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3 Center Stage: The Crucial Role of Macrophytes in Regulating Trophic Interactions in Shallow Lake Wetlands

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3.1 Introduction

Hydrophilic, or water-loving, macrophytes characterize wetland ecosystems, indicating prerequisite conditions of hydric soils and sufficient hydrology. The presence of such macrophytes is a key descriptor in multiple wetland definitions (Lewis 2001a) and macrophytes may be further used to actually describe particular types of wetlands, such as cattail marshes. Macrophytes contribute significant biomass to wetland systems and represent a critical component of wetland biogeochemistry as primary producers and drivers of organic matter cycling within aquatic systems. In this chapter, we argue that macrophytes occupy the center of trophic interactions in shallow lakes, influencing outcomes through structural, behavioral and chemical interactions. We define shallow lakes as permanently flooded wetlands that often contain submerged or floating macrophytes and that may be surrounded by emergent vegetation (i.e. marshy habitat). Shallow remains a relative term in limnology circles, but typically is less than 3 m average depth, such that macrophytes can fill a substantial portion of the water column and stratification is neither predictable nor long-term. Such systems may be termed lakes, ponds or wetlands, depending on their size and the ecological context. Macrophytes may regulate trophic interactions in ephemeral systems without permanent inundation.

3.2 Central Position of Aquatic Vegetation

Terrestrial ecologists historically have focused on vegetation. However, early aquatic studies also noted the dominance of plants in aquatic systems. For example, in *The lake as a microcosm*, Forbes (1925) derided areas 'clogged with weeds', but then elaborated on how these weeds (*Chara*, *Potamogeton*, *Ceratophyllum*) swarmed with life, including fishes, invertebrates, zooplankton and algae. Lindeman (1942) included pondweeds as an important component of lake food webs and Teal (1962) went a step further and quantified the energy flow between trophic levels in a salt marsh. Thus, historical precedent exists for focusing attention on macrophytes as part of the aquatic community. First to emphasize ecosystem processes, Carpenter and Lodge (1986) summarized the impacts of submerged macrophytes on abiotic and biotic components of aquatic systems. With a similar aim, Jeppesen et al. (1997a) published a comprehensive book documenting the structuring role of submerged macrophytes in lakes. We extend their discussion of trophic interactions and also consider other macrophyte architectures (i.e. floating-leaved, emergent, freely-floating).

Reinforced by multiple mechanisms, macrophytes promote water clarity, help stabilize a clear-water state (Jeppesen 1998; Scheffer 1998) and enhance biodiversity (Declerck et al. 2005). Several of those feedbacks depend on structural or chemical effects that, in turn, influence behaviors of multiple trophic levels. To evaluate our progress in understanding the role of macrophytes in wetland systems since Jeppesen et al. (1997a), we performed an extensive literature search (1997–2004) regarding aquatic macrophytes. Using four search engines [Web of Science, Science Direct (Elsevier), BioOne, Kluwer-Online] our inquiry discovered 126 papers that involved trophic interactions with macrophytes.

The vast majority (74 %) of recent studies focused on behavioral interactions with macrophytes, with an additional 13 % exploring this within a chemical context. The remaining 13 % focused on single structural–chemical interactions, largely between macrophytes and phytoplankton. Macrophytes, fish and zooplankton composed the most common suite of organisms studied together (12 %), although 35 % of the studies involved three groups and 56 % only examined a single interaction. Thirteen studies (10 %) examined more complex food webs in shallow wetland systems; however, only four of these studies (3 %) examined five trophic levels. Surprisingly, similar numbers of single-interaction studies involved both fish and invertebrates, dominated by studies including fish (44 %). Only 10 % of the studies included an additional primary producer (periphyton or phytoplankton) besides macrophytes. These complex trophic connections that occur with macrophytes dramatically alter the carbon flow through the system (Fig. 3.1). With this context, we used the literature survey to identify four key themes regarding the regulation of trophic interactions by macrophytes.

