

Comparative ecology of submersed grass beds in freshwater, estuarine, and marine environments¹

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Abstract

Worldwide, there are 500–700 species of submersed angiosperms adapted to freshwater and estuarine environments compared with 50 species adapted to marine waters. In their evolution from freshwater ancestors, seagrasses have undergone extensive anatomical changes (e.g. reduction in floral and leaf structures, reduction of xylem tissue with a lacunal gas transport system), as well as physiological adaptations (bicarbonate utilization in photosynthesis). Seagrasses appear to have more annual production than do their freshwater counterparts because they develop greater standing crops and have the capacity to store photosynthetic products in extensive rhizome systems in the sediments. For example, maximum productivity of $> 10 \text{ g C m}^{-2} \text{ d}^{-1}$ has been reported for tropical seagrass species (*Cymodocea nodosa* and *Thalassia testudinum*), but the maximum productivity of temperate freshwater species such as *Myriophyllum* or tropical freshwater species such as *Hydrilla* is usually $< 5 \text{ g C m}^{-2} \text{ d}^{-1}$. In addition, the marine environment provides ample supplies of inorganic carbon (C) and increased mixing energies, making CO_2 limitation less likely. One calculation suggests that marine macrophytes impact the global C budget by sequestering as much as 10^9 t of C per year.

Secondary productivities of seagrass communities can also be high. For example, stable isotopic ratios suggest that macrophytic C is important in sustaining several species of commercial fish species in Australia, accounting for $> 50\%$ of their diets. Also, sea urchins (*Diadema antillarum*) consume plant material, creating bare halos around tropical patch reefs in the Caribbean Sea. It is difficult to generalize regarding brackish submersed aquatics in estuaries because their coverage is variable due to light limitation and algal overgrowth from eutrophication. Freshwater macrophytes seem rarely grazed by fish (except via exotic introductions of *Tilapia* or carp), but waterfowl use is often significant at the end of the growing season. Thus, trophic relations in freshwater macrophyte beds may be qualitatively different and much more pulsed than in seagrass systems, with more *r*-selection in lakes and more *K*-selection in marine environments.

Shallow marine environments along continental margins have been regarded as having the highest productivities (Odum 1971), particularly in terms of macrophytic vegetation (Mann 1973). The angiosperms—one important component of the systematically diverse grouping of macrophytes—have their evolutionary origins in terrestrial environments. Although the initial array of angiosperm types was predominantly adapted to dry upland climates (Takhtajan 1969), fossil evidence (protozosteroids and cymodoceoids) suggests that there were a few primitive species of angiosperms developing distinctively aquatic habits by the upper Cretaceous (Den Hartog 1970b).

There is evidence not only of modern genera of submersed angiosperms such as *Posidonia* and *Cymodocea* in the Paleocene and Eocene, but also of foraminiferous fossils characteristic of present seagrass communities (Brasier 1975). Because of gaps, it is not yet clear from the fossil record that freshwater angiosperms were ancestral to seagrass species. In addition, despite an increasing number of studies of chromosomal complements of selected genera of submersed angiosperms (e.g. Cook and Luond 1982; Kalkman and Van Wijk 1984) and chemical constituents (Drew 1983), such evolutionary investigations are not yet available on a broad enough scale to reconstruct phylogenetic relationships.

Anatomical and morphological features, however, indicate that the seagrasses are derived from several genera of freshwater macrophytes (Schenk 1886). Although freshwater and estuarine angiosperms come from both monocot and dicot evolutionary lines, all seagrasses are monocots (Tomlin-

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son 1980). For example, in the family Hydrocharitaceae, the seagrass *Thalassia* appears to be derived from a basic plan represented by freshwater genera such as *Hydrocharis* (Tomlinson 1969). In addition, salt tolerance is a highly specialized physiological trait in the angiosperms which have only a small percentage of halophytes. Of the submersed aquatics studied by Haller et al. (1974), most grew best under 3‰ salinity while exposure to >18‰ was toxic to most species found in estuaries (e.g. *Myriophyllum spicatum*; McGahee and Davis 1971). Harborne (1977) postulated that the successful adaptation to inorganic salts by seagrasses may depend on their ability to inactivate sulfate by conjugation with various phenolic compounds. The lack of salt tolerance may be one reason there are only about 50 species of true seagrasses worldwide, distributed in as few as 12 genera (Den Hartog 1970a). By contrast, there are an estimated 500–700 freshwater species of submersed angiosperms representing 50 genera (Sculthorpe 1967). Genetic isolation in lakes may also help account for higher species diversity of macrophytes in freshwater environments.

Factors beyond salinity are important in the comparison of freshwater, estuarine, and marine environments (Table 1). Regular tidal motion in estuaries and coastal waters provides more mixing energy than is typical for lakes, reducing “unstirred boundary layers” surrounding leaves. Smith and Walker (1980) have pointed out that laminar boundary layers often limit photosynthesis in aquatic plants and may be the reason for comparatively high productivity in flowing freshwater environments such as Silver Spring, Florida (Odum 1956). Regular changes of water level must be adapted to in coastal environments, but these changes are often small compared to the large excursions plants encounter in managed lakes and reservoirs (Gaudet 1979). Bottom sediments in the shallows of quiescent lakes are finer grained than in coastal environments because of wave and tidal action in the latter. However, this difference is often obscured since macrophytes frequently reduce water velocities enough to accelerate deposition of fine-grained materials in dense

grass beds (Fonseca et al. 1982; Bulthuis et al. 1984; Ward et al. 1984). Light availability at comparable depths is often greater in lakes and tropical marine waters than in rivers and estuaries where continual resuspension of sediment can cause light limitation. The growing season tends to be longer in marine environments because high specific heat moderates oceanic environments. There is also more variability in the water chemistry of lakes producing greater adaptational variety than in seawater, which has a more constant salt supply, including bicarbonate. This last difference produces less likelihood of pH shifts in marine waters and provides a more even supply of CO₂ in the water column.

The purpose of this synthesis is to draw on earlier reviews and to make broad comparisons concerning the ecology of freshwater and marine species of submersed angiosperms. Earlier treatises explored the submersed macrophytes as a group (Arber 1920; Gessner 1955, 1959; Westlake 1963; Sculthorpe 1967), but these treatments are now out of date in terms of photosynthesis and comparative primary productivity. The recognition of fundamental differences in photosynthetic pathways in submersed aquatics (see Holaday and Bowes 1980; Lucas and Berry 1985) presents several new hypotheses to account for the productivity of major plant groups in aquatic environments. The burgeoning amount of information concerning submerged angiosperms has restricted recent reviews either to freshwater (Hutchinson 1975; Westlake 1975; Wetzel 1975) or seagrass systems (Den Hartog 1970a; Odum 1974; Phillips 1974; McRoy and Helfferich 1977; Phillips and McRoy 1980). Such polarization often precludes ecological comparison of submersed aquatic ecosystems at opposite ends of the salinity spectrum. Unfortunately, a disjointed view of macrophytic communities results, especially in estuaries where little synthesis has been attempted (Stevenson and Confer 1978) despite the potential importance of submersed aquatics to overall productivity in these environments (Thayer et al. 1975). Although a detailed review is not possible here, several key questions are addressed.

Table 1. Characteristics of various shallow-water environments.

Parameter	Freshwater	Estuarine	Marine (includes lagoons)
Physical			
Water levels	Often variable	Irregular tides	Regular tidal
Currents	Slow in lakes	Highly variable	Variable
Sediments	Finer in lakes	Variable	Often coarse
Light availability	Variable	Low	High
Growing season	Short (in temperate regions)	Often truncated	Long (even in temperate)
Temperature	More variable (especially in temperate)	Intermediate	More stable
Chemical			
pH	Very wide range, 3 to >10	Variable in headwaters	Circumneutral
HCO ₃ ⁻	Very variable	Spatially variable	Abundant
CO ₂	Sometimes low	Occas. depleted	Stable
N source	Water column	Water column	N fixation
P source	Sediments	Water column	Sediments

• What are the major ecological adaptations as we follow the angiosperms from freshwater to progressively higher salinity environments?

• Are there quantitative differences in standing crop or primary productivity in freshwater and marine environments, and do limiting factors differ in this transition?

• To what extent do trophic relationships of submersed aquatic ecosystems qualitatively change in lake, riverine, estuarine, and marine systems?

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Ecological adaptations

Reproductive biology—The evolutionary rise of the angiosperms was characterized by the dominance of a genetically diploid sporophyte generation with its large conspicuous insect-pollinated flowers having male and female parts on the same individual (i.e. monoecious). Most freshwater genera of submersed angiosperms appear to be monoecious and some (e.g. *Heteranthera*,

Hydrilla, *Egeria*, etc.) even hold their flowers above the water surface for a short period of time during pollination. However, most marine genera are dioecious with male and female flowers on separate individuals (Pettitt 1984). Since there is also progressive reduction in conspicuous perianth structures (usually associated with insect pollination) with increasing salinity, it suggests that the means of sexual reproduction are very different in freshwater and marine environments. There is a trend toward hydrophilous pollination in brackish and marine species (Cox 1983) with some genera having pollen releases timed with gas bubble formation to facilitate pollination, as in *Ruppia* (Verhoeven 1979).

Another difference between freshwater and marine submersed aquatics is in the regularity of sexual reproduction. In lakes, flowering in submersed species such as *Myriophyllum* regularly occurs near peak biomass and sometimes more than once a season (Adams and Prentki 1982). Getsinger and Dillon (1984) found that flowering in *Egeria densa* in South Carolina varies in intensity from year to year, but basically has two maxima—one in June, the other in September. In contrast, flowering is rarely seen in many tropical seagrasses (McMillan et al. 1980), and it is surmised that asexual reproduction (through fragmentation of shoots) is the dominant dispersal mechanism. However, marine angiosperms seem

fully capable of flowering, despite submer-
sion in seawater, when the proper combi-
nation of environmental cues is present
(Pettitt 1984). For example, Lot (1977) re-
ported abundant flowering and seed pro-
duction in *Thalassia testudinum* at Isla
Verde Reef (Vera Cruz, Mexico). In the
Florida Keys, Tomlinson (1969) observed
that flowering of *Thalassia* was highly vari-
able from year to year. Lewis and Phillips
(1980) reported that spatial separation of
male and female flowers in the beds de-
creases chances for successful pollination.
Even so, Durako and Moffler (1985) re-
ported substantial seed production during a
3-yr study just outside the mouth of Tampa
Bay, Florida, despite the finding that the
inside of the bed had male flowers while the
fringes had female. Thus, even though spo-
radic, there may be more reliance on sexual
reproduction in *Thalassia* than previously
believed (Zieman 1975).

In *Zostera marina*, the dominant seagrass
in the Northern Hemisphere, sexual repro-
duction is associated with stress in the in-
tertidal regions in the central portion of its
range (Phillips et al. 1983). Furthermore, in
extreme environments, such as the warm
waters of the Gulf of California, this tem-
perate seagrass can take on the strategy of
an annual, with complete die-off of vege-
tative parts and complete dependence on
seeds for reproduction (Felger and McRoy
1974). Keddy and Patriquin (1978) found a
similar reproductive strategy for *Zostera* in
intertidal habitats (where desiccation is a
stress) associated with marshes in Nova
Scotia. Another recent investigation (Church-
ill 1983) indicates that *Zostera* seeds are
much more viable than Tutin (1938) indi-
cated earlier. It appears, therefore, that the
basic angiosperm pattern of sexual repro-
duction via flowering, with the evolutionary
advantages of genetic recombination, is still
intact in seagrasses but that it may often be
enhanced by stress. This may help account
for the irregularity of flowering in seagrasses
in the tropics where physical stresses that
trigger flowering responses are relatively
rare. Pettitt (1984) found that floral initia-
tion can also be triggered by slightly cooler
winter sea temperatures followed by a
warming period.

Another critical stage in the life cycle of
any species is dispersal. After seeds are
formed in freshwater and marine species,
there is comparatively limited distribution
because the seeds do not float. Unlike man-
groves and other species in the littoral zone
such as coconut palms, which developed
flotation mechanisms, seeds of submersed
aquatics sink soon after release (Sculthorpe
1967). The only long-range transport mech-
anism of seeds in these plants may lie, as
Darwin (1859) originally suggested, in their
being ingested by animal grazers (waterfowl,
turtles, etc.), which do not digest seeds with
tough seedcoats. This strategy is akin to that
of land plants that depend on animal vec-
tors for transport. However, unlike their ter-
restrial ancestors, the submersed aquatics in
both freshwater and marine environments
depend more heavily on vegetative frag-
mentation for dispersal. This is evident in
species such as *Hydrilla verticillata*, a fresh-
water species belonging to the Hydrochar-
itaceae, which has become a global pest de-
spite its lack of sexual reproduction in many
biotypes (Pieterse 1981).

Plant morphology—One of the more ob-
vious structural features of the most com-
mon marine species (e.g. *Zostera* and *Tha-
lassia*) is a tendency to form dense meadows
of linear leaves with basal meristems. In the
warmest waters on the shoreward edge of
the beds, where desiccation is occasionally
a problem, leaves are often terete (e.g. *Halo-
dulse*). In contrast, submersed angiosperms
in quiescent lakes and ponds often have very
dissected (or even fenestrated) leaves lying
on or near the surface of the water (Fig. 1),
which increases surface area and enhances
exchange processes (Wetzel 1975). Also,
freshwater beds have very dense layering
with a surface canopy where terminal
meristems often lie at the tips of erect stems
(*Potamogeton* spp.). The lack of canopy for-
mation in marine meadows allows the
species to slough off leaves efficiently and
seems primarily due to the higher energy
regime encountered in the sea shallows
where meristems need more protection from
wave action. An equivalent adaptation of
linear ribbonlike leaves is also found in
freshwater macrophytes in vigorously flow-
ing streams. In deeper tropical waters, when

wave action is low, species such as *Halophila* often do not have linear leaves. Instead, leaves are ovate with prostrate stems—a life form reminiscent of terrestrial geophytes (Raunkaier 1934). Thus, some marine species adopt a strategy of shade-adapted understory species and do not ascend to the surface (Fig. 1). It is clear that submersed angiosperms display a broad range of adaptations of leaf forms in different aquatic environments (Gaudet 1968).

