

EFFECTS OF SUBMERSED MACROPHYTES ON ECOSYSTEM PROCESSES

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ABSTRACT

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Both natural and managed ecosystems experience large fluctuations in submersed macrophyte biomass. These fluctuations have important consequences for ecosystem processes because of the effects of macrophytes on the physical/chemical environment and littoral biota.

The first part of this paper reviews the effects of submersed macrophytes on the physical environment (light extinction, temperature, hydrodynamics, substrate), chemical environment (oxygen, inorganic and organic carbon, nutrients) and the biota (epiphytes, grazers, detritivores, fishes). This extensive literature suggests that variations in macrophyte biomass could have major effects on aquatic ecosystems.

The second part of this paper considers the ecosystem consequence of several common changes in submersed macrophytes: replacement of vascular macrophytes by bryophytes during lake acidification; short-term biomass changes caused by invasions of adventive species, cultural eutrophication or macrophyte management; and changes in littoral grazers. These scenarios illustrate the importance of macrophytes in ecosystems, but raise many questions which cannot be answered at present. Controlled, whole-lake macrophyte experiments are needed to resolve these open questions.

INTRODUCTION

Submersed macrophytes have major effects on productivity and biogeochemical cycles in fresh water because they occupy key interfaces in stream and lake ecosystems. Most macrophytes are rooted, and constitute a living link between sediments and the overlying water. Macrophytes grow between the shoreline and open waters dominated by plankton, and can potentially intercept or modify material flows from land to the pelagial zone. Finally, the life cycles of macrophytes are intermediate in length, much longer than those of plankton but generally shorter than those of fish. In temperate lakes, the production—decomposition cycle of macrophytes, and the associated biogeochemical fluxes, follow an annual cycle (Carpenter, 1980a).

Nutrient cycling by plankton has a turnover time of days (Lehman, 1980), whereas the residence time of nutrients in fishes is many years (Kitchell et al., 1975). In general, the macrophyte nutrient pool, which is often quite large (Carpenter and Adams, 1977), cycles at an intermediate rate at the interfaces of water with sediment, and terrestrial ecosystems with freshwater ecosystems.

To determine the effects of macrophytes on ecosystem processes, we must study the effects of macrophytes on their environment. This line of inquiry is much less popular than its converse, the study of environmental effects on macrophytes. To illustrate this point, we classified 193 papers published in volumes 15–21 of *Aquatic Botany* (1983–1985). Ninety-four papers were ecological; that is, in contrast to purely morphological, physiological or systematic papers, they dealt primarily with interactions between macrophytes and their environment. Seventy-two papers emphasized the effects of environmental factors on macrophytes, but only 22 papers emphasized the effects of macrophytes on the environment. This imbalance in the literature implies that ecosystem effects of macrophytes are less well known than their physiological ecology.

Nevertheless, research on the ecosystem effects of macrophytes is extremely important for the advancement of aquatic ecology in general, and for fulfillment of the requests that society makes of aquatic ecologists. Natural ecosystems experience massive changes in macrophyte biomass over time scales of decades to centuries. Such changes can have major consequences for commercially important animal species (Orth and Moore, 1983). Management practices produce equally large biomass changes over shorter time scales. We know enough to expect large ecosystem responses from such natural or man-made fluctuations in macrophyte biomass. However, the critical ecosystem-level experiments needed to test these expectations have not been carried out.

This paper summarizes the effects of submersed macrophytes on the freshwater environment and presents recommendations for further research. The first part of the paper, a review, examines effects of macrophytes on physical and chemical factors, and biotic interactions which involve the use of macrophytes as habitat or food by other aquatic organisms. Collectively, these reductionistic studies suggest that changes in the macrophyte component should have powerful effects on freshwater ecosystems. However, most of these hypothesized effects have not been subjected to experimental tests at the ecosystem level. The second part of this paper describes hypotheses that emerge from the literature and are testable by experiments at the ecosystem level.

REVIEW: EFFECTS OF MACROPHYTES ON THEIR ENVIRONMENT

Effects on the physical environment

As the largest sessile organisms in fresh water ecosystems, macrophytes have great effects on the physical environment. From an ecosystem standpoint, the most important physical effects of macrophytes are those on light, temperature, water flow and substrate.

Light extinction

Light is attenuated exponentially with depth within the macrophyte canopy (Westlake, 1964; Owens et al., 1967). Titus and Adams (1979) fit Eqn. 1 to light profiles within macrophyte canopies:

$$I_z = I_0 \exp(-k_w z - k_m M) \quad (1)$$

I_z and I_0 are photosynthetically active radiation at depth z and the surface respectively; k_w and k_m are the extinction coefficients of lake water and macrophyte shoot tissue; and M is the dry mass of macrophyte shoots above depth z . Light attenuation by the canopy significantly alters the depth profile of photosynthesis in macrophyte stands (Adams et al., 1974). Extinction coefficients of macrophyte canopies vary about 4-fold among species (Westlake, 1964; Owens et al., 1967; Titus and Adams, 1979). Light extinction by *Myriophyllum spicatum* L., which concentrates biomass near the water surface, does not depend on sun angle, while the rosulate *Vallisneria americana* Michx attenuates more light at low sun angles than at high sun angles (Titus and Adams, 1979). Such interspecific differences in light extinction have obvious implications for neighbor relations among submersed plants and for growth of epiphytes.

Temperature

The vertical temperature gradient within macrophyte stands is as steep as 10°C m^{-1} , compared to gradients of less than 0.2°C m^{-1} in neighboring unvegetated areas (Dale and Gillespie, 1977a). At a typical Q_{10} of 2, this temperature gradient would halve the metabolic rates of macrophytes, epiphytes and epifauna with each meter of depth in the canopy. Dale and Gillespie (1977a) found a strong linear relationship between the vertical temperature gradient during the day and the logarithm of macrophyte biomass m^{-3} over the range 30–1000 g dry mass m^{-3} in Lake Opinicon, Ontario. In experimental work using artificial macrophytes, the temperature gradient varied on a diel cycle (Dale and Gillespie, 1978). Steepness of the gradient depended on the ratio of solar radiation to wind speed, leaf area index and the vertical profile of leaf density. Time of day of the maximum temperature gradient depended on leaf area index and the vertical profile of leaf density.

Water circulation tends to obliterate the thermal gradients induced by macrophytes (Dale and Gillespie, 1977b). Differences among lakes are likely to result from morphometric factors related to circulation such as fetch and wave-mixed depth. Differences in morphometry and circulation between Lake Opinicon and Lake Wingra may explain the relatively weak thermal gradients found in dense *Myriophyllum spicatum* stands in the latter lake (Adams et al., 1974). Water circulation is fairly rapid in the littoral zone of Lake Wingra (Prentki et al., 1979) and probably accounts for the thermal homogeneity of neighboring vegetated and unvegetated plots (Carpenter and Gasith, 1978).

