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Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences

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Abstract

Macroalgal blooms are produced by nutrient enrichment of estuaries in which the sea floor lies within the photic zone. We review features of macroalgal blooms pointed out in recent literature and summarize work done in the Waquoit Bay Land Margin Ecosystems Research project which suggests that nutrient loads, water residence times, presence of fringing salt marshes, and grazing affect macroalgal blooms.

Increases in nitrogen supply raise macroalgal N uptake rates, N contents of tissues, photosynthesis-irradiance curves and P_{max} , and accelerate growth of fronds. The resulting increase in macroalgal biomass is the macroalgal bloom, which can displace other estuarine producers. Fringing marshes and brief water residence impair the intensity of macroalgal blooms. Grazing pressure may control blooms of palatable macroalgae, but only at lower N loading rates. Macroalgal blooms end when growth of the phytoplankton attenuates irradiation reaching the bottom. In estuaries with brief water residence times, phytoplankton may not have enough time to grow and shade macrophytes. High phytoplankton division rates achieved at high nutrient concentrations may compensate for the brief time to divide before cells are transported out of the estuary.

Increased N loads and associated macroalgal blooms pervasively and fundamentally alter estuarine ecosystems. Macroalgae intercept nutrients regenerated from sediments and thus uncouple biogeochemical sedimentary cycles from those in the water column. Macroalgae take up so much N that water quality seems high even where N loads are high. Macroalgal C moves more readily through microbial and consumer food webs than C derived from seagrasses that were replaced by macroalgae. Macroalgae dominate O_2 profiles of the water columns of shallow estuaries and thus alter the biogeochemistry of the sediments. More frequent hypoxia and habitat changes associated with macroalgal blooms also changes the abundance of benthic fauna in affected estuaries.

Approaches to remediation of the many pervasive effects of macroalgal blooms need to include interception of nutrients at their watershed sources and perhaps removal by harvest of macroalgae or by increased flushing. Although we have much knowledge of macroalgal dynamics, all such management initiatives will require additional information.

The appearance of dense canopies of macroalgae in benthic communities of shallow water bodies is an increasingly common phenomenon along virtually all the world's shorelines. Even a short list of published studies attests to the widespread distribution of macroalgal blooms (Table 1).

Macroalgal blooms in temperate, relatively nutrient-rich waters (concentration of dissolved inorganic N, DIN > a few μM), consist of extraordinary growth and dominance of a relatively small group of taxa (Table 1). These so-called nuisance seaweeds are largely filamentous, unattached forms and are predominantly green algal species, at least in nutrient-rich, temperate waters. Occasionally, other taxonomic groups of macroalgae form blooms: a brown alga (*Pilayella littoralis*) has bloomed for decades in loose bundles of free-living fronds within a Massachusetts bay subject to some nitrogen loading by wastewater (Wilce et al. 1982; Pregnall

and Miller 1988). In nutrient-poor or tropical waters, macroalgal blooms may be more taxonomically diverse (Lapointe 1987). Growth of blooms of nuisance species in almost every case displaces seagrasses, corals, or brown and red algae (Table 1).

Macroalgal blooms are unlike microalgal blooms in at least three ways: they lack direct chemical toxicity, have a broader range of ecological effects, and last longer. The term "harmful algal blooms" generally has been used to refer to episodic increases in abundance of microalgal organisms that have some direct chemical-based toxic effect on animal or human health, or cause damage in other ways, such as biomass decomposition and anoxia. The harmful effects of macroalgal blooms are generally not mediated by toxic substances, probably as a fortuitous accident of taxonomy. Green algae are the most common seaweeds involved in bloom episodes, at least in temperate waters (Table 1), and greens also turn out to be the group of macroalgae least likely to contain and release toxic compounds (Hay and Fenical 1988).

Both microalgal and macroalgal blooms may have intensive consequences; the contrast is in the breadth of effects. The effects of macroalgal blooms are rather indirect and extensive, in contrast to the more direct and narrowly focused, often toxic, effects of most microalgal blooms. The multifaceted effects of macroalgal blooms may thoroughly alter

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Table 1. Selected examples of studies documenting the occurrence of seaweed blooms.

Locality	Seaweed taxa	Some effects	Reference
Peel-Harvey estuary, Australia	<i>Cladophora</i> , <i>Ulva</i> , <i>Enteromorpha</i>		Lavery et al. 1991
Great Barrier Reef, Australia	—	Replaced corals	Bell 1992
Kanehoe Bay, Hawaii	<i>Dictyosphaeria</i>	Replaced corals	Smith et al. 1981
Venice Lagoon, Italy	<i>Ulva</i>		Sfriso et al. 1992
N. Mediterranean coasts	<i>Caulerpa</i>	Replaced <i>Cymodocea</i> , <i>Posidonia</i>	Meinesz et al. 1993
NW Black Sea	<i>Enteromorpha</i> , <i>Cladophora</i>	Replaced <i>Zostera</i> , <i>Phyllophora</i>	Zaitsev 1992
Baltic Sea	<i>Cladophora</i> , <i>Enteromorpha</i>	Replaced <i>Fucus</i>	Baden et al. 1990
Bermuda	<i>Cladophora</i>		Lapointe and O'Connell 1989
Coos Bay, U.S.	<i>Enteromorpha</i>		Pregnall and Rudy 1985
Branford River, U.S.	<i>Ulva</i>		Walsh 1980
Waquoit Bay, U.S.	<i>Cladophora</i> , <i>Gracilaria</i>	Replaced <i>Zostera</i>	Valiela et al. 1992; Peckol et al. 1994
Great Lakes, U.S.	<i>Cladophora</i>		Auer 1982
Nahant Bay, U.S.	<i>Pilayella</i>		Wilce et al. 1982; Pregnall and Miller 1988

function and structure of affected ecosystems; the range of ecological effects is discussed in more detail below.

Blooms of macroalgae tend to last much longer than the more short-lived blooms of dinoflagellates or other microalgae. Bloom seaweeds may remain in an environment for years to decades, as in the Peel Harvey estuary of Western Australia, where a bloom of *Cladophora* lasted for a dozen or so years (Gordon and McComb 1989). In Waquoit Bay, Massachusetts, blooms of *Cladophora* and *Gracilaria* have been present for >20 yr (Valiela et al. 1992). Macroalgal blooms therefore last much longer than even the multiyear (1990-present) brown tides—the longest-lasting microalgal blooms recorded (Buskey 1997).

The mechanisms that control rates of net production in macroalgae (e.g. temperature, light, grazing, and nutrients) are the same as in other producers (Norin and Waern 1973; Lowthion et al. 1985; Tewari and Joshi 1988). Temperature limits geographic boundaries or imposes seasonal patterns on net macroalgal production. Light intensity also directly creates seasonal patterns in macroalgal growth and thus controls the biomass present. Removal of grazers from shallow-water environments may also prompt increases in macroalgal standing crops that could be considered to be blooms. Hughes (1994), for example, argued that removal of grazers by overfishing and disease resulted in increased the area covered by fleshy macroalgae from 4 to 92% of the shallow coastal habitats previously supporting corals in Jamaica. As it turns out, lowered abundance of herbivores may not be the sole reason for the increases in macroalgal cover in this example. Lapointe (1997) pointed out that there were contemporaneous increases in nutrient loading to this system, so that the proliferation of macroalgae may be yet another instance of bottom-up control by increased nutrient supply. It appears that most cases of macroalgal proliferation are the result of increased nutrient availability. In this paper we therefore emphasize the role of nutrients and the interaction

between nutrients and other factors in the control of macroalgal blooms.

Limnologists concerned with controls of food webs have coined the terms “bottom up” and “top down” to refer to situations in which the supply of resources or the actions of consumers control populations within food webs (Carpenter et al. 1985; McQueen et al. 1986). These terms economically subsume concepts that would otherwise require many words to describe. Below we start with a look at two mechanisms that seem important in initiation and maintenance of macroalgal blooms; the bottom-up effects of nitrogen loading, and grazer-related top-down processes. We then examine key processes that might prompt the termination of macroalgal blooms. Lastly, we speculate on some ecosystem consequences of macroalgal blooms.

