

## CHAPTER EIGHT

# ESTUARINE BENTHIC ALGAE

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### 8.1 INTRODUCTION

Benthic algae play a key role in regulating carbon and nutrient turnover and in supporting food webs in shallow-water coastal environments. They are especially important in the wide diversity of estuarine habitats found worldwide. Benthic producers are generally divided into macroalgae and microalgae (also known as *microphytobenthos*). Macroalgae contribute between 4.8% and 5.9% of the total marine net primary productivity (calculated from Duarte and Cebrian, 1996). Although lower than total oceanic (81.1%) and coastal (8.5%) phytoplankton, the local macroalgal productivity (per square meter) is comparable to some of the most productive terrestrial ecosystems such as tropical forests. Benthic microalgae often form visible brown or green mats on the sediment surface. These mats are thin, as the microalgae are confined to the photic zone (1–3 mm) of the sediment, yet the density of algae and other microorganisms is usually high, often 100–1000 times higher than in the water column. In shallow estuaries, benthic microalgae normally account for 20–50% of the total primary production (Underwood and Kromkamp, 1999). In this chapter, we discuss the benthic algal communities that inhabit the soft-bottom (mud/sandflat, seagrass bed, marsh), hard-bottom (rocky intertidal, shallow subtidal), and coral reef habitats that lie within estuarine ecosystems.

### 8.2 TAXONOMY

All algae at some stage of their life cycles are unicellular (usually as reproductive stages such as spores or zygotes), and they are viewed as “primitive” photosynthetic organisms because of their relatively simple construction and their long evolutionary history. Prokaryotic “blue-green algae,” or cyanobacteria, are the oldest group, with fossils dating back almost 3000 million years. These first algal fossil remains include stromatolites, which are structures formed in shallow tropical waters when cyanobacterial mats accrete layers by trapping, binding, and cementing sediment grains. Photosynthesis by these early primary producers was responsible for much of the oxygen that eventually built up to the levels that occur today. Evolution of eukaryotic algae occurred much later, about 700–800 million years ago, although this date is difficult to determine more exactly as most groups were composed of soft tissue that would not have been preserved reliably in the fossil record.

Marine macroalgae or “seaweeds” are a functional rather than phylogenetic group comprising members from two kingdoms and at least four major phyla (divisions). There is a wide variation in algal classification schemes among systematists, but the traditional divisions for macroalgae are *Cyanobacteria* (prokaryotic blue-green algae, sometimes termed

*Cyanophyta*), *Chlorophyta* (green algae), *Phaeophyta* (brown algae), and *Rhodophyta* (red algae) (Littler and Littler, 2000).

Marine green algae range from cold temperate to tropical waters. Green algae reach highest diversity and abundance in tropical regions, with several families such as the *Caulerpaceae* and *Udoteaceae* being very abundant in coral reef and associated seagrass habitats. Often overlooked, but very abundant, are filamentous green algae that bore into coral skeleton and proliferate widely, with high rates of productivity (Littler and Littler, 1988). Opportunistic green algae form nuisance blooms in estuaries worldwide; in eutrophic systems, they form almost monospecific mats of extremely high biomass.

Brown algae are almost exclusively marine and are dominant in temperate waters where hard-bottomed habitats occur. Some genera of structurally robust forms such as *Laminaria* and *Sargassum* dominate in very high energy zones. Kelps are "ecoengineers" that form extensive forests in coastal areas where nutrients are supplied by upwelling. Other groups of fast growing and more opportunistic genera such as *Dictyota* may form seasonal blooms in tropical and subtropical regions.

The majority of seaweed species is in the *Rhodophyta*. At present, the approximately 4000 named species of red algae exceed the number of species in all other groups combined (Lee, 1999). Although red algae are extremely speciose in tropical and subtropical regions, their biomass is low relative to that in temperate areas. The most common forms of red algae in the tropics include crustose members of the family *Corallinaceae* as well as a high diversity of small, less obvious filamentous species that comprise algal turfs. However, there are some genera of upright and branching calcifying forms such as *Galaxaura* and branching or flattened foliose red algae in the genera *Laurencia*, *Asparagopsis*, and *Halymenia* that can be quite conspicuous and abundant on reefs under certain conditions. The highest biomass of red algae is found in temperate and boreal regions. Some large fleshy members of the *Rhodophyta* with descriptive names such as "Turkish towels" blanket rocky intertidal and subtidal regions. Other genera, such as *Gracilaria*, form blooms in estuaries and lagoons.

In most cases, the benthic microalgal community in estuarine habitats is a mixture of several taxonomical groups, although blooms tend to be dominated by one or few species. The taxa that form typical visible microbial mats on the sediment surface in the photic zone are mostly diatoms (phylum *Bacillariophyta*) and cyanobacteria (the prokaryotic phylum *Cyanophyta* or *Cyanobacteria*). The term microbial mat originally

referred to consortia dominated by prokaryotic phototrophs (Stal and Caumette, 1992), but here it is used in a broader sense, including all types of mats consisting of microscopic phototrophic organisms.

Diatoms are by far the most common taxonomic group, giving the sediment a brown color because of the pigment fucoxanthin. Benthic diatoms are different from planktonic diatoms in that they mostly represent the pennate diatoms, with more or less bilateral symmetry (classes *Fragilariophyceae* and *Bacillariophyceae*; according to the systematics in Round et al., 1990). They are solitary, and when they have a raphe (a slitlike structure) on both valves of their silica frustule (or covering), they are motile. Those that have no raphe, or a raphe only on one valve, can form short colonies. Some centric diatoms (class *Coscinodiscophyceae*) can be common on sediments, for example, *Paralia sulcata*. The size of benthic diatoms ranges from a few micron to 500  $\mu\text{m}$ ; the sigmoid cells belonging to the genera *Gyrosigma* and *Pleurosigma* are some of the largest. Because many benthic diatoms are small (<10  $\mu\text{m}$ ), it is difficult to identify live cells to species level in a light microscope. When the organic cell contents are removed by oxidation to prepare "diatom slides," the taxonomically important ornamentation of the silica frustule can be viewed.

Cyanobacteria are widespread both on soft and hard substrates. They form mats along reef margins or on coral (Smith et al., 2009), may be epiphytic on other algae (Fong et al., 2006), rapidly colonize open space opportunistically after disturbances (Belk and Belk, 1975), and may bloom in response to nutrient enrichment (Armitage and Fong, 2004). Cyanobacterial mats are also common on salt marshes, particularly in subtropical and tropical estuaries and extreme habitats such as hypersaline lagoons. They are laminated systems that form interdependent layers of vertically stratified phototrophic, heterotrophic, and chemotrophic microorganisms. They function as laterally compressed ecosystems that support most of the major biochemical cycles within a vertical dimension of a few millimeters (Paerl and Pinckney, 1996). Typical benthic genera are the filament-forming *Oscillatoria* and *Microcoleus* and the colony-forming *Merismopedia*. Many filamentous benthic cyanobacteria fix nitrogen gas ( $\text{N}_2$ ) (Paerl and Pinckney, 1996). See Chapter 4.

Flagellates such as dinoflagellates (*Dinophyta*), euglenophytes (*Euglenophyta*), chlorophytes (*Chlorophyta*), and cryptophytes (*Cryptophyta*) are also found in estuarine microphytobenthos. Dense populations of dinoflagellates of the genus *Amphidinium* can occasionally give the sediment surface a red brown

color. See Chapter 4. As for phytoplankton, photopigments can be used to identify and quantify the presence of major taxonomical groups of benthic microalgae in surface sediments (Chapter 4).

### 8.3 FUNCTIONAL FORMS

Structurally, benthic algae include diverse forms that range from single cells to giant kelps over 45 m in length with complex internal structures analogous to vascular plants. Species diversity may be extremely high in benthic algal communities (Guiry and Guiry, 2007; see <http://www.algaebase.org>), and can be simplified by classifying algae by functional-form categories. Steneck and Dethier (1994) classified algae into the following groups based on productivity and susceptibility to grazing: microalgae, filamentous, crustose, foliose, corticated foliose, corticated macrophyte, leathery macrophyte, and articulated calcareous.

For macroalgae, a classification scheme based on a broader set of characteristics was put forward by Littler and Littler (1984): sheet, filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose forms (Table 8.1). These groups of functional forms have characteristic rates of nutrient uptake and mass-specific productivity, turnover rates, and resistance to herbivory that allow them to perform similarly in response to environmental conditions, despite differences in taxonomy. A key characteristic that drives these differences in function based on form is the ratio of surface area to volume ( $SA:V$ ) of the

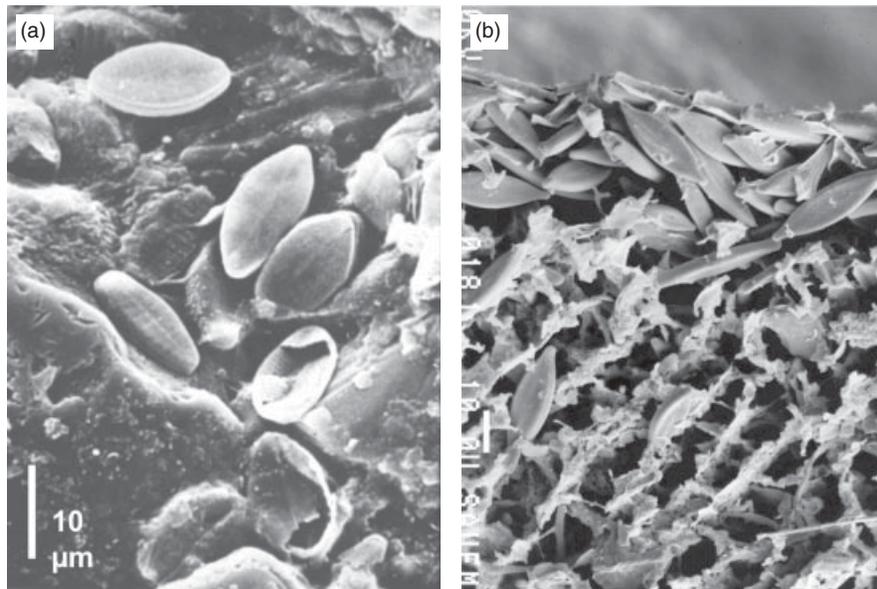
thallus. Macroalgae are also grouped more generally into “ephemeral” or “perennial” forms. Ephemeral macroalgae typically have a high thallus  $SA:V$  and inherently rapid nutrient uptake and growth rates. Most of the bloom-forming macroalgae that occur in response to nutrient overenrichment (eutrophication) (e.g., *Ulva* sp., *Chaetomorpha* sp., *Gracilaria* sp., *Polysiphonia* sp.) are ephemeral, and usually comprise very simple thallus forms such as those in the first three categories of Littler and Littler (1984). They tend to live floating and unattached or loosely attached to hard surfaces (i.e., shells, worm tubes) on the sediment (Schories and Reise, 1993; Thomsen and McGlathery, 2005). Perennial species such as crustose and calcareous macroalgae tend to live in low nutrient or stressful habitats (e.g., low light, low temperature) where a slow growth rate or perennial life form confers an advantage.

For benthic microalgae that live in sediments, the energy regime of the habitat determines the dominant life forms. In wave-exposed, well-sorted sands, life forms that are firmly attached to sand grains dominate and are called *epipsammic* (attached to sand grains). In high energy sand, most epipsammic diatoms are found in the crevices of the sand grains, where they are protected from abrasion. Typical genera are *Achnanthes*, *Cocconeis* (with raphe on one valve), and small-sized *Navicula*-like genera and *Amphora* (raphe on two valves) (Fig. 8.1a). These life forms attach by mucopolysaccharides extruded through their raphe. In less wave-exposed sands, solitary cells or colonies

**TABLE 8.1** Functional-form groups of predominant macroalgae, their characteristics, and representative taxa

	Functional-form Group	External Morphology	Comparative Anatomy	Thallus Size/texture	Example Genera
1.	Sheetlike algae	Flattened or thin tubular (foliose)	One–several cell layers thick	Soft, flexible	<i>Ulva</i> <i>Halymenia</i>
2.	Filamentous algae	Delicately branched	Uniseriate, multiseriate, or lightly corticated	Soft, felxible	<i>Chaetomorpha</i> <i>Cladophora</i> <i>Gelidium</i> <i>Caulerpa</i>
3.	Coarsely branched algae	Terete, upright, thicker branches	Corticated	Wiry to fleshy	<i>Acanthophora</i> <i>Laurencia</i>
4.	Thick leathery macrophytes	Thick blades and branches	Differentiated, heavily corticated, thick walled	Leathery-rubbery	<i>Sargassum</i> <i>Turbinaria</i>
5.	Jointed calcareous algae	Articulated, calcareous, upright	Calcified genicula, flexible intergenicula	stony	<i>Galaxaura</i> <i>Amphiroa</i>
6.	Crustose algae	Epilithic, prostrate, encrusting	Calcified, heterotrichous	Stony and tough	<i>Porolithon</i> <i>Hydrolithon</i>

Source: Adapted from Littler and Littler (1984).



**FIGURE 8.1** Benthic diatom assemblages viewed by scanning electron microscopy (SEM). (a) Epipsammic diatoms (*Achnanthes* and *Navicula*) in the cavity of a sand grain. (b) Vertical cut of a sediment surface at low tide photographed in a low temperature SEM. Motile diatoms have moved to the sediment surface where they form a dense microalgal mat. Strings forming networklike patterns consist of extracellular polymeric substances (EPS) excreted by diatoms (the pattern is an artifact produced by the method). *Source:* Photograph (a) by H. Håkansson and K. Sundbäck, (b) by A. Miles, Sediment Ecology Research Group, University of St. Andrews, Scotland.

of small diatoms are found protruding from the sediment particles. Such genera include *Fragilaria* and *Opephora*, which lack raphe, but attach through a mucopolysaccharide pad extruded from apical pores. The more sheltered the sediment is from wave exposure, the more common are motile life forms (*epipellic*; originally meaning “living on mud”). These are the diatoms that form visible, cohesive microbial mats on the sediment surface, particularly on muddy tidal flats (Fig. 8.1b). The cohesiveness is due to extracellular polymeric substances (EPS) that are extruded from the raphe and from pores in the silica frustule. The production of EPS is related to the motility of raphe-bearing life forms (genera such as *Navicula*, *Amphora*, *Nitzschia*, *Gyrosigma*, etc.; for systematics of the diatom genera, see Round et al., 1990). In fine sediments, epipsammic life forms are found attached to flocs of organic matter consisting of detritus and fecal pellets.

## 8.4 HABITATS

### 8.4.1 Soft-Bottom: Mud/Sandflats, Seagrass Beds, and Marshes

Benthic algae are important members of the primary producer community in shallow soft-sediment

systems worldwide where light penetrates to large areas of the benthos. In those systems subject to low nitrogen loading rates, macroalgae occur in relatively low abundance attached to the benthos, are epiphytic on seagrass blades, or form drifting mats. Within tropical seagrass beds, calcareous and/or siphonaceous green macroalgae such as *Halimeda* and *Caulerpa* are commonly attached to the benthos; calcification and chemical defenses provide protection from most herbivores. Calcified macroalgae ultimately contribute significantly to the accumulation and stabilization of tropical sands (MacIntyre et al., 2004). In both tropical and temperate seagrass beds, macro- and microalgae attach epiphytically to seagrass blades. Although even low abundances of epiphytes can have negative effects on seagrasses due to shading and interference with gas and nutrient exchange, in seagrass systems with low nutrient loading and intact herbivore populations epiphyte biomass accumulation is modest and contributions to food webs are significant (Williams and Ruckelshaus, 1993). In low nutrient soft-sediment systems, drift macroalgae are also present in low abundance, but are ecologically important as they may provide protection from predation and aid in dispersal of invertebrates and fishes (Salovius et al., 2005; Holmquist, 1994). However, when abundances increase, drifting mats can have negative effects on

their seagrass hosts, reducing density through smothering and shading (Huntington and Boyer, 2008).

Macroalgae can occasionally be abundant in the lower salt marsh zone in estuaries. Examples include the ephemeral green algae (*Blidingia*, *Rhizoclonium*, and *Ulva* (including former *Enteromorpha*)), slow-growing stress tolerant and long-lived brown algae (*Fucus* and *Ascophyllum*), inconspicuous slow-growing red algae (*Bostrychia* and *Caloglossa*), and invasive species (e.g., *Gracilaria vermiculophylla*). Many macroalgae in the understory of salt marsh vegetation are complexed with cyanobacteria and diatom mats. Productivity of these mixed algal communities can be very high, at times equaling or exceeding the productivity of the vascular plant canopy (Zedler, 1982). When algae are abundant in the understory of the vascular plant community, they may affect primary production rates, biogeochemical cycling, trophic interactions, and environmental conditions, such as evapotranspiration, infiltration, and sediment characteristics (Brinkhuis, 1977; Moseman et al., 2004; Boyer and Fong, 2005; Thomsen et al., 2009).

Similar to macroalgae, benthic microalgae are also important primary producers on illuminated shallow-water sediments. On sediments where there are no macroscopic primary producers, they are the only benthic primary producers, forming the base for benthic food webs. Benthic microalgae are most well studied on tidal mud- and sandflats, but are also important in subtidal habitats, particularly in microtidal estuaries, where the water column often stays clear through most of the day because of the lack of strong tidally induced turbidity. In large deep estuaries, such as Chesapeake Bay, a high percentage of the sea floor is within the photic zone, enabling primary production to occur over large areas.

#### 8.4.2 Hard-Bottom: Rocky Intertidal, Shallow Subtidal

Rocky intertidal and shallow subtidal zones worldwide are dominated by macroalgae, microalgae, and sessile invertebrates. While common along open coasts, some rocky areas exist in sheltered estuarine systems such as fjords and sounds. The rocky intertidal zone is characterized by environmental extremes (temperature, salinity, desiccation, nutrient supply), yet there are also strong biotic interactions that combine to produce striking patterns of zonation along elevational gradients. Both macroalgae and microalgae play important roles as *in situ* producers, forming the base of local food webs.

