POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	54	4	701–707	2006

Short review

Zeynep PEKCAN-HEKIM, Anne LILJENDAHL-NURMINEN, Jukka HORPPILA

Department of Biological and Environmental Sciences/Aquatic Sciences, University of Helsinki, Finland, P.O.B. 65, FIN-00014, e-mail: zeynep.pekcan@helsinki.fi

CHAOBORUS FLAVICANS IN THE FOOD WEB – COMPETITOR OR RESOURCE FOR FISH?

ABSTRACT: In lakes, chaoborids can be a food resource and also act as competitors for planktivorous fish. Usually their density varies reciprocally with the density of planktivorous fish, which forage on chaoborids. Results from Lake Hiidenvesi show, however, that in deep clay-turbid lakes chaoborids may be the main regulators of herbivorous zooplankton although the density of planktivorous fish is high. This is because turbidity reduces the feeding efficiency of fish while the feeding of chaoborids is not affected by the high turbidity levels.

KEY WORDS: *Chaoborus*, smelt, white bream, clay-turbidity, predation

1. INTRODUCTION

The significant role of invertebrate predators in lake food webs, and their ability to regulate the species composition and size structure of plankton communities, has been emphasized during recent decades (Gliwicz *et al*. 1978, Lane 1978, Lair 1990). Phantom midges (Diptera, Chaoboridae) are invertebrate predators that have aquatic larvae which form dense populations in many water bodies. They have been a target of intensive research because they are very effective predators on zooplankton and can regulate zooplankton communities (Black and Hairston 1988, Lair 1990, Wissel and Benndorf 1998, Liljendahl-Nurminen *et al*. 2003). In food web management, the aim is to improve water quality by enhancing the grazing pressure on phytoplankton through fish stock manipulations (Shapiro *et al*. 1975). It may happen, however, that invertebrate predators, such as chaoborids, increase in abundance after the reduction of planktivorous fish and contribute to the failure of lake restoration (Benndorf 1995, Wissel and Benndorf 1998).

Invertebrate predators are difficult to fit into the food chain theory behind food web management, since they can be a food resource and also act as competitors for planktivorous fish (Persson *et al.* 1992). Additionally, water quality should be taken into consideration because the interactions in the food web will differ in turbid lakes compared with clear lakes (Cuker 1993, Horppila and Liljendahl-Nurminen 2005). Hence, clarification of the role of chaoborids in the food web of lakes with differing water quality and morphometry is crucial for the prediction of their effects on food web manipulations. In this article, we discuss the role of chaoborids as prey and as predator,

especially concentrating on results derived from a clay-turbid Lake Hiidenvesi (southern Finland).

2. LAKE HIIDENVESI

Lake Hiidenvesi (area 30.3 km^2) in southwestern Finland (60°24′N, 24°18′E), has several separate basins differing in morphometry and water quality. The shallow, non-stratifying basins (maximum depth <5 m) are the most eutrophic, the total average phosphorus concentration exceeding 80 µg L^{-1}. In the stratifying parts of the lake (c. 10 km^2), total phosphorus concentration is on average 40 µg L^{-1}. The lake is also clay-turbid due to resuspended sediments and external loading of inorganic suspended solids from agricultural areas. In the shallow basins, water turbidity frequently exceeds 50 NTU (Nephelometric Turbidity Units), while in the epilimnion of the stratifying areas it usually remains around 10 NTU. Food web management through removal of planktivorous and benthivorous fish has been applied, but no considerable effects on water quality have been detected (Olin *et al.* 2006). More detailed description of the lake, its plankton, fish and macrophyte communities can be found in Tallberg *et al.* (1999), Nurminen (2003), Horppila (2005a), and Olin and Ruuhijärvi (2005).