Bottom-up control of macroalgal blooms

Nutrient enrichment seems involved in the initiation of virtually every macroalgal bloom. The voluminous literature on the identity of key limiting nutrients, the role of nutrient enrichment, and mechanisms underlying macroalgal blooms were reviewed by Sand-Jensen and Borum (1991) and Duarte (1995). Here we use these reviews, some newer publications, and relevant new data collected for the Waquoit Bay Land Margin Ecosystems Research project (WBLMER) to summarize key interactions that seem to initiate and maintain macroalgal blooms. We first discuss factors that influence the identity of the limiting nutrient. We then examine how increases in nitrogen loading might change macroalgal physiology and anatomy, macroalgal standing crops, and dominance of different producers. We then discuss some powerful modifiers of the effects of land-derived nitrogen loading, in particular the presence of fringing wetlands and the effects of different water residence times.

Identity of the limiting nutrient—The identity of the specific nutrient that limits macroalgal growth and production depends on time of year, nature of the sedimentary substrate, and taxonomic composition of the macroalgal bed.

Nitrogen supply seems to control the peak seasonal rates of growth or net primary production by macroalgae in most coastal systems (Twilley et al. 1985; Fujita et al. 1989; Thybo-Christensen et al. 1993; Peckol et al. 1994). Phosphorus alone (Lapointe 1987; Peckol et al. 1994) or both N and P (Gordon et al. 1981; Lapointe 1987; Short et al. 1990) may limit production of macrophytes at certain times of year in some cases.

The chemistry of sediment substrate can make one or another element more or less available. For example, phosphate is strongly adsorbed to carbonates; consequently, phosphate may limit growth rates of macroalgae in tropical carbonate-rich waters (Lapointe et al. 1992). P limitation tends to be more common in tropical than in temperate waters, but knowledge about the mechanisms involved in such possible regional differences is limited.

The identity of the limiting nutrient may also depend on the macroalgal taxon; different species of macroalgae can be limited by nitrogen or by phosphorus in the same estuary. In the Peel-Harvey estuary, for example, *Ulva* was nitrogen limited (Lavery 1989), but *Cladophora* was phosphorus limited (Lavery et al. 1991), or both were P and N limited (Gordon et al. 1981). In the Belize Barrier Reef, growth of fleshy macroalgae (*Dictyota*, *Acanthophora*) was P limited, but that of the calcareous *Halimeda* was N limited (Lapointe et al. 1987). Too little is known about the reasons for such interspecific differences to generalize freely.

Ecophysiological and anatomical changes in macroalgae—Increases in nutrient supply alter the physiology of macroalgae (Lapointe and Tenore 1981; Lapointe and O'Connell 1989; Gordon and McComb 1989; Peckol et al. 1994). In general, macroalgae growing in estuaries with increased nutrient supply show elevated nutrient uptake rates, tissue nutrient contents, initial slopes of the $P:I$ curve (α) and maximum photosynthetic rates (P_{max}), and macroalgal growth rates. The quantitative specifics of each of these responses depends on the species of macroalgae, but the patterns hold in general.

Nutrient supply-related differences in nutrient uptake (Wallentinus 1984) and other physiological variables (Gordon et al. 1981; Peckol et al. 1994) seem, in turn, tied to differences in frond architecture. Differing nutrient supply regimes may thus change the morphology of macroalgae. Morphological changes of fronds of a single species exposed to different nutrient supply may even rival differences in morphology among species (Littler and Littler 1983; Littler et al. 1988). For example, mats of *Cladophora vagabunda* are most often made up of ball-shaped (aegagropiloid!) filament bundles in estuaries of Waquoit Bay subject to lower rates of nitrogen loading (pers. obs.). In estuaries subject to high loading rates, the blooming macroalgal canopies are made up of longer filaments, intertwined in shapeless mats. Perhaps different frond shape provide different surface-to-volume ratios, which in turn alter nitrogen uptake. Hein et al. (1995) showed that the ratio of surface to volume in

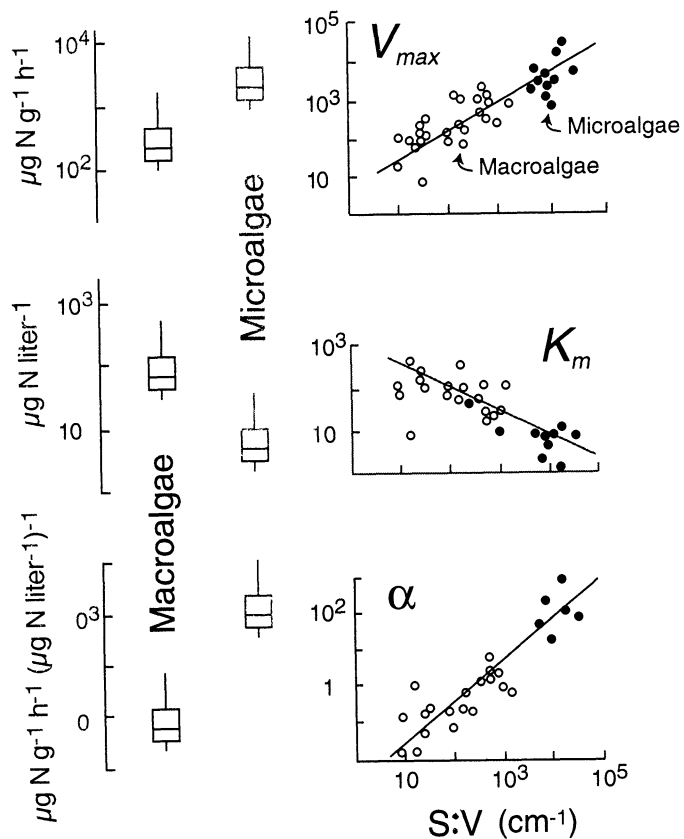


Fig. 1. Left. Values of maximum nitrate uptake rates (V_{max})(top), half-saturation coefficients (K_m)(middle), and nitrate assimilation efficiencies (α)(bottom) for many different species of macro- and microalgae. The line within boxes is the median; the boxes span the 25th to the 75th quartiles; the vertical lines extend to the 95% confidence limits. Right. Relationship of V_{max} (top), K_m (middle), and α (bottom) to ratio between surface area (S) and volume (V) of the organisms. (Redrawn from Hein et al. 1995.)

macroalgae is strongly linked to nitrogen uptake kinetics (Fig. 1, right panels). Although the relationship was first studied in phytoplankton (Malone 1980), it is macroalgae that show the most evident differences in maximum uptake rates, half-saturation coefficients, and uptake efficiencies relative to surface-to-volume ratios (Duarte 1995; Hein et al. 1995).

Effect of progressive nitrogen loading on macroalgal biomass—Increased nitrogen supply usually bolsters macroalgal standing crops. Strong evidence of these second-order effects of nutrient supply on macroalgal growth is provided by the reduction in macroalgal cover after sewage was diverted away from Kanehoe Bay (Smith et al. 1981) and by increased growth that followed manipulative additions of N and P in several nutrient-enrichment experiments (Twilley et al. 1985; Lapointe 1987; Short et al. 1990; Peckol et al. 1994; Taylor et al. 1995).

To quantify the relationship between land-derived nitrogen loadings and effects on macroalgae in the estuaries of Waquoit Bay, we measured the biomass of macroalgae in estuaries subject to different loading rates. We use the Waquoit

