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Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral

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SUMMARY

1. In some shallow lakes, *Daphnia* and other important pelagic consumers of phytoplankton undergo diel horizontal migration (DHM) into macrophytes or other structures in the littoral zone. Some authors have suggested that DHM reduces predation by fishes on *Daphnia* and other cladocerans, resulting in a lower phytoplankton biomass in shallow lakes than would occur without DHM. The costs and benefits of DHM, and its potential implications in biomanipulation, are relatively unknown, however.
2. In this review, we compare studies on diel vertical migration (DVM) to assess factors potentially influencing DHM (e.g. predators, food, light, temperature, dissolved oxygen, pH). We first provide examples of DHM and examine avoidance by *Daphnia* of both planktivorous (PL) fishes and predacious invertebrates.
3. We argue that DHM should be favoured when the abundance of macrophytes is high (which reduces planktivory) and the abundance of piscivores in the littoral is sufficient to reduce planktivores. Food in the littoral zone may favour DHM by daphnids, but the quality of these resources relative to pelagic phytoplankton is largely unknown.
4. We suggest that abiotic conditions, such as light, temperature, dissolved oxygen and pH, are less likely to influence DHM than DVM because weaker gradients of these conditions occur horizontally in shallow lakes relative to vertical gradients in deep lakes.
5. Because our understanding of DHM is rudimentary, we highlight potentially important research areas: studying a variety of systems, comparing temporal and spatial scales of DHM in relation to DVM, quantifying positive and negative influences of macrophytes, focusing on the role of invertebrate predation, testing the performance of cladocerans on littoral versus pelagic foods (quantity and quality), investigating the potential influence of temperature, and constructing comprehensive models that can predict the likelihood of DHM. Our ability to biomanipulate shallow lakes to create or maintain the desired clear water state will increase as we learn more about the factors initiating and influencing DHM.

Keywords: *Daphnia*, food quality, macrophytes, predation, shallow lakes

Introduction

The abundance and quality of the world's freshwater resources are declining rapidly (Naiman *et al.*, 1995; Brown *et al.*, 2000). Changes in land use degrade natural freshwaters and reduce biodiversity by eliminating valuable habitats and adding excess nutrients

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(Vitousek, 1994). Increased introductions of exotic species have also reduced biodiversity (Kolar & Lodge, 2000). Of these threats, cultural eutrophication has been the most serious for freshwaters for the past 25 years (Lodge, Blumenshine & Vadeboncoeur, 1998a) and continues to be a major global threat (Sala *et al.*, 2000). While pollution of large, deep lakes attracts more scientific focus and publicity (Wetzel, 1990; Moss, 1998), eutrophication adversely impacts many of the far more abundant, small, shallow lakes that provide habitat for wildlife as well as recreational and biological services to the general public (Moss, 1998). These shallow lakes often reside within agricultural areas, recycle nutrients internally, and contain smaller volumes of water to dilute added nutrients from fertilizers (Jeppesen, 1998). Excess nutrients in shallow lakes can cause a shift in the fish community from large, piscivorous fishes (PI) towards small, planktivorous (PL) or benthivorous fishes (Persson *et al.*, 1988). In deep lakes at least, decreasing the proportion of piscivores to planktivores (PI : PL) and increasing density of planktivores results in a decrease in the zooplankton : phytoplankton ratio that, along with increasing nutrient concentrations, leads to increasing phytoplankton abundance. Thus, changes in fish dominance translate through the food web into changes in water quality (Carpenter, Kitchell & Hodgson, 1985). However, our understanding of food web dynamics in deep lakes may only be partially applicable to shallow lakes (Moss, McGowan & Carvalho, 1994; Jeppesen *et al.*, 1997a, 2000; Beklioglu, 1999).

Herbivorous zooplankton reduce algal biomass and change algal community structure (Elser & Goldman, 1990). Large-bodied *Daphnia*, in particular, graze a wider size-range of phytoplankton (Lampert, 1987) than smaller-bodied zooplankton, but are more vulnerable to fish predation (Brooks & Dodson, 1965). Thus, restoration efforts aimed at reducing algal biomass by increased grazing often strive to increase *Daphnia* abundance, even amid increased predation pressure (Perrow *et al.*, 1997; Deneke & Nixdorf, 1999). Predator pressure on *Daphnia* may be amplified in shallow lakes because of the absence of a hypolimnetic refuge and a stronger impact of fishes (Jeppesen *et al.*, 1997a). In deep lakes, *Daphnia* avoid visual predators by day by migrating vertically into colder, darker, hypolimnetic water (O'Brien, 1979; Lampert, 1993). In shallow lakes, light may penetrate to the

bottom of water and, because they do not stratify for an extended time, they often lack a hypolimnetic refuge. Thus, in shallow lakes where diel vertical migration (DVM) is probably less advantageous, pelagic zooplankters may migrate into vegetated, littoral zones during the day. This behaviour is termed diel horizontal migration (DHM) (Timms & Moss, 1984; Lauridsen & Buenk, 1996; Lauridsen *et al.*, 1998) and is assumed to be an alternative predator avoidance strategy. Refuge from predation could help sustain *Daphnia* populations or other grazing zooplankters (Bertolo *et al.*, 1999) and contribute to the maintenance of a clear, macrophyte-dominated, rather than a turbid, algal-dominated, state (Lauridsen *et al.*, 1998; but see Blindow *et al.*, 2000).

In this paper, we discuss evidence for the occurrence of DHM and evaluate possible mechanisms behind it, including predator-avoidance. We focus primarily on daphnids because large-bodied *Daphnia* most strongly influence water quality, outcompete other zooplankton for food, and suffer most from predation (de Bernardi & Peters, 1987). We include limited discussion of other filter-feeding zooplankton (e.g. *Ceriodaphnia*, *Bosmina*, *Sida*, *Simocephalus*) that might compete with *Daphnia* (Frank, 1952; DeMott & Kerfoot, 1982), which we differentiate from more littoral, plant-associated taxa that are primarily scrapers (e.g. *Chydorus*, *Eurycercus*) (Paterson, 1994). First, we address the evidence for DHM by reviewing the literature on the horizontal distribution of *Daphnia* in shallow lakes. Secondly, we discuss potential mechanisms behind DHM by drawing on the literature related to DVM. We discuss the potential influences on DHM of macrophytes, predators, food resources, light, temperature, pH and dissolved oxygen.

Occurrence of DHM

Diel horizontal migration occurs in some shallow lakes, but has so far not been well-documented in stratified lakes (although see White, 1998). Timms & Moss (1984) first documented daytime aggregations of *Daphnia* under water lilies in the shallow Norfolk Broads. Since then, documentation of pelagic cladocerans in littoral zones has been published for *D. hyalina lacustris* (Straus) in British gravel pits (Davies, 1985), *D. magna* (Straus) and *D. hyalina* (Leydig) in Danish lakes Ring and Væng (Lauridsen & Buenk, 1996), *Scapholeberis mucronata* (Müller) in a

Belgian small pond (DeMeester *et al.*, 1993), *Daphnia* spp. and *Ceriodaphnia dubia* (Richard) in the Norfolk Broads (Stansfield *et al.*, 1997; Moss, Kornijów & Measey, 1998), *Bosmina longirostris* (Müller) in a Finnish Lake (Walls *et al.*, 1990), *D. longispina* (Müller) and helmeted *D. galeata* (Sars) in small Norwegian lakes (Kvam & Kleiven, 1995; Lysebo, 1995) and *D. retrocurva* (Birge) and *D. catawba* (Coker) in Ranger Lake, Canada (Visman, McQueen & Demers, 1994). Hitherto, studies of DHM have focused on northern temperate lakes. No studies have directly examined DHM in the subtropics and tropics, although many well-vegetated shallow lakes occur in these areas (Steinman *et al.*, 1997).

The DHM may also be more common than we realize because most sampling programmes for zooplankton are not designed to detect it (Lauridsen *et al.*, 1999). Methodological difficulties exist even in studies designed to detect DHM. Collecting more animals at night (than expected by mass balance of all samples) is a frequent concern in DVM studies (Bollens & Frost, 1989) and also often occurs in DHM studies (Verreth, 1990; DeStasio, 1993; Lauridsen & Buenk, 1996; White, 1998). Large zooplankton may avoid samplers better in the daytime (Omori & Hamner, 1982), but it is more likely that animals are located on or near the sediments during the day, thus avoiding visual predators (DeStasio, 1993; Jeppesen, 1998). Sampling among vegetation can also be difficult (Marklund, 2000). Traditional zooplankton sampling methods, which avoid sediment, potentially underestimate DHM as well as small-scale DVM in the littoral zone during the day. Sediment samples are time-consuming to process. In addition, large sample variability often results. For these reasons, it may remain impractical to sample sediments routinely. However, an intensive sampling (including sampling of the surficial sediments) in lakes where DHM apparently occurs could provide better documented examples of DHM and help determine whether DVM often occurs simultaneously with DHM.

Factors influencing costs and benefits of DHM

There is substantial information regarding the costs and benefits of DVM that could effectively steer further research. (for recent reviews of DVM, see Haney, 1993; Lampert, 1993; Ringelberg, 1993). Predators, food resources and abiotic factors (e.g. light,

temperature, dissolved oxygen and pH) all influence DVM. In shallow lakes, macrophytes also appear to play an important role in DHM (Lauridsen & Buenk, 1996; Moss *et al.*, 1998). Below, we evaluate how each of these factors may contribute to the costs and benefits of DHM for zooplankton.

Predators

Predator-avoidance is commonly accepted as the ultimate reason for DVM (Lampert, 1993) and is also the favourite hypothesis for why daphnids undergo DHM (Lauridsen *et al.*, 1996; Scheffer, 1998). The decisive 'benefit' of vertical migration is a reduction in the risk of predation by visual predators, whose effectiveness is reduced in darker, colder, often hypoxic, deeper water (O'Brien & Vinyard, 1978). A reduction in predation may also result from horizontal migration, but by different mechanisms. However, migrating to avoid pelagic predators could introduce daphnids to littoral zone predators. In an enclosure (7.1-m depth) experiment in stratified Ranger Lake (Canada), *D. pulex* (Leydig) displayed vertical migration and simultaneously avoided deep areas occupied by *Chaoborus americanus* (Johannsen) as well as near-surface areas occupied by another predator (*Notonecta* spp.) (Nesbitt, Riessen & Ramcharan, 1996). With regard to DHM, the challenge is to measure the relative threat of pelagic and littoral predators, and to discover how daphnids respond to multiple predators (Sih, Englund & Wooster, 1998) in shallow lakes.

Alone, or in combination with light stimuli, the presence of a predator elicits multiple responses from daphnids (Kats & Dill, 1998; Riessen, 1999). Chemical cues (von Elert & Pohnert, 2000) released from both vertebrate (Macháček, 1991; van Gool & Ringelberg, 1995; Sakwińska, 1998) and invertebrate predators (Stibor, 1992; Repka, Ketola & Walls, 1994; Riessen, 1994; Engelmayer, 1995) influence a wide range of *Daphnia* life-history traits, morphological parameters (Larsson & Dodson, 1993), and behaviour (Jensen, Jakobsen & Kleiven, 1998). In laboratory experiments, *Daphnia* swim away from chemical clues from invertebrate predators, both vertically (Lüning, 1992; Black, 1993; Watt & Young, 1994) and horizontally (Kleiven, Larsson & Hobæk, 1996; Lauridsen & Lodge, 1996). Cues from PL fish prompt daphnids to swim downward (van Gool & Ringelberg, 1998), but more focused investigations of daphnid swimming are

needed to fully evaluate the costs of swimming horizontally during DHM. Diel vertical migration in freshwater occurs anywhere from the cm-scale (within laboratory beakers) to over 100 m within deep lakes (Hutchinson, 1967). Less is known about the scale of DHM, but observations to date suggest that it ranges from the cm-scale in laboratory aquaria (Lauridsen & Lodge, 1996) to at least 30 m in field studies (Davies, 1985; Kvam & Kleiven, 1995; Lauridsen & Buenk, 1996).