3. *CHAOBORUS* AS PREY

Chaoborids are popular food items for fish and therefore high chaoborid densities are often related to the absence or low density of fish (Pope *et al.* 1973). The coexistence of chaoborids with fish is usually limited to species that are able to conduct vertical migrations (Von Ende 1978, McQueen *et al.* 1999). Chaoborids are very tolerant of low concentrations of dissolved oxygen, and they can inhabit the hypolimnion of stratified lakes during daytime and migrate at night into the epilimnion to forage on zooplankton (e.g. Luecke 1986). Alternatively, chaoborids can burrow into the sediment during daytime (Sæther 1997). One of the chaoborid species using the vertical migration strategy and coexisting with fish is *Chaoborus flavicans* (Meigen), which is common widely in the holarctic region (Nilssen 1974, Borkent 1981). *C. flavicans* has a high biomass in Lake Hiidenvesi, its density frequently exceeding 5000 ind. m^{-2} (Liljendahl-Nurminen *et al.* 2002).

What is unusual in Lake Hiidenvesi is that *C. flavicans* occupy relatively well oxygenated water layers throughout the day, their distance from dense swarms of planktivorous fish (*Osmerus eperlanus* (L.) smelt) being only few metres (Fig. 1). Thus it can be concluded that the close coexistence of chaoborids and smelts is facilitated by a metalimnetic turbidity maximum that chaoborids use as a refuge against fish predation (Liljendahl-Nurminen *et al.* 2003, Horppila 2005b) (Fig. 1). The day time separation of *C. flavicans* and dense swarms of smelt could also be explained by vertical temperature and oxygen gradients. However, since adult smelts have an upper temperature limit of 16–18 °C (Appenzeller and Leggett 1995) and the water temperature during the summer in the epilimnion is >18 °C (Fig. 1), they should prefer the cooler deeper layers. Also the concentration of dissolved oxygen in the metalimnion is not low enough to form a strict boundary for fish.

Inorganic turbidity combined with reduced light lowers the feeding efficiency of planktivorous and piscivorous fish (Vinyard and O'Brien 1976, Utne-Palm 1999, De Robertis *et al.* 2003). Experimental studies on the predator-prey interaction between smelts and *C. flavicans* have shown that darkness alone does not protect chaoborids very effectively against predation by smelts, but that inorganic turbidity exceeding 30 NTU together with light intensity below 0.1 µE m^{-2} s^{-1} provides an efficient refuge (Horppila *et al.* 2004). The same phenomenon can be seen also from field data on the diurnal variation in the diet composition of smelts. The diets of smelts captured from the epilimnion during the day do not include *C. flavicans* which hide in the turbid water layers. At night in the dark, when the swarms of *C. flavicans* migrate into the epilimnion to feed on zooplankton, they form a considerable percentage (50%) of smelt diets (M. Vinni – unpublished).

In eutrophic lakes, the intensive predation by planktivorous fish depresses large-

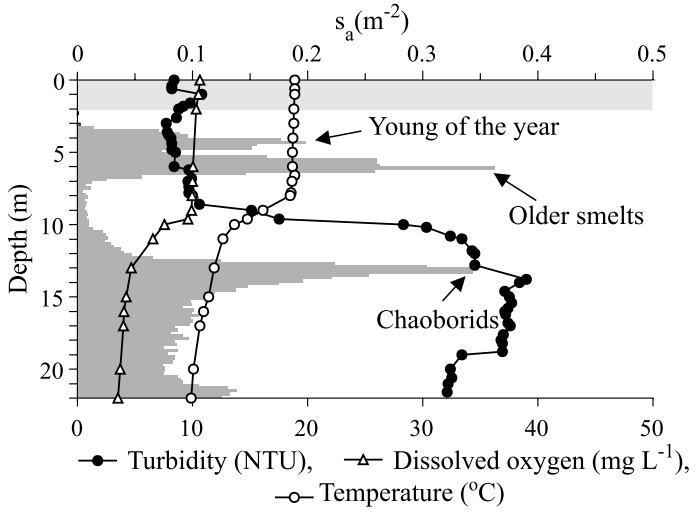

Fig. 1. Top axis (bars): the vertical daytime distribution of echo integrals in Lake Hiidenvesi on 26 August 2001. The blind zone of the echosounder at the water surface is indicated by a shadowed layer. Bottom axis: profiles of water turbidity, dissolved oxygen (DO), and temperature in the deep basin of Lake Hiidenvesi on 26 August 2001. Modified from Horppila (2005b).

sized herbivorous zooplankton and therefore predatory macroinvertebrates may form an important food resource for fish (Van Densen *et al.* 1996). The behaviour of chaoborids may thus affect the competitive interactions between different fish species that have variable abilities to forage in turbid environments (e.g. Lammens et al. 1987). The dominance of cyprinids in eutrophic lakes is a common phenomenon (Persson *et al.* 1991, Jeppesen *et al.* 2000). It has been suggested that cyprinids forage efficiently at low light intensities (Townsend and Risebrow 1982, Diehl 1988). Recent laboratory experiments (Pekcan-Hekim and Horppila in press) have suggested that compared with smelt, the cyprinid white bream (*Abramis björkna* (L.)) is a more efficient forager on chaoborids at inorganic turbidity levels exceeding 30 NTU (Fig. 2). White bream is a common cyprinid species abundant in turbid and eutrophic north temperate lakes (Olin *et al.* 2002, Horppila 2005b). The success of cyprinids can be related to their ability to feed effectively in turbid waters (Lammens *et al.* 1987, Persson 1987).

Chaoborids inhabit only the stratifying areas of Lake Hiidenvesi (water depth >10 m). In the shallow basins, *C. flavicans* are absent although water turbidity is even higher than in the stratifying areas (Liljendahl-Nurminen *et al.* 2002). It seems that the close co-existence of chaoborids and fish in the water column is only possible when a thermocline exists and facilitates the development of a metalimnetic turbidity maximum, which separates the schools of fish from chaoborids. Shallow eutrophic lake basins often show high densities of benthivorous fish and even burrowing into the sediment may not protect chaoborids from fish predation.

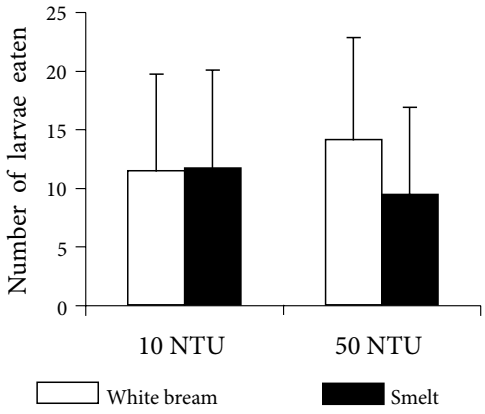

Fig. 2. Average number of *Chaoborus* eaten by white bream and smelt at clay-turbidities of 10 and 50 Nephelometric Turbidity Units (NTU) in two-hour experiments, conducted in 45-litre bags at light intensities of 0–1.5 μE m^{-2} s^{-1}. Vertical bars show the standard deviation. More detailed description of the experimental design can be found in Horppila *et al.* 2004.

4. *CHAOBORUS* AS PREDATOR

Usually, the seasonal succession of zooplankton in stratifying eutrophic lakes includes a spring biomass peak followed by a summer decline and often also a moderate autumn biomass peak (Sommer *et al.* 1986). In the stratifying area of Lake Hiidenvesi, the spring peak is missing and the highest biomass of cladocerans takes place in mid summer, simultaneously with the emergence of chaoborids. Studies on food consumption of *Chaoborus* and smelts have confirmed that chaoborids are the main predators on cladocerans in the stratifying area of Lake Hiidenvesi and in early summer their consumption clearly exceeds the production of cladocerans (Liljendahl-Nurminen *et al.* 2003, 2005). Such effective predation by chaoborids is not a unique phenomenon, but has been reported earlier from other lakes (Kajak and Rybak 1979, Elser *et al.* 1987, Ramcharan *et al.* 2001).