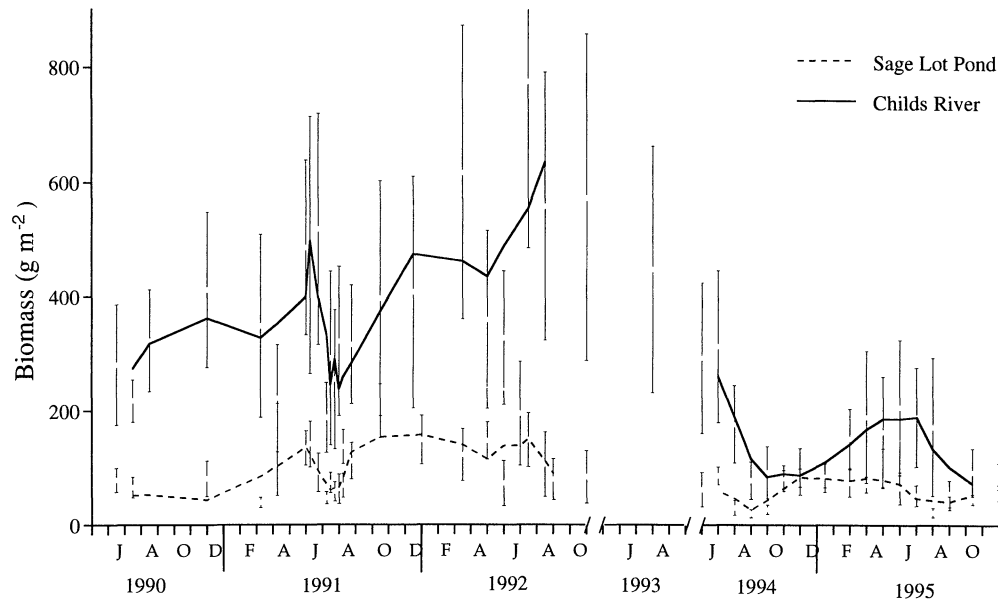


Fig. 2. Long-term time-course of macroalgal biomass in two estuaries of Waquoit Bay: Childs River (subject to high N loading rates), and Sage Lot Pond (subject to low N loading rates). The thick lines show the three-point running means for the two estuaries. The means for each date are shown as gaps in the vertical SE bars. Ten depth-stratified samples of benthic algae were used to calculate each mean. Funding available allowed only one sampling date in 1993. Data from Hersh (1996) and J. McClelland (unpubl. WBLMER data).

Bay estuaries subject to different nitrogen loading rates at present (Valiela et al. 1992) as a space-for-time substitution (Pickett 1991), which permits a view of changes brought about by increased rates of nitrogen loading across many years. We can also follow specific estuaries through several years as macroalgae bloom (data from 1990–1992, left side of Fig. 2).

Data on macroalgal biomass were collected from 10 stations in seven estuaries of Waquoit Bay from 1990 to 1995. In Fig. 2 we show data only for Childs River and Sage Lot Pond, estuaries that have the highest and lowest nitrogen-loading rates in the Waquoit Bay system ($>20\times$ difference, Valiela et al. 1997). Macroalgal biomasses in additional estuaries subject to intermediate loading rates fall between those shown in Fig. 2 (J. McClelland and D. Hersh unpubl. data).

Macroalgal biomass was consistently greater in Childs River, the estuary that received the largest nitrogen load, than in Sage Lot Pond, the estuary subject to the lowest nitrogen loading rate (Fig. 2). Macroalgal biomass in Childs River was variable, but increased ~ 2 fold from 1990 to 1993. Some degree of climatic control is evident from the multiyear changes in macroalgal biomass in Sage Lot Pond. The clear 6-fold difference between the two estuaries at any one time before 1993, however, can be attributed to differences in nitrogen availability on the basis of differences in physiological state of the fronds in the two estuaries (Peckol et al. 1994). Post-1993 data of Fig. 2 are discussed below in the section on bloom termination. The macroalgae growing in Childs River had higher rates of photosynthesis, uptake of dissolved nitrogen, and growth compared to macroalgae in Sage Lot Pond (Peckol et al. 1994). Childs River

macroalgae grow in the presence of higher concentrations of nitrogen (Valiela et al. 1992). The differences in physiological state of the macroalgae—largely prompted by the continued availability of higher nitrogen concentrations—result in the observed differences in standing crops seen in Fig. 2.

Stable isotopic data from Waquoit Bay provide evidence that nitrogen inputs from land are directly identifiable in macroalgae in the estuaries. The land-derived inputs come from wastewater, use of fertilizers, and atmospheric deposition. The bay provides a set of estuaries in which the proportion of wastewater nitrogen input varies from 0 to 60% of the total nitrogen load entering the specific estuaries. Wastewater bears a $\delta^{15}\text{N}$ signature distinct from those of atmospheric sources and fertilizer (Lajtha and Michener 1994). The $\delta^{15}\text{N}$ ratios of all producers in the Waquoit estuaries increase linearly by 3–4‰ as the wastewater contribution increases from 0 to 60% of the total nitrogen load (McClelland et al. in press). The increase in $\delta^{15}\text{N}$ ratios is likely due to the increased proportion of wastewater-derived nitrogen in groundwater entering the estuaries. These data indicate a direct link between land and estuary: estuarine producers contain the same isotopic mix of N as found in the nitrogen loaded from the adjoining watershed.

Effects of macroalgal blooms on other estuarine producers—Bottom-up controls—largely through nitrogen supply—differentially affect different producers. Duarte (1995), Taylor et al. (1995), and others have suggested that in waters where nutrient supply increases, seagrasses are replaced by macroalgae, which in turn can be replaced by phytoplankton as the dominant producers. Here we use data from different estuaries of Waquoit Bay to put together a quantitative de-

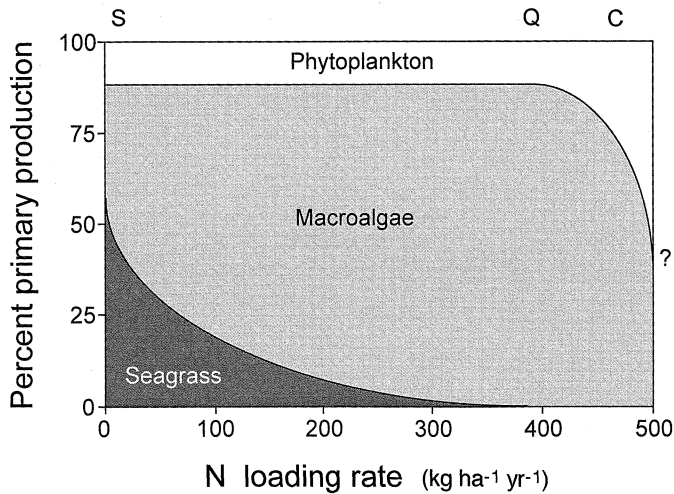


Fig. 3. Proportion of total net production that is carried out by phytoplankton, macroalgae, and eelgrass in three estuaries (Sage Lot Pond—S; Quashnet River—Q; Childs River—C) of Waquoit Bay that are subject to different nitrogen loading rates. The initials indicate the position of the three estuaries along the nitrogen loading axis. (Unpubl. WBLMER data.)

picture of how seagrasses might be replaced by macroalgae and phytoplankton as the dominant producers, under the influence of progressive nitrogen enrichment (Fig. 3). If we assume that these three estuaries can be used as a space-for-time substitution, Fig. 3 provides a quantified way to discuss how increases in nitrogen loads might alter the composition of major producer types in shallow temperate estuaries. Increases in nitrogen loading rates to the Waquoit estuaries shift the relative contribution of seagrasses, macroalgae, and phytoplankton to total estuarine production. The expansion of macroalgal dominance as nitrogen loading rate increases from left to right in Fig. 3 is, in essence, a depiction of a macroalgal bloom.

Seagrasses tend to dominate shallow temperate waters exposed to low nutrient inputs. We see this in Waquoit Bay estuaries: primary production by a seagrass (*Zostera marina*) is largest in magnitude in near-pristine estuaries with low rates of nitrogen loading (Fig. 3). Seagrasses thus characterize shallow waters in which other competitors are scarce because of low nutrient supply. Seagrasses dominate such waters by solving the problem of nutrient acquisition by taking up nutrients largely via their roots (Short and McRoy 1984; Pedersen and Borum 1992). In addition, seagrasses store substantial amounts of nitrogen in their thick leaves, stems, and rhizomes for translocation and use at critical times of year. As a result, net production in temperate-zone seagrasses is seldom nutrient limited; rather, seagrass growth is generally light limited (Dennison and Alberte 1985; Zimmerman et al. 1987). Growth of seagrasses might be nutrient limited in some oligotrophic or tropical waters (Powell et al. 1989; Short et al. 1990; Lapointe 1987), but in temperate latitudes light is probably more important as the limiting factor.

In contrast to seagrasses, growth of macroalgae and phytoplankton in shallow temperate estuaries tends to be nutrient limited rather than light limited. Macroalgae and phy-

toplankton make more effective use of lower levels of irradiation than seagrasses (Fig. 4 top center). Such differences in photosynthetic abilities are corroborated by the different depth distributions of these three groups of producers. For example, seagrasses grow on sediments at depths receiving 11% of incident light (Duarte 1991). Macroalgae, in contrast, can grow down at depths where only 0.12% (for species with thick fronds) and <0.003% (for thin macroalgae) of incident light penetrate (Markager and Sand-Jensen 1992). Such results might explain the presence of nearly monospecific beds of *Ulva*, a thin-bladed macroalga, in Venice Lagoon, a highly nitrogen-enriched coastal estuary with impressive phytoplankton standing crops (Sfriso et al. 1992).