Across broad scales and diverse systems, the presence of invertebrate and vertebrate predators is known to invoke DVM. However, predator-avoidance by *Daphnia* in shallow, patchily vegetated systems is much more complex than in homogeneous, deep lakes (Scheffer, 1998). Besides contending with increased fish predation (see next section), daphnids must also confront the difficulties of hiding in macrophytes, which may harbour invertebrate predators and constitute inferior habitat in other ways (see later sections). Understanding what predation scenarios favour DHM by *Daphnia* involves examining multiple interacting parameters in shallow lakes (Jeppesen *et al.*, 1998). When applicable in the following sections, we describe how factors differ across nutrient gradients, because evaluating the impact of nutrients on complex interactions involving *Daphnia* may help predict when DHM would be expected.

Fishes

Predation by PL fishes is one factor strongly and likely to drive DHM. Planktivorous fishes produce a higher predation impact in shallow than deep lakes, because shallow lakes contain a higher biomass of fishes per unit volume than deep lakes (Jeppesen, 1998). Increased benthic area provides abundant food for both pelagic and benthivorous fishes (Blumenshine *et al.*, 1997). Benthic resources, in turn, support higher densities of fishes that control pelagic zooplankton (Jeppesen, 1998). Furthermore, large PI fishes keep smaller, PL fishes in check, thus releasing predation pressure on *Daphnia* that can then control algae (Pace *et al.*, 1999). However, the degree of top-down control may depend on trophic state. Piscivorous fishes only increase in abundance once enough planktivores occur to support them. At high nutrients, the proportion of large piscivores in the entire fish stock usually decreases because of a loss of complex habitat. This

habitat loss leads to increased cannibalism, enhanced competition between planktivores and juvenile piscivores, and environmental conditions that are adverse for piscivores (e.g. low dissolved oxygen) (Persson *et al.*, 1988). In contrast, the abundance of PL fishes increases with nutrients (Kitchell *et al.*, 1977; Jeppesen *et al.*, 1997a, 2000). As nutrients increase from oligotrophic conditions, the ratio of piscivorous to planktivorous fishes (PI : PL) increases initially and then steadily declines (Persson *et al.*, 1988; Jeppesen, 1998). Consequently, the costs and benefits to DHM may depend not only on fish density, but also on the interactions between these two trophic levels (Carpenter, 1988; Persson, 1993).

Fish-related factors favouring DHM

Cascading trophic interactions are more complex in shallow than in deep lakes. Therefore, it is often difficult to predict the effect of fishes on daphnid populations. At a high PI : PL ratio, there are enough piscivores to depress the effect of PL fishes, either numerically, behaviourally, or both (Eklöv & Diehl, 1994). However, this benefit may depend on the piscivore (Persson, 1993). If a littoral predator dominates, such as pike (*Esox lucius* Linnaeus), then the planktivores fish are forced out of the vegetation and into contact with pelagic predators such as adult perch (*Perca fluviatilis* Linnaeus) (Grimm & Backx, 1990; Berg, Jeppesen & Søndergaard 1997; Jacobsen & Perrow, 1998). This situation may enhance the littoral zone refuge for daphnids. Alternatively, more pelagic piscivores may force PL fishes to seek refuge in macrophytes (Eklöv, 1992; Bean & Winfield, 1995; Persson & Crowder, 1998; Schindler, 1999), probably reducing the efficiency of the refuge (see next section). Yet, maintenance of a refuge is not the only potential benefit of PI fishes to zooplankters. Piscivores, as well as planktivores, may further benefit daphnids undergoing DHM if the fish feed on alternative food resources, such as predacious pelagic (Herzig, 1995; Wissel & Bendorff, 1998) or benthic invertebrates (Christensen & Persson, 1993; Blumenshine *et al.*, 1997). For management purposes, a reasonable hypothesis is that the best stocking policy for promoting DHM is to add piscivores that prefer the littoral habitat. When PI fish wait for prey among macrophytes, refuge for *Daphnia* should be maximized. Direct experimental

tests of this hypothesis would be valuable for management purposes.

Fish-related factors discouraging DHM

As PI : PL ratios decline with increasing nutrients (or from other causes), predation on daphnids by PL fishes is likely to intensify. In low nutrient systems, predation pressure on daphnids is high and populations are low because clear water enhances zooplanktivory by fishes and because macrophytes are scarce and offer little refuge (Jeppesen *et al.*, 1997b, 1999). At moderate nutrient concentration, availability of a refuge among macrophytes may prolong the presence of *Daphnia* (see *Macrophyte-related factors favouring DHM*). Increasing evidence suggests that predation by numerous young-of-the-year (0+) fishes causes a midsummer decline in littoral zooplankton (Whiteside, 1988), particularly *Daphnia* (Wright & Shapiro, 1990; Simonian *et al.*, 1995; Mehner *et al.*, 1998; but see Hülsmann & Lampert, 1999). Therefore, in systems with a moderate or high nutrient concentration, seasonal changes in the horizontal distribution of juvenile fishes may also hold implications for daphnids undergoing DHM. Young-of-the-year (YOY) perch (*P. fluviatilis*) often move to the littoral zone in mid-summer (both by day and night) and are efficient foragers among vegetation (Winfield, 1986). Roach (*Rutilus rutilus* Lacustris), in contrast, stay near vegetation during the day but predominately move into the pelagic at night (Jacobsen & Perrow, 1998). Particularly if plant density is low, predation pressure on zooplankton may be higher if YOY perch dominate, as they probably co-occur with zooplankton in the vegetation during the day more than YOY roach.

Based on the strong influence of YOY fishes in temperate lakes, we might hypothesize that DHM may not be as prevalent in subtropical and tropical lakes because of the frequent spawning of small species, such as the mosquitofish (*Gambusia affinis* Baird & Girard), that prefer vegetated habitat (Chick & McIvor, 1997). These effective predators within vegetation (Linden & Cech, 1990) may eliminate any macrophyte refuge in these types of lakes, although more experimental evidence is required to draw any strong conclusions about patterns in these systems. However, *Daphnia* cannot survive where abundant predators nullify any refuge afforded by macrophytes (Persson, 1991; Venugopal & Winfield, 1993; Diehl &

Kornijów, 1998). Perrow *et al.* (1999) suggest that only 1 PL fish m⁻² is sufficient to prevent large populations of herbivorous zooplankton from establishing in beds of floating-leaved macrophytes.

The critical fish density that eliminates *Daphnia* may be higher in systems with higher nutrient concentrations (Scheffer, Sergio & Kuznetsov, 2000), allowing a partial refuge effect. If the foraging activity of PL fishes is reduced among macrophytes (Stansfield *et al.*, 1997), then the net impact of PL fishes on *Daphnia* in littoral habitats could be negligible in the absence of other littoral-associated predators. Furthermore, at high nutrients, low dissolved oxygen and high pH in vegetated habitats may cause fish kills (Barica & Mathias, 1979; Beklioğlu & Moss, 1995; Jeppesen *et al.*, 1998), or at least avoidance of such habitat by fish, perhaps allowing daphnid populations to persist. The survival of *Daphnia* is therefore strongly linked to predation pressure from PL fishes, which depends on interactions with piscivores.

Invertebrate predators: pelagic

Up to this point, we have considered DHM in relation to vertebrate predators, particularly PL fishes. However, invertebrate predators in the pelagic, such as *Chaoborus* spp., *Leptodora kindtii* (Focke), and *Bythotrephes cederstroemi* (Schoedler), can also strongly reduce zooplankton populations (Leucke & Litt, 1987; Mumm, 1997; Schulz & Yurista, 1999; Wahlström & Westman, 1999) and influence DVM (Gonzalez & Tessier, 1997), especially in fishless lakes (Vanni, 1988). In these fishless systems, significant predation pressure may also result from invertebrates commonly considered as scavengers, such as *Gammarus lacustris* (Sars) (Wilhelm & Schindler, 1999). While the influence of these pelagic invertebrates on daphnids probably diminishes as nutrients increase (as a result of consumption of these predators by PL fishes) (Jeppesen *et al.*, 1997a), pelagic invertebrates may still be dominant in oligotrophic lakes or hypereutrophic lakes that have experienced fish kills (Wissel & Benndorf, 1998).

Pelagic invertebrate predators are known to affect *Daphnia* populations in deep lakes, but are poorly studied in shallow lakes. Evidence that pelagic invertebrate predators prompt DHM is scarce. However, some recent studies suggest that the peak activity time of these predators could help predict when daphnids should seek refuge in vegetation (Table 1). Yet, these

predictions become more difficult if pelagic invertebrates also choose to migrate horizontally when PL fishes are numerous (Voss & Mumm, 1999). In studies of vertical migration, daphnids are able to avoid multiple invertebrate predators simultaneously by altering their migration (Nesbitt *et al.*, 1996). Circumstantial evidence suggests that this may also be the case for horizontal migration, although experimental studies are needed to test this inference. Wissel & Benndorf (1998) suggest that the impact of invertebrate predators on *Daphnia* populations could equal or exceed that of PL fishes in deep lakes, although this is unlikely for most systems (Hansson & Tranvik, 1996). Rather, in shallow lakes, the impacts of fishes and pelagic invertebrate predators may be additive and increase the likelihood that daphnids seek refuge in the littoral zone, although this has not been tested experimentally.

Invertebrate predators: littoral

In shallow lakes, *Daphnia* may face predacious benthic and epiphytic invertebrates in the littoral zone (Blois-

Heulin *et al.*, 1990; Sih *et al.*, 1998) in addition to pelagic invertebrate predators. Therefore, the benefit of escaping from pelagic predators must be balanced with the costs of confronting predators in the littoral zone. Direct predation on zooplankton by epiphytic and benthic invertebrates is thus a potentially large, and overlooked, cost of DHM (Burks *et al.*, 2001a). Macrophytes are habitat for many invertebrate predators of zooplankton, such as larval odonates (Johnson *et al.*, 1987; Lombardo, 1997), dytiscid beetles (Arts, Maly & Pasitschniak, 1981; Kornijów & Kairesalo, 1994), notonectids (Murdoch, Scott & Ebsworth, 1984; Barry, 1997; Arnér *et al.*, 1998), corixids (Ranta & Espo, 1989), water mites (Matveev, Martinez & Frutos, 1989; Davids, Ten Winkel & De Groot, 1994), hydra (Elliott, Elliott & Leggett, 1997) and flatworms (Beisner, McCauley & Wrona, 1996). Other invertebrates (e.g. amphipods) associated with vegetation readily consume ephippia of *Daphnia*, possibly influencing the population dynamics of pelagic zooplankton (Caceres & Hairston, 1998). Furthermore, macroinvertebrate density often increases with increasing surface area and structural complexity (Brown & Lodge, 1993;

Table 1. Scenarios for potential influences of predacious pelagic invertebrates on diel horizontal migration by daphnids

Are pelagic fishes present?	Are pelagic predacious invertebrates present?	In the pelagic, are invertebrates active at day or night?	Prediction on where and when daphnids should congregate in macrophytes	Example	Reference
Yes	No	Not Applicable	Macrophytes during day	<i>D. magna</i> and <i>D. hyalina</i> in Danish Lakes Ring and Væng	Lauridsen & Buenk (1996)
No	Yes	Day	Macrophytes during day	<i>D. longispina</i> occurred in dense swarms (4000 L ⁻¹) in a Norwegian lake	Kvam & Kleiven (1995)
No	Yes	Night	Macrophytes at night	<i>Daphnia</i> in fishless Central Long Lake, USA, congregated in open water during day and macrophytes at night	Lauridsen <i>et al.</i> (1998)
Yes	Yes	Day	Unknown: Possibly macrophytes during day?	None with daphnids. Yet, third and fourth instar <i>Chaoborus</i> migrated horizontally in German Lake Plusssee in response to fish predation	Voss & Mumm (1999)
Yes	Yes	Night	?	No known example	

Kornijów & Kairesalo, 1994; Cattaneo *et al.*, 1998). Therefore, the impact of macrophyte-associated or benthic predators may add to the impact of PL fishes.

