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SHALLOW LAKES

Waterfowl, macrophytes, and the clear water state of shallow lakes

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Abstract The importance of lake ecosystems for waterfowl remains a topic of debate. In order to assess how temporal variations in lake features, specifically shifts between alternative stable states, may interact with the waterfowl fauna, we performed a long-term (22 years) study of the shallow Lake Krankesjön, southern Sweden. Lower total numbers of waterfowl occurred during periods with low macrophyte cover and turbid water, than when submersed macrophytes flourished and the water was clear. Some specific functional groups of waterfowl, such as herbivores, invertebrate, and fish feeders, showed a positive relation to clear water and high macrophyte cover. Hence, our data suggest that some migratory waterfowl may select lakes based on water quality, thereby adjusting their large-scale migratory routes. On the other hand, omnivorous waterfowl exhibited their highest abundances during turbid conditions. Furthermore, waterfowl not primarily relying on food from the lake showed no response to fluctuations in turbidity or macrophyte cover, but followed regional trends in population dynamics. In our study lake, L. Krankesjön, we estimated that waterfowl remove less than 3% of the macrophyte biomass during a stable clear-water state with lush macrophyte beds. However, during transition periods between alternative stable states, when macrophyte biomass is lower and the plants already stressed, the consumption rate of waterfowl may have a stronger effect on lake ecosystem functioning.

Keywords Waterfowl · Bird · Alternative stable state · Lake · Macrophyte · Herbivory · Grazing

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This paper is dedicated to the late Gunnar Andersson for his pioneering work on interactions between limnology and waterfowl dynamics.

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Introduction

Waterfowl generally warrant an important component of shallow lakes, which are often considered sites of special interest for environmental conservation, e.g., the Ramsar convention (http://www.ramsar.org/) and the EU water framework directive (http://ec.europa.eu/environment/water/water-framework), as well as for biodiversity and nutrient retention (Hansson et al., 2005). Besides their environmental value, many shallow lakes and wetlands also attract interest for recreation, such as bird watching and ecotourism. Many such habitats are protected, e.g., as national parks, but surprisingly little information exists about the interactions between waterfowl and organisms below the water surface. This lack of research seems paradoxical as a high productivity of the aquatic community often serves as a prerequisite for a rich bird life. Interactions with aquatic biota may differ in strength and affect waterfowl populations differently. For example, benthivorous fish and birds may show strong competition for invertebrate food (Wagner & Hansson, 1998; Haas et al., 2007), resulting in a negative relation between fish and waterfowl abundances. On the other hand, fish feeding birds may gain from high numbers of fish, and instead have a positive relation to fish abundances. In contrast, some functional groups of waterfowl, e.g., birds feeding on vegetation, may be unrelated to fish densities and instead show a positive relation with macrophytes (Milberg et al., 2002). Hence, we may hypothesize that different functional groups of waterfowl will respond differently to characteristics of the lake ecosystem, such as macrophyte cover, fish, and invertebrate abundances. Further, the amount of phytoplankton in the lake may constrain visual foragers through changes in turbidity.

Many shallow lakes, including our study lake, L. Krankesjön (Brönmark et al., 2009) shift between two alternative stable states, either a clear water state, with lush macrophyte growth, or a turbid state dominated by planktonic algae (Jeppesen et al., 1990; Moss, 1990; Scheffer, 1990; Blindow et al., 1993; Moss et al., 2004). Since many features, including turbidity and abundances of fish, invertebrates, and macrophytes, change considerably as a lake shifts between clear and turbid states, also the quality of the lake as a habitat for waterfowl changes. Thus, the characteristics of the lake may affect the attractiveness as a breeding or stop-over site for waterfowl. Moreover, high abundances of waterfowl may affect the lake ecosystem considerably, for example, by the birds feeding on macrophytes (van Donk & Otte, 1996) and through deposition of faeces (Mitchell & Wass, 1995; Chaichana et al., 2009).

In our study, we analyzed data from a long term (22 years) study of a shallow lake which has gone through regime shifts between clear and turbid states (Blindow et al., 1993; Hargeby et al., 2007; Brönmark et al., 2009), and we address the issue of how different functional groups of waterfowl (herbivores, omnivores, fish, and invertebrate feeders) respond to such shifts. We particularly took interest in the period of the year when macrophytes primarily occur, i.e., May–October. Our aim sought to provide insight into potential causes behind fluctuations in waterfowl abundance and diversity. Moreover, knowledge on whether local changes in lake habitat quality relate to bird migratory routes may be valuable for our understanding of large-scale migratory patterns of waterfowl. Such insights will improve our ability to manage and restore lakes and wetlands important for both breeding and migrating waterfowl.