Water flow

Retardation of flow by macrophyte beds is well known to stream ecologists, and lowland streams are often dredged to remove macrophytes and decrease the risk of flooding (Sculthorpe, 1967). Effects of macrophytes on circulation in lakes are not as well known. Sear (1977) used a laboratory flume to determine the effects of macrophytes on flow in lake water. His results were incorporated in a three-dimensional flow model which showed that *Myriophyllum spicatum* beds decreased water flux through the littoral zone of Lake Wingra by 36% (Weiler, 1978). While it is clear that macrophyte beds retard water flow in lakes, we know little about the quantitative importance of this effect and its dependence on macrophyte biomass and canopy structure.

Substrate

Hydrodynamics and substrate characteristics are closely linked, because currents and waves are responsible for the erosion and deposition that produce the mosaics of substrate types in stream beds and littoral zones. The interacting effects of hydrodynamics and substrate on macrophyte zonation were reviewed with insight by Spence (1982). Spence emphasized the importance of the wave-mixed depth in determining substrate characteristics and hence submersed vegetation. Erosion and sorting of littoral sediments above the wave-mixed depth lead to coarser sediments than those found in the purely depositional zone below the wave-mixed depth.

Because of their effects on water movements, macrophyte beds enhance deposition of fine sediments that would otherwise be eroded. For example, macrophyte vegetation significantly reduces losses of suspended solids in waters ebbing from tidal flats (Bulthuis et al., 1984). In stream ecosystems, the export of macrophyte detritus is inversely related to living macrophyte biomass (Fisher and Carpenter, 1976), suggesting that macrophyte stands act as a sieve retaining coarse particulate detritus. Terrestrial allochthonous material is retained in macrophyte beds and decomposed to a much greater extent than in unvegetated reaches of streams (Dawson, 1980). In lakes, macrophytes contribute refractory organic matter directly to sediments upon senescence (see below).

Effects on the chemical environment

Biogeochemical consequences of macrophyte growth

Oxygen. Diel oxygen changes as large as 8 mg l^{-1} occur in the waters of dense submersed macrophyte stands (Ondok et al., 1984). Submersed macrophytes oxygenate the water more effectively than floating-leaved macrophytes (Pokorny and Rejmankova, 1983). Mats of duckweeds actually decrease oxygen concentrations by inhibiting reoxygenation from the atmosphere (Morris and Barker, 1977). In a river with dense macrophyte stands, diel and annual oxygen dynamics were strongly dependent on macrophyte biomass (Kelly et al., 1983). The diel oxygen flux in a dense *Myriophyllum spicatum* stand was about twice as great as that of an adjacent harvested plot (Carpenter and Gasith, 1978).

Submersed vascular plants also oxidize their rhizospheres. Photosynthetically-produced oxygen diffuses to the roots through the aerenchyma, and subsequently diffuses across the epidermis into the sediment (Oremland and Taylor, 1977; Sand-Jensen and Prahl, 1982; Smith et al., 1984). Oxygen release rates are enhanced by light (Sand-Jensen et al., 1982; Carpenter et al., 1983). Among submersed macrophytes, rhizosphere oxidation was first reported for rosette plants of oligotrophic lakes (Wium-Andersen and Andersen, 1972). In these small rosettes, release of photosynthetic oxygen is favored by thick leaves and cuticles, chloroplasts lining the aerenchyma, relatively large lacunae, large root surface area and short diffusional pathways (Sand-Jensen et al., 1982). Numerous flexuous-stemmed plants of more productive waters are also capable of rhizosphere oxidation, but at somewhat lower rates (Sand-Jensen et al., 1982; Carpenter et al., 1983).

The degree to which sediments are oxidized depends on the balance between oxygen release by the macrophytes and reductant formation by chemical and microbiological processes in the sediment. In oligotrophic lake sediments, oxidized zones many centimeters thick develop below macrophyte beds (Wium-Andersen and Andersen, 1972; Tessenow and Baynes, 1975; Jaynes, 1985). In contrast, highly reducing eutrophic lake sediments quickly consume oxygen released by *Myriophyllum verticillatum* L. and no detectable oxidized zone is formed (Carpenter et al., 1983).

Rhizosphere oxidation has important biogeochemical consequences. Iron and manganese diffusing upward from deep, reduced sediments are precipitated at the base of the oxidized zone (Tessenow and Baynes, 1978). Transplants of vascular macrophytes into reduced sediments lowered pore water iron and phosphorus fractions and diminished phosphorus diffusion from sediments as iron-phosphorus complexes accumulated (Jaynes and Carpenter, 1986). Therefore, in oligotrophic systems, rosette macrophytes slow phosphorus recycling by oxidizing surficial sediments (Jaynes and Carpenter, 1986). Apparently this process is ineffective in more eutrophic systems because of the greater flux of reductants in sediments and the lower rates of oxygen release by macrophytes (Sand-Jensen et al., 1982; Carpenter et al., 1983).

Inorganic carbon. Metabolism of submersed macrophytes can strongly influence dissolved inorganic carbon speciation and pH. For example, Ondok et al. (1984) report the following diel changes in a stand of *Elodea canadensis* Michx: pH, 7.5–9.5; free CO_2 , 0–4 mg l^{-1} ; HCO_3^- , 45–100 mg l^{-1} . Macrophytes remove inorganic carbon from the water by both assimilation into organic matter and precipitation as carbonate salts on the leaves (Wetzel, 1960). The latter process leads to the formation of marl sediment zones which have a distinctive benthos and have been used as sources of agricultural lime (Wetzel 1960, 1970).

In softwater lakes, sediment pore waters are a major source of dissolved inorganic carbon, and up to 95% of the carbon fixed by macrophytes enters from the roots (Wium-Andersen, 1971; Sand-Jensen and S ndergaard, 1978; S ndergaard and Sand-Jensen, 1979a). Root uptake of inorganic carbon is a minor source for marine macrophytes (Wetzel and Penhale, 1979) and macrophytes of hardwater lakes (Loczy et al., 1983).

Dissolved organic carbon. Actively growing macrophytes release 1–10% of their photosynthetically-fixed carbon to the water as dissolved organic compounds (Wetzel, 1969; Hough and Wetzel, 1975; S ndergaard, 1981). This organic matter contributes to the metabolism of bacteria in the complex of carbonate deposits and epiphytic microorganisms on the macrophyte surface (Allen, 1971). Organic matter released by macrophytes is used more rapidly by the epiphytic assemblage than by the bacterioplankton (S ndergaard, 1983). Littoral zones are net sources of dissolved organic matter to lake water (Mickle and Wetzel, 1978; Prentki et al., 1979).