In terms of overall distribution of biomass, there is a tendency for marine species to have a higher percentage of rhizome and roots than freshwater species (Table 2). Despite the large variability even within the same species at different locations (*Zostera* and *Potamogeton perfoliatus* in Table 2), it is obvious that seagrass species often have a root (including rhizome): shoot ratio (RSR) > 1 . In comparison, the RSR (at peak biomass) of fresh and brackish submersed species is usually < 1 . Among freshwater species, *Vallisneria americana* has one of the highest values of RSR, while *M. spicatum* (Titus and Adams 1979) has an RSR of ~ 0.1 . *Hydrilla verticillata* has an extremely low RSR (0.01). The higher RSR of *Vallisneria* has been suggested as the reason that it can outcompete *Myriophyllum* in the shallows where physical forces such as waves can shear aboveground biomass (Adams and Prentki 1982). Increased rhizomatous growth in marine environments may help protect loss of perennial meristems from wave action and conserve energy and nutrients within the beds (Kenworthy and Thayer 1984). In addition, since the roots of aquatic vascular plants are functional in terms of nutrient uptake (Bristow and Whitcombe 1971), large root biomass (and surface area) provides increased nutrition from the sediments in oligotrophic coastal waters (McRoy and Barsdate 1970). Although the rhizomes themselves may not be as important in uptake, they provide “safe storage” for nutrients and photosynthetic products protected both from wave action and from most grazers.

Transport systems—Another basic angiosperm characteristic is a well-developed vascular system in which vessel elements of the xylem tissue conduct nutrients and water

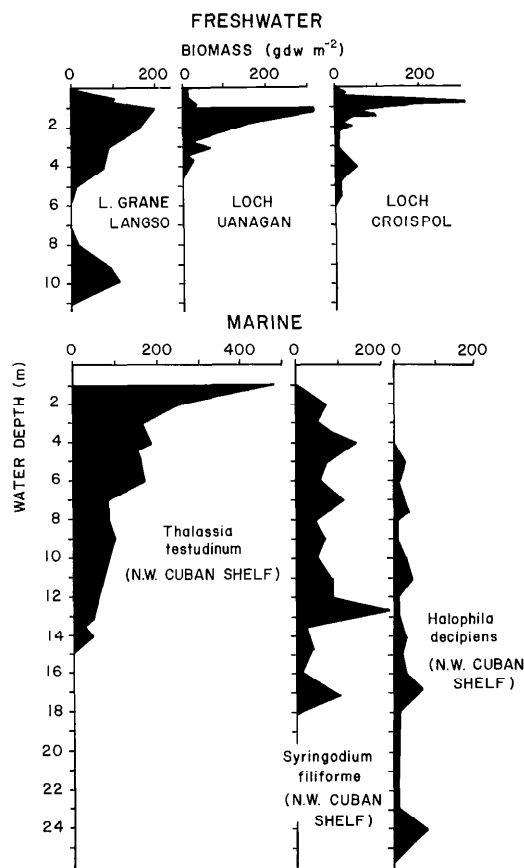


Fig. 1. The vertical distribution of biomass in the canopies of submersed angiosperms in marine and freshwater environments. Data from the three lakes is for communities of mixed species typical of freshwater (from Spence 1976); the Cuban shelf measurements are for relatively pure stands of typical marine species (from Buesa 1974).

from roots to broad leaves containing stomates and cuticles. In ecological terms, considerable net primary productivity is necessary in land plants to maintain rigid support in a nonbuoyant gaseous environment. Rigid support is provided by heavily lignified fibers associated with the transport system. However, as the development of angiosperms progressed, several evolutionary lines became less woody, and the stems became prostrate rhizomes. There are several ecological advantages to rhizomatous architecture for plants (Bell and Tomlinson 1980), including efficient reproduction through fragmentation of vegetative units

Table 2. The root:shoot ratio (RSR) of freshwater submersed aquatic plants and seagrass species at peak biomass. "Shoots" include stems and leaves in the water column; "roots" include all sedimentary biomass (rhizomes as well as roots).

Species (S, %)†	Location	RSR	Reference
Seagrass			
<i>Halodule</i> sp.	Pine Channel, Fla. Keys	3.70	Zieman 1982
<i>Posidonia australis</i>	Port Hacking, Aust.	4.80	Kirkman and Reid 1979
<i>Syringodium</i> sp.	Pine Channel	3.14	Zieman 1982
<i>Thalassia testudinum</i>	Laguna de Terminos, Mexico	1.56	Madden pers. comm.
<i>T. testudinum</i>	Pine Channel	8.10	Zieman 1982
<i>Zostera marina</i> (9–23)	Øresund, Denmark	13.46	Sand-Jensen and Borum 1983
<i>Z. marina</i> (18–23)	Vellerup Vig, Denmark	0.96	Sand-Jensen and Borum 1983
<i>Z. marina</i>	Izembek Lagoon, Alaska	1.80	McRoy 1974
<i>Z. marina</i>	Nabeta Bay, Japan*	0.32	Mukai et al. 1979
<i>Z. marina</i> (30–35)	Odawa Bay, Japan	0.23	Aioi 1980
Freshwater			
<i>Egeria densa</i>	Lake Marion, S.C.	0.05	Getsinger and Dillon 1984
<i>Heteranthera dubia</i>	Chautauqua Lake, N.Y.	0.23	Nicholson and Best 1974
<i>Hydrilla verticillata</i>	Upper Chesapeake Bay, Md.	0.01	Staver and Stevenson in prep.
<i>Myriophyllum spicatum</i>	Lake Wingra, Wis.	0.09	Titus and Adams 1979
<i>M. spicatum</i>	Chautauqua Lake	0.11	Nicholson and Best 1974
<i>Potamogeton perfoliatus</i>	Mikolajskie Lake, Poland	0.63	Ozimek et al. 1976
<i>P. perfoliatus</i>	Choptank estuary, Md.†	0.12	Kemp et al. 1984
<i>Vallisneria americana</i>	Lake Wingra	0.18	Titus and Adams 1979
<i>V. americana</i>	Chenango Lake, N.Y.	0.25	Titus and Stephens 1983
<i>V. americana</i>	Upper Chesapeake Bay	0.25	Staver and Stevenson in prep.
<i>V. americana</i>	Mikolajskie Lake	0.89	Ozimek et al. 1976

* Plants were taken from the bay and grown in outdoor tanks.

† Actually brackish, varying from 12–17 ‰.

(ramets), indeterminate growth potential, and reduced energy drains on NPP. Although not well adapted to many terrestrial situations (except as vines or epiphytes), rhizomatous herbs have been highly successful in wetland environments and adjacent shallows. The aquatic environment provides support and to some extent transport, which relieves the selection pressure toward an efficient vascular system (Sculthorpe 1967).

A classic example of the reduction in vascularization of submersed aquatics was demonstrated a century ago in the genus *Potamogeton* where there is a transition from amphibious to fully submersed and even estuarine species with concurrent reduction in xylem (Schenck 1886). Replacing the xylem are open air spaces (lacunae) that are capable of both gaseous storage and gaseous transport between stems and roots (Hartman and Brown 1967). The transport of oxygen to sediments by the lacunal system tends to increase the rates of nitrogen cycling because nitrification is more rapid in

the presence of oxygen (Iizumi and Hattori 1982; Kemp et al. 1984).

The ability of the vascular system to transport nutrients in submersed aquatics has been a topic of continuing debate since the last century, when it was believed (Schenk 1886) that very little uptake and transport occurred through the root and rhizome system. Arber (1920) was among the first to conclude from several dye experiments that translocation was possible in submersed species. More recently it has been established, using isotopic labeling, that roots can take up phosphorous (Bristow and Whitcombe 1971) and nitrogen (Toetz 1974). The extent of efficient transport between major plant organs is still unclear (Denny 1980). Iizumi and Hattori (1982) found that translocation of nitrogen was higher during the day, suggesting photosynthetically driven transport. Since the phloem is still intact, it is most likely the major conducting tissue, as in rice when it is submersed (Tatsumi and Kono 1981), but I have found no experimental evidence of this

in submersed aquatics. When submersed plants are under low-oxygen conditions and energy derived from aerobic respiration is limited, it may not be possible to supply nutrients internally through the phloem system to photosynthetic sites; thus, external supplies in the water column may be critical.

It is unlikely that the lacunar system can transport solutes other than by passive diffusion. The large gas storage and transport potential has other ecological implications for submersed aquatic plants. The potential sensitivity of surrounding tissues to volume changes due to pressure differences is one (Gessner 1961). However, recent work with more elaborate hydrostatic testing has failed to show any adverse changes in growth to a depth of 23 m for 18 species of freshwater angiosperms from 12 plant families (Dale 1984). Thus, adapting to pressure does not appear to pose a significant problem for a wide variety of submersed aquatic species. Instead, growth limitation below 10 m is probably due to diminished light availability (Jupp and Spence 1977).

Photosynthesis—Another controversial aspect of lacunae lies in the potential effects of internal storage of gaseous O_2 and CO_2 on photosynthesis. At saturating light, when photosynthesis is rapid, the boundary layers surrounding plant leaves may become depleted of CO_2 (Raven 1970). Thus, the basic material necessary to run the Calvin cycle via incorporation by ribulose biphosphate (RuBP) carboxylase (Cooper et al. 1969) can become limiting. Highly productive terrestrial species, such as sugarcane and maize, circumvent CO_2 depletion by the C-4 pathway (Hatch and Slack 1966) where CO_2 is initially incorporated into malic and/or aspartic acids which have a high affinity for CO_2 . Although theoretically at equilibrium with the atmosphere at 10 μM , depletion of CO_2 is much more likely in aquatic environments because it diffuses at 10^{-5} cm s $^{-1}$, five orders of magnitude more slowly than in air (Raven 1970). Thus, any group of aquatic macrophytes (including algal species) must cope with increasing probabilities of carbon depletion—especially in quiescent waters and when pH is elevated (Walker 1985).

Most of the seagrasses investigated thus far lack the specialized bundle sheath cells (Kranz anatomy)—a key feature of the C-4 pathway in terrestrial plants—and only develop small pools of aspartate or malate after $^{14}CO_2$ labeling (Andrews and Abel 1979). Although no aquatic angiosperms have been shown to possess conventional C-4 photosynthesis (Sternberg et al. 1984), several freshwater species such as *H. verticillata* (Holaday and Bowes 1980), *Scirpus subterminalis* (Beer and Wetzel 1981), and *Valisneria* (Helder and Harmelan 1982) seem to have a variant of the C-4 pathway termed crassulacean acid metabolism. This pathway in submersed aquatics is now termed aquatic acid metabolism (AAM) (Cockburn 1985). The presence of AAM indicates strong pressure for trapping CO_2 to maintain productivity. However, not all submersed aquatic species (e.g. *Lobelia dortmanna*) have been shown to use AAM (Sand-Jensen and Prahl 1982) and some may have limited CO_2 uptake ability.

The lacunal system also may have ecological importance in storing available CO_2 from respiration for reutilization by photosynthesizing cells in the leaves (Søndergaard 1979). Søndergaard and Wetzel (1980) found that about 30% of the CO_2 in *S. subterminalis* is recycled internally by the lacunal system. Furthermore, it may actually transport CO_2 formed in the sediments by roots and rhizomes to leaves, as has been reported in *Juncus bulbosus* and *Isoetes* found in soft-water lakes of very low carbon content (Richardson et al. 1984; Wetzel et al. 1985). In seagrasses, Andrews and Abel (1979) hypothesized that the generally less negative $\delta^{13}C$ isotopic values may be attributable to efficient recycling in the lacunal system. The converse of this has been advanced to explain the anomalously negative $\delta^{13}C$ carbon values of *Thalassia* in Rookery Bay, Florida, where the predominant carbon source may be exogenously derived from mangrove detritus (Zieman 1986).

Efficient trapping of CO_2 is especially critical since many aquatic species have significant photorespiration where oxygen competes with CO_2 in photosynthetic tissues, producing a pool of glycolate which reduces the rate of carbohydrate production (Weber

BICARBONATE UPTAKE BY SUBMERSED MACROPHYTES

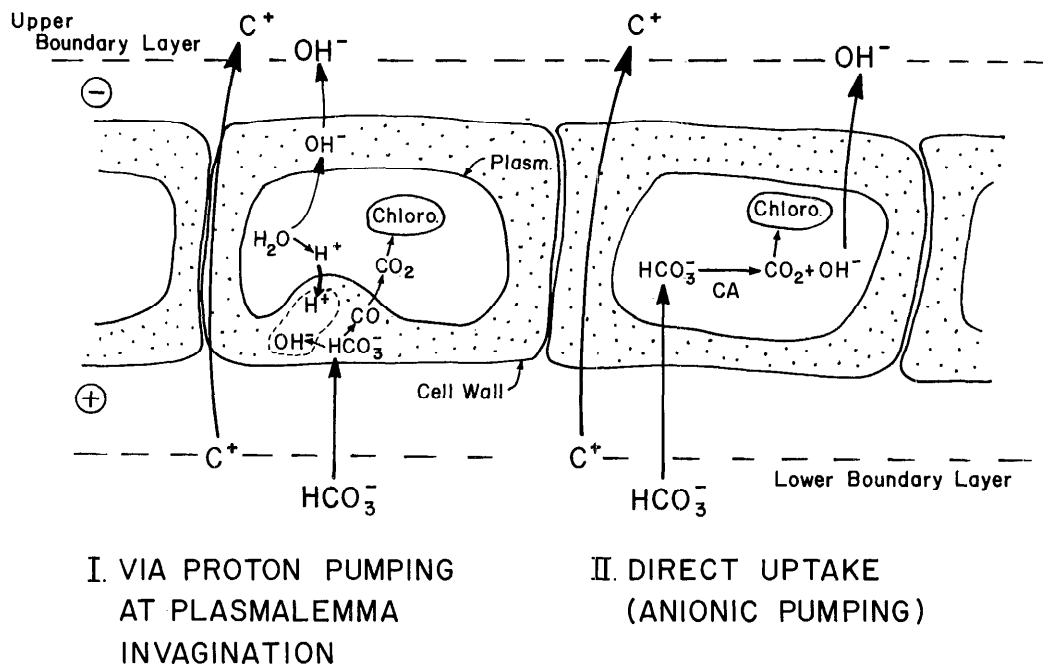
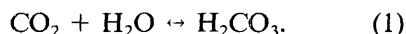


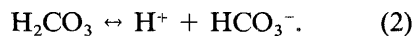
Fig. 2. Two mechanisms of bicarbonate uptake by cells in the polarized leaves of submersed macrophytes. I. Bicarbonate conversion in association with an acidic invagination of the plasmalemma (Plasm.) resulting from proton pumping (Prins et al. 1982) and subsequent migration of CO_2 into the chloroplast (Chloro.). II. Direct uptake of HCO_3^- into cytoplasm where it is converted to CO_2 and OH^- via the enzyme carbonic anhydrase (CA). In both pathways, hydroxyl ions are extruded at the upper (adaxial) surface, as well as cations (C^+) such as potassium, which can migrate through the apoplasm (stippled). Further details are given by Lucas and Berry (1985).

et al. 1981). For example, in the freshwater species, *Najas flexilis*, Hough (1974) reported significant rates of photorespiration at least partially attributable to high oxygen concentrations in the lacunal spaces. It would appear, therefore, that lacunal storage may provide both advantages and disadvantages to submersed aquatics.