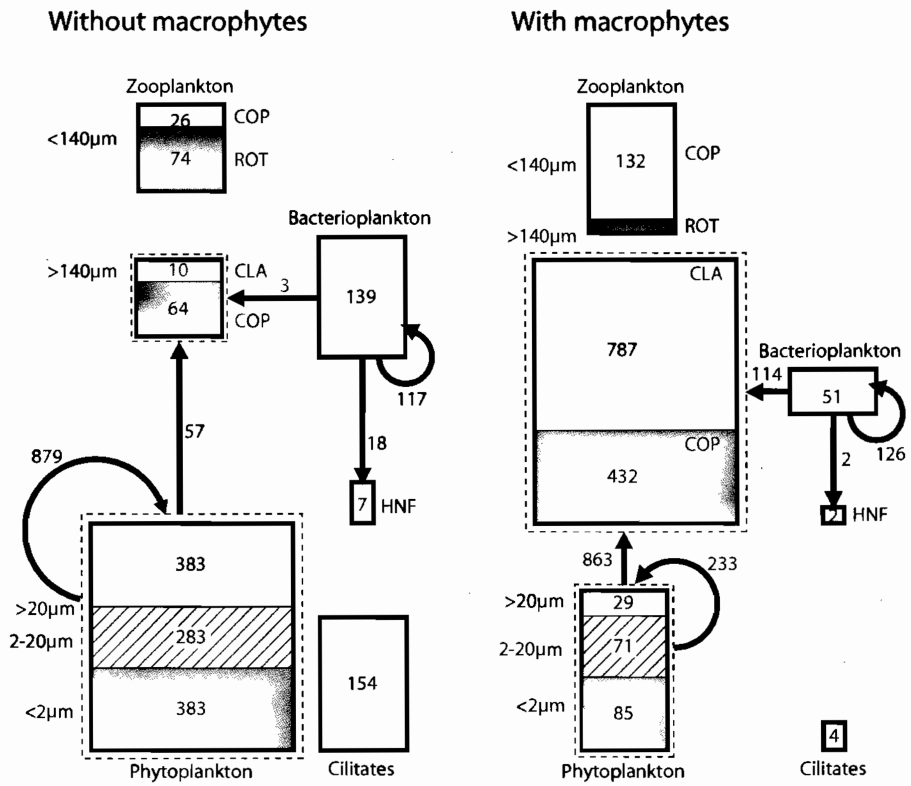

Fig. 3.1 Illustration of the dramatic alteration of energy flow in the presence of macrophytes (originally published by Jeppesen et al. 2002). The figure illustrates the cascading trophic interactions within enclosures placed in the littoral zone of a shallow Danish lake (Stigsholm). The data illustrate carbon flow between trophic levels in enclosures with and without submerged macrophytes for the first diel periods where day and night sampling occurred. *Boxes* represent the biomass (µg C l^{-1}) of different trophic components and the *arrows* measure flux per day. *COP* Copepods, largely cyclopoids, *ROT* rotifers, *CLA* cladocerans, *HNF* heterotrophic nanoflagellates. *Broken box outlines* indicate that phytoplankton production and zooplankton grazing are community estimates for all groups within the boxes. Note that zooplankton grazing by far exceeded phytoplankton production in the macrophyte state, suggesting extremely high grazing on phytoplankton and likely benthic facilitation of the zooplankton. The latter may, in turn, ensure a steady high abundance of zooplankton and thus high grazing on phytoplankton when zooplankton migrate to the open water at night

3.2.1 Central Themes: Zooplankton Depend on Macrophytes as Habitats

While many historical studies noted the abundance of macroinvertebrates among macrophytes (e.g. for damselflies, see Lombardo 1997; for snails, see Brönmark and Vermaat 1997), fewer studies recognized the role of macrophytes as providing refuge for zooplankton. Limnologists generally restrict their discussion of refuges for zooplankton to the hypolimnetic refuge provided by deep lakes for large-bodied zooplankton undergoing diel vertical migration (i.e. *Daphnia*). However, littoral-associated cladocerans (i.e. *Alona, Chydorus, Simocephalus, Ceriodaphnia*) commonly occur among macrophytes in large lacustrine wetlands (Hann and Zrum 1997) and small glacial kettleholes (Gaiser and Lang 1998). Recent studies from shallow lake and wetland systems demonstrated that macrophyte presence can bolster pelagic zooplankton, as large-bodied species such as *Daphnia* migrate horizontally into macrophytes to seek refuge from predators (for a review, see Burks et al. 2002).

Zooplankton dependence on macrophyte beds acts as a positive feedback mechanism that helps maintain clear-water conditions in lakes, especially eutrophic systems with high macrophyte biomass (Jeppesen et al. 1999; although see Blindow et al. 2000). Multiple scenarios exist, however, for the relationship between zooplankton size (at the individual or population scale) and macrophyte density. One possibility is a non-linear relationship based on the assumptions that increased prey size leads to increased vulnerability (Brooks and Dodson 1965) and that increased structural complexity makes foraging more difficult for some predators in a non-linear way (Jeppesen et al.1997a; Burks et al. 2001a). This refuge scenario suggests that some threshold of macrophytes is required, which is corroborated by a large mesocosm experiment that showed smaller rotifers and cyclopoid copepods comprised the zooplankton in plant-free controls while large-bodied cladocerans dominated enclosures with plants, when plant density exceeded a certain threshold (Fig. 3.1; Jeppesen et al. 1997a, 2002).

With horizontal migration, the extent of entry into macrophytes by zooplankton varies, depending on the costs of inhabiting macrophytes. These costs include competition with other zooplankton, food scarcity, chemical inhibition, or adverse abiotic conditions (Burks et al. 2002). Such costs might be responsible for the horizontal patchiness that occurred in Rybak and Weglenska's (2003) study, where sparse beds showed more limnetic species of Cladocera while dense beds held more littoral species. Intense predation pressure from macrophyte-associated invertebrates (Burks et al. 2001b) also may factor into the non-linear relationship between macrophyte density and zooplankton size and contribute to patterns commonly observed in the field. Invertebrate density across vertical and horizontal dimensions varies among macrophytes. The substantial surface area of submerged macrophytes likely supports higher abundances of macroinvertebrates than floating or emergent plants (Cattaneo et al. 1998). Marklund et al. (2001) found higher densities of invertebrate grazers in the layers closer to the sediment than near the surface of *Chara* beds. Their results also showed higher densities at the macrophytes' edge versus the innermost parts for some species. The latter corroborates earlier results by Lauridsen et al. (1996). Thus, for zooplankton, macrophyte beds may form a horizontal transition zone in predation, from invertebrate predation inshore to fish predation offshore (Tolonen et al. 2001).