Macroalgae in rocky intertidal habitats are highly diverse and abundant, especially in temperate

regions. Virtually every functional form of macroalgae can be found in hard-bottomed habitats, from delicate branching genera such as *Plocamium* to large and fleshy reds and browns such as *Mastocarpus* (Turkish Towel) and *Egregia* (Feather Boa Kelp). Many classical studies have identified the importance of top-down forces in controlling the structure of rocky intertidal communities (e.g., Connell, 1972; Paine, 1974). More recent work has begun to focus on bottom-up processes as well as the relationship between biodiversity and ecosystem functions such as productivity and nutrient retention (e.g., Worm and Lotze, 2006; Bruno et al., 2008). Although rocky intertidal and shallow subtidal systems in tropical regions are far less studied, there is some evidence to suggest that macroalgal communities in some areas, such as the Pacific coast of Panama, are controlled by the same ecological processes as temperate systems (Lubchenco et al., 1984). In polar regions, the extreme and variable light climate and continuous near-freezing temperatures impose constraints on macroalgal production and depth distribution, as areas are typically ice covered for all but two months of the year. Despite these harsh conditions, crustose coralline macroalgae can be found down to 50 m depth in Arctic estuaries where the light level is only 0.004% of surface irradiance (Rysgaard et al., 2001). Large brown algae in the genera *Laminaria* and *Fucus* are often the community dominants in the 2–20-m-depth region attached to rocks, stones, and even gravel in protected areas (Witman and Dayton, 2001; Krause-Jensen et al., 2007). Physical disturbance by ice scouring often limits the distribution at shallow depths, and light limitation and possibly also disturbance from walrus feeding activities sets the lower limit of distribution in Arctic waters (Borum et al., 2002; Krause-Jensen et al., 2007).

Although macroalgae are the most prominent vegetation of rocky shores, there is also another less evident, but ecologically important algal community, the microscopic *epilithic* (growing on rock) community. Rocky surfaces are covered by a biofilm comprising microalgae, cyanobacteria, and newly germinated stages of macroalgae. This often slippery biofilm also includes bacteria, protozoans, and meiofauna. In the upper intertidal, cyanobacteria give the rock surface a dark, almost black color. Typical cyanobacterial genera are *Rivularia* and *Calothrix*. However, the black color can also be due to salt-tolerant lichens, such as *Verrucaria maura*. Epilithic diatoms often include life forms that are stalked and form colonies (for example, the genera *Gomphonema*, *Fragilaria*). The biofilm is an important food source for limpets and periwinkles

and also influences the settlement of invertebrate larvae. In addition to a top-down control by grazers, the algae in the intertidal biofilm are controlled by physical stress caused by high insolation (Thompson et al., 2004).

### 8.4.3 Coral Reefs

Coral reefs are productive, diverse, and economically important ecosystems that dominate hard-bottomed habitats in low nutrient tropical and subtropical waters. They proliferate in open nearshore habitats and in sheltered lagoons along tropical and subtropical coasts. On pristine coral reefs, fleshy macroalgae are rarely spatially dominant (Littler and Littler, 1984); rather, tropical reefs in low nutrient waters are dominated by crustose coralline and turf-forming algae. These algae form the base of benthic food chains, contribute to biodiversity, and stabilize reef framework. Crustose coralline algae play an important role in reef accretion, cementation, and stabilization (Littler et al., 1995). Algal turfs, comprising filamentous algae and cropped bases of larger forms, are ubiquitous throughout tropical reefs and are characterized by high rates of primary productivity. An exception to dominance by corallines and turfs on pristine reefs can occur when mechanisms exist which limit the efficacy of herbivores. Physical or chemical defenses produced by macroalgae such as *Dictyota* and *Sargassum*, and spatial refuges from herbivory such as surrounding sand planes or the bases of branching corals, can support fleshy macroalgae (Hay, 1984; Smith et al., 2010). Human impacts on reefs such as overfishing of herbivorous fishes (Jackson et al., 2001; Hughes et al., 2003) and increased nutrient supplies (Smith et al., 1981; Lapointe et al., 2005) may also produce dominance by macroalgae.

## 8.5 SPATIAL PATTERNS OF BIOMASS AND PRODUCTIVITY

### 8.5.1 Broad Geographic Scale—Latitudinal Differences

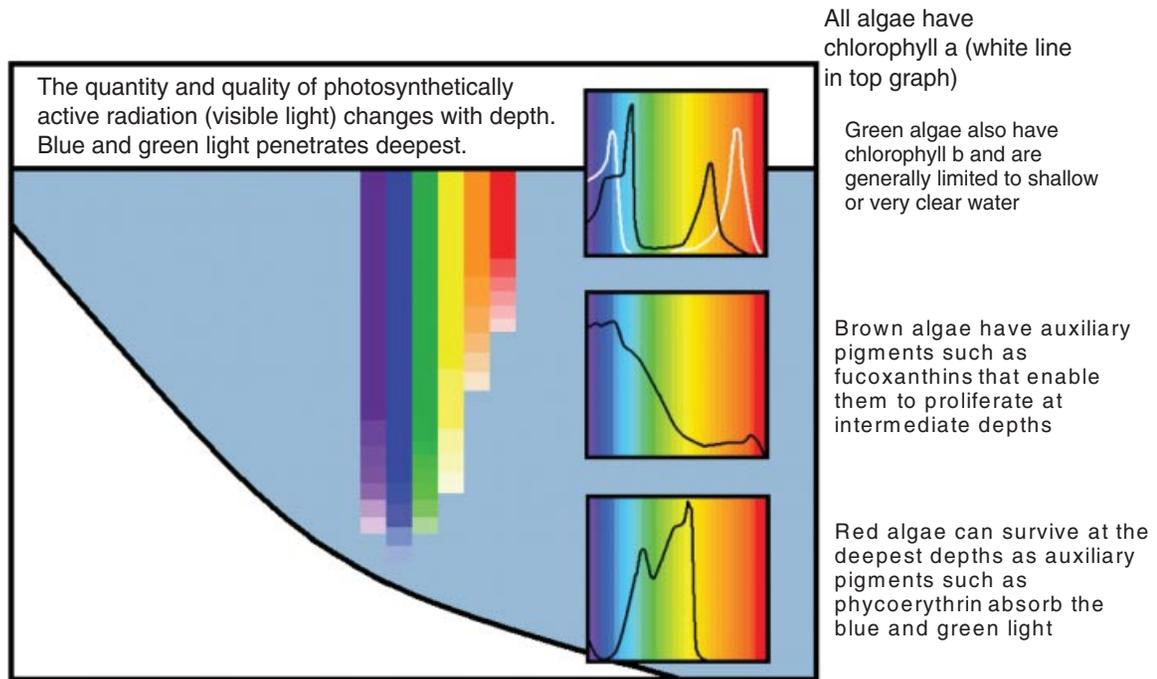
Benthic macroalgae are found in subtidal and intertidal estuarine habitats from tropical to polar regions. Some macroalgal species have broad geographic distributions, indicating their ability to acclimate to climatic variations in temperature and irradiance. For example, the foliose *Laminaria saccharina* occurs in rocky subtidal habitats from Spain to North Greenland (Lüning, 1990), and coralline algae inhabit waters throughout tropical and polar regions (Steneck, 1986).

Mesoscale differences in annual rates of productivity are related predictably to temperature and irradiance levels. Rates of productivity can be as high as 2500 g C/m<sup>2</sup>/year (Valiela, 1995), and highest annual rates are in tropical communities where growth and temperature conditions are favorable throughout the year. In regions where water column productivity is low, as in the tropics and some polar regions, benthic macroalgal production can exceed pelagic production on an areal basis (Duarte and Cebrian, 1996; Krause-Jensen et al., 2007).

Benthic microalgae are found on every surface that is reached by light. While benthic microalgae exist in all climatic zones, their temporal and depth distribution varies with latitudinal light conditions and the transparency of the water column. The range of annual benthic microalgal primary production varies from 5 to over 3000 g C/m<sup>2</sup>/year, but most values are within the range 20–500 g C/m<sup>2</sup>/year (Cahoon, 1999), and the highest values are from tropical regions. Areal values of both daily net primary production (NPP) and chlorophyll *a* (a rough measure of microalgal biomass) are often similar in magnitude to those for phytoplankton in shallow, clear water of the coastal regions. In shallow (1–3 m) estuaries, benthic microalgae can account for up to 70% of the total primary production (Underwood and Kromkamp, 1999; Baird et al., 2004), and in areas that lack macroscopic primary producers, they constitute the only autochthonous benthic source of primary production. Even in temperate seagrass meadows, the contribution of benthic microalgae can be 20–25% of the total benthic primary production (Asmus and Asmus, 1985). In tropical and subtropical seagrass-vegetated sediments, the biomass of benthic microalgae can be as high as that in adjacent unvegetated sediments, even though the seagrass canopy reduces light availability at the sediment surface (Miyajima et al., 2001).

### 8.5.2 Depth Distribution

Benthic macroalgae contain accessory pigments that allow capture of different wavelengths of light and efficient utilization of changing light quantity and quality with depth in the water column (Fig. 8.2). Red algae contain accessory pigments such as phycoerythrin that absorb green and blue-green wavelengths that penetrate deep in clear coastal waters. Crustose coralline red algae are the deepest living marine macroalgae, and have been found at depths of 268 m in the clear, tropical waters of the Bahamas where irradiances were less than 0.001% of the surface irradiance (Lüning and Dring, 1979). These macroalgae are characterized by slow growth rates. Light attenuation with depth, and the changing quality of light



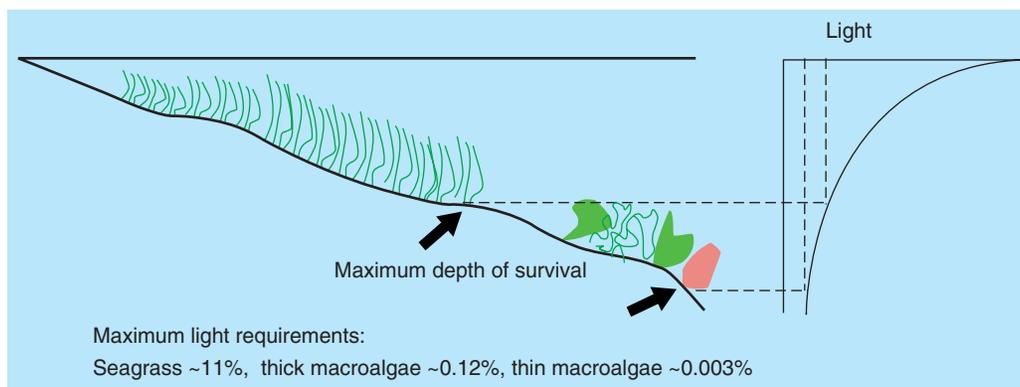
Although auxiliary pigments enable algae to extend their ranges deeper, this does not mean that they are limited to those depths! Red algae, for example, can live intertidally as well as deep. In addition, other factors such as grazing, wave energy, and disturbance control algal depth zonation.

Artwork by Kendal Fong

**FIGURE 8.2** Different divisions of algae have adapted to the varied light regimes that occur along depth gradients in estuaries.

limits the potential depth distribution of macroalgae, although disturbance and grazing losses also influence the actual depth distribution (Fig. 8.2). The minimum light requirements for thick macroalgae ( $\sim 0.12\%$  of surface irradiance) and thin macroalgae ( $< 0.005\%$ ) are substantially less than those for most seagrasses ( $\sim 10\text{--}25\%$ , see Chapter 5), and as a result their depth penetration is much greater than that for the vascular plants (Fig. 8.3).

As for macroalgae, the depth at which benthic microalgal primary production is important depends on the transparency of the water body. In clear waters, benthic microalgal NPP can be substantial at depths  $> 20$  m and can be sustained at a light level of  $5\text{--}10 \mu\text{mol photons/m}^2/\text{s}$  (Cahoon, 1999). At a site in NE Greenland, the maximum depth limit for benthic microalgae matched the 50 m depth limit for crustose coralline macroalgae, where light was  $0.004\%$  of the



**FIGURE 8.3** Comparison of minimum light requirements between macroalgae and seagrass. Depth limits are set by light attenuation in the water column.

surface irradiance during the open-water season (Rysgaard et al., 2001).

### 8.5.3 Energy Regime

Flow velocities around macroalgal thalli can have positive effects on rates of nutrient uptake and photosynthesis by reducing the thickness of the boundary layer and increasing the exchange of gases and solutes across the thallus surface (Hurd, 2000; Hepburn et al., 2007). In dense macroalgal communities, flow velocity is reduced due to the drag imposed by the thalli and this increases particle deposition and decreases particle resuspension (Gaylord et al., 2007; Morrow and Carpenter, 2008). Reduced flow rates can also influence macroalgal growth. For example, Stewart et al. (2009) showed that in dense beds of the giant kelp *Macrocystis pyrifera*, fronds on the seaward edge of the bed had faster elongation rates, larger blades, and greater carbon and nitrogen accumulation than interior fronds that were exposed to lower flows. Flow velocities also decrease with depth in the subtidal, and maximum velocities typically occur at the subtidal–intertidal fringe (Denny et al., 1985). Biomechanical models for high energy systems (up to 15 m/s) can be used to calculate velocities that cause macroalgal thalli to break and thus predict survival against hydrodynamic forces (Denny, 1995). The two most important factors determining break forces for macroalgae are substrate type and thallus size (Malm et al., 2003). In low energy systems, water speeds as low as 0.22 m/s can cause both breakage and “pruning” (thallus fragments left for regrowth) for attached algae with delicate thalli such as *Ulva* (Kennison, 2008). The macroalgal form can vary in response to flow regimes, with exposed areas having algae with flatter, narrower fronds to reduce drag and protected areas having wider, undulate fronds to increase turbulent flow and decrease boundary layer effects. This can reflect both morphological plasticity and genetic differentiation (Hurd et al., 1997; Roberson and Coyer, 2004).

The largest accumulations of macroalgae are found in poorly flushed systems, such as sheltered embayments and estuaries, with elevated nutrient concentrations where bloom-forming species occur (e.g., *Ulva* sp., *Chaetomorpha* sp., *Gracilaria* sp., *Polysiphonia* sp.) (Viaroli et al., 1996; Pihl et al., 1999). Advective transport of macroalgae, both between habitats within an estuary (i.e., subtidal to intertidal) and from the estuary to the coastal ocean, can be important in terms of nutrient exchange. Macroalgal material moves either as bedload or as floating mats at the water surface, depending on their specific gravity (which is influenced by photosynthesis

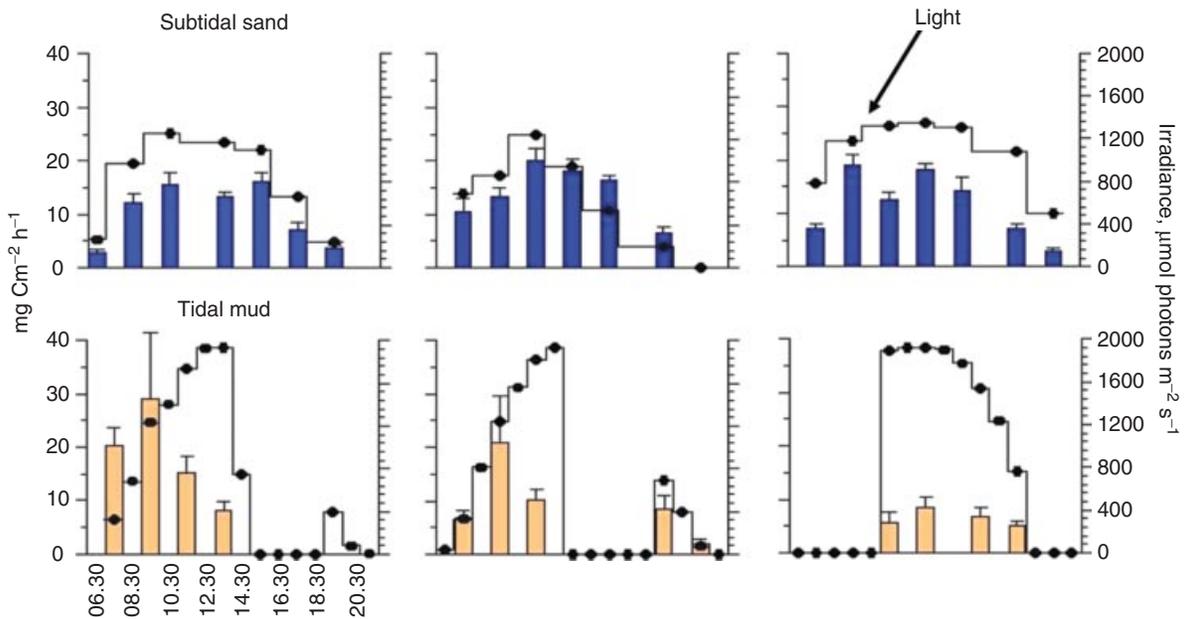
rates and invertebrates that colonize mat-forming macroalgae). Unattached, living macroalgae move at current velocities as low as 2 cm/s (Flindt et al., 2004), and these current velocities are common in estuaries where both winds and tides affect current speeds at the sediment surface (Lawson et al., 2007; Kennison, 2008). Macroalgae also settle 1000 to 5000 times faster than phytoplankton, and hence if transported out of estuaries usually settle on the ocean floor rather than being returned on the flood tide (Flindt et al., 2004). Few studies include mass transport of nutrients bound in plant material and as a result nutrient retention in estuaries can be overestimated.

Generally, benthic microalgal production is higher in fine sediments than in sandy sediments exposed to wave action (Underwood and Kromkamp, 1999). The explanation for this finding is that fine sediments, with high organic matter concentration and rapid bacterial mineralization, contain more nutrients in the pore water than sandy sediments with less accumulation of organic matter. Moreover, the biomass of benthic microalgae (measured as chlorophyll *a* content of the sediment) in the upper few millimeters of muddy sediments can be much higher than in sandy sediments. But the NPP can occasionally be as high, or even higher, in sandy than in muddy sediments. One reason is the higher availability of light, because of a thicker photic zone, so that photosynthesis can occur deeper in sandy sediments than in muddy sediments. In addition, advective flushing can reduce nutrient limitation in inundated permeable sands (Billerbeck et al., 2007). In high energy environments, such as tidal sand flats, a large part of the benthic microalgal community can be resuspended during the tidal cycle, contributing to pelagic production. Up to half of the food resource of filter feeders can consist of resuspended benthic microalgae (de Jonge and Beusekom, 1992). The turnover of benthic microalgal biomass on sandy tidal flats is typically higher than that on muddy flats (Middelburg et al., 2000).