The requirement for carbon in aquatic plants apparently can be met in another way than by exogenous sources of CO_2 (Lucas 1983) if species have HCO_3^- assimilation capabilities and carbonic anhydrase (carbonate hydrolase). This enzyme is widely distributed in the photosynthetic cells of plants and catalyzes the reversible hydration of carbon dioxide (Raven 1970):



Carbonic acid (H_2CO_3) is in equilibrium with bicarbonate (HCO_3^-):



The suggestion that various species of submersed aquatics can use HCO_3^- in photosynthesis was first made by Angelstein (1911) and elaborated on by Arens (1933) who established that *Potamogeton* and *Elodea* leaves were polarized, with the lower surface capable of bicarbonate uptake. Although controversial, these observations were later confirmed by Steemann Nielsen (1947). He found that freshwater and estuarine species such as *Elodea canadensis*

and *M. spicatum* are able to photosynthesize with bicarbonate when CO_2 levels are depleted, in contrast to *Fontinalis* (an aquatic moss) which cannot.

More elaborate experiments using microelectrodes (Prins et al. 1982) indicate that an H^+ extrusion pump is present in the plasmalemma of the lower leaf cells of *Elodea* and *Potamogeton* which balances the OH^- output on the upper leaf surface. Thus, transport of bicarbonate, by whatever physiological pathway (Fig. 2), seems to be a key ecological adaptation enabling submersed angiosperms to invade marine waters and successfully compete with algal macrophytes. It also appears that bicarbonate utilization in photosynthesis is widespread in red, brown, and green seaweeds, as well as in unicellular species such as *Chlamydomonas* and *Chlorella* (Badger et al. 1980; Beardall and Raven 1981). This suggests that any submersed angiosperm not having similar abilities would be at a distinct disadvantage in seawater at its normal pH (8.2) when bicarbonate ions are at least $10\times$ more prevalent than CO_2 . In less buffered shallow freshwaters, where pH can exceed 10 in the afternoon (Staver and Stevenson in prep.), bicarbonate utilization is essential to maintain photosynthesis. Weaver and Wetzel (1980) surveyed carbonic anhydrase (CA) activity from several freshwater environments. They concluded that plants with low CA had very much lower production rates, especially in comparison to emergent marsh plants that have very high CA. Thus, the evolution of bicarbonate uptake may be one of the most critical physiological mechanisms enabling submersed angiosperms to exploit many aquatic environments (Lucas 1983).

Sand-Jensen and Gordon (1984) recently reported wide variance in the ability of macrophytic species to use bicarbonate compared to CO_2 (Table 3). Marine species such as *Z. marina* appear to have high affinity for HCO_3^- , whereas freshwater species such as *Elodea* and *Potamogeton crispus* have very low HCO_3^- affinity. However, Milhouse and Strother's (1986) finding that *Zostera muelleri* cannot efficiently use HCO_3^- as a substrate in photosynthesis (the apparent K_m is around 20 mM and quite

Table 3. Half-saturation constants and ratios of $\text{CO}_2:\text{HCO}_3^-$ affinity for photosynthesis of various macrophytes (Sand-Jensen and Gordon 1984).

Habitat and species	K_0 (CO_2) (mM)	K_0 (HCO_3^-) (mM)	$\text{CO}_2:\text{HCO}_3^-$ affinity
Marine			
<i>Zostera marina</i>	0.27	0.60	1.7
<i>Fucus vesiculosus</i>	0.28	0.54	1.9
<i>Ulva lactuca</i>	0.26	0.60	2.4
Brackish			
<i>Myriophyllum spicatum</i>	0.18	0.06	5.4
<i>Potamogeton lucens</i>	0.20	0.07	6.0
<i>Potamogeton pectinatus</i>	0.38	1.25	9.8
<i>Egeria densa</i>	0.08	—	8–12
<i>Nitella flexilis</i>	0.10	8.0	10.1
Freshwater			
<i>M. spicatum</i>	0.15	4.5	30
<i>Hydrilla verticillata</i>	0.17	6.4	38
<i>Ceratophyllum demersum</i>	0.17	6.4	38
<i>Elodea canadensis</i>	0.30	16.0	52
<i>Potamogeton crispus</i>	0.20	23.0	66

dependent on pH) is at variance with *Z. marina*. In addition, since *T. testudinum* (Benedict et al. 1980) and *Thalassia hemprichii* (Abel 1984) have been reported to use CO_2 exclusively in photosynthesis, it is not clear that tropical seagrasses follow the same trends as temperate species. To what extent bicarbonate utilization is inducible when plants are abruptly exposed to low CO_2 environments is also not clear (Weaver and Wetzel 1980; Sand-Jensen and Gordon 1984). Nonetheless, the relative ability to switch from CO_2 to bicarbonate in photosynthesis may decide competitive interactions when CO_2 is limited. Whether it helps explain the trends in productivity of marine vs. freshwater species is an open question.

Differences in productivity

Comparative productivity—Although the potential importance of submersed aquatic populations to the fishery yield of coastal waters was postulated very early (Petersen 1918), there has been long-standing debate concerning which productivity technique is reliable enough to make accurate assessments of overall production. Petersen's (1918) analysis of eelgrass production along the North Sea consisted of doubling the

STANDING CROPS of FRESHWATER, BRACKISH and
MARINE SUBMERSED AQUATICS (g/m^2)

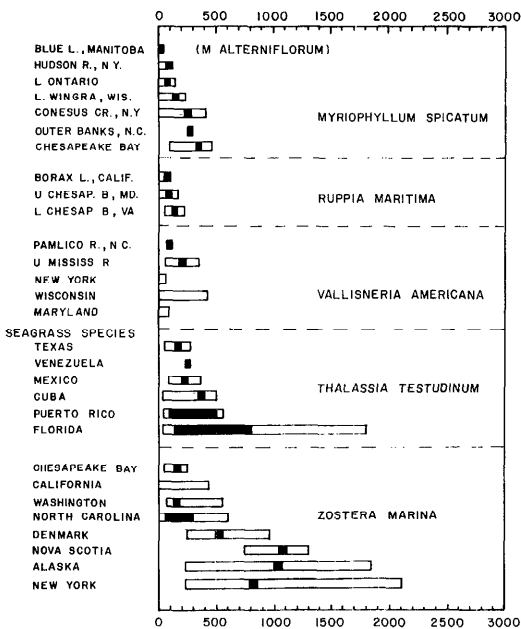


Fig. 3. Representative total above- and belowground biomass (g dw) for freshwater macrophytes and seagrass species. Black regions on bars show mean or range of peak biomass; white portions indicate entire range of reported values.

maximum standing crop for an estimate of losses to obtain estimates of annual production (assuming 50% disappears before peak biomass is reached). The inference of productivity from standing crop estimates is still widely used and is the most commonly reported parameter in production studies. The sampling of biomass is itself subject to methodological problems, but these often can be reduced by taking many small samples instead of a few large (1 m^2) ones (Downing and Anderson 1985). Although Zieman (1974) suggested that leaf tagging could be used to assess productivity in *Thalassia*, it has limitations in species with different leaf morphology and only measures aboveground production. Although accurate for leaf production, Patriquin's (1973) biometric estimation of productivity also underestimates total production. The production of O_2 was also used in several early investigations (Meyer 1939;

Gessner 1955; Odum and Hoskin 1958), but the technique was questioned by Hartman and Brown (1967) because of lag problems involving the lacunal storage system. Citing oxygen storage in lacunae and some comparative measurements, Wetzel (1964) also concluded that ^{14}C measurements were most reliable for making productivity rate measurements in submersed aquatics; this caused oxygen measurements to fall into disfavor (Zieman and Wetzel 1980).

Wetzel (1964) seems to have overlooked the fact that his own oxygen measurements were often substantially higher than those obtained by simultaneous measurements of carbon incorporation—the opposite of that expected if oxygen lags cause productivity to be underestimated. Indeed, Nixon and Oviatt (1972) concluded that the lag was inconsequential to the determination of production rates in *Zostera*. It now seems that carbon incorporation methods seriously underestimate productivity because the lacunal storages provide tight coupling between respired and “reused carbon” in photosynthesis (Benedict et al. 1980), and carbon is lost to excretion (Penhale and Smith 1977). This led Kemp et al. (1986) to conclude that each technique has its strengths and weaknesses and that each is probably useful in some situations. Thus, it appears that rates of oxygen production, carbon incorporation, and biomass production should all be considered in comparing freshwater and marine environments.

Earlier reviews (McRoy and McMillan 1977; Zieman and Wetzel 1980) concluded that seagrasses potentially have both high standing crop and productivity (up to $10\text{--}20 \text{ g C m}^{-2} \text{ d}^{-1}$). Comparison with reviews of freshwater macrophytes (Westlake 1963, 1975) suggests that those species have lower production rates and biomass (Fig. 3). In more recent literature (Table 4), the trend for seagrasses to have higher total biomass is clear, but productivity may have been overstated in some species. Especially when productivity is expressed per unit of tissue (as opposed to area), freshwater and marine species seem to have similar rates. For example, Odum et al. (1959) reported very high productivity ($8\text{--}15 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) for *Thalassia* in Puerto Rico. When the pro-

ductivity is expressed per unit weight, however, it is among the lower values for any of the species considered. In other words, it is the ability of seagrasses to maintain substantial standing crops throughout the year that allows them to have higher annual production than freshwater species. An argument might be raised that this conclusion is an artifact of productivity studies of freshwater species carried out mostly in the temperate regions. However, Van et al. (1976) pointed out that tropical species such as *Hydrilla* have many of the same physiological growth characteristics of temperate species. Thus, the critical question becomes: is there some overall limitation which prevents high macrophyte biomass (and thus overall production) in freshwaters?

Limiting factors—Solar radiation is often regarded as the ultimate limiting factor in any autotrophic ecosystem (Odum 1971). Brylinsky and Mann (1973) concluded that solar energy is more important in determining the productivity of lakes than are nutrient conditions. Figure 4 uses energy flow symbols (Odum 1971) to illustrate differences among freshwater, estuarine, and marine environments. Incoming light energy (circle at the left) has been shown to control the biomass and productivity in freshwater streams (Dawson and Kern-Hansen 1979) and in seagrass beds (Backman and Barilotti 1976; Dennison and Alberte 1982, 1985). Shallow, quiescent freshwaters often provide excellent environments for growth of submersed aquatics, but light is limiting in the deeper areas (Jupp and Spence 1977). In the lower portions of large rivers and estuaries, light attenuation in the water column is often severe (Fig. 4A) due to high turbidity associated with sediment and phytoplankton which limit the extent of submersed aquatic plant distribution (Orth and Moore 1983). Also, because many temperate estuaries have relatively high nutrient loadings, macrophytes can be heavily colonized with epiphytic algae which reduce the light available for photosynthesis (Kemp et al. 1983; Twilley et al. 1985). This mechanism is also important in limiting macrophyte growth in eutrophic freshwaters (Phillips et al. 1978). In marine waters, the light field is considerably more

favorable along temperate coastlines as well as in tropical seas, which partially accounts for increased productivity. In temperate estuaries which are not affected by excessive nutrient input, submersed angiosperms account for about half of the net primary production (Table 5). Interestingly, the well-documented productivity at Lawrence Lake (Wetzel 1975) is even higher than the two estuarine systems, and the contribution by submersed macrophytes is also substantial. However, due to nutrient inputs and greater overall depth, the organic carbon budget in large temperate estuaries (and large lakes) is dominated by plankton production.

Other factors that influence productivity are currents, waves, and tides; all can provide mixing energies needed to transport nutrients. In this regard, Conover (1968) reported a strong linear relationship between current speed up to 50 cm s^{-1} and productivity in eelgrass. Microcosm studies (Odum and Hoskin 1958) have also indicated higher metabolic rates when a turbulent flow regime is maintained. Presumably moderate tidal amplitudes can enhance productivity, provided sediment resuspension is not too severe. Water movement may also help to provide gaseous exchange and thus influence the metabolism of submersed macrophytes (Gessner 1955). However, it appears from field observations that the standing crop of *Zostera* declines sharply when current speeds exceed 50 cm s^{-1} (Conover 1968). This response is even more pronounced in *Callitriche stagnalis*, a submersed angiosperm found in Danish streams, which has an optimal threshold velocity of $8\text{--}12 \text{ mm s}^{-1}$ for photosynthesis beyond which it is inhibited (as much as 30% at 4 cm s^{-1} ; Madsen and Søndergaard 1983). The relative response to current by these species corresponds closely to prevailing environmental conditions. B. Kjerfve (pers. comm.) suggests that mean current speeds in lakes are on the order of 0.1 m s^{-1} , whereas in coastal waters they are about 10 times faster.