The use of macrophytes as a refuge by zooplankton is also likely to decline with increasing turbidity. While several studies document the use of submerged and floating plants as a refuge, the ability of emergent plants to provide a refuge for zooplankton remains questionable. Nurminen and Horppila (2002) investigated the importance of emergent macrophytes as refugia for littoral cladocerans in lakes of differing trophic status. No tendency toward horizontal migration into emergent macrophytes occurred in a clearwater system. In the turbid system, Nurminen and Horppila (2002) found reverse migration by large-bodied filter feeders (*Limnosida frontosa*, *Sida crystallina*), possibly in response to high densities of small fishes among the vegetation. This agrees well with a recent study of changes along a chlorophyll *a* (turbidity) gradient in the proportion of fish near the shore versus the open water. Numerous Danish lakes showed an increasing share of the most abundant fish species in the littoral as turbidity increased (Jeppesen et al. 2006). In contrast, the anti-predator behavior of juvenile fish, such as using macrophytes for refuge, may occur less frequently in turbid water, where hunting by sight-dependent predator fish is less successful (Abrahams and Kattenfeld 1997). Under clear-water conditions, juvenile pike (*Esox lucius*) spent more time foraging among complex structures compared to an even distribution between complexity and open water under turbid conditions (Skov et al. 2002). In a survey of 33 interconnected shallow ponds, Cottenie et al. (2001) found that zooplankton community structure depended strongly on predation intensity and macrophyte cover and that the clear-water state coincided with macrophytes, piscivorous fish and large *Daphnia* species.

Besides the influence of turbidity, the ability of macrophytes to serve as a refuge for zooplankton also declines when macrophytes play host to other predators, suggesting the avoidance of macrophytes by zooplankton. If one considers its root network, water hyacinth (*Eichhornia crassipes*) may possess a comparable surface area to submerged plants. However, *Eichhornia* does not support a similar high diversity of invertebrates, including zooplankton (Meerhoff et al. 2003). Lower colonization of macrophytes than predicted may be due to chemical deterrence (Burks et al. 2000, 2001a), differences in water chemistry from the floating plant canopy or high fish predation (Meerhoff et al. 2003 and unpublished results). However, the few studies on free-floating plants make such generalizations difficult and more research is needed to understand if this architectural type differs in function from submerged or emergent macrophytes. Despite any potential differences, high fish predation can occur outside all types of macrophyte architectures. Romare et al. (2003), for example, found that roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) congregated outside dense emergent vegetation in a small Danish lake, thus likely eliminating the advantage of horizontal migration for cladocerans. This negative relationship may exist with the carnivorous macrophyte bladderwort, *Utricularia* (Guisande 2000; Englund and Harms 2003), depending on zooplankton size. Furthermore, larval dragonflies also pose a serious predation threat to zooplankton undergoing diel horizontal migration, particularly at low macrophyte densities (Burks et al. 2001b). Alternatively, littoral fishes may reinforce the refuge effect for zooplankton if they prefer macroinvertebrates (Sagrario and Balseiro 2003). Overall, macrophytes act as effective refuges for zooplankton or planktivorous fishes when the diversity or density is sufficient enough to depress the predation rates of planktivores (Priyadarshana et al. 2001) or piscivores, respectively (e.g. largemouth bass, *Micropterus salmoides*; Valley and Bremigan 2002). Further experiments and field studies that investigate patterns of zooplankton size, macrophyte density and composition will help resolve the ambiguity associated with these multiple scenarios and lend further insight into how carbon cycling occurs across multiple trophic interactions (Fig. 3.1).

3.2.2 Central Themes: Chemical Ecology Spans Trophic Levels

Biochemical interactions between (submerged) macrophytes and competing primary producers, termed 'allelopathy' (*sensu* Molisch 1937), often appear in the literature, but at the same time ignite much controversy. Allelopathy is unlikely to act as a determining factor of a clear versus turbid state, but it certainly influences the interactions between the main opponents. Multiple laboratory studies document inhibitory effects of extracts, exudates or intact macrophytes on algae (summarized e.g. in Gross 2003a; for a recent example from freely-floating plants, see Mulderij et al. 2005a). Most studies show differential sensitivity among algal groups, with cyanobacteria often the most sensitive and chlorophytes and diatoms less susceptible (e.g. Gross et al. 1996; but see Mulderij et al. 2005b). Macroalgae, such as charophytes, also employ allelopathic chemicals in their interactions with other primary producers (Van Donk and van de Bund 2002; Mulderij et al. 2003). Relative to other macrophyte growth forms, the likelihood of allelopathic interactions increases in dense stands of submerged macrophytes where more stagnant water prevails. Based on our literature survey, we provide a ranked list of macrophyte species that we think best represent allelopathic species (Table 3.1).

Knowledge of chemical ecology in freshwater systems lags behind marine and terrestrial systems (Burks and Lodge 2002), but we see substantial progress. Our literature survey indicated that 25 % of recent studies included an aspect of chemical influence, suggesting that more investigations of this nature are underway. The practicality of both realistic laboratory and in situ experiments will increase as we identify more compounds. For now, we noticed particularly the variety of ways in which chemical cues or allelopathic compounds altered trophic interactions. The impacts often depended on species identity and commonly involved macroinvertebrates.

Table 3.1 Ranking allelopathic potential of aquatic macrophytes (based on evidence presented in studies cited by Wium-Andersen 1987; Gopal and Goel 1993; Gross 2003a). Evidence was considered high when different authors reported the same or similar observations and/or when proof for the release of active compounds occurred. The asterisk (*) indicates that evidence was not as strong as for "high" species. Note that not all *Chara* species showed indications of allelopathic properties

Allelopathic potential	Species	Common name
High	*Myriophyllum spicatum*	Eurasian water milfoil
↓	*Chara globularis*, *Ch. aspera*, *Ch. contraria*	Stonewort or charophyte
↓	*Ceratophyllum demersum*	Coontail
↓	*Stratiotes aloides*	Water soldier
Medium/high*	*Elodea* spp	Waterweed, water pest
↓	*Eleocharis acicularis*	Spike rush
↓	*Myriophyllum brasiliense*	Parrotfeather, Brasilian milfoil
↓	*Myriophyllum verticillatum*	Whorl-leaf watermilfoil
Medium	*Berula erecta* (*Sium erectum*)	Water parsnip
↓	*Eichhornia crassipes*	Water hyacinth
↓	*Egeria densa*	Common waterweed
↓	*Najas marina* ssp. *intermedia*	Spiny naiad
↓	*Nuphar lutea*	Yellow water lily
Low	*Potamogeton* spp	Pondweeds

Some species showed higher tendencies to be allelopathic than others (Table 3.1). For example, Körner and Nicklisch (2002) demonstrated that *Myriophyllum spicatum* and *Ceratophyllum demersum* both inhibited photosystem II activity of phytoplankton, but they found no effect by *Potamogeton pectinatus*. Based on the absence of plant fragments in fish guts, Nurminen et al. (2003) also implied selective avoidance of the first two species (*M. spicatum*, *C. demersum*) by rudd (*Scardinius erythrophthalmus*). Macrophyte species may influence both behavioral and chemical interactions. For example, water incubated with *Stratiotes* (i.e. water soldier) demonstrated a highly significant inhibitory effect on the green alga *Scenedesmus obliquus* (Mulderij et al. 2005a), cyanobacterium *Microcystis* and eustigmatophyte *Nannochloropsis* (Mulderij et al. 2005b). Furthermore, the presence of *Stratiotes aloides*, especially young plants, increased colony formation by *S. obliquus*. Sinking rates of the algae also increased, leading to improved water clarity and light conditions for the macrophyte (Mulderij et al. 2005a). In the reverse direction, cyanobacterial compounds can have detrimental impacts on submerged vegetation. For example, Microcystin-LR shows allelopathic properties against *M. spicatum* and *C. demersum* (Pflugmacher 2002).

The deterrent chemical nature of some macrophytes may strongly regulate the biological community. One study suggests that aquatic plants repellent to grass carp could serve as areas of amphibian rehabilitation (Murphy et al. 2002). Endangered odonate larvae (*Aeshna viridis*) also preferred *Stratiotes aloides*, as it also served as a refuge from perch predation (Rantala et al. 2004). Other work connects herbivores and predators through the chemical nature of the macrophyte. For example, *Hyallela azteca* (Amphipoda) readily grazes on roots of emergent macrophytes (*Berula erecta*, water parsnip), even though they may be chemically defended (Rowell and Blinn 2003). Consequently, these amphipods exhibited lower susceptibility to fish predation. Although common in the marine literature, this study provided the first experimental evidence of reduced predation on a freshwater herbivore that consumed a chemically defended plant (Rowell and Blinn 2003).

Of all the aquatic macrophytes, one species (*Myriophyllum spicatum*, Eurasian watermilfoil; EWM) clearly stood out as the most influential chemically (Table 3.1) because of multiple interactions that occur with herbivores and competing phototrophs. On the whole-lake scale, macroinvertebrate biomass on dominant plant species in a lake may decline as the percentage of EWM cover increases (Cheruvelil et al. 2001). Furthermore, Lindén and Lehtiniemi (2005) found that chemicals excreted by dense EWM resulted in high mortality (73–89 %) of mysids (*Neomysis integer*, *Praunus felxuosus*) and lowered the feeding efficiencies of three-spined sticklebacks (*Gasterosteus aculeatus*). At a smaller scale, *Acentria* (Lepidoptera) exhibited higher feeding rates on *Myriophyllum* than on *Elodea* (Gross et al. 2001). In choice experiments, *Acentria* larvae clearly preferred EWM. By selectively removing apical tissue with the highest concentrations of allelopathically active compounds (Choi et al. 2002), herbivory by *Acentria* might weaken the allelopathic strength of this species, indirectly altering competitive interactions and the plant's susceptibility to bacterial infection. Overall, the magnitude of herbivory on EWM may shape competitive interactions between submerged macrophytes, change invertebrate biomass and perhaps alter ecosystem processes, such as primary production (Gross 2003a).

Remarkably, many invasive species, such as *M. spicatum* in Northern America or *Elodea* spp in Europe (Gross et al. 1996; Erhard and Gross 2005), act as allelopathically active species (Table 3.1). Significant differences in allelopathic activity between native and invasive specimens remain uncertain for aquatic systems, although Bais et al. (2003) documented such an occurrence with invasive, spotted knapweed (*Centaurea maculosa*). In addition, the extent to which allelopathic interactions add significantly to successful invasion also merits further attention. The concentration of active compounds in EWM may vary strongly, depending on environmental conditions (Gross 2003b) and may vary between native and invaded ranges of plants. Therefore, the role of macrophytes as chemical signalers under field conditions strongly depends on the macrophyte species present, the density or spatial heterogeneity of their patches, the velocity of breakdown of active compounds and possibly the nutrient state of both donor (macrophyte) and target organisms (e.g. phytoplankton).

The magnitude of the deterrent effect of macrophytes on trophic interactions also may differ among species and in the presence of other predatory cues. For example, *Daphnia* actively avoided submerged macrophytes in the absence of fish, but then overcame this repellency and sought refuge when fish arrived (Burks et al. 2001a), despite the possible costs of reduced zooplankton growth (Burks et al. 2000). In the absence of fish, Van de Meutter et al. (2004a) found an additional, although weak, avoidance of macrophytes that housed *Ischnura elegans* (10 % less within vegetation). Unfortunately, the predictability of macrophyte avoidance by *Daphnia* varies, perhaps depending on the clone, the presence of conspecific cues or the presence of other predators. In a similar study, Van de Meutter et al. (2004b) found no horizontal migration response toward the open water in the presence of *Ischnura elegans* alone. However, when *Ischnura* co-occurred with *Chaoborus*, daphnids showed an increased avoidance of plants. Van de Meutter et al. (2004b) attributed this to an increased risk of predation in the vegetation. If strong enough, chemical cues from littoral predators may contribute to the already repellent nature of macrophytes and override the tendency for zooplankton to seek refuge from fish, suggesting a hierarchal nature of chemical cues.