A more unconventional observation was that in Lake Hiidenvesi the mean size of cladocerans increased when predation pressure by chaoborids was reduced during the emergence period (Liljendahl-Nurminen *et al.* 2003). Usually it has been assumed that predation by invertebrate predators causes the size spectrum of prey to shift to large plankton (Lampert and Sommer 1997). It seems that in Lake Hiidenvesi, the combined predation pressure from fish and chaborids prevents cladocerans from reaching a body length large enough to escape from chaoborid predation (Liljendahl-Nurminen *et al.* 2003). Similar to other lakes (Elser *et al.* 1987, Lüning-Krizan 1997), the main prey of fourth instar *Chaoborus* larvae in Lake Hiidenvesi are cladocerans (*Bosmina*, *Daphnia* and *Chydorus*) (Fig. 3). In June and August, however, their diet is complemented with adult copepods and rotifers. Younger instars prey first mainly on rotifers and protozoans, and later (third instar) also on copepodits and small cladocerans. Chaoborids can be regarded as flexible predators and the spatial and temporal variation in their diets may be the result of behavioral plasticity, differences in the availability of prey or a combination of both factors (Pastorok 1981). The ontogenetic diet shifts probably reduce food

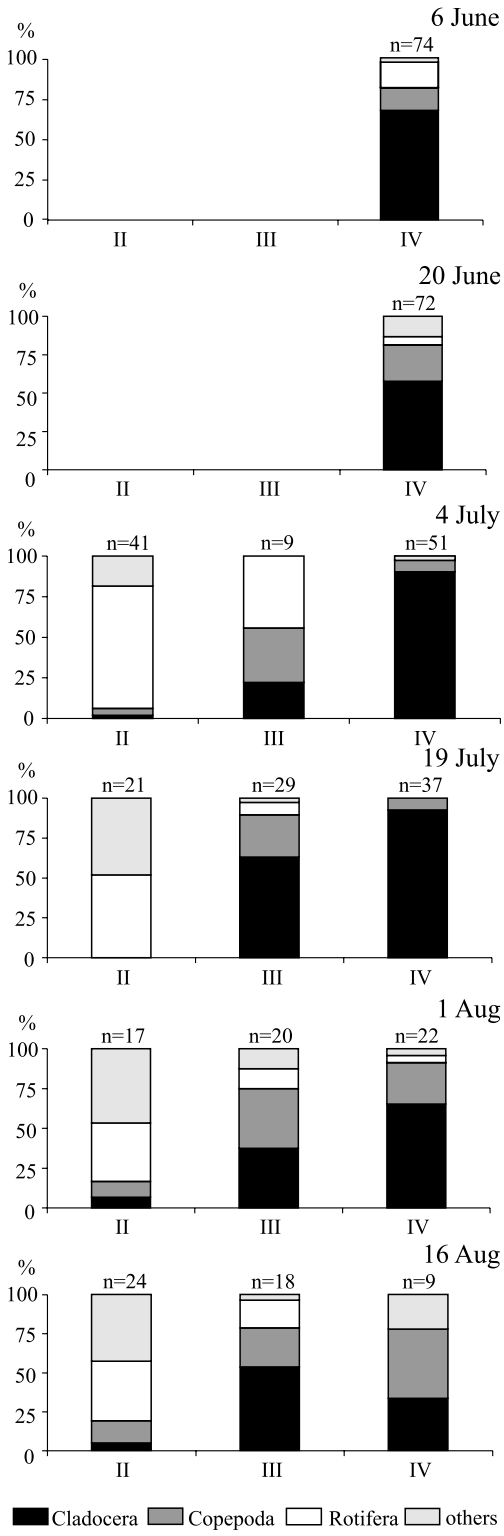

Fig. 3. Diet (frequency of occurrence) of instars II-IV of *Chaoborus flavicans* in Lake Hiidenvesi in year 2000. For materials and methods see Liljendahl-Nurminen *et al.* 2003.

competition between different chaoborid instars. It seems that the community structure of zooplankton in Lake Hiidenvesi is suitable for each instar of *Chaoborus*.