## 8.6 TEMPORAL PATTERNS OF BIOMASS AND PRODUCTIVITY

### 8.6.1 Diel Cycle

The diel cycle of benthic microalgal primary production is well described, and generally differs between tidal and subtidal sediments (Fig. 8.4; Miles and Sundbäck, 2000). On muddy tidal flats, there are large variations in the light climate during the day because



**FIGURE 8.4** Diel pattern of microphytobenthic primary production (bars) on a shallow-water subtidal sandy site (Kattegat, microtidal west coast of Sweden) and an intertidal muddy site (Tagus estuary, Portugal). Measurements were made by the  $^{14}\text{C}$  technique with subsequent 2-h incubations during three full days. Filled circles show irradiance measured at sediment surface. Because of high turbidity, no light penetrated to the sediment surface during high tide in the Tagus estuary. *Source:* Redrawn from Miles and Sundbäck (2000).

of tide-induced turbidity, and photosynthesis occurs only when the sediment is immersed during daylight. This pattern is strengthened by the endogenous (i.e., controlled by “internal clocks”) vertical migration rhythm of particularly motile diatoms. The algae start to migrate down 30–60 min before the tide returns (Kromkamp and Forster, 2006) and emerge again to the surface for the low tide period (Fig. 8.1b). High resolution techniques, such as low temperature scanning electron microscopy and single-cell pulse–amplitude–modulation (PAM) chlorophyll fluorescence, have shown that the algal composition at the sediment surface changes during the photoperiod (Underwood et al., 2005). This vertical migration can be explained as a way of taking advantage of the favorable light conditions during low tide and avoiding resuspension by the tidal waves. A more stable habitat with higher concentrations of nutrients also provides more favorable conditions for cell growth and division deeper in the sediment compared to the sediment surface (Saburova and Polikarpov, 2003). On sandy tidal flats, the water column may stay clear during high tide, and primary production can continue when the sediment is submerged. In subtidal habitats and on microtidal coasts, the light climate is often not affected by tidal turbidity, and benthic photosynthesis can proceed

throughout the daylight period (Fig. 8.4), showing the highest production at midday. Benthic diatoms also migrate daily in subtidal conditions so that they emerge before sunrise and submerge in the evening (Longphuir et al., 2006).

### 8.6.2 Seasonal Cycle

Seasonality in benthic algal growth is highest in polar regions and decreases toward lower latitudes. For perennial macroalgae in polar regions, shade adaptation is one way of dealing with the dark winter months and the ice cover 10 months of the year. Laminarians that dominate these regions have inherently slow growth rates, storage of carbon reserves during the summer period of high productivity, a long life span, and a high resistance to grazing (Lüning, 1990). Macroalgae need to maintain low respiration to minimize carbon losses during the long winter months, high photosynthetic efficiency at low light when ice still covers the water surface, and the ability to maximize continuous light in the summer. Laminarians increase their blade surface area to increase light capture and produce new thin blades before the break up of ice cover using stored reserves in old overwintering thalli and are poised for rapid growth as soon as the ice-free period begins (Chapman and Lindley, 1980; Dunton, 1985). In temperate soft-bottom

systems, macroalgae may be present year-round, and different species have different thermal tolerances and optimum temperatures for photosynthesis, respiration, and growth, so species composition can change with increasing temperature. In general, the respiration rate increases more rapidly with rising temperature than photosynthesis rate, leading to a decrease in the photosynthesis:respiration ratio ( $P/R$ ).

Ephemeral macroalgae go through boom and bust cycles in many regions, with the mid-growing season population crashing due to high temperatures and self-shading. In some areas such as southern California, floating blooms can occur during any season, with the magnitude and frequency related to land use in watersheds and patterns of nutrient input (Kamer et al., 2001; Boyle et al., 2004). Intertidal macroalgae on rocky shores, especially in higher tidal zones, respond to interactions among monthly and seasonal changes in the tidal amplitude, temperature, and light by changing biomass (Menge and Branch, 2001). Seasonality is much less pronounced in tropical systems, although some exceptions occur. Some coral reef algae show marked seasonal variation in standing stock of carbon (Lirman and Biber, 2000). On Panamanian reefs, algal productivity and biomass accumulation is much higher during the upwelling season (Smith, 2005), suggesting that algal communities are regulated by nutrients in the absence of upwelling.

Seasonal variability in thallus photosynthesis is higher for ephemeral macroalgae than for perennial genera such as *Cladophora* and *Ulva* that grow fast and store little nutrient reserves (Sand-Jensen et al., 2007). Respiration rates typically vary systematically over the year, and increase as temperature and irradiance levels increase. For temperate species, this leads to higher minimum light requirements during summer than winter for photosynthesis to balance respiration. While there are significant changes in the actual production as light and temperatures vary with seasons, the maximum potential production (at saturating light) varies less (Middelboe et al., 2006). This is in part due to changes in species composition and abundance that favor species that have optimal performance at different times of the year.

Long-term studies on seasonality of benthic microalgae are rare. One of the longest seasonal studies (12 years, 14 stations) on benthic microalgal biomass and production is from a tidal flat on the coast of the Netherlands (Cadée and Hegeman, 1977). This study shows that, in temperate areas, the biomass peaks during the warm season. Occasional dips in benthic chlorophyll *a* during summer are explained by strong grazing pressure, particularly by

mud snails (such as *Hydrobia ulvae*). This seasonal pattern agrees with patterns found in shallow subtidal and microtidal areas in temperate estuaries, although well-developed diatom mats have also been found on the sediment surface under sea ice. Such proliferation of benthic diatoms under ice can be explained by the presence of shade-tolerant species, good nutrient availability, and low grazing pressure. In tropical areas, seasonal variations in benthic microalgal abundance can be influenced by the monsoon, such that abundance is lowest during the monsoon and highest during the postmonsoon period (Mitbavkar and Anil, 2006). In polar regions, the length of the productive season for benthic primary production is only about 80–90 days. During this period, the daily microbenthic primary production (172–387 mg C/m<sup>2</sup>/day) at depths  $\leq 20$  m has been found to exceed that of phytoplankton (Glud et al., 2002).

## 8.7 METHODS FOR DETERMINING PRODUCTIVITY

For macroalgae, various methods are used to estimate production, based either on short-term estimates of carbon assimilation/oxygen production or on longer-term growth estimates.

1. **Growth Measurements** Frond-marking is a common technique used to estimate growth rates of large, attached macroalgae such as kelps. The fronds, or blades, are marked with holes at the junction between the stipe and the blade where the growth zone is located. The holes are displaced upward as the blade grows and the distance between the hole and the stipe/blade junction represents new growth (Krause-Jensen et al., 2007). This is similar to the leaf-marking technique that is commonly used to measure seagrass growth. Rates of elongation are then converted to production as mass (gram dry weight, gdw) or carbon using conversion rates. For unattached mats or rafts of macroalgae with diffuse growth (growth throughout the thallus), the biomass can be measured directly as wet weight. Algae are collected from a known area of benthos or volume of water, cleaned of mud and fauna, and, if desired and possible, separated into species. Techniques to assure a consistent wet weight are varied, but include blotting the thalli dry or spinning in a salad spinner for a consistent time and rate. The change in the average biomass over time estimates productivity.

2. **Photosynthesis Measurements** Measurements of net or gross production as gas ( $O_2$  or  $CO_2$ ) exchange

provide shorter-term estimates of production, and these can be scaled spatially and temporally based on availability of incident irradiance. Changes in oxygen or dissolved inorganic carbon (DIC) can be measured on individual thalli in light or dark bottles or chambers to estimate the NPP and respiration. Photosynthesis–irradiance ( $P$ – $I$ ) curves can be constructed for each species to derive data on maximum photosynthetic rate ( $P_{\max}$ ), efficiency of light utilization ( $a$ ), respiration ( $R$ ), and the saturation and compensation irradiances ( $I_s$  and  $I_c$ ) (Chapter 4). These parameters can be related to light availability at specific water depths using an equation (e.g.,  $P = P_{\max}[1 - \exp(-aI/P_{\max})] + R$ ; Platt et al., 1980) and scaled to areal rates of production.

Since macroalgae can grow in dense accumulations, models are used to account for self-shading within the macroalgal communities (Brush and Nixon, 2003; McGlathery et al., 2001). These models scale production in macroalgal mats based on incident irradiance reaching the canopy, known patterns of light attenuation with depth in macroalgal mats, and  $P$ – $I$  relationships for individual thalli. This approach is similar to terrestrial canopy models. Sand-Jensen et al. (2007) have modified this approach further to consider variations in thallus light absorbance, canopy structure, and density. The model has been tested for single-species communities of the sheetlike *Ulva lactuca* and the leathery *Fucus serratus* and for mixed-species communities. An interesting result of the model is the stabilizing effect of species richness, whereby multiple species complement each other in absorbing light.

The PAM chlorophyll  $a$  fluorescence technique is also used to determine relative measures of photosynthetic activity of algal species. These measurements typically provide a snapshot (seconds–minutes) of photosynthetic capacity to acclimate to light conditions. However, they do not easily translate into quantitative measures of photosynthesis in terms of oxygen production or carbon fixation. The PAM technique can be used *in situ* and measures the activity of photosystem II, giving an estimate of the electron transport rate (ETR). Although there is a fairly good linearity between ETR, oxygen production, and  $^{14}\text{C}$  incorporation, this relationship can become nonlinear at high irradiances. For a review on this technique see Kromkamp and Forster, (2006).

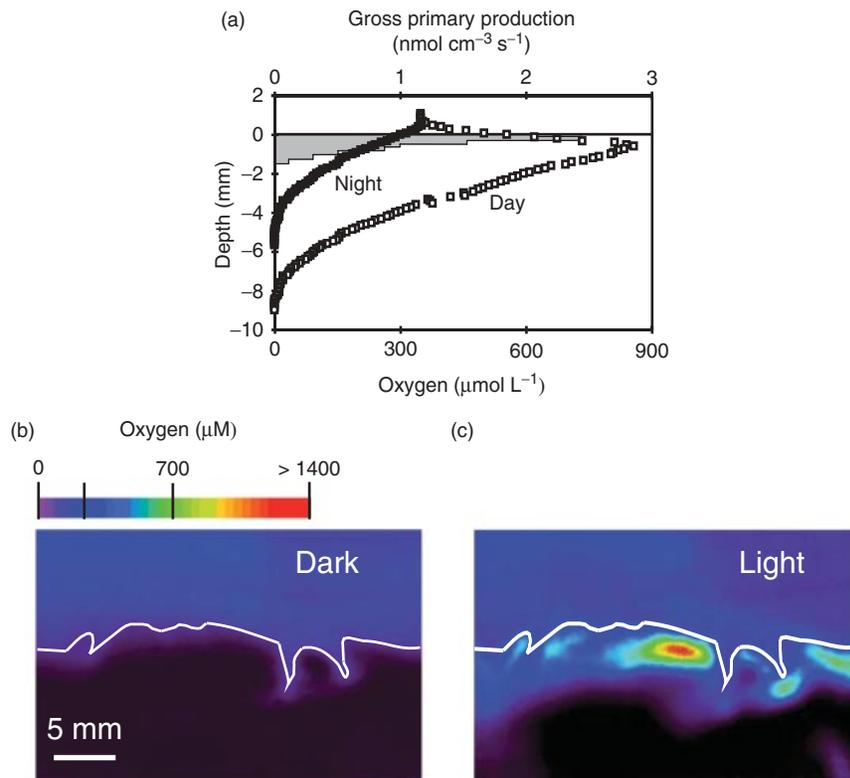
For benthic microalgae, the best methods for primary production measurements are those that do not disturb the natural physical, chemical, and biological microgradients in the sediment. There are four principal methods that are used for primary production

measurements in sediments. All these techniques have their limitations, and primary production rates determined by the different methods can be slightly different because they measure different aspects of photosynthesis.

1. **Sediment–Water  $\text{O}_2$  or  $\text{CO}_2$  Exchange** Oxygen flux is measured as changes in the concentration of oxygen in well-mixed overlying water in benthic chambers or sediment cores. The advantage of this method is that the measurements integrate over a sediment area and that measurements both in the light and dark give three ecologically relevant rates: net primary production (NPP), community respiration (CR), and gross primary production (GPP). Field measurements of benthic primary production on tidal flats during immersion are possible by measuring  $\text{CO}_2$  fluxes in benthic chambers (Migné et al., 2004). Disadvantages are that cores and chambers do not replicate natural hydrodynamic and light conditions and may underestimate the flux.

2. **Uptake of Radioactively Labeled Carbon ( $^{14}\text{C}$ -Bicarbonate)** This is a suitable technique for tracking the fate of carbon in food webs. In sandy sediments,  $^{14}\text{C}$  can be percolated a few millimeters into the photic zone of the sediment (Jönsson, 1991). In muddy sediments, percolation does not usually work, and the technique relies on diffusion of the label into the sediments, which results in underestimation of primary production. Slurry incubations disrupt the microgradients in the sediment, but are suitable in experiments where the maximum potential primary production is used as a variable. The stable isotope  $^{13}\text{C}$  also can be used for tracking carbon through the food webs (Middelburg et al., 2000).

3. **Oxygen Microsensors (with a Tip of Only a Few Microns) and Planar Optodes** These are used for high-resolution nondestructive measurements of oxygen microgradients in the sediment, from which primary production can be calculated by modeling (Fig. 8.5). The dark–light shift microelectrode technique can also be used to measure oxygen production (Revsbech et al., 1981). The classic oxygen microsensor is the oxygen electrode with a guard cathode (Revsbech, 1989), but there are also oxygen optodes that are based on fiber optics (Glud, 2006). The use of microsensors has contributed greatly to our understanding of the temporal and spatial variations among the processes operating in the top few millimeters of the sediment. Planar optodes make it possible to get a two-dimensional picture of the  $\text{O}_2$  distribution and dynamics at a given area over many days (Fig. 8.5; Glud, 2006). Such measurements have provided new



**FIGURE 8.5** Influence of microphytobenthos on oxygen distribution in surface sediment. (a) Oxygen profiles in light and dark measured by oxygen microelectrodes. Also shown is a vertical profile of modeled rates of primary production (bars). (b) and (c) Oxygen distribution in light and dark in bioturbated sandy silt measured by planar oxygen optodes (Section 8.7). The bright red spot indicates the high rate of photosynthetic oxygen production in light by an assemblage of benthic diatoms just below the sediment surface. *Source:* (a) Redrawn from Glud et al. (2009) and (b) redrawn from Fenchel and Glud (2000).

insights into oxygen dynamics around rhizospheres, faunal structures, structures in permeable sands, and within phototrophic communities.

4. **PAM Chlorophyll *a* Fluorescence** The fluorescence technique can be used to estimate photosynthesis in the sediment microalgal community and also to measure photosynthetic activity of individual cells using a modified fluorescence microscope (Underwood et al., 2005)

Finally, for all types of benthic producers, there is a new *in situ* method based on the eddy correlation flux technique that is commonly used to measure oxygen exchange across the land–air interface in terrestrial and intertidal ecosystems. This technique has been adapted to subtidal conditions and has the advantage that it measures community metabolism under natural hydrodynamic and light conditions, can capture short-term (minutes) variation in production/respiration, and integrates over a much larger area (>100 m<sup>2</sup>) than conventional techniques (<1 m<sup>2</sup>) (Berg et al., 2003, 2007).

## 8.8 FACTORS REGULATING PRODUCTIVITY AND COMMUNITY COMPOSITION

The mechanisms that control the net production of benthic algae in estuarine ecosystems are the same as those for other primary producers: geographic limits for growth are set by temperature and light. Within the geographical limits, biomass accumulation is controlled by many interacting biotic and abiotic factors including light quantity and quality, nutrient availability, water motion, temperature, intra- and interspecific competition, grazing, and physical disturbance. Here we discuss light, nutrients, and grazing; additional factors are included in other sections.

### 8.8.1 Light

Similar to all primary producers, benthic macro- and microalgae use visible light in the 400–700 nm

spectrum, which is termed *photosynthetically active radiation* (PAR). Accessory pigments in benthic algae allow certain groups to capture wavelengths that would otherwise be inaccessible by chlorophyll *a* alone (Fig. 8.2). Light is attenuated exponentially with depth in the water column following the Beer–Lambert law,  $I_z = I_0 e^{-K_{dz}}$ , where  $I_z$  is the irradiance at depth  $z$ ,  $I_0$  is the surface irradiance, and  $K_{dz}$  is the attenuation coefficient for diffuse downwelling irradiance. This is described in detail in Chapter 4. The surface irradiance reaching the benthos at a given depth is influenced by properties of the water that affect the attenuation coefficient, including suspended sediment, organic (e.g., phytoplankton) and detrital particles, and colored organic matter (CDOM).

Light is attenuated rapidly within dense macroalgal communities. For the bloom-forming species *Cladophora prolifera* and *Chaetomorpha linum*, 90% of the available irradiance hitting the surface of the mat can be absorbed in the top few centimeters (Krause-Jensen et al., 1996). The extent of this light attenuation will depend on the thallus form (canopy structure) and density of the algae, the absorbance of the algae, and species composition. Complementarity of light use between different algal species in mixed-species communities often means that the total community production is higher for a given irradiance level than for single-species communities (Middelboe and Binzer, 2004). Benthic macroalgae can acclimate rapidly (within minutes) to changing light conditions. This can be an adaptation for optimizing production in a short growing season (Borum et al., 2002) or to a variable light climate due to short-term changes in incident irradiance (e.g., cloud cover) or water column light attenuation (e.g., wind/wave induced sediment resuspension). A general adaptation to reduced light levels is an increase in pigment content and light utilization efficiency. This results in reduced compensation and saturation irradiances ( $I_c, I_s$ ) for photosynthesis. These characteristics allow macroalgae to more effectively photosynthesize at low light levels. However, the production and maintenance of higher pigment content and enzyme activities increase respiratory costs in low light plants. At high irradiance levels, pigment concentrations are typically lower, compensation and saturation irradiances are higher, and maximum photosynthesis is high. Photoinhibition may occur at high irradiances or under high UV stress, and the damage to the photosystem that causes this inhibition is not necessarily reversible (Chapter 4).

Benthic microalgae also function in a wide range of light climates and are able to adapt to widely fluctuating light conditions. Diatoms can optimize their photosynthetic apparatus efficiently to current light conditions (within minutes) (Glud et al., 2002). Moreover, as epipelagic life forms are able to migrate vertically in the sediment, they can position themselves in favorable light conditions. In this way, physiological photoinhibition is avoided at high ambient light levels. Because of back-scattering effects, the light intensity at the sediment surface can be up to 200% higher than the ambient light above the sediment (Kühl et al., 1994). While the photic zone in the water column is generally measured in meters, the photic zone in shallow-water sediments is measured in micro- and millimeters. Fiber-optic microsensors enable high resolution measurements of the light quantity and quality in microbial mats and surface sediments (Kühl et al., 1994). Light penetrates deepest in sandy sediments (~3 mm), while in fine sediments the photic zone is less than 1 mm. The light climate in the sediment also differs from that in the water column in that red light penetrates deepest in sediments. The vertical change in the light quantity and spectrum often results in stratified microbial mats consisting of layers of organisms with different optimal light requirements (e.g., a sequence of diatoms on the top, followed by cyanobacteria, and then by photosynthetic purple sulphur bacteria, which prefer anaerobic conditions). Live microalgae can be found far below the photic zone in the sediment. Episammic diatoms on sand grains can be mixed down to 10 cm depth in wave-exposed sediments. They survive long periods (weeks, months) of darkness, and rapidly resume photosynthesis when transported up to the photic zone by mixing of the sediment.