Figure 4B depicts less severe physical factors in lacustrine environments. However, large deep lakes and those in which water levels fluctuate drastically (reservoirs) present serious problems for growth of sub-

Table 4. Comparison of biomass and productivity of selected freshwater, brackish, and marine macrophytes.

Species/location	Peak biomass* (g dw m ⁻²)			Rates of productivity†			Reference
	Above	Below	Total	(mg O ₂ h ⁻¹ g ⁻¹ ff)	(g C m ⁻² d ⁻¹)	NPP‡ (g m ⁻² d ⁻¹)	
Freshwater and brackish							
<i>Vallisneria spiralis</i>							
L. Merrimajean, Aust.	463	66	529			2.1	Briggs and Maher 1985
<i>Vallisneria americana</i>							
New York State	50	13	63			1.5	Titus and Stephens 1983
Wisconsin	344	64	408				Titus and Adams 1979
Mississippi R.	180	38	218			3.2	Donnermeyer and Smart 1985
Maryland	53	38	91	3.8–10.6			Staver and Stevenson in prep.
<i>Myriophyllum spicatum</i>							
Wisconsin	407	39	446				Titus and Adams 1979
Wisconsin	220 ¹			2–17	3.35		Adams and McCracken 1974
Wisconsin					2–4		McCracken et al. 1975
New York State	387				1.2–1.8		Peverly 1979
New York State	878			8.0	4.44		Peverly et al. 1974
Maryland							Staver and Stevenson in prep.
<i>Hydrilla verticillata</i>							
Florida	161.4						Haller and Sutton 1975
Florida	280						Cassani and Caton 1985
Maryland	322 ¹	4	326	2.8–5.4			Staver and Stevenson in prep.
<i>Ruppia maritima</i>							
Chesapeake Bay, Va.	80–150					0.92	Wetzel and Penhale 1983
Redfish Bay, Texas	160	50	210		0.98		Pulch 1985
Borax Lake, Calif.	64						Wetzel 1964
Caimanero Lagoon, Mex.			1,000	0.9–9.7			Edwards 1978
Marine							
<i>Posidonia oceanica</i>							
Mediterranean, Italy	600–1,700					0.8–4.4 ²	Ott and Maurer 1977
<i>Posidonia australis</i>							
Port Hacking, Aust.	80	195	275			1.9 ²	Kirkman and Reid 1979
N. S. Wales, Aust.	137–453		847–25,550			1.9–5.2 ²	West and Larkum 1979
Spencer Gulf, Aust.	616		2,457			5.5 ²	West and Larkum 1979

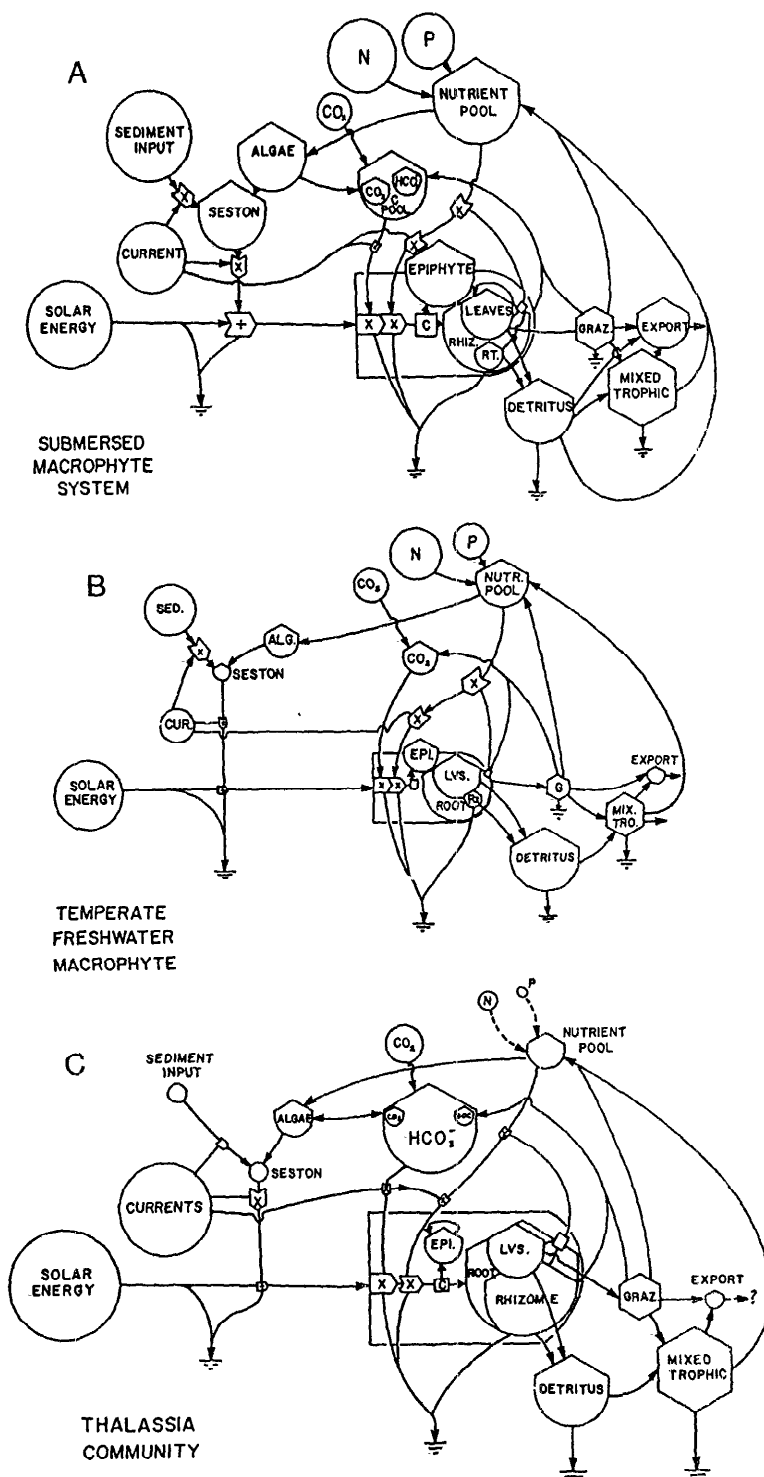


Fig. 4. Energy flow diagrams (see Odum 1971 for description of symbols) showing limiting factors involved in (A) an estuarine submersed macrophyte system, (B) a freshwater submersed aquatic community, and (C) seagrasses. Differences in the sizes of compartments show relative importance of various components in each environment.

Table 5. The annual primary production of two estuarine systems and a temperate lake

Component	Sydfynske Ohav, Denmark*		Beaufort estuary, N.C.†		Lawrence Lake, Mich.‡	
	(g C m ⁻²)	(% total)	(g C m ⁻²)	(% total)	(g C m ⁻²)	(% total)
Phytoplankton	53	33	66	48	43	25
Epiphytic and epibenthic algae	17	11	13	9	40	23
Submersed macrophytes	89	56	58	42	88	52
Total	159		137		171	

* Sand-Jensen and Borum 1983.

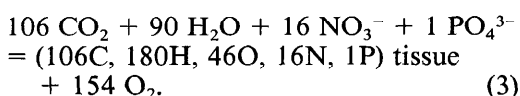
† Penhale and Smith 1977.

‡ Wetzel 1975.

mersed aquatics. Gaudet (1979) summarized data from artificial African lakes suggesting that floating mats (e.g. *Cyperus papyrus*, *Salvinia molesta*, *Eichornia crassipes*) dominate the system for the first several years of succession. Submersed weeds such as *Potamogeton* spp. and *Ceratophyllum demersum* have difficulty in adjusting to variability in littoral depth and appear later in succession if lake levels stabilize. Natural seasonal variation in water level also encourages floating aquatic plants (at the expense of submersed species) in lakes along the Amazon River in South America (T. Fisher pers. comm.).

It is important to emphasize that the original context of limiting factors, as first defined by Liebig (1840), did not refer to energy (which was taken as a boundary condition), but to elements that could be added to agricultural systems to increase *maximum standing crops*. Much of the confusion and controversy in the recent literature concerning nutrient limitation is due to a departure from Liebig's sense of limiting nutrients over a growing season toward very short-term (i.e. hours) productivity studies or supplementation of laboratory cultures or chemostats where growth of a particular population is measured. Of primary interest in this review of submersed aquatics is whether there are different limiting factors that account for the higher standing crops in marine vs. freshwater environments. Wetzel and Hough (1973) pointed out that the littoral region of lakes is confounded by a myriad of controlling factors. Nonetheless, certain generalizations can be made from scattered ecological observations and physiological studies.

In considering the basic stoichiometry of primary production (Odum 1971), the compound most needed for plant growth is carbon dioxide:



Although nitrogen and phosphorus are usually considered to be the main elements limiting overall productivity of aquatic environments (Wetzel 1975), some lakes are disproportionately low in total inorganic carbon (Boston and Adams 1983). Only aquatic mosses and isoetid relatives of submersed angiosperms can survive in these environments because of their ability to use CO₂ from sediments (Richardson et al. 1984). In lakes with enough inorganic carbon to allow growth of submersed angiosperms, there is probably a strong selective pressure to use bicarbonate as well as carbon dioxide, especially where pH exceeds 8 and HCO₃⁻ becomes the dominant ion. Presumably, species such as *Elodea*, which have comparatively high carbonic anhydrase levels (Weaver and Wetzel 1980), would be most competitive.

Another possible adaptation to quiescent, carbon-limited freshwaters might lie in the lush canopy formation by some species such as *M. spicatum* and *H. verticillata*. When leaves lie close to the air-water interface, their ability to absorb carbon from the atmosphere must increase considerably. A similar buoyancy mechanism for floating algae has been proposed by Paerl (1988). The lacunal system in submersed angiosperms may provide leaves with enough buoyancy in early evening hours (when desiccation

would not be excessive) to capture CO_2 from the air, which could be trapped and converted to C-4 acids via AAM (Cockburn 1985). Thus, it seems that much of the adaptive physiology of freshwater submersed species may be explained by the need to cope with carbon limitation in lakes. This argument assumes that most lakes are not limited by nitrogen because of nitrogen fixation (Schindler 1974) and that phosphorus (P) can be extracted from the sediments by submersed aquatics (Bristow and Whitcombe 1971; Carignan and Kalff 1980; Smith and Adams 1986).

Under some circumstances there may be problems with nutrient uptake when organic carbon levels in the sediments become high enough to cause oxygen depletion around the roots (Barko and Smart 1986). Although short-term diel root anoxia in eelgrass has not been shown to be excessively stressful (Pregnall et al. 1984), long-term anoxia in the rhizosphere of species with less subsurface structure (freshwater species) may curtail nutrient uptake ability (which depends on energy derived from respiratory processes to maintain membrane potentials). Thus, eutrophication can lead to many problems for submersed angiosperms in freshwaters, not the least of which is overgrowth of epiphytes on leaves (Phillips et al. 1978).

In streams and rivers there is much less chance of carbon limitation due to high mixing and reaeration. Not surprisingly, the highest productivity and biomass estimates in freshwaters come from clear flowing waters (Odum 1956; Dawson and Kern-Hansen 1979). However, high light attenuation because of elevated silt loads prevents extensive growth of submersed angiosperms in many rivers. When rivers mix with seawater in estuaries, light attenuation becomes even more severe due to flocculation and resuspension. Also, salinity in estuaries can fluctuate drastically at any particular location, making long-term survival of particular species marginal. As a result, growth of submersed aquatics is restricted under estuarine conditions, despite an often adequate supply of C, N, and P (Stevenson and Confer 1978).

Total estimates of standing crop suggest that protected, shallow marine environ-

ments are ideal for submersed aquatics. The most significant difference is the large amount of sub-sediment biomass, which creates a comparatively high root-to-shoot ratio (RSR). High RSR in macrophytes has been attributed (among other factors) to the need for efficient nutrient uptake in lean environments (Nicholson and Best 1974). This implies that nutrients may limit seagrass standing crops.

Patriquin (1972) hypothesized that nitrogen is the nutrient generally in short supply in tropical marine systems dominated by *Thalassia* and that nitrogen requirements are met largely by N fixation (Patriquin and Knowles 1972). Although initial measurements of N fixation suggested there might be a surplus of N produced by N-fixers associated with seagrasses, recent studies indicate that about a fourth of the N can be accounted for by fixation (Capone 1983). It thus appears that other sources of N (upwelling or land runoff) or recycling are often needed to satisfy the N requirement of seagrasses (Stevenson et al. in press). Comparatively low rates of N fixation are associated with brackish submersed aquatics in temperate estuarine environments, no doubt reflecting the large input of N from terrestrial sources (Lipschultz et al. 1979). Furthermore, Short et al. (1985) have postulated that there may be situations where the tropical seagrass *Syringodium* is phosphorus limited due to the strong adsorptive capacity of carbonate sediments. On other grounds, Smith (1984) has recently reopened the issue of whether P is more limiting than N to biological productivity in marine environments. Even if P proves to be more limiting to species in some shallow marine systems, it nonetheless appears that the critical constraint on the productivity of seagrasses is nutrient availability (Fig. 4C). This is in sharp contrast to estuaries where an overabundance of nutrients in the water column adversely impacts growth of submersed aquatics (Kemp et al. 1983) and to freshwaters where carbon limitation may be as much a problem for macrophytes as N and P availability.

Fate of production

Despite the changes in invertebrate communities brought about by the wasting dis-

ease (Allee 1923; Cottam 1935; Stauffer 1937), Petersen's (1918) early view that *Zostera* communities were important to fish stocks in the North Sea has been discredited because there was no noticeable effect on fish harvests (Rasmussen 1977). There is some evidence that significant quantities of seagrass may not enter pelagic food chains at all, but are swept into deep oceanic waters and sequestered in the sediments. Pratt (1962) reported *Thalassia* blades from the Puerto Rico Trench at over 7,000 m, and Menzies et al. (1967) noted similar sightings of *Thalassia* on the deep-sea floor off North Carolina. Although species with larger lacunal spaces may be predominantly exported (e.g. *Syringodium*), a substantial amount of *Thalassia* production may be deposited in situ in the sediments of the bed (Zieman et al. 1979). Similarly, Kirkman and Reid (1979) found that only 12% of the leaf production at Port Hacking, Australia, was carried out of the *Posidonia australis* bed and 37% remained to supplement the carbonaceous sediments.