Dissolved nutrients. Since we are concerned with ecosystem effects of macrophytes, this section will emphasize plant–water exchanges of phosphorus. We selected phosphorus because of its importance as a limiting nutrient in lakes and streams. For a broader physiological perspective on uptake, translocation and excretion of phosphorus and other nutrients by submersed macrophytes, we recommend the thorough, critical review by Denny (1980).

Roots are the major avenue for entry of phosphorus into macrophytes (Smith, 1978; Barko and Smart, 1980; Carignan and Kalff, 1980). Phosphorus is translocated to shoots, where it may eventually enter the lake water by release from living or decaying shoots.

Phosphorus, in contrast to organic carbon, is not released from living submersed macrophytes at ecologically significant rates. Denny (1980) argued that most reports of phosphorus excretion resulted from leakage of radioactive phosphorus from root to shoot compartments of experimental chambers. There are at least three studies that appear exempt from Denny's criticisms, all of which show that phosphorus release by living shoots is a minor flux. Smith (1978) used pre-labeled shoots of *Myriophyllum spicatum* to show that release rates were less than 5% of uptake rates throughout the year. Barko and Smart (1980) used a mass balance approach in closed

laboratory systems, and concluded that release was only a few percent of the seasonal phosphorus flux through *Egeria densa* Planch., *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum*. Carignan and Kalff (1982) used fully-labeled plants of 9 species in situ to show that epiphytes obtained only 3–9% of their phosphorus from the macrophyte host and that *Myriophyllum spicatum* accounted for less than 10% of the phosphorus released from the total macrophyte–epiphyte complex.

Biogeochemical consequences of macrophyte decomposition

Decay rates of macrophyte shoots depend on several environmental factors, especially temperature, oxygen concentration and nitrogen concentration (Godshalk and Wetzel, 1978; Carpenter and Adams, 1979; Carpenter, 1980). Decay rates of *Myriophyllum spicatum* shoots were enhanced by nitrate, but not by phosphate (Carpenter and Adams, 1979). Under aerobic conditions, most of the variance in shoot decay rates can be explained by temperature and shoot nitrogen content (Carpenter, 1980a). The temperature response, which is exponential, dominates the nitrogen response, which is linear or hyperbolic (Carpenter and Adams, 1979; Carpenter, 1980a). From an ecosystem standpoint, the most important consequences of macrophyte decay are release of dissolved substances, deoxygenation and sediment accretion.

Release of dissolved substances. Leaching of dissolved organic carbon is rapid, especially in the early stages of macrophyte decay (Otsuki and Wetzel, 1974; Godshalk and Wetzel, 1978). For example, as much as 29% of the dry mass of *Nymphoides peltata* (Gmel.) O. Kuntze was released to the water as dissolved organic compounds (Brock, 1984). Organic matter leached from decaying macrophytes is readily metabolized by suspended bacteria (Carpenter et al., 1979) and consequently has rapid turnover rates (Godshalk and Wetzel, 1978). In contrast, humic materials derived from lignified tissues over longer time periods have slow turnover rates and can suppress the productivity of phytoplankton (Jackson and Hecky, 1980).

Phosphorus is released more rapidly than carbon during decomposition (Carpenter, 1980a; Brock, 1984; Pomogyi et al., 1984). Phosphorus leaching rates are strongly dependent on shoot phosphorus content, but do not depend on water temperature (Carpenter, 1980a). Over 75% of leached phosphorus is in a soluble reactive form that co-elutes with phosphate in Sephadex gel filtrations (Carpenter and Adams, 1978; Carpenter, 1980a). Phosphorus released by decaying macrophytes is rapidly assimilated by phytoplankton, leading to increased chlorophyll concentrations (Landers, 1982).

Nitrogen, in contrast to phosphorus, tends to be released more slowly than carbon during decay (Nichols and Keeney, 1973; Carpenter and Adams, 1979; Boston and Perkins, 1982; Brock, 1984). Much of the soluble nitrogen is released as ammonium (Landers, 1982; Brock et al., 1983), consistent

with the rapid disappearance of protein carbon from the detritus (Pomogyi et al., 1984).

Deoxygenation. Decaying macrophytes consume large amounts of oxygen (Godshalk and Wetzel, 1978), and macrophyte leachate stimulates oxygen consumption by suspended bacteria (Carpenter et al., 1979). Oxygen depletion around masses of detritus causes decay rates to decrease (Godshalk and Wetzel, 1977). It seems likely that localized deoxygenated patches must occur in littoral zones during periods of macrophyte senescence, with important consequences for nutrient recycling from both sediments and decaying macrophytes. Larger-scale oxygen depletions are most likely to occur in warm, shallow, poorly circulated waters in which dense macrophyte stands senesce rapidly (Carpenter and Greenlee, 1981).

Sediment accretion. Macrophyte decay rates decrease as decay progresses, so that recently dead shoots decompose most rapidly (Godshalk and Wetzel, 1978). The relative content of refractory organic matter increases during decay, causing decay rates to decline even in aerated systems at constant temperature (Godshalk and Wetzel, 1978). In lakes, burial in colder anoxic sediments further decreases decay rates (Godshalk and Wetzel, 1977). Several models have been proposed to explain such declining decay rates (Carpenter, 1981a). The best-fitting model postulates two detrital pools with independent decay rates, one labile with rapid decay and the other refractory with slow decay (Carpenter, 1982; Brock et al., 1985).

The accumulation of refractory macrophyte detritus in lake sediments has important long-term effects on lake succession (Wetzel, 1979). Accretion of sediments causes expansion of the littoral zone, resulting in a positive feedback that accelerates lake succession (Carpenter, 1981b). Eventually, sediment organic content becomes high enough to limit macrophyte growth (Barko and Smart, 1983). This process hastens the transition from a vegetation of submersed macrophytes into a vegetation of emergent macrophytes which are more tolerant of highly organic sediment conditions (Barko and Smart, 1983). Greater dominance by emergent macrophytes further accelerates sediment accretion and lake succession (Wetzel, 1979).

Macrophyte stands: nutrient source or sink?

One of the most important questions about the role of littoral zones in ecosystems is the extent to which macrophyte beds act as sources or sinks of dissolved materials. The answer depends upon the particular material flux of interest (Table I). In general, macrophyte stands are sinks for particulate matter and sources of dissolved phosphorus and organic carbon.