Increased availability of nutrients therefore prompts growth of benthic macroalgae, of epiphytic macro- and microalgae on seagrass leaf surfaces, and of phytoplankton in shallow coastal waters. All these producers intercept photons, and increased biomass of these producers are detrimental to the already light-limited seagrasses. The seagrasses are unavoidably rooted to the bottom and hence subject to shading by the unattached benthic algae, epiphytes, and by phytoplankton (Twilley et al. 1985; Sand-Jensen and Borum 1991; Lapointe et al. 1994; Duarte 1995). Fast-growing macroalgae can take up nutrients at fast rates (Fig. 4, top right), can store nutrients (Fig. 4, bottom left), and can grow relatively well at low irradiances (Fig. 4, top center). As a result, even if the water is turbid, canopies of macroalgae are found on seafloors of nutrient-enriched shallow waters in sites such as those of Table 1.

Nutrient enrichment enhances already extant differences in tolerance of low light regimes (Fig. 4, top center) and in nitrogen uptake rates (Fig. 4, top right) between seagrasses and macroalgae. Increased nitrogen loads add to the physiological advantages of macroalgae over seagrasses and enhance the likelihood that macroalgae growing on the seafloor and on seagrass leaves will shade and eventually replace seagrasses as the dominant macroproducer. Progressive eutrophication of shallow waters generally increases benthic macroalgal production, and these alterations are soon followed by reduction of seagrass meadows (Valiela et al. 1992; Thybo-Christesen et al. 1993; Duarte 1995). Even at modest increases in nitrogen loadings from watersheds, the macroalgal bloom and replace seagrasses as the dominant producers (Fig. 3).

Burkholder et al. (1992) claimed that increased nitrate in water may even be toxic to seagrasses in North Carolina. If true in general, this provides yet another mechanism that further favors dominance of macroalgae at the expense of seagrasses.

Extensive losses of seagrass habitat have taken place as a result of eutrophication of many shallow temperate coastal areas (Nienhuis 1983; Cambridge and McComb 1984; Giesen et al. 1990; Zaitsev 1991; Valiela et al. 1992; Thybo-Christesen et al. 1993). The conversion from seagrass to macroalgal habitats is often considered a degradation of coastal environments because seagrass beds support a wide variety of consumers—some of commercial interest (Valiela et al. 1992)—and are nurseries for juveniles of many deeper water fish species. The same holds for the coral habitats that are

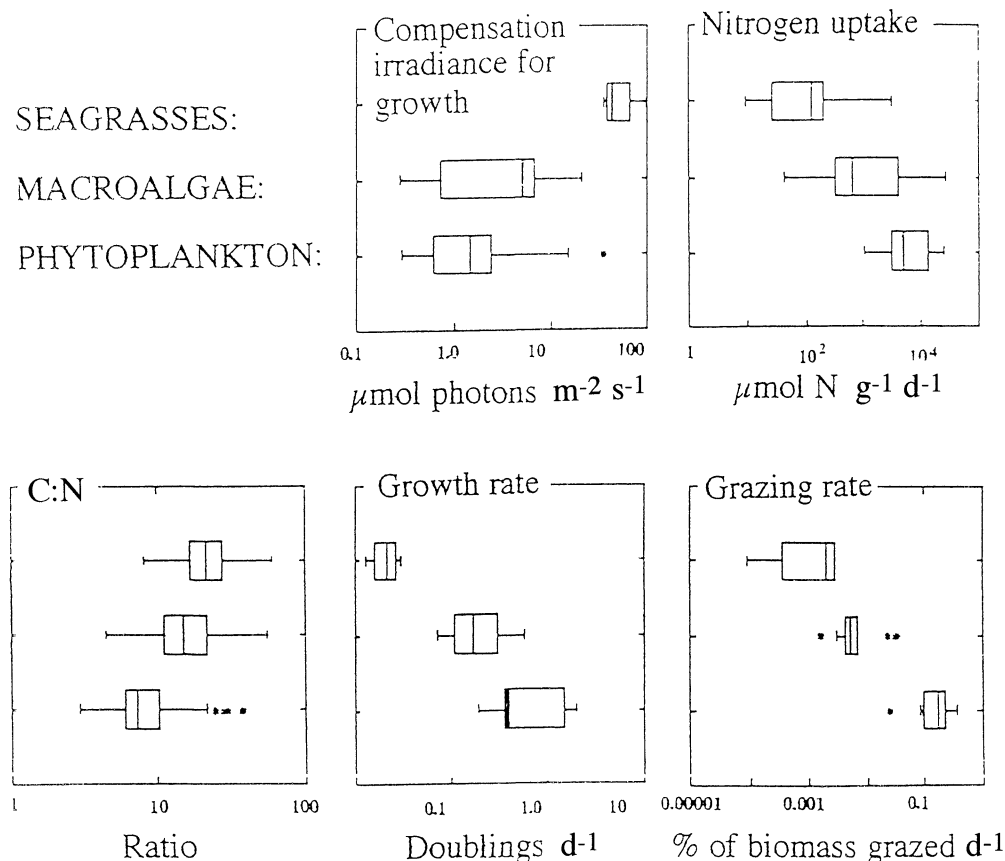


Fig. 4. Comparisons of values of various features of seagrasses, macroalgae, and phytoplankton that are involved in the response of these three groups of producers to eutrophication. The line within boxes is the median; the boxes span the 25th to the 75th quartiles; the horizontal lines extend to the 95% confidence limits, and the dots show outliers beyond the 95% confidence limits. (Adapted from Duarte 1995.)

taken over by nuisance seaweeds in tropical regions (Bell 1992).

To summarize, even relatively small increases in nitrogen loading to shallow estuaries favor blooms of macroalgae. Increased biomass of benthic and epiphytic macroalgae shades seagrasses and prompts significant changes in the relative production by the different groups of producers, mainly by replacement of seagrass beds with macroalgal mats (Fig. 3). The alteration of relative contribution by different types of primary producers in shallow estuaries, however, is unlikely to be a simple function of nitrogen loading rate alone. Below we discuss two complicating factors—presence of fringing salt marsh and differences in water residence time—that may significantly modify the response of macrophytes to nitrogen loading from watersheds.

Interaction among loading rate, macroalgal blooms, and salt-marsh fringe habitats—In many coastal areas there is a fringe of wetlands interposed between land and the open estuary. In temperate latitudes, these fringes are salt marshes, largely covered by halophytic grasses. Below we review results from Waquoit Bay that suggest that fringing salt marshes intercept a significant fraction of land-derived nitrogen,

thereby to some extent lowering the nitrogen loads to receiving estuarine waters.

If the relationship between macroalgal biomass and nitrogen load from watersheds was straightforward, we might simply find a positive relationship between these two variables, in which macroalgal biomass was larger in estuaries subject to larger nitrogen loads. Data from five different estuaries of the bay subject to different rates of nitrogen loading do show that macroalgal biomass increases as nitrogen load to the estuary increases (Fig. 5, top left). We might also expect that, in view of the postulated effect of macroalgae on eelgrass, there is a negative relation of loading and eelgrass biomass, and we in fact do find that eelgrass biomass decreases as loading rate increases (Fig. 5, top right). The points around the regression line, however, are considerably scattered. To see whether we could account for some of the scatter, we turned to an examination of the area of fringing salt marsh in each estuary.

Different estuaries of Waquoit Bay have different areas of fringing salt marsh interposed between land (the source of allochthonous nitrogen) and the aquatic system where macrophytes grow. As the area of salt marsh increases, the biomass of eelgrass increases, and macroalgal abundance de-

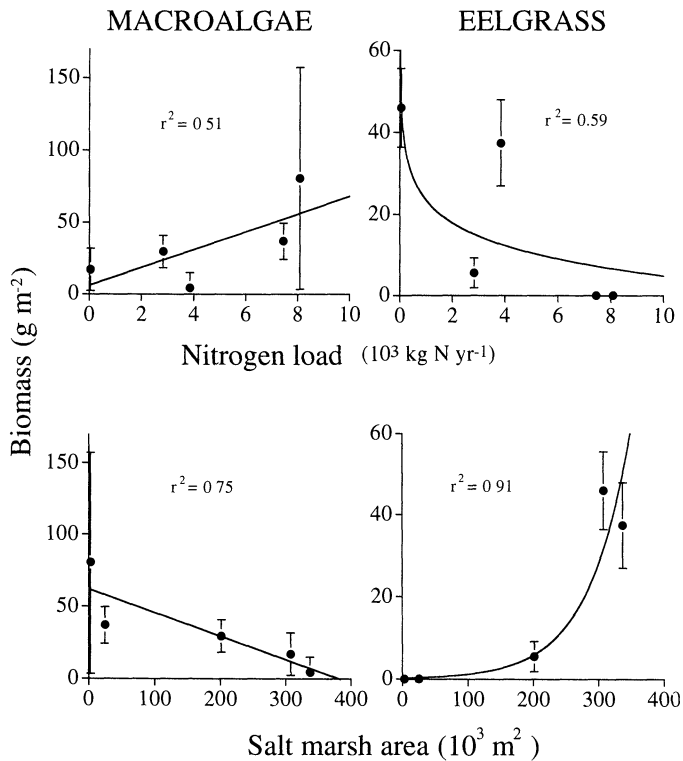


Fig. 5. Top. Relationship of macroalgal and eelgrass biomass to rate of nitrogen loading received by different estuaries of Waquoit Bay. Bottom. Relationship of macroalgal and eelgrass biomass to area of fringing salt marsh interposed between land and water in estuaries of the bay. Regression lines calculated from the means, rather than using the individual measurements, to avoid the issue of pseudoreplication. (Adapted from Lyons et al. 1995 and unpubl. WBLMER data.)

creases (Fig. 5, bottom panels). Moreover, the scatter of the points in the graph of eelgrass and macroalgal vs. salt-marsh area is notably less than the scatter in the graph in which nitrogen load was plotted on the x-axis (cf. values of r , Fig. 5, top panels). This result suggests that perhaps the effects of nitrogen loads from land (which ultimately have to drive the changes in macroalgae and eelgrass) are mediated by some area-dependent process in salt marshes.

We hypothesize that as groundwater percolates through the aquifer, seeps into springs, and flows over the salt-marsh surface or through tidal creeks, concentrations of land-derived nitrogen are decreased by some process. That process may be denitrification, which is active in salt marshes (Valiela and Teal 1979). Denitrification in salt marshes could reduce the amount of land-derived nitrate (the principal nitrogen species transported in groundwater: Valiela et al. 1997) that enters receiving estuarine waters. Alternatively, there could be increased storage of land-derived nitrogen within salt-marsh sediments, as occurs in experimentally fertilized salt-marsh plots (Valiela et al. 1973).

It is apparent that the coupling of land to sea via nitrogen transport, and its consequent role in creation and maintenance of macroalgal blooms, is not straightforward. Rather, for any given rate of watershed-derived nitrogen loading, intervening units of coastal landscape such as salt marshes

modify the influence of nitrogen loadings generated by the land-cover mosaic on aquatic macrophytes. The data from Waquoit estuaries suggest that more eelgrass biomass and habitat area remain and less macroalgae are present in estuaries with larger areas of fringing salt marsh (Valiela et al. unpubl. data). Thus, the spatial mosaic of adjoining habitats matters: intensity of macroalgal blooms depends not only on the rate at which nutrients are delivered from land, but also on the extent of fringing salt-marsh habitat interposed between watershed and receiving estuary.

Interaction of water residence time and responses to N loading—Differences in residence time of water within estuaries might also modify the responses of different producers—including macroalgae—in estuaries. Duarte's (1995) comparison of nitrogen uptake in a variety of different species of macro- and microalgae (Fig. 4, top right) shows that uptake by phytoplankton is faster than uptake by macroalgae. Hein et al. (1995) summarized differences in uptake kinetics of nitrate and ammonium in macro- and microalgae in more detail. Macroalgae generally have lower V_{max} , higher K_m , and lower α than microalgae (Fig. 1, left) and are therefore poorer at harvesting nitrogen from water than microalgae, regardless of the concentration of nitrogen in the water. Given this result, it seems therefore odd that the proportion of primary production in Waquoit Bay estuaries that is carried out by phytoplankton remains relatively low and is relatively constant through most of the nitrogen loading range (Fig. 3). We have shown in batch enrichment experiments that net growth of phytoplankton in Waquoit estuaries is nitrogen limited (Tomasky et al. in prep.), so we expected that as nitrogen load increased, phytoplankton would have an advantage at making use of any added nitrogen and would increasingly proliferate. Nonetheless, the data of Fig. 3 suggest that it is only at higher rates of nitrogen loading that phytoplankton begin to replace macroalgae as the dominant producer.

One explanation for the unexpected slow response by phytoplankton in Waquoit estuaries to increased nitrogen loads may be that the cells lack sufficient time to grow within the estuaries. Water resides in the Waquoit estuaries for relatively brief periods of time (27–64 h, T. Isaji unpubl. data). The range of water residence times in coastal water bodies is a few days to months (Nixon et al. 1996). Phytoplankton divide ~ 0.5 –3 times d^{-1} (Fig. 4, bottom center), and the division rate in part depends on the supply of limiting nutrients. Thus, at low nitrogen loads, the intervals of time that we calculate as residence times for water in Waquoit estuaries may be so short that there is not enough time to allow the cell divisions needed to produce a well-developed phytoplankton population response to in situ nitrogen concentrations. Perhaps we can conceive of these estuaries as chemostats in which flow rates are set so fast that cell growth just barely compensates for fast flow rates.

Increased nitrogen loads, not surprisingly, lead to higher nitrogen content of the water (Valiela et al. 1992). Phytoplankton division rates depend on the concentration of limiting substrate, so we might expect that in estuaries subject to high nutrient loads, nutrient supply may be high enough to create faster cell division. It might be that in highly loaded

estuaries, phytoplankton could divide more than once a day, and these division rates could create higher cell densities. From this argument, and the data of Fig. 3, we hypothesize that the higher cell density of the more rapidly dividing phytoplankton could thus shade and perhaps eliminate macroalgae from estuaries receiving relatively high nitrogen loads from land.

We conjecture that as nitrogen loads increase, nutrient concentrations rise, nitrogen uptake by phytoplankton increases, and cells divide faster. If the division rates do increase sufficiently, it might be that even within the brief time available within estuaries with relatively short water residence times, densities of phytoplankton might become higher. This effect might be a result of increases in V_{\max} as well as of higher K_m . Under this scenario, phytoplankton may therefore bloom where nitrogen loads have become high enough so that nutrient concentrations become relatively high. Peaks in phytoplankton abundance could be due to chronic increases across years or within-year seasonal peaks (see Fig. 8). In such nitrogen-enriched situations, phytoplankton biomass may increase sufficiently to shade and eventually replace bottom-dwelling macroalgae. Macroalgae might be unable to survive the lowered light intensities, and phytoplankton then become the dominant producers. The blooms of phytoplankton thus could produce the seasonal troughs in macroalgal biomass, as well as the multiyear reduction visible in Waquoit Bay between 1992 and 1994 (Fig. 2) or the biomass collapses seen in 1987 or 1991 in Venice Lagoon (Sfriso et al. 1992).

Of course, not all shallow temperate estuaries have the same water residence times, and not all shallow estuaries have residence times as brief as those of Waquoit estuaries (Nixon et al. 1996). We should expand our model of the relationship of nitrogen load to dominance of different estuarine producers to include the modifying effect of water residence time (Fig. 6). Longer residence times may reconfigure the transition depicted in Fig. 3 and Fig. 6 (top), to the hypothetical situation of Fig. 6 (bottom). In shallow estuaries where residence times may be weeks or even months, such as in Laguna Madre, Texas, or Sarasota Bay, Florida, for instance, we might predict that phytoplankton—because of their advantage in nitrogen uptake kinetics and sufficient time to grow—could readily respond to even small increases in nitrogen loading rates. In such slower-moving waters, we predict that phytoplankton may become the dominant producers at much lower rates of N loading. Interception of light by the increased phytoplankton might shade and exclude macroalgae much earlier in the process of eutrophication, at much lower nitrogen loading rates (Fig. 6, bottom), than is the case in Waquoit Bay and other sites with shorter residence times. We might also predict—because of the nitrogen kinetics of seagrasses shown in Fig. 4 (top right)—that shading would lead to decline in seagrass contributions at even lower nitrogen loading rates than would be the case in estuaries with shorter water residence times (Fig. 6).