Thus, in order to understand the fate of seagrass production, there has been emphasis on the decomposition processes of macrophytes (see Marshall 1970; Fenchel 1977; Pellikan 1984) and detrital utilization (Rice and Tenore 1981; Mann 1988). For example, Nienhuis and Van Ierland (1978) found that only 4% of eelgrass production (60 g C m^{-2}) was actually eaten by macroconsumers in Lake Grevelingen (Netherlands), whereas >50% of the production entered detrital food chains. Although Harrison and Mann (1975) found that *Z. marina* is much more resistant to decay than is *Spartina*, most submersed macrophytes have higher rates of decomposition than emergent marsh plants and may provide labile material for dependent organisms (Twilley et al. 1986). In addition to macrophyte detritus, submersed aquatic canopies capture organic materials by filtering incoming currents (Short and Short 1984), often making them even richer in detritus than are surrounding waters.

There seem to be rich invertebrate communities that feed on detrital material associated with temperate *Zostera* beds (Orth 1973) and various tropical species (Bell et al. 1984). These invertebrates are thought

to be the principal intermediaries in providing sustenance for young fish that use temperate *Zostera* beds as nursery areas (Kikuchi 1974; Adams 1976). In addition, some invertebrates, such as snails, even enhance macrophyte growth by feeding on periphyton as documented by Brönmark (1985) for *Ceratophyllum demersum*.

Unfortunately, the answer to how much macrophyte production is coupled to fisheries is illusive for several reasons. McMillan et al. (1980) found that most seagrasses have sulfated phenolic compounds that may reduce the palatability of leaf tissue and deter potential grazing by fish. There is also a lack of quantitative sampling of fish in submersed aquatic beds, although most surveys have shown low standing stocks of fish ($<2 \text{ g dw m}^{-2}$) in grass beds (Table 6). However, a recent study using more efficient gear shows high fish biomass (up to 80 g dw m^{-2}) in freshwater segments of estuaries (Serafy et al. in press). Serafy et al. (in press) concluded that fish biomass could be underestimated one to two orders of magnitude with conventional seining and electrofishing techniques and that fish biomass varies significantly over 24-h time periods in *Vallisneria* and *Hydrilla* beds. In the tropics it is well documented that fish associated with coral reefs during the day forage over seagrass beds at night (Weinstein and Heck 1979; Tribble 1981). Furthermore, fish appear to move into *Thalassia* beds at night in Laguna de Terminos, Mexico, from various other habitats (Yáñez-Arancibia et al. 1980; Yáñez-Arancibia and Day in press). Furthermore, the tendency of species to forage at either high or low tides (Robertson 1980) leads to undersampling, because few early studies were oriented to detecting temporal variations.

Diel behavior can be very important in the Caribbean where sea urchins (*Diadema antillarum*) migrate from coral reef crevices in the late afternoon to graze the perimeters of *Thalassia* beds so heavily that distinctive halos are formed around patch reefs (Ogden et al. 1973). Other studies indicate that almost half of the total leaf production ($42 \text{ g dw m}^{-2} \text{ week}^{-1}$) of *Thalassia* was ingested by sea urchins in Kingston Harbour, Jamaica (Greenway 1976). Although Thayer et al. (1984) pointed out that densities of

Table 6. Comparison of fish standing stocks in selected submersed aquatic communities.

Standing stocks g dw m ⁻²		Location	Habitat	Collection method	Reference
Annual mean	Range				
Marine					
1.3		Australia	<i>Zostera</i> bed	10- and 50-m seines	Robertson 1980
	0.2–3.8	Florida	<i>Thalassia</i> bed	47-m ² drop net	Brook 1977
1.5		North Carolina	<i>Zostera</i> bed	9-m ² drop net	Adams 1976
	0.04–0.4	Rhode Island	<i>Zostera</i> bed	15-m seine	Nixon and Oviatt 1972
1.2		Texas	Mixed seagrass	253- and 1,012-m ² drop nets	Hellier 1958
0.04–0.5		Texas	<i>Thalassia</i> bed	—	Hoese and Jones 1963
0.4		Texas	Guadalupe Bay	25-m ² drop net	Mosely and Cope-land 1969
Brackish and freshwater					
0.9	0–2.8	Parson's Island (Chesapeake)	<i>Potamogeton pectinatus</i>	31-m haul seine	Kemp et al. 1981
6.8	1.6–27.2	Todd's Cove (Chesapeake)	<i>Potamogeton perfoliatus</i>	31- and 1.8-m haul seines	Kemp et al. 1981
	1.6–40.7	Upper Chesapeake	<i>Vallisneria</i> and <i>Hydrilla</i>	3 × 3-m ² pop nets	Serafy et al. in press

sea urchins in Kingston Harbour were unusually high (20 m⁻²) during the Greenway study, her work at least demonstrates the possibility of a major grazing pathway in *Thalassia* beds. Moreover, there has been severe overfishing in most reef and seagrass systems, especially of green turtles (*Chelonia mydas*), which have been observed maintaining "grazing plots" in *Thalassia* by consistently feeding in particular parts of beds (Bjorndal 1980). Bjorndal (1980) argued persuasively that although Caribbean grass beds are generally considered to be detrital-based systems, this was not true in the past. Old records indicate extensive turtle populations acting as major herbivores in *Thalassia*.

Since submersed angiosperms have less negative values of stable carbon isotope ratios ($\delta^{13}\text{C}$) than algal species and C-3 species from terrestrial environments, analysis of $\delta^{13}\text{C}$ in consumer species has proven a useful tool in determining the origins of secondary production in various shallow marine systems (Thayer et al. 1978; Fry and Parker 1979; Mann 1988). Fry et al. (1982) suggested that 48–76% of the carbon of grazing fish in *Thalassia* beds at St. Croix may originate from either algal or angiosperm mac-

rophytes. However, Lobel and Ogden (1981) attributed most of the nutrition of parrot fish (*Sparisoma radians*) to epiphytic algae associated with *Thalassia* leaves at St. Croix. Similarly, Kitting et al. (1984) concluded that epiphytic algae are a more important basis of estuarine food webs than seagrasses in the northwest Gulf of Mexico. In contrast, $\sigma^{13}\text{C}$ studies in Australia (Klumpp and Nichols 1983; Nichols et al. 1985) clearly indicate that at least two species of commercial fish in Victoria depend heavily on seagrass (as opposed to algal) production.

Although marine macrophytes are > 50% of the diet of many of the consumers analyzed thus far (Table 7), there is still considerable debate concerning the direct utilization of seagrass carbon in secondary production. Stephenson et al. (1984) found considerable variability in $\delta^{13}\text{C}$ in kelp (*Laminaria*) and to a lesser degree in *Zostera*, which may make interpretation of $\delta^{13}\text{C}$ values difficult. More work is needed to separate algal and angiosperm nutrition—possibly by analysis of distinctive production products in food chains such as lipids (Nichols et al. 1985). The $\delta^{13}\text{C}$ isotopic analysis of freshwater systems has been little studied until recently (Fry and Sherr 1984), but there

Table 7. Percentage of diet of selected animals originating from seagrass.

Plant species (location)	Animal species (common name, type)	Diet (%)	Reference
<i>Halodule wrightii</i> * (L. Madre, Redfish B., Tex.)	<i>Diopatra cuprea</i> (polychaete worm)	50	Fry and Parker 1979
<i>Heterozostera tasmanica</i> (Corner Inlet, Aust.)	<i>Hyporhamphus melanochir</i> (southern sea garfish)	65–80	Nichols et al. 1985
<i>Posidonia australis</i> (Corner Inlet)	<i>Platycephalus laevigatus</i> † (rock flathead, fish)	40–60	Nichols et al. 1985
<i>P. australis</i> (Port Hacking, Aust.)	<i>Monacanthus chinensis</i> (leather-jacket, fish)	42	Kirkman and Reid 1979
<i>Thalassia testudinum</i> (Miskito Cays, Nicaragua)	<i>Chelonia mydas</i> (green turtle)	87	Mortimer 1976
<i>T. testudinum</i> (St. Johns, Virgin Is.)	<i>Acanthurus chirurgus</i> (doctor fish)	6	Randall 1965
<i>T. testudinum</i> (West Indies)	<i>Sparisoma radians</i> (bucktooth parrotfish)	88	Randall 1967
<i>Zostera marina</i> (E. coast of U.S.)	<i>Branta bernicla horta</i> (Atlantic brant, waterfowl)	>80	Cottam 1934
<i>Z. marina</i> (Newport estuary, N.C.)	<i>Bittium varium</i> (snail, epifauna)	58	Thayer et al. 1978
<i>Z. marina</i> (Newport estuary)	<i>Ophioderma brevispinum</i> (brittle star, echinoderm)	61	Thayer et al. 1978
<i>Z. marina</i> (Newport estuary)	<i>Lytechinus variegatus</i> (sea urchin, echinoderm)	60	Thayer et al. 1978
<i>Z. marina</i> (Newport estuary)	<i>Palaemonetes vulgaris</i> (grass shrimp)	49	Thayer et al. 1978
<i>Z. marina</i> (Newport estuary)	<i>Angopecten irradians</i> (bay scallop, bivalve)	30	Thayer et al. 1978
<i>Z. marina</i> (Newport estuary)	<i>Syngnathus floridae</i> (pipefish)	58	Thayer et al. 1978

* *Thalassia testudinum* and *Halophila engelmanni* are codominants.

† Major food item in the diet of *P. laevigatus* is the rock crab *Nectocarcinus integrifrons* which feeds predominantly on living leaves of *P. australis* (Klumpp and Nichols 1983).

seems to be less direct utilization by fish despite reports that some species “nest” in grass beds. Thus, although freshwater macrophytes appear less important in terms of fish production, marine and estuarine macrophytes may have once supported extensive grazing food chains. They may still be important in areas where grazers have been protected, for example manatees (*Trichechus manatus*) in Florida (Zieman 1982) and green turtles in St. Johns, Virgin Islands (S. Williams pers. comm.).

Waterfowl grazing by Brant geese has been reported on temperate communities of eelgrass at the end of the season (Cottam 1934). Stevenson and Confer (1978) also found evidence that when *Vallisneria* beds were prolific in upper Chesapeake Bay they supported large populations of migratory waterfowl. Although *Zostera* beds in Lake Grevelingen (an impounded estuary) are not reported to be grazed extensively (Nienhuis and Van Ierland 1978), Kiorboe (1980)

found that waterfowl consumption of plant production was comparatively high (from 15 to 60%) in Tipper Grund, a Danish fjord. Therefore, it seems that grazing in submersed macrophyte systems is sporadic, but can be more intense than in many other wetland systems (see Cahoon and Stevenson 1986).

Conclusions and overview

The overall impression from earlier reviews that macrophytes in freshwater and marine systems have marked differences in productivity has not been supported by a systematic comparison of the literature. There do not seem to be substantive differences in maximum productivity on a unit-tissue basis between freshwater and marine angiosperms, but they do have very different adaptive strategies. Despite the probability that freshwater species are ancestral, they retain many of the characteristics of colonizing species with comparatively low

Table 8. Comparison of submersed aquatic species in various environments.

Parameter	Freshwater	Estuarine	Marine (includes lagoons)
Flowers	Often conspicuous, monoecious		Usually dioecious
Total biomass	Usually $< 500 \text{ g m}^{-2}$		Can be $> 2,500 \text{ g m}^{-2}$
Architecture	Forms dense canopies in quiescent water, with ribbonlike leaves in streams		Open meadows with linear leaves and robust rhizomes
RSR		0.01–1.0	Usually > 1.0
Aerial production ($\text{g C m}^{-2} \text{ d}^{-1}$)		Up to 5	May be > 10
Most often limiting	Carbon, nutrients	Light	Nutrients
Consumers	Waterfowl	Fish, crabs, and waterfowl	Fish, sea urchins, sirenians, crabs, and turtles
Export	Small	Variable	Potentially high

biomass (Table 8). Although several freshwater species such as *Myriophyllum* and *Hydrilla* have high rates of productivity per unit weight, there is less energy put into long-lived plant structures, especially in terms of belowground biomass (reflected in the lower RSR). It is still unclear which of the differences in lake and marine ecosystems (Table 1) are responsible for the alternative patterns of biomass allocation in submersed angiosperms. However, meager sedimentary storage by freshwater species leads to a strategy of “boom–bust” productivity.

The productivity pulses of most freshwater macrophytes do not seem to be grazed regularly by fish (except when exotic species are introduced), but some systems may be at least partially consumed by migratory waterfowl at the end of the growing season (Perry et al. 1981). This may reflect the lack of fish species in lakes with cellulases in their stomachs capable of using submersed angiosperms. Recently formed lakes often have depauperate fish faunas (e.g., Crater Lake in Oregon had no fish until they were introduced by man) and often lack highly specialized species. In older tropical lakes and rivers where there is higher diversity, specialist species may graze the macrophytes because dense beds of submersed aquatics are often conspicuously absent. Efforts have been made to control the biomass of aquatic macrophytes in several lakes by introducing African *Tilapia*, which effectively uses the nutrient and caloric contents of species such as *Najas guadalupensis* (Buddington 1979).

The carbon from freshwater angiosperms not assimilated by consumers ends up as detritus, often decomposing in situ and substantially increasing the oxygen demand, which is inhibitory to most submersed aquatics (Barko and Smart 1986). This autotoxic feedback may help explain the cyclic behavior of submersed aquatics in freshwater ecosystems where they exhibit many “*r*-selected” traits, including high rates of reproduction (Phillips et al. 1983).