All assessments of macrophyte effects on material cycles are dependent upon the time scale of the study. For example, macrophyte stands in streams act as sinks for particulate organic matter during the growing season, but export organic matter upon senescence (Dawson, 1980). On an annual

TABLE I

Effects of submersed macrophyte stands on concentrations of selected materials in lake water. "Source" means that there was a net flux from the plant beds to the water during the course of the study; "sink" means that there was a net flux from the water to the plant beds

Material	Effect	Reference
Coarse particulate organic matter	Sink	Dawson, 1980
Suspended solids	Sink	Bulthuis et al., 1984
Particulate phosphorus	Sink	Bulthuis et al., 1984
Particulate phosphorus	Sink	Adams and Prentki, 1982
Particulate silica	Sink	Bulthuis et al., 1984
Dissolved organic carbon	Source	Mickle and Wetzel, 1978
Dissolved organic carbon	Sink	Prentki et al., 1979
Dissolved calcium	Sink	Mickle and Wetzel, 1978
Dissolved magnesium	No effect	Mickle and Wetzel, 1978
Dissolved potassium	Sink	Mickle and Wetzel, 1978
Dissolved inorganic nitrogen	Sink	Mickle and Wetzel, 1978
Dissolved phosphorus	Source	Prentki et al., 1979

scale, most macrophyte stands are net sources of particulate organic matter. During periods of active growth, macrophytes and epiphytes are a net sink for phosphorus (Howard-Williams, 1981), while during periods of senescence the plants are a net source (Landers, 1982).

Very few data sets provide estimates of net annual phosphorus flux to and from macrophyte beds. In a *Potamogeton pectinatus* L. stand, the phosphorus cycle was relatively closed (Howard-Williams and Allanson, 1981). These authors concluded that phosphorus released by decaying macrophytes was rapidly assimilated by periphyton and epiphyton, which in turn decomposed on littoral sediments that effectively retained phosphorus. However, net phosphorus fluxes were not measured directly. In a *Myriophyllum spicatum* stand where net fluxes were directly measured, somewhat different results were obtained (Adams and Prentki, 1982). The littoral zone was a significant source of dissolved phosphorus, exceeding the total phosphorus loading from the watershed during summer. The major pathway of phosphorus transfer was from sediments to macrophyte shoots, via uptake and translocation, and then to the water via decomposition (Carpenter, 1980a). Adams and Prentki (1982) estimated many within-littoral phosphorus transfers as well as the net fluxes and concluded, like Howard-Williams and Allanson (1981), that internal recycling of phosphorus much exceeded net fluxes across littoral zone boundaries.

Macrophyte community composition influences the magnitude of dissolved phosphorus and organic carbon fluxes from the littoral zone (Carpenter, 1983). In oligotrophic lakes, biomass is low and turns over slowly, surficial sediments are oxidized and therefore retain phosphorus, and net

fluxes to and from the littoral zone are small. In contrast, eutrophic lakes support high macrophyte biomasses with high turnover rates, surficial sediments are reduced and therefore release phosphorus, and fluxes to and from the littoral zone are comparatively large.

Biotic interactions of macrophytes

The importance of submersed macrophytes in biotic interactions is proportional to their biomass and productivity. Both of these vary substantially among lakes. For example, in oligotrophic Mirror Lake, *Lobelia dortmanna* L. has a maximum annual biomass of 7 g dry mass m⁻² and an annual net production of 5 g dry mass m⁻² (Moeller, 1978). In contrast, *Myriophyllum spicatum* in eutrophic Lake Wingra has a maximum annual biomass of more than 340 g dry mass m⁻² and an annual net production in excess of 600 g dry mass m⁻² (Adams and McCracken, 1974). Mirror Lake and Lake Wingra are low and high extremes, respectively, which bracket most of the reported values for submersed macrophyte production (Carpenter, 1983). Therefore, the inter-lake variability of macrophyte biomass and production is about two orders of magnitude.

The diversity of methods used complicates comparisons of macrophyte production. Commonly used methods include leaf marking techniques (Moeller, 1978), modifications of the Allen Curve (Carpenter, 1980b) and the ¹⁴C technique combined with biomass and environment data (Adams and McCracken, 1974). From an ecosystem standpoint, methods based on diel gas exchange are attractive because they integrate the metabolism of the entire system. Unfortunately, these methods have not been commonly applied, perhaps because of earlier reports that lacunar gas storage prevented accurate measurements of respiration and photosynthesis using gas concentration changes in the surrounding water (Hartman and Brown, 1967). These concerns are negated by recent studies showing rapid exchange of oxygen between aerenchyma of macrophytes and the water (Westlake, 1978; Kelly et al., 1981). Carbon dioxide, like oxygen, is sequestered in the lacunae of submersed plants. Equilibration of the internal atmosphere with the water occurs within a few minutes and poses no serious difficulties for photosynthesis and respiration measurements (Titus et al., 1979; Moeslund et al., 1981). However, in ¹⁴C experiments inorganic carbon in the water takes as much as 30 min to reach equilibrium with CO₂ in the internal atmosphere, causing serious errors in short incubations (Søndergaard and Sand-Jensen, 1979b).

Epiphytes

Macrophytes are colonized by a rich array of microbes, algae and consumers, particularly in hard water lakes where carbonate deposits provide a matrix for the epiphytes (Allanson, 1973). Productivity of the epiphyte complex ranges from 4 to 93% of host macrophyte productivity (see Jones,

1984, p. 1902). Epiphytes appear to be much more active than their hosts in dissolved nutrient exchanges with the water (Howard-Williams, 1981; Carignan and Kalff, 1982).

Organic carbon and phosphorus behave somewhat differently in the macrophyte—epiphyte complex. Organic carbon released by macrophytes is a major substrate for epiphytic bacteria (Allen, 1971; Søndergaard, 1983). In contrast, little phosphorus is released by living macrophytes (Smith, 1978; Barko and Smart, 1980) and epiphytic algae obtain less than 10% of their phosphorus from the host macrophyte (Carignan and Kalff, 1982). On the other hand, epiphyte algae may rapidly assimilate phosphorus released from decomposing macrophytes (Howard-Williams and Allanson, 1982), and provide food for many macrophyte-associated grazers.

Periphyton—macrophyte—grazer interactions

High invertebrate densities typically associated with macrophytes relative to other substrates (e.g. Voigts, 1976; Pip, 1978; Dvorak and Best, 1982; Lodge, 1985; cf. Rooke, 1984) may result from epiphyte food available on macrophyte surfaces (Sculthorpe, 1967). Other explanations for macrophyte—invertebrate associations, to be discussed in later sections, include the use by invertebrates of live macrophytes as food (Pip and Stewart, 1976), and protection from predators (Crowder and Cooper, 1982). It is certainly true that many of the invertebrates associated with macrophytes eat the epiphyte—detritus complex on the surface of macrophytes rather than the macrophyte itself (Reavell, 1980; Cattaneo, 1983; Orth and van Montfrans, 1984). This close association of macrophytes, epiphytes and grazers has spawned a hypothesis about symbiotic relationships among macrophytes, grazers and epiphytes (Hutchinson, 1975, pp. 547—548; Thomas, 1982; Rogers and Breen, 1983).

