

29. Structuring Role of Macrophytes in Lakes: Changing Influence Along Lake Size and Depth Gradients

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Introduction

Emergent, floating-leaved, and submergent macrophytes grow in the littoral region of most lakes. These aquatic macrophytes are influenced by geomorphology, environmental conditions, and biotic interactions (Sculthorpe, 1967; Hutchinson, 1975), while exerting their own influence on the lake environment and biota (Carpenter and Lodge, 1986; Engel, 1988). The capacity of macrophytes to provide a substrate for colonization of algae and invertebrates (Sozka, 1975; Cattaneo and Kalff, 1980; Dvorak and Best, 1982; Cattaneo, 1983; Morin, 1986; Schram et al., 1987; Miller et al., 1989), to affect water and sediment chemistry as well as other limnological conditions (Carpenter and Gasith, 1978; Prentki et al., 1979; Jaynes and Carpenter, 1986), and to influence biogeochemical cycles and productivity (Wetzel and Hough, 1973; Godshalk and Wetzel, 1978; Wetzel, 1979; Carpenter, 1980; Cattaneo and Kalff, 1980; Carpenter, 1983; Wetzel, 1990) and biotic interactions (Crowder and Cooper, 1982; Heck and Crowder, 1991; Schriver et al., 1995; see also this volume) is well recognized. The understanding of the role of macrophytes in lacustrine systems is based mostly on process studies, small-scale investigations (ponds, test plots), observations in small lakes, and modeling (Carpenter and Lodge, 1986). It is intuitively obvious that the influence of macrophytes in most small or shallow aquatic systems is proportional to their abundance (density, biomass, or extent of cover) and productivity. Little is known about the role of macrophytes in situations in which they are less conspicuous, as in large

deep lakes. Danehy et al. (1991), Gasith (1991), and Gasith and Gafny (this volume, Chapter 24) argue that the potential influence of littoral resources, including those provided by macrophytes to the biotic functioning of large deep lakes, has been overlooked. Both abundance and productivity of macrophytes vary about two orders of magnitude among lakes of different trophic levels (Carpenter, 1983), regardless of lake size. It is less clear, however, how the role of macrophytes varies in lakes of similar trophic status that differ in size and depth. The purpose of this discussion is to assess how the potential structuring role of macrophytes can change along lake size (surface area) and depth gradients.

We first point out the inherent difficulty in the terminology used to describe a lake size; we then consider the factors that interact with lake size and depth and affect plant growth; and finally, we assess the changing role of macrophytes along lake size and depth gradients.

The macrophyte-epiphyte complex is functionally inseparable. Whenever we generally use the term *macrophytes*, it is inclusive of their epiflora. For sake of the required brevity, we also fail to distinguish among the different macrophyte types and growth forms, despite evidence for possible type or growth form-specific effects as well as effects of mixed plant associations (Emery, 1978; Guillory et al., 1979; Eadie and Keast, 1984; Conrow et al., 1990; Dionne and Folt, 1991; Lillie and Budd, 1992; Chick and McIvor, 1994).

Large Versus Small and Deep Versus Shallow

Lakes are commonly categorized as small or large and shallow or deep despite lack of clear-cut morphological definitions. Generally, large lakes tend to be deeper and have longer retention times than small lakes. Only large deep lakes have truly pelagic communities that are usually more important in the overall cycling and production processes than the littoral zone and bottom communities (Tilzer, 1990). The term *shallow* is often associated with lakes that do not thermally stratify and where continuous sediment-water interaction makes internal nutrients cycling more efficient than in deeper lakes that stratify. This definition ignores the important presence of aquatic macrophytes. Thus, a definition more pertinent to the aim of this discussion is that shallow lakes are those whose bottom is significantly covered by submerged macrophytes (Moss, 1995). In general, large deep lakes have less aquatic macrophytes than small shallow lakes, with the exception that highly turbid, shallow lakes may be devoid of submerged vegetation.

Factors Affecting Plant Growth: Interaction with Lake Size and Depth

Here, we consider lake size (surface area) and depth on a relative scale in connection to the potential growth of aquatic macrophytes. Unless stated otherwise, we assume similar growth conditions for the lakes compared, except for those arising from the gradients in surface area and depth.