The functional response of larval odonates feeding on *Daphnia* is a classic example found in several ecology textbooks (Thompson, 1975; Begon, Harper & Townsend, 1990). Laboratory studies commonly use daphnids as prey to examine odonate foraging tactics and feeding rates (Thompson & Pickup, 1984; Lombardo, 1997; Hirvonen, 1999). However, few field studies examine daphnids as prey for odonates (Burks *et al.*, 2001a). Larval odonates are predators of moving prey in the littoral zone. Large-bodied *Daphnia* are therefore highly susceptible to these predators (Hirvonen, 1999), and this susceptibility could influence the advantages of DHM. For example, the higher relative density of *Enallagma* (Order Odonata, Suborder Zygoptera) and *Chaoborus* in the littoral zone than the pelagic zone may explain the lack of DHM in Crooked Lake, Indiana, USA (Smiley & Tessier, 1998).

Besides predacious epiphytic or benthic macroinvertebrates, epineustonic predators may also prey on *Daphnia* (Murdoch *et al.*, 1984; Herwig & Schindler, 1996; Arnér *et al.*, 1998). For example, water striders (Family Gerridae), backswimmers (Notonectidae) and diving beetles (Dytiscidae), rely on movement, besides light, to detect prey. Thus, these predators are likely to hone in on jerky swimming movements of *Daphnia* (O'Brien & Vinyard, 1978; Arts *et al.*, 1981). To evaluate the value of DHM to *Daphnia*, the benefit of reduced mortality from pelagic predation must be compared with increased susceptibility to predation by littoral invertebrates. Such research has not been carried out.

Macrophytes

Although we have discussed interactions between PI and PL fishes in macrophytes, as well as the potential impact of macrophyte-associated predators, we now turn our attention to the direct implications for DHM, including the potential benefits and costs of macrophytes.

Macrophyte-related factors favouring DHM

Foraging for zooplankton within macrophytes is difficult for some fishes (Diehl, 1988; Engels, 1988),

decreasing their foraging efficiency (Winfield, 1986; Tatrái & Herzig, 1995). The effectiveness of a refuge for *Daphnia*, however, may differ with macrophyte growth form, density, or species (Lauridsen *et al.*, 1996; Moss *et al.*, 1996; Jacobsen *et al.*, 1997; Stansfield *et al.*, 1997; Burks *et al.*, 2001b). In addition, the seasonal development of macrophytes will certainly influence refuge effectiveness as will the nutrient status of the lake.

Lakes that are colonized with macrophytes early in the spring often show a higher abundance of daphnids and a longer duration of clear water (Jeppesen *et al.*, 1999; Meijer *et al.*, 1999). With regard to macrophyte density, theory suggests that refuge effectiveness should be maximized in the summer after dense stands of macrophytes have developed in mesotrophic and eutrophic lakes (Jeppesen *et al.*, 1998). At the oligotrophic and hypereutrophic extremes, we would expect little seasonal variation in refuge potential, because submerged macrophytes are usually scarce or absent (Jeppesen *et al.*, 1997b). In mesotrophic and eutrophic lakes with macrophytes, the seasonal response becomes more complex and depends on whether PL fishes are present. If there is a high density of small fish, we would expect a spring maximum in daphnid abundance, then a subsequent decline over the summer as predation increases, and perhaps an autumn recovery (Whiteside, 1988). If fish density is low or macrophytes are particularly dense (i.e. they provide an effective refuge), daphnid abundance may increase in spring and remain stable through the summer (Whiteside, 1988; Jeppesen *et al.*, 1998). Refuge potential may be higher in lakes in which macrophytes persist through the winter, although little is known about daphnid population dynamics in shallow lakes during winter. In addition, as previously discussed, a simultaneous seasonal increase in small fish may nullify the effect of any refuge. Therefore, in our discussion about macrophyte-related factors that favour horizontal migration, we focus on examples where macrophytes provide a refuge for daphnids during spring or summer.

Floating-leaved and submerged macrophytes can protect large-bodied zooplankton from fish predation. Despite high perch (*P. fluviatilis*) density, thick stands of floating water lilies (*Nuphar lutea* Linnaeus) provide a refuge for *Daphnia* (Moss *et al.*, 1998) and *Ceriodaphnia* (Stansfield *et al.*, 1997) during

the summer. Local elimination of *Daphnia* by 0+ fish (perch and roach) is also delayed where there are extensive stands of submerged macrophytes (Stansfield *et al.*, 1997; Perrow *et al.*, 1999). Finely dissected submerged macrophytes, such as *Potamogeton pectinatus* (Linnaeus), *Ceratophyllum demersum* (Linnaeus), *Myriophyllum exalbescens* (Fernald) or *Elodea canadensis* (Michx.), may significantly reduce *Daphnia* mortality more than floating leaved macrophytes, although this idea has not been tested experimentally. Relative to floating-leaved and submerged plants, less experimental evidence exists for emergent plants as a refuge, although *S. mucronata* congregated in *Carex* stands in a small pond with fish (DeMeester *et al.*, 1993), and large *Bosmina* swarms ($>3000\text{ L}^{-1}$) accumulated in stands of another emergent, *Equisetum fluviatile* Linnaeus (Kairesalo, 1980). Refuge effectiveness for cladocerans, however, will depend not only on plant architecture, but also on plant density.

Refuge efficiency from PL fishes increases with increasing macrophyte density (Jeppesen *et al.*, 1997a; Burks *et al.*, 2001b). Yet, even relatively sparse submerged macrophytes, e.g. 15–20% 'volume infested' (PVI, *sensu* Canfield *et al.*, 1984), allows *Daphnia*, *Bosmina* and *Ceriodaphnia* to persist in enclosures with a low fish density, when compared with cladoceran abundances in the absence of macrophytes (Schriver *et al.*, 1995). PVI is a metric used to describe macrophyte coverage (originally used for nuisance macrophytes in Florida) and is calculated as the area of macrophyte coverage multiplied by the plant height divided by the water depth (Canfield *et al.*, 1984). Nevertheless, sparse to moderate densities of macrophytes are not likely to provide a predation refuge for *Daphnia* if they are accessible to abundant small fishes (Venugopal & Winfield, 1993). Perch forage particularly efficiently among complex structure (Winfield, 1986). In one study, wood bundles, which enhanced *Daphnia* populations in the short term in the presence of fish, eventually failed to provide refuge against sustained predation by perch (Irvine, Moss & Stansfield, 1990). A density of floating-leaved macrophytes exceeding 40% is needed to protect large cladocerans in shallow ponds, such as the Norfolk Broads (Perrow *et al.*, 1999). In contrast, small, dense patches of submerged macrophytes can be an effective refuge for daphnids undergoing DHM (Lauridsen *et al.*, 1996). Despite

this existing evidence, more experimental studies are required to understand the persistence of *Daphnia* as a function of the species and abundance of macrophytes, invertebrates and fishes.

Macrophyte-related factors discouraging DHM

The benefits of a refuge must be weighed against potential costs to *Daphnia* of inhabiting macrophytes. Submerged macrophytes, e.g. *Elodea canadensis*, release chemical substances that reduce the growth of *Daphnia* (Burks, Jeppesen & Lodge, 2000). Prolonged exposure (i.e. 5 days) to exudates (e.g. resorcinol) from water lilies (*N. lutea*) even caused significant daphnid mortality (Sütfield, Petereit & Nahrstedt, 1996). Reduced growth and reproduction or increased mortality among macrophytes may offer one explanation for the apparent paradox between the historical documentation of daphnids avoiding macrophytes and recent studies of DHM. Early work demonstrating that *Daphnia* avoided macrophytes (Hasler & Jones, 1949; Pennak, 1973; Dorgelo & Heykoop, 1985) apparently convinced limnologists that it was true under all circumstances. However, Lauridsen & Lodge (1996) showed that, when confronted with fish chemical cues, *Daphnia* chose to reside in macrophytes, despite their initially repellent properties. Extensive testing of how chemicals from macrophytes influence *Daphnia* behaviour, filtering ability (Burns & Dodds, 1999) and life history traits (as DVM studies do with predator chemicals) will help determine when the benefits of DHM outweigh the costs.

Food resources

In addition to the direct negative effects of macrophytes on daphnids, indirect effects via phytoplankton are probably also important (Phillips, Perrow & Stansfield, 1996). Macrophytes, such as *Myriophyllum*, release chemicals that depress phytoplankton (Phillips, Eminson & Moss, 1978; Gross & Sütfield, 1994; Jasser, 1995; Gross, Meyer & Schilling, 1996). In shallow lakes, macrophytes and phytoplankton compete for nutrients and light, which may drive the shift from the clear to turbid state (Scheffer *et al.*, 1993). For *Daphnia*, this competition creates another potential cost of inhabiting macrophytes, reduced food quantity or quality.

Food quantity

Daphnia swarm in response to high food concentration (Cuddington & McCauley, 1994; Neary, Cash & McCauley, 1994), influencing their vertical distribution. Dagg (1985) hypothesized that zooplankton should migrate vertically (i.e. spend time in a habitat with less food) when there is an abundance of food in their preferred habitat: increased food availability in one habitat allows zooplankton to seek refuge in otherwise suboptimal conditions. In shallow systems, where DVM is less advantageous, this idea of seeking refuge in a less treacherous habitat as a trade-off to finding quality food in a riskier habitat may apply to DHM. *Daphnia* migrate horizontally from pelagic zones with abundant phytoplankton to potentially safer littoral zones where resources may be limited. We now examine how differences in resource quantity in the littoral zone could discourage or favour DHM.

Lack of phytoplankton may discourage DHM

A clear negative correlation exists between the abundance of phytoplankton and submerged macrophytes (Phillips *et al.*, 1978; Schriver *et al.*, 1995). Therefore, it is clear that, with regard to phytoplankton abundance, there is a cost to daphnids inhabiting the littoral versus the pelagic zone (Søndergaard & Moss, 1998). However, that cost may entail an overall net gain where pelagic phytoplankton abundance is high. Scarcity of phytoplankton restricts vertical migrations of *D. longispina* in enclosure experiments (Johnsen & Jakobsen, 1987) and *D. pulex* in Lake Maarsseveen (Flik & Ringelberg, 1993). Furthermore, White (1998) suggested that zooplankters migrated in parallel to horizontal gradients of food availability after dark. Thus, the quantity of available food is an important consideration in evaluating whether DHM is possible.

Increased resources may favour DHM

In contrast to phytoplankton, a higher quantity of periphyton and bacteria is found among macrophytes than in open water. Periphyton and bacteria may be an incentive for daphnids to migrate into the littoral zone, but only if *Daphnia* can facultatively switch from filter feeding to browsing (Horton *et al.*, 1979) and

make use of these alternative resources. Most daphnids can feed on bacteria and detritus that accumulate in the littoral (Riemann & Bosselmann, 1984; Lampert, 1987; Nagata & Okamoto, 1988). Ojala *et al.* (1995) found that *D. longispina* reproduced well when fed littoral zone resources, despite the low abundance of phytoplankton. However, the animals which fed on resources from the littoral zone were smaller and overall net production was lower than occurred in control treatments where daphnids received phytoplankton. Bacteria may serve as a 'life-support' system, enabling survival when algae are scarce (Ojala *et al.*, 1995). However, browsing by daphnids is not very well studied and deserves further attention. Use of stable isotopes (Peterson & Fry, 1987; Gannes, O'Brien & Del Rio, 1997), or additional experiments designed to measure *Daphnia* growth when fed with littoral versus pelagic food (like Ojala *et al.*, 1995), would shed light on whether *Daphnia* can benefit from the potentially greater food availability in the littoral zone.