5. CONCLUDING REMARKS

In many lakes, chaoborids cannot compete with abundant planktivorous fish, but are themselves regulated by fish predation. As suggested by Cuker (1993) and Horppila and Liljendahl-Nurminen (2005), it seems though that elevated inorganic turbidity levels tend to shift the dominance from fish to chaoborids. Chaoborids are particularly successful in deep, clay turbid lakes where they can stay high in the water column close to their epilimentic prey without having to diurnally migrate long distances (Liljendahl-Nurminen *et al.* 2002). It is also observed that when chaoborids are able to coexist with fish in the water column, the size structure of zooplankton is suitable for them. This is due to selective predation by fish shifting the zooplankton size structure towards small size-classes that are suitable food for chaoborids. It must also be remembered that inorganic suspendoids are not the only cause of water turbidity. In eutrophic lakes, high turbidity values can result from dense phytoplankton populations as well. There are, however, reasons to believe that inorganic turbidity is more favorable for chaoborids than phytoplankton-originated turbidity. Firstly, their effect on the light environment is different. Suspended inorganic particles predominantly cause light scattering, while phytoplankton has more effect on absorption (Kirk 1994). This is important, since the contrast between the prey and its background is more important for vision-oriented fish to detect their prey, than the absolute light level (Hemmings 1966, Hinshaw 1985). Clay turbidity is especially harmful for feeding of planktivorous fish, since light scattering interferes with the background light level and reduces contrast (Hinshaw 1985, Giske *et al.* 1994). Secondly, high phytoplankton biomasses are also mostly restricted to the euphotic zone, which reduces their usefulness as refuges.

Chaoborids play an important role in the food web and can act both as a resource and as a competitor for planktivorous fish. Water quality can be a significant factor that determines their role as prey or as a predator. It seems that increasing clay-turbidity tends to shift their role from being a resource to a competitor for planktivorous fish. Water depth is an important factor determining the possibility of vertical migration of chaoborids to avoid planktivourous fish, thus amplifying their role as prey to a predator.

6. REFERENCES

Appenzeller A.R., Leggett W.C. 1995 – An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*) – Can. J. Fish. Aquat. Sci. 52: 504–511.

Benndorf J. 1995 – Possibilities and limits for controlling eutrophication by biomanipulation – Int. Rev. ges. Hydrobiol. 80: 519–534.

Black R.W., Hairston N.G.Jr. 1988 – Predator driven changes in community structure – Oecologia, 77: 468–479.

Borkent A. 1981 – The distribution and habitat preferences of the Chaoboridae (Culicomorpha: Diptera) of the holarctic region – Can. J. Zool. 59: 122–133.

Cuker B.E. 1993 – Suspended clays alter trophic interactions in the plankton – Ecology, 74: 944–953.

De Robertis A., Ryer C.H., Veloza A., Brodeur R.D. 2003 – Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish – Can. J. Fish. Aquat. Sci. 60: 1517–1526.

Diehl S. 1988 – Foraging efficiency of three freshwater fishes: Effects of structural complexity and light – Oikos, 53: 207–214.

Elser M.M., von Ende C.N., Sorranno P., Carpenter S.R. 1987 – *Chaoborus* populations: response to food web manipulations and potential effects on zooplankton communities – Can. J. Zool. 65: 2846–2852.

Giske J., Aksnes D.L., Fiksen Ø. 1994 – Visual predators, environmental variables and zooplankton mortality risk – Vie et Milieu, 44: 1–9.

Gliwicz Z.M., Hillbricht-Ilkowska A., Węgleńska T. 1978 – Contribution of fish and invertebrate predation to the elimination of zooplankton biomass in two Polish lakes – Verh. Internat. Verein. Limnol. 20: 1007–1011.