## 8.8.2 Nutrients

### 8.8.2.1 Sources

Benthic algae obtain nutrients from both the sediments and the water column and the source of nutrients are from both external (allochthonous) and recycled (autochthonous) sources. Sources of “new” or allochthonous nutrients include terrestrial inputs via rivers from coastal watersheds, nitrogen fixation, groundwater, atmospheric deposition, and upwelling (Nixon, 1995; Smith et al., 1996; Whittall and Paerl, 2001). With the possible exception of upwelling and N-fixation, all of these sources are rapidly increasing as a result of anthropogenic alterations of global nutrient cycles (for a review, see Vitousek et al., 1997). Autochthonous sources of nutrients include recycling from other biota and regeneration from the sediments during decomposition.

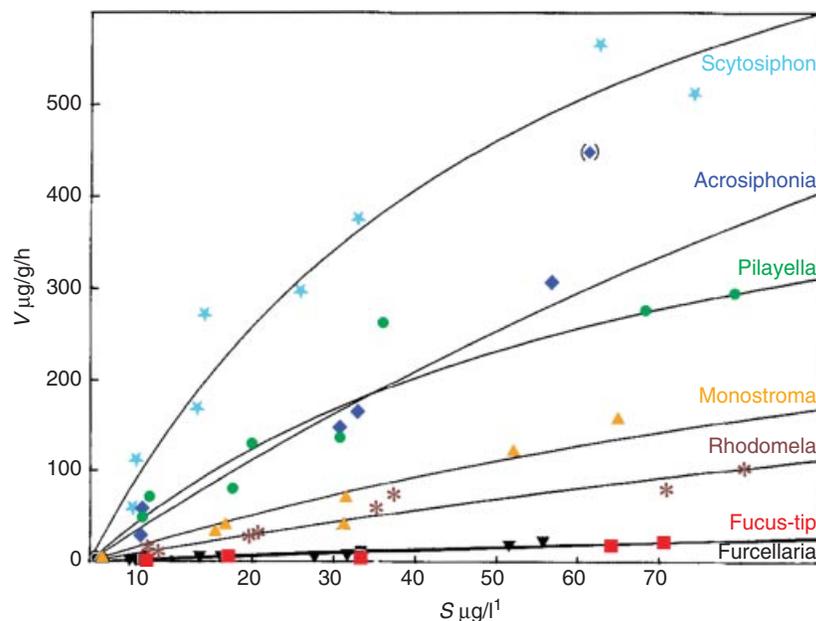
### 8.8.2.2 Uptake and Storage

The relationship between the nutrient concentration in the water and the rate at which nutrients are taken up by benthic macro- and microalgae can be described by a hyperbolic function. The Michaelis–Menten equation for enzyme uptake kinetics is often used to describe this function, and this is also described in detail for phytoplankton in Chapter 4. The Michaelis–Menten equation describes uptake as follows:  $V = V_{\max} * [S / (K + S)]$ , where  $V$  is the uptake rate at a given substrate (nutrient) concentration,  $S$  is the substrate concentration,  $K$  is the half-saturation concentration—where uptake is equal to  $1/2$  of the maximum uptake rate, and  $V_{\max}$  is the maximum uptake rate at high substrate concentration. From a biological perspective, there are two important components of this relationship: (i) nutrient uptake rates become saturated as nutrient concentration increases and (ii) the initial slope of the curve at low concentrations provides a useful index of an alga's affinity for nutrients at low levels. This latter characteristic may be important in determining the competitive abilities of algae when nutrients are in critically low supply. The  $V_{\max}$  rate varies depending on the nutrient status of the plant. Algae that have lower nitrogen contents in more nitrogen-limiting environments would be expected to have higher maximum nutrient uptake rates.

For macroalgae, uptake rates are higher for thin-structured sheetlike or filamentous thalli that

have a high surface area to volume ratio than for more coarsely branched species (Fig. 8.6, Wallentinus, 1984). In addition, some nitrogen-starved ephemeral macroalgae have the capacity for very rapid (“surge”) uptake during the first minutes of exposure to nutrients, which results in a three-phase pattern of nutrient uptake as a function of external supply (Pedersen, 1994). The capacity for surge uptake is assumed to be advantageous for ephemeral algae subject to short-term nutrient pulses that might result from animal excretion or temporarily high mineralization rates. For macroalgae, there are two primary ways to measure nutrient uptake: (i) the “multiple flask” method, where different substrate concentrations are added to individual flasks containing macroalgae, the disappearance of substrate is measured over a short (15-min) incubation, and then the data are pooled to obtain an uptake versus concentration curve; and (ii) the “perturbation” method, where thalli are exposed to a high concentration of substrate and a time series of substrate concentration is measured (Pedersen, 1994).

Both macro- and microalgae can store nutrients, and their capacity to do this varies depending on their inherent growth rates and the frequency and magnitude of nutrient pulses. The general pattern that emerges is that fast-growing ephemeral macroalgae such as *Ulva* and *Chaetomorpha* store little reserves compared to slow-growing perennial species such as *Fucus*, which has reserves that can support growth for longer periods of time. This influences the duration



**FIGURE 8.6** Maximum uptake rates of  $\text{NH}_4\text{-N}$  versus concentration for macroalgae with different ratios of surface area to volume. Source: From Wallentinus (1984).

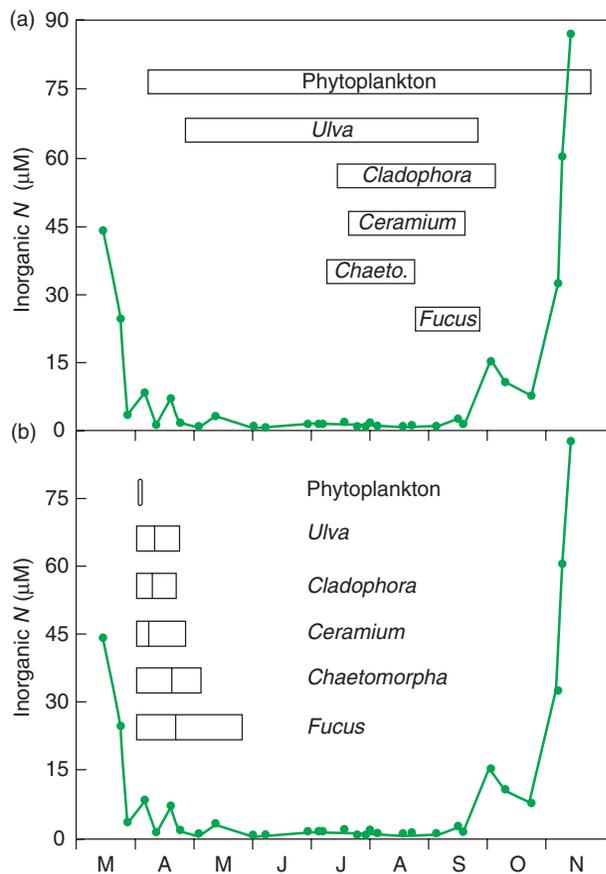
of nutrient limitation that often occurs in temperate regions in response to a seasonal (summer) depletion of nutrients. For example, Pedersen and Borum (1996) showed that while different algal species, from phytoplankton to slow-growing perennial macroalgae, had similar storage reserves (mg N/gdw), the storage capacity, that is, the ability to support growth in the absence of an external nutrient supply, varied from less than 1 day for phytoplankton to greater than 15 days for perennial macroalgae (Fig. 8.7). On shorter time scales (hours–days), macroalgae have rapid, but transient, responses to variability in N availability, with uptake rates influenced by changing tissue N pools (McGlathery et al., 1996). Also, the coupling of C metabolism (photosynthesis and storage) and N metabolism over the short term implies that algal growth rate acts as a feedback regulator to maintain balanced C-N metabolism, except under extreme conditions of high irradiance and low N supply. Such self-regulation may be especially beneficial

to algae growing in estuarine environments that are characterized by high spatial and temporal variability in nutrient and light availability (McGlathery and Pedersen, 1999).

### 8.8.2.3 Limitation of Growth

In most temperate and polar estuaries, nitrogen is considered to be the primary limiting nutrient for growth, in part due to high rates of denitrification relative to nitrogen fixation. For macroalgae in tropical/subtropical systems dominated by carbonate sediments, phosphorus often limits growth, largely due to the binding of phosphorus by the carbonate sands. There are exceptions to this generalization that are related to the ratio of N:P in external loading, variations in the relative rates of nitrogen fixation and denitrification, and the adsorption capacity of carbonate sediments in different systems. Large data sets on C:N:P ratios of marine plants indicate that macrophytes (macroalgae and seagrasses) have different characteristic atomic ratios of tissue nutrients than phytoplankton. Atkinson and Smith (1983) examined marine plants and found a ratio of 550:30:1 for benthic marine plants, and Duarte (1992) showed that the ratio for 46 macroalgal species was 800:49:1. These ratios compare to the “Redfield Ratio” of phytoplankton of 106:16:1 (Chapter 4), and suggest that macroalgae have a higher nitrogen demand. As with phytoplankton, these ratios are often used to infer nutrient availability and possible nutrient (N vs P) limitation.

Increases in nutrient supplies that relieve nutrient limitation in subtidal soft-sediment habitats result in enhanced macroalgal production and potentially in the loss of seagrasses, which tend to dominate under low nutrient conditions (see Chapter 5 and Duarte, 1995; Valiela et al., 1997; McGlathery et al., 2007). In salt marshes, water column nutrients sequestered by understory macroalgae are retained within the salt marsh community, and become available to support vascular plant growth when macroalgae senesce (Boyer and Fong, 2005). Transitions from macroalgae to toxic cyanobacterial mats occur in estuaries on the West Coast of the United States (Armitage and Fong, 2004), perhaps due to higher tidal amplitudes, lower residence times, and broad areas of intertidal mudflats (large areas of suitable habitat). Nutrient-driven community shifts also occur in rocky intertidal areas (Worm et al., 2002; Worm and Lotze, 2006). In these studies, experimental nutrient enrichment increased macroalgal abundance, and grazing by consumers moderated that response. However, macroalgae in areas with low ambient nutrients responded to enrichment with increased thallus complexity and diversity,



**FIGURE 8.7** Periods of nutrient-limited growth (a) and storage capacity (ability to support growth in the absence of an external nutrient supply) (b) for phytoplankton and macroalgae in a Danish Fjord compared to ambient nutrient concentrations. *Source:* From Pedersen and Borum (1996).

while macroalgae in more enriched areas responded with decreases in diversity due to a shift in dominance to opportunists.

For coral reefs, there is considerable debate about whether algae are limited by nutrients. Effects of experimental nutrient additions have varied from no effects (Delgado et al., 1996; Larkum and Koop, 1997; Koop et al., 2001) to orders of magnitude differences in effects on photosynthesis, growth, and biomass accumulation (Lapointe and O'Connell, 1989). Interpretation of experimental results is limited, in part, by the difficulty of relating results of laboratory or microcosm studies to natural growth in the high energy, high flow environments with variable nutrient supply typical of coral reefs (Fong et al., 2006), and by the related methodological challenge of effectively conducting *in situ* experiments in these same environments (reviewed in McCook, 1999).

It was once generally assumed that benthic microalgae are not likely to be limited by nutrients in the same manner as phototrophic organisms in the water column. This is often the case for fine sediments, but in sandy sediments, benthic microalgae can be nutrient limited (Nilsson et al., 1991). For short periods, however, nutrient limitation can also occur in fine, cohesive sediments during, for example, tidal emersion (Thornton et al., 1999). Studies on nutrient fluxes in well-sorted permeable sandy sediments exposed to wave action have, on the other hand, partly changed our view on the nutrient limitation in sandy sediments. In permeable sediments, nutrient availability can be enhanced by efficient advective transport, resulting in high microbenthic primary production (Billerbeck et al., 2007).

### 8.8.3 Grazing

Preferential feeding by herbivores can influence the abundance and species composition of macroalgae. Many studies show an association between high nutrient content of primary producers and high consumption rates; however, other factors such as herbivore abundance, per capita grazing rates of the dominant herbivores, and feeding preferences also play important roles in determining patterns of herbivory (Cebrian, 1999, 2002).

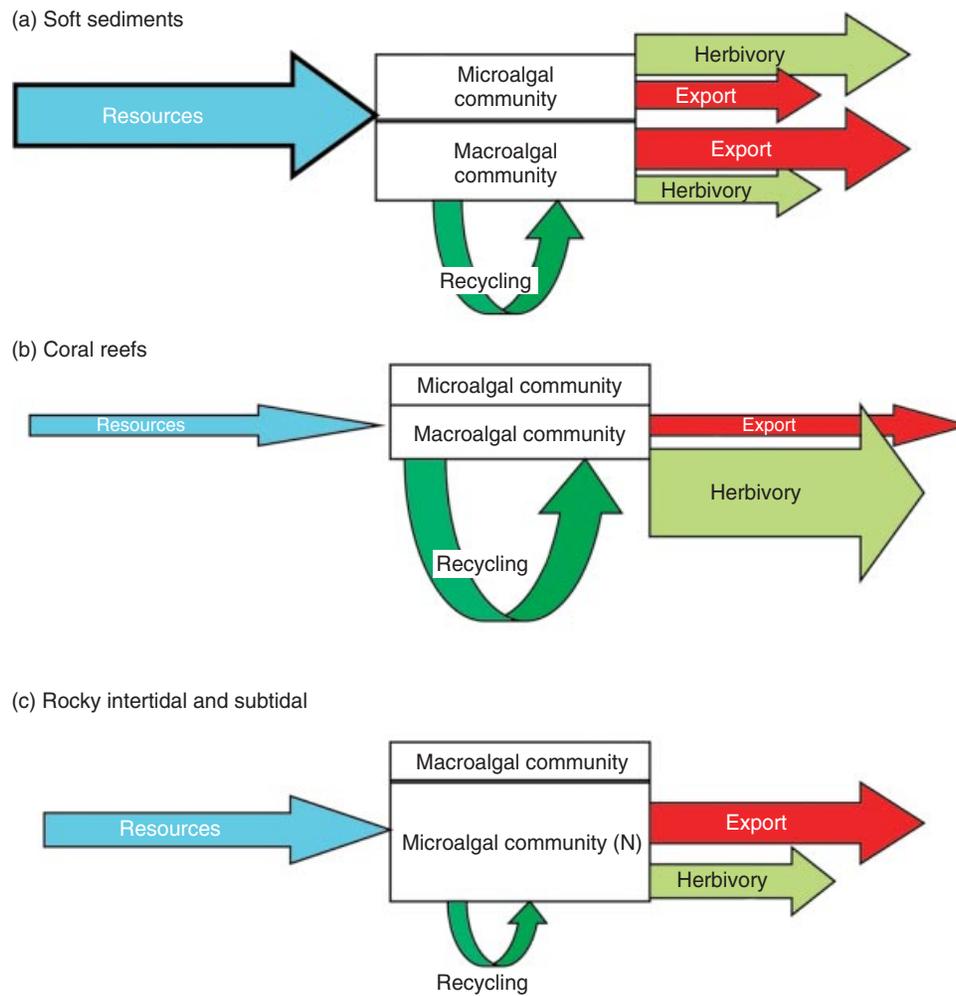
Herbivory has been shown to control algal biomass accumulation with community-level effects. For example, grazers such as amphipods and gastropods can control the abundance of algal epiphytes on seagrasses and hard substrates, and can mediate the negative shading effects of epiphytes in response to nutrient loading (Williams and Ruckelshaus, 1993; Hillebrand et al., 2000). Likewise, grazers can mediate the impact of macroalgal blooms in eutrophic

environments (Worm et al., 2000). On coral reefs, at low to intermediate nutrient supplies, herbivores can control macroalgal abundance and maintain the competitive dominance of slower-growing community types (Hughes et al., 2003; Pandolfi et al., 2003). Rapid growth with nutrient enrichment allows algae to escape control by herbivores and also biomass to accumulate, which ultimately leads to a phase shift. Chemical and structural defenses also provide a refuge from control by herbivores, allowing algal biomass to accumulate even in heavily grazed areas. In soft-sediment communities, enhanced algal growth from high nutrient loading can saturate the grazing potential and decrease per capita consumption rates; grazer abundance can be impacted negatively by the change in physicochemical conditions (i.e., low oxygen, high sulfide and  $\text{NH}_4^+$ ) that result from the decomposition of algal blooms (Hauxwell et al., 1998).

Microbenthic primary production can enter the food web through several pathways, including through grazers, detritus, or dissolved organic carbon (DOC). Field studies show that a large fraction of benthic microalgal biomass can pass through macrograzers (>1 mm), particularly mud snails (*Hydrobia*) (Asmus and Asmus, 1985; Andresen and Kristensen, 2002). In addition, some microphytobenthic production can pass through the "small food chain" consisting of microfauna (unicellular fauna such as ciliates) and meiofauna (<100  $\mu\text{m}$ ) (Fenchel, 1968; Kuipers et al., 1981; Pinckney et al., 2003). Meiofauna have been estimated to occasionally graze up to 100% or more of the benthic microalgal standing stock, although benthic primary production is generally sufficient to supply food resources for meiofaunal grazers (Pinckney et al., 2003).

## 8.9 ENERGY FLOW

The amount of energy sequestered in primary producers and the proportion flowing through algal-dominated benthic estuarine communities varies among soft sediment, coral reef, and rocky intertidal and subtidal ecosystems (Fig. 8.8). In all systems, the amount of energy that is fixed into algal biomass and made available to higher trophic levels is dependent on resources, usually light and nutrients. Overall, systems more closely associated with terrestrial environments, and those that experience restricted water exchange, such as those composed of soft sediments, are assumed to be subject to and affected the most by increasing external nutrient supplies.



**FIGURE 8.8** Energy flow diagrams for different macroalgal communities. The size of the arrow represents the magnitude of flow in the different pathways.

### 8.9.1 Recycling of Nutrients

Across estuarine systems, recycling of nutrients from sediments and biota is most likely greatest in soft sediment and coral reefs and least in rocky intertidal and subtidal systems. In soft-sediment estuaries and lagoons, fluxes of nutrients regenerated from sediments are an important source of recycled nutrients (McGlathery et al., 1997; Fong and Zedler, 2000; Tyler et al., 2003). In some seasons, fluxes meet up to 100% of macroalgal nutrient demand (Sundbäck et al., 2003). Interception of nutrients by macroalgae may reduce supplies to other producer groups and change the path and rate of carbon flow. Macroalgal communities may also be sustained by nutrient release from senescent or self-shaded thalli, or by recycling of nutrients from nearby vascular plant communities such as seagrass beds (for a review, see McGlathery

et al., 2007). In coral reef ecosystems, recycling from sediments is only likely to be significant in enriched systems (Stimpson and Larned, 2000). Other recycled sources in coral reefs include flocculent material settling on the surfaces of algal thalli (Schaffelke, 1999) and animals that release nitrogenous waste products (Williams and Carpenter, 1988). Release of waste products from closely associated animals is also a recycled source of nutrients in intertidal and subtidal systems (Hurd et al., 1994; Bracken, 2004).