Food quality

Besides food quantity, food quality may also be important for daphnids in the littoral and may change over a nutrient gradient (Gliwicz & Lampert, 1990). Daphnids may be limited by food quantity in oligotrophic systems, but by food quality in nutrient-rich systems. Little information is available about the composition or quality of littoral versus pelagic resources for daphnids. Nevertheless, we examine various measures used to assess phytoplankton quality (Porter & Orcutt, 1980), and hypothesize how each type of food limitation might differ in littoral versus pelagic zones.

Assessing quality of littoral versus pelagic resources for daphnids

For daphnids, food quality depends on multiple factors including size and shape (Orcutt & Porter, 1983), toxicity (Porter & Orcutt, 1980; de Bernardi & Giussani, 1990), elemental ratios (Sterner & Robinson, 1994; Urabe, Clasen & Sterner, 1997; Elser *et al.*, 2000), fatty acid composition (DeMott & Müller-Navarra, 1997; Gulati & DeMott, 1997), cell coverings (Gliwicz & Lampert, 1990) and colony formation (Lampert, 1987). Thus, many parameters are necessary to

evaluate the nutritional value of a resource for daphnids. Therefore, it is often difficult to decide what constitutes high quality food for daphnids (Sterner & Schulz, 1998).

As daphnids are generalist filterers, large species, such as *D. magna* and *D. pulex* can handle a wide size range of phytoplankton, up to 60 µm (Lampert, 1987). Algae greater than 15 µm may be too large to ingest for small daphnids, such as *D. dubia* (Herrick) (Lampert, 1987), although some small daphnids can ingest certain filaments (Epp, 1996; Repka, 1998). Ingestion ability of daphnids also may be modified by texture (DeMott, 1995). Experiments that use plastic beads as substitutes for different sized algae may underestimate ingestion of some taxa, such as soft algae (i.e. naked and gelatinous flagellates) (DeMott, 1995). Experiments that are designed to overcome these methodological issues are needed to fully assess the limitations of algal size. Most daphnids partially filter small particles including bacteria and picoplankton, although filtering is less efficient than occurs with larger particles (Lampert, 1987; Sterner, 1989). To our knowledge, no studies actually compare the size of algae in the littoral and pelagic zones, but some relevant patterns in composition emerge from the literature.

In combination with grazers, macrophytes may also affect the species and size distribution of phytoplankton. Edible cryptophytes (*Cryptomonas*, *Rhodomonas*) often increase with increasing macrophyte density in the presence of pelagic grazers (Schriver *et al.*, 1995; Van den Berg *et al.*, 1998). At low grazer densities in Lake Stigsholm (Denmark), larger (and therefore likely less edible) algae occurred in the presence versus the absence of macrophytes (Søndergaard & Moss, 1998). With regard to DHM, studies of shallow lakes suggest that increased grazing of daphnids in the littoral zone may increase the proportion of edible algae (Van den Berg *et al.*, 1998), although this has not been tested with specific experiments.

At high grazing, large, slow-growing algae are eliminated because they never reach a size at which they can avoid grazers (Lampert, 1987; Søndergaard & Moss, 1998). The pattern found in shallow lakes is that large-sized algae only dominate at intermediate grazing pressure (Jeppesen *et al.*, 1997a, 1998). Small, fast-growing algae (e.g. flagellates) survive high grazing pressure because they have high growth rates (Schriver *et al.*, 1995), or are mixotrophic (Jeppesen

et al., 1997a; Søndergaard & Moss, 1998). Small, edible algae would benefit *Daphnia* that migrate into littoral zones. In contrast, poor quality food, such as colonial benthic diatoms (i.e. *Tabellaria fenestrata* Lyngbye) and large filamentous algae can also dominate the littoral (Kairesalo, 1980; Ahlgren *et al.*, 1997). In addition, toxic cyanobacteria covered in gelatinous sheaths (Sterner, 1989) could potentially limit daphnid growth and reproduction (de Bernardi & Giussani, 1990), but it is largely unknown whether littoral phytoplankton is more or less favourable for *Daphnia*.

Low C : P ratios (Urabe *et al.*, 1997; Sterner & Schulz, 1998) and high polyunsaturated fatty acid (PUFA) content (DeMott & Müller-Navarra, 1997; Gulati & DeMott, 1997) are other important factors known to influence *Daphnia* population growth positively. Stoichiometric constraints may exist in littoral habitats. In Crooked Lake, Michigan, USA, daphnids fed on littoral seston performed poorly when compared with daphnids fed with pelagic seston (Smiley & Tessier, 1998), but the mechanisms behind these results are unclear. In an enclosure study, *Daphnia* and *Ceriodaphnia* reached their highest abundances when saturated fatty acids were added (Boersma & Stelzer, 2000). In a field study, Ahlgren *et al.* (1997) found similar C : P content (~50 : 1) in pelagic seston (net samples) and benthic sediment (traps) but higher PUFA content in pelagic versus benthic samples. However, at this time, no clear stoichiometric trends or patterns in fatty acid allocation have been found between littoral and pelagic zones.

Light availability (see next section) may also alter the stoichiometry of food for daphnids in shallow lakes. When light energy is high relative to nutrient availability (as might occur in clear, oligo-mesotrophic lakes), the base of the food web is predicted to be rich in carbon and poor in phosphorus (Sterner *et al.*, 1997). Alternatively, when light is less available compared with nutrients (which would most probably be the case in eutrophic, shallow systems), algae are predicted to be relatively rich in phosphorus (Sterner *et al.*, 1997). The light : nutrient ratio in shallow lakes has important implications in ecosystem function, although, more investigation is required to understand its relationship to DHM. In general, more experiments that test performance of daphnids on littoral versus pelagic foods will provide insight into whether food resources are an important consideration for horizontal migration and how these

resources may be influenced by stoichiometry or abiotic factors.

Abiotic factors

Light

Besides predators, macrophytes and food resources, abiotic factors may also influence DHM. Light is often the most plausible proximate cue for DVM because it accounts for the timing of the behaviour (Ringelberg, 1993). In deep lakes, the depth to which light penetrates limits the foraging space of pelagic visual predators (Li *et al.*, 1985), and defines a low light refuge that allows *Daphnia* to coexist with PL fishes. In DVM, vertical gradients of declining light frequently coincide with other gradients of declining temperature and dissolved oxygen, which further inhibit some predators. Because of the ways in which horizontal gradients of light and other variables differ from vertical gradients, their influence on DHM may differ from that on DVM.

Shade under macrophyte beds could potentially provide refuge for daphnids, although enough light may penetrate into dense macrophyte beds to allow adequate foraging by fishes (Moss *et al.*, 1998). In laboratory studies of DVM, low light (4.2×10^{-3} W m⁻² or 1 Lux (lx) approximately) served as a refuge for *Daphnia* against pumpkinseed (*Lepomis gibbosus* Linnaeus) predation (Hartleb & Haney, 1998). Light limitation of visual predators ranges widely between species (Li *et al.*, 1985; O'Brien & Wright, 1985). Lake herring (*Coregonus artedii* Lesueur) foraging is impaired at light supply less than 10-lx (4.2×10^{-2} W m⁻²) (Link & Edsall, 1996), while both roach (*Rutilus rutilus*) and bream (*Abramis brama* Linnaeus) forage with similar effectiveness in total darkness or under high light conditions (125-lx or 5.2×10^{-2} W m⁻²) (Diehl, 1988). Sufficient light (25-lx or 1.05×10^{-1} W m⁻²) exists for perch to forage effectively under dense stands of imitation *Chara tomentosa* Linnaeus (900 stems m⁻²), although perch captured *Daphnia* less efficiently under total darkness (Diehl, 1988) and captured only larger *Daphnia* under low light conditions (2.1 lx) (Mills, Confer & Kretchmer, 1986). Therefore, the capacity of light to provide a refuge for daphnids depends not only on the light, but also on the predator involved.

Because most studies measure only light attenuation or penetration within macrophyte beds, instead of quantifying light absolutely, it is difficult to generalize whether low light conditions under macrophyte beds would provide an effective refuge for daphnids against fishes or predacious invertebrates. A decrease in light is unlikely to protect daphnids against epineustonic predators that rely primarily on movement to detect prey. However, in clear-water shallow lakes, increased light may prompt zooplankton to initiate small-scale vertical migration (Ringelberg, 1993) and seek whatever cover may exist at the sediment–water interface (DeStasio, 1993), either in the open water or under macrophyte beds (Beklioglu & Jeppesen, 1999). In turbid shallow lakes, reduced light may lower predation on *Daphnia*, although fish density in these eutrophic systems is often sufficient to negate any refuge effect, especially in the absence of macrophytes (Jeppesen *et al.*, 1999). Furthermore, because light often penetrates to the sediment surface and probably does not limit visual predators, refuge for daphnids at the sediment–water interface under macrophytes is unlikely to be as effective as that in a dark hypolimnion in a stratified lake.

Temperature

Temperature plays an important role at every scale of zooplankton ecology – from individual physiology to population dynamics (Burns, 1969; Goss & Bunting, 1983; Mourelatos & Lacroix, 1990; Barry, 1997) — and may interact with influences of light. Most daphnids thrive in water between 15 and 25 °C, although some species, such as *D. parvula* (Fordyce) and *D. ambigua* (Scourfield), survive and reproduce well at temperatures as high as 30 °C (Mallin & Partin, 1989). Arctic species, such as *D. middendorffiana* (Fischer) and *D. pulex*, grow and reproduce below 15 °C (Røen, 1962; Peterson, Hobbie & Haney, 1978). Therefore, for any given population of daphnids, differences in temperatures between pelagic and littoral zones more than ambient lake temperatures are likely to impact daphnids undergoing DHM.

Early researchers of vertical migration hypothesized that daphnids increased their fitness by minimizing activity and conserving energy in the colder water of deep lakes (McLaren, 1974; Geller, 1986), but recent authors strongly disagree (Gliwicz, 1986; Lampert, 1993; Loose & Dawidowicz, 1994). In contrast,

the implications of different temperature in different areas of shallow lakes are unknown for daphnids. Temperature within macrophyte stands varies on a diel basis (Carpenter & Lodge, 1986), and surface temperature in plant beds is often higher than beneath the macrophytes (Frodge, Thomas & Pauley, 1990). Cooler water beneath macrophytes may deter fishes from foraging. For example, at temperatures less than 15 °C, pumpkinseed sunfish forage less efficiently than at a higher temperature (Hartleb & Haney, 1998). However, the temperature of this foraging threshold may overlap with the tolerance of many daphnid species. Notwithstanding, the infrequent occurrence of stratification in shallow lakes makes them less likely than deep lakes to experience horizontal patches of low temperature. Water in the shallows of a lake can heat and cool more quickly than that in deep lakes, which results in convection currents between zones (Monismith, Imberger & Morison, 1990; Barko & James, 1998). Although, these convection currents carrying cooler water are rare and occur at night and would not provide refuge from visual, daytime predators. Therefore, we argue that lower temperature is unlikely to influence daphnids undergoing DHM.

It is still necessary, however, to consider potential indirect effects of higher temperature. Few studies document temperature differences between the pelagic and the littoral. However, if the littoral is consistently warmer during the day than the pelagic, indirect metabolic consequences of higher temperature are likely to reduce daphnid fitness. Daphnid fecundity generally declines above 20 °C (Moore, Folt & Stemberger, 1996) and costs associated with respiration, development and feeding also increase with increasing temperature (McMahon & Rigler, 1963; Lampert, 1987). Achenbach & Lampert (1997) found that larger species of daphnids (*D. galeata*) continued to out-compete smaller species (*D. ambigua*) for food at higher temperatures. With respect to daphnids in littoral zones, increased filtering may further reduce resource availability (Barry, 1997) in an already limiting environment. Increased temperature in littoral relative to pelagic zones during the day may also increase the level of predator activity (Moore & Townsend, 1998). For example, recruitment of YOY fishes is enhanced by warmer water and these young fish are efficient predators on zooplankton (Mehner *et al.*, 1998; Romare, Bergman & Hansson, 1999). Yet,

in general, adequate understanding of how temperature influences daphnid migration in shallow lakes requires more studies that compare conditions between the littoral and pelagic zones.