Comparison of the role of macrophytes along lake size and depth gradients is complicated because plant development is variable even in lakes of similar morphometry (Sculthorpe, 1967; Hutchinson, 1975). Several site-specific environmental factors affecting the abundance and distribution of aquatic macrophytes in lakes have been identified. These include climatic factors such as irradiance, temperature, wave action generated by winds, size and edaphic features of the catchment basin that affect nutrient loading and general water chemistry, and biotic factors of grazing by invertebrates, fish, and birds. We limit our discussion to those factors that interact with lake size and depth.

Light availability and wave action are directly and indirectly influenced by morphometric features. Due to exponential light attenuation in water, depth is one of the most critical environmental factors determining the lakeward growth of macrophytes and their species richness (Hutchinson, 1975; Chambers and Kalff, 1985; Duarte et al., 1986). As a general rule of thumb, submerged macrophytes will grow to a depth of two to three times the Secchi depth (Canfield et al., 1985; Chambers and Kalff, 1985). Thus, macrophyte growth will be limited in lakes with small or large surface areas where the majority of lake bottom exceeds the above Secchi depth. Additionally, even if a lake is physically shallow and does not thermally stratify (i.e., 1–2 m, mean depth), if the Secchi depth is less than 0.5 m there is a strong probability that submerged aquatic macrophytes will be absent. With some exceptions, a depth range between 10 and 15 m appears to be a limit for most angiosperms. Lakes in which most of the basin is deeper than 10–15 m are not expected to have abundant submerged aquatic macrophytes. Emergent and floating-leaved aquatic macrophytes seldom grow in waters exceeding a depth of 3 m (Canfield and Hoyer, 1992). Climatic differences associated with lake latitude appear to have a strong influence on the relationship between depth distribution of submerged plants and water transparency (Duarte and Kalff, 1987). At low latitudes, angiosperms colonize deeper and reach maximum biomass at greater depth than those growing in lakes of similar transparency at higher latitudes. Warmer water, greater irradiance, and longer growing period in lower latitude lakes may account for the difference.

Basin slope (square root of the area divided by mean depth; Hakanson, 1981), surface area, and basin configuration are among the most important morphological features that influence the potential development of macrophytes in lakes (Pearsall, 1917; Spence, 1982; Duarte and Kalff, 1986). These factors interact directly and indirectly with other environmental factors such as light, nutrient availability, substrate characteristics, and wind-generated erosion to determine the site-specific extent of plant development and macrophyte types.

Maximum biomass of submerged macrophytes is inversely related to slope (Duarte and Kalff, 1986). The probable reasons for this relation is the difference in the relative area suitable for plant growth and in sediment stability and quality between gently and steeply sloped littoral zones. The area of littoral zone available for emergent growth declines with increasing slope of the basin. In addition, steep-sided basins are areas of erosion and sediment transport (Pearsall, 1917; Hakanson, 1977), whereas nearshore regions of gently sloped basins are sites of

accretion of fine, relatively more stable, and nutrient-rich sediment, where macrophytes can become established. Pearsall (1920) demonstrated that the variation in the quantity and quality of silts largely controls the distribution of submerged vegetation. Thus, irrespective of lake size, steep-sided lakes will have lower cover and biomass of submerged macrophytes than lakes with gently sloped basins.

A large lake has a long fetch and a greater wave energy than a smaller lake. Exposure to waves can directly and indirectly affect plant distribution and abundance in lakes (Keddy, 1983; Chambers, 1987; Coops et al., 1991). Wave action and currents also affect sediment transport and distribution in lakes (Davidson-Arnott and Pollard, 1980; Keddy, 1982), concomitantly affecting the distribution of aquatic plants (Spence, 1982). Unless physically protected, points and shallows where wave energy is highest tend to be swept clean of fine sediments (Lorang and Stanford, 1993) and have little or no growth of macrophytes. Bays and areas below the wave-mixed depth tend to silt in providing more stable sediments, suitable for the establishment of macrophytes (Pearsall, 1929). Waves and strong currents can also retard vegetation growth by exerting a mechanical stress on the plants (Hutchinson, 1975; Coops et al., 1991). High concentration of suspended solids generated by wind mixing of bottom sediments (Kristensen et al., 1992) can limit light for plant growth particularly in large, shallow, unstratified lakes, whereas in stratified lakes suspended particles tend to settle out of the mixed layer (Osgood, 1988). High wave energy, currents, and turbidity in the shallows often restrict macrophyte growth in large deep lakes to protected bays and coves (Duarte et al., 1986). Overall, lakes with large surface areas and longer fetch are expected to have fewer vegetated littoral regions in relation to the amount of open water than smaller lakes (Rounsefell, 1946; Spence, 1982).