In simple outline, the symbiosis hypothesis suggests the following costs and benefits. Epiphytes benefit macrophytes because epiphytes distract grazers from macrophytes (Hutchinson, 1975). Macrophytes benefit epiphytes by providing a substrate and nutrients. Thus selection has favored macrophytes that leak organic carbon and other nutrients and stimulate epiphytic growth (see previous section; Wetzel, 1983a; cf. Harrison and Chan, 1980). However, excessive epiphytic growth decreases macrophyte photosynthesis (Phillips et al., 1978; Bulthuis and Woelkerling, 1983). Grazers then benefit the macrophyte by removing algal (Orth and van Montfrans, 1984) and bacterial (Rogers and Breen, 1983) epiphyton and making excretory nitrogen available for macrophyte uptake (Miura et al., 1978). Therefore, macrophytes that attract epiphyton grazers (e.g. with amino- and organic acids (Sterry et al., 1983)) may benefit. Macrophytes benefit grazers by providing epiphyton food, refuge from predation, oviposition sites, access to the air—water interface, amino acids and by removing toxic ammonia (Thomas, 1982; Sterry et al., 1983).

We propose the following related, but more parsimonious, hypothesis

that suggests epiphytes are a passive mediating influence in the relationship between macrophytes and epiphyte grazers. Epiphytes do not defend macrophytes from grazers. Instead, epiphytes are preferred over macrophytes because many aquatic grazers do not have mouth parts capable of puncturing or tearing macrophyte tissues (which are tough and low in nitrogen relative to periphyton) and/or macrophytes may be intrinsically unpalatable to many grazers. Macrophytes leak organic carbon and other nutrients (because the costs of being impermeable are too high), epiphyton takes advantage of the leaked nutrients, and grazers eat the epiphyton. Because of the several advantages (discussed above) offered to invertebrates by macrophyte habitats, there is selection for those grazers possessing distant chemoreception to macrophytes (see Sterry et al., 1983). Because periphyton grazers do benefit macrophytes, exudates attractive to grazers are selected in macrophytes. In an experimental test of the central predictions of this hypothesis, Brönmark (1985) found that the growth of *Ceratophyllum demersum* L. was higher in the presence of periphyton-grazing snails than without grazers. Intact *Ceratophyllum* attracted the snail *Lymnaea peregra* (Müller), but damaged *Ceratophyllum* repelled snails. Brönmark (1985) concluded that *Ceratophyllum* was protected from herbivore attack by repellent substances and a hard texture.

Substrate and feeding selectivity at the macrophyte—epiphyte and periphyton—grazer interfaces have been largely ignored in the model just outlined. Whether a result of specific macrophyte exudates (see Wetzel, 1983a) or a micro-climate created by macrophyte architecture, there are specific associations of epiphytes and macrophytes (Eminson and Moss, 1980; Lodge, 1985). The interaction of macrophyte—epiphyte associations and the selectivity of periphyton grazing by invertebrates determine the micro-distribution of some grazers (Lodge, 1986). Such interactions may therefore determine the site and rate of nutrient turnover by littoral grazers.

Macrophyte herbivory

Although many aquatic herbivores consume periphyton only, there is abundant evidence that many grazers eat living macrophytes (see Berg, 1949; Frohne, 1956; Gaevskaya, 1966; and below). Yet the view that macrophytes are an inert substrate for grazers, entering the food web only at their senescence, has been perpetuated by recent authors (Porter, 1977; Wetzel, 1983b, p. 543; Gregory, 1983).

However, there are few reasons to expect low consumption of macrophytes. Hutchinson (1975) is quoted as supporting the idea that algae and bacteria are used by the macrophytes to “placate grazers” (Porter, 1977), and while macrophytes do have high carbon to nitrogen ratios relative to most algae (Gregory 1983), many terrestrial grazers thrive on plants of nutritional value similar to macrophytes (see Mattson, 1980). Aquatic macrophytes also seem to lack digestion-inhibiting and toxic compounds abundant in many terrestrial plants (McClure, 1970; cf. Otto, 1983; Valiela

and Rietsma, 1984). The continued emphasis in ecosystem analysis on macrophytes as detritus only is certainly a simplification.

Although detrital pathways including macrophytes are extremely important in energy transfer in marine and freshwater littoral communities (Watson et al., 1984), recent detailed food web studies suggest a very important role for macrophyte herbivory. In seagrass systems in the southeastern U.S.A., the adult diets of the most abundant fish, *Lagodon rhomboides* (Linnaeus) (Stoner, 1980), and the most important invertebrate consumer, *Penaeus duorarum* Burkenroad (Leber, 1985; cf. Morgan and Kitting, 1984), comprise > 50 and 3–24% (by dry weight) living seagrass, respectively. In a southeastern U.S.A. coastal salt marsh, snow geese removed 58% of the emergent biomass and reduced macrophyte productivity (Smith and Odum, 1981). Along the northeastern U.S.A. coast, grazing by the snail *Littorina littorea* (L.) reduces the growth of *Spartina alterniflora* Lois. stands (Bertness, 1984). Similar interactions, which have major impacts on sedimentation rates (Bertness, 1984) and nutrient cycling, may occur in freshwater littoral zones.

Food web studies of freshwater littoral zones are sorely needed, especially since much of the available evidence suggests herbivory of macrophytes is much more common than appreciated. In one case, 9–14% of the annual net biomass production of *Typha latifolia* L. was consumed or used in lodge construction by muskrats (Pelikan et al., 1971). In the Great Salt Lake marsh (Utah, U.S.A.), waterfowl and mammalian grazers reduced production of *Typha* by 48% (Smith and Kadlec, 1985). In other cases, the impact of grazing on freshwater emergent macrophytes has not been quantified, but observations suggest it is significant (Boorman and Fuller, 1981; Brinson et al., 1981).

In many situations, the impact on submersed macrophytes of avian, mammalian, fish and invertebrate grazing may be as great, but has rarely been quantified. Waterfowl often consume significant portions of annual consumption: 40% peak standing crop of *Potamogeton pectinatus* in Delta Marsh, Manitoba, Canada (Anderson and Low, 1976); 30% peak standing crop of *P. filiformis* Pers. in Loch Leven, Scotland (Jupp and Spence, 1977); and about 50% peak standing crop of an assemblage of submersed macrophytes in Tipper Grund, Denmark (Kjørboe, 1980).

Macrophytes also provide a significant portion of the diet of many temperate fishes. Nearly all the littoral fishes of Europe consume some plant material; submersed macrophytes comprise a significant portion of the diet for roach (*Rutilus rutilus* (L.)), and rudd (*Scardinius erythrophthalmus* (L.)) and ide (*Leuciscus idus* (L.)) (Prejs, 1984). The diet of rudd, one of the most common littoral fish in eutrophic European lakes, includes 65–90% submersed macrophyte tissue (Prejs, 1984). The grass carp (*Ctenopharyngodon idella* Val.), introduced into waters of Europe, the U.S.S.R. and North America from Asia, dramatically reduces macrophyte standing crop (Mitzner, 1978). The diets of certain *Tilapia* species also consist pri-

marily of submersed macrophytes (Bowen, 1982). Fish—macrophyte interactions similar to those occurring in tropical and European littoral zones may also occur in other, e.g. North American, temperate lakes. Yet few studies address this possibility (see Robson, 1977).