Dissolved oxygen and pH

In addition to light and temperature, changes in pH or dissolved oxygen may also influence DHM. Lower dissolved oxygen (DO) conditions often form underneath macrophyte beds that have a large canopy, because gas exchange is limited between surface water and the atmosphere (Frodge *et al.*, 1990; Andersen & Olsen, 1994; Beklioğlu & Moss, 1995). Higher pH (>9) may occur during the day in the littoral than in the pelagic (Kairesalo, 1980; Frodge *et al.*, 1990), but more evidence is required before generalizations can be made about pH trends.

Low dissolved oxygen or high pH may limit the volume in which fish can forage in shallow lakes, although less evidence exists for these mechanisms than in deep lakes. In Little Mere, UK, areas of high pH (10) served as a refuge for *Daphnia magna* Straus (Beklioğlu & Moss, 1995), as littoral fish, such as young perch, decreased their foraging or suffered mortality. However, a pH exceeding 10.5 negatively impacts growth, reproduction and survival of most *Daphnia* species (Hansen, Christensen & Sortkjaer, 1991; Vijverberg, Kalf & Boersma, 1996; but see Jensen *et al.*, 1992). Cladocerans in Little Mere, such as *Ceriodaphnia*, *B. longirostris*, and *Polyphemus pediculus* (Linnaeus), all declined with increasing pH (Beklioğlu & Moss, 1995). *Daphnia* could potentially hide in macrophytes because they can tolerate low DO, surviving anoxia for 1–3 h by producing haemoglobin (Peters, 1987). However, daphnids require refuge from visual predators during the day, and lower dissolved oxygen usually occurs at night. In addition, while daphnids tolerate low DO conditions for a brief time, continual low values (0.1–3.5 mg O₂ L⁻¹, depending on species and haemoglobin content) are lethal (Peters, 1987). Furthermore, anoxic areas in macrophyte beds are never far from oxygenated water and therefore are unlikely to serve as refuge. Although light, temperature and dissolved oxygen gradients work as refuges in deep lakes, they are probably less effective in shallow lakes. Based on the few studies that exist, we suggest that dissolved oxygen and pH are unlikely to influence DHM

strongly because of the less severe and inconsistent abiotic gradients in shallow lakes.

Conclusions

We argue that DHM should be favoured when macrophyte density is high and littoral-associated piscivores are sufficiently abundant to control planktivores or restrict their habitat to open water. The potential benefits to *Daphnia* of DHM (e.g. reduced mortality from fishes, alternate littoral zone resources, enhanced growth) must outweigh the probable costs (e.g. increased predation from littoral invertebrates, higher metabolism, poor food quality) for DHM to be advantageous (Table 2). As with DVM, predator avoidance seems to be the most probable selective force behind DHM. However, so little is known about littoral versus pelagic resources and conditions that it

is difficult to speculate how the frequency or magnitude of DHM may be influenced by these factors. Furthermore, if the selective advantage behind DHM is avoidance of visual predators, logic dictates that light and temperature could influence the initiation, amplitude and duration of DHM as is true for DVM. Direct tests of daphnid performance in littoral versus pelagic zone are needed to discover the roles that resource availability and abiotic factors play in DHM. The present management challenge is to learn how to manipulate multiple factors to enhance *Daphnia* populations that can maintain shallow lakes in the desired clear water state.

Current management practices aimed at increasing water clarity in shallow lakes often include stocking of piscivores (Berg *et al.*, 1997; Horppila *et al.*, 1998; Hansson *et al.*, 1998), mass removal of planktivores (Jeppesen *et al.*, 1990a,b; Van Donk *et al.*, 1990; Meijer

Table 2. Summary of factors likely to favour or discourage diel horizontal migration (DHM) of *Daphnia* into macrophytes

	Favors DHM into macrophytes	Unknown factors	Discourages DHM into macrophytes
Predators			
Fishes	Littoral piscivores keep pelagic planktivores out of macrophytes		Pelagic piscivores force planktivores into vegetation Excessive fishes nullify macrophyte refuge
Pelagic Invertebrates	Alternative food for planktivorous fishes	Variation possible, see Table 1	
Littoral Invertebrates	Alternative food for fishes	Relative magnitude of littoral versus pelagic predation	Predation from littoral predators
Macrophytes	Refuge from predation by fishes	Influences on phytoplankton (which is food for <i>Daphnia</i>)	Reduced daphnid growth Altered life history traits Potential mortality
Food resources			
Quantity	Alternative resources available in littoral zone (e.g. periphyton)	Whether daphnids can feed effectively on alternative resources	Less phytoplankton in littoral than pelagic
Quality		How quality differs between lake zones	
Abiotic factors			
Light	Shading under plants could provide refuge		
Temperature		Temperatures in littoral in relation to pelagic	If littoral temperature greater than pelagic, indirect metabolic costs likely
Dissolved oxygen		Tolerances of <i>Daphnia</i> to changes in dissolved oxygen relative to that of predators	
pH	pH 9–10 discourages foraging by some fishes		pH > 10.5 reduces daphnid growth & reproduction

et al., 1999), and protection of macrophytes from herbivory (Lauridsen, Jeppesen & Andersen, 1993, Lauridsen, Jeppesen & Søndergaard 1994; Lodge *et al.*, 1998b). Unfortunately, many biomanipulation efforts fail to promote daphnid populations (Theiss, Zielinski & Lang, 1990; Perrow *et al.*, 1997, 1999). One reason may be that the role of DHM as a response to biomanipulation, and the factors controlling DHM, are not well understood (Hansson *et al.*, 1998; Jeppesen *et al.*, 1998; Lauridsen *et al.*, 1998). Reducing PL fishes is often the first step to increasing refuge availability for daphnids. However, follow-up efforts that include increasing the area of the lake colonized by macrophytes may be essential to facilitating DHM, thereby preserving daphnid populations (Lauridsen *et al.*, 1996; Jeppesen *et al.*, 1998). We briefly highlight eight areas important for building a knowledge-base about DHM. This list is not comprehensive, but includes topics most applicable to management. Some of these research efforts are underway, while others have been completely neglected.

1. Studies that rigorously document DHM in shallow lakes that differ in nutrient loading, water clarity and the magnitude of zooplanktivory (especially including tropical and subtropical systems that are currently understudied).
2. Studies that investigate methodically the temporal and spatial scales of DHM in contrast to DVM, paying particular attention to improving upon current sampling methods.
3. Experiments that quantify the refuge potential of different macrophyte species (and stand density), and test how the effectiveness of that refuge depends on the relative proportion of PI versus PL fishes.
4. Increased research efforts that focus on the role played by invertebrate predation (littoral and pelagic) in DHM, taking into consideration possible interaction with fishes.
5. Experiments that test the impact of different macrophyte exudates on daphnid survival, growth, reproduction and life history traits.
6. Experiments that test how the growth and survival of cladocerans differ when fed with littoral versus pelagic resources (paying particularly to both food quantity and quality).
7. Surveys that document diel and seasonal differences in temperature between littoral and pelagic zones, followed by experiments that examine how

daphnids respond behaviourally to these differences.

8. Construction of daphnid population models that depict how the components of the littoral zone environment (e.g. structure, macrophyte chemicals and food availability) influence the costs and benefits for *Daphnia* populations performing DHM.

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References

- Achenbach L. & Lampert W. (1997) Effects of elevated temperatures on threshold food concentrations and possible competitive abilities of different sized cladoceran species. *Oikos*, **79**, 469-476.
- Ahlgren G., Goedkoop W., Markensten H., Sonesten L. & Boberg M. (1997) Seasonal variations in food quality for pelagic and benthic invertebrates in Lake Erken - the role of fatty acids. *Freshwater Biology*, **38**, 555-570.
- Andersen F.O. & Olsen K.R. (1994) Nutrient cycling in shallow, oligotrophic Lake Kvie, Denmark. II. Effects of isoetids on the exchange of phosphorus between sediment and water. *Hydrobiologia*, **275/276**, 267-276.

- Arner M., Koivisto S., Norberg J. & Kautsky N. (1998) Trophic interactions in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. *Freshwater Biology*, **39**, 79–90.
- Arts M.T., Maly E.J. & Pasitschniak M. (1981) The influence of *Acilius* (Dytiscidae) redation on *Daphnia* in a small pond. *Limnology and Oceanography*, **36**, 1172–1175.
- Barica J. & Mathias J.A. (1979) Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. *Journal of the Fisheries Research Board of Canada*, **36**, 980–986.
- Barko J.W. & James W.F. (1998) Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K.Christoffersen), pp. 197–216. Springer Verlag, New York.
- Barry M.J. (1997) Effects of food limitation, notonectid predation, and temperature on the population dynamics of *Daphnia carinata*. *Internationale Revue der Gesamten Hydrobiologie*, **82**, 545–562.
- Bean C.W. & Winfield I.J. (1995) Habitat use and activity patterns of roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus* (L.)), perch (*Perca fluviatilis*) and pike (*Esox lucius*) in the laboratory: the role of predation threat and structural complexity. *Ecology of Freshwater Fish*, **4**, 37–46.
- Begon M., Harper J.L. & Townsend C.R. (1990) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, London.
- Beisner B.E., McCauley E. & Wrona F.J. (1996) Temperature-mediated dynamics of planktonic food chains: the effect of an invertebrate carnivore. *Freshwater Biology*, **35**, 219–232.
- Beklioglu M. (1999) A review on the control of eutrophication in deep and shallow lakes. *Turkish Journal of Zoology*, **23**, 327–336.
- Beklioglu M. & Jeppesen E. (1999) Behavioural response of plant-association *Eurycercus lamellatus* (Ö.F. Müller) to different food sources and fish cues. *Aquatic Ecology*, **33**, 167–173.
- Beklioglu M. & Moss B. (1995) The impact of pH on interactions among phytoplankton algae, zooplankton and perch (*Perca fluviatilis*) in a shallow, fertile lake. *Freshwater Biology*, **33**, 497–509.
- Berg S., Jeppesen E. & Søndergaard M. (1997) Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng (Denmark). *Hydrobiologia*, **342/343**, 311–318.
- de Bernardi R. & Peters R.H. (1987) Why *Daphnia*? In: *Daphnia* (Eds R.H. Peters & R. de Bernardi), pp. 1–9. Memorie Dell'istituto Italiano Di Idrobiologia, Pallanza, Italy.
- de Bernardi R. & Giussani G. (1990) Are blue-green algae a suitable food for zooplankton? An overview. *Hydrobiologia*, **200/201**, 29–41.
- Bertolo A., Lacroix G., Lescher-Moutoué F. & Sala S. (1999) Effects of physical refuges on fish–plankton interactions. *Freshwater Biology*, **41**, 795–808.
- Black R.A. (1993) Predator-induced phenotypic plasticity in *Daphnia pulex*: life history and morphological responses to *Notonecta* and *Chaoborus*. *Limnology and Oceanography*, **38**, 986–996.
- Blindow I., Hargeby A., Wagner B.M.A. & Andersson G. (2000) How important is the crustacean plankton for the maintenance of water clarity in shallow lakes with abundant submerged vegetation? *Freshwater Biology*, **44**, 185–197.
- Blois-Heulin C., Crowley P.H., Arrington M. & Johnson D.M. (1990) Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. *Oecologia*, **84**, 295–306.
- Blumenshine S.C., Vadeboncoeur Y., Lodge D.M., Cottingham K.L. & Knight S. (1997) Benthic–pelagic links: responses of benthos to water-column nutrient enrichment. *Journal of the North American Benthological Society*, **16**, 466–479.
- Boersma M. & Stelzer C.-P. (2000) Response of a zooplankton community to the addition of unsaturated fatty acids: an enclosure study. *Freshwater Biology*, **45**, 179–188.
- Bollens S.M. & Frost B.W. (1989) A predator-induced diel vertical migration in a planktonic copepod. *Journal of Plankton Research*, **11**, 1047–1065.
- Brooks J.L. & Dodson S.I. (1965) Predation, body size and composition of plankton. *Science*, **150**, 28–35.
- Brown K.M. & Lodge D.M. (1993) Gastropod abundance in vegetated habitats: the importance of specifying null models. *Limnology and Oceanography*, **38**, 217–225.
- Brown L.R., Flavin C., French H *et al.* (2000) *State of the World 2000*. The Worldwatch Foundation, New York.
- Burks R.L., Jeppesen E. & Lodge D.M. (2000) Chemicals from macrophytes and fishes suppress *Daphnia* growth and alter life history traits. *Oikos*, **88**, 139–147.
- Burks R.L., Jeppesen E. & Lodge D.M. (2001a) Pelagic prey and benthic predators: the impact of odonates on *Daphnia*. *Journal of the North American Benthological Society*, **20**, 615–628.
- Burks R.L., Jeppesen E. & Lodge D.M. (2001b) Littoral zone structures as refugia for *Daphnia* against fish predation. *Limnology and Oceanography*, **46**, 230–237.
- Burns C.W. (1969) Relation between filtering rate, temperature, and body size in four species of *Daphnia*. *Limnology and Oceanography*, **14**, 693–700.

