoplankton growth. However, in shallow embayments and lagoons, eutrophication often results in blooms of fast-growing filamentous and sheet-like macroalgae, which form loose mats either lying close to the sediment surface or floating at the surface of the shallow water column [e.g., Valiela et al., 1997; Astill and Lavery, 2001; McGlathery et al., 2001]. Accumulations of macroalgae at the sediment surface impact biogeochemical processes in the sediment and the exchange of solutes at the sediment–water interface [e.g., Lavery and McComb, 1991; Sfriso et al., 1992; Viaroli et al., 1996; McGlathery et al., 1997; Tyler et al., 2003]. The MPB community also can form visible mats at the sediment surface [Underwood and Kromkamp, 1999; Cahoon, 1999], regulate biogeochemical processes and sediment–water exchanges of oxygen and nutrients [e.g., Sundbäck et al., 2000, and references therein], and stabilize sediments [Yallop et al., 2000]. Although both types of mats exist in shallow-water embayments, few studies have considered them simultaneously [McGlathery et al., 2001; Havens et al., 2001; Eyre and Ferguson, 2002; Sundbäck et al., 2003; Dalsgaard, 2003]. Even fewer studies exist where the interactions between these mats have been studied experimentally [Fong et al., 1993; Sundbäck et al., 1990, 1996; Tyler et al., 2003].

The aim of this chapter is to examine the interactions, direct and indirect, between macro- and microalgal mats. To do this, we will first give a general description of the characteristics of the two types of algal mats and then give examples from areas that differ in tidal amplitude and climate. We will focus primarily on shallow embayments and lagoons from the two geographic areas that are most familiar to us: the west coast of Sweden, representing a cool temperate area with a negligible tidal amplitude (0.1–0.3 m), and the coast of Virginia (USA), representing a somewhat warmer temperate area with a clear tidal variation (1.2–1.5 m). Some questions we hope to elucidate are: What are the modes of interaction between the two types of algal mats? What is the role of these algal communities in nutrient cycling and retention in shallow embayments?

Characteristics of Macro- and Microalgal Mats

Macroalgal Mats

The problem of increasing occurrences of MA mats has been recognized for at least 20 years, and there is a vast literature considering their growth dynamics [e.g., Harlin and Thorne-Miller, 1981; Cambridge and McComb, 1984; Lapointe and O’Connell, 1989; McGlathery, 1995; Pihl et al., 1996; Viaroli et al., 1996; Campbell, 2001] and impacts on benthic biogeochemistry [e.g., Lavery and McComb, 1991; Viaroli et al., 1996] as well as populations of other organisms, such as seagrasses [Hartog, 1994; Hauxwell et al., 2000; Havens et al., 2001] and benthic fauna [e.g., Norkko and Bonsdorff, 1996; Rafaelli, 2000; Cummins et al., 2004, and references therein]. Effects on the functioning of food webs have also been shown [Isaksson et al., 1994].
In this review, we will give only a short summary of the characteristics of MA mats. Most often, MA mats consist of fast-growing green algae (hence “green tides”) that are either filamentous (e.g., *Cladophora*, *Enteromorpha*, and *Chaetomorpha* species) or sheet-like (e.g., *Ulva* spp.). Mats of filamentous red algae, such as *Gracilaria*, *Spyridea*, and *Laurencia*, also occur in enriched areas [McGlathery, 1995; Valiela et al., 1997; Astill and Lavery, 2001; McGlathery et al., 2001]. Although the growth of these algae starts from benthic propagules attached to sand grains and shells [Schories et al., 2000], they typically establish themselves as loose mats over the sediment surface. One notable exception to this is where tube-forming polychaetes, such as *Arenicola marina* and *Diopatra cuprea*, facilitate MA distribution in soft-sediment environments by attachment of algal fragments to the tube cap [Schories and Reise, 1993; Thomsen and McGlathery, in press]. The largest accumulations of MA mats are found in poorly flushed systems, such as sheltered embayments and lagoons, with elevated sediment organic content and sediment nutrient efflux [Viaroli et al., 1996; Pihl et al., 1999; Astill and Lavery, 2001; McGlathery et al., 2001]. This has led to the hypothesis that such embayments may have become, after several decades of nutrient loading, self-perpetuating systems that favour the growth of opportunistic macroalgae [Hodgkin and Birch, 1986; Pihl et al. 1999; Stimson and Larned, 2000; Tyler et al., 2003].

The position of MA mats in relation to the sediment varies, depending on their composition, growth phase and biomass and water movements in the area. For example, in sheltered embayments of the cool and relatively nutrient-poor microtidal Kattegat–Skagerrak area, vital MA mats are often found floating at the water surface, where wind and currents move them around. These mats, consisting primarily of filamentous species, start to grow in May. Eventually they cover 30–50% of the soft sediment habitats during summer and start to decompose in August–September [Pihl et al., 1999]. In the more eutrophic and warmer microtidal lagoons in Italy, *Ulva* mats, which grow to 50–70 cm thick, appear earlier in spring and collapse in midsummer, causing dystrophic crises [Bartoli et al., 1996; Viaroli et al., 1996]. These mats develop initially on the sediment surface and eventually float up into the water column, presumably buoyed by oxygen bubbles produced during photosynthesis. In the warm temperate region of Virginia, macroalgae are present year-round, reaching maximum biomass in midsummer (June–July); the algal bloom typically collapses in late summer, presumably due to high temperatures and self-shading within the MA mats [McGlathery et al., 2001]. The MA mats in this system are situated on the sediment surface, although during bloom periods the mat can occupy the entire water column (0.5 m at low water). In Australia, Astill and Lavery [2001] report MA mats accumulating on the sediment surface that vary in height but rarely exceed 25 cm, regardless of water depth. The biomass of MA mats typically is 100–600 g dw m$^{-2}$ (ca 25–150 g C m$^{-2}$, assuming that C-content is 25–30% of the dry weight) [Lapointe and O’Connell, 1989; Valiela et al., 1992; Pihl et al., 1999; Astill and Lavery, 2001; McGlathery et al., 2001], although peak biomass of >2 kg dw m$^{-2}$ has been recorded [McGlathery et al., in prep]. Macroalgal mats contribute significantly to annual net production in estuaries [McGlathery et al., 2001], even if the accumulations are transient, lasting only 1–2 months [Dalsgaard, 2003].