In contrast to freshwater species, seagrasses seem to put less energy into flowering and to store more of their production. Consequently, seagrasses have larger standing stocks of aboveground as well as belowground biomass (Table 8), which results in increased annual production and stability (see Ott 1981). Similarly, Harrison (1979) suggested that in intertidal zones *Z. marina* behaves as an *r*-strategist, but in deeper waters it has more attributes associated with *K*-strategists. When fully submersed in marine waters (where substantial tidal action provides mixing and ample supplies of bicarbonate make carbon limitation remote), seagrasses can maintain high rates of photosynthesis throughout the comparatively long growing season. By contrast, freshwater angiosperms in quiescent waters (where carbon and/or other nutrients are potentially limiting on a seasonal and even on a diel basis) have less overall production. Marine mammals, reptiles, fish, and invertebrates have all been reported to use macrophyte production in coastal environments, but there is much controversy concerning the

importance of detrital vs. grazing pathways in seagrass systems. McRoy (1974) concluded that macrophyte systems in Alaska produce five times the amount of carbon as the contiguous oceanic environments and must be regarded as important in budgeting materials. Furthermore, Smith (1981) suggested that marine macrophytes may sequester as much as 10^9 t of carbon annually; this could account for a large portion of the "missing carbon" in current global budgets (see Moore and Bolin 1986). In comparison, although not as important in a global sense since they are more geographically restricted, freshwater macrophytes undoubtedly play a major role in the mass balances of many lake ecosystems (Wetzel 1975).

References

- ABEL, K. M. 1984. Inorganic carbon source for photosynthesis in the seagrass *Thalassia hemprichii* (Ehrenb.) Aschers. *Plant Physiol.* **76**: 776–781.
- ADAMS, M. S., AND M. D. MCCracken. 1974. Seasonal production of the *Myriophyllum* component of the littoral of Lake Wingra, Wisconsin. *J. Ecol.* **62**: 457–465.
- , AND R. T. PRENTKI. 1982. Biology, metabolism and functions of littoral submersed weedbeds of Lake Wingra, Wisconsin, USA: A summary and review. *Arch. Hydrobiol. Suppl.* **62**, p. 333–409.
- ADAMS, S. M. 1976. The ecology of eelgrass *Zostera marina* (L.) fish communities. 1. Structural analysis. *J. Exp. Mar. Biol. Ecol.* **22**: 291–293.
- AIOTI, K. 1980. Seasonal change in the standing crop of eelgrass (*Zostera marina* L.) in Odawa Bay, central Japan. *Aquat. Bot.* **8**: 343–354.
- ALLEE, W. C. 1923. Studies in marine ecology: 3—Some physical factors related to the distribution of littoral invertebrates. *Biol. Bull.* **44**: 205–253.
- ANDREWS, T. J., AND K. M. ABEL. 1979. Photosynthetic carbon metabolism in seagrass. *Plant Physiol.* **63**: 650–656.
- ANGELSTEIN, U. 1911. Über die Kohlensäureassimilation submerser Wasserpflanzen in Bikarbonat- und Karbonatlosungen. *Beitr. Biol. Pflanz.* **10**: 87–117.
- ARBER, A. 1920. *Water plants*. Cambridge.
- ARENS, K. 1933. Physiologisch polarisierter Massenaustausch und Photosynthese bei submersen Wasserpflanzen. 1. *Planta* **20**: 621–658.
- BACKMAN, T. W., AND D. C. BARILOTTI. 1976. Irradiance reduction: Effects on standing crop of the eelgrass *Zostera marina* in a coastal lagoon. *Mar. Biol.* **34**: 33–40.
- BADGER, M. R., A. KAPLAN, AND J. A. BERRY. 1980. Internal inorganic carbon pool of *Chlamydomonas reinhardtii*: Evidence for a carbon dioxide-concentrating mechanism. *Plant Physiol.* **66**: 407–413.
- BARKO, J. W., AND R. M. SMART. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* **67**: 1328–1340.
- BEARDALL, J., AND J. A. RAVEN. 1981. Transport of inorganic carbon and the CO_2 concentrating mechanism in *Chlorella emersonii* (Chlorophyceae). *J. Physiol.* **64**: 892–895.
- BEER, S., AND R. G. WETZEL. 1981. Photosynthetic carbon metabolism in the submerged aquatic angiosperm *Scirpus subterminalis*. *Plant Sci. Lett.* **21**: 199–207.
- BELL, A. D., AND P. B. TOMLINSON. 1980. Adaptive architecture in rhizomatous plants. *Bot. J. Linn. Soc.* **80**: 125–160.
- BELL, S. S., K. WALTERS, AND J. C. KERN. 1984. Meiofauna from seagrass habitats: A review and prospectus for future research. *Estuaries* **7**: 331–338.
- BENEDICT, C. R., W. L. WONG, AND J. H. H. WONG. 1980. Fractionation of the stable isotopes of inorganic carbon by seagrasses. *Plant Physiol.* **65**: 512–517.
- BITTAKER, H. F., AND R. L. IVERSON. 1976. *Thalassia testudinum* productivity: A field comparison of measurement methods. *Mar. Biol.* **37**: 39–46.
- BJORNDAAL, K. A. 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar. Biol.* **56**: 147–156.
- BOSTON, H. L., AND M. S. ADAMS. 1983. Evidence of crassulacean acid metabolism in two North American isoetids. *Aquat. Bot.* **15**: 381–386.
- BRASIER, M. D. 1975. An outline history of seagrass communities. *Palaeontology* **18**: 681–702.
- BRIGGS, S. V., AND M. T. MAHER. 1985. Limnological studies of waterfowl habitat in south-western New South Wales. 2. Aquatic macrophyte productivity. *Aust. J. Mar. Freshwater Res.* **36**: 707–715.
- BRISTOW, J. M., AND M. WHITCOMBE. 1971. The role of roots in the nutrition of aquatic vascular plants. *Am. J. Bot.* **58**: 8–13.
- BRÖNMARK, C. 1985. Interactions between macrophytes, epiphytes and herbivores: An experimental approach. *Oikos* **45**: 26–30.
- BROOK, I. M. 1977. Trophic relationships in a seagrass community (*Thalassia testudinum*), in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. *Trans. Am. Fish. Soc.* **106**: 219–229.
- BRYLINSKY, M., AND K. H. MANN. 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnol. Oceanogr.* **18**: 1–14.
- BUDDINGTON, R. K. 1979. Digestion of an aquatic macrophyte by *Tilapia zillii* (Gervais). *J. Fish. Biol.* **15**: 449–455.
- BUESA, R. J. 1974. Population and biological data on turtle grass (*Thalassia testudinum* König, 1805) on the northwestern Cuban shelf. *Aquaculture* **4**: 207–226.
- BULTHUIS, D. A., G. W. BRAND, AND M. C. MOBLEY. 1984. Suspended sediments and nutrients in water ebbing from seagrass-covered and denuded tidal mudflats in a southern Australian embayment. *Aquat. Bot.* **20**: 257–266.
- , AND W. J. WOELKERLING. 1983. Seasonal variation in standing crop, density and leaf growth rate of the seagrass, *Heterozostera tasmanica*, in

- western Port and Port Phillip Bay, Victoria, Australia. *Aquat. Bot.* **16**: 111–136.
- BURKHOLDER, P., AND L. M. BURKHOLDER. 1959. Some chemical constituents of turtle grass *Thalassia testudinum*. *Bull. Torrey Bot. Club* **86**: 88–93.
- CAHOON, D. R., AND J. C. STEVENSON. 1986. Production, predation, and decomposition in a low-salinity *Hibiscus* marsh. *Ecology* **67**: 1341–1350.
- CAPONE, D. G. 1983. N_2 fixation in seagrass communities. *Mar. Technol. Soc. J.* **17**: 32–37.
- , P. A. PENHALE, R. S. OREMLAND, AND B. F. TAYLOR. 1979. Relationship between productivity and $N_2(C_2H_4)$ fixation in a *Thalassia testudinum* community. *Limnol. Oceanogr.* **24**: 117–125.
- CARIGNAN, R., AND J. KALFF. 1980. Phosphorus sources for aquatic weeds: Water or sediments? *Science* **207**: 987–989.
- CASSANI, J. R., AND W. E. CATON. 1985. Effects of chemical and biological weed control on the ecology of a south Florida pond. *J. Aquat. Plant Manage.* **23**: 51–58.
- CHURCHILL, A. C. 1983. Field studies on seed germination and seedling development in *Zostera marina* L. *Aquat. Bot.* **16**: 21–29.
- COCKBURN, W. 1985. Variation in photosynthetic acid metabolism in vascular plants: CAM and related phenomena. *New Phytol.* **101**: 3–24.
- CONOVER, J. T. 1968. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. *Bot. Mar.* **11**: 1–9.
- COOK, C. D. K., AND R. LUOND. 1982. A revision of the genus *Hydrilla* (Hydrocharitaceae). *Aquat. Bot.* **13**: 485–504.
- COOPER, T. G., D. FILMER, M. WISHNIK, AND D. M. LANE. 1969. The active species of “ CO_2 ” utilized by ribulose diphosphate carboxylase. *J. Biol. Chem.* **224**: 1082–1083.
- COTTAM, C. 1934. The eelgrass shortage in relation to waterfowl. *Trans. Am. Game Conf.* **20**: 272–279.
- . 1935. Wasting disease of *Zostera marina*. *Nature* **135**: 306.
- COX, P. A. 1983. Search theory, random motion, and the convergent evolution of pollen and spore morphology in aquatic plants. *Am. Nat.* **121**: 9–31.
- DALE, H. M. 1984. Hydrostatic pressure and aquatic plant growth: A laboratory study. *Hydrobiologia* **111**: 193–200.
- DARWIN, C. R. 1859. On the origin of the species by means of natural selection, or, the preservation of favored races in the struggle for life. John Murray.
- DAWSON, F. H., AND U. KERN-HANSEN. 1979. The effect of natural and artificial shade on the macrophytes of lowland streams and the use of shade as a management technique. *Int. Rev. Gesamten Hydrobiol.* **64**: 437–455.
- DEN HARTOG, C. 1970a. The sea-grasses of the world. North-Holland.
- . 1970b. Origin, evolution and geographical distribution of the sea-grasses. *Verh. K. Ned. Akad. Wet. Nat.* **59**: 12–38.
- DENNISON, W. C., AND R. S. ALBERTE. 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. *Oecologia* **55**: 137–144.
- , AND ———. 1985. Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). *Mar. Ecol. Progr. Ser.* **25**: 51–61.
- DENNY, P. 1980. Solute movement in submerged angiosperms. *Biol. Rev.* **55**: 65–95.
- DONNERMEYER, G. N., AND M. M. SMART. 1985. The biomass and nutritive potential of *Vallisneria spiralis* Michx. in navigation pool 9 of the Upper Mississippi River. *Aquat. Bot.* **22**: 33–44.
- DOWNING, J. A., AND M. R. ANDERSON. 1985. Estimating the standing biomass of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.* **42**: 1860–1869.
- DREW, E. A. 1983. Sugars, cyclitols and seagrass phylogeny. *Aquat. Bot.* **15**: 387–408.
- DURAKO, M. J., AND M. D. MOFFLER. 1985. Observations on reproductive ecology of *Thalassia testudinum* (Hydrocharitaceae). 3. Spatial and temporal variations in reproductive patterns within a seagrass bed. *Aquat. Bot.* **22**: 265–276.
- EDWARDS, R. R. C. 1978. Ecology of a coastal lagoon complex in Mexico. *Estuarine Coastal Mar. Sci.* **6**: 75–92.
- FELGER, R., AND C. P. MCROY. 1974. Seagrasses as potential food plants, p. 62–68. *In* G. F. Somers [ed.], Seed-bearing halophytes as food plants. Univ. Delaware, Coll. Mar. Stud.
- FENCHEL, T. 1977. Aspects of the decomposition of seagrasses, p. 123–145. *In* C. P. McRoy and C. Helfferich [eds.], Seagrass ecosystems: A scientific perspective. Dekker.
- FONSECA, M. S., J. S. FISHER, J. C. ZIEMAN, AND G. W. THAYER. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine Coastal Shelf Sci.* **15**: 351–364.
- FRY, B., R. LUTES, M. NORTHAM, P. L. PARKER, AND J. OGDEN. 1982. A $^{13}C/^{12}C$ comparison of food webs in Caribbean seagrass meadows and coral reefs. *Aquat. Bot.* **14**: 389–398.
- , AND P. L. PARKER. 1979. Animal diet in Texas seagrass meadows: $\delta^{13}C$ evidence for the importance of benthic plants. *Estuarine Coastal Shelf Sci.* **8**: 499–509.
- , AND E. SHERR. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* **27**: 15–27.
- GAUDET, J. J. 1968. The correlation of physiological differences and various leaf forms of an aquatic plant. *Physiol. Plant.* **21**: 594–601.
- . 1979. Aquatic weeds in African man-made lakes. *Pans* **25**: 279–286.
- GESSNER, F. 1955. Hydrobotanik. 1. Energichaushalt. VEB Deutscher.
- . 1959. Hydrobotanik. 2. Stoffhaushalt. VEB Deutscher.
- . 1961. Hydrostatischer Druck und Pflanzenwachstum, p. 668–690. *In* W. Ruhland [ed.], Encyclopedia of plant physiology. Springer.
- GETSINGER, K. D., AND C. R. DILLON. 1984. Quiescence, growth and senescence of *Egeria densa* in Lake Marion. *Aquat. Bot.* **20**: 329–338.
- GREENWAY, M. 1974. The effects of cropping on growth of *Thalassia testudinum* (Konig) in Jamaica. *Aquaculture* **4**: 199–206.