- Burns C.W. & Dodds A. (1999) Food limitation, predation and allelopathy in a population of *Daphnia carinata*. *Hydrobiologia*, **400**, 41–53.
- Caceres C.E. & Hairston N.G. Jr (1998) Benthic-pelagic coupling in planktonic Crustaceans: the role of the benthos. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **52**, 163–174.
- Canfield D.E. Jr, Shireman J.V., Colle D.E., Haller W.T., Watkins C.E. II & Maceina M.J. (1984) Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 497–501.
- Carpenter S.R. (1988) *Complex Interactions in Lake Communities*. Springer-Verlag, New York.
- Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading trophic interactions and lake productivity. *Bioscience*, **35**, 635–639.
- Carpenter S.R. & Lodge D.M. (1986) Effects of submerged macrophytes on ecosystem processes. *Aquatic Botany*, **26**, 341–370.
- Cattaneo A., Galanti G., Gentinetta S. & Romo S. (1998) Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. *Freshwater Biology*, **38**, 725–740.
- Chick J.H. & McIvor C.C. (1997) Habitat selection by three littoral zone fishes: effects of predation pressure, plant density and macrophyte type. *Ecology of Freshwater Fish*, **6**, 27–35.
- Christensen B. & Persson L. (1993) Species specific antipredator behaviours: effects on prey choice in different habitats. *Behavioural Ecology and Sociobiology*, **32**, 1–9.
- Cuddington K.M. & McCauley E. (1994) Food-dependent aggregation and mobility of the water fleas *Ceriodaphnia dubia* and *Daphnia pulex*. *Canadian Journal of Zoology*, **72**, 1217–1226.
- Dagg M.J. (1985) The effects of food limitation on diel migratory behavior in marine zooplankton. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **21**, 247–255.
- Davids C., Ten Winkel E.H. & De Groot C.J. (1994) Temporal and spatial patterns of water mites in Lake Maarsseveen I. *Netherlands Journal of Aquatic Ecology*, **28**, 11–17.
- Davies J. (1985) Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. *Hydrobiologia*, **120**, 103–105.
- DeMeester L., Maas S., Dierckens K. & Dumont H.J. (1993) Habitat selection and patchiness in *Scapholeberis*: horizontal distribution and migration of *S.mucronata* in a small pond. *Journal of Plankton Research*, **15**, 1129–1139.
- DeMott W.R. (1995) The influence of prey hardness on *Daphnia's* selectivity for large prey. *Hydrobiologia*, **307**, 127–138.
- DeMott W.R. & Kerfoot W.C. (1982) Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. *Ecology*, **63**, 1949–66.
- DeMott W.R. & Müller-Navarra D.C. (1997) The importance of highly unsaturated fatty acids in zooplankton nutrition: evidence from experiments with *Daphnia*, a cyanobacterium and lipid emulsions. *Freshwater Biology*, **38**, 649–664.
- Deneke R. & Nixdorf B. (1999) On the occurrence of clear-water phases in relation to shallowness and trophic state: a comparative study. *Hydrobiologia*, **408/409**, 251–262.
- DeStasio B.T. Jr (1993) Diel vertical and horizontal migration by zooplankton: population budgets and the diurnal deficit. *Bulletin of Marine Science*, **53**, 44–64.
- Diehl S. (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos*, **53**, 207–214.
- Diehl S. & Kornijów R. (1998) Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 24–26. Springer Verlag, New York.
- Dorgelo J. & Heykoop M. (1985) Avoidance of macrophytes by *Daphnia longispina*. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 3369–3372.
- Eklöv P. (1992) Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Animal Behaviour*, **44**, 313–326.
- Eklöv P. & Diehl S. (1994) Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia*, **98**, 344–353.
- von Elert E. & Pohnert G. (2000) Predator specificity of kairomones in diel vertical migration of *Daphnia*: a chemical approach. *Oikos*, **88**, 119–128.
- Elliott J.K., Elliott J.M. & Leggett W.C. (1997) Predation by *Hydra* on larval fish: field and laboratory experiments with bluegill (*Lepomis macrochirus*). *Limnology and Oceanography*, **42**, 1416–1423.
- Elser J.J. & Goldman C.R. (1990) Zooplankton effects on phytoplankton in lakes of contrasting trophic status. *Limnology and Oceanography*, **36**, 64–90.
- Elser J.J., Sterner R.W., Galford A.E., Chrzanowski T.H., Findlay D.L., Mills K.H., Paterson M.J., Stainton M.P. & Schindler D.W. (2000) Pelagic C : N : P stoichiometry in a eutrophied lake: responses to a whole-lake food-web Manipulation. *Ecosystems*, **3**, 293–307.
- Engelmayer A. (1995) Effects of predator-released chemicals on some life history parameters of *Daphnia pulex*. *Hydrobiologia*, **307**, 203–206.

- Engels S. (1988) The role and interactions of submersed macrophytes in a shallow Wisconsin lake. *Journal of Freshwater Ecology*, **4**, 329–240.
- Epp G.T. (1996) Grazing on filamentous cyanobacteria by *Daphnia pulicaria*. *Limnology and Oceanography*, **41**, 560–567.
- Flik B.J.G. & Ringelberg J. (1993) Influence of food availability on the initiation of diel vertical migration (DVM) in Lake Maarsseveen. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **39**, 57–65.
- Frank P.W. (1952) A laboratory study of intraspecies and interspecies competition in *Daphnia pulicaria* (Forbes) and *Simocephalus vetulus* (Ö. F. Müller). *Physiological Zoology*, **25**, 178–204.
- Frodge J.D., Thomas G.L. & Pauley G.B. (1990) Effects of canopy formation on floating and submerged aquatic macrophytes on the water quality of two shallow Pacific NW lakes. *Aquatic Botany*, **38**, 231–248.
- Gannes L.Z., O'Brien D.M. & Del Rio C.M. (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology*, **78**, 1271–1276.
- Geller W. (1986) Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): a starvation avoidance mechanism? *Archiv für Hydrobiologie*, **74** (Suppl.), 1–60.
- Gliwicz M.Z. (1986) Predation and the evolution of vertical migration in zooplankton. *Nature*, **320**, 746–748.
- Gliwicz M.Z. & Lampert W. (1990) Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology*, **71**, 691–702.
- Gonzalez M.J. & Tessier A.J. (1997) Habitat segregation and interactive effects of multiple predators on a prey assemblage. *Freshwater Biology*, **38**, 179–191.
- van Gool E. & Ringelberg J. (1995) Swimming of *Daphnia galeata x hyalina* in response to changing light intensities: influence of food availability and predator kairomone. *Marine and Freshwater Behavior and Physiology*, **26**, 259–265.
- van Gool E. & Ringelberg J. (1998) Quantitative effects of fish kairomones and successive light stimuli on downward swimming responses of *Daphnia*. *Aquatic Ecology*, **39**, 291–296.
- Goss L.B. & Bunting D.L. (1983) *Daphnia* development and reproduction: responses to temperature. *Journal of Thermal Biology*, **8**, 375–380.
- Grimm M.P. & Backx J. (1990) The restoration of shallow eutrophic lakes and the role of northern pike, aquatic vegetation and nutrient concentration. *Hydrobiologia*, **201**, 557–566.
- Gross E.M. & Sütfield R. (1994) Polyphenols with algicidal activity in the submerged macrophyte *Myriophyllum spicatum* L. *Acta Horticulturae*, **381**, 710–716.
- Gross E.M., Meyer H. & Schilling G. (1996) Release and ecological impact of algicidal hydrolysable polyphenols in *Myriophyllum spicatum*. *Phytochemistry*, **41**, 133–138.
- Gulati R. & DeMott W.R. (1997) The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. *Freshwater Biology*, **38**, 753–768.
- Haney J.F. (1993) Environmental control of diel vertical migration behaviour. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **39**, 1–17.
- Hansen A.-M., Christensen J.V. & Sortkjaer O. (1991) Effect of high pH on zooplankton and nutrients in fish-free enclosures. *Archiv für Hydrobiologie*, **123**, 143–164.
- Hansson L.-A., Annadotter H., Bergman E., Hamrin-Stellan F., Jeppesen E., Kairesalo T., Luokkanen E., Nilsson P.-A., Søndergaard M. & Strand J. (1998) Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems*, **1**, 558–574.
- Hansson L.-A. & Tranvik L.J. (1996) Quantification of invertebrate predation and herbivory in food chains of low complexity. *Oecologia*, **108**, 542–551.
- Hartleb C.F. & Haney J.F. (1998) Use of a thermal and light refugium by *Daphnia* and its effects on foraging pumpkinseeds. *Environmental Biology of Fishes*, **51**, 339–349.
- Hasler A.D. & Jones E. (1949) Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. *Ecology*, **30**, 359–364.
- Herwig B.R. & Schindler D.E. (1996) Effects of aquatic insect predators on zooplankton in fishless ponds. *Hydrobiologia*, **324**, 141–147.
- Herzig A. (1995) *Leptodora kindtii*: efficient predator and preferred prey item in Neusiedler See, Austria. *Hydrobiologia*, **307**, 273–282.
- Hirvonen H. (1999) Shifts in foraging tactics of larval damselflies: effects of prey density. *Oikos*, **86**, 443–452.
- Horppila J., Peltonen H., Malinen T., Luokkanen E. & Kairesalo T. (1998) Top-down or bottom-up effects by fish: issues of concern in biomanipulation of lakes. *Restoration Ecology*, **6**, 20–28.
- Horton P.A., Rowan M., Webster K.E. & Peters R.H. (1979) Browsing and grazing by cladoceran filter feeders. *Canadian Journal of Zoology*, **57**, 206–212.
- Hülsmann S. & Lampert W. (1999) Adult, not juvenile mortality as a major reason for the midsummer decline of a *Daphnia* population. *Journal of Plankton Research*, **22**, 151–168.
- Hutchinson G.E. (1967) *Introduction to Lake Biology and the Limnoplankton*, Vol. 2. *A Treatise of Limnology*. John Wiley & Sons, New York, p. 1115.

