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~ *Algas* ✾ *Alto interés* ~ Algae ✾ Highlights ~

ВОДОРОСЛИ ✾ ВАЖНЕЙШИЕ МОМЕНТЫ ~ أَخْبَارُ ✾ الطَّحَالِبِ

MACROALGAL BLOOMS CONTRIBUTE TO THE DECLINE OF SEAGRASS IN NUTRIENT-ENRICHED COASTAL WATERS

Nutrient over-enrichment of coastal waters has led to widespread decline in seagrass populations worldwide. It has been well documented in numerous observational and experimental studies that this loss is in large part caused by excessive microalgal growth. Phytoplankton biomass (as well as total suspended particles) increases in nutrient-enriched waters and reduces light penetration through the water column to benthic plant communities (e.g. Kemp et al. 1983, Monbet 1992, Johansson and Lewis 1992, Moore et al. 1996). Epiphytic microalgae also become more abundant on seagrass leaves in eutrophic waters and contribute to light attenuation at the leaf surface (e.g. Borum 1985, Twilley et al. 1985, Short et al. 1995), as well as to reduced gas and nutrient exchange (Sand-Jensen 1977). The result of light interception by these fast-growing alga taxa is a decrease in the maximum depth limit and areal coverage of seagrasses (Dennison et al. 1993, Duarte 1995, Krause-Jensen et al. 2000).

Eutrophication of shallow estuaries and lagoons also can lead to the proliferation of bloom-forming "ephemeral" macroalgae. This has been observed at least for the last two decades throughout nutrient-enriched temperate and tropical regions (e.g. Harlin and Thorne-Miller 1981, Cambridge and McComb 1984, Lapointe and O'Connell 1989, Lavery et al. 1991, McGlathery 1995, Sfriso et al. 1992, Valiela et al. 1997, Kinney and Roman 1998). Recent reviews highlight the role of massive and persistent macroalgal blooms in shading seagrass populations and eventually in displacing seagrasses as the dominant benthic autotrophs in nutrient-enriched waters (Valiela et al. 1997, Raffaelli et al. 1998). These "nuisance" macroalgae are typically filamentous or sheet-like forms (e.g. *Ulva, Cladophora, Chaetomorpha, Gracilaria*)—many are chlorophytes—that accumulate in extensive, thick, unattached mats over seagrasses or the sediment surface (Fig. 1). Some of these macroalgal species also occur as epiphytes on seagrass leaves (e.g. Neckles et al. 1994). In highly enriched waters, it is not unusual for macroalgal populations to attain peak biomass of over 0.5 kg·m^{-2} and for canopy heights to exceed 0.5 m. Recently, it has been suggested that the loss of top predators and the release of herbivores from predation in overfished areas also can contribute to algal overgrowth of seagrasses (Heck et al. 2000, reviewed by Williams and Heck 2001). Given the pervasiveness of macroalgal blooms, it is surprising that until recently there have not been more direct studies of the effects of macroalgal accumulations on seagrass biomass and production.

In their recent study, Hauxwell et al. (2000) provide some of the first experimental evidence that the occurrence of dense macroalgal canopies leads to the decline of the temperate eelgrass *Zostera marina*. They showed this by enclosing mixed macroalgal mats (*Cladophora vagabunda, Gracilaria tikvahiae*) of varying thickness, ranging from 0 to 25 cm, in two estuaries of Waquoit Bay, MA, that were subject to different nutrient loading rates. Previous work in Waquoit Bay had shown that as a result of differences in housing densities in the watersheds, nitrogen-loading rates varied nearly 10-fold among the different estuaries (5 kg·ha^{-1}·yr^{-1} to 410 kg·ha^{-1}·yr^{-1}). Data collected over a 7-year period indicated that macroalgal biomass in Waquoit Bay was consistently greater in the estuary that received the highest nitrogen load (Valiela et al. 1997, Hauxwell et al. 2000). For their study, Hauxwell et al. (2000) used one estuary with a forested watershed and a low nitrogen-loading rate of 5 kg·ha^{-1}·yr^{-1} and another with a relatively urbanized watershed and a higher nitrogen loading rate of 30 kg·ha^{-1}·yr^{-1}. They monitored shoot density and growth of eelgrass in 1-m^2 experimental plots over the summer growth period (14 wk), and then during the following spring, and used this to calculate aboveground summer net production of eelgrass and the persistence of macroalgal effects on the seagrass population. As one might expect, they found that eelgrass loss rates increased with increasing macroalgal canopy height and that this resulted in an exponential decrease in aboveground summer production of eelgrass. A decrease in recruitment of new shoots and rates of leaf appearance in existing shoots accounted for the decline in eelgrass density and production.