Microphytobenthos

Microphytobenthos is the only benthic autochthonous source of primary production on sediments that lack macrophytic vegetation; however even with macrophytes present,
the contribution of MPB can be 20–35% of the total primary production in temperate shallow soft-bottom areas [Asmus and Asmus, 1985; and review by Underwood and Kromkamp, 1999]. In tropical and subtropical seagrass-vegetated sediments, benthic chlorophyll can be as high as that in adjacent unvegetated sediments, even though the seagrass canopy reduces light availability at the sediment surface [Kemp and Cornwell, 2001; Miyajima et al., 2001]. Microphytobenthos often form brownish-yellow or green visible mats on the sediment surface. Although these mats are thin, the microalgae being confined to the restricted photic zone (1–3 mm) of the sediment, the density of algae, as well as other microorganisms, is very high. Occasionally, the POC content of microbial mats (including both live autotrophic and heterotrophic organisms and dead POM) can be as high as 50–70 g C m⁻², which is comparable to the POC content of floating green MA mats (50–100 g C m⁻²) [Sundbäck et al., 1996]. These microbial mats are often dominated by diatoms [e.g., Admiraal, 1984], although cyanobacteria can also be common, and well-developed cyanobacterial mats occur particularly under extreme conditions, such as hypersaline, polar or hot habitats [Stal and Caumette, 1992]. Occasionally, blooms of benthic dinoflagellates and euglenoids occur on the sediment surface [Admiraal, 1984; Larsen, 1985]. Microphytobenthos occur and are generally active throughout the year in most systems, regardless of temperature (tropical vs. temperate) or tidal amplitude (microtidal vs. macrotidal) [Rizzo et al., 1992; Rysgaard et al., 1995; Sundbäck et al., 2000; McGlathery et al., 2001; Dalsgaard, 2003; Ferguson et al., 2003]. In polar seas, MPB activity is limited to the ice-free season [Glud et al., 2002, and references therein]; we cannot, however, exclude the possibility that MPB communities can survive under the ice cover, since benthic diatoms, in particular, can survive long periods of darkness [e.g., Gargas and Gargas, 1982]. The MPB biomass is typically 1–4 g C m⁻² but is occasionally higher (20–30 g C m⁻²), as calculated from chlorophyll a concentrations from Cahoon [1999], assuming a C/chl a ratio of 30 [Jonge, 1980]. The MPB production per m² is within the same magnitude as that of phytoplankton (≈50–300 mg C m⁻² y⁻¹), and can account for up to 60% of total primary production in some estuaries Underwood and Kromkamp, 1999). In shallow embayments, the contribution of MPB primary production to total benthic primary production can vary between ≈5 and 100%, depending on the season [McGlathery et al., 2001].

Macroalgal Effects on Benthic Light and Oxygen Conditions

A basic resource of MPB that is affected directly by MA mats is light. However, MA mats may also affect MPB indirectly, through the input of particulate organic matter into the sediments and by affecting benthic oxygen conditions. All these changes can be expected to affect the trophic state and biogeochemistry of the sediment. The degree of impact on MPB is a function of both the nature of the MA mats themselves (thickness, persistence, physiological state and spatial distribution) and the environment in which they occur (water residence time, tidal amplitude and the carbon content of the sediment). Shading generally decreases or inhibits MPB due to light limitation, but some MPB communities appear to be well adapted to co-exist with MA mats.

Shading by Macroalgal Mats

Dense MA mats (≈100–500 g dw m⁻²) decrease light levels at the sediment surface by >90% [Krause-Jensen et al., 1996; Peckol and Rivers, 1996; Sundbäck et al., 1996; Astill
and Lavery, 2001]. Consequently, MA mats can be expected to decrease or even inhibit the production of MPB. This has been demonstrated in Hog Island Bay, Virginia, a shallow back-barrier island lagoon, which is dominated by benthic macro- and microalgae [McGlathery et al., 2001]. Macroalgal mats accumulate in the midlagoon shoal areas where relict oyster reefs capture drifting algae. Tyler et al. [2003] showed that in sediments underlying MA mats there was an inverse relationship over the year between MA biomass and production of both MPB chlorophyll and sediment-dissolved oxygen. The sediments were net heterotrophic, and maximum net heterotrophy coincided with maximum MA biomass. Together these data suggest that MA mats reduce production of MPB in the underlying sediments. An increased input of organic matter from decaying MA mats can also stimulate heterotrophic bacterial activity in the sediments [Trimmer et al. 2000].

Even though light attenuation by MA mats overlying the sediment surface would be expected to decrease MPB production, this is not always the case, as found at a site with floating Enteromorpha mats on the microtidal Swedish west coast. Sundbäck et al. [1996] found in a series of 2–6-wk experiments that the biomass of a cohesive benthic diatom mat dominated by large sigmoid diatoms (Gyrosigma balticum and Pleurosigma formosum) did not decrease despite severely decreased light levels below the green algae. Although only <1–4% of the surface light reached the sediment surface, $^{14}$C uptake of the diatom mat remained at 30–50% of that of sediment with no MA cover. Moreover, oxygen microprofiles suggested a higher photosynthetic efficiency within the shaded mats [Sundbäck et al., 1996]. This apparent lack of proportionality in the decline of MPB production with reduced PAR may be due to the fact that, with no MA shading, the MPB community may have already reached the declining, “photoinhibited” part of the photosynthesis/irradiance (P/I) curve, as cells had migrated away from the sediment surface as a response to strong light. A different vertical position of the cells was hinted at by the different sediment colours: dark brown below the MA but grey with no MA [cf. Jonsson et al., 1994]. Thus, while overall we can expect increased MA biomass to result in reduced PAR and MPB production, there are also situations where we can expect more complex interactions between the degree of shading by MA and the ecophysiological adaptation of MPB to low-light climates.