Materials and methods

Study area

Lake Krankesjön is situated in Southern Sweden (55°42′N, 13°28′E) and has a drainage area of 53 km^2, mainly consisting of open fields (about 70%), and forests (15%). The lake covers an area of 2.9 km^2 and has a mean depth of 0.9 m (Hargeby et al., 1994). With an average summer total phosphorus concentration of 38 $\mu g\ l^{-1}$, 1.3 $mg\ l^{-1}$ nitrogen and 17 $\mu g\ l^{-1}$ chlorophyll-*a*, Lake Krankesjön is moderately eutrophic (Hargeby et al., 1994). During periods with clear water, submersed plants cover the bottom, especially charophytes, which dominate the bottom vegetation of most of the lake. Smaller areas with *Potamogeton pectinatus* also occur. The lake is fringed by reeds *Phragmites australis* that form more extensive beds in the western and southeastern parts of the lake. In the eastern part, a few small, isolated clumps of reeds occur as well as low, island-like stands of mainly *Acorus calamus* and *Sparganium*. We estimated the cover (%) of submersed macrophytes by mapping from boat during July or August, complemented with estimates from aerial photographs.

The planktivorous fish roach (*Rutilus rutilus*) represents the most abundant fish species in the lake. Other planktivorous and benthivorous species common in Krankesjön include rudd (*Scardinius erythrophtalmus* (L.)), tench (*Tinca tinca*), bream (*Abramis brama* (L.)), and white bream (*Blicca bjoerkna* (L.)). Piscivorous fish species common in Krankesjön include perch (*Perca fluviatilis*) and pike (*Esox lucius*) (Hansson et al., 2007).

We categorized dominant waterfowl taxa into functional groups, including fish feeders (Great Crested Grebe; *Podiceps cristatus* and Common merganser; *Mergus merganser*), invertebrate feeders (Goldeneye; *Bucephala clangula*, tufted duck; *Aythya fuligula*), herbivores (Coot: *Fulica atra*, Mute Swan: *Cygnus olor*, and Eurasian Wigeon: *Anas penelope*), omnivores (Common Pochard: *Aythya ferina*), and waterfowl not primarily relying on food resources in the lake, such as Mallard (*Anas platyrhynchos*) and Common teal (*Anas crecca*). The waterfowl were counted, using binoculars and (mainly) spotting scopes, from two bird towers, one on the southern shore and the other in the east. Birds were generally counted twice a month from 1985 to 2007. In most years, counts started in mid-April and continued until mid-October. However, after 2003, counts occurred more frequently and have been carried out year-round. A few gaps exist in the data series, including 1997 and 2000 when no counts were conducted, and in 2001 when counts did not start until July (Källander et al., 2009).

We have focused on the period from May to October when submersed macrophytes can affect the waterfowl, i.e., data include both breeding and migratory birds. The number of waterfowl within each functional group (described above) was summarized for each counting day, and mean abundances for the period May–October was then calculated. Abundances during this period were used for analyses of relations between waterfowl and submersed macrophytes.

In order to assess whether waterfowl fluctuations in L. Krankesjön follow regional trends or whether they result from processes at the local scale, i.e., changing conditions in the lake such as the macrophyte cover, we used data from the Swedish Bird Survey, a nationwide bird-monitoring scheme that is a part of the Environmental Monitoring Programme of the Swedish Environmental Protection Agency (Lindström et al., 2009). This program started in 1975, and consists of about 1000 routes, each with 20 point counts. At each point, participants counted all birds heard or seen during 5 min. The sum of all birds observed at each route in 1 year formed the basis of our analyses. The same observer evaluated a given route once a year at a route-specific date (±5 days) and starting hour (±30 min). Routes were performed once in summer and once in winter to account for both breeding and migrating waterfowl. About 90% of the routes occurred in the southern half of Sweden to mirror regional trends in waterfowl abundances.

We calculated population trends using TRIM (TRends and Indices for Monitoring data; Pannekoek & van Strien, 2001), a statistical package developed especially for monitoring data. TRIM analyzes time series of counts with missing observations using Poisson regression, taking serial correlation and overdispersion into account. We used the "time-effect model" to estimate overall trends as well as yearly indices. For more information, see Pannekoek & van Strien (2001). Following the standard of the national scheme, we normalized all values based on the numbers counted in 1998. In order to include both breeding and migrating birds, we used the normalized average form winter and summer routes.