- , 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. *Aquat. Bot.* **2**: 117–126.
- HALLER, W. T., AND D. L. SUTTON. 1975. Community structure and competition between *Hydrilla* and *Vallisneria*. *Hyacinth Control J.* **13**: 48–50.
- , —, AND W. C. BARLOWE. 1974. Effects of salinity on growth of several aquatic macrophytes. *Ecology* **55**: 891–894.
- HARBORNE, J. B. 1977. Flavonoid sulphates: A new class of natural product of ecological significance in plants. *Prog. Phytochem.* **4**: 189–208.
- HARRISON, P. G. 1979. Reproductive strategies in intertidal populations of two co-occurring seagrasses (*Zostera* spp.). *Can. J. Bot.* **57**: 2635–2638.
- , AND K. H. MANN. 1975. Detritus formation from eelgrass (*Zostera marina* L.): The relative effects of fragmentation, leaching, and decay. *Limnol. Oceanogr.* **20**: 924–934.
- HARTMAN, R. T., AND D. L. BROWN. 1967. Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. *Ecology* **48**: 252–258.
- HATCH, M. D., AND C. R. SLACK. 1966. Photosynthesis by sugarcane leaves. A new carboxylation reaction and the pathway of sugar formation. *Biochem. J.* **101**: 103–111.
- HELDER, R. J., AND M. V. HARMELAN. 1982. Carbon assimilation pattern in the submerged leaves of the aquatic angiosperm: *Vallisneria spiralis* L. *Acta Bot. Neerl.* **3**: 281–295.
- HELLIER, T. R., JR. 1958. The drop-net quadrat, a new population sampling device. *Publ. Inst. Sci. Univ. Texas* **5**: 165–168.
- HOESE, H. D., AND R. S. JONES. 1963. Seasonality of larger animals in a Texas turtlegrass community. *Publ. Inst. Sci. Univ. Texas* **9**: 37–47.
- HOLADAY, A. S., AND G. BOWES. 1980. C4 acid metabolism and dark CO₂ fixation in a submerged aquatic macrophyte (*Hydrilla verticillata*). *Plant Physiol.* **65**: 331–335.
- HOUGH, R. A. 1974. Photorespiration and productivity in submersed aquatic vascular plants. *Limnol. Oceanogr.* **19**: 912–927.
- HUTCHINSON, G. E. 1975. A treatise on limnology. V. 3. Wiley.
- IIZUMI, H., AND A. HATTORI. 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. 3. The kinetics of nitrogen uptake. *Aquat. Bot.* **12**: 245–256.
- JACOBS, R. P. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquat. Bot.* **7**: 151–172.
- JUPP, B. P., AND D. H. N. SPENCE. 1977. Limitations of macrophytes in a eutrophic lake, Loch Leven. 1. Effects of phytoplankton. *J. Ecol.* **65**: 175–186.
- KALKMAN, L., AND R. J. VAN WIJCK. 1984. On the variation in chromosome number in *Potamogeton pectinatus* L. *Aquat. Bot.* **20**: 343–349.
- KEDDY, C. J., AND D. G. PATRIQUIN. 1978. An annual form of eelgrass in Nova Scotia. *Aquat. Bot.* **5**: 163–170.
- KEMP, W. M., W. R. BOYNTON, J. C. STEVENSON, R. W. TWILLEY, AND J. C. MEANS. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. *Mar. Technol. Soc. J.* **17**: 78–89.
- , —, R. R. TWILLEY, J. C. STEVENSON, AND L. G. WARD. 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay, p. 367–394. *In* V. S. Kennedy [ed.], *The estuary as a filter*. Academic.
- , M. R. LEWIS, AND T. JONES. 1986. Comparisons of methods for measuring production by the submersed macrophyte, *Potamogeton perfoliatus* L. *Limnol. Oceanogr.* **31**: 1322–1334.
- , J. C. STEVENSON, W. R. BOYNTON, AND J. C. STEVENSON. 1981. Submerged aquatic vegetation in Chesapeake Bay: Its ecological role in bay ecosystems and factors leading to its decline. Final Rep. U.S. EPA, Chesapeake Bay Program.
- KENTULA, M. E., AND C. D. MCINTIRE. 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. *Estuaries* **9**: 188–199.
- KENWORTHY, W. J., AND G. W. THAYER. 1984. Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems. *Bull. Mar. Sci.* **5**: 364–379.
- KIKUCHI, T. 1974. Japanese contribution on consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* **4**: 145–160.
- KJØRBOE, T. 1980. Distribution and production of submerged macrophytes in Tipper Grund (Ringkøbing Fjord, Denmark), and the impact on grazing. *J. Appl. Ecol.* **17**: 675–687.
- KIRKMAN, H., AND D. D. REID. 1979. A study of the role of the seagrass *Posidonia australis* in the carbon budget of an estuary. *Aquat. Bot.* **7**: 173–183.
- KITTING, C. L., B. FRY, AND M. D. MORGAN. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* **62**: 145–149.
- KLUMPP, D. W., AND P. D. NICHOLS. 1983. A study of food chains in seagrass communities. 2. Food of the rock flathead *Platycephalus laevis* Cuvier, a major predator in a *Posidonia australis* seagrass bed. *Aust. J. Mar. Freshwater Res.* **34**: 745–754.
- LEWIS, R. R., AND R. C. PHILLIPS. 1980. Occurrence of seeds and seedlings of *Thalassia testudinum* Banks ex König in the Florida Keys (USA). *Aquat. Bot.* **9**: 377–380.
- LIEBIG, J. 1840. Chemistry in its application to agriculture and physiology. Taylor and Walton.
- LIPSCHULTZ, F., J. J. CUNNINGHAM, AND J. C. STEVENSON. 1979. Nitrogen fixation associated with four species of submersed angiosperms in the central Chesapeake Bay. *Estuarine Coastal Shelf Sci.* **9**: 813–818.
- LOBEL, P. S., AND J. C. OGDEN. 1981. Foraging by the herbivorous parrot fish *Sparisoma radians*. *Mar. Biol.* **64**: 173–183.
- LOT, A. 1977. General status of research on seagrass ecosystems in Mexico, p. 233–245. *In* C. P. McRoy

- and C. Helfferich [eds.], *Seagrass ecosystems: A scientific perspective*. Dekker.
- LUCAS, W. J. 1983. Photosynthetic assimilation of exogenous HCO_3^- by aquatic plants. *Annu. Rev. Plant Physiol.* **34**: 71–104.
- , AND J. A. BERRY. 1985. Inorganic carbon uptake by aquatic photosynthetic organisms. *Am. Soc. Plant Physiol.*
- MCCRACKEN, M. D., M. S. ADAMS, J. TITUS, AND W. STONE. 1975. Diurnal course of photosynthesis in *Myriophyllum spicatum* and *Oedogonium*. *Oikos* **26**: 355–361.
- MCGAHEE, C. F., AND G. J. DAVIS. 1971. Photosynthesis and respiration in *Myriophyllum spicatum* L. as related to salinity. *Limnol. Oceanogr.* **16**: 826–829.
- MCMILLAN, C., O. ZAPATA, AND L. ESCOBAR. 1980. Sulphated phenolic compounds in seagrasses. *Aquat. Bot.* **8**: 267–278.
- MCRORY, C. P. 1974. Seagrass productivity: Carbon uptake experiments in eelgrass, *Zostera marina*. *Aquaculture* **4**: 131–137.
- , AND R. J. BARSDATE. 1970. Phosphorus absorption in eelgrass. *Limnol. Oceanogr.* **15**: 6–13.
- , AND C. HELFFERICH. 1977. *Seagrass ecosystems: A scientific perspective*. Dekker.
- , AND C. MCMILLAN. 1977. Production ecology and physiology of seagrasses, p. 53–87. In C. P. McRoy and C. Helfferich [eds.], *Seagrass ecosystems: A scientific perspective*. Dekker.
- MADSEN, T. V., AND M. SØNDERGAARD. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. *Aquat. Bot.* **15**: 187–193.
- MANN, K. H. 1973. Seaweeds: Their productivity and strategy for growth. *Science* **182**: 975–981.
- . 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol. Oceanogr.* **33**: 910–930.
- MARSHALL, N. 1970. Food transfer through the lower trophic levels of the benthic environment, p. 52–66. In J. A. Steele [ed.], *Marine food chains*. Oliver and Boyd.
- MENZIES, R. J., J. S. ZANEVELD, AND R. M. M. PRATT. 1967. Transported turtle grass as a source of organic enrichment of abyssal sediments off North Carolina. *Deep-Sea Res.* **14**: 111–112.
- MEYER, B. S. 1939. The daily cycle of apparent photosynthesis in a submerged aquatic. *Am. J. Bot.* **26**: 755–760.
- MILHOUSE, J., AND S. STROTHER. 1986. The effect of pH on the inorganic carbon source for photosynthesis in the seagrass *Zostera muelleri* Irmish ex Aschers. *Aquat. Bot.* **24**: 199–209.
- MOORE, B., AND B. BOLIN. 1986. The oceans, carbon dioxide, and global climate change. *Oceanus* **29**: 9–15.
- MORTIMER, J. A. 1976. Observations on the feeding ecology of the green turtle, *Chelonia mydas*, in the western Caribbean. M.S. thesis, Univ. Florida.
- MOSELEY, F. N., AND B. J. COPELAND. 1969. A portable drop-net for representative sampling of nekton. *Publ. Inst. Mar. Sci. Univ. Texas* **14**: 37–45.
- MUKAI, H., AND OTHERS. 1979. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific Coast of Japan. 1. Growth analysis in spring-summer. *Aquat. Bot.* **7**: 47–56.
- NICHOLS, P. D., D. W. KLUMP, AND R. B. JOHNS. 1985. A study of food chains in seagrass communities. 3. Stable carbon isotope ratios. *Aust. J. Mar. Freshwater Res.* **36**: 683–690.
- NICHOLSON, S. A., AND D. G. BEST. 1974. Root:shoot and leaf area relationships of macrophyte communities in Chautauqua Lake, New York. *Bull. Torrey Bot. Club* **101**: 96–100.
- NIENHUIS, P. H., AND B. H. H. DE BREE. 1980. Production and growth dynamics of eelgrass (*Zostera marina*) in brackish Lake Grevelingen (The Netherlands). *Neth. J. Sea Res.* **14**: 102–118.
- , AND E. T. VAN IERLAND. 1978. Consumption of eelgrass, *Zostera marina* by birds and invertebrates during the growing season in Lake Grevelingen (S.W. Netherlands). *Neth. J. Sea Res.* **12**: 180–194.
- NIXON, S. W., AND C. A. OVIATT. 1972. Preliminary measurements of midsummer metabolism in beds of eelgrass, *Zostera marina*. *Ecology* **53**: 150–153.
- ODUM, E. P. 1971. *Fundamentals of ecology*. Saunders.
- ODUM, H. T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* **1**: 102–117.
- . 1963. Productivity measurements in Texas turtlegrass and the effects of dredging an intra-coastal channel. *Publ. Inst. Mar. Sci. Texas* **9**: 48–58.
- . 1974. Tropical marine meadows, p. 442–487. In H. T. Odum et al. [eds.], *Coastal ecological systems of the United States*. Conserv. Found.
- , R. P. BURKHOLDER, AND J. RIVERO. 1959. Measurements of productivity of turtle grass flats, reefs, and the Bahia Fosforescente of southern Puerto Rico. *Publ. Inst. Mar. Sci. Univ. Texas* **6**: 159–170.
- , AND C. M. HOSKIN. 1958. Comparative studies of the metabolism of marine waters. *Publ. Inst. Mar. Sci. Texas* **5**: 16–46.
- OGDEN, J. C., R. A. BROWN, AND N. SALESKY. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science* **182**: 715–717.
- ORTH, R. J. 1973. Benthic infauna of eelgrass, *Zostera marina*, beds. *Chesapeake Sci.* **14**: 258–269.
- , AND K. A. MOORE. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* **222**: 51–53.
- OTT, J. A. 1981. Adaptive strategies at the ecosystem level: Examples from two benthic systems. *Mar. Ecol.* **2**: 113–158.
- , AND L. MAURER. 1977. Strategies of energy transfer from marine macrophytes to consumer levels: The *Posidonia oceanica* example, p. 493–502. In B. B. Keegan et al. [eds.], *The biology of benthic organisms*. Pergamon.
- OZIMEK, T., A. PREJS, AND K. PREJS. 1976. Biomass and distribution of underground parts of *Potamogeton perfoliatus* L. and *P. lucens* in Mikolajskie Lake, Poland. *Aquat. Bot.* **2**: 309–316.