The results of these studies suggest that in the short term (weeks–month), diatom-dominated microbial mats are not necessarily outcompeted by overlying MA mats. A tentative explanation for the lack of a negative impact of MA on this specific type of MPB community could be a combination of shade adaptation and good nutrient availability in the sediment, probably through an efficient recycling of both inorganic and organic nutrients within the microbial mat (cf. Fig. 1, bottom). Photoacclimation studies (P/I curves) of subtidal diatom communities have shown an acclimation to low light levels [e.g., Robinson et al., 1995; Light and Beardall, 2000] and benthic diatoms also can survive long periods of full darkness [Gargas and Gargas, 1982; Sundbäck and Granéli, 1988]. Mats dominated by large sigmoid diatoms may be characteristic of shaded habitats (<10% of surface light), as such mats also have typically been found at depths >10 m [Gillespie et al., 2000; Sundbäck et al., 2004]. Organic substances in the pore water may also have contributed to the survival of the MPB. Admiraal and Peletier [1979] showed that several benthic diatoms, including a Gyrosigma species, grew well at low light levels (0.12 mol photons m$^{-2}$ day$^{-1}$, equivalent to a mean light level of ca. 2 μmol photons m$^{-2}$ s$^{-1}$ during a 14-h light period) when provided with organic substances. Recent experiments have shown that dissolved free amino acids can stimulate the growth of MPB communities [Linares, 2003], presumably because the amino acids provide both a carbon and a nitrogen source for the algae [cf. Mulholland et al., 2002]. We do not yet know how common these shade-adapted types of MPB communities are in shallow-water areas and cannot therefore generalize for other areas where MA mats occur.
Macroalgal Influence on Benthic Oxygen Conditions

Macroalgal mats influence benthic oxygen conditions both by oxygen production and by creating hypoxia and anoxia at the sediment surface. When the MA mats are dense, or when they decompose, the effects on the sediment community below can be considerable [cf. Lavery and McComb, 1991]. The decomposition phase of macroalgae can be slow and gradual or can occur as a sudden collapse, leading to dystrophic events. Dystrophic crises are typical of microtidal lagoons in Italy, which are covered by thick mats of
the sheet-like *U. rigida* [Viaroli et al., 1996; Sfriso et al. 1992], and also sometimes occur in temperate macrotidal lagoons [McGlathery et al., 2001; Tyler et al., 2001].

In dense MA mats, the combination of reduced light levels below the mat and respiration and decomposition within the MA mat induces hypoxia or anoxia at the sediment surface during the night and also during the day when mats are dense enough to severely reduce light levels in the lower mat and on the underlying sediment surface [Krause-Jensen et al., 1996; Astill and Lavery, 2001]. The presence of dense MA mats can move the location of the oxic–anoxic interface up from the sediments into the MA mat, since only the upper few centimeters of the mat may be within the photic zone [Krause-Jensen et al., 1999; Astill and Lavery, 2001]. Anoxia at the sediment surface influences sediment–water nutrient fluxes, generally resulting in the release of nutrients from the sediment. The impact of anoxia on sediment–water nutrient fluxes will be discussed in more detail in the next section. Ultimately, anoxia leads to H$_2$S production, which is toxic to aerobic organisms, including MPB, fauna [e.g., Sundbäck et al., 1990] and aerobic bacteria, such as nitrifiers [Joye and Hollibaugh, 1995].

Experimental evidence indicates that benthic diatom communities show a high resistance to anoxia and thus could aid in the recovery of sediment systems after anoxic events [Sundbäck et al., 1990; McGlathery et al., 2001]. MPB mats were well-developed in sediments when sampled 1 month after a MA population crash and dystrophic event in Hog Island Bay, Virginia. Underlying sediments were anoxic both during the peak growth phase of MA (due to shading from the MA mats) and after their collapse, in total probably for more than a month. Following the summertime collapse, MPB production (80 mmol C m$^{-2}$ d$^{-1}$) was about four times higher than it was in late spring, before the MA mat developed [McGlathery et al., 2001]. In an experiment on the west coast of Sweden, the decomposition of a filamentous red algal mat created a 2-week period of anoxia and high H$_2$S production that lasted $\approx$2 wk and had a negative effect on the biomass of both benthic microfauna and meiofauna [Sundbäck et al., 1990]. However, the response of the various algal groups of the MPB community differed. Although the biomass of cyanobacteria and photosynthetic flagellates decreased by 50%, the biomass of diatoms remained unchanged. This agrees with previous findings that many benthic diatom species are tolerant to sulphides [Admiraal and Peletier, 1979; Kennet and Hargraves, 1985]. After the anoxic event, diatoms quickly resumed photosynthesis, thereby re-oxygenating the sediment surface. Benthic diatoms, which are also rapid colonizers, may thus play an important role in the recovery of sediment systems after disturbances [Sundbäck et al., 1990; Underwood and Paterson, 1993; Wulff et al., 1997; McGlathery et al., 2001]. This has been recently verified by manipulative experiments looking specifically at the resilience of shallow-water sediment systems after disturbance [Larson and Sundbäck, 2003, and unpublished].

**Nutrient Interactions**

**General Effects of Algal Mats**

When MA mats are positioned just above the sediment surface, their effect on nutrient cycling is similar to that of MPB, in that they influence nutrient transformations at the sediment–water interface, as well as in the sediment. Their photosynthetic production of oxygen and assimilation of pore-water nutrients influence the concentrations and depth distributions of both inorganic and organic nutrient fractions. Active communities of both types of mats are generally net sinks for inorganic nutrients [e.g., Cerco and Seitzinger, 1997; Sundbäck et al., 2000; Suzumura et al., 2002; Dalsgaard, 2003; Tyler et al., 2003].
Nutrient assimilation by these benthic primary producers can reduce the efflux of remineralized nutrients from the sediments to the overlying water. This “filter effect” can effectively decouple nutrient turnover within the sediments from water-column processes, reducing nutrient availability for phytoplankton and bacteria, as well as for floating MA mats, in the overlying water. However, persistent MA mats can, by creating anoxia at the underlying sediment surface, also switch underlying sediments to being sources of N and P to the water column [Tyler et al., 2003; see also further below].