Hemmings C.C. 1966 – Factors influencing the visibility of objects underwater (In: Light

as an ecological factor, Eds. R. Bainbridge, G.C. Evans, O. Rackham) – Blackwell Scientific Publications, Oxford, pp. 359–374.

Hinshaw J.M. 1985 – Effects of illumination and prey contrast on survival and growth of larval yellow perch *Perca flavescens* – Trans. Am. Fish. Soc. 114: 540–545.

Horppila J. 2005a – Project background and lake description – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 59: 1–11.

Horppila J. 2005b – Expected and unexpected phenomena – experiences from Lake Hiidenvesi research – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 59: 219–232.

Horppila J., Liljendahl-Nurminen A. 2005 – Clay-turbid interactions may not cascade – a reminder for lake managers – Restor. Ecol. 13: 241–245.

Horppila J., Liljendahl-Nurminen A., Malinen T. 2004 – Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids – Can. J. Fish. Aquat. Sci. 61: 1862–1870.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T., Landkildehus F. 2000 – Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient – Freshwat. Biol. 45: 201–218.

Kajak Z., Rybak J. 1979 – The feeding of *Chaoborus flavicans* Meigen (Diptera, Chaoboridae) and its predation on lake zooplankton – Int. Rev. Ges. Hydrobiol. 64: 361–378.

Kirk J.T.O. 1994 – Light and photoynthesis in aquatic ecosystems – Cambridge University Press, Cambridge, 509 pp.

Lair N. 1990 – Effects of invertebrate predation on the seasonal succession of a zooplankton community: a two year study in Lake Aydat, France – Hydrobiologia, 198: 1–12.

Lammens E.H.R.R., Geursen J., MacGillavry P.J. 1987 – Diet shifts feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes – Proc. V Congr. Europ. Ichtyol. Stockholm, 1985: 153–162.

Lampert W., Sommer U. 1997 – Limnoecology: The ecology of lakes and streams – Oxford University Press, Oxford – New York, 382 pp.

Lane P.A. 1978 – Role of invertebrate predation in structuring zooplankton communities – Verh. Internat. Verein. Limnol. 20: 480–485.

Liljendahl-Nurminen A., Horppila J., Eloranta P., Malinen T., Uusitalo L. 2002 – The seasonal dynamics and distribution of *Chaoborus flavicans* in adjacent lake basins of different morphometry and degree of eutrophication – Freshwat. Biol. 47: 1283–1295.

Liljendahl-Nurminen A., Horppila J., Eloranta P., Alajärvi E., Malinen T., Valtonen S., Vinni M. 2003 – The supremacy of invertebrate predators over fish – factors behind the unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi – Arch. Hydrobiol. 158:75–96.

Liljendahl-Nurminen A., Horppila J., Eloranta P., Valtonen S., Pekcan-Hekim Z. 2005 – Searching for the missing peak – an enclosure study on the seasonal succession of cladocerans in Lake Hiidenvesi – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 59: 85–103.

Luecke C. 1986 – A change in the pattern of vertical migration of *Chaoborus flavicans* after the introduction of trout – J. Plankton Res. 8: 649–657.

Lüning-Krizan J. 1997 – Selective feeding of third- and fourth instar larvae of *Chaoborus flavicans* in the field – Arch. Hydrobiol. 140: 347–365.

McQueen D.J., Ramcharan C.W., Demer E., Yan N.D., Conforti L.M., Perez-Fuentetaja A. 1999 – *Chaoborus* behavioural responses to changes in fish density – Arch. Hydrobiol. 145: 165–179.

Nilssen J.P. 1974 – On the ecology and distribution of the Norwegian larvae of *Chaoborus* (Diptera, Chaoboridae) – Norw. J. Entomol. 21: 37–44.