While many invertebrates graze only periphyton, others, including insects (Berg, 1949; Frohne, 1956; Wallace and O'Hop, 1985), isopod (Marcus et al., 1978) and decapod (Flint and Goldman, 1975; Lorman and Magnuson, 1978) crustaceans and gastropod molluscs (Pip and Stewart, 1976) graze submersed macrophytes (see also Gaevskaya, 1966). While the impacts of natural grazer densities on submersed macrophyte diversity, biomass and productivity are in most cases not known, two well-studied examples from north temperate lakes demonstrate the potential for major reductions in macrophyte biomass and diversity by invertebrate grazing, i.e. omnivorous crayfish and herbivorous snails.

Building on previous observations suggesting crayfish played a major role in determining macrophyte abundance in the north central lake district of Wisconsin (Magnuson et al., 1975; Lorman and Magnuson, 1978; Lorman, 1980), Lodge and Lorman (Lodge and Lorman, 1987; Lodge et al., 1985) conducted enclosure—exclosure experiments with natural densities of *Orconectes rusticus* (Girard) in four different macrophyte assemblages in three lakes. In all experiments, there was a reduction in shoot number of some macrophyte species. In two of the five experiments, total biomass was significantly reduced. In the diverse, high biomass macrophyte assemblage of Trout Lake, one adult crayfish m^{-2} (a density commonly exceeded in nature) reduced total macrophyte biomass by 64%. In some area lakes, crayfish have eliminated submersed macrophytes (Lodge et al., 1985).

Whereas snails often graze periphyton only (Reavell, 1980), at high densities (under low predation pressure) grazing on submersed macrophytes by *Physa* can significantly reduce macrophyte biomass and species diversity (Pip and Stewart, 1976; Sheldon, 1984). In laboratory and field experiments, Sheldon (1984) found that those macrophyte species with higher growth rates (in the absence of grazers) were the preferred food of *Physa*. Minnesota lakes with high snail densities had low macrophyte diversity, with the macrophyte species preferred by *Physa* in low abundance or absent (Sheldon, 1984).

The recent evidence, then, suggests that consumption of live freshwater macrophytes by birds, mammals, fish and invertebrates may be a widespread phenomenon important in determining macrophyte abundance, diversity and productivity. Herbivory may therefore influence the timing and magnitude of nutrient turnover by macrophytes and the biomass of senescent macrophytes entering the littoral detrital pool.

Detritivory

In the sense that most of the organic carbon in freshwaters is in dead organic matter, lake ecosystems are detrital based (Wetzel, 1983b, ch. 22).

Yet the standing crop of detritus and the rate of its decomposition are at least partly determined by herbivory and detritivory, respectively. Much of the macrophyte tissue that ends up as detritus is consumed by detritivores, but the ability of many invertebrate and vertebrate detritivores to digest detrital cellulose is limited (Calow and Calow, 1975; Monk, 1976), and little detritus is assimilated in one gut passage (Hargrave, 1970; Calow, 1975; Berrie, 1976; Roman, 1984; cf. Bowen, 1982). In fact, most detritivores assimilate the bacterial fraction of detritus (Calow, 1974; Motyka et al., 1985), increasing the detrital C:N ratio (see earlier section on decomposition). Even so, detritivores probably stimulate bacterial turnover and increase the rates of decomposition (Watson et al., 1984) and nutrient turnover. However, recent reviews of detritivory and decomposition by Polunin (1984) and Merritt and colleagues (Merritt et al., 1984) point out the dearth of information on detritivore—bacterial interactions. They point out the necessity of understanding such interactions before nutrient cycling effects can be understood.

EXPERIMENTAL APPROACHES TO MACROPHYTE EFFECTS ON ECOSYSTEMS

Our title (Effects of Submersed Macrophytes on Ecosystem Processes) treats macrophytes as an independent variable and ecosystem processes as dependent variables. This wording suggests that experiments in which macrophytes are manipulated and the response of the ecosystem is measured would answer many of the open questions pointed out by this review. However, such experiments have not been performed.

Three kinds of studies pertinent to effects of macrophytes on ecosystems have been reported. First, there are many studies of particular processes (e.g. organic carbon secretion, decomposition, production) which have implications for ecosystem response. The preceding review is based almost entirely on this reductionistic approach.

Second, there are many small-scale studies (in artificial pools, ponds or test plots) of the consequences of macrophyte management, especially by herbicides. These studies show that major short-term responses to herbicides are indirect, result from the decay of the plants and include: declines in oxygen, pH and alkalinity; increases in free CO₂ concentration; loss of habitat, cover and attachment sites for epiphytes and epifauna; and changes in food resources leading to replacement of a herbivorous fauna by a detritivorous fauna (Brooker and Edwards, 1975). Longer-term impacts of macrophyte reduction in controlled pond experiments with herbicides and grass carp (Boyle, 1979; Terrell, 1983) include increases in sediment redox potential and decreases in aqueous N, P, phytoplankton standing crop and pelagic primary production. Mitzner (1978) showed that in the three years following the introduction of grass carp in Red Haw Lake (Iowa, U.S.A.), standing crop of submersed macrophytes declined by 91%, alkalinity increased and BOD, turbidity, dissolved nitrate and pelagic primary production

all decreased. However, none of these studies have used controlled whole-lake manipulations.

Third, several modelling exercises have examined ecosystem responses to macrophyte manipulations (e.g. Mitsch, 1976; several papers in Breck et al., 1979; Carpenter and Greenlee, 1981). Many important hypotheses and scenarios have emerged from these models, but in most cases the necessary experimental tests at the ecosystem level have not been performed.

Because of the complexity of lake and stream ecosystems, we attach considerable uncertainty to arguments based on isolated process studies, small-scale experiments and uncontrolled lake manipulations. For example, Stanley (1974) found that in laboratory experiments grass carp increased the rate of nutrient recycling. Yet in pond and lake experiments (cited above), the opposite was true: nutrient concentrations and primary production decreased. For these reasons, we believe that ecosystem-level macrophyte manipulations will reveal many surprises and new insights. Sound ecosystem experiments should include both reference (or control) and manipulated ecosystems, and measurements of long-term responses so that variation induced experimentally can be compared with natural ecosystem variability (Likens, 1985).