Diel and seasonal variations attributable to MA and MPB oxygen production and consumption, as well as N uptake, also influence rates of nitrification and denitrification in the sediments, although the effect of MA appears to be less than that of MPB [e.g., Risgaard-Petersen et al., 1994; Krause-Jensen et al., 1999; Trimmer et al., 2000; Dalsgaard, 2003]. Generally, both types of mats decrease denitrification, due to algal competition for dissolved inorganic N (DIN) with bacteria, particularly when DIN levels are low [Risgaard-Petersen, 2003; Dalsgaard, 2003]. When ammonium concentrations are high, an increased supply of oxygen by MPB photosynthesis can instead stimulate nitrification-coupled denitrification [Risgaard-Petersen et al., 1994; An and Joye, 2001]. The implication of both MA mats and MPB on the nutrient turnover in shallow-water sediments will be treated in more detail below.

**Influence of Macroalgal Mats on Benthic Nutrient Cycling and Microphytobenthos**

Macroalgal mats, regardless of whether they are lying on the sediment surface or floating at the water surface, enhance nutrient cycling in the sediments due to an increased input of organic matter [Lavery and McComb, 1991; Jeffrey et al., 1995; Trimmer et al., 2000; Tyler et al., 2003]. Mats floating in the water column that do not shade the sediment surface to the same extent as the sediment MA mats may indirectly stimulate MPB growth by enhancing the nutrient supply. In thick mats lying on the sediment surface, light does not penetrate to the deeper layers; NH$_4^+$ from decomposition and reduced algal uptake builds up as the oxic–anoxic interface is shifted from the sediment into the MA mat [McGlathery et al., 1997; Krause-Jensen et al., 1999; Astill and Lavery, 2001]. Anoxic conditions at the sediment–water interface results in the release of phosphate (through chemical desorption) and ammonium (through decreased nitrification-coupled denitrification) out of the sediment [McGlathery et al., 1997; Trimmer et al., 2000; Astill and Lavery, 2001]. Bioturbating infauna also may become extinct because of anoxic conditions created by dense or decomposing MA mats, and this may inhibit nitrification and result in higher NH$_4^+$ concentrations in the lower part of the mat and in the underlying sediments [Hansen and Kristensen, 1997]. In actively growing MA mats lying just above the sediment surface, this enhanced nutrient release typically is intercepted by the macroalgae and never reaches the water column, thereby uncoupling sediment–water column interactions [Thybo-Christesen et al., 1993; McGlathery et al., 1997; Tyler et al., 2003] (Fig. 1 top). This benthic nutrient release can be interpreted as a feedback mechanism by which the nutrient availability for MA growth can be sustained.

Even when MA mats overlie the sediment surface for only short periods, they generally make the benthic community a strong net sink for nutrients [Dalsgaard, 2003; Tyler et al., 2003]. The effectiveness of the MA nutrient-filter function depends on the biomass and productivity of the macroalgae, as well as on the stability of MA accumulations. Unattached MA mats tend to be patchy and unstable, but oxygen and nutrient gradients develop quickly, in as little as 24 h, suggesting that this filter function occurs even in dynamic environments [Astill and Lavery, 2001]. On a seasonal time scale, it is common
for macroalgae in eutrophic waters to switch from being a net sink early in the growing season to being a net source of nutrients in late summer, when productivity declines due to self-shading within the mat and high temperatures increase respiration. When dense MA mats collapse, the release of plant-bound nutrients following these dystrophic events typically stimulates phytoplankton and bacterial metabolism in the water column [Valiela et al., 1997; McGlathery et al., 2001].

Most studies have focused on MA interception of dissolved inorganic nutrient fluxes [e.g., Thybo-Christesen et al., 1993; McGlathery et al., 1997; Dalsgaard, 2003]; however, macroalgae are also important in regulating the flux of dissolved organic nutrients across the sediment–water interface. Tyler et al. [2003] showed that when the macroalga Ulva lactuca was present in a shallow Virginia lagoon, the benthic community became a net source of organic N (as dissolved combined amino acids; DCAA) to the water column on an annual basis. This occurred even though the benthic community (sediment + macroalgae) was a net sink for DIN on an annual basis (no MA collapse occurred this year). Urea and dissolved free amino acids (DFAA) that were released by the sediments were sequestered by macroalgae, but up to 22% of the total N (DIN + dissolved organic N [DON]) uptake by macroalgae was released into the water column as DCAA, which could stimulate bacterial growth in the water column. DON also may be released from macroalgae due to grazing, as has been shown for phytoplankton [Eyre and Ferguson, 2002].

In situations where the MPB community is nutrient-limited, nutrient uptake from the water column by MA mats may have a negative effect on MPB growth. Nutrient limitation of MPB production occurs especially in sandy sediments during summer months [Nilsson et al., 1991; Flothmann and Werner, 1992]. When the nutrient supply from mineralization in the sediments or within the MA mat is insufficient to meet MA demand, which also likely occurs during the summer months when MA biomass is highest, there generally will be a nutrient flux from the water column into the MA mat [McGlathery et al., 1997; Dalsgaard, 2003]. This may, in turn, limit the water column nutrient supply for the MPB community. When the MA mat eventually decomposes, the large release of mineralized nutrients, in addition to the high light availability at the sediment surface, may stimulate MPB production [McGlathery et al., 2001].

**Influence of Microphytobenthos on Nutrient Turnover and Macroalgal Mats**

Today it is well established that MPB can significantly reduce, and even fully intercept, the flux of remineralized nutrients from the sediment to the overlying water column, particularly in the light [e.g., Henriksen et al., 1981; Rizzo, 1990; Sundbäck et al., 1991; Reay et al., 1995; Thornton et al., 1999; Anderson et al., 2003]. When the sediment nutrient sources are insufficient to meet the growth demand of MPB [e.g., Nilsson et al., 1991], there is a downward flux from the water to the sediment; i.e., the sediment becomes a sink of nutrients. Studies performed in different type of shallow-water ecosystems, ranging from cool temperate [Rizzo et al., 1992; Cerco and Seitzinger, 1997; Sundbäck and Miles, 2000] to warm temperate [Eyre and Ferguson, 2002] and subtropical and tropical areas [Miyajima et al., 2001; Suzumura et al., 2002], have indeed shown that sediments can, due to MPB assimilation, function as temporary sinks of nutrients during a large part of the year. This appears to particularly apply to autotrophic sediments under nutrient-poor conditions [e.g., Christensen, 1998; McGlathery et al., 2001; Sundbäck et al., 2003; Tyler et al., 2003]. Under such conditions, MPB also can outcompete bacteria, such as nitrifiers, suppressing denitrification [Rysgaard et al., 1995; Risgaard-Petersen, 2003]. In general, MPB nutrient uptake probably represents a major fate of mineralized N compared to
coupled nitrification–denitrification in net autotrophic sediments [Cabrita and Brotas, 2000; Sundbäck et al., 2000; Trimmer et al., 2000; Anderson et al., 2003].