Nurminen L. 2003 – Macrophyte species composition reflecting water quality changes in adjacent water bodies of Lake Hiidenvesi, SW Finland – Ann. Bot. Fenn. 40: 199–208.

Olin M., Rask M., Ruuhijärvi J., Kurkilahti M., Ala-Opas P., Ylönen O. 2002 – Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient – J. Fish Biol. 60: 593–612.

Olin M., Rask M., Ruuhijärvi J., Keskitalo J., Horppila J., Tallberg P., Taponen T., Lehtovaara A., Sammalkorpi I. 2006– Effects of biomanipulation on fish and plankton communities in ten eutrophic lakes of southern Finland – Hydrobiologia, 553: 67–88..

Olin M., Ruuhijärvi J. 2005 – Fish communities in the different basins of L. Hiidenvesi in 1997–2001: effects of trophic status and basin morphology – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 59: 125–140.

Pastorok R.A. 1981 – Selection of prey by *Chaoborus* larvae: A review and new evidence for

behavioral flexibility (In: Evolution and ecology of zooplankton communities, Ed. W.C. Kerfoot) – The University Press of New England, Hanover, New Hampshire, pp. 538–554.

Peckan-Hekim Z. Horppila J. – Feeding efficiency of white bream at different inorganic turbidities and light climates – J. Fish Biol. (in press)

Persson L. 1987 – Effects of habitat and season on competitive interactions between roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) – Oecologia, 73: 170–177.

Persson L., Diehl S., Johansson L., Andersson G., Hamrin S.F. 1991 – Shifts in fish communities along the productivity gradient of temperate lakes – patterns and the importance of size-structured interactions – J. Fish Biol. 38: 281–293.

Persson L., Diehl S., Johansson L., Andersson G., Hamrin S. 1992 – Trophic interactions in temperate lake ecosystems: a test of food chain theory – Am. Nat. 140: 59–84.

Pope G.F., Carter J.C.H., Power G. 1973 – The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River System, Québec – Trans. Am. Fish. Soc. 102: 707–722.

Ramcharan C.W., McQueen D.J., Pérez-Fuentetaja A., Yan N.D., Demers E., Rusak J. 2001 – Complex responses of *Chaoborus* to changes in fish populations – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 56: 81–100.

Sæther O.A. 1997 – Diptera Chaoboridae, Phantom midges (In: Aquatic insects of North Europe 2, Ed. A. Nilsson) – Apollo Books, Stenstrup, pp. 149–161.

Shapiro J., Lamarra V., Lynch M. 1975 – Biomanipulation: an ecosystem approach to lake restoration (In: Water quality management through biological control, Eds. P.L. Brezonit, J.L. Fox) – University of Florida, Gainesville, pp. 85–96.

Sommer U., Gliwicz Z.M., Lampert W., Duncan A. 1986 – The PEG-model of seasonal succession of planktonic events in fresh waters – Arch. Hydrobiol. 106: 433–471.

Tallberg P., Horppila J., Väisänen A., Nurminen L. 1999 – Seasonal succession of phytoplankton and zooplankton along a trophic gradient in a eutrophic lake – implications for food web management – Hydrobiologia, 412: 81–94.

Townsend C.R., Risebrow A.J. 1982 – The influence of light level on the functional response of a zooplanktonivorous fish – Oecologia, 53: 293–295.

Utne-Palm A.C. 1999 – The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey – J. Fish Biol. 54: 1244–1258.

Van Densen W.L.T., Ligtvoet W., Roozen R.W.M. 1996 – Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items – Ann. Zool. Fennici, 33: 495–506.

Vinyard G.L., O'Brien J. 1976 – Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*) – J. Fish. Res. Board Can. 33: 2845–2849.

Von Ende C.N. 1978 – Regional coexistence of four *Chaoborus* species – Verh. Internat. Verein. Limnol. 20: 2630–2633.

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 – Arch. Hydrobiol. 143: 129–146.

(Received after revising December 2005)