Lake ecosystems routinely experience massive changes in macrophyte biomass. Over time spans of millenia, morphometric changes in lakes increase the influence of the littoral zone on lake metabolism, which leads to further and accelerating changes in the ecosystem (Wetzel, 1979; Carpenter, 1981b, 1983). Over shorter spans of centuries, oscillations of macrophyte vegetation have been documented and related to climatic trends (Davis, 1985). Over periods of a few decades, substantial changes in macrophyte abundance and species composition result from eutrophication (Lind and Cottam, 1969; Orth and Moore, 1983) and acidification (Roelofs, 1983). For the time scale of a decade or so, large fluctuations in macrophyte biomass result from invasions and declines of exotic macrophyte species (Carpenter, 1980c) and irruptions of grazers (Lodge et al., 1985). For annual time scales, ecosystem responses are linked to phenological change (Carpenter, 1980a), natural disturbances (Lodge and Kelly, 1985; Carpenter and McCreary, 1985) and macrophyte management (Brooker and Edwards, 1975; Breck et al., 1979). In summary, macrophytes are highly variable components of aquatic ecosystems, and this variability could have major consequences for ecosystem behavior.

In the remainder of this paper, we present scenarios for ecosystem changes resulting from variations in macrophyte biomass. These scenarios, which illustrate the potential importance of macrophytes in ecosystems, are complex hypotheses testable directly by whole-lake macrophyte manipulations.

Transitions between vascular macrophyte and bryophyte vegetation

Compositional shifts from vascular macrophyte to bryophyte vegetations are associated with lake acidification (Roelofs, 1983). Transplant experi-

ments showed that such changes in vegetation lowered sediment redox potential, increased filterable iron and phosphorus percentages and increased diffusion of phosphorus from sediment (Jaynes and Carpenter, 1986). These chemical changes resulted from the inability of mosses to oxidize sediments around their rhizoids and shoots. The results suggest that specification of other metals sensitive to redox potential would be altered as mosses replaced vascular plants. Increased dissolved organic matter in sediment pore waters would provide chelators, thereby increasing the mobility of metal ions.

At the ecosystem level, replacement of vascular macrophytes by mosses is predicted to decrease decomposition rates in sediment and increase diffusion of phosphorus, iron and perhaps other metal ions into the lake water. Phosphorus mobilization would increase water column productivity, especially of periphyton which can intercept phosphorus diffusing from sediments. However, direct effect of acidity and mobilized toxic metals may override the stimulatory effects of phosphorus release. Experiments are needed to compare these contrasting effects.

Changes in macrophyte biomass

The ecosystem consequences of long-term changes in macrophyte biomass during lake succession have been reviewed by Wetzel (1979) and Carpenter (1981b). Here, we consider the consequences of increases and decreases in macrophyte biomass over a few years. Possible causes of such fluctuations include invasions and declines of adventive macrophyte species, macrophyte management or irruptions of grazers. Variability in benthic grazer populations may result from variable population dynamics of their fish predators (Strong, 1986). Consequences of fluctuations in predator, grazer or macrophyte biomass could easily be studied in experiments with manipulated and control ecosystems, although this has not been attempted at a whole-lake scale.

We predict that increased macrophyte biomass following invasion of a lake by an adventive species would lead to increased ecosystem productivity through both enhanced phosphorus recycling from sediments and effects on fishes (Fig. 1). Phosphorus taken up from sediments supports macrophyte shoot production and is recycled to periphyton and phytoplankton as shoots senesce. At the same time, increased cover for spawning and young of the year (YOY) fish leads to increased predation on both littoral grazers and zooplankton. Decreased grazer biomass leads to increased biomass and production by all autotrophic components of the ecosystem. Shifts in the relative productivity of phytoplankton, periphyton and macrophytes due to nutrient-light interactions are likely (Sand-Jensen and Søndergaard, 1981). For simplicity, we assume in this and subsequent scenarios that production is proportional to biomass.

Effects of macrophyte removal by mechanical harvesting have been modelled by several authors in Breck et al. (1979). Harvesting macrophyte

INVASION BY ADVENTIVE MACROPHYTE

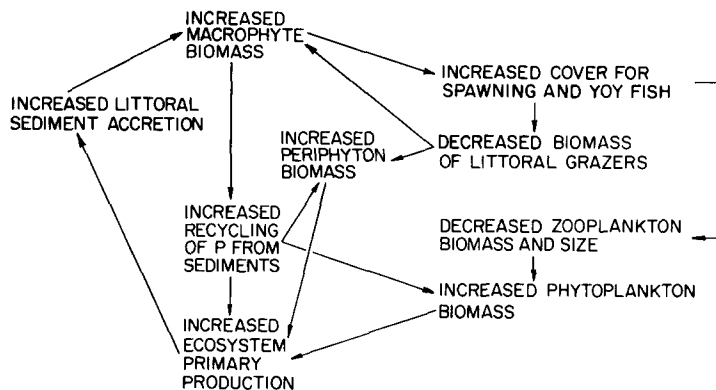


Fig. 1. Hypothesized responses of lake ecosystem to increased macrophyte biomass during invasion by an adventive species. YOY stands for young-of-the-year.

biomass is predicted to decrease phosphorus recycling from sediment and decrease cover for fish. Declining fish recruitment should lead to increased zooplankton biomass (Breck and Kitchell, 1979) and decreased phytoplankton biomass (Bartell and Breck, 1979). These changes lead to a decline in overall ecosystem productivity (Fontaine and Ewel, 1979). From the preliminary tests discussed above, it appears that the impact of grass carp is the same as that predicted for mechanical harvesting. However, the consequences of macrophyte reduction for littoral grazers and periphyton are not clear. Predation on littoral grazers would decrease, but so would the colonizable surface formerly provided by macrophytes. The density of grazers per unit substrate would increase, but composition of the grazer assemblage and its impact on the periphyton could change dramatically. The consequences for the periphyton of simultaneous changes in substrate type and predation on grazers are not intuitively obvious.

Changes in littoral grazers

Sheldon (1984) documented the effects of grazing by the snail *Physa gyrina* (Say) on assemblages of submersed macrophytes, but did not examine changes in ecosystem processes. Combining Sheldon's (1984) findings with the modelling and experimental studies discussed above, we have generated a series of predictions about the effects on system productivity of changes in the littoral food web (Fig. 2). We predict that ecosystem effects of snail grazing are essentially the same as those of mechanical harvesting. One important difference, however, is that changes in snail abundance are largely predator-driven (Sheldon, 1984; Lodge et al., 1985). There may be predator-mediated density thresholds above which snails change from periphyton-grazers to macrophyte-grazers. A second important

