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An evaluation of the role of daphnids in controlling phytoplankton biomass in clear water versus turbid shallow lakes

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Abstract

Phytoplankton and zooplankton were monitored during 2 years in four eutrophic shallow lakes (two turbid and two clear water) from two wetland reserves in Belgium. In each wetland, phytoplankton biomass was significantly higher in the turbid lake than in the clear water lake. Although total macrozooplankton biomass and the contribution of daphnids to total zooplankton biomass was comparable in the clear water and the turbid lakes, the grazing pressure of macrozooplankton on phytoplankton as estimated from zooplankton to phytoplankton biomass ratios was higher in the clear water lakes. Estimated grazing by daphnids in the clear water lakes was always high in spring. In summer, however, daphnid biomass was low or daphnids were even absent during prolonged periods. During those periods phytoplankton was probably controlled by smaller macrozooplankton or by submerged macrophytes through nutrient competition, allelopathic effects or increased sedimentation rates in the macrophyte vegetation.

Keywords: Shallow lakes; Phytoplankton; Macrozooplankton; *Daphnia*; Macrophytes

Introduction

The alternative stable states theory predicts that meso- to eutrophic shallow lakes can have two alternative equilibrium states at a given nutrient loading: a clear water or a turbid state (Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). The clear water state is characterized by a low phytoplankton biomass and a dense submerged macrophyte vegetation while the turbid state has a high phytoplankton biomass and usually lacks submerged macrophytes. These two alternative stable equilibrium states are stabilized by ecological feedback mechanisms. Large zooplankton like daphnids (*Daphnia* or *Ceriodaphnia*) are considered to play a central role in stabilizing the clear water and turbid states (e.g. Jeppesen et al., 1997; Scheffer, 1999). These daphnids are slow swimmers that are sensitive to fish predation (Brooks & Dodson, 1965; Pace, 1984). Daphnids are also efficient in controlling phytoplankton as they graze on a broad size-range of phytoplankton (Hall, Threlkeld, Burns, & Crowley, 1976). In clear water lakes,

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daphnids can attain a high biomass and can control phytoplankton because the submerged macrophytes provide them with a refuge from fish predation (Burks, Jeppesen, & Lodge, 2001; Timms & Moss, 1984). In turbid lakes, daphnids have no shelter from fish predation and cannot attain a sufficiently high biomass to control phytoplankton.

In 1998 and 1999, two pairs of connected shallow lakes were monitored in two wetlands in Belgium. The two lakes in both wetlands fitted each well into one of the alternative stable states categories. In each wetland, the clear lake had a significantly higher phytoplankton biomass than the turbid lake and, in the clear lake, submerged macrophytes covered about half of the lake surface while macrophytes were absent in the turbid lake (Muylaert et al., 2003). In this paper, we evaluate the importance of daphnids in regulating phytoplankton biomass in the clear water versus turbid lakes of the two wetlands.

Materials and methods

Study site

Two lakes were located in the Blankaart reserve, a wetland of international importance situated in the western part of Belgium, close to the coast (Fig. 1). The lakes in this wetland were created by peat digging and are on average about 1 m deep. The lakes are situated in an area characterized by intensive agriculture and livestock farming, which results in high inputs of nutrients to the lakes. The turbid lake, Lake Blankaart, is relatively large (32 ha) and receives surface water inputs through several rivulets. The clear water lake, Lake Visvijver, is small (0.6 ha) and receives no direct surface water inputs. During periods of high rainfall in winter, flooding connects the two lakes, resulting in an exchange of water and dissolved nutrients. In Lake Visvijver, submerged macrophytes cover about half of the lake surface. During the study period, *Chara globularis* was the dominant macrophyte in spring but it was replaced by floating beds of filamentous green algae towards the end of summer. Fish were absent from Lake Visvijver during the study period because of a summer fish kill in 1997. In Lake Blankaart, benthivorous and planktivorous fish species like white bream (*Blicca bjoerkna*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) attain high biomass, while piscivorous species are virtually absent (Muylaert et al., 2003).

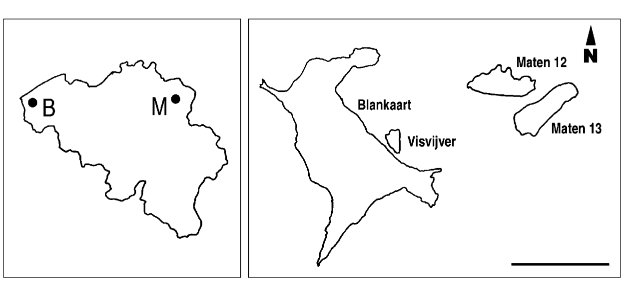

Fig. 1. The location of the 'De Blankaart' (B) and 'De Maten' (M) wetland reserves in Belgium (left) and detailed maps at identical scale of the four lakes studied (right). Scale bar is 500 m.

The two other lakes were located in the De Maten wetland, which is situated in the northeastern part of Belgium (Fig. 1). The De Maten wetland consists of 32 small lakes that are all interconnected by a system of overflows and receive surface water inputs by two main rivulets (Cottenie, Nuytten, Michels, & De Meester, 2001; Michels, Cottenie, Neys, & De Meester, 2001). Like the lakes in the Blankaart wetland, the De Maten lakes were created by peat digging and are about 1 m deep. The two lakes studied, Lake Maten 12 and Lake Maten 13, are situated next to each other and have a similar size (Lake Maten 12: 3.2 ha, Lake Maten 13: 3.3 ha). Both lakes are fed by the same rivulet and Lake Maten 13 flows into Lake Maten 12. In Lake Maten 13, macrophytes cover about half of the lake surface while submerged macrophytes are virtually absent in Lake Maten 12. The dominant macrophytes in Lake Maten 13 during the study period were *Drepanocladus fluitans*, *Polygonum amphibium* and *Nitella translucens*. Fish biomass as measured by fyke nets in 2000 was higher in Lake Maten 12 when compared to Lake Maten 13 (Muylaert et al., 2003). Brown bullhead (*Ameiurus nebulosus*), roach and rudd (*Scardinius erythrophtalmus*) dominated the fish community in Lake Maten 12, while rudd and tench (*Tinca tinca*) were the dominant fish species in Lake Maten 13.

Sampling and analyses

The four lakes were sampled monthly during winter and biweekly during summer during two consecutive years (1998–1999). The two lakes in each wetland reserve were always sampled on the same day. Samples were collected during daytime at a fixed location in each lake. Before taking samples, Secchi depth was measured at the sampling location using a black and white disc. Subsurface samples for phytoplankton were fixed in the field using Lugol's solution. Macrozooplankton was sampled using a Schindler-Patalas trap. The trap was deployed at two depths to sample the entire water column. Macrozooplankton samples were fixed in the field with sucrose-saturated formalin (Haney & Hall, 1973). A water sample was kept refrigerated in the dark and transported to the lab to be subsampled for nutrients and suspended particulate matter (SPM). Samples for dissolved nutrients (nitrite, nitrate,