Using model calculations to estimate light attenuation by the different autotrophs (phytoplankton, epiphytes, macroalgae), Hauxwell et al. (2000) confirm

Fig. 1. Nutrient over-enrichment of shallow estuaries and lagoons can lead to the proliferation of bloom-forming ephemeral macroalgae. Extensive and persistent macroalgal blooms intercept light and can eventually displace seagrasses as the dominant benthic autotrophic in eutrophic coastal waters. Shown here is the eelgrass (*Zostera marina*) and the ephemeral macroalga *Chaetomorpha linum* in Kertinge Nor, Denmark. (Photo courtesy of Michael Bo Rasmussen.)

that the primary cause of eelgrass loss associated with the occurrence of macroalgal blooms is light reduction by the macroalgal canopy. For temperate seagrasses, it is well documented that light availability is usually the most important factor controlling growth (Dennison and Alberte 1982). Temperate seagrasses can largely meet their nutrient requirements through uptake, use of stored nutrients, internal recycling, and exploitation of sediment nutrient sources (Pedersen and Borum 1996). Even in tropical waters where seagrasses are more limited by nutrient (phosphorus) availability, fast-growing micro- and macroalgae can replace seagrasses as the dominant primary producers in enriched systems. Hauxwell et al. (2000) found that light interception by macroalgae was most important for newly recruiting shoots. In dense canopies of *C. vagabunda* and *G. tikvahiae*, over 95% of incident irradiation was attenuated within the first 6 to 8 cm. A similar result was found by Krause-Jensen et al. (1996) for the bloom-forming macroalga *Chaeotomorpha linum*. For older shoots that extend above the macroalgal canopy, water column and epiphyte shading understandably had a more pronounced effect.

There may be other, secondary, effects of light attenuation by the macroalgal canopy on seagrass growth. Hauxwell et al. (2000) and others (Thybo-Christesen et al. 1993, Krause-Jensen et al. 1996, McGlathery et al. 1997) have documented marked increases in ammonium concentrations within macroalgal mats due to the remineralization of senescent macroalgal tissue deep within the canopy where light does not penetrate. One recent study has shown that these levels (>25 μM) may be toxic to eelgrass (van Katwijk et al. 1997). Again, this effect is likely to be most important for newly recruiting shoots that exist entirely within the macroalgal canopy. Another effect is the decrease

in redox potential and the increase in sediment sulfide concentrations resulting from decomposition in the anoxic organic-rich sediments and decaying macroalgal layer. Elevated sediment sulfide has been shown experimentally to reduce both light-limited and light-saturated photosynthesis and to increase the minimum light requirements for survival in eelgrass (Goodman et al. 1995), although this may not always be the case (Terrados et al. 1999). Decreased photosynthetic oxygen production at all light levels also reduces the potential for oxygen translocation and release to the rhizosphere and creates a positive feedback that reduces sulfide oxidation around the roots and further elevates sediment sulfide levels. High sulfide and low oxygen concentrations also may reduce growth and production of seagrasses by decreasing nutrient uptake and plant energy status (Pregnall et al. 1984).

Even though these unattached macroalgal mats are patchy and unstable, Hauxwell's data suggest that the negative effects on seagrasses persist beyond a single growing season. The partial or total replacement of seagrass by macroalgal blooms in highly enriched waters has significant ecosystem consequences. Where mass accumulations of macroalgae occur, their characteristic bloom and die-off cycles influence oxygen dynamics in the entire ecosystem. This results in frequent episodes of oxygen depletion throughout the water column rather than the seasonal bottom-water anoxia that occurs in stratified, deeper estuaries (Sfriso et al. 1992, D'Avanzo and Kremer 1994, Boynton et al. 1996). Because of their position at the sediment-water interface and their ability to store nutrients, macroalgae uncouple benthic-pelagic linkages by intercepting the flux of nutrients regenerated in the sediments to the water column (Thybo-Christesen et al. 1993, Krause-Jensen et al. 1996; McGlathery et al. 1997). As a result,

water quality often appears high (low chlorophyll, low dissolved nutrients) despite high external nutrient loads. Retention of nutrients in macroalgal biomass, however, is temporary. Because fast-growing benthic macroalgae typically have a low C/N content and decompose rapidly, the dominance of macroalgae over seagrasses can feedback to accelerate nutrient cycling rates. When macroalgal blooms collapse, nutrients released to the water column temporarily stimulate phytoplankton production (Sfriso et al. 1992). This results in a dynamic switching between benthic and pelagic production in eutrophic shallow waters. Because ephemeral macroalgae are rich in nitrogen and low in structural carbohydrates compared to seagrasses (Enriquez et al. 1993), their decomposition is also likely to stimulate bacterial metabolism to a greater extent. Sediment resuspension and high turbidity events are more common in macroalgal-dominated systems because the patchy, ephemeral macroalgal mats do not provide the same stabilizing effect as the seagrass root/rhizome structure and dense leaf canopy. Lastly, conversion of seagrass beds to ephemeral macroalgal mats invariably results in changes in trophic interactions and loss of invertebrate and fish species that use the seagrass habitat for food, protective cover, or as a nursery ground (e.g. Norkko and Bonsdorff 1996). Ultimately, these nutrient-induced habitat changes may lead to a decrease in biodiversity of the benthic community (National Research Council 2000).

Dominance by ephemeral macroalgae and the associated changes in benthic fauna in eutrophic estuaries also may influence the extent to which the system acts as a "filter" to process nitrogen inputs on their transport to the coastal ocean. The activities of bioturbating infauna and irrigating invertebrates both tend to stimulate mineralization and coupled nitrification-denitrification in the sediments (Kristensen 1988, Pelegri et al. 1994); if populations decline in shallow estuaries that experience episodic anoxic events, then relative nitrogen losses may decrease with greater nitrogen loading. Likewise, because oxygen release from roots of submerged macrophytes during photosynthesis stimulates nitrification and denitrification (Caffrey and Kemp 1990), decreased abundance of rooted macrophytes in eutrophic systems also should reduce relative nitrogen losses.

The study by Hauxwell et al. (2000) indicates that the effects of nutrient enrichment and the proliferation of bloom-forming macroalgae on seagrass are reversible. This depends on the persistence and spatial scale of the bloom, the seagrass belowground carbon reserves available to support new growth following bloom termination, and the availability of new propagules. Macroalgal mats also are frequently disturbed by winds and tides and may collapse due to self-shading and high temperatures in the middle of the growing season before long-term effects are realized. One might expect that some tropical seagrasses, such as the turtle grass *Thalassia testudinum,* that have a proportionately greater allocation to belowground biomass may be more resilient

to ephemeral shading by macroalgal canopies. Even with the potential for recovery, however, it is clear that eutrophication of coastal waters and the proliferation of bloom-forming macroalgae pose a real threat to seagrass habitats worldwide.

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2002 ANNUAL MEETING OF THE PHYCOLOGICAL SOCIETY OF AMERICA

The Phycological Society of America will hold its 56th annual meeting at the University of Wisconsin-Madison, 3 to 8 August, 2002. The PSA meeting will be held in conjunction with the meetings of the Botanical Society of America at the Pyle Center, located on the shore of Lake Mendota, the site of classic immunological studies by Birge and Juday and others. Lake Mendota is currently one of the research sites included in the North Temperate Lakes (NTL) Long Term Ecological Research (LTER) Program funded by the National Science Foundation. Lake Mendota is connected to nearby Lake Monona, whose algae were studied in the early 1900s by the famous phycologist Gilbert Morgan Smith. The Pyle Center is within walking distance of State Street, which links the University of Wisconsin Campus with the State Capitol, and the UW Memorial Union, a center of student life.