The flux of nutrients out of the sediment is known to be important for sustaining MA growth [Thybo-Christesen et al., 1993; Jeffrey et al., 1995; Sfriso et al., 1992; Lavery and McComb, 1991; Stimson and Lamed, 2000; Tyler et al., 2003]. Thus, provided that MPB communities remain active below MA mats, they could control the availability of sediment-regenerated nutrients to the macroalgae, thereby limiting further growth and the thickness of MA mats. Such a scenario could be possible when macroalgae form loose floating mats at the water surface, as suggested by experiments on the microtidal Swedish west coast [Sundbäck et al., 1996].

From these experiments it was concluded tentatively that shade-adapted (and probably photoheterotrophic) diatom mats that remain active below MA mats could, at least in the short-term, control the growth of MA mats by decreasing nutrient outflow from the sediment [Sundbäck et al., 1996]. The question remained, however, whether MPB could be expected to also control the actual onset of the growth of MA mats in spring. As the MPB community is already well established at the normal time of the initiation of MA growth (May, in cool temperate areas), it could be assumed to compete with MA for the pool of remineralized nutrients in the sediment. Such a competition scenario could be plausible if the sediments were the primary source of nutrients for algal growth because nutrient levels in the water column during the normal initiation period for MA mats were too low to trigger the onset of MA growth. This could be the case if there were no or little land runoff of nutrients to the water column, either because of little rain or because of actions taken to reduce anthropogenic nutrient loading. In such a situation, the initiation of MA growth would depend on the sediment pool of nutrients. The regular reoccurrence of MA mats, despite actions taken to reduce external nutrient loading, has led to the idea that MA growth is triggered by the efflux of remineralized nutrients accumulated in the sediments, perhaps during decades of increased nutrient load to the coastal zone (cf. the self-perpetuation hypothesis mentioned earlier). Such a mechanism has also been suggested to sustain benthic MA growth in temperate lagoons in Virginia [27–75% of MA demand; Tyler et al., 2003] and in subtropical lagoons in Hawaii [Stimson and Lamed, 2000].

Some support for the above scenario was found in a study that was done just before and during the normal onset of MA growth in two bays on the Swedish west coast where MA mats have occurred regularly during the last decade [Sundbäck et al., 2003]. In one of the bays, sediment efflux accounted for 50–100% of the calculated N demand and 30–70% of the P demand of the initial growth of MA mats; in the other bay the corresponding percentages were lower [15–35% for N and 10–20% for P; Sundbäck et al., 2003]. This difference between bays was related to the trophic state (balance autotrophy/heterotrophy) of the sediment. In one of the bays, in which sediment had been rendered net autotrophic through MPB photosynthesis, the sediment supply of nutrients to the water column was more strongly controlled by MPB than in the bay with heterotrophic sediment. In these autotrophic sediments, MPB decreased the efflux of both DIN and DIP by up to 100% (i.e., sediment was turned into a sink) during the period that was crucial for the onset of MA growth [Sundbäck and Miles, 2002]. This suggests that MPB could delay or even prevent the start of MA blooms by trapping nutrients in the sediment. In fact, during the study period, no MA mats appeared in the bay with autotrophic sediment, whereas MA mats started to establish in the bay with heterotrophic sediments, which also contained more bioturbating fauna, generally further enhancing nutrient efflux [e.g., Berg et al., 2001; Christensen et al., 2000]. This agrees with the previous findings that autotrophic sediments function as sinks and heterotrophic sediments serve as sources of nutrients [Eyre and Ferguson, 2002; Tyler et al., 2003]. The tentative conclusions of
the role of MPB in controlling the onset of macroalgal growth must, however, be corroborated by further studies involving more sites and sediment types.

Role of Algal Mats in the Carbon and Nutrient Turnover

Relative Contribution of Benthic Macro- and Microalgal Mats to Benthic Primary Production

Given the general negative effect of shading and anoxia on MPB communities, we would expect seasonal variation in the importance of MPB to benthic production in systems with seasonal dense MA mats. This was found in Hog Island Bay, Virginia, where dense MA mats occur locally in midlagoon shoal areas. During early to midsummer and in late fall at these sites, MA mats accounted for 96 and 68% of total benthic production, respectively, and MPB mats accounted for the remaining 4 and 32% (Fig. 2). MPB mats increased in importance (99% of benthic production) following the midsummer die-off of MA mats, suggesting competition for light and possibly nutrients limiting MPB production when MA densities were high. In a subsequent study at this same site, Tyler et al. [2003] found that sediments underlying MA mats were net heterotrophic, except during the late fall and winter when densities were lower. Densities in MA accumulations during summertime peak in biomass reached 2600 g dw m\(^{-2}\), whereas in the fall, winter, and early spring, MA biomass ranged from 10 to 250 g dw m\(^{-2}\) [McGlathery et al., unpubl.].

This same seasonality of MPB production in relation to MA accumulations was found in one of two shallow stations located in a eutrophic shallow estuary in Denmark [Dalsgaard, 2003]. At these sites, transient MA mats consisting of the green algae *Ulva*, *Enteromorpha*, and *Chaetomorpha* accumulate during 1–2 months in the summer, reaching densities of 100–300 g dw m\(^{-2}\) in 3–5-cm-deep unattached mats overlying the sediment surface. At one of the sites, the sediment was net autotrophic due to MPB photosynthesis from late autumn through early summer and net heterotrophic in summer and early autumn, the time when MA mats typically attain highest biomass. At the other site, the sediment was net autotrophic on an annual basis, despite the transient accumulation of an overlying MA mat during the summer. At this latter site, gross primary production (GPP) was 85% higher on an annual basis, probably partly due to a considerably higher (1.7×) MPB biomass than at the site that was dominated by net heterotrophy. This suggests that the presence of well-developed MPB can contribute to the resilience of the sediment system at short-term shading by overlying MA mats [cf. Sundbäck et al., 1996]. At both sites, total benthic GPP increased substantially (4–12×) in the presence of the MA mats.

Relative Contribution of Micro- and Macroalgal Mats to Nitrogen Assimilation

Shifts in primary producer dominance have an impact on the rates and pathways of nutrient retention and transformations within the system. There have been some attempts to compare the importance of benthic microalgal and MA assimilation of nutrients in coastal embayments in which the assimilation rate of N by benthic microalgae has been found to be similar to, or even exceed, that of macroalgae [e.g., McGlathery et al., 2001; Sundbäck and Miles, 2002]. Here we attempt to estimate the role of MA and MPB mats in the retention of N in some temperate shallow-water embayments (Figs. 2 and 3, Table 1).
Calculations of benthic microalgal N demand are subject to potential errors of either over- or underestimation. These calculations can be based on measurements of either net primary production [NPP; Sundbäck and Miles, 2000] or GPP [Anderson et al., 2003]. If NPP estimates are based on sediment–water fluxes of dissolved oxygen or dissolved inorganic carbon (DIC) measured in sediment cores, sediment community respiration will result in an underestimation of microalgal NPP and, therefore, of N demand. Estimates based on GPP eliminate this problem if they are corrected for bacterial respiration [estimated as 10% of GPP; Cloern, 1987]. These estimates, however, may overestimate N demand since GPP does not take into account exudation, which may be a large component (up to 75%) of the carbon fixed by MPB [Goto et al., 1999; Middelburg et al., 2000; Smith and Underwood, 2000; Wolfstein et al., 2002]. Here we discuss N assimilation of the MPB...
Figure 3. Nitrogen assimilation by microphytobenthos (MPB), green macroalgal mats (MA) and sediment denitrification (isotope pairing) in two shallow microtidal bays in East Skagerrak, Sweden, during the period April–June. MPB assimilation is based on 90% of gross primary production. 1) Calculated from MA growth during the study period; 2) calculated from mean growth rate of Enteromorpha sp. in cage experiments [Pihl et al., 1996]. For further methods of calculation, see Table 1.

Community based on 90% GPP (Ass$_{GPP}$), but we also present values based on NPP (Ass$_{NPP}$) (Table 1). To convert MPB oxygen production to N assimilation, we have used a photosynthetic quotient of 1.2 and a C/N ratio of 9 [for justification see Sundbäck et al., 2000; Hillebrand and Kahlert, 2002]. Calculations of macroalgal assimilation for Hog Island Bay, Virginia, and two bays in East Skagerrak are based on in situ growth rates (increase in biomass) and measured C/N ratios. For Hog Island Bay, where MA densities ranged from 0 to 2600 g dw m$^{-2}$, corrections were made for the effects of self-shading within the MA mats on growth and N assimilation. Several studies have documented the reduction in productivity with exponentially decreasing light availability within mats of Chaetomorpha linum, Cladophora vagabunda, and Gracilaria tikvahiae [Krause-Jensen et al., 1996; Peckol and Rivers, 1996]. We used these relationships to scale the maximum growth rate (at full surface irradiance) measured in the field to actual growth rates per m$^{-2}$ taking into account the measured densities of macroalgae [McGlathery et al., 2001]. Without making such a correction, our N assimilation rates based on maximum growth rates would be overestimates by >90% at the highest field densities. This is because in dense MA mats, only the top few centimeters are within the photic zone and are actively growing. Our calculations represent net nitrogen assimilation by macroalgae (i.e., that amount retained in standing biomass), and not total uptake. Like phytoplankton, macroalgae release substantial quantities of assimilated N as DON compounds. This release can be high, from 17% to 99% of gross N uptake in macroalgae [Tyler, 2002], compared to 11–28% for phytoplankton [Bronk and Ward, 2000]. These high leakage rates indicate that considerably more N passes through the MA pool than is accounted for by the N demand for growth.

In Hog Island Bay, Virginia, maximum N assimilation rates estimated for the three primary producer groups (MA, MPB, phytoplankton) were remarkably similar despite orders of magnitude differences in standing biomass (Fig. 2, and McGlathery et al., unpubl.). At the midlagoon shoal sites, estimated maximum N assimilation by macroalgae (7.2 mmol N m$^{-2}$ d$^{-1}$) occurred in midsummer when MA biomass peaked (average 766 g dw m$^{-2}$ d$^{-1}$). However, this N assimilation rate was matched by phytoplankton (6.9 mmol m$^{-2}$ d$^{-1}$), which peaked immediately after the MA bloom, even though phytoplankton biomass was low (<20 µg L$^{-1}$). Likewise, the MPB community had highest estimated N assimilation rates during the summer at the mainland creek and barrier island sites where MA biomass was relatively low (0–70 g dw m$^{-2}$). Maximum N assimilation
TABLE 1. Calculated nitrogen assimilation (mmol m\(^{-2}\) d\(^{-1}\)) of microphytobenthos (MPB) and macroalgal mats (MA) in two temperate shallow-water areas. Shown are mean values for four seasons (data for the Skagerrak sites exist only for spring and summer). MPB assimilation of N is calculated from net primary (oxygen) production (\(\text{Ass}_{\text{NPP}}\)), as well as from 90% gross primary production (\(\text{Ass}_{\text{GPP}}\)), applying a photosynthetic quotient of 1.2 and a C/N ratio of 9. MA assimilation of N is based on increase of biomass and measured C/N ratios, thus presenting net assimilation.

<table>
<thead>
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<th>Season</th>
<th>Hog Bay, VA</th>
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<td></td>
<td>Ass(<em>{\text{NPP}}) Ass(</em>{\text{GPP}})</td>
<td>Ass(<em>{\text{NPP}}) Ass(</em>{\text{GPP}})</td>
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<tr>
<td>Spring</td>
<td>0 0.32 0.43</td>
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<td><strong>0.69 1.18 0.07</strong></td>
<td><strong>2.64 4.55 0.33</strong></td>
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<td>Creeks</td>
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<tr>
<td>Shoals</td>
<td>0 1.83 1.14</td>
<td>0 0.84 6.17</td>
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<tr>
<td>Islands</td>
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<tr>
<td>Bassholmen</td>
<td>0 1.57 2.32(^1), 5.4(^2)</td>
<td>0 2.97 2.32(^1), 5.4(^2)</td>
</tr>
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\(^1\)Calculated from MA growth during the study period.

\(^2\)Calculated from mean growth rate of Enteromorpha sp. in cage experiments [Pihl et al., 1996].
rates estimated for the MPB community were 6.2 mmol N m$^{-2}$ d$^{-1}$. These rates agree well with those measured in spring in two bays in the East Skagerrak, where green MA mats have been common during the last two decades (Fig. 3). Estimated N assimilation by MPB was highest in June in both bays but was twice as high (7.4 mmol N m$^{-2}$ d$^{-1}$) in the bay with sediment rendered autotrophic by MPB photosynthesis than in the bay with heterotrophic sediments (3.4 mmol N m$^{-2}$ d$^{-1}$). Estimated MA assimilation of N (2.3–5.4 mmol N m$^{-2}$ d$^{-1}$) in the one bay where MA mats formed was within the same range as that of MPB. In the autotrophic sediment, estimated N assimilation by MPB exceeded N-removal by denitrification by a factor of 5, whereas in the heterotrophic sediment, denitrification rates were within the same range as MPB N assimilation [Fig. 3 and Sundbäck and Miles, 2002]. The similarity between the N assimilation rates estimated for the different primary producer groups implies that the turnover time of nutrients bound in algal tissue is an important factor influencing the role of primary producers in nutrient retention in these shallow estuaries.

Summarizing calculations from the two temperate shallow-water areas shows that the estimated magnitude of N assimilation by MA and MPB lies within the same order of magnitude (Table 1), despite the biomass of MA being an order of magnitude higher. However, given differences in the seasonal variation of MA and MPB biomass, there may be a temporal separation of this N acquisition. Mean seasonal MPB Ass$_{GPP}$ varied between 0.32 and 7.5 mmol N m$^{-2}$ d$^{-1}$ (mean 3.0 ± SE 0.6), and the seasonal means of MA assimilation, when based on biomass increase, varied between 0.07 and 6.17 mmol N m$^{-2}$ d$^{-1}$ (mean 1.88 ± SE 0.5) (Table 1). The mean N assimilation rate for MPB based on NPP (Ass$_{NPP}$ in Table 1) was about 70% lower than that based on GPP. However, Ass$_{NPP}$ rates of MPB (0–4 [mean 0.84 ± SE 0.28] mmol N m$^{-2}$ d$^{-1}$) are still occasionally within the same range as those of MA mats.

More work is needed to determine the turnover rate of nutrients bound in MA and MPB tissue in order to understand the consequences of the shifting dominance of these communities as the trophic status of an estuary changes. In particular, we need to determine the fate of assimilated N in algal biomass under different environmental conditions. Retention and turnover of N in MPB and MA biomass occur on multiple time scales through direct grazing on live material, heterotrophic bacterial mineralization of detritus, and exudation of organic material (DOC, DON). DON may be released by passive release, excretion, sloppy feeding or direct excretion during grazing, and viral lysis. To our knowledge, no studies have demonstrated exudation of DON by benthic microalgae, although DON release has been observed for phytoplankton [Glibert and Bronk, 1994; Bronk, 1999]. However, because MPB releases large amounts of extracellular polymeric substances [Smith and Underwood, 2000; Wolfstein et al., 2002, and references therein], it can be assumed that dissolved matter is released as well. Like phytoplankton, the composition of DON released from MA includes DFAA, DCAA, dissolved primary amines, and urea, and release of dissolved organic matter appears to be a photosynthetically driven process [Tyler et al., 2003]. Grazing may be an important fate of MA under low to moderate nutrient loading and prevents biomass from accumulating [Hauxwell et al., 2000; Giannotti and McGlathery, 2001]. Field studies have shown that also a large fraction of MPB biomass can pass through macrograzers [Asmus and Asmus, 1985; Herman et al., 2000; Andresen and Kristensen, 2002]. Meiofauna has been estimated to occasionally graze up to 100% or more of the MPB standing stock, although MPB primary production is generally sufficient to supply food resources for meiofaunal grazers [Sundbäck et al., 1996; Pinckney et al., 2003, and reference therein]. In situ $^{13}$C-labeling experiments on a tidal flat showed that assimilated C from MPB was transferred within a few days through the heterotrophic components in the order of bacteria > macrofauna > meiofauna [Middelburg et al., 2000].
Whole ecosystem comparisons suggest that detrital pathways of consumption become relatively more important when the turnover times of the dominant autotrophs in the system are short [Duarte and Cebrian, 1996]. It also has been suggested that higher rates of organic matter supply, as would occur with enhanced algal production in nutrient-enhanced systems, can cause a shift in the relative importance of microbial activity over metazoan activity [Malone and Conley, 1996]. MPB and MA represent a source of labile C and N that turns over on the scale of days [Duarte and Cebrian, 1996; Tyler et al., 2001; Ferguson et al., 2003], but relatively little is known about the presence and composition of refractory material in algal detritus and the extent to which this would enhance nutrient burial and retention in the marine systems [Banta et al., 2004]. Current estimates of refractory material in marine primary producers are highly variable [Cebrian, 2002].

Conceptual Models of Interactions Between Micro- and Macroalgal Mats

As shown by the above examples, interactions between MA and MPB are complicated, varying with season and the nature of the ecosystem. This suggests that there is no single general model for these interactions, but rather several parallel models, or even a continuum of models. The type and strength of the interactions between the mats change with the growth phase, the physiological state, and the spatial location of the mats in relation to each other (Fig. 1, upper). Moreover, the strength of interaction/competition may also depend on the type of water body (water exchange, tidal amplitude, climate and nutrient status of the area, including the sediments). Here we show two conceptual models—one where the MA mat exists close to the sediment surface (Fig. 1, upper) and one where the MA mat is floating at the water surface (Fig. 1, lower). Our graphic presentation follows that of a model previously presented by Astill and Lavery [2001].

At times, there appears to be a close coupling between the MA mat and the underlying sediment, with exchange of both particulate and dissolved matter, regardless of the position of the MA mat (Fig. 1, upper, and right side lower). This coupling can further be strengthened through feedback mechanisms, such as release of sediment nutrients under anoxic conditions induced by MA oxygen consumption (Fig. 1, right side of both models). On other occasions, the two systems can be decoupled (Fig. 1, lower left side). This scenario appears to apply particularly to autotrophic (often sandy) sediments with low nutrient levels in the overlying water column. In such situation, pore-water nutrients (both inorganic and organic) are efficiently trapped in the sediment by the MPB community, which can sustain its productivity by efficient recycling of nutrients within the microbial mat [Kristensen, 1993; Lomstein et al., 1998; Anderson et al., 2003]. A similar efficient recycling seems also to apply for tropical carbonate sediments [Miyajima, 2001; Suzumura et al., 2002]. A decoupling also occurs between the water column and the benthic system (although MA mats remain coupled with the water column) when macroalgae are situated on the sediment surface (Fig. 1, upper left side). High rates of nutrient uptake by these benthic MA mats effectively intercept the flux of remineralized nutrients from the sediment to the overlying water column. This has been shown both for inorganic nutrients [Thybo-Christesen et al., 1993; McGlathery et al., 1997; Tyler et al., 2003] and for organic nutrients [urea and DFAA; Tyler et al., 2003]. However, even when the MA mat intercepts the sediment efflux, the macroalgae leak DCAA compounds and so appear to be a source of organic N to the water column [Tyler et al., 2003]. It is also possible that decoupling between the sediment and water column can occur if mineralization of floating
MA mats takes place in the water column and the lower part of the algal mat and is then transported away via water flow. In this case, particulate organic matter does not enter the sediment system. Such a scenario was suggested in an experiment with decomposing red algae, where the TOC content in the sediment below did not increase during the decomposition of the MA mats [Sundbäck et al., 1990].

Nutrient Cycling and Shifts in Primary Producer Dominance

The generally accepted conceptual models of eutrophication [Sand-Jensen and Borum, 1991; Duarte, 1995; Valiela et al., 1997] predict that increasing nutrient loading will decrease benthic primary production and sediments will become increasingly heterotrophic, resulting in increased nutrient efflux from the sediment to the water column. Ultimately, this will cause accelerating eutrophication through internal loading of nutrients. Some empirical evidence supporting this series of events has been found [e.g., Rizzo et al., 1992; Meyercordt and Meyer-Reil, 1999; Eyre and Ferguson, 2002].

Initially, MPB will be stimulated by increased nutrient levels, particularly in sandy, rather nutrient-poor sediments [Cadée, 1984; Nilsson et al., 1991; Flothman and Werner, 1992]. At the same time, however, the growth of filamentous macroalgae and epiphytes will be stimulated [Nilsson et al. 1991; Havens et al. 2001], resulting in increased shading of the benthos. Whether and when MA mats outcompete MPB (and other benthic primary producers) by shading will depend on the duration and extent of bloom events. We hypothesise that, with proceeding eutrophication and light attenuation from dense MA mats, the negative impact on the MPB community will be more gradual and slower than for macroscopic benthic primary producers, such as seagrasses. Thus, a partially beneficial “buffering” effect of benthic microalgae on shallow-water sediment systems may persist even in more heavily eutrophied systems, as has been shown by Krom et al. [1991] for a hypertrophic fish pond. This hypothesis is based on the assumption that MPB communities possess, due to high diversity and functional redundancy, a certain degree of plasticity, as well as a high potential for rapid colonization. These traits can contribute to the overall resilience of shallow-water sediment systems after pelagic bloom events, as discussed earlier in the context of deteriorating light and oxygen conditions. This scenario, with MPB communities surviving despite deteriorating conditions, may apply particularly to cool moderately eutrophic waters, where MA bloom events last only a few months [e.g., Pihl et al., 1999; McGlathery et al., 2001; Dalsgaard, 2003], leaving the rest of the year open to benthic microalgal primary production. In warmer, more eutrophic systems, MPB can be outcompeted by shading from more persistent MA mats and also by dystrophic events when the MA blooms eventually collapse [Viaroli et al., 1996].

As eutrophication proceeds, the efflux of N and P from the sediments will increase due to prolonged shading of the benthos, as suggested by experiments using varying light intensities [Rizzo et al., 1992; Sundbäck and Granéli, 1988; Cerco and Setzinger, 1997]. The more heterotrophic the sediment system becomes, the more the pelagic primary productivity will be stimulated. Ultimately, the systems will become self-perpetuating and demonstrate hysteresis; e.g., internal nutrient loading from the sediments will continue to sustain the growth of ephemeral MA mats for some time after the nutrient loads begin to decrease [Pihl et al., 1999].

When nutrient loadings to coastal waters are reduced, e.g., to abate negative impacts of eutrophication, a reversed scenario has been predicted, where benthic primary producers, such as MPB, are favoured because of better light conditions. This should accelerate the process of recovery by reoxygenation of the sediment, interception of the nutrient flux,
and increased retention of nutrients in the sediment. This scenario accords with the model presented for Danish coastal waters [Christensen et al., 1998], which predicts that MPB will dominate sediment nutrient turnover in clear shallow waters with a low nutrient content. A practical example of this has been seen in a shallow fjord in Denmark (Kertinge Nor). Reduced land-runoff of nutrients decreased both sedimentation of organic matter and benthic oxygen consumption, allowing MPB to colonize the sediments due to a clearer water column [Dalsgaard et al., 1999]. The release rate of the sediment N pool also can be significantly lower only a few years after the nutrient load to the water column has been decreased [Dalsgaard et al., 1999]. Given the strong correlation between nitrogen loading and MA biomass in temperate estuaries [Kinney and Roman, 1998], one would expect a decline in MA biomass as both these external and internal N sources decrease. Growth by bloom-forming macroalgae such as Ulva, Cladophora, and Chaetomorpha can only be sustained by stored nutrients on a time scale of several days to a week [Borum, 1996; McGlathery and Pedersen, 1999], so a relatively constant high supply of nutrients is required to support the nitrogen growth demands of these MA populations.

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