Because both the regional trends in population dynamics and macrophyte cover (i.e., the local environment) may affect the amount of waterfowl in L. Krankesjön, we used stepwise multiple regressions (backward removal; F-to-remove $\geq$0.100) to determine their relative importance. Regional population density and macrophyte cover acted as independent variables and local density of each specific functional waterfowl group as the dependent variable.

Results

At the start of the time series, the lake existed in a turbid state and had almost no submersed macrophytes. Eventually, the macrophyte cover increased from only a few percent of the lake's area in the mid-1980s to above 45% 5 years later (1990), and although no recordings were made between 1994 and 2004, observational data indicate that no major changes in macrophyte cover occurred during that period, but that the cover has been stable at between 30 and 50% since 1993. Over the time period, an increase in water clarity occurred, resulting in a positive relation between macrophyte cover and Secchi depth ($r = 0.71$; $t = 2.56$; $P < 0.030$; Fig. 1).

The main herbivore waterfowl species (Mute Swan, Coot and Wigeon) occurred in low numbers during the 1980s, but increased considerably in the beginning of the 1990s (Fig. 2). After a minor dip in abundance during the late 1990s, the numbers again increased and showed a maximum in 2001. The herbivore waterfowl also represent the function group

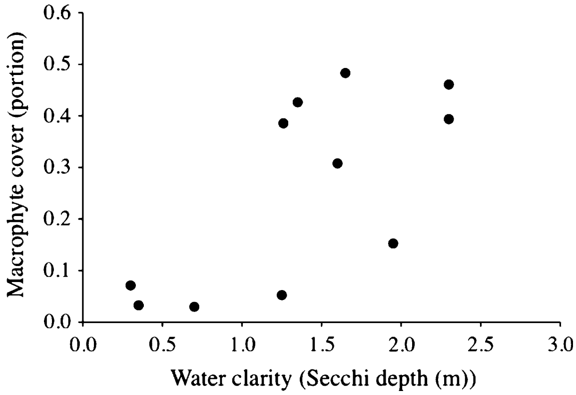

Fig. 1 The relation between water clarity, expressed as Secchi depth (m) and submersed macrophyte cover (portion) in L. Krankesjön

that showed the strongest positive linear relation with macrophyte cover ($r = 0.86$; Table 1; Fig. 3). In addition to being related to macrophyte cover in L. Krankesjön, they also showed a positive tendency in abundances at a regional scale ($r = 0.35$; NS; Fig. 3). However, a stepwise multiple regressions showed a strong relation between macrophyte cover and herbivorous waterfowl in L. Krankesjön, whereas the regional fluctuations in abundances do not add further explanatory power (Table 1).

Invertebrate feeders (including Goldeneye and Tufted duck) also occurred in low numbers in L. Krankesjön during the late 1980s, and then steadily increased in abundances until the end of the 1990s (Fig. 2). After this period, they have shown a steady decline. At a regional scale, invertebrate feeders showed a weak positive trend between 1985 and 2007 (Fig. 2), whereas they, just as the herbivores, showed a strong positive relation to macrophyte cover in the lake ($r = 0.68$; $t_{19} = 4.14$; $P < 0.001$; Fig. 3). Accordingly, regional population changes do not explain any variance beyond what the macrophyte cover in the lake does (Table 1). The fish-feeding waterfowl, such as Crested grebe and Common merganser, also occurred in low numbers in the lake during the late 1980s, then reached a maximum in the mid-1990s, and have since then decreased to mean abundances of about 50 individuals between May and October (Fig. 2). The regional trend among fish feeders was similar to that in the lake during the 1980s.

However, in contrast to what we observed in the lake, fish feeders showed a strong regional increase from about year 2000 (Fig. 2). Their relation to macrophyte cover was strongly positive ($r = 0.82$; Table 1; Fig. 3), and regional fluctuations in population size did not explain any further variation (Table 1). In contrast to the other functional groups of waterfowl in L. Krankesjön, the omnivorous species, Common Pochard, showed its highest abundances in the late 1980s and have since then steadily declined (Fig. 2), although no such trend has occurred at the regional scale (Fig. 2). Their abundances in relation to macrophyte cover showed a negative tendency ($r = -0.50$; Table 1; Fig. 3). Abundances of waterfowl taxa that spend a considerable time in the lake, but mainly feed on land, including Mallard and Teal, showed, as expected, no relation to macrophyte cover in the lake (Table 1; Fig. 3), whereas their population dynamics were weakly related to regional fluctuations (Table 1).