The modifying effect of presence of fringing salt marsh might have simpler consequences than those of water residence time. It might be feasible to merely consider that the presence of a given area of salt marsh lowers the land-derived nitrogen load by a certain factor, so that the effect of

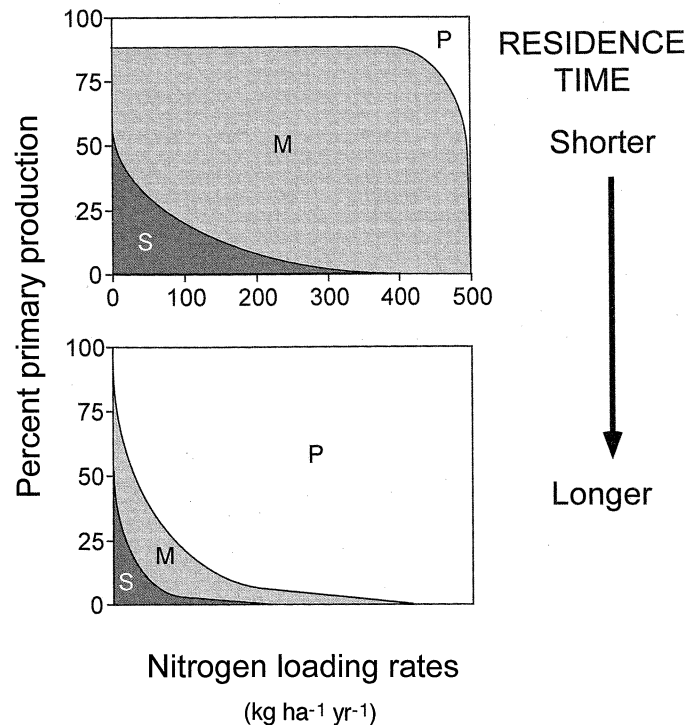


Fig. 6. Conceptual scheme showing hypothetical pattern of change in the relative contribution by three major groups of producers (phytoplankton—P; macroalgae—M; eelgrass—S) in response to changes in nitrogen loading rate in shallow temperate estuaries with shorter and longer water residence times.

fringe marsh might be considered merely an adjustment toward the left along the x-axis of the conceptual loading-residence time models diagrammed in Fig. 6.

Top-down controls of macroalgal blooms

In addition to the bottom-up controls on macroalgal biomass mentioned so far, reduced top-down effects could be involved in macroalgal blooms. Differential susceptibility of seagrasses, macroalgae, and phytoplankton to consumption (Fig. 4, bottom right) would suggest that grazer activity, where important, could favor dominance of relatively unpalatable macrophytes (Hay and Fenical 1988). Presumably, from Fig. 4 (bottom right) we can expect that, all else being equal, differential grazing pressure could prevent macroalgal takeovers and sustain a seagrass-dominated producer assemblage. The differential effects of grazing have been documented, for example, in rocky tidal habitats and account for the dominance of a tough, unpalatable macroalga, irish moss (*Chondrus crispus*), in rocky shore habitats exposed to grazers (Lubchenco 1978).

The palatability of different kinds of macroalgae to herbivores is a function of toughness, feeding deterrents, and cues of nutritional value. Phytoplankton and most fast-growing green macroalgae lack the chemical protection often found in vascular plants and certain slower growing red and brown macroalgae (Hay and Fenical 1988). Phytoplankton may be nutritionally more desirable to grazers than macro-

algae, and certainly than seagrasses; hence grazing rates by herbivores may vary accordingly (Fig. 4, bottom right). If we take C:N as a rough index of nutritive quality and accept that nitrogen is often limiting for herbivores (Mattson 1980), the ranking of the three producer groups as potential foods for grazers is phytoplankton > macroalgae > seagrasses (Fig. 4, bottom left). Seagrasses, being poor foods, seem unlikely to be exposed to strong grazing pressure. Zimmerman et al. (1987) concluded that grazers much prefer macroalgae growing as epiphytes (including many fast-growing greens) on eelgrass than the eelgrass itself.

Differences in herbivory by preferential consumption of the major producer groups may change the array of producers present in an estuary. As grazers selectively feed on preferred macroalgae, they limit abundance of the palatable groups of producers. Grazers of phytoplankton and macroalgae therefore may be instrumental in maintaining dominance of seagrasses in waters subject only to low rates of nutrient loading; in such situations, grazing pressure and competitive advantages among producers determine what producers dominate the canopies. The situation may differ where nutrient loading increases because food quality, grazer abundance, and competitive advantages are bound to change under increased nutrient inputs.

To evaluate the relative magnitude of, and possible interaction between control by benthic grazers and by nitrogen loading rates, we made model calculations of potential control of macroalgal biomass by amphipod and isopod herbivores in estuaries of Waquoit Bay subject to different rates of land-derived nitrogen inputs (Hauxwell et al. in press). For the sake of brevity, here we only report results from the estuaries with the highest and lowest nitrogen loading rates. The model calculations are based on measurements that show that increased nitrogen loading rates have the following effects: increased macroalgal growth rates (Peckol et al. 1994) and biomass (Hersh 1996, and Fig. 7, top); increased feeding rates by herbivores fed on macroalgae from nitrogen-loaded estuaries; and decreased abundance of herbivorous amphipods and isopods (Fig. 7, middle). To assess the potential for top-down control of macroalgal biomass, we calculated the percent of macroalgal growth that could be consumed per day by the population of herbivores present in each of the estuaries (Fig. 7, bottom). This statistic would show whether the rate of consumption of macroalgae by herbivores would or would not be larger than the in situ growth rate by the algae. We can judge whether grazers are likely to be effective controls in Fig. 7 (bottom) by seeing whether points lie above or below the dashed line that shows the position where growth by macroalgae is equal to consumption by herbivores. Points that lie above the dashed line show when grazers can restrict biomass of the macroalgae; points that lie below the dashed line show instances in which macroalgal growth is larger than grazer consumption. Potential control of macroalgae by grazers is likely only in the estuary subject to low rates of N loading, and only during summer (Fig. 7, bottom).

The relative effectiveness of grazers as controls has been thought to depend largely on chemical cues that determine herbivore-macroalgal relationships. WBLMER results point out the potential importance of other top-down and bot-

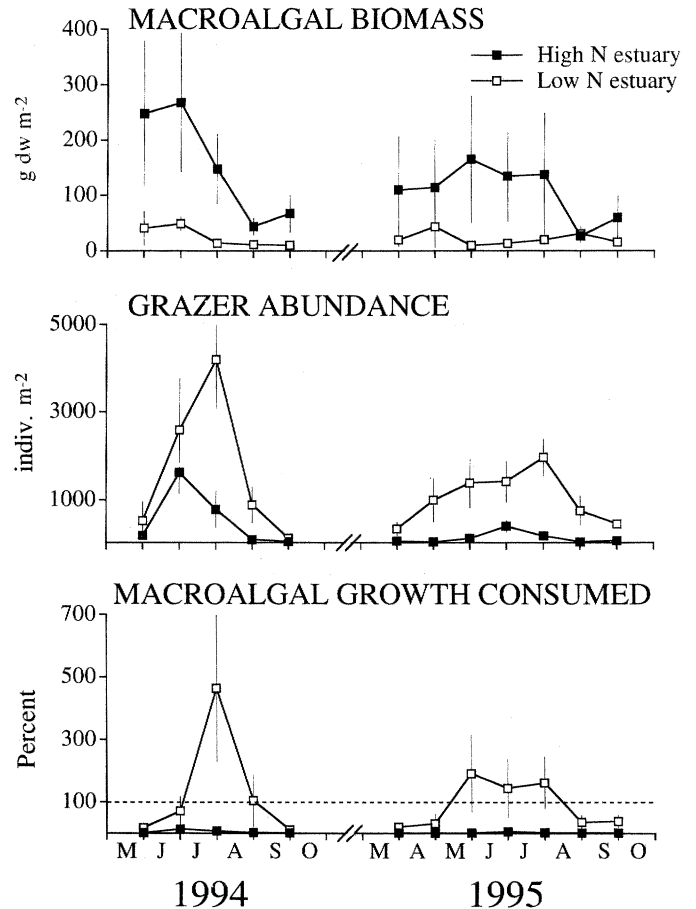


Fig. 7. Top. Biomass of the macroalga *Cladophora vagabunda* in estuaries of Waquoit Bay subject to high (Childs River) and low (Sage Lot Pond) rates of nitrogen loading (*C. vagabunda* comprises 40–80% of total macroalgal biomass in these estuaries). Middle. Abundance of herbivorous invertebrates, including six spp. of amphipods, and three spp. of isopods. Bottom. Potential grazer impact, estimated by calculating total consumption of *C. vagabunda* by extant grazers relative to total *C. vagabunda* growth in the same two estuaries. Dashed line shows where consumption by the herbivores equals macroalgal growth. Data in top and middle panels are means \pm standard errors of 10 depth-stratified benthic samples taken from each estuary on each date. Data in bottom panel are means \pm propagated standard errors. (Summarized from Hauxwell et al. in press).

tom-up control mechanisms in producers living in oligotrophic to eutrophic gradients: density of herbivores and biomass and growth rates of macroalgae. Waquoit estuaries subject to higher nitrogen loads harbor lower (avg $\frac{1}{4}\times$) densities of herbivores (Fig. 7, middle). These lower densities are partially responsible for the lower calculated impact of the herbivores on macroalgal biomass. The lowered density of grazers might be caused by more frequent hypoxic conditions created by higher rates of nitrogen loading (D'Avanzo and Kremer 1994). Macroalgae in Waquoit estuaries subject to higher loads also support faster rates of growth (avg $2\times$) of higher standing stocks (avg $3\times$) of macroalgae (Peckol et al. 1994). The enhanced growth effect was even larger than the lower grazer density effect, and at higher rates of nitrogen loading, fast-growing seaweeds may overcome controls

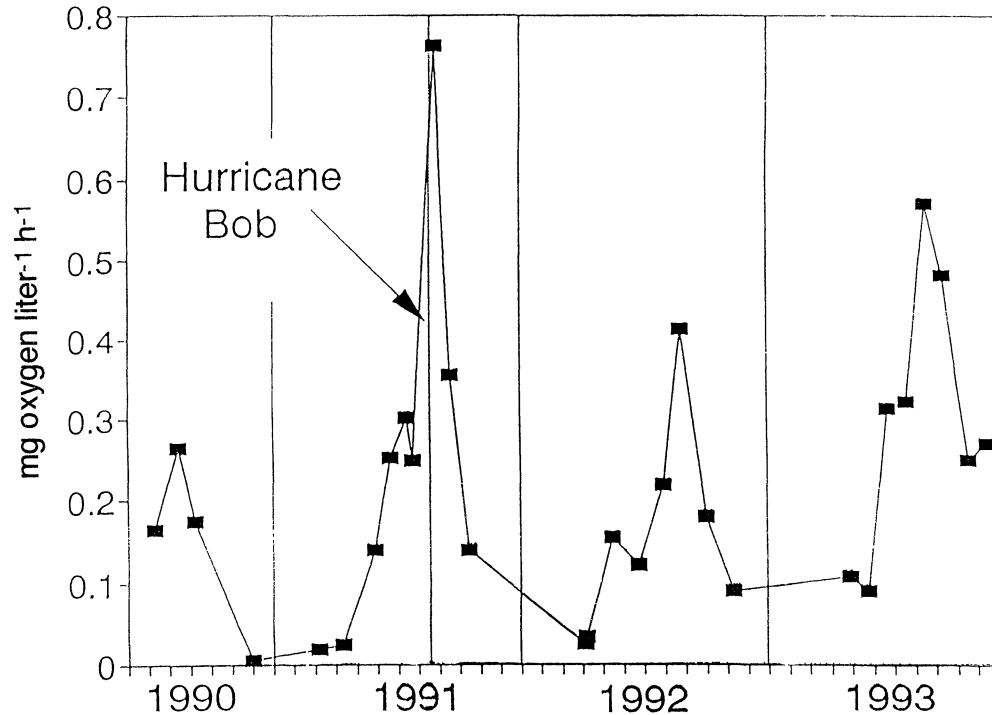


Fig. 8. Multiyear time-course of gross phytoplankton production, average of seven stations in Waquoit Bay, obtained by oxygen microelectrodes. The seasonal and multiyear trends are reasonably regular and suggest a slow increase over several years. There is one extraordinarily high outlier in August 1991 caused by passage of Hurricane Bob; the events and mechanisms underlying that disturbance are discussed elsewhere (Valiela et al. 1996).

by grazers. In such situations, shallow estuaries may continue to be dominated by macroalgal blooms, which replace seagrasses or other producers.

The potential predicted effect of grazers on macroalgal blooms have strong temporal patterns. Cold temperatures restrict abundance of herbivores during winter and spring (Fig. 7, middle), so that macroalgal standing crops increase during the cold seasons (Fig. 2). Predicted effects of grazers are greatest in summer (Fig. 7, bottom), the time when herbivores are most abundant and active (Fig. 7, middle). During late summer, it may be that predation by fish lowers density of the herbivorous amphipods and isopods, which are a major prey of fish (Wiltse et al. 1984). The fish may therefore indirectly release macroalgae from consumption pressure late in summer. We therefore speculate that seasonal effects of grazers might be a result of fairly complicated and still undefined relationships among temperature, macroalgae-animal, and animal-animal interactions.

Termination of macroalgal blooms

Many documented blooms of macroalgae have ended or suffered unexplained collapses after increases in nutrient loads through a period of years. These collapses include *Cladophora* in Moriches Bay, New York (E. Cosper pers. comm.), and in the Peel-Harvey estuary, Australia (Lavery et al. 1991), *Ulva* in certain areas of Venice Lagoon (Sfriso et al. 1992; A. Zittelli and M. Cardinaletti pers. comm), and

Cladophora and *Enteromorpha* in bays in the Baltic (Baden et al. 1990), among others.

The mechanisms involved in termination or collapses of macroalgal blooms are not well understood. There may be several mechanisms—grazing, nitrate toxicity, physiological responses, all previously mentioned—that might be responsible for ending macroalgal blooms. The simplest explanation might be what we articulated in relation to the conceptual loading/residence time model—increasing nutrient supply stimulates phytoplankton growth and this in turn increases light interception in the water column and shading of macrophytes below.

We see interannual evidence consistent with such an explanation in Waquoit Bay data. The interpretation is speculative and by no means excludes other explanations; we offer it here mainly as a way to prompt further testing of the supposed relationships.

First, there were increases in phytoplankton abundance and activity measured during multiyear studies in different parts of the bay (Fig. 8). The multiyear increase is evident in the increasing peaks (late summer) and troughs (late winter) in gross phytoplankton production. Second, macroalgae became less abundant in the most nitrogen-enriched estuary after 1992, and the reductions continued through 1995 (Fig. 2). The losses of macroalgal biomass might have resulted from increased phytoplankton biomass and reduced light supply to the macroalgae below. Third, after 1992 we begin to see, for the first time, clear seasonal patterns in the much

lowered macroalgal biomass. Before 1992, at the peak of the macroalgal bloom, processes that impose seasonality may have been simply overwhelmed by fast macroalgal growth. Circumstantial evidence of the possible interaction of phytoplankton and macroalgal crops is that the troughs of the macroalgal biomass coincide nicely with the annual peaks in phytoplankton (cf. July–August data, 1994–1995 in Figs. 2 and 8). After 1993, winter macroalgal biomass remained low, in striking contrast with standing crops at other times of year.

Ecosystem consequences of macroalgal blooms

In estuaries subject to increased nutrient enrichment the dominance of nuisance seaweeds engenders a series of other ecosystem-level changes. The changes result because of the differences between bloom macroalgae and the producers that they replace and because bloom macroalgae affect other components of ecosystems once macroalgal canopies are established.