Lakes with a large surface area tend to be deeper than smaller lakes (a positive correlation exists between lake area and mean depth; Duarte et al., 1986). The cover and biomass of submerged macrophytes are expected to decline with increasing lake size if only for the reason that larger lakes have greater proportion of area below the compensation depth for macrophytes. In analyzing 139 lakes, Duarte et al. (1986) indeed found that the percentage surface area covered by submerged plants is not a constant proportion of the lake area but tends to be smaller in bigger lakes. Rather surprising, however, was their finding that emergent macrophytes colonized on average a constant proportion (7%) of the lake area regardless of the size of the lake. A similar relation was reported for Polish lakes, showing that emergents covered a relatively narrow range of lake surface areas (9.3–12.3%; Planter, 1973). This contradicts the expectation of declining growth of macrophytes with increasing fetch and greater wave action in the littoral zone (Spence, 1982). Duarte et al. (1986) suggested that a greater number of sheltered bays and floodplains in larger lakes where macrophytes can grow compensates for decreases in vegetation caused by greater wave action. If this is indeed so, it is apparently sufficient to compensate for the lower growth of emergents in shoals of large lakes but not of submerged macrophytes. Duarte et al.

(1986) concluded that on average submerged macrophytes are more important in small lakes and emergent plants will become more important with increasing lake size. It should be pointed out, however, that an opposite trend of a transition from submergents' dominance to that of emergent vegetation is part of the natural process of lake succession, which is most accelerated in small shallow productive lakes. The accumulation of refractory macrophyte detritus further limits growth of submerged macrophytes and hastens the transition to emergent vegetation that is more tolerant of organic rich sediments (Wetzel, 1979; Carpenter, 1981; Barko and Smart, 1983).

The proportion of littoral zone areas in a lake declines with increasing depth and lake size (Gasith, 1991) and increases with increasing shoreline irregularity (high shore development figure). Therefore, highly irregular lakes may have a higher proportion of vegetation zones compared with lakes of similar area but with a more regular shoreline.

The trophic status of lakes is inversely related to mean depth (Vollenweider, 1975; Canfield and Bachmann, 1981). Deep lakes tend to be more oligotrophic and support lesser growth of aquatic macrophytes than shallow lakes. A study by Canfield and Hoyer (1992) shows that oligotrophic and mesotrophic lakes rarely have aquatic macrophyte abundance exceeding 20% volume infested (PVI), whereas eutrophic and hypereutrophic lakes have the potential to reach 100 PVI. High turbidity may limit growth of submerged macrophytes in these lakes even though nutrients availability can support extensive growth.

Structuring Role of Macrophytes: Changing Importance Along Size and Depth Gradients

When established in a lake, aquatic macrophytes can influence the lake ecosystem in multiple ways (reviewed in Carpenter and Lodge, 1986) and mediate biotic interactions (Crowder and Cooper, 1982; Savino and Stein, 1982; Diehl, 1988; see also this volume). The structuring role of macrophytes in a lake ecosystem falls into three main categories: (1) limnological effects related to changes in physical and chemical conditions in the water and sediment; (2) metabolic effects related to production and processing of organic matter and nutrient cycling; and (3) effect on biotic interactions and community structure related to the role of macrophytes in providing a structured habitat.

It may be useful to approach the question of how the role of macrophytes changes along lake size and depth gradients by considering each of the above categories separately. We suggest that the limnological and metabolic effects of macrophytes in lakes diminish with increasing depth and lake size faster than their importance in providing structured habitats (Fig. 29.1). This implies that, by providing structure, macrophytes may still play a role affecting biotic interactions in situations in which they may have no significant effect on water-quality, nor are they important for nutrient cycling, nor as a source of organic matter.