### 8.9.2 Carbon Storage

The capacity of ecosystems to store energy, represented by the amount of carbon in the biomass of producers and consumers, varies across estuarine ecosystems. An example is the tremendous difference in producer biomass between coral reef algae (0.03–0.6 kg wet weight/m<sup>2</sup> based on a wet:dry

weight ratio of 10:1, Foster, 1987) and rocky subtidal reefs (3.5 kg wet weight/m<sup>2</sup>, Manley and Dastoor, 1987). Although both are highly productive in terms of gross primary productivity, they occupy different ends of a spectrum in terms of biomass accumulation and therefore carbon storage. In general, opportunistic species with simple thallus forms such as those that dominate coral reef turfs have low levels of biomass; therefore, they can store little carbon despite having relatively rapid growth rates. The low biomass is due to short life spans, susceptibility to removal and export by physical disturbance, and high rates of grazing by herbivores. In contrast, more complex macroalgae that dominate rocky subtidal and intertidal areas often have high standing stocks of carbon. This is due to the longevity of individual thalli, investment in structure to withstand physical disturbances, and lower rates of carbon transfer to herbivores due to protection by chemical and physical defenses. One exception to this generalization is opportunistic macroalgae in shallow soft-sediment estuaries that go through periods of boom and bust and cycle carbon quickly.

### 8.9.3 Herbivory

The amount of energy that is transferred from macroalgae through consumption can vary by orders of magnitude across estuary types. On a global scale, direct consumption by grazers was estimated to be 33.6% of the net carbon fixed by macroalgae, demonstrating their general importance as the base of food webs in coastal ecosystems (Duarte and Cebrian, 1996). Herbivory on coral reefs is extremely high, with large herbivorous fishes and invertebrates acting as “lawn mowers” that keep algal standing stocks very low and carbon transfer very high (for a review see McCook, 1999; Jackson et al., 2001). In rocky subtidal habitats, grazing is important in maintaining diversity, but cannot always overcome the effects of increased resources (Worm and Lotze, 2006). Within soft-sediment systems, rates of primary consumption can vary greatly (Fong et al., 1997; Giannotti and McGlathery, 2001), and consumption of benthic microalgae can be very important (Asmus and Asmus, 1985; Armitage and Fong, 2004).

Benthic microalgal production forms the basis for the benthic food webs in sediments where macroscopic primary producers are lacking. The main pathway of this fixed carbon into the food web is generally considered to be through macrofaunal and meiofaunal grazers (Duarte and Cebrian, 1996), although the detrital pathway is also important. The microbial film (epilithon) on rocky surfaces is an important component in the cycling of carbon, particularly on exposed

and moderately exposed shores with large numbers of limpets and other grazers (Hawkins and Jones, 1992).

### 8.9.4 Detrital Pathway

Death and subsequent decomposition of macroalgal detritus results in the release and recycling of stored carbon. Processing of carbon through detrital pathways comprises about a third of macroalgal net primary productivity globally (Duarte and Cebrian, 1996). However, like grazing, the relative importance of recycling varies across habitats. For example, high energy rocky areas recycle much less carbon from detritus within the system compared to lagoons, while the estimates for recycling within coral reef algae are very high (Duarte and Cebrian, 1996). When algae decompose, they release organic carbon to the water and, in soft sediments systems, to the sediments (for a review see McGlathery et al., 2007). The detrital pathway is also important for benthic microalgal production (Admiraal, 1984). As much as 70% of the NPP by benthic microalgae on a tidal flat was found to enter the food web as detritus (particulate organic carbon, POC), and was further transferred to bacteria and detritus-feeding fauna (Baird et al., 2004).

### 8.9.5 Dissolved Organic Carbon

Substantial DOC also “leaks” from healthy macroalgal thalli (Tyler et al., 2003; Fong et al., 2003). Some organic compounds in the water can be taken up directly by consumers and may alter food webs toward heterotrophic bacteria pathways (Valiela et al., 1997). A large portion (>50%) of the photosynthetic product of benthic microalgae can also be released as DOC, particularly under low nutrient conditions. This DOC enters food webs rapidly through bacteria (Middelburg et al., 2000), forming the benthic equivalent of the pelagial microbial loop. About 40% to 75% of the carbon fixed by motile benthic diatoms can be released as colloidal organic matter or EPS (Goto et al., 1999; Smith and Underwood, 2000) and rapidly transferred to sediment bacteria.

### 8.9.6 Export of Carbon

The rate of carbon exported from benthic estuarine communities varies tremendously across ecosystem types and is a function of standing stock, water motion, and algal morphology. Duarte and Cebrian (1996) have calculated that a global average of 43.5% of macroalgal NPP is exported; however, the range is perhaps the more important metric, varying from approximately 0–85% across macroalgal-dominated habitats. Rocky subtidal systems export a far larger

amount of carbon than coral reefs despite vigorous wave action in both systems due to the larger standing stock. In contrast, pristine soft sediment lagoonal systems export less carbon than rocky systems as there is both less physical disturbance and lower water exchange to detach and remove biomass. Thus, seagrasses in lagoons represent a large and relatively stable reservoir of carbon. In contrast, in eutrophic systems there is often accumulation of large floating algal rafts, resulting in faster turnover and more rapid export of carbon to the ocean (Flindt et al., 1997; Salomonsen et al., 1999). In sediments exposed to strong tidal or wave action, benthic microalgae are easily resuspended together with sediment particles and hence can be transported away (Admiraal, 1984). A large study in the Ems-Dollart Estuary (North Sea coast) showed that, on an annual basis, 14–25% of the microphytobenthic carbon was found in the water column as a result of resuspension (de Jonge and Beusekom, 1995).

## 8.10 FEEDBACKS AND INTERACTIONS

### 8.10.1 Feedbacks on Biogeochemical Cycling in Soft-Sediment Estuaries

Both macro- and microalgal mats have a large impact on the biogeochemical cycling in shallow-water habitats. This effect can be both direct, through nutrient assimilation, retention, and release, and indirect through oxygen production and consumption, affecting mineralization and other redox-sensitive processes. Despite large differences in biomass, the quantitative role of macroalgal and microalgal mats on biogeochemical processes (for example, nitrogen assimilation) can be similar, making the turnover time of algae-bound nutrients a key factor in nutrient retention in shallow systems (McGlathery et al., 2004). Nutrients that are assimilated by benthic algae are, for the most part, only temporarily retained within individual algal thalli on a time scale of days to months. Tissue turnover times vary for the different autotrophs, with seagrasses having a longer retention time (weeks–months) than bloom-forming macroalgae (days–weeks) and microalgae (days). This suggests that nutrients will be recycled faster in systems dominated by microalgae and ephemeral macroalgae than in those dominated by perennial macrophytes (Duarte, 1995).

Both types of benthic algal mats strongly influence the degree of benthic–pelagic coupling by reducing the flux of remineralized nutrients from the

sediment pore water to the overlying water column (Sundbäck et al., 1991; Fong and Zedler, 2000; Anderson et al., 2003; Tyler et al., 2003; see also Section 8.10.5). Benthic algae can outcompete phytoplankton for nutrients if the major nutrient supply is internal flux from the sediments. Therefore, in shallow coastal systems, short-lived phytoplankton blooms often coincide with low benthic algal biomass (Sfriso et al., 1992; Valiela et al., 1992; McGlathery et al., 2001). The influence of benthic microalgae on sediment–water nutrient fluxes is often observed as lower fluxes—or no flux at all—out of the sediment in light when compared with that in the dark (Sundbäck et al., 1991; Sundbäck and McGlathery, 2005). When sediment nutrient sources are insufficient to meet the growth demand of benthic microalgae, there is a downward flux from the water to the sediment, such that the sediment functions as a temporary *nutrient sink* instead of a nutrient source. This applies particularly to autotrophic sediments (oxygen production exceeds oxygen consumption, Engelsen et al., 2008). Also, dissolved organic nutrients, such as dissolved nitrogen (DON), are influenced by both benthic micro- and macroalgae (Tyler et al., 2003; Veuger and Middelburg, 2007).

Benthic algal mats influence the vertical profiles of oxygen and this affects biogeochemical cycling. The presence of dense macroalgal mats can move the location of the oxic–anoxic interface up from the sediments into the mat since only the upper few centimeters of the mat are in the photic zone where oxygen is produced by photosynthesis (Krause-Jensen et al., 1996; Astill and Lavery, 2001). Below the photic zone, decomposing macroalgae release nutrients that can diffuse upward to support production. Unattached macroalgal mats tend to be patchy and unstable, but oxygen and nutrient gradients develop quickly, in as little as 24 h, suggesting that this filtering function occurs even in dynamic environments (Astill and Lavery, 2001). Overall, sediment nutrient cycling is enhanced by the presence of macroalgae, presumably due to the input of organic matter and faster decomposition (Trimmer et al., 2000; Tyler et al., 2003). In the surface layer of the sediment, dynamic oxygen gradients created by benthic microalgal activity also control the rate and vertical position of the sequence of redox-sensitive processes in the sediment, such as nitrification, denitrification, sulfate, iron and manganese reduction, and methane production.

Benthic micro- and macroalgae have an important influence on rates of denitrification and nitrification. Rates tend to be low in sediments underlying macroalgal mats, likely due to algal competition with bacteria for  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . In addition, high free sulfide

concentrations in organic-rich sediments underlying macroalgal accumulations may inhibit nitrification (Trimmer et al., 2000; Dalsgaard, 2003). In dense macroalgal mats, the zone of denitrification may be moved up from the sediments into the oxic–anoxic interface of the mat (Krause-Jensen et al., 1999). The combined use of oxygen and nitrogen microsensors has shown that benthic microalgae can both reduce and enhance denitrification. During photosynthesis, the oxygenated sediment layer gets deeper, and it takes longer for the  $\text{NO}_3^-$  to diffuse from the water column to the denitrification zone of the sediment, reducing the rate of denitrification. Under low nitrogen conditions, benthic microalgae will also compete with nitrifying bacteria for  $\text{NH}_4^+$ , reducing the availability of substrate ( $\text{NO}_3^-$ ) for the denitrifiers. Such an effect by benthic microalgae can still occur down to a water depth of 15 m (Sundbäck et al., 2004). When ambient N concentrations are high, oxygen production will instead stimulate nitrification (an aerobic process), and thereby also stimulate nitrification-coupled denitrification (Risgaard-Petersen, 2003). The alternative pathway of bacterial nitrogen removal, anaerobic ammonium oxidation (anammox), is negatively affected by the presence of active benthic microalgae (Risgaard-Petersen et al., 2004).

### 8.10.2 Feedbacks on Sediment Stabilization

Macroalgal mats may either stabilize or destabilize sediments, depending on algal abundance. Dense macroalgal mats stabilize sediments by decreasing shear flow at the sediment surface (Escartín and Aubrey, 1995) and thus sediment suspension (Sfriso and Marcomini, 1997; Romano et al., 2003). Thick macroalgal mats (equivalent to 3.5 to 6.2 kg wet wt/m<sup>2</sup>) displace velocities vertically and can deflect 90% of the flow over the mat, with only 10% of the flow traveling through the mat (Escartín and Aubrey, 1995). However, macroalgae also exist at low densities and in patchy distributions that are often dependent on available substratum for attachment or on advection of drift algae (Thomsen et al., 2006) and may act to destabilize sediments. At low densities, flow causes macroalgae to move and scour the sediment, increasing sediment suspension relative to bare sediments. This sediment destabilization is akin to the well-documented phenomenon of saltating or abrading particles increasing erosion in cohesive sediments (e.g., Houser and Nickling, 2001; Thompson and Amos, 2002, 2004). In cohesive beds, the critical stress required to initiate erosion is often greater than the stress required to maintain the sediment in suspension. Macroalgae that scrape the bed while

moving across it can dislodge particles and increase sediment suspension/erosion.

The influence of benthic microbial mats on surface sediment stability is well studied (e.g., Paterson, 1989; de Brouwer et al., 2006). The mechanism behind this stabilizing effect is the production and extrusion of EPS by diatoms through the raphe during their gliding movements. Its composition can be complex and varies between species, but mainly consists of carbohydrates, proteins, and sulfate groups. EPS bind sediment particles together so that the shear stress needed for erosion of sediment is increased, and therefore the sediment is less easily eroded and resuspended. Besides gluing sediment particles together, EPS also have physiological and ecological implications. On tidal flats, there are large diel changes in environmental variables (light, temperature, salinity, water content, oxygen, and erosive forces). By secreting EPS, the diatoms become embedded in a cohesive matrix that can create more stable conditions. This sediment stabilization is a seasonal phenomenon at least in temperate systems, and the deposited material may be resuspended at times of the year when the microalgae are less productive (Widdows et al., 2004).

### 8.10.3 Effects on Faunal Biomass, Diversity, and Abundance

Macroalgae can have positive and negative effects on associated organisms. On the positive side, they can provide a food source through direct assimilation or through detritus-based food chains, as well as a protective refuge from predators (Norkko and Bonsdorff, 1996). The complex structure of some macroalgal species, such as *Gracilaria vermiculophylla*, could potentially create a predation refuge for commercially valuable blue crab and fish recruits as well as shrimps and amphipods in both the subtidal and lower intertidal zones of estuaries (Hay et al., 1990; Thomsen et al., 2009). Macroalgae also may provide an important link between estuarine habitats (subtidal to intertidal, sand flats to seagrass beds), as associated organisms are transferred with advecting macroalgae between habitats (Holmquist, 1994; Thomsen et al., 2009).

The negative effects of dense macroalgae on benthic fauna include harmful exudates that are toxic to some organisms, low dissolved oxygen within and under dense macroalgal mats (Hull, 1987; Isaksson and Pihl, 1992), and high dissolved  $\text{NH}_4^+$  concentrations that also can be toxic (Hauxwell et al., 1998). These negative effects have been associated with observed reductions in abundance of various macrofauna, including bivalves, gastropods, amphipods, and fish, as well as increases in certain polychaetes,

oligochaetes, and amphipods (Norkko and Bonsdorff, 1996; Raffaelli, 2000; Wennhage and Pihl, 2007).

Both macro- and microalgal mats can cause negative upward cascades in estuarine food webs. For example, microalgal mats subjected to high nutrient loads shifted to dominance by cyanobacteria and purple sulfur bacteria and increased the mortality of the dominant herbivore, the mudsnail *Cerithidia californica*, threefold over mats subjected to lower nutrients that were dominated by diatoms (Armitage and Fong, 2004). Changes in benthic fauna associated with macroalgal blooms may cause resident and migratory shorebirds to change foraging behavior. For example, sandpipers spend more time probing in their search for food when they are foraging on top of macroalgal mats, but more time repeatedly pecking when mats are absent (Green, 2010). As infauna are a major food source for birds and other secondary consumers, macroalgal impacts that reduce this link in the food chain may impair this vital ecosystem function. There is also growing evidence that indirect positive effects in the form of “facilitation” cascades mediated by habitat created or modified by macroalgal species can enhance biodiversity and organismal abundances (Thomsen et al., 2010).

#### 8.10.4 Facilitation by Fauna

Macroalgae in soft-bottom environments can be facilitated by fauna, such as tube-dwelling polychaetes and bivalves, that provide hard substrate for settlement and growth. For example, the tube-cap forming polychaete, *Diopatra cuprea*, facilitates macroalgal assemblages in shallow lagoons. These organisms create and maintain attachment sites by incorporating algal fragments into tube caps, thus increasing algal residence time on mudflats compared to unattached algae (Thomsen et al., 2005). This association both increases population stability and resilience by providing a stable substrate that retains algae against hydrodynamic forces such as tidal flushing and storm surge, and by providing new fragments to populate new areas or repopulate areas after a storm disturbance. Oyster reefs and mussel and clam beds likewise provide substrate for algal attachment and increase both biomass and diversity relative to nearby bare sediments (McCormick-Ray, 2005). These biotic substrates also enhance algal growth by local fertilization effects. Grazers such as the California Horn Snail can facilitate the development of macroalgal mats by consuming microalgal competitors and releasing nutrients for uptake by macroalgae (Fong et al., 1997). Also, on coral reefs, Carpenter and Williams (1993) showed that urchin grazing facilitated algal turf production by reducing self-shading within the dense algal turf community. Invertebrate grazers that remove microalgal

films that sometimes form on macroalgal thalli, but do not damage the macroalgae, may facilitate macroalgal growth by enhancing nutrient and gas exchange.

#### 8.10.5 Competition between Benthic Algal Primary Producers

Competition between benthic and pelagic algae was mentioned briefly in Section 8.10.1. Here we discuss the interplay between mats of benthic microalgae and loose mats of opportunistic macroalgae in shallow water in more detail (Fig. 8.9).

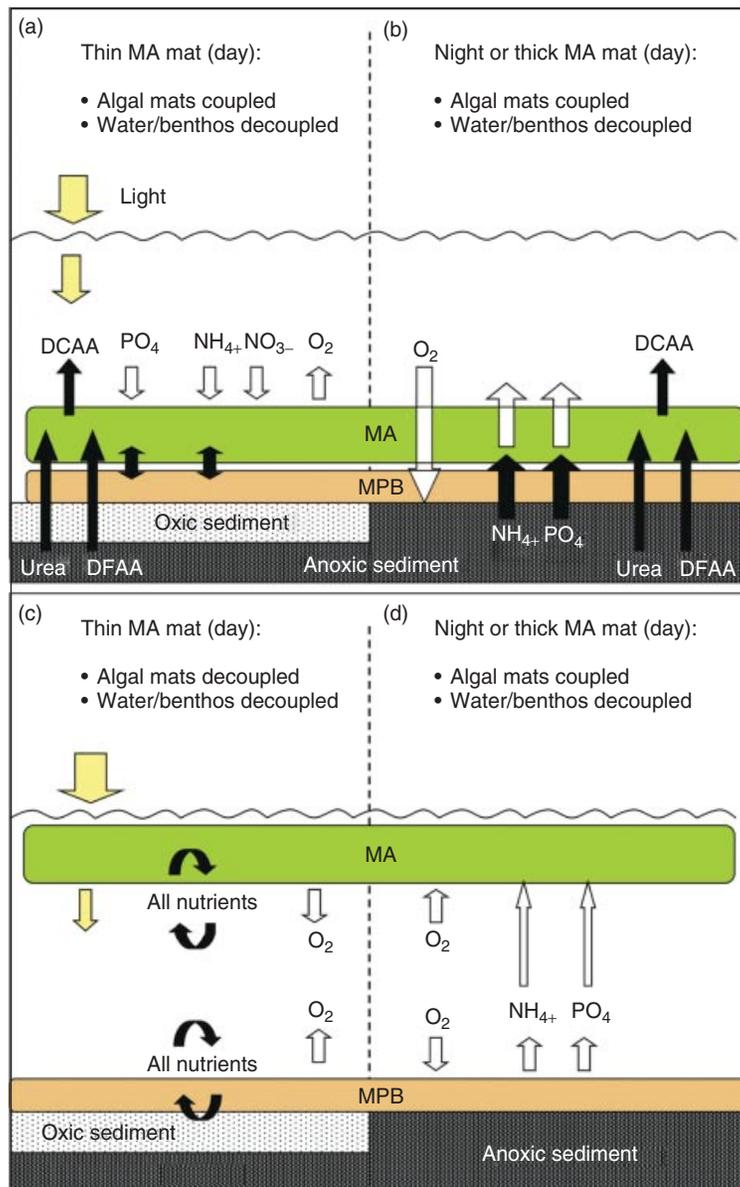
Benthic micro- and macroalgae interact, directly and indirectly, through their impact on light, oxygen, and nutrient conditions. The type and strength of the interactions change with the growth phase, physiological state, the spatial location of the mats in relation to each other, and the type of the water body as it relates to tidal amplitude. Shading by dense macroalgal mats generally decreases benthic microalgal production. However, shade-adapted microphytobenthic communities that remain active—and even thrive—below macroalgal mats are also present, provided that at least some light penetrates to the sediment surface (Sundbäck and McGlathery, 2005). An example of such a shade-adapted species is the large sigmoid diatom *Gyrosigma balticum*. Benthic microalgae, particularly diatoms, are in fact often resistant to short-term (days, few weeks) hypoxia and anoxia and promote recovery of sediment systems by rapidly reoxygenating the sediment surface after hypoxic and anoxic events (Larson and Sundbäck, 2008).

When nutrient concentrations in the water column are low, primary producer groups compete for nutrients. In such a situation, the importance of sediments as a source of remineralized nutrients increases. At the same time, an active benthic microalgal mat will decrease the availability of sediment nutrients, limiting the growth of loose macroalgal mats, as well as phytoplankton. In Figure 8.9, two conceptual models are shown: one where the macroalgal mat (MA) exists close to the sediment surface (Fig. 8.9 a, b) and the other where the macroalgal mat is floating at the water surface (Fig. 8.9 c, d). The coupling also depends on the thickness of the macroalgal mat and the time of the day (day/night, tidal cycle).

## 8.11 ENVIRONMENTAL IMPACTS

### 8.11.1 Eutrophication

As estuarine systems become increasingly eutrophied and macroalgal blooms occur, the decomposing macroalgal mats contribute significant amounts of organic matter to the water and sediments (Trimmer



**FIGURE 8.9** Conceptual models of interactions between mats of benthic microalgae (microphytobenthos, MPB) and loose macroalgae (MA). Upper panel (a and b): macroalgal mat lying close to the sediment surface, a situation common on tidal coasts during low tide. Lower panel (c and d): macroalgal mat floating at the water surface, a typical situation in microtidal waters. In (a), the two closely coupled mats intercept nutrient release from the sediment to the overlying water, whereas in case (b) nutrients are released from the anoxic sediment and the coupled mats to the overlying water. When the two algal mats are spatially separated (c and d), there is no nutrient exchange between the two mats or between the sediment and water column. Instead, algal productivity is sustained by efficient recycling of nutrients within the mats themselves (c). This scenario applies particularly to autotrophic (often sandy) sediments in microtidal areas when nutrient levels in the overlying water column are low. At night, or when a thick floating macroalgal mat does not allow light to penetrate to the sediment surface (d), pore-water nutrients are released to the water column where they can be used by floating macroalgae. DFAA refers to dissolved free amino acids, and DCAA refers to dissolved combined amino acids. *Source:* Model drawings were inspired by the model in Astill and Lavery (2001) and redrawn from Sundbäck and McGlathery (2005).

et al., 2000; Tyler et al., 2003; Nielsen et al., 2004). This decomposing organic matter turns over relatively quickly and is a positive feedback mechanism that increases nutrient availability to sustain large

algal standing stocks. Other consequences of algal bloom formation in eutrophic estuaries include decreases in fish/invertebrate abundance and diversity, anoxia, and loss of seagrasses, corals,

and perennial algae (see 8.10). Eutrophication can lead to phase shifts from seagrass communities to algal-dominated communities (Hauxwell et al., 2001; Valentine and Duffy, 2006), similar to what has been observed in lakes and several other ecosystems (Scheffer et al., 2001; Scheffer and van Nes, 2004). It is essential to know whether these transitions are reversible phase shifts or if they represent an alternative state stabilized by negative feedbacks (Fig. 8.10).

Tropical estuaries with coral reefs may also undergo phase shifts from coral to algal domination (Knowlton, 2004), although the link to eutrophication is less well established than for soft-sediment habitats. One classic study in Kaneohe Bay (Hawaii, USA) established that hard-bottomed communities shifted from coral to algae and back to coral again with changes in nutrient loading. In this system, sewage outfalls into the Bay increased nutrients and stimulated phytoplankton blooms. Lower light penetration stressed corals, shifting the competitive advantage to the macroalga *Dictyosphaeria cavernosa*, the “green bubble algae” that was able to creep over the substrate and replace coral. After sewage was diverted to an offshore outfall, water clarity increased and coral gradually recolonized and replaced the algae. However, while Kaneohe Bay is a clear example of a eutrophication-driven transition from coral- to algal-dominated tropical reef communities, several other studies suggest that co-occurring stressors, such as the loss of grazers, must be in play to shift these communities (Pandolfi et al., 2003).

The growth of benthic microalgae also may respond to increased nutrient load, particularly in sandy sediments with lower concentrations of pore-water nutrients than finer sediments (Nilsson et al., 1991). It appears that microphytobenthic communities are highly resilient to eutrophication-related disturbances and may play an important role in the resilience of the sediment community after, for example, hypoxic and anoxic events (McGlathery et al., 2007; Larson and Sundbäck, 2008). The negative impact of eutrophication on the benthic microalgal community may be more gradual and slower than for benthic macroscopic primary producers such as seagrasses. Thus, a partial beneficial “buffering” effect of benthic microalgae on shallow sediment systems may persist even in more heavily eutrophied systems. Microphytobenthic communities possess, owing to high diversity and functional redundancy, a certain degree of plasticity, increasing the overall resilience of shallow-water sediment systems after pelagic bloom events. Benthic diatoms can survive

periods of only a few % of incident light (or even darkness), and high sulfide levels, and can rapidly resume photosynthesis when exposed to light or after an anoxic event (Larson and Sundbäck, 2008 and references therein). This scenario, with benthic microalgae surviving despite deteriorating conditions, may apply particularly to areas where macroalgal bloom events last only a few months (Pihl et al., 1999; McGlathery et al., 2001; Dalsgaard, 2003), leaving the rest of the year open to benthic microalgal primary production. In warm, eutrophic microtidal systems with long-lasting macroalgal blooms, benthic microalgae can be outcompeted by shading and also by dystrophic events when the macroalgal blooms eventually collapse (Viaroli et al., 1996).

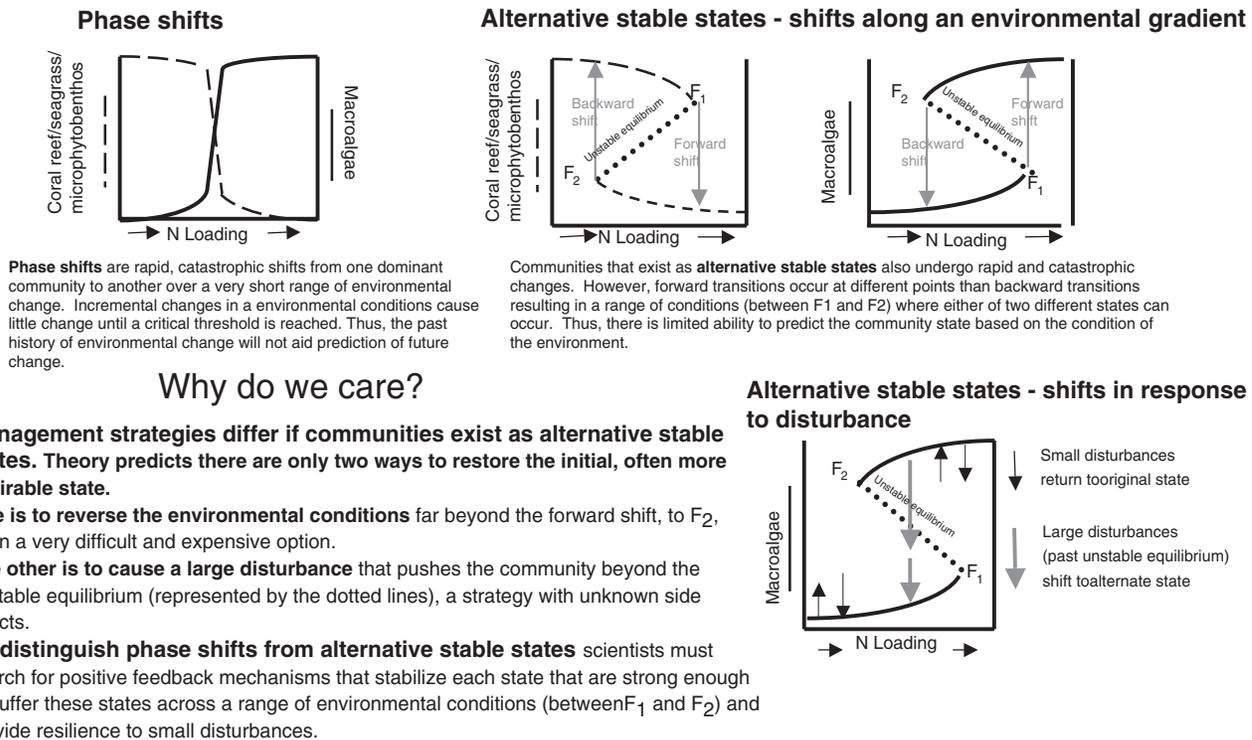
### 8.11.2 Invasions

A recent review by Williams and Smith (2007) identified a total of 277 introduced macroalgal species in marine waters worldwide. The primary vectors for invasion are boat traffic and aquaculture. Most reports are from temperate regions; there is a general lack of information on introduced species from tropical waters, especially coral reef habitats (Coles and Eldredge, 2002). The taxonomic distribution of invasive species identified in the review included 165 Rhodophytes, 66 Phaeophytes, 45 Chlorophytes, and 1 Charophyte. Most successful invaders were foliose and filamentous forms, followed by leathery and siphonous forms (Williams and Smith, 2007).

Several characteristics of successful invaders have been identified: rapid reproduction and the potential for successful evolution in new habitats, rapid colonization (including fragmentation as a source of new propagules), vegetative growth for population stability, rapid nutrient uptake and growth potentials (“weedy” species), antiherbivore defenses, and a wide environmental tolerance (Nyberg and Wallentinus, 2005). Both physical disturbance (by killing natives and opening space) and eutrophication (by relaxing resource competition) can make estuarine habitats more easily invaded. Some well-known invasions are those of *Caulerpa taxifolia*, *Gracilaria vermiculophylla*, *G. salicornia*, *Kappaphycus alvarezii*, *Hypnea musciformis*, *Sargassum muticum*, and *Codium fragile* (Fig. 8.11). In general, the community-level effects of invasive macroalgae are negative when accumulations are dense, and include shading of native algal species leading to decreases in abundance and diversity, decline in epifaunal and fish abundance, diversity and reproduction, loss of seagrass, and increases in incidences of anoxia and

## The Nature of Community Collapse: Phase Shifts or Alternative Stable States?

Macroalgae are taking over benthic estuarine communities worldwide. Catastrophic collapses from long-lived seagrass and coral dominated ecosystems to opportunistic and shorter-lived macroalgae have focused research on the nature of these shifts. One important question is whether these are simple and reversible phase shifts, or if they represent alternative stable states with stabilizing mechanisms that inhibit recovery to the initial state (Scheffer et al. 2001, Beisner et al. 2003, Didham and Watts 2005).



**FIGURE 8.10** The Nature of Community Collapse: Phase Shifts or Alternative Stable States?

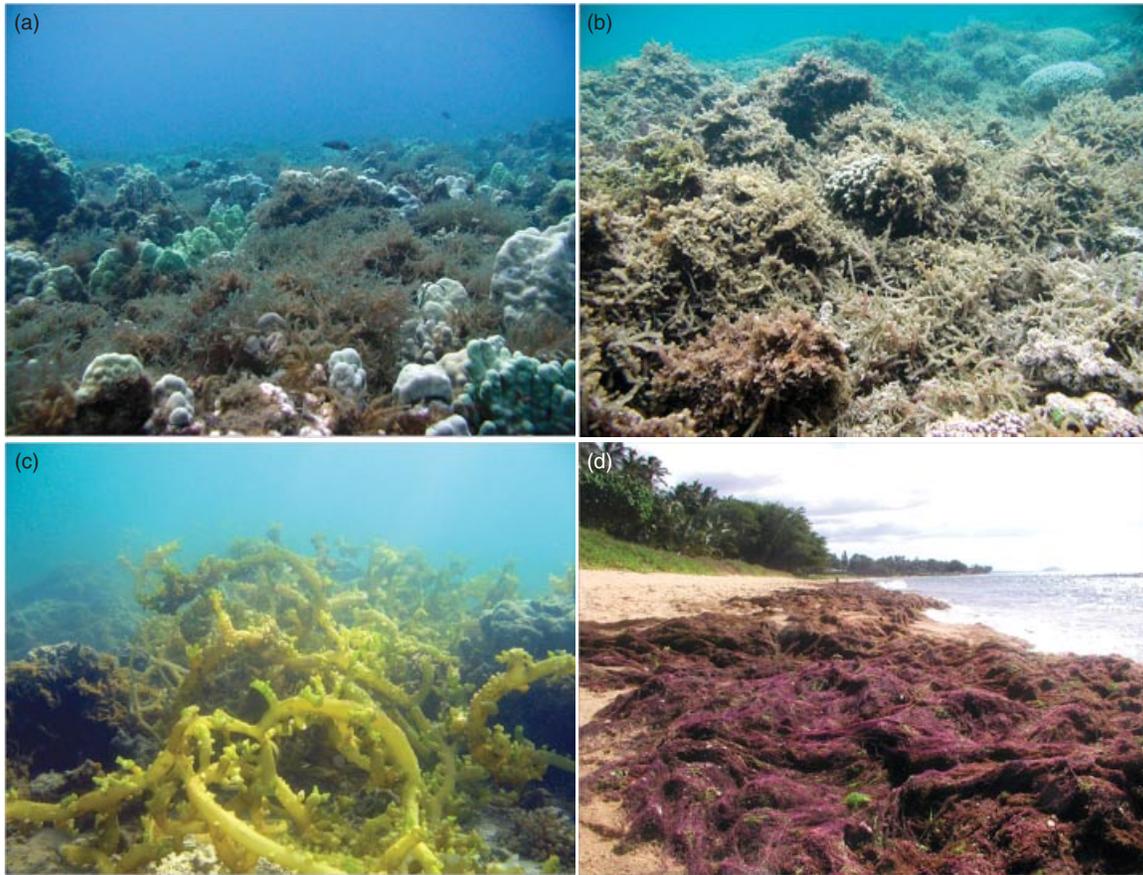
hypoxia. There may be cases where introduced seaweeds increase habitat structure and complexity on unvegetated mudflats, as is the case with *G. vermiculophylla* in some Virginia coastal lagoons, and have a positive effect on faunal abundances as long as algal populations stay below bloom proportions (Thomsen et al., 2009).

### 8.11.3 Climate Change

Climate change impacts on benthic algae include sea-level rise, increased temperature, increased  $\text{CO}_2$  in the air and water, ocean acidification, and changes in weather patterns (Parmesan and Yohe, 2003). Rising temperatures have been predicted to cause poleward shifts in geographic ranges of species and ultimately alter the composition of marine communities (for a review see Hawkins et al., 2008), including benthic primary producers in estuaries. In temperate latitudes, warming may result in deepening thermoclines

and relaxation of cold upwelling, thus enabling warm water species to more easily jump gaps in distribution, especially along the western margins of major continents. Continued temperature increases in tropical systems will likely result in further increases in dominance of benthic algae as a result of coral bleaching and mortality (Hoegh-Guldberg, 1999). Changes in storm frequency may influence the distribution and abundance of benthic primary producers in estuaries by reducing or enhancing intertidal and shallow subtidal habitat via sedimentation, reducing water clarity and the depth of the photic zone, and increasing scouring (Zedler and West, 2008). For example, experimentally simulated scouring by sediments shifted the algal community from a diverse assemblage of macroalgae to more opportunistic forms (Vaselli et al., 2008) with high temporal variability (Bertocci et al., 2005) in rocky coastal habitats.

Some experimental evidence as well as studies of aquaculture optimization techniques suggests



**FIGURE 8.11** Many species of invasive red algae proliferate on Hawaiian coral reefs including (a) *Acanthophora spicifera* (b) *Gracilaria salicornia*, and (c) *Kappaphycus alvarezii*. (d) In some areas, such as the coast of Maui, blooms of *Hypnea musciformis* become so large that they detach, form floating rafts, and deposit on the beach. *Source:* Photographs by Jennifer Smith.

that increased  $\text{CO}_2$  concentrations and the resultant acidification of seawater may have strong effects on estuarine algae. Experiments with elevated  $\text{CO}_2$  and lowered pH have revealed strong negative effects on tropical crustose calcareous algae (Jokiel et al., 2008; Anthony et al., 2008), and also show that *Porphyra* growth decreased with increased  $\text{CO}_2$ , most likely due to increases in dark respiration rates (Israel et al., 1999).

There is also evidence that complex interactions among factors may be important. For example, while increased temperature and nutrients may increase algal recruitment and growth up to some threshold, they should also increase the number of grazers, driving intertidal communities toward opportunistic species and away from dominance by fucoids (Lotze and Worm, 2002). O'Connor (2009) found that warming strengthens herbivore–algal interactions, shifting important trophic pathways. Recent multifactorial experiments show that certain stages in complex life cycles may be more sensitive to interactions among

climate-related factors and may be important bottlenecks limiting the ability of algal dominants to survive climate change over the long term. For example, while adult kelp sporophytes in polar regions are relatively hardy to changes in temperature, UV light, salinity and their interactions, germination of zoospores is much more sensitive (Fredersdorf et al., 2009). Aquaculture studies have identified an important interaction between rising  $\text{CO}_2$  and nutrients, with positive  $\text{CO}_2$  effects on growth of *Gracilaria* being accelerated with pulsed nutrient supplies (Friedlander and Levy, 1995), suggesting that storms combined with rising  $\text{CO}_2$  will facilitate algal blooms in estuaries. Other studies suggest that interactions among climate change factors may result in changes in habitats. In sheltered embayments of the North Sea, rising sea level and eutrophication combined to cause shifts from *Zostera* to opportunistic green macroalgae (Reise et al., 2008). Overall, it appears that interacting factors associated with climate change will enhance algal blooms, and may shift communities to greater algal dominance.

## REFERENCES

- Admiraal W. The ecology of estuarine sediment-inhabiting diatoms. In: Round FE, Chapman DJ, editors. *Progress in Phycological Research*. Volume 3, Bristol: Biopress Ltd; 1984. p 269–314.
- Anderson IC, McGlathery KJ, Tyler AC. Microbial mediation of 'reactive' nitrogen transformations in a temperate lagoon. *Mar Ecol Prog Ser* 2003;246:73–84.
- Andresen M, Kristensen E. The importance of bacteria and microalgae in the diet of the deposit-feeding polychaete *Arenicola marina*. *Ophelia* 2002;56:179–196.
- Anthony KRN, Kline DI, Diaz-Pulida G, Hoegh-Guldberg O. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc Natl Acad Sci* 2008;105:17442–17446.
- Armitage AR, Fong P. Upward cascading effects of nutrients: shifts in a benthic microalgal community and a negative herbivore response. *Oecologia* 2004;139:560–567.
- Asmus H, Asmus R. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. *Helgol Meeresunters* 1985;39:273–301.
- Astill H, Lavery P. The dynamics of unattached benthic macroalgal accumulations in the Swan-Canning Estuary. *Hydrol Processes* 2001;15:2387–2399.
- Atkinson MJ, Smith SV. C:N:P ratios of marine benthic plants. *Limnol Oceanogr* 1983;28:568–574.
- Baird D, Asmus H, Asmus R. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. *Mar Ecol Prog Ser* 2004;279:45–61.
- Belk MS, Belk D. Observation of algal colonization on *Acropora aspera* killed by *Acanthaster planci*. *Hydrobiologia* 1975;46:29–32.
- Berg PB, Roy H, Janssen F, Meyer V, Jorgensen BB, Huettel M, de Beer D. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. *Mar Ecol Prog Ser* 2003;261:75–83.
- Berg PB, Roy H, Wiberg PW. Eddy correlation flux measurements: the sediment surface area that contributes to the flux. *Limnol Oceanogr* 2007;52:1672–1684.
- Bertocci I, Maggi E, Vaselli S, Benedetti-Cecchi L. Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. *Ecology* 2005;86:2061–2067.
- Billerbeck M, Roy H, Bosselmann K, Huettel M. Benthic photosynthesis in submerged Wadden Sea intertidal flats. *Estuar Coast Shelf Sci* 2007;71:704–716.
- Borum J, Pedersen MF, Krause-Jensen D, Christensen PB, Nielsen K. Biomass, photosynthesis and growth of *Laminaria saccharina* in a High-Arctic fjord, NE Greenland. *Mar Biol* 2002;141:11–19.
- Boyer KE, Fong P. Macroalgal-mediated transfers of water column nitrogen to intertidal sediments and salt marsh plants. *J Exp Mar Biol Ecol* 2005;321:59–69.
- Boyle KA, Fong P, Kamer K. Spatial and temporal patterns in sediment and water column nutrients in an eutrophic southern California estuary. *Estuaries* 2004;27:254–267.
- Bracken ME. Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. *J Phycol* 2004;40:1032–1041.
- Brinkhuis BH. Comparisons of salt-marsh fucoid production estimated from 3 different indexes. *J Phycol* 1977;13:328–335.
- de Brouwer JFC, Neu TR, Stal LJ. On the function of secretion of extracellular polymeric substances by benthic diatoms and their role intertidal mudflats. In: Kromkamp JC, de Brouwer JFC, Blanchard GF, Forster RM, Creach V, editors. *Functioning of Microphytobenthos in Estuaries*. Amsterdam: Royal Netherlands Academy of Arts and Sciences; 2006. p 45–61.
- Bruno JF, Boyer KE, Duffy JE, Lee SC. Relative and interactive effects of plant and grazer richness in a benthic marine community. *Ecology* 2008;89:2518–2528.
- Brush MJ, Nixon SW. Biomass layering and metabolism in mats of the macroalga *Ulva lactuca* L. *Estuaries* 2003;26:916–926.
- Cadée GC, Hegeman J. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balgzand, Dutch Wadden Sea. *Neth J Sea Res* 1977;11:24–41.
- Cahoon LB. The role of benthic microalgae in neritic ecosystems. *Oceanogr Mar Biol: Ann Rev* 1999;37:47–86.
- Carpenter RC, Williams SL. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. *Limnol Oceanogr* 1993;38:687–694.
- Cebrián J. Patterns in the fate of production in plant communities. *Am Nat* 1999;154:449–468.
- Cebrián J. Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnol Oceanogr* 2002;47:11–22.
- Chapman ARO, Lindley JE. Seasonal growth of *Laminaria solidongula* in the Canadian high Arctic in relation to irradiance and dissolved nutrient concentrations. *Mar Biol* 1980;57:1–5.
- Coles SL, Eldredge LG. Nonindigenous species introductions on coral reefs: A need for information. *Pac Sci* 2002;56:191–209.
- Connell JH. Community interactions on marine rocky intertidal shores. *Annu Rev Ecol Syst* 1972;3:169–192.
- Dalsgaard T. Benthic primary production and nutrient cycling in sediments with benthic microalgae and transient accumulation of macroalgae. *Limnol Oceanogr* 2003;48:2138–2150.
- Denny MW. Predicting physical disturbance: Mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol Mongr* 1995;55:69–102.
- Denny MW, Daniel TL, Koehl MAR. Mechanical limits to size in wave-swept organisms. *Ecol Mongr* 1985;51:69–102.
- Delgado O, Rodriguez-Prieto C, Gacia E, Ballesteros E. Lack of severe nutrient limitation in *Caulerpa taxifolia* (Vahl) C. Agardh, an introduced seaweed spreading over the oligotrophic Northwestern Mediterranean. *Botanica Marina* 1996;39:61–67.

- Duarte CM. Nutrient concentration of aquatic plants: Patterns across species. *Limnol Oceanogr* 1992;37:882–889.
- Duarte CM. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 1995;41:87–112.
- Duarte CM, Cebrian J. The fate of marine autotrophic production. *Limnol Oceanogr* 1996;41:1758–1766.
- Dunton KH. Growth of dark-exposed *Laminaria saccharina* (L.) Lamour. and *Laminaria solidungula* J. Ag. (Laminariales: Phaeophyta) in the Alaska Beaufort Sea. *Journal of Experimental Marine Biology and Ecology* 1985;94:181–189.
- Engelsen A, Hulth S, Pihl L, Sundbäck K. Benthic trophic status and nutrient fluxes in shallow-water sediments. *Estuar Coast Shelf Sci* 2008;78:783–795.
- Escartín J, Aubrey DG. Flow structure and dispersion within algal mats. *Estuar Coast Shelf Sci* 1995;40:451–472.
- Fenchel T. The ecology of marine microbenthos II. The food of marine benthic ciliates. *Ophelia* 1968;5:123–136.
- Fenchel T, Glud RN. Benthic Primary production and O<sub>2</sub>-CO<sub>2</sub> dynamics in a shallow water sediment: spatial and temporal heterogeneity. *Ophelia* 2000;53:159–171.
- Flindt M, Salomonsen J, Carrer M, Bocci M, Kamp-Nielsen L. Loss, growth, and transport dynamics of *Chaetomorpha aerea* and *Ulva rigida* in the Lagoon of Venice during and early summer campaign. *Ecol Model* 1997;102:133–141.
- Flindt MR, Neto J, Amos CL, Pardal MA, Bergamasco A, Pedersen CB, Andersen FØ. Plant bound nutrient transport: Mass transport in estuaries and lagoons. In: Nielsen SL, Banta GT, Pedersen MF, editors. *Estuarine Nutrient Cycling: The Influence of Primary Producers*. Dordrecht: Kluwer Academic Publishers; 2004. p 93–128.
- Fong P, Desmond JS, Zedler JB. The effect of a horn snail on *Ulva expansa* (Chlorophyta): consumer or facilitator of growth? *J Ecol* 1997;33:353–359.
- Fong P, Zedler JB. Sources, sinks, and fluxes of nutrients (N + P) in a small highly-modified estuary in southern California. *Urban Ecosyst* 2000;4:125–144.
- Fong P, Fong J, Fong C. Growth, nutrient storage, and release of DON by *Enteromorpha intestinalis* in response to pulses of nitrogen and phosphorus. *Aquatic Botany* 2003;78:83–95.
- Fong P, Smith T, Wartian M. Protection by epiphytic cyanobacteria maintains shifts to macroalgal-dominated communities after the 1997–98 ENSO disturbance on coral reefs with intact herbivore populations. *Ecology* 2006;87:1162–1168.
- Foster SA. The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. *J Exp Mar Biol Ecol* 1987;105:1–20.
- Fredersdorf J, Müller R, Becker S, Wienke C, Bischof K. Interactive effects of radiation, temperature, and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia* 2009;160:483–492.
- Friedlander M, Levy I. Cultivation of *Gracilaria* in outdoor tanks and ponds. *J Appl Phycol* 1995;7:315–324.
- Gaylord B, Rosman JH, Reed DC, Koseff JR, Fram J, MacIntyre S, Arkema K, McDonald C, Brzezinski MA, Largier J, Monismith SG, Raimondi PT, Mardian B. Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnol Oceanogr* 2007;52:1838–1852.
- Giannotti AL, McGlathery KJ. Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta*. *J Phycol* 2001;37:1–7.
- Glud RN. Microscale techniques to measure photosynthesis: a mini-review. In: Kromkamp JC, de Brouwer JFC, Blanchard GF, Forster RM, Creach V, editors. *Functioning of Microphytobenthos in Estuaries*. Amsterdam: Royal Netherlands Academy of Arts and Sciences; 2006. p 31–41.
- Glud RN, Kühl M, Wenzhöfer F, Rysgaard S. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance of ecosystem primary production. *Mar Ecol Prog Ser* 2002;238:15–29.
- Glud RN, Woelfel J, Karsten U, Kuhl M, Rysgaards S. Rysgaard Benthic microalgal production in the Arctic: Status of the current database. *Botanica Marina*, Submitted.
- Goto NT, Kawamura T, Mitamura O, Terai H. Importance of extracellular organic carbon production in the total primary production by tidal-flat diatoms in comparison to phytoplankton. *Mar Ecol Prog Ser* 1999;190:289–295.
- Green L. Macroalgal mats control trophic structure and shorebird foraging behavior in a Southern California estuary. Ph.D dissertation. Los Angeles: University of California; 2010. pp. 190
- Guiry MD, Guiry GM. *AlgaeBase Version 4.2*. Galway: National University of Ireland; 2007. Worldwide electronic publication. Available at <http://www.algaebase.org>; accessed 2011.
- Hawkins SJ, Moore PJ, Burrows MT, Poloczanska E, Mieszkowska N, Herbert RJH, Jenkins SR, Thompson RC, Genner MJ, Southward AJ. Complex interactions in a rapidly changing world: Responses of rocky shore communities to recent climate change. *Clim Res* 2008;37:123–133.
- Hay ME. Pattern of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 1984;65:446–454.
- Hay ME, Duff JE, Fenical W. Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. *Ecology* 1990;71:733–743.
- Hauxwell J, Cebrián J, Furlong C, Valiela I. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 2001;82:1007–1022.
- Hauxwell J, McClelland J, Behr PJ, Valiela I. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 1998;21:347–360.
- Hepburn CD, Holborow JD, Wing SR, Frew RD, Hurd CL. Exposure to waves enhances growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. *Mar Ecol Prog Ser* 2007;339:99–108.
- Hillebrand HB, Worm B, Lotze HK. Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. *Mar Ecol Prog Ser* 2000;204:27–38.

- Hoegh-Guldberg O. Climate change, coral bleaching, and the future of the world's coral reefs. *Mar Freshw Res* 1999;50:839–866.
- Holmquist JG. Benthic macroalgae as a dispersal mechanism for fauna: influence of a marine tumbleweed. *J Exp Mar Biol Ecol* 1994;180:235–251.
- Houser CA, Nickling WG. The factors influencing the abrasion efficiency of saltating grains on a clay-cruste playa. *Earth Surf Processes and Landforms* 2001;26:491–505.
- Hughes TP, Baird AH, Bellwood DR, Card M, Connoll SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J. Climate change, human impacts, and the resilience of coral reefs. *Science* 2003;301:929–933.
- Hull SC. Macroalgal mats and species abundance: a field experiment. *Estuar Coast Shelf Sci* 1987;25:519–532.
- Huntington BE, Boyer KE. Effects of red macroalgal (*Grallariopsis* sp.) abundance on eelgrass *Zostera marina* in Tomales Bay, California, USA. *Mar Ecol Prog Ser* 2008;367:133–142.
- Hurd CL. Water motion, marine macroalgal physiology, and production. *J Ecol* 2000;36:453–472.
- Hurd CL, Durante KM, Chia F-S, Harrison PJ. Effect of bryozoan colonization on inorganic nitrogen acquisition by the kelps *Agarum fimbriatum* and *Macrocystis integrifolia*. *Mar Biol* 1994;121:167–173.
- Hurd CL, Stevens CL, Laval BE, Lawrence GA, Harrison PJ. Visualization of seawater flow around morphologically distinct forms of the giant kelp *Macrocystis integrifolia* from wave-sheltered and exposed sites. *Limnol Oceanogr* 1997;42:156–163.
- Isaksson I, Pihl L. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Neth J Sea Res* 1992;30:131–140.
- Isreal A, Katz S, Dubinsky Z, Merrill J, Friedlander M. Photosynthetic inorganic carbon utilization and growth of *Porphyra linearis* (Rhodophyta). *J Applied Phycol* 1999;5:447–453.
- Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 2001;293:629–638.
- Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT. Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 2008;27:473–483.
- de Jonge VN, Beusekom JEE. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. *Neth J Sea Res* 1992;30:91–105.
- de Jonge VN, Beusekom JEE. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems Estuary. *Limnol Oceanogr* 1995;40:766–778.
- Jönsson B. A <sup>14</sup>C-incubation technique for measuring microphytobenthic primary productivity in intact sediment cores. *Limnol Oceanogr* 1991;36:1485–1492.
- Kamer , Krista , Karleen A, Boyle , Peggy Fong . Macroalgal bloom dynamics in a highly eutrophic southern California estuary. *Estuaries* 2001;24:623–635.
- Kennison RL. Evaluating ecosystem function of nutrient retention and recycling in excessively eutrophic estuaries. PhD dissertation. Los Angeles: University of California; 2008. pp. 186
- Knowlton N. Multiple 'stable' states and the conservation of marine ecosystems. *Prog Oceanogr* 2004;60:387–396.
- Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar Pollut Bull* 2001;41:91–120.
- Krause-Jensen D, Christensen PB, Rysgaard S. Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. *Estuaries* 1999;22:31–38.
- Krause-Jensen D, Kuhl M, Christensen PB, Borum J. Benthic primary production in Young Sound, Northeast Greenland. In: Rysgaard S Glud RN, editors. *Carbon Cycling in Arctic Marine Ecosystems: Case Study Young Sound*. Meddr. Gronland, Bioscience, Volume 58, 2007. p 160–173.
- Krause-Jensen D, McGlathery K, Rysgaard S, Christensen PB. Production within dense mats of the filamentous macroalga *Chaetomorpha linum* in relation to light and nutrient availability. *Mar Ecol Prog Ser* 1996;134:207–216.
- Kromkamp JC, Forster RM. Developments in microphytobenthos primary productivity studies. In: Kromkamp JC, de Brouwer JFC, Blanchard GF, Forster R, Creach V, editors. *Functioning of Microphytobenthos in Estuaries*. Amsterdam: Royal Netherlands Academy of Arts and Sciences; 2006. p 9–30.
- Kühl M, Lassen C, Jørgensen BB. Light penetration and light intensity in sandy marine sediments measured with irradiance and scalar irradiance fiber-optic microprobes. *Mar Ecol Prog Ser* 1994;105:139–148.
- Kuipers BR, de Wilde PAWJ, Creutzberg F. Energy flow in a tidal flat ecosystem. *Mar Ecol Prog Ser* 1981;5:215–221.
- Lapointe BE, O'Connell J. Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda—Eutrophication of a confined, phosphorus-limited marine ecosystem. *Estuar Coast Shelf Sci* 1989;28:347–360.
- Lapointe BE, Barile PJ, Littler MM, Littler DS. Macroalgal blooms on southeast Florida coral reefs II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. *Harmful Algae* 2005;4:1106–1122.
- Larkum AWD, Koop K. ENCORE, algal productivity and possible paradigm shifts. *Proc Int Coral Reef Symp* 1997;2:881–884.
- Larson F, Sundbäck K. Role of microphytobenthos in recovery of functions in a shallow-water sediment system after hypoxic events. *Mar Ecol Prog Ser* 2008;357:1–16.

- Lawson SE, Wiberg PL, McGlathery KJ, Fugate DC. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuar Coasts* 2007;30:102–111.
- Lee RE. *Phycology*. Cambridge: Cambridge University Press; 1999.
- Lirman D, Biber P. Seasonal dynamics of algal communities in the northern Florida reef tract. *Botanica Marina* 2000;43:305–314.
- Littler DS, Littler MM. *Caribbean Reef Plants*. Washington (DC): Offshore Graphics; 2000.
- Littler MM, Littler DS. A relative-dominance model for biotic reefs. Proceedings of the Joint Meeting of the Atlantic Reef Committee Society of Reef Studies; Miami, Florida; 1984.
- Littler MM, Littler DS. Structure and role of algae in tropical reef communities. In: Lembi CA, Waaland JR, editors. *Algae and Human Affairs*. Cambridge: Cambridge University Press; 1988. p 29–56.
- Longphui SN, Leynaert A, Guarini JM, Chauvaud L, Claquin P, Herlory O, Amice E, Huonnic P, Ragueneau O. Discovery of microphytobenthos migration in the subtidal zone. *Mar Ecol Prog Ser* 2006;328:143–154.
- Littler MM, Littler DS, Taylor PR. Selective herbivore increases biomass of its prey: a chiton-coral reef-building association. *Ecology* 1995;76(5):1661–1681.
- Lotze HK, Worm B. Complex interactions of climatic and ecological controls on macroalgal recruitment. *Limnol Oceanogr* 2002;47:1734–1741.
- Lubchenko J, Menge BA, Garrity SD, Lubchenko PJ, Ashkenas LR, Gaines S. Structure, persistence, and the role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *J Exp Mar Biol Ecol* 1984;78:23–73.
- Lüning K. *Seaweeds—Their Environment, Biogeography, and Ecophysiology*. New York: John Wiley & Sons, Inc; 1990.
- Lüning K, Dring MJ. Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgol Mar Res* 1979;32:403–424.
- MacIntyre IG, Toscano MA, Bond GB. Modern sedimentary environments, Twin Cays, Belize, Central America. *Atoll Res Bull* 2004;509:1–12.
- Malm T, Kautsky L, Claesson T. The density and survival of *Fucus vesiculosus* L. (*Fucales*, *Phaeophyta*) on different bedrock types on a Baltic Sea moraine coast. *Bot Mar* 2003;46:256–262.
- Manley SL, Dastoor MN. Methyl halide (CH<sub>3</sub>X) production from the giant kelp, *Macrocystis*, and estimates of global CH<sub>3</sub>X production by kelp. *Limnol Oceanogr* 1987;32:709–715.
- McCook LJ. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 1999;18:357–367.
- McCormick-Ray J. Historical oyster reef connections to Chesapeake Bay—a framework for consideration. *Estuar Coast Shelf Sci* 2005;64:119–134.
- McGlathery KJ, Anderson IC, Tyler AC. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Mar Ecol Prog Ser* 2001;216:1–15.
- McGlathery KJ, Pedersen MF, Borum J. Changes in intracellular nitrogen pools and feedback controls on nitrogen uptake in *Chaetomorpha linum* (Chlorophyta). *J Phycol* 1996;32:393–401.
- McGlathery KJ, Pedersen MF. The effect of growth irradiance on the coupling of carbon and nitrogen metabolism in *Chaetomorpha linum* (Chlorophyta). *J Phycol* 1999;35:721–731.
- McGlathery KJ, Sundbäck K, Anderson IC. The importance of primary producers for benthic nitrogen and phosphorus cycling. In: Nielsen SL, Banta GT, Pedersen MF, editors. *The Influence of Primary Producers on Estuarine Nutrient Cycling*. Dordrecht, Boston, London; Kluwer Academic Publishers; 2004.
- McGlathery KJ, Sundbäck K, Anderson IC. Eutrophication patterns in shallow coastal bays and lagoons. *Mar Ecol Prog Ser* 2007;348:1–18.
- Medlin LK, Kaczmarek I. Evolution of the diatoms: V. Morphological and cytological support for the major clades and taxonomic revision. *Phycologia* 2004;43:245–270.
- Menge BA, Branch GM. Rocky intertidal communities. In: Bertness MD, Gaines SD, Hay ME, editors. *Marine Community Ecology*. Massachusetts: Sinauer Associates, Inc; 2001. p 221–254.
- Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR. The fate of intertidal microphytobenthos carbon: an in situ <sup>13</sup>C-labelling study. *Limnol Oceanogr* 2000;45:1224–1234.
- Middelboe AL, Binzer T. The importance of canopy structure on photosynthesis in single- and multi-species assemblages of marine macroalgae. *Oikos* 2004;107:442–432.
- Middelboe AL, Sand-Jensen K, Binzer T. Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. *Oecologia* 2006;150:464–476.
- Migné A, Spilmont N, Davoul D. In situ measurements of benthic primary production during emersion: seasonal variations and annual production in the Bay of Somme (eastern English Channel, France). *Cont Shelf Res* 2004;24:1437–1449.
- Miles A, Sundbäck K. Diel variation of microphytobenthic productivity in areas with different tidal amplitude. *Mar Ecol Prog Ser* 2000;205:11–22.
- Mitbavkar S, Anil AC. Diatoms of the microphytobenthic community in a tropical intertidal sand flat influenced by monsoons: spatial and temporal variations. *Mar Biol* 2006;148:693–709.
- Miyajima T, Suzumura M, Umezawa Y, Koike I. Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. *Mar Ecol Prog Ser* 2001;217:273–286.
- Morrow KM, Carpenter RC. Macroalgal morphology mediates particle capture by the corallimorpharian *Corynactis californica*. *Mar Biol* 2008;155:273–280.
- Moseman SM, Levina LA, Curri C, Forder C. Colonization, succession, and nutrition of macrobenthic assemblages in a restored wetland at Tijuana Estuary, California. *Estuar Coast Shelf Sci* 2004;60:755–770.

- Nielsen SL, Banta GT, Pedersen MF. Decomposition of marine primary producers: consequences for nutrient recycling and retention in coastal ecosystems. In: Nielsen SL, Banta GT, Pedersen MF, editors. *Estuarine Nutrient Cycling: The Influence of Primary Producers*. Netherlands: Springer; 2004. p 187–216.
- Nilsson P, Jönsson B, Swanberg IL, Sundbäck K. Response of a marine shallow-water sediment system to an increased load of inorganic nutrients. *Mar Ecol Prog Ser* 1991;71:275–290.
- Nixon SW. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* 1995; 41:199–219.
- Norkko A, Bonsdorff E. Population responses of coastal zoobenthos to stress by drifting algal mats. *Mar Ecol Prog Ser* 1996;140:141–151.
- Nyberg C, Wallentinus I. Can species traits be used to predict marine macroalgal introduction?. *Biol Invasions* 2005;7:265–279.
- O'Connor MI. Warming strengthens an herbivore-plant interaction. *Ecology* 2009;90:388–398.
- Paerl HW, Pinckney JL. A mini-review of microbial consortia: Their roles in aquatic production and biogeochemical cycling. *Microb Ecol* 1996;31:225–247.
- Paine RT. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 1974;15: 93–120.
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 2003;301:955–958.
- Parnesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 2003;421:37–42.
- Paterson DM. Short-term changes in erodibility of intertidal cohesive sediments related to the migratory behavior of epipelagic diatoms. *Limnol Oceanogr* 1989;34:223–234.
- Platt T, Gallegos CL, Harrison WG. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J Mar Res* 1980;38:687–701.
- Pedersen MF. Transient ammonium uptake in the macroalga *Ulva lactuca* L. (Chlorophyta): nature, regulation and consequences for choice of measuring technique. *J Phycol* 1994;30:980–986.
- Pedersen MF, Borum J. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar Ecol Prog Ser* 1996;142:261–272.
- Pihl L, Svenson A, Moksnes PO, Wennhage H. Distribution of green algal mats throughout shallow soft bottoms of the Swedish Skagerrak archipelago in relation to nutrient sources and wave exposure. *J Sea Res* 1999;41:281–294.
- Pinckney JL, Carman KR, Lumsden SE, Hymel SN. Microalgal-meiofaunal trophic relationships in muddy intertidal estuarine sediments. *Aquat Microb Ecol* 2003;31:99–108.
- Raffaelli D. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. *Helgol Mar Res* 2000;54:71–79.
- Reise K, Herre E, Sturm M. Mudflat biota since the 1930s: change beyond return? *Helgol Mar Res* 2008;62:13–22.
- Revsbech NP. An oxygen microsensor with a guard cathode. *Limnol Oceanogr* 1989;34:474–478.
- Revsbech NP, Joergensen BB, Brix O. Primary production of microalgae in sediments measured by oxygen microprofile,  $H^{14}CO_3^-$  fixation, and oxygen exchange methods. *Limnol Oceanogr* 1981;26:717–730.
- Risgaard-Petersen N. Coupled nitrification-denitrification in autotrophic and heterotrophic estuarine sediments: On the influence of benthic microalgae. *Limnol Oceanogr* 2003;48:93–105.
- Risgaard-Petersen N, Nicolaisen MH, Revsbech NP, Lomstein BAa. Competition between ammonia-oxidizing bacteria and benthic microalgae. *Appl Environ Microbiol* 2004;70:5528–5537.
- Roberson LM, Coyer JA. Variation in blade morphology of the kelp *Eisenia arborea*: incipient speciation due to local water motion?. *Mar Ecol Prog Ser* 2004;282:115–128.
- Romano C, Widdows J, Brinsley MD, Staff FJ. Impact of *Enteromorpha intestinalis* mats on near-bed currents and sediment dynamics: flume studies. *Mar Ecol Prog Ser* 2003;256:63–74.
- Rysgaard S, Kuhl M, Glud RN, Hansen JW. Biomass, production and horizontal patchiness of sea ice algae in a high-Arctic fjord (Young Sound, NE Greenland). *Mar Ecol Prog Ser* 2001;223:15–23.
- Round FE, Crawford RM, Mann DG. *The Diatoms: Biology and Morphology of the Genera*. New York: Cambridge University Press; 1990.
- Saburova MA, Polikarpov IG. Diatom activity within soft sediments: behavioural and physiological processes. *Mar Ecol Prog Ser* 2003;251:115–126.
- Salomonsen J, Flindt M, Geertz-hansen O, Johansen C. Modelling advective transport of *Ulva lactuca* (L) in the sheltered bay, MØllekrogen, Roskilde Fjord, Denmark. *Hydrobiologia* 1999;397:241–252.
- Salovius S, Nyqvist M, Bonsdorff E. Life in the fast lane: macrobenthos use temporary drifting algal habitats. *J Sea Res* 2005;53:169–180.
- Sand-Jensen K, Binzer T, Middelboe AL. Scaling of photosynthetic production of aquatic macrophytes—a review. *Oikos* 2007;116:280–294.
- Schaffelke B. Particulate organic matter as an alternative nutrient source for tropical Sargassum species (Fucales, Phaeophyceae). *Journal of Phycology* 1999;35:1150–1157.
- Scheffer M, Carpenter S, Foley JA, Folkes C, Walker B. Catastrophic shifts in ecosystems. *Nature* 2001;413: 591–596.
- Scheffer M, van Nes EH. Mechanisms for marine regime shifts: can we use lakes as microcosms for oceans? *Prog Oceanogr* 2004;60:303–319.
- Schories D, Reise K. Germination and anchorage of *Enteromorpha* spp. in the sediment of the Wadden Sea. *Helgol Meeresunters* 1993;47:275–285.

- Sfriso A, Marcomini A. Macrophyte production in a shallow coastal lagoon. Part I: Coupling with chemico-physical parameters and nutrient concentrations in waters. *Mar Env Res* 1997;44:351–375.
- Sfriso A, Pavoni B, Marcomini A, Orio AA. Macroalgae, nutrient cycles, and pollutants in the lagoon of Venice. *Estuaries* 1992;15:517–528.
- Smith SV, Chambers RM, Hollibaugh JT. Dissolved and particulate nutrient transport through a coastal watershed-estuary system. *J Hydrol* 1996;176:181–203.
- Smith T. The Dynamics of Coral Reef Algae in an Upwelling System. Ph.D. dissertation. Florida: University of Miami; 2005. pp. 156
- Smith TB, Fong R, Kennison J, Smith J. Spatial refuges and associational defenses promote harmful blooms of the alga *Caulerpa sertularioides* onto coral reefs. *Oikos*, in press. 2010;164:1039–1048. DOI 10.1007/s00442-010-1698-x.
- Smith SV, Kimmerer WJ, Laws EA. Kaneohe Bay sewage diversion experiment—perspective on ecosystem responses to nutrient perturbation. *Pac Sci* 1981;35:279–395.
- Smith JE, Kuwabara J, Coney J, Flanagan K, Beets J, Brown D, Stanton F, Takabayashi M, duPlessis S, Griesemer BK, Barnes S, Turner J. An unusual cyanobacterial bloom in Hawaii. *Coral Reefs* 2009;27. pp. 851
- Smith DJ, Underwood GJC. The production of extracellular carbohydrates by estuarine benthic diatoms: The effects of growth phase and light and dark treatments. *J Phycol* 2000;36:321–333.
- Stal LJ, Caumette P. *Microbial Mats. Structure, Development and Environmental Significance*. NATO ASI Series G: Ecological Science, Volume 35, 1992.
- Steneck RS. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu Rev Ecol Syst* 1986;17:273–303.
- Steneck RS, Dethier MN. A functional group approach to the structure of algal-dominated communities. *Oikos* 1994;69:476–498.
- Stewart HL, Fram JP, Reed DC, Williams SL, Brzezinski MA, MacIntyre S. Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. *Mar Ecol Prog Ser* 2009;375:101–112.
- Stimpson J, Larned ST. Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. *J Exp Mar Biol Ecol* 2000;252:159–180.
- Sundbäck K, Enoksson V, Granéli W, Pettersson K. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. *Mar Ecol Prog Ser* 1991;74:262–279.
- Sundbäck K, Linares F, Larson F, Wulff A, Engelsen A. Benthic nitrogen fluxes along a depth gradient in a microtidal fjord: role of denitrification and microphytobenthos. *Limnol Oceanogr* 2004;49:1095–1107.
- Sundbäck K, McGlathery K. Interactions between benthic macroalgal and microalgal mats (review). In: Kristensen E, Haese RR, Kostka JE, editors, *Interactions Between Macro- and Microorganisms in Marine Sediments*. AGU Series: Coastal and Estuarine Studies, Volume 60, 2005. p 7–29.
- Sundbäck K, Miles A, Hulth S, Pihl L, Engström P, Selander E, Svenson A. Importance of benthic nutrient regeneration during initiation of macroalgal blooms in shallow bays. *Mar Ecol Prog Ser* 2003;246:115–126.
- Sundbäck K, Nilsson P, Nilsson C, Jönsson B. Balance between autotrophic and heterotrophic components and processes in microbenthic communities of sandy sediments: A field study. *Estuar Coast Shelf Sci* 1996;43:689–706.
- Thompson CEL, Amos CL. The impact of mobile disarticulated shells of *Cerastoderma edulis* on the abrasion of a cohesive substrate. *Estuaries* 2002;25:204–214.
- Thompson CEL, Amos CL. Effect of sand movement on a cohesive substrate. *J Hydraul Eng-ASCE* 2004;130:1123–1125.
- Thomsen MS, Gurgel CFD, Fredericq S, McGlathery KJ. *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in Hog Island Bay, Virginia: a cryptic alien and invasive macroalga and taxonomic corrections. *J Phycol* 2005;42:139–141.
- Thomsen M, McGlathery KJ. Facilitation of macroalgae by the sedimentary tube-forming polychaete *Diopatra cuprea*. *Estuar Coast Shelf Sci* 2005;62:63–73.
- Thomsen MS, McGlathery KJ, Tyler AC. Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. *Estuar Coasts* 2006;29:470–478.
- Thomsen MS, McGlathery KJ, Schwartzchild A, Silliman BR. Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. *Biol Invasions* 2009;11:2303–2316.
- Thomsen M, Wernberg T, Altieri A, Tuya F, Gulbrandsen DJ, McGlathery KJ, Holmer M, Silliman BR. Habitat cascades: the conceptual context and global relevance of indirect facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology* 2010;50:158–175.
- Thompson RC, Norton TA, Hawkins SJ. Physical stress and biological control regulate the producer–consumer balance in intertidal biofilms. *Ecology* 2004;85:1372–1382.
- Thornton DCO, Underwood GJC, Nedwell DB. Effect of illumination and emersion period on the exchange of ammonium across the estuarine sediment-water interface. *Mar Ecol Prog Ser* 1999;28:11–20.
- Trimmer M, Nedwell DB, Sivyer DB, Malcolm SJ. Seasonal benthic organic matter mineralisation measured by oxygen uptake and denitrification along a transect of the inner and outer River Thames estuary, UK. *Mar Ecol Prog Ser* 2000;197:103–119.
- Tyler AC, McGlathery KJ, Anderson IC. Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnol Oceanogr* 2003;48:2125–2137.

- Underwood GJC, Kromkamp J. Primary production by phytoplankton and microphytobenthos in estuaries. *Adv Ecol Res* 1999;29:93–153.
- Underwood GJC, Perkins RG, Consalvey MC, Hanlon ARM, Oxborough K, Baker NR. Patterns in microphytobenthic primary productivity: Species-specific variation in migratory rhythms and photosynthetic efficiency in mixed-species biofilms. *Limnol Oceanogr* 2005;50:755–767.
- Valentine JF, Duffy JE. The central role of grazing in seagrass ecology. In: Larkum WD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, Ecology, and Conservation*. Berlin: Springer; 2006. p 463–501.
- Valiela I. *Marine Ecological Processes*. New York: Springer-Verlag; 1995. pp. 686
- Valiela I, Foreman K, LaMontagne M, Hersh D, Costa J, Peckol P, DeMeo-Andreson B, D'Avanzo C, Babione M, Sham S, Brawley J, Lajtha K. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries* 1992;15:443–457.
- Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 1997;42:1105–1118.
- Vaselli S, Bertocci I, Maggi E, Benedetti-Cecchi L. Effects of mean intensity and temporal variance of sediment scouring events on assemblages of rocky shores. *Mar Ecol Prog Ser* 2008;364:57–66.
- Veuger B, Middelburg JJ. Incorporation of nitrogen from amino acids and urea by benthic microbes: role of bacteria versus algae and coupled incorporation of carbon. *Aquat Microb Ecol* 2007;48:35–46.
- Viaroli P, Bartoli M, Bondavalli C, Christian RR. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. *Hydrobiologia* 1996;329:105–119.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 1997;7:737–750.
- Wallentinus I. Comparisons of nutrient uptake rates for Baltic macroalgae with different thallus morphologies. *Mar Biol* 1984;80:215–225.
- Wennhage H, Pihl L. From flatfish to sticklebacks: assemblage structure of epibenthic fauna in relation to macroalgal blooms. *Mar Ecol Prog Ser* 2007;335:187–198.
- Whitall DR, Paerl HW. Spatiotemporal variability of wet atmospheric nitrogen deposition to the Neuse River Estuary, North Carolina. *J Environ Qual* 2001;30:1508–1515.
- Widdows J, Blauw A, Heip CHR, Herman PMJ, Lucas CH, Middelburg JJ, Schmidt S, Brinsley MD, Twisk F, Verbeek H. Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. *Mar Ecol Prog Ser* 2004;274:41–56.
- Williams SL, Carpenter RC. Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. *Mar Ecol Prog Ser* 1988;47:145–152.
- Williams SL, Ruckelshaus MH. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 1993;74:904–918.
- Williams SL, Smith JE. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annu Rev Ecol Syst* 2007;38:327–359.
- Witman JD, Dayton PK. Rocky Subtidal Communities. In: Bertness MD, Gaines SD, Hay ME, editors. *Marine Community Ecology*. Massachusetts: Sinauer Associates, Inc; 2001. p 339–366.
- Worm B, Lotze HK. Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnol Oceanogr* 2006;51:569–576.
- Worm B, Lotze HK, Sommer U. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. *Limnol Oceanogr* 2000;45:339–349.
- Worm B, Lotze HK, Hillebrand H, Sommer U. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 2002;417:848–851.
- Zedler JB. *The Ecology of Southern California Coastal Salt Marshes: A Community Profile*. Washington (DC): U.S. Fish and Wildlife Service, Biological Services Program; 1982. FWS/OBS-81/54, p 110.
- Zedler JB, West JM. Declining diversity in natural and restored salt marshes: A 30-year study of Tijuana Estuary. *Restor Ecol* 2008;16:249–262.