PREDICTED IMPACT OF HERBIVOROUS SNAILS

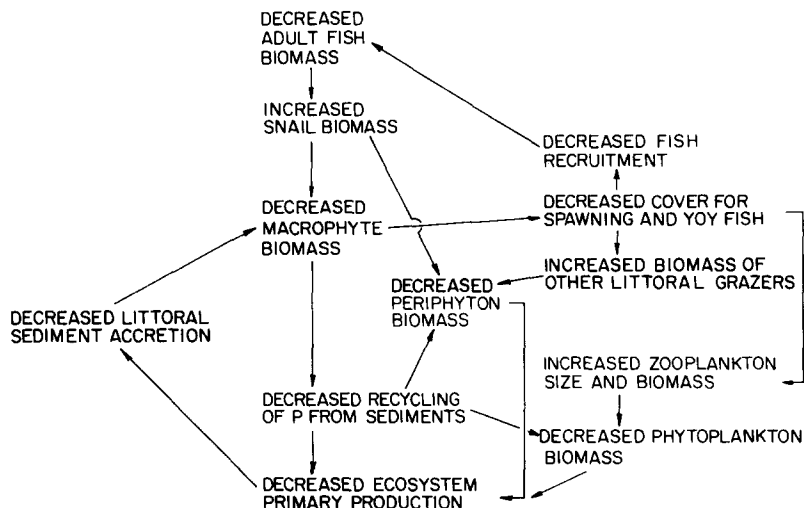


Fig. 2. Hypothesized responses of a lake ecosystem to an irruption of herbivorous snails. YOY stands for young-of-the-year.

difference that may accentuate reductions in productivity is that snails graze selectively on fast growing macrophyte species (Sheldon, 1984). Other potentially complicating factors are noted in the following summary of the predictions.

A decrease in the abundance of molluscivorous fishes would lead to increased snail biomass (Fig. 2). Many species of fishes consume snails of various sizes and some are specialists on snails (Lodge et al., 1986). Small snails with thin shells, like *Physa*, are particularly vulnerable to predators like pumpkinseed sunfish (*Lepomis gibbosus* L.), that crush the snail (Stein et al., 1984). Fish populations are notoriously variable (Strong, 1986), and snail populations may boom in years of low predator abundance. Such an occurrence might initiate a positive feedback sequence in which macrophytes are significantly reduced by increased snail grazing and fish recruitment is reduced as a result of macrophyte habitat destruction by snails.

However, empirical studies have not yielded a consensus on the impact of macrophyte reduction on fish populations. Krzywosz et al. (1980) attributed a loss of fish species to the destruction of macrophyte habitat following the introduction of grass carp. Yet Bailey (1978) found that changes in the populations of sport-fish following grass carp introductions were not predictable. These inconsistent results probably arise in part because different species of fish are affected differently by changes in macrophyte biomass. For example, Keast (1984) found that with increasing *Myriophyllum spicatum* biomass, bluegill sunfish (*Lepomis macrochirus* L.) were displaced from their spawning beds while other fishes were not affected. The evidence suggests that an intermediate density of macrophytes benefits

molluscivorous fishes, both as spawning grounds and predation-refuge (Crowder and Cooper, 1982; Savino and Stein, 1982). If we assume, however, that macrophytes are rarely dense enough to inhibit molluscivorous fishes, reductions in macrophytes by grazing snails are likely to result in reductions of the snail's fish predators.

Also as result of reduced fish predation, other littoral grazers of periphyton (e.g. insects) and large zooplankton will probably increase in abundance and reduce periphyton and phyto plankton biomass, respectively. Alternatively, species diversity and abundance of other periphyton grazers might decline as a result of competition with snails. As already suggested, snails may not significantly reduce macrophyte abundance until snail densities are high and periphyton standing crop has been significantly reduced. Grazing by snails could therefore reduce (instead of enhance) the densities of other periphyton grazers (see Cuker, 1983). However, regardless of the interactions among grazers, the overall magnitude of periphyton grazing, whether by snails or other grazers, will increase. Ecosystem production will decrease as a result of decreases in all three major production compartments; macrophytes, periphyton and phytoplankton (Fig. 2).

The overall impact of macrophyte reduction by crayfish is probably similar to that resulting from snail grazing (Fig. 3). However, since crayfish (i) achieve a size refuge from most predators (Stein and Magnuson, 1976) and (ii) eat fish eggs (and other invertebrates in addition to periphyton and macrophytes), they are more likely to escape population control by predaceous fishes (Lodge et al., 1985; cf. Saiki and Tash, 1979). Therefore, if, as we suggest, the littoral grazing systems have alternate stable points (one at high fish, low grazer and high macrophyte biomass, and another

PREDICTED IMPACT OF OMNIVOROUS CRAYFISH

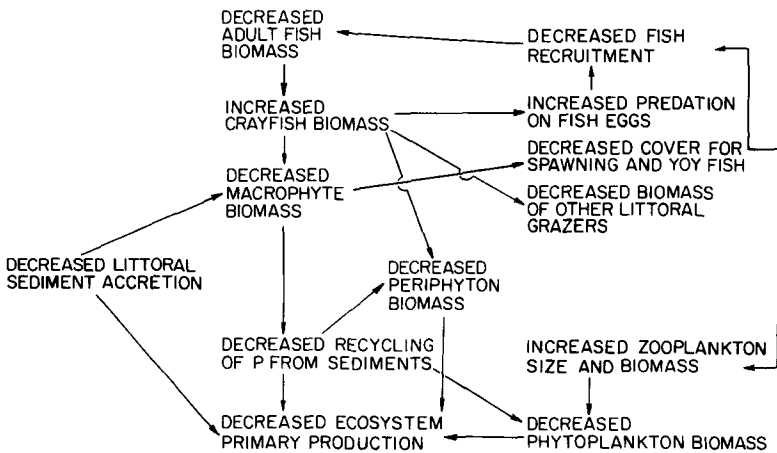


Fig. 3. Hypothesized responses of a lake ecosystem to an irruption of omnivorous crayfish. YOY stands for young-of-the year.

at low fish, high grazer and low macrophyte biomass) systems with crayfish are more likely than those with only snails to be at the low primary productivity stable point.

Because crayfish predation probably reduces abundance of other littoral grazers, it may be that periphyton (especially as expressed per unit macrophyte surface area) would actually increase with increasing crayfish herbivory. Probably, however, periphyton and macrophyte grazing by crayfish would overwhelm any such effect.

Except for the more complex trophic interactions of crayfish, we predict that the direction of impact on ecosystem productivity of macrophyte reductions via snails and crayfish is similar. However, because of the more diverse diet and great possibility of uncontrolled population growth in crayfish, we predict that crayfish have a more frequent and greater impact on lake productivity.

In conclusion, interactions between macrophytes and littoral fauna are probably very important for ecosystem processes. The seasonal cycle, macrophyte species invasions, macrophyte management and littoral grazers all change macrophyte species composition and/or macrophyte standing crop. In turn, changes in macrophytes have dramatic impacts on lake physicochemical conditions, nutrient cycling, and macrophyte-associated biota. We predict that such modifications in macrophyte composition or biomass lead to significant changes in ecosystem structure and productivity. However, these predictions are based primarily on recent population or community studies, and point to many uncertainties about the system-wide effects of interactions among macrophytes, grazers and fish. The overall impact of such interactions on ecosystem processes can only be tested with controlled, whole-lake manipulations of macrophytes.

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