- PAERL, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.* **33**: 823–847.
- PATRIQUIN, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm *Thalassia testudinum*. *Mar. Biol.* **15**: 35–46.
- . 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* Konig. *Carib. J. Sci.* **13**: 111–121.
- , AND R. KNOWLES. 1972. Nitrogen fixation in the rhizosphere of marine angiosperms. *Mar. Biol.* **16**: 49–58.
- PELLIKAN, G. C. 1984. Laboratory experiments on eelgrass (*Zostera marina* L.) decomposition. *Neth. J. Sea Res.* **18**: 360–383.
- PENHALE, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *J. Exp. Mar. Biol. Ecol.* **26**: 211–224.
- , AND W. O. SMITH. 1977. Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) and its epiphytes. *Limnol. Oceanogr.* **22**: 400–407.
- PERRY, M. C., R. E. MUNRO, AND G. M. HARAMIS. 1981. Twenty-five year trends in diving duck populations in Chesapeake Bay. *Trans. N. Am. Wildl. Nat. Resour. Conf.* **46**: 299–310.
- PETERSEN, C. G. J. 1918. The sea bottom and its production of food. *Rep. Dan. Biol. Sta.* **25**: 1–62.
- PETTITT, J. M. 1984. Aspects of flowering and pollination in marine angiosperms. *Oceanogr. Mar. Biol. Annu. Rev.* **22**: 315–342.
- PEVERLY, J. H. 1979. Elemental distribution and macrophyte growth downstream from an organic soil. *Aquat. Bot.* **7**: 319–338.
- , G. MILLER, W. H. BROWN, AND R. L. JOHNSON. 1974. Aquatic weed management in the Finger Lakes. Cornell Univ. Water Res. Mar. Sci. Center, Tech. Rep. 90.
- PHILLIPS, G. L., P. EMINSON, AND B. MOSS. 1978. A mechanism to account for macrophytic decline in progressively eutrophicated waters. *Aquat. Bot.* **4**: 103–126.
- PHILLIPS, R. C. 1974. Temperate grass flats, p. 244–299. *In* H. T. Odum et al. [eds.], *Coastal ecological systems of the United States*. Conserv. Found.
- , W. S. GRANT, AND C. P. McROY. 1983. Reproductive strategies of eelgrass (*Zostera marina* L.). *Aquat. Bot.* **16**: 1–20.
- , AND C. P. McROY. 1980. *Handbook of seagrass biology*. Garland.
- PIETERSE, A. H. 1981. *Hydrilla verticillata*—a review. *Abstr. Trop. Agric.* **7**: 9–33.
- PRATT, R. M. 1962. The ocean bottom. *Science* **138**: 492–495.
- PREGNALL, A. M., R. D. SMITH, T. A. KURSAR, AND R. S. ALBERTE. 1984. Metabolic adaptation of *Zostera marina* (eelgrass) to diurnal periods of root anoxia. *Mar. Biol.* **83**: 141–147.
- PRINS, H. B. A., J. F. H. SNEL, AND P. E. ZANSTRA. 1982. The mechanism of photosynthetic bicarbonate utilization, p. 120–126. *In* J. J. Symoens et al. [eds.], *Studies on aquatic vascular plants*. R. Bot. Soc. Belg.
- PULCH, W. M. 1985. Seasonal growth dynamics of *Ruppia maritima* L. sl. and *Halodule wrightii* Aschers in southern Texas and evaluation of sediment fertility status. *Aquat. Bot.* **23**: 53–66.
- RANDALL, J. E. 1965. Grazing effect on seagrasses by herbivorous reef fish in the West Indies. *Ecology* **46**: 255–260.
- . 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr. Miami* **5**: 665–847.
- RASMUSSEN, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on the environmental factors and fauna, p. 1–51. *In* C. P. McRoy and C. Helfferich [eds.], *Seagrass ecosystems: A scientific perspective*. Dekker.
- RAUNKAER, C. 1934. The life forms of plants and statistical plant geography. Clarendon.
- RAVEN, J. A. 1970. Exogenous inorganic carbon sources in plant photosynthesis. *Biol. Rev.* **45**: 167–221.
- RICE, D. L., AND K. R. TENORE. 1981. Dynamics of carbon and nitrogen during the decomposition of detritus derived from estuarine macrophytes. *Estuarine Coastal Shelf Sci.* **13**: 681–690.
- RICHARDSON, K., H. GRIFFITH, M. L. REED, J. A. RAVEN, AND N. M. GRIFFITHS. 1984. Inorganic carbon assimilation in the isoetids, *Isoetes lacustris* and *Lobelia dortmanii*. *Oecologia* **61**: 115–121.
- ROBERTSON, A. I. 1980. The structure and organization of an eelgrass fish fauna. *Oecologia* **47**: 79–82.
- SAND-JENSEN, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia* **14**: 185–201.
- , AND J. BORUM. 1983. Regulation of growth of eelgrass (*Zostera marina* L.) in Danish coastal waters. *Mar. Technol. Soc. J.* **17**: 15–21.
- , AND D. M. GORDON. 1984. Differential ability of marine and freshwater macrophytes to utilize HCO_3^- and CO_2 . *Mar. Biol.* **80**: 247–253.
- , AND C. PRAHL. 1982. Oxygen exchange with the lacunae and across leaves and roots of the submerged vascular macrophyte *Lobelia dortmanna* L. *New Phytol.* **91**: 103–120.
- SCHENCK, H. 1886. *Vergleichende Anatomie der submersen Gewächse*. Bibl. Bot. **1**: 1–67.
- SCHINDLER, D. W. 1974. Eutrophication and recovery in experimental lakes: Implications for lake management. *Science* **184**: 260–262.
- SCULTHORPE, C. D. 1967. *The biology of aquatic vascular plants*. Arnold.
- SERAFY, J. E., H. M. HARRELL, AND J. C. STEVENSON. In press. Quantitative sampling of small fishes in dense vegetation: Design and field testing of portable “pop-nets.” *J. Appl. Ichthyol.*
- SHORT, F. T., M. W. DAVIS, R. A. GIBSON, AND C. F. ZIMMERMAN. 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine Coastal Shelf Sci.* **20**: 419–430.
- , AND C. A. SHORT. 1984. The seagrass filter: Purification of estuarine and coastal waters, p. 395–413. *In* V. S. Kennedy [ed.], *The estuary as a filter*. Academic.

- SMITH, C. S., AND M. S. ADAMS. 1986. Phosphorus transfer from sediments by *Myriophyllum spicatum*. *Limnol. Oceanogr.* **31**: 1312-1322.
- SMITH, F. A., AND N. A. WALKER. 1980. Photosynthesis by aquatic plants: Effects of unstirred layers in relation to assimilation of CO_2 and HCO_3^- and to carbon isotopic discrimination. *New Phytol.* **86**: 245-259.
- SMITH, S. V. 1981. Marine macrophytes as a global carbon sink. *Science* **211**: 838-840.
- . 1984. Phosphorus versus nitrogen limitation in the marine environment. *Limnol. Oceanogr.* **29**: 1149-1160.
- SØNDERGAARD, M. 1979. Light and dark respiration and the effect of the lacunal system on refixation of CO_2 in submerged aquatic plants. *Aquat. Bot.* **6**: 269-283.
- , AND R. G. WETZEL. 1980. Photorespiration and internal recycling of CO_2 in the submersed angiosperm *Scirpus subterminalis*. *Can. J. Bot.* **58**: 591-598.
- SPENCE, D. H. N. 1976. Light, zonation and biomass of submerged freshwater macrophytes, p. 335-345. *In* E. A. Drew et al. [eds.], *Underwater research*. Academic.
- STAUFFER, R. C. 1937. Changes in the invertebrate community of a lagoon after disappearance of the eelgrass. *Ecology* **18**: 427-431.
- STEEMANN NIELSEN, E. 1947. Photosynthesis of aquatic plants with special reference to the carbon sources. *Dan. Bot. Ark.* **12**: 1-71.
- STEPHENSON, R. L. K., F. C. TAN, AND K. H. MANN. 1984. Stable carbon isotope variability in marine macrophytes and its implications in food web studies. *Mar. Biol.* **81**: 223-230.
- STERNBERG, L., M. J. DENIRO, AND J. E. KEELEY. 1984. Hydrogen, oxygen, and carbon isotope ratios of cellulose from submerged aquatic crassulacean acid metabolism and non-crassulacean acid metabolism plants. *Plant Physiol.* **76**: 68-70.
- STEVENSON, J. C., AND N. M. CONFER. 1978. Summary of available information on Chesapeake Bay submerged vegetation. U.S. Fish Wildl. Serv. OBS/USFWS.
- , C. MADDEN, AND C. S. HOPKINSON. In press. Sources of new nitrogen in a tropical lagoon system receiving inputs from a continental landmass, p. 1-10. *In* A. Yáñez-Arancibia and J. W. Day, Jr. [eds.], *Ecology of a coastal ecosystem in the southern Gulf of Mexico, with special reference to Terminos Lagoon*. Univ. Nacl. Auto. Mexico. UNAM/CONACYT.
- TAKHTAJAN, A. 1969. Flowering plants, origin and early evolution angiosperms. *Smithson. Inst.*
- TATSUMI, J., AND Y. KONO. 1981. Translocation of foliar-applied nitrogen to rice roots. *Jpn. J. Crop Sci.* **50**: 302-310.
- THAYER, G. W., K. A. BJØRNDAL, J. C. OGDEN, S. L. WILLIAMS, AND J. C. ZIEMAN. 1984. Role of larger herbivores in seagrass communities. *Estuaries* **7**: 351-376.
- , P. L. PARKER, M. W. LACROIX, AND B. FRY. 1978. The stable isotope ratio of components of an eelgrass, *Zostera marina*, bed. *Oecologia* **35**: 1-12.
- , D. A. WOLFE, AND R. B. WILLIAMS. 1975. The impact of man on seagrass systems. *Am. Sci.* **63**: 288-296.
- TITUS, J. E., AND M. S. ADAMS. 1979. Comparative carbohydrate storage and utilization patterns in the submersed macrophytes, *Myriophyllum spicatum* and *Vallisneria americana*. *Am. Midl. Nat.* **102**: 263-272.
- , AND M. D. STEPHENS. 1983. Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. *Oecologia* **56**: 23-29.
- TOETZ, D. W. 1974. Uptake and translocation of ammonia by freshwater hydrophytes. *Ecology* **55**: 199-201.
- TOMLINSON, P. B. 1969. On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae). 3. Floral morphology and anatomy. *Bull. Mar. Sci.* **19**: 286-305.
- . 1980. Leaf morphology and anatomy in seagrasses, p. 7-28. *In* R. C. Phillips and C. P. McRoy [eds.], *Handbook of seagrass biology*. Garland.
- TRIBBLE, G. W. 1981. Reef-based herbivores and the distribution of two seagrasses (*S. filiforme* and *T. testudinum*) in the San Blas Islands (western Caribbean). *Mar. Biol.* **65**: 277-281.
- TUTIN, T. G. 1938. The autecology of *Zostera marina* L. in relation to its wasting disease. *New Phytol.* **37**: 50-71.
- TWILLEY, R. R., G. EJDUNG, P. ROMARE, AND W. M. KEMP. 1986. A comparative study of decomposition, oxygen consumption and nutrient release for selected aquatic plants occurring in an estuarine environment. *Oikos* **47**: 190-198.
- , W. M. KEMP, K. W. STAYER, AND J. C. STEVENSON. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* **23**: 179-191.
- VAN, T. K., W. T. HALLER, AND G. BOWES. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiol.* **58**: 761-768.
- VERHOEVEN, J. T. A. 1979. The ecology of *Ruppia*-dominated communities in western Europe. 1. Distribution of *Ruppia* representatives in relation to their autecology. *Aquat. Bot.* **6**: 197-268.
- WALKER, N. A. 1985. The carbon species taken up by *Chara*: A question of unstirred layers, p. 31-37. *In* W. J. Lucas and J. A. Berry [eds.], *Inorganic carbon uptake by aquatic photosynthetic organisms*. Am. Soc. Plant Physiol.
- WARD, L. G., W. M. KEMP, AND W. R. BOYNTON. 1984. The influence of waves and seagrass communities on suspended sediment dynamics in an estuarine embayment. *Mar. Geol.* **59**: 85-103.
- WEAVER, C. I., AND R. G. WETZEL. 1980. Carbonic anhydrase levels and internal lacunar CO_2 concentrations in aquatic macrophytes. *Aquat. Bot.* **8**: 173-186.
- WEBER, J. A., J. D. TENHUNEN, S. S. WESTRIN, C. S. YOCUM, AND D. M. GATES. 1981. An analytical model of photosynthetic response of aquatic plants to inorganic carbon and pH. *Ecology* **62**: 697-705.

- WEINSTEIN, M. P., AND K. L. HECK, JR. 1979. Ichthyofauna of seagrass meadows along the Caribbean west of Panama and the Gulf of Mexico: Composition, structure and community ecology. *Mar. Biol.* **50**: 97–107.
- WEST, R. J., AND A. W. D. LARKUM. 1979. Leaf productivity of the seagrass, *Posidonia australis* in eastern Australian waters. *Aquat. Bot.* **7**: 57–65.
- WESTLAKE, D. F. 1963. Comparisons of plant productivity. *Biol. Rev.* **38**: 385–425.
- . 1975. Primary production of freshwater macrophytes, p. 189–206. *In* J. P. Cooper [ed.], *Photosynthesis and productivity in different environments*. Cambridge.
- WETZEL, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large shallow lake. *Int. Rev. Gesamten Hydrobiol.* **49**: 1–61.
- . 1975. *Limnology*. Saunders.
- , E. S. BRAMMER, K. LINDSTRÖM, AND C. FORSBERG. 1985. Photosynthesis of submersed macrophytes in acidified lakes. 2. Carbon limitation and utilization of benthic CO₂ sources. *Aquat. Bot.* **22**: 107–120.
- , AND R. A. HOUGH. 1973. Productivity and role of aquatic macrophytes in lakes: An assessment. *Pol. Arch. Hydrobiol.* **20**: 9–19.
- WETZEL, R. L., AND P. A. PENHALE. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Mar. Technol. Soc. J.* **17**: 22–31.
- WIUM-ANDERSON, S., AND J. BORUM. 1980. Biomass and production of eelgrass (*Zostera marina* L.) in the Øresund, Denmark. *Ophelia Suppl.* **1**, p. 49–55.
- YÁÑEZ-ARANCIBIA, A., F. AMEZCUA LUNARES, AND J. W. DAY, JR. 1980. Fish community structure and function in Terminos Lagoon, a tropical estuary in southern Gulf of Mexico, p. 465–482. *In* V. S. Kennedy [ed.], *Estuarine perspectives*. Academic.
- , AND J. W. DAY, JR. In press. Ecology of a coastal ecosystem in the southern Gulf of Mexico, with special reference to Terminos Lagoon. *Univ. Nacl. Auto. Mexico. UNAM/CONACYT*.
- ZIEMAN, J. C. 1974. Methods for the study of the growth and production of turtle grass, *Thalassia testudinum* König. *Aquaculture* **4**: 139–143.
- . 1975. Seasonal variation of turtle grass, *Thalassia testudinum* König, with special reference to temperature and salinity effects. *Aquat. Bot.* **1**: 107–123.
- . 1982. The ecology of the seagrasses of south Florida: A community profile. *Biol. Serv. Program. U.S. Fish Wildl. Serv. FWX/OBX/82/25*.
- . 1986. Variations of stable isotope ratios in seagrasses and in macrophyte based food webs as a function of source habitat [abstract]. *EOS* **67**: 989.
- , G. W. THAYER, M. B. ROBBLEE, AND R. T. ZIEMAN. 1979. Production and export of seagrasses from a tropical bay, p. 21–34. *In* R. J. Livingston [ed.], *Ecological processes in coastal and marine systems*. Plenum.
- , AND R. G. WETZEL. 1980. Productivity in seagrasses: Methods and rates, p. 87–116. *In* R. C. Phillips and C. P. McRoy [eds.], *Handbook of seagrass biology*. Garland.