3.2.3 Central Themes: Impacts of Grazer–Epiphyton Interactions with Macrophytes

Although the term periphyton encompasses the whole community of organisms that colonize surfaces, we use epiphyton to stress the competitive interactions between algae and macrophytes. Macrophytes can serve as a habitat, a refuge from predators, or can act as a substrate which potential food sources can colonize (Fig. 3.2). Most epiphytes belong to the classes Bacilliophyta (diatoms) and Chlorophyta (green algae), but nuisance, grazing-resistant forms, such as filamentous blue-greens (Cyanobacteria) and *Cladophora*, can occur when the community is grazed by invertebrates which are selective in their feeding (Jones et al. 2000). Snail densities on macrophytes depend in part on plant palatability, periphyton density and algal quality and growth form (Brönmark and Vermaat 1997; Jones et al. 2000; Lombardo and Cooke 2002). Besides snails, other insects (including caddisflies, mayflies, beetles, corixids), along with several crustaceans (e.g. amphipods, cladocerans, ostracods) consume ample amounts of epiphyton (Jones et al. 1997).

We often recognize the importance of top-down control of phytoplankton by zooplankton grazing and its central role in maintaining the clear-water state (Jeppesen et al. 1997b). However, the distinction between the origin and maintenance of alternative equilibria is often not made; and it may be that

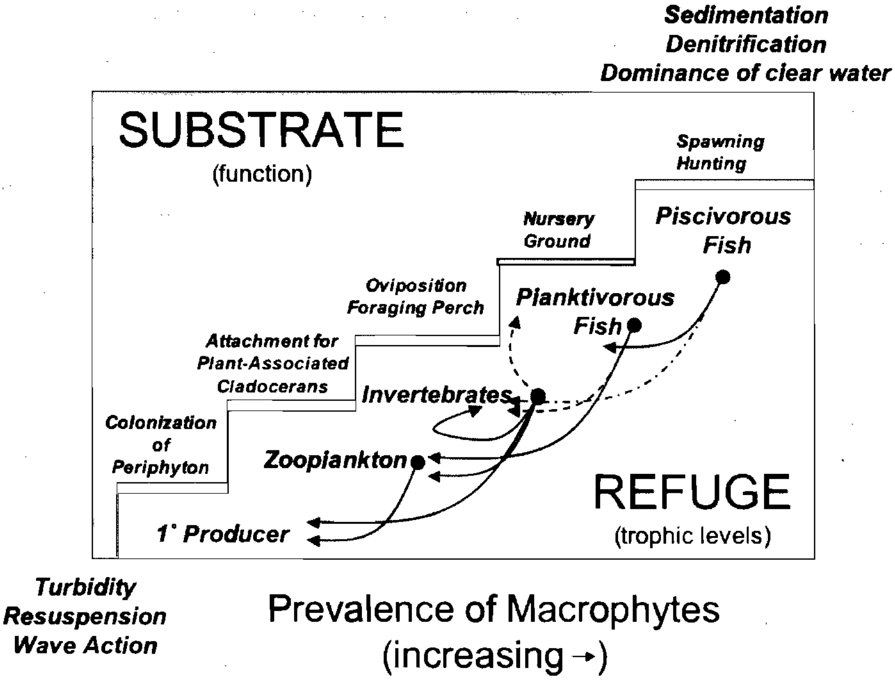

Fig. 3.2 Multi-faceted dual roles of macrophytes as both refuge and substrate across trophic levels. The *steps* suggest that the refuge potential of macrophytes increases with increasing macrophyte density after a threshold is established (i.e. the plateaus). *Arrows* show the predator–prey relationships that necessitate the need for macrophyte refuge. *Solid lines* illustrate the most predicted prey choice (*origin* with predator, *arrow* points to prey). *Dotted lines* illustrate prey choices that could occur with ontogenetic diet shifts. Four arrows originate from invertebrates because of the versatility of functional groups (i.e. predators, grazers, filterers). Increasing refuge provided by macrophytes leads to sedimentation and the dominance of clear-water, while the absence of macrophytes increases turbidity and promotes wave action and resuspension

phytoplankton plays a less important role in precipitating the shift from a turbid to a clear-water state. Macrophytes lead to increased sedimentation, through reduced water movement, which results in an influx of particles to the sediment. Consequently, there is less phytoplankton available to zooplankton in macrophytes, thus increasing the importance of epiphyton. Traditional approaches centered on the response of epiphyton to increased nutrient availability (Phillips et al. 1978), but recent work provides insight into how higher trophic levels affect the interaction between periphyton and plants, and accordingly shallow lake function.

Shading by periphyton shortened the clear-water phase associated with optimum growth conditions for submerged plants (e.g. *P. pectinatus*) in Lake Müggelsee (Germany; Roberts et al. 2003). Nutrients alone, however, do not appear to determine whether epiphyton can reach sufficient densities to negatively impact macrophytes. Experimental work suggests that other mechanisms are important for the loss of macrophytes (Jones et al. 2000; Williams et al. 2002). These experiments, previous work (Brönmark and Vermaat 1997) and a survey of 17 macrophyte-dominated lakes in the United Kingdom (Jones and Sayer 2003) have led to a proposal that the strength of a trophic cascade in the littoral zone determines the fate of macrophytes (Fig. 3.3). We agree with a recent review (Vadeboncoeur et al. 2002) that argued that benthic organisms, including epi- or periphyton and grazers, form integral links in lake food webs and deserve more emphasis in studies of trophic interaction.