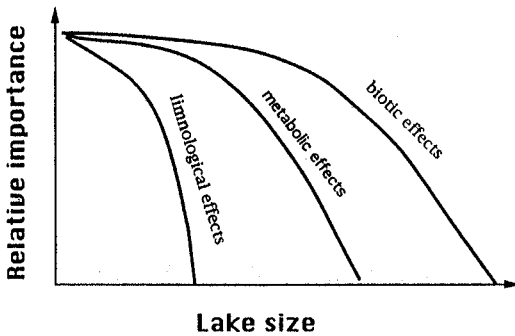


Figure 29.1. Comparison of the changing relative importance of limnological, metabolic and biotic effects of macrophytes along increasing lake size gradient. A positive relation between size (surface area) and depth is assumed.

It is reasonable to assume that a PVI exceeding 40% is required for macrophytes to be able to change the water-quality conditions of an entire lake ecosystem (Canfield and Jones, 1984); this would be a situation more typical of marshes and shallow eutrophic lakes (Canfield and Hoyer, 1992). Large-scale oxygen depletion, for example, is most likely to occur following rapid senescence of dense macrophyte stands in warm, poorly circulated waters (Carpenter and Greenlee, 1981). Indeed, the fish community of densely vegetated wetlands is composed of the most tolerant species that are able to function in dense vegetation and survive periodic high temperatures and low dissolved oxygen levels (MacCrimmon, 1980; Johnson, 1989). The effects of macrophytes on sediment and water quality (Carpenter and Greenlee, 1981; Carpenter and Lodge, 1986) are expected to be restricted to the plant bed, particularly in large and deep water bodies. It is possible, however, that biotic changes in the littoral zone in response to chemical-physical gradients (e.g., change in composition and abundance of prey organisms) will be carried across habitat boundary and influence limnetic communities using littoral resources.

Organic matter originating from the littoral zone may have metabolic importance especially in small shallow lakes where macrophytes are highly productive (Sculthrope, 1967; Wetzel and Hough 1973; Wetzel, 1979; Carpenter, 1983; Carpenter and Lodge, 1986). In large and deep lakes, the proportion occupied by the littoral region is often less than 10% of the total lake area (Gasith, 1991). In the Great Lakes, for example, the important spawning and nursery areas of most fish species are in littoral water less than 10 m deep (Goodyear et al., 1982; O'Gorman, 1983). In addition, large lakes are often more oligotrophic and support a lesser growth of aquatic macrophytes. In these and in highly eutrophic lakes, phytoplankton may dominate the production of organic matter and control the recycling of nutrients (Carpenter, 1983; Hough et al., 1989; Tilzer, 1990).

The effect of decreasing plant abundance with increasing lake size on biotic interactions is unclear. Biotic interactions can be influenced over a wide range of

plant abundance. In the absence of alternative sources for physical structure, even sparse vegetation or isolated patches of macrophyte beds can be important in providing substrate for colonization, refuge, feeding, and spawning grounds. For example, in Orange Lake (Florida) young bluegills were found primarily in small isolated islands of panic grass (*Panicum* spp.), which constituted less than 2% of the lake's area (Conrow et al., 1990). Bluegills have been reported to prefer lateral concealment (Casterlin and Reynolds, 1978) and probably favored panic grass, which provided both protection from predators as well as access to open-water zooplankton (Conrow et al., 1990). In another case, Danehy (1984) and Danehy et al. (1991) found greater diversity and abundance of fish at relatively isolated cobbles and rubble sites than at sandy sites in Lake Ontario. Moreover, Danehy et al. (1991) found that yellow perch captured at the structured sites grew faster than those collected from the sandy sites. They attributed this difference in growth to lower energy expenditure associated with greater cover and lower predation risk as well as to higher food availability at the structured sites. At the sandy sites, individuals may have been required to "commute" more in search of cover and food. This led them to conclude that even small structured habitats may be important to local fish populations. The significance that this may have in the context of the whole lake ecosystem is yet to be evaluated. Another example in which a relatively limited plant structure can be important in a large lake situation is illustrated by the evidence that although spawning on macrophytes is unusual for salmonids, at least a portion of the population of lake trout (*Salvelinus namaycush*) in Lake Tahoe spawns in deepwater mounds (40–60 m deep) over beds of *Chara* (Beauchamp et al., 1992). No evidence of spawning was found over rocky formations that exist at various depths in the lake. Apparently, the *Chara* mounds are favored as they provide the basic requirements for successful egg incubation by anchoring the eggs against currents and providing protection from effective invertebrate and small vertebrate egg predators (Beauchamp et al., 1992). Similarly, it has been suggested that macrophyte beds provide cover for predation-vulnerable grazers such as large herbivorous zooplankton (Timms and Moss, 1984; Davies, 1985; Jeppesen et al., 1991; Moss et al., 1994; Lauridsen and Lodge, 1996; Jeppesen et al., this volume, Chapter 5; Lauridsen et al., this volume, Chapter 13). Survival of herbivorous zooplankton even in limited macrophyte coverage may accelerate establishment of larger populations (Lauridsen et al., 1996) that may, in turn, play a role in the switch from algae dominance to macrophytes (Scheffer et al., 1993; Hargeby et al., 1994; Jeppesen et al., this volume, Chapter 28). Due to their limited capacity for horizontal movement relative to fish, zooplankton would probably benefit less from scattered isolated plant beds than would fish. Restricted plant cover may therefore be expected to provide more effective refuge for zooplankton populations in small rather than large lake situations. Fish, however, are probably able to exploit isolated plant beds over a wider lake size range.

Freshwater fish use vegetation for cover (Crowder and Cooper, 1982; Tabor and Wurtsbaugh, 1991), foraging on benthos, epifauna, and prey organisms in the water among the vegetation (Fairchild, 1982; Mittelbach, 1984; Heck and Crowder, 1991; Diehl and Kornijów, this volume, Chapter 2) directly as food (Prejs,

1984) and as spawning and nursery sites (Goodyear et al., 1982; O'Gorman, 1983; Beauchamp et al., 1992). Most of the information on the use of structured habitats by fish is based on daytime studies. There is evidence, however, of much higher fish density in littoral habitats at night (Beauchamp et al., 1994) as well as a difference in size distribution of the fish between the day and night-time littoral zone assemblages (Gasith, Gafny, and Goren, unpublished data, Lake Kinneret). Further studies are needed to assess the importance of diurnal shifts in fish abundance, size, and species composition of littoral habitats.

As lake size and depth increase, macrophyte abundance declines, and structured habitats and associated resources may become in short supply (Gasith, 1991; Beauchamp et al., 1994). Consequently, competition over littoral resources (Mittelbach, 1988), particularly among species moving from the limnetic zone into the littoral region, is expected to increase with increasing lake size and depth (Gasith and Gafny, this volume, Chapter 24). In addition, unlike abiotic structures (e.g., rocky formations) macrophytes undergo temporal and spatial variations. In lakes where physical structure is provided mostly by macrophytes, organisms using littoral resources are forced to synchronize with the "window of opportunity" provided by macrophyte growth. If this is indeed so, competitive interactions over macrophyte-supported resources should be highest in large deep lakes where the abundance of macrophytes is low and in lakes where the period of macrophyte growth is shortest (e.g., high latitudes).

Conclusion

The changing influence of macrophytes along lake size and depth gradients is currently mostly speculative. Generally, the importance of macrophytes is expected to be proportional to their abundance in the water body, and thus their influence will decline with increasing lake size and depth. Existing information suggests that macrophytes can affect biotic interactions in situations in which they have no more limnological or metabolic significance. We therefore may conclude that only in shallow and small lakes can macrophytes potentially have significant effects on the physical-chemical condition in the water and sediment, on internal nutrient loading, and on lake productivity as well as on biotic interactions. In large deep lakes, macrophyte influence on lake ecosystem diminishes and is probably limited to some effect on biotic interactions.

Relatively small and isolated plant beds may have greater importance than have so far been assumed. In this connection, it is possible that cases of unexplained changes in zooplankton community structure and in fish population size and juvenile growth rate were linked to overlooked changes in the availability of structured habitats in the littoral zone.

A better understanding of macrophyte importance in relation to lake morphometry may require separate assessment of macrophyte effects on limnological conditions, metabolic processes, and biotic interactions. Due to the experimental limitations of ecosystem manipulation, particularly of large lakes, this will probably

be achieved by long-term and comparative studies and possibly by more extensive use of artificial structures in lakes of various sizes.

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