- Irvine K., Moss B. & Stansfield J. (1990) The potential of artificial refugia for maintaining a community of large-bodied cladocera against fish predation in a shallow, eutrophic lake. *Hydrobiologia*, **200/201**, 379–389.
- Jacobsen L. & Perrow M.R. (1998) Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. *Ecology of Freshwater Fish*, **7**, 78–86.
- Jacobsen L., Perrow M.R., Landkildehus F., Hjerne M., Lauridsen T.L. & Berg S. (1997) Interactions between piscivores, zooplanktivores and zooplankton in submerged macrophytes: preliminary observations from enclosure and pond experiments. *Hydrobiologia*, **342/343**, 197–205.
- Jasser I. (1995) The influence of macrophytes on a phytoplankton community in experimental conditions. *Hydrobiologia*, **306**, 21–32.
- Jensen K.H., Jakobsen P.J. & Kleiven O.T. (1998) Fish kairomone regulation of internal swarm structure in *Daphnia pulex* (Cladocera: Crustaceae). *Hydrobiologia*, **368**, 123–127.
- Jensen H.S., Kristensen P., Jeppesen E. & Skytthe A. (1992) Iron: phosphorus ratio in surface sediment as an indicator of phosphate release from aerobic sediments in shallow lakes. *Hydrobiologia*, **235/236**, 731–743.
- Jeppesen E. (1998) *The Ecology of Shallow Lakes – Trophic Interactions in the Pelagial*. D. Sc. Dissertation. NERI Report no. 247, Ministry of Environment and Energy, National Environmental Research Institute, Silkeborg, Denmark.
- Jeppesen E., Søndergaard M., Mortensen E. *et al* (1990a) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case studies. *Hydrobiologia*, **200/201**, 205–218.
- Jeppesen E., Jensen J.P., Kristensen P., Søndergaard M., Mortensen E., Sortkjær O. & Olrik K. (1990b) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia*, **200/201**, 219–227.
- Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T., Pedersen L.J. & Jensen L. (1997a) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, **342/343**, 151–164.
- Jeppesen E., Lauridsen T., Mitchell S.F. & Burns C. (1997b) Do planktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand Journal of Marine and Freshwater Research*, **31**, 163–173.
- Jeppesen E., Lauridsen T.L., Kairesalo T. & Perrow M.R. (1998) Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffer- sen), pp. 91–114. Springer Verlag, New York.
- Jeppesen E., Søndergaard M., Kronvang B., Jensen J.P., Svendsen L.M. & Lauridsen T. (1999) Lake and catchment management in Denmark. In: *Ecological Basis for Lake and Reservoir Management* (Eds D. Harper, A. Ferguson, B. Brierley & G. Phillips), *Hydrobiologia*, **395/396**, 419–432.
- Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T. & Landkildehus F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a nutrient gradient. *Freshwater Biology*, **45**, 201–219.
- Johnsen G.H. & Jakobsen P.J. (1987) The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnology and Oceanography*, **32**, 873–880.
- Johnson D.M., Pierce C.L., Martin T.H., Watson C.N., Bohanan R.E. & Crowley P.H. (1987) Prey depletion by odonate larvae: combining evidence from multiple field experiments. *Ecology*, **68**, 1459–1465.
- Kairesalo T. (1980) Diurnal fluctuations within a littoral plankton community in oligotrophic Lake Pääjärvi, southern Finland. *Freshwater Biology*, **10**, 533–537.
- Kats L.B. & Dill L.M. (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.
- Kitchell J.F., Johnson M.G., Minss C.K., Loftus K.H., Greig L. & Olver C.H. (1977) Percid habitat: the river analogy. *Journal of the Fisheries Research Board of Canada*, **34**, 1959–1963.
- Kleiven O.T., Larsson P. & Hobæk A. (1996) Direct distributional response in *Daphnia pulex* to a predator kairomone. *Journal of Plankton Research*, **18**, 1341–1348.
- Kolar C.S. & Lodge D.M. (2000) Freshwater nonindigenous species: interactions with other global changes. In: *Invasive Species in a Changing World* (Eds H.A. Mooney & R.J. Hobbs), pp. 3–30. Island Press, Washington DC.
- Kornijów R. & Kairesalo T. (1994) *Elodea canadensis* sustains rich environment for macroinvertebrates. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **25**, 2270–2275.
- Kvam O.V. & Kleiven O.T. (1995) Diel horizontal migration and swarm formation in *Daphnia*. response to *Chaoborus*. *Hydrobiologia*, **307**, 177–184.
- Lampert W. (1987) Feeding and nutrition in *Daphnia*. In: *Daphnia* (Eds R.H. Peters & R. de Bernardi), pp. 143–192. Memorie Dell'istituto Italiano Di Idrobiologia, Pallanza, Italy.
- Lampert W. (1993) Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **39**, 79–88.

- Larsson P. & Dodson S.I. (1993) Invited review: chemical communication in planktonic animals. *Archiv für Hydrobiologie*, **129**, 129–155.
- Lauridsen T.L. & Buenk I. (1996) Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Archiv für Hydrobiologie*, **137**, 167–176.
- Lauridsen T.L., Jeppesen E. & Andersen F.O. (1993) Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: impact of sediment composition and waterfowl grazing. *Aquatic Botany*, **46**, 1–15.
- Lauridsen T.L., Jeppesen E. & Søndergaard M. (1994) Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish manipulation. *Hydrobiologia*, **275/276**, 233–242.
- Lauridsen T.L. & Lodge D.M. (1996) Avoidance by *Daphnia magna* of fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. *Limnology and Oceanography*, **41**, 794–798.
- Lauridsen T., Pedersen L.J., Jeppesen E. & Søndergaard M. (1996) The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *Journal of Plankton Research*, **18**, 2283–2294.
- Lauridsen T.L., Jeppesen E., Søndergaard M. & Lodge D. (1998) Horizontal migration of zooplankton: predator-mediated use of macrophyte habitat. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 233–239. Springer Verlag, New York.
- Lauridsen T.L., Jeppesen E., Mitchell S.F., Lodge D.M. & Burks R.L. (1999) Horizontal distribution of zooplankton in lakes with contrasting fish densities and nutrient levels. *Hydrobiologia*, **408/409**, 241–250.
- Leucke C. & Litt A.H. (1987) Effects of predation by *Chaoborus flavicans* on crustacean zooplankton of Lake Lenore, Washington. *Freshwater Biology*, **18**, 185–192.
- Li K.T., Wetterer J.K. & Hairston N.G. Jr (1985) Fish size, visual resolution, and prey selectivity. *Ecology*, **66**, 1729–1735.
- Linden A.L. & Cech J.J. Jr (1990) Prey selection by mosquitofish (*Gambusia affinis*) in California rice fields: effects of vegetation and prey species. *Journal of the American Mosquito Control Association*, **6**, 115–120.
- Link J. & Edsall T.A. (1996) The effect of light on Lake Herring (*Coregonus artedii*) reactive volume. *Hydrobiologia*, **332**, 131–140.
- Lodge D.M., Blumenshine S.C. & Vadeboncoeur Y. (1998a) Insights and application of large-scale, long-term ecological observations and experiments. In: *The State of Experimental Ecology: Questions, Levels, and Approaches* (Eds W.J. Resetarits & J. Bernardo), pp. 202–235. Oxford University Press, Oxford.
- Lodge D.M., Cronin G., Van Donk E. & Froelich A.J. (1998b) Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 149–174. Springer Verlag, New York.
- Lombardo P. (1997) Predation by *Enallagma* nymphs (Odonata, Zygoptera) under different conditions of spatial heterogeneity. *Hydrobiologia*, **356**, 1–9.
- Loose C.J. & Dawidowicz P. (1994) Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*, **75**, 2255–2263.
- Lüning J. (1992) Phenotypic plasticity of *Daphnia pulex* in the presence of invertebrate predators: morphological and life history responses. *Oecologia*, **92**, 383–390.
- Lysebo E.M. (1995) Behavioural and morphological changes in polymorphic *Daphnia* related to different predation regimes. *Hydrobiologia*, **307**, 185–191.
- Machàček J. (1991) Indirect effect of planktivorous fish on the growth and reproduction of *Daphnia galeata*. *Hydrobiologia*, **225**, 193–197.
- Mallin M.A. & Partin W.E. (1989) Thermal tolerances of common Cladocera. *Journal of Freshwater Ecology*, **5**, 45–51.
- Marklund O. (2000) A new sampler for collecting invertebrates in submerged vegetation. *Hydrobiologia*, **432**, 229–231.
- Matveev V.F., Martinez C.C. & Frutos S.M. (1989) Predatory-prey relationships in subtropical zooplankton: water mite against cladocerans in an Argentine lake. *Oecologia*, **79**, 489–495.
- McLaren I.A. (1974) Demographic strategy of vertical migration by a marine copepod. *American Naturalist*, **108**, 91–102.
- McMahon J.W. & Rigler F.H. (1963) Mechanisms regulating the feeding rate of *Daphnia magna* Straus. *Canadian Journal of Zoology*, **41**, 321–332.
- Mehner T., Hülsmann S., Worischka S., Plewa M. & Benndorf J. (1998) Is the midsummer decline of *Daphnia* really induced by age-0 fish predation? Comparison of fish consumption and *Daphnia* mortality and life history parameters in a biomanipulated reservoir. *Journal of Plankton Research*, **20**, 1797–1811.
- Meijer M. -L., de Boois I., Scheffer M., Portielje R. & Houser H. (1999) Biomanipulation in shallow lakes in the Netherlands: an evaluation of 18 case studies. *Hydrobiologia*, **408/409**, 13–30.

- Mills E.L., Confer J.L. & Kretchmer D.W. (1986) Zooplankton selection by young yellow perch: the influence of light, prey density, and predator size. *Transactions of the American Fisheries Society*, **115**, 716–725.
- Monismith S.G., Imberger J. & Morison M.L. (1990) Convective motions in the sidearm of a small reservoir. *Limnology and Oceanography*, **35**, 1676–1702.
- Moore M., Folt C.L. & Stemberger R.S. (1996) Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Archiv für Hydrobiologie*, **135**, 289–319.
- Moore M.K. & Townsend V.R. Jr (1998) The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. *Oikos*, **81**, 329–336.
- Moss B., McGowan S. & Carvalho L. (1994) Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. *Limnology and Oceanography*, **39**, 1020–1029.
- Moss B., Stansfield J., Irvine K., Perrow M. & Phillips G. (1996) Progressive restoration of a shallow lake: a 12-year experiment in isolation, sediment removal and biomanipulation. *Journal of Applied Ecology*, **33**, 71–86.
- Moss B. (1998) Shallow lakes biomanipulation and eutrophication. *Scientific Committee on Phosphates in Europe Newsletter*, **29**, 45.
- Moss B., Kornijów R. & Measey G.J. (1998) The effects of nymphaeid (*Nuphar lutea*) density and predation by perch (*Perca fluviatilis*) on the zooplankton communities in a shallow lake. *Freshwater Biology*, **39**, 689–697.
- Mourelatos S. & Lacroix G. (1990) In situ filtering rates of Cladocera: effect of body length, temperature, and food concentration. *Limnology and Oceanography*, **35**, 1101–1111.
- Mumm H. (1997) Effects of competitors and Chaoborus predation on the cladocerans of a eutrophic lake: an enclosure study. *Hydrobiologia*, **360**, 253–264.
- Murdoch W.W., Scott M.A. & Ebsworth P. (1984) Effects of the general predator, *Notonecta* (Hemiptera) upon a freshwater community. *Journal of Animal Ecology*, **53**, 791–808.
- Nagata T. & Okamoto K. (1988) Filtering rates on natural bacteria by *Daphnia longispina* and *Eodiaptomus japonicus* Lake Biwa. *Journal of Plankton Research*, **10**, 835–850.
- Naiman R.J., Magnuson J.J., McKnight D.M. & Stanford J.A. (1995) *The Freshwater Imperative*. Island Press, Washington DC.
- Neary J., Cash K. & McCauley E. (1994) Behavioural aggregation of *Daphnia pulex* in response to food gradients. *Functional Ecology*, **8**, 377–383.
- Nesbitt L.M., Riessen H.P. & Ramcharan C.W. (1996) Opposing predation pressures and induced vertical migration responses in *Daphnia*. *Limnology and Oceanography*, **41**, 1306–1311.
- O'Brien W.J. (1979) The predator-prey interaction of planktivorous fish and zooplankton. *American Scientist*, **67**, 572–581.
- O'Brien W.J. & Vinyard G.L. (1978) Polymorphism and predation: the effect of invertebrate predation on the distribution of two varieties of *Daphnia carinata* in South India ponds. *Limnology and Oceanography*, **23**, 452–460.
- O'Brien W.J. & Wright D.I. (1985) Potential limits on the daytime planktivorous feeding depth of the white crappie. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 2527–2533.
- Ojala A., Kankaala P., Kairesalo T. & Salonene K. (1995) Growth of *Daphnia longispina* L. in a polyhumic lake under various availabilities of algal, bacterial and detrital food. *Hydrobiologia*, **315**, 119–134.
- Omori M. & Hamner W.M. (1982) Patchy distributions of zooplankton: behavior, population assessment and sampling problems. *Marine Biology*, **72**, 193–200.
- Orcutt J.D. & Porter K.G. (1983) Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnology and Oceanography*, **28**, 720–730.
- Pace M.L., Cole J.J., Carpenter S.R. & Kitchell J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Paterson M.J. (1994) Invertebrate predation and the seasonal dynamics of microcrustacea in the littoral zone of a fishless lake. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **1/2**, 1–36.
- Pennak R.W. (1973) Some evidence for aquatic macrophytes as repellents for a limnetic species of *Daphnia*. *Internationale Revue der Gesamten Hydrobiologie*, **60**, 569–576.
- Perrow M.R., Jowitt A.J.D., Stansfield J.H. & Tench L.D. (1999) The practical importance of the interactions between fish, zooplankton and macrophytes in shallow lake restoration. *Hydrobiologia*, **395/396**, 199–210.
- Perrow M.R., Meijer M.-L., Dawidowicz P. & Coops H. (1997) Biomanipulation in shallow lakes: state of the art. *Hydrobiologia*, **342/343**, 355–365.
- Persson L. (1991) Behavioral response to predators reverses the outcome of competition between prey species. *Behavioral Ecology and Sociobiology*, **28**, 101–105.
- Persson L. (1993) Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos*, **68**, 12–22.
- Persson L., Anderson G., Hamrin S.F. & Johansson L. (1988) Predation regulation and primary production along the productivity gradient of temperate lake

- ecosystems. In: *Complex Interactions in Lake Communities* (Ed. S.R. Carpenter), pp. 45–65. Springer Verlag, New York.
- Persson L. & Crowder L.B. (1998) Fish–habitat interactions mediated via ontogenetic niche shifts. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 3–23. Springer Verlag, New York.
- Peters R.H. (1987) Metabolism in *Daphnia*. In: *Daphnia* (Eds R.H. Peters & R. de Bernardi), pp. 1–9. Memorie Dell'istituto Italiano Di Idrobiologia, Pallanza, Italy.
- Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.
- Peterson B.J., Hobbie J.E. & Haney J.F. (1978) *Daphnia* grazing on natural bacteria. *Limnology and Oceanography*, **23**, 1039–1044.
- Phillips G.L., Emlinon D.F. & Moss B. (1978) A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany*, **4**, 103–126.
- Phillips G.L., Perrow M.R. & Stansfield J.H. (1996) Manipulation of the fish–zooplankton interaction in shallow lakes: a tool for restoration. In: *Aquatic Predators and Their Prey* (Eds S.P.R. Greenstreet & M.L. Tasker), pp. 174–183. Blackwell Scientific Publications, Oxford, England.
- Porter K.G. & Orcutt J.D. (1980) Nutritional adequacy, manageability, and toxicity as factors that determine food quality of green and blue-green algae for *Daphnia*. *American Society of Limnology and Oceanography Special Symposium*, **3**, 268–281.
- Ranta E. & Espo J. (1989) Predation by the rock-pool insects *Arctocoris carinata*, *Callicorixa producta* (Heteroptera, Corixidae) and *Potamonectes griseostriatus* (Coleoptera, Dytiscidae). *Annales Zoologici Fennici*, **26**, 53–60.
- Repka S. (1998) Effects of food type on the life history of *Daphnia* clones from lakes differing in trophic state. I. *Daphnia galeata* feeding on *Scenedesmus* and *Oscillatoria*. *Freshwater Biology*, **38**, 675–683.
- Repka S., Ketola M. & Walls M. (1994) Specificity of predator-induced neck spine and alteration in life history traits in *Daphnia pulex*. *Hydrobiologia*, **294**, 129–140.
- Riemann B. & Bosselmann S. (1984) *Daphnia* grazing on natural populations of bacteria. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 795–799.
- Riessen H.P. (1994) Morphological response of *Daphnia* to *Chaoborus* predation. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **25**, 2382–2386.
- Riessen H.P. (1999) Predator-induced life history shifts in *Daphnia*: a synthesis of studies using meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2487–2494.
- Ringelberg J. (1993) Phototaxis as a behavioural component of diel vertical migration in a pelagic *Daphnia*. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **39**, 45–55.
- Røen U.I. (1962) Studies on freshwater Entomostraca in Greenland. II. Localities, ecology, and geographical distribution of the species. *Medd Om Greenland*, **170**, 249.
- Romare P., Bergman E. & Hansson L.-A. (1999) The impact of larval and juvenile fish on zooplankton and algal dynamics. *Limnology and Oceanography*, **44**, 1655–1666.
- Sakwińska O. (1998) Plasticity of *Daphnia magna* life history traits in response to temperature and information about a predator. *Freshwater Biology*, **39**, 681–687.
- Sala O.E., Chapin F.S. III, Armesto J.J. et al. (2000) Global biodiversity scenarios for the Year 2100. *Science*, **287**, 1770–1774.
- Scheffer M. (1998) *Community Dynamics of Shallow Lakes*. Chapman & Hall, London. p. 357.
- Scheffer M., Hosper S.H., Meijer M.-L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, **8**, 275–279.
- Scheffer M., Sergio R. & Kuznetsov Y.A. (2000) Effects of fish on plankton dynamics: a theoretical analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1209–1219.
- Schindler D.E. (1999) Migration strategies of young fishes under temporal constraints: the effect of size-dependent overwinter mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 61–70.
- Schriver P., Bøgstrand J., Jeppesen E. & Søndergaard M. (1995) Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology*, **33**, 255–270.
- Schulz K. & Yurista P.M. (1999) Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. *Hydrobiologia*, **380**, 179–193.
- Sih A., Englund G. & Wooster D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.
- Simonian A., Tătrai I., Bíró P., Paulovits G., Tóth L.G. & Lakatos G. (1995) Biomass of planktonic crustaceans and the food of young cyprinids in the littoral zone of Lake Balaton. *Hydrobiologia*, **303**, 39–48.
- Smiley E.A. & Tessier A.J. (1998) Environmental gradients and the horizontal distribution of microcrustaceans in lakes. *Freshwater Biology*, **39**, 397–409.
- Søndergaard M. & Moss B. (1998) Impact of submerged macrophytes on phytoplankton in shallow freshwater

- lakes. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 115–132. Springer Verlag, New York.
- Stansfield J.H., Perrow M.R., Tench L.D., Jowitt A.J.D. & Taylor A.A.L. (1997) Submerged macrophytes as refuge for grazing Cladocera against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. *Hydrobiologia*, **342/343**, 229–240.
- Steinman A.D., Meeker R.H., Rodusky A.J., Davis W.P. & Hwang S.J. (1997) Ecological properties of charophytes in a large subtropical lake. *Journal of the North American Benthological Society*, **16**, 781–793.
- Sterner R.W. (1989) The role of grazers in phytoplankton succession. In: *Plankton Ecology: Succession in Plankton Communities* (Ed. U. Sommer), pp. 107–170. Springer Verlag, New York.
- Sterner R.W. & Robinson J.L. (1994) Thresholds for growth in *Daphnia magna* with high and low phosphorus diets. *Limnology and Oceanography*, **39**, 1228–1232.
- Sterner R.W., Elser J.J., Fee E.J., Guildford S.J. & Chrzanowski T.H. (1997) The light : nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. *American Naturalist*, **150**, 663–684.
- Sterner R.W. & Schulz K.L. (1998) Zooplankton nutrition: recent progress and a reality check. *Aquatic Ecology*, **32**, 261–279.
- Stibor H. (1992) Predator induced life-history shifts in a freshwater cladoceran. *Oecologia*, **92**, 162–165.
- Süttfeld R., Petereit F. & Nahrstedt A. (1996) Resorcinol in exudates of *Nuphar lutea*. *Journal of Chemical Ecology*, **22**, 2221–2231.
- Tatrái I. & Herzig A. (1995) Effects of habitat structure on the feeding efficiency of young stages of razor fish (*Pelecus cultratus* L.): an experimental approach. *Hydrobiologia*, **200/201**, 229–240.
- Theiss J., Zielinski K. & Lang H. (1990) Biomanipulation by introduction of herbivorous zooplankton. A helpful shock for eutrophic lakes? *Hydrobiologia*, **200/201**, 59–68.
- Thompson D.J. (1975) Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *Journal of Animal Ecology*, **44**, 907–916.
- Thompson D.J. & Pickup J. (1984) Feeding rates of zygoptera larvae within an instar. *Odonatologica*, **13**, 309–315.
- Timms R.M. & Moss B. (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnology and Oceanography*, **29**, 472–486.
- Urabe J., Clasen J. & Sterner R.W. (1997) Phosphorus-limitation of *Daphnia* growth: it is real? *Limnology and Oceanography*, **42**, 1436–1443.
- Van den Berg M.S., Coops H., Meijer M.-L., Scheffer M. & Simons J. (1998) Clear water associated with a dense. *Chara* vegetation in the shallow and turbid Lake Veluwemeer, the Netherlands. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen), pp. 339–352. Springer Verlag, New York.
- Van Donk E., Grimm M.P., Gulati R.D. & Klein Breteler J.P.G. (1990) Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. *Hydrobiologia*, **200/201**, 275–291.
- Vanni M.J. (1988) Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small species community. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1758–1770.
- Venugopal M.N. & Winfield I.J. (1993) The distribution of juvenile fishes in a hypereutrophic pond: can macrophytes potentially offer a refuge for zooplankton? *Journal of Freshwater Ecology*, **8**, 389–396.
- Verreth J. (1990) The accuracy of population density estimates of horizontally distributed zooplankton community in Dutch fish ponds. *Hydrobiologia*, **203**, 53–61.
- Vijverberg J., Kalf D.F. & Boersma M. (1996) Decrease in *Daphnia* egg viability at elevated pH. *Limnology and Oceanography*, **41**, 789–794.
- Visman V., McQueen D.J. & Demers E. (1994) Zooplankton spatial patterns in two lakes with contrasting community structure. *Hydrobiologia*, **284**, 177–191.
- Vitousek P.M. (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.
- Voss S. & Mumm H. (1999) Where to stay by night and day: size-specific and seasonal differences in horizontal and vertical distribution of *Chaoborus flavicans* larvae. *Freshwater Biology*, **42**, 201–213.
- Wahlström E. & Westman E. (1999) Planktivory by the predacious cladoceran *Bythotrephes longimanus*: effects on zooplankton size structure and abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1865–1872.
- Walls M., Rajasilta M., Sarvala J. & Salo J. (1990) Diel changes in horizontal microdistribution of littoral cladocera. *Limnologia*, **20**, 253–258.
- Watt P.J. & Young S. (1994) Effect of predator chemical cues on behaviour in both horizontal and vertical planes. *Animal Behaviour*, **48**, 861–869.
- Wetzel R.G. (1990) Land–water interfaces: metabolic and limnological regulators. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **24**, 6–24.

- White M.D. (1998) Horizontal distribution of pelagic zooplankton in relation to predation gradients. *Ecography*, **21**, 44–62.
- Whiteside M.C. (1988) 0+ fish as major factors affecting abundance patterns of littoral zooplankton. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 1710–1714.
- Wilhelm F.M. & Schindler D.W. (1999) Effects of *Gammarus lacustris* (Crustacea: Amphipoda) on plankton community structure in an alpine lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1401–1408.
- Winfield I.J. (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. *Journal of Fish Biology*, **29**, 37–48.
- Wissel B. & Benndorf J. (1998) Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. *Archiv für Hydrobiologie*, **143**, 129–146.
- Wright D. & Shapiro J. (1990) Refuge availability: a key to understanding the summer disappearance of *Daphnia*. *Freshwater Biology*, **24**, 43–62.

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