In eutrophic to hypertrophic lakes, macrophyte biomass exhibits a negative relationship with epiphyton growth, with the density of epiphyton being, in turn, dependent on the density of grazing macroinvertebrates, but not nutrients (Fig. 3.3; Jones and Sayer 2003). A 20-fold increase in nutrient loading had no effect on the abundance of epiphyton growing on the surface of *Elodea nuttallii* in artificial ponds, whereas epiphyton density negatively correlated with increased grazers (Jones et al. 2002). In experimental ponds constructed to simulate reservoir wetlands, Balci and Kennedy (2003) also found that macroinvertebrate abundance correlated well with epiphyton biomass, although epiphyton biomass varied between exotic EWM and native water stargrass, *Heteranthera dubia* (Balci and Kennedy 2003). Fish biomass also served as a reliable predictor for the density of invertebrates (Jones and Sayer 2003) and accordingly epiphyton. Williams et al. (2002) showed that epiphyton chlorophyll *a* in experimental mesocosms increased significantly with increasing fish biomass (0–700 kg ha^{-1}). Interestingly, Jones and Waldron (2003) found that the proportion of periphyton in the diets of zooplankton increased with fish density, possibly as a result of increased horizontal migration. For these reasons, we highlight the strong potential for epiphyton–grazer interactions with macrophytes, mediated through interactions with fish, to facilitate shifts between turbid and clear states (see Section 3.2.4).

Colonization by epiphytes generally places macrophytes at a substantial disadvantage, due to increased competition for light, nutrients and carbon (Jones et al. 2000; Williams et al. 2002). By continuously grooming macrophyte hosts of unwanted algae and sediments, grazers may help maintain littoral communities (James et al. 2000). The periphyton removal rate generally increases allometrically with grazer biomass (Jones et al. 1997). Most grazing studies focus on snails (Gastropoda, see Brönmark and Vermaat 1997) because they are among the largest and most visible grazers on aquatic plants and can remove substantial biomass. While it may be advantageous for macrophytes to host snails, Jones et al. (2000) suggest that it is unlikely that macrophytes alter the community composition of epiphytes to increase their attractiveness to snails. However, see Brönmark's (1985) study that showed how macrophyte exudates (dissolved organic matter excreted from *Cerato-*

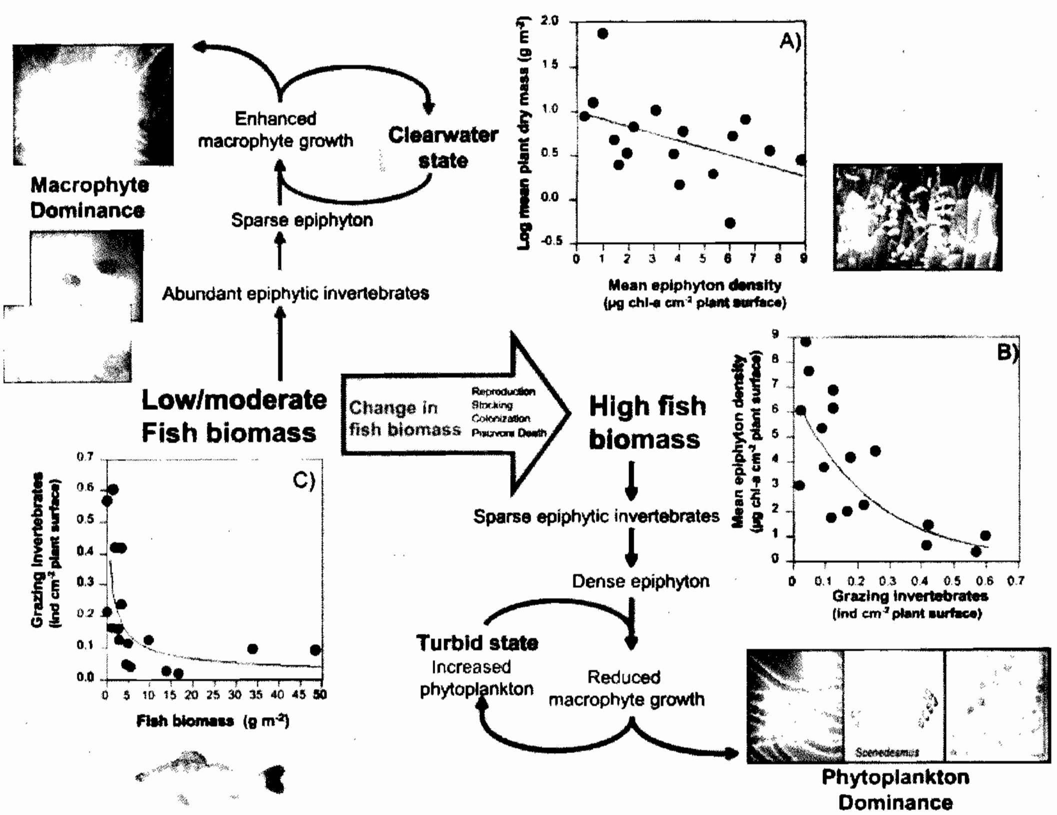

Fig. 3.3 Illustration of a littoral trophic cascade that could mediate the shift from turbid to clear conditions in shallow lakes (graphs originally published by Jones and Sayer 2003). In 17 British shallow lakes, plant biomass was negatively correlated with mean periphyton density (*graph A*: r^2=0.240, P=0.046). Periphyton density was then strongly negatively related to the density of grazing invertebrates (*graph B*: r^2=0.714, P<0.0001). Last, grazing invertebrate density declined significantly with increasing fish biomass (*graph C*: r^2=0.395, P=0.007). Overall, this suggests that a high abundance of fish would eliminate epiphyton grazers, allowing epiphyton to accumulate on plant surfaces. Consequently, macrophyte loss would occur due to light limitation and the absence of macrophytes would allow and a turbid state to dominate (*pictures* illustrate different types of phytoplankton blooms). *Images* show representative trophic levels. Note that the biomass of plankto-benthivorous fish increases with increasing nutrient levels. Thus, the scenario to the right is the most typical in eutrophic lakes unless high eutrophication leads to fish kills

phyllum demersum) attracted periphyton grazers (i.e. the snail *Lymnaea peregra*).

Direct consumption of macrophytes also alters trophic interactions. Some large invertebrates, including the invasive channeled applesnail *Pomacea canaliculata* (Lach et al. 2000) or crayfish (Lodge et al. 1994), may consume or destroy macrophytes copiously, decreasing the habitat available for colonization. For example, *Procambarus clarkii* reduced the macrophyte cover in a mesotrophic, Spanish shallow lake from 97 % to below 10 % in less than three years (Rodríguez et al. 2003). However, species-specific impacts occur, e.g. Hessen et al. (2004) demonstrated that the crayfish *Astacus astacus* failed to control rapid growth of *Elodea*. In addition, macrophytes differ in their palatability to snails and other invertebrates (Elger and Willby 2003), therefore changing plant species composition through selective herbivory (Elger et al. 2002).

The large size and omnivorous nature of crayfish differentiate them from other macroinvertebrates, underlining their importance in littoral habitats (Lodge et al. 1994). With a demonstrated preference for herbivory over carnivory and for native versus exotic macrophytes (i.e. *Eichhornia*), *P. clarkii* could be responsible for the extirpation of native aquatic macrophytes in Lake Naivasha, Kenya (Smart et al. 2002). In small Michigan ponds, vascular macrophytes failed to establish in the presence of crayfish, blue-green algae came to dominate and two epiphyton herbivores (i.e. tadpoles, snails) did not co-exist with crayfish (Dorn and Wojdak 2004). Beyond just consuming macrophytes, Dorn and Wojdak's (2004) study showed that crayfish preyed heavily on fish eggs, reducing fish recruitment (Fig. 3.2) and indirectly enhancing zooplankton biomass. Crayfish also influenced the life history traits and habitat choice of snails. Increased abundance led to the aggregation of snails on food-poor macrophytes and reduced snail growth (Lewis 2001b). Crayfish can structure the abundance and size distribution of thin-shelled snails through size-selective predation, although crayfish effects on snail size distribution may be less pronounced in complex habitats, such as macrophyte beds (Nyström and Pérez 1998). Collectively, these results indicate that crayfish can have dramatic direct and indirect impacts on littoral pond communities via feeding links with multiple trophic levels and non-trophic activities.

3.2.4 Central Themes: Prevalance of Fish Influence in Shallow Lakes

Tight coupling makes it challenging to discuss the role of macrophytes in shallow lakes without routinely acknowledging the prevalence of fishes in the littoral. Multiple interactions highlighted in our literature survey involved fish. Particular littoral fish communities exist in both temperate (Weaver et al. 1997; Lewin et al. 2004) and tropical systems (Vono and Barbosa 2001; Jeppesen et al. 2005). Such fishes spend their time predominately within macrophyte beds, although the proportion of that time may change with ontogenetic shifts (Persson and Crowder 1997). For example, juvenile pike (*Esox lucius*) inhabit littoral vegetation, but as they grow larger, pike associate with open water along the edges of macrophyte beds (Bry 1996) or less complex structure(s) of emergent macrophytes (i.e. *Typha*; Skov and Berg 1999).

Apart from ontogenetic habitat shift, the time spent in the littoral by fish also varies on a diel and a seasonal scale (Romare et al. 2003). For instance, many juvenile littoral fish perform diel horizontal migrations into the open water at night (e.g. Jacobsen and Perrow 1998; Shoup et al. 2003). Limited knowledge exists regarding winter behavior in shallow lake fish, but the littoral structure might act as a winter refuge, possibly resulting in a lower ratio of zooplankton to phytoplankton compared to summer (Jeppesen et al. 2004). This suggests a lower potential for zooplankton grazing. Habitat use of macrophytes by lower taxa strongly depends on the presence and species identity of littoral fishes. As suggested earlier, the water clarity of the system also influences interactions between macrophytes and fish. For example, Jacobsen et al. (2004) showed roach hide under water lilies during daytime in a clear-water lake inhabited by piscivorous bird species. Therefore, floating-leaved macrophytes might provide an effective cover for fish if the predation threat comes from above.

Macrophytes also serve as substrate for spawning (Fig. 3.2; Winfield 2004). Pike prefer a short dense structure, even flooded grasslands, for spawning. As for several other species, eggs require a structure on which to adhere. Some fish even use vegetation for nest-building during spawning, especially large sticklebacks (*Gasterosteus aculeatus*; Kraak et al. 2000). Littoral fish density and identity, however, fail to tell the whole story. The structural complexity of some macrophytes negatively impact the foraging rates of some fishes (Warfe and Barmuta 2004). Predation risk and competition can influence the distribution of fish species and age or size structure. For example, small bluegills (*Lepomis*) spent more time in artificial macrophytes during day than night when predators were present (Shoup et al. 2003), while large bluegill (>200 mm), in contrast used open water, emergent vegetation and submerged vegetation similarly during the day (Paukert and Willis 2002). No single factor controls habitat use of macrophytes by fishes, although macrophyte density, predation risk and prey availability may be the most influential.

Macrophytes also affect the trophic structure and interactions by enhancing fish kills under ice in lakes with long-lasting ice-cover. Canadian studies have shown higher oxygen depletion under ice in shallow lakes with abundant macrophyte biomass (Meding and Jackson 2001). This may, in turn, affect the entire trophic dynamic and water clarity quite substantially in such lakes (Bayley and Prather 2003). Grazing by fishes also may alter the biomass and species composition of submerged macrophytes (Van Donk and Otte 1996). Furthermore, some fishes may not intentionally consume macrophytes, but instead inflict damage at a critical developmental stage when they forage for macroinvertebrates (Körner and Dugdale 2003). Despite these known impacts, the complexity of interactions associated with macrophytes and fish seems limitless and warrants further study.

3.3 In the Wings: Research Areas Worthy of Attention

Our synthesis of the role of macrophytes in regulating trophic interactions suggests the need for more information to answer several key questions.

3.3.1 Predictability of Macrophyte Function in Trophic Interactions Across a Climatic Gradient

Most studies of macrophytes have been confined to North temperate lakes (Jeppesen et al. 2003), while little information exists from warm temperate to tropical lakes (Jeppesen et al. 2005). We might expect that higher temperature and favorable growth conditions during winter promote the growth of macrophytes (Rooney and Kalff 2000; Liboriussen et al. 2005). We must also consider that floating plants and floating-leaved plants are more prominent in the tropics and subtropics, but these architectures have not been as well studied as submerged plants. In dry areas, a lower water table also might promote macrophyte growth (Blindow et al. 1993). However, some macrophyte species, such as *Elodea*, may be broadly resilient to small increases associated with warming (Mckee et al. 2002). Recent enclosure studies along a climatic gradient in Europe suggested a less positive role of macrophytes on water clarity in warmer versus colder temperate lakes (Moss et al. 2004). Bachmann et al. (2002) draw similar conclusions from a cross-comparison of data from Florida lakes. One explanation may be that increased omnivory and a shift to small fish size in warm lakes also increase the use of macrophytes as a habitat for fish, making the plants a less useful refuge for zooplankton and macroinvertebrate grazers (Fig. 3.3; Blanco et al. 2003; Meerhoff et al. 2003; Jeppesen et al. 2005). In the tropics, the life cycles of some fish species are completely coupled to plants (Sazima and Zamprogno 1985; Agonstinho et al. 2003). More comparative studies of submerged, free-floating, floating-leaved and emergent plant communities are needed to understand exactly how architecture influences the dual roles of macrophytes (Fig. 3.2). We advise more studies to consider this temporal scale and to explore how macrophyte age and the ontogeny of other organisms (fish, zooplankton, invertebrates) affect the use of macrophytes as substrates, habitats, or refuges. We especially encourage more studies along climatic gradients to gain needed insight into how climate affects the role of macrophytes in lakes. Such studies are also needed to provide knowledge of how global warming may affect plants and their role in lake ecosystems.

3.3.2 Relative Importance of Chemical Ecology Across Trophic Levels

As others often propose, we also stress the need for collaboration between chemists and ecologists to identify allelopathic compounds of aquatic macrophytes. Such identification would produce incredible potential for experiments that provide definitive answers to testable hypotheses. Experimental evidence for in situ allelopathic activity on epiphyte density is challenging because of natural heterogeneity due to wave action, grazers and macrophyte structure. Thus, no general proof clearly exists for lower epiphyte density on allelopathically active macrophytes (Wium-Andersen 1987; Gross et al. 2003a), but different classes of compounds may differentially affect primary producers. For example, after investigating the allelopathic properties of *Ceratophyllum demersum* and *Najas marina*, Gross et al. (2003b) suggested that water-soluble allelochemicals may inhibit phytoplankton, whereas lipophilic allelochemicals may act through direct cell–cell contact, e.g. against epiphytes. Although difficult, we argue for more field studies that examine allelopathy. For example, we could benefit from more detailed knowledge on how changes in dissolved organic matter (i.e. concentration, composition, or source) or turbidity alter interactions inside and outside macrophyte beds.

3.3.3 Disproportional Impacts of Certain Invertebrates and Exotic Species

Fish undoubtedly drive interactions in pelagic communities (Jeppesen 1998). However, in littoral communities, macroinvertebrates, acting as grazers or predators, may be nearly as important in regulating trophic interactions among macrophytes. We recommend that studies continue to focus on invertebrates, especially large individuals such as snails and crayfish. Our literature review also indicated that epiphyton (in combination with grazers) and benthic–pelagic interactions may play a significant role in pushing systems toward a clear or turbid state. We recommend more field experiments that explore this possibility and its relation to lake/wetland management. Last, we encourage wetland scientists and ecologists to examine how macrophytes may facilitate the introduction of exotic species and the implications of macrophytes themselves as exotic species. The introduction of exotic species has the potential to alter primary production and nutrient cycling as well as native biodiversity. Furthermore, climate warming may further facilitate the invasiveness of exotic species.

3.4 Returning to Center Stage: Macrophytes are Common Players in Trophic Interactions

Any wetland textbook will enumerate the many ways in which macrophytes alter biogeochemical cycles. Recognition of the importance of macrophytes in regulating ecosystem processes is not novel (Carpenter and Lodge 1986). The take-home message of our chapter, however, focuses on examining macrophytes at the level of the community and emphasizing the multi-faceted interactions that result. Macrophytes compete with other primary producers, serve as "prey" for herbivores, function as habitat or substrate for multiple trophic levels and may serve as vectors for exotic species. Our chapter broadens the discussion from Jeppesen et al. (1997a) by speculating about how floating-leaved, free-floating and emergent macrophytes may structure interactions beyond what is known for submerged macrophytes. We also discuss how regulation of such interactions could differ between temperate and tropical systems. Regardless of locality, we strongly suggest that the presence of aquatic macrophytes drives interactions within the rest of the food web and determines which trophic interactions play a role in influencing shifts between alternative states.

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