Macroalgal blooms uncouple biogeochemical cycles in sediments from those in water columns to a significant degree. Under higher rates of nutrient loading, macroalgae that take nutrients up from water replace plants that “mine” nutrients from sediments using roots. Macroalgal canopies over the sediment–water interface, moreover, partially intercept “old” nutrients released by regeneration from sediments. This interception of ammonium regenerated from sediments is quantitatively important during the day and lower at night; this suggests that nutrient uptake might be coupled to photosynthetic activity in these seaweeds (Bierzychudek et al. 1993; D’Avanzo et al. 1996). In any case, the presence of macroalgal canopies seems likely to sequester nutrients that otherwise might have entered the water column and may enhance recycling of nutrients near the sediment surface.

The amounts of carbon and nutrients stored as seaweed biomass are certainly important at the level of an ecosystem. The magnitude of macroalgal biomass can be impressive: in Venice Lagoon the biomass of *Ulva* may exceed 10 kg wet wt m⁻² (Maroli et al. 1993). It has even been argued that the carbon stores in seaweeds may be large enough to account for a reasonable fraction of the carbon “missing” at the global level (Smith 1981); this may be stretching the point but suggests that macroalgal blooms in coastal areas can be large enough to create significant biogeochemical changes. In Waquoit Bay, for example, the stored nitrogen is of the same magnitude as the annual nitrogen load delivered from the watershed (Hersh 1996). The partial interception of regenerated nutrients in macroalgal canopies is large enough to maintain lowered nutrient concentrations in the overlying water (Hersh 1996). Seaweeds store large amounts of nutrients (and carbon) in their fronds. Because of this storage, and because of the interception of old nutrients, water quality in seaweed-dominated shallow waters seems considerably better than would be the case in a phytoplankton-dominated water body subject to the same rate of nitrogen loading.

Uptake of nutrients by macroalgae varies through the year, and the changes might set the seasonal patterns of activity

of the other producers. Macroalgae, for as yet unknown reasons, have considerably lowered activity in late summer (Peckol et al. 1994). During late summer, therefore, we surmise that greater amounts of old nutrients from sediments manage to cross the overlying macroalgal canopy and mix upward in the water column. We suspect that this is the mechanism that might be responsible for the prominent late-summer seasonal peak in phytoplankton seen in Waquoit Bay (Tomasky et al. in prep.) and in many other shallow bays and estuaries (Sfriso et al. 1992). The late-summer peak in phytoplankton is in strong contrast with the more common late-winter or early-spring bloom characteristic of deeper coastal waters (Valiela 1995). This is one more example of nutrient-mediated interaction between macroalgal blooms and other components of estuarine ecosystems.

Faunas of consumers associated with macroalgal-dominated systems differ widely from those of more pristine systems. As already mentioned, bloom macroalgae are, in broad terms, nutritionally better than seagrasses and vascular plants in general, and their defensive chemical armories might, as a whole, be somewhat less developed than those of vascular plants. We speculate that carbon fixed by macroalgae might therefore move through trophic webs faster than carbon fixed by seagrasses or vascular plants (Alber and Valiela 1994a,b,c, 1995), with corresponding faster nutrient regeneration.

Seaweeds release surprisingly large amounts of dissolved organic matter (Khailov and Burlakava 1969). Apparently, these producers frequently fix carbon in excess of metabolic needs for growth and exude the unused DOC. Exudation from live seagrasses may reach 2% of carbon fixation (Velimirov 1986), while macroalgal fronds may release 39% of gross production; after senescence most of the remaining fixed carbon is released (Buchsbaum et al. 1991; Alber and Valiela 1994a). The change from seagrass- to macroalgal-dominated canopies in response to increased nutrient loads thus is likely to augment the delivery of labile carbon compounds to estuarine waters. The released DOC may be used by microbes, and substantial quantities may enter the microbial food web (Alber and Valiela 1994a). Microbes cause aggregation of the DOC into amorphous particles that resemble marine snow in appearance, and the aggregates may be ingested and assimilated by larger animals (Alber and Valiela 1994b, 1995). The released DOC may be sufficient to increase biological oxygen demand and is perhaps involved in the increased frequency of anoxic events often found in enriched waters (D’Avanzo and Kremer 1994). These anoxic events may be responsible (together with the changes in producer species) for the marked changes in faunas that often accompany macroalgal blooms in eutrophic estuaries (Norkko and Bonsdorff 1996) and that, as we have argued above, alter the ability of consumers to carry out top-down controls of macroalgae. The shift from seagrass to macroalgal systems is therefore accompanied by a series of indirect effects that are likely to propagate throughout entire trophic webs.

Vertical profiles of oxygen in shallow waters dominated by seaweeds are largely determined by photosynthetic and respiratory activity by the macroalgal canopy (D’Avanzo and Kremer 1994). The activity of the canopy causes the bottom waters to be oxic during sunny days and hypoxic at

night. This has several critical consequences. One result is that the intercanopy water is subject to daily wide excursions of redox potential; these changes could provide ideal circumstances many types of microbes. Activity of denitrifiers, for example, is enhanced by macroalgal canopies containing interdigitated small parcels of oxic and anoxic water, and the mix of conditions changes from day to night. The mix of conditions provides a way for nitrate to be made available to bacteria within anoxic waters. In addition, the macroalgae release DOM, which powers denitrification of the nitrate. Coupled denitrification could be favored in such circumstances. It is likely that the activity of the macroalgal canopy in daily alternation of oxic and hypoxic conditions of the near-bottom water also causes important changes to the carbon, sulfur, and phosphorus cycles. The activity of the macroalgal biomass, the large storage on materials in algal biomass, and the position of the canopy directly over sediments therefore must have major consequences for the biogeochemistry of enriched estuarine ecosystems.

Conclusions

Macroalgal blooms are generated by nutrient loading to shallow waters where the bottom is within the photic zone. The effects of nutrients loads on producer mosaics that include macroalgae are modified by presence of fringing wetlands or by water residence times. Grazers may also modify the loading-producer interaction, in particular at lower rates of nutrient loading.

Macroalgal blooms have fundamental and pervasive effects seen in the physiology of the macroalgae themselves, changes in the relative contribution by different producers to production of coastal habitats, alterations to microbial and macrofaunal food webs, and alteration of redox conditions that in turn alter biogeochemical transformations of N, C, S, and P of nitrogen-enriched coastal ecosystems. Eutrophication of shallow coastal environments is occurring in most shorelines of the world. The intense local effects of the macroalgal blooms—one symptom of eutrophication—that we have described above are therefore taking place in innumerable sites across the globe. In a real sense, it can be argued that the current proliferation of macroalgal blooms upscales by addition into a major biotic change at a global scale.

Although the paragraphs above have focused on basic issues, it should be clear that presence of blooms of nuisance seaweeds is increasingly more common. We will need much knowledge about the controls of macroalgal-related process to inform the ever-increasing need to make management decisions. New knowledge will be needed for either of two general approaches to solve the problem of macroalgal blooms: to intercept nutrient sources on land before nitrogen enters receiving estuaries, or to hasten loss of nitrogen by harvest of macroalgal biomass or by increased flushing of water through the estuary.

Interception of nutrient sources may be the most effective because it simply reduces entry from known sources into the watersheds and estuaries. To propose reasonable preemptory interception as a solution to macroalgal bloom problems, however, we will need much environmental information as

to nutrient sources on land, relative losses during transport and recycling in the estuary, relative storage in seaweed biomass, and some notion of the likelihood and time lags needed before macroalgae decline and seagrass recovers.

Removal from estuaries by increased flushing or harvest of biomass seems more problematic. If we propose to dredge to hasten water renewal rates, we need to know much more about nutrient uptake rates and about the relative importance of internal regeneration within the estuary, as well as hydrography and geological conditions. Some of the required knowledge is available, much is not. To propose collecting macroalgal biomass as a means to remove nutrients, we will need to find effective, affordable techniques, estimate effective harvest rates, and devise a suitable harvest regime, and we will need to explore the inevitable consequent effects on water quality.

In addition to the significant need for environmental information, there are likely to be many social and economic constraints that will affect decisions. We are poised at a cusp in this field: we have a solid foundation of observation, experiment, and theory, and some synthesis has been achieved. The growing occurrence of macroalgal blooms has forced renewed attention on finding practical solutions. Progress in basic knowledge has raised many good questions that will simultaneously test the synthesis and advance the field, but we will need to provide much more information to understand the basics, as well as to address coastal zone management issues.

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