Discussion

Quantitative changes in submersed macrophyte cover may have strong effects on several trophic levels, because they create substrate and shelter for many organisms and increase the diversity as well as abundances of invertebrates and zooplankton (Hargeby et al., 1994), but also of waterfowl (Milberg et al., 2002; Rybicki & Landwehr, 2007). However, the reasons for fluctuations in macrophyte cover remains unclear, although many shallow eutrophic lakes undergo conspicuous and repeated state shifts between a turbid, phytoplankton dominated state, and a state dominated by macrophytes and clear water (Scheffer, 1990; Blindow et al., 1993; Hargeby et al., 1994, 2004). Because the clearwater state is preferred over the turbid state, techniques to improve the conditions for macrophyte establishment have been developed, including chemical, physical as well as biological restoration methods (Hansson et al., 1998; Søndergaard et al., 2007).

One of these techniques, biomanipulation, has been used with varying success with the aim to improve the water clarity and re-establish submersed macrophytes (Hansson et al., 1998; Søndergaard et al., 2007). The theory behind biomanipulation includes removing fish that feed on herbivorous zooplankton, thereby increasing the grazing pressure on phytoplankton. This will, at least in theory, lead to clear water and thus to light reaching the sediment surface, allowing

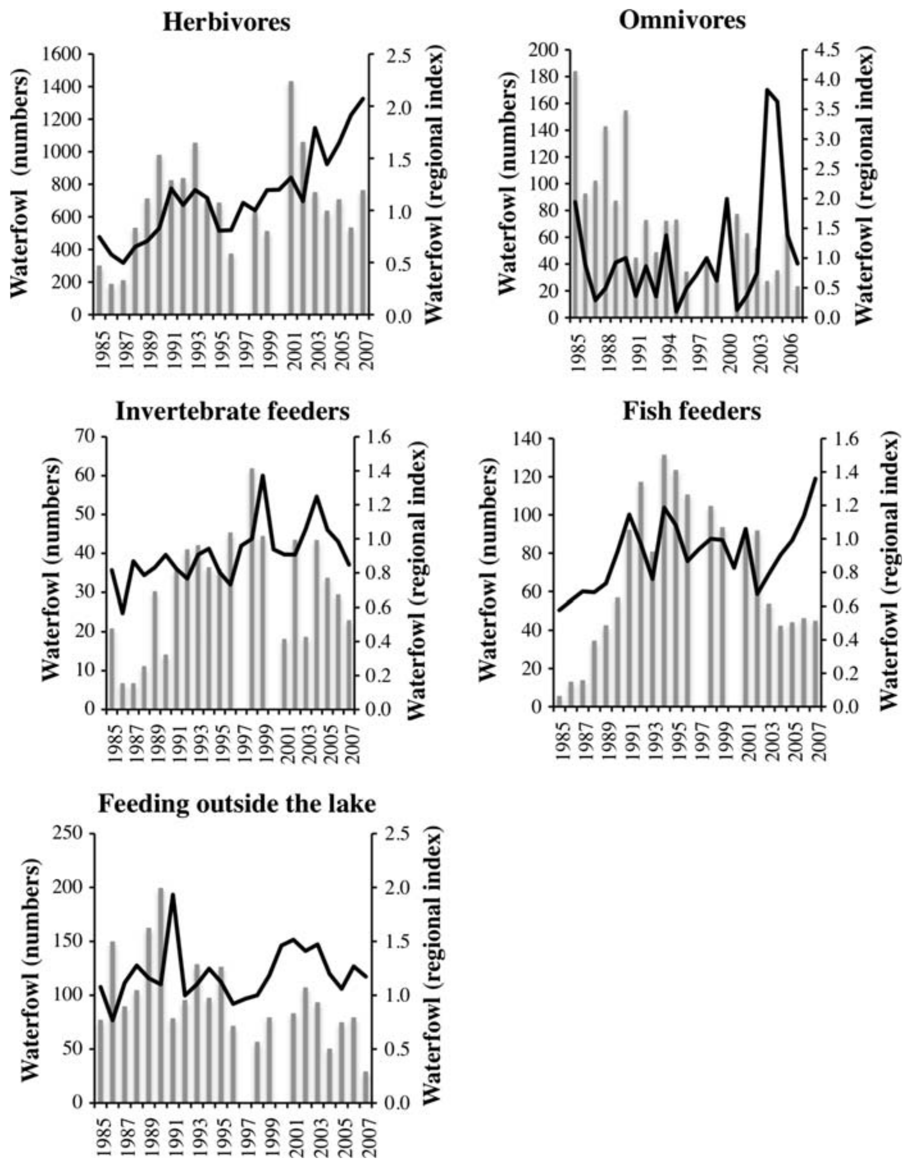

Fig. 2 Abundances of different functional groups of waterfowl in L. Krankesjön during May–October from 1985 to 2007 (*bars*), and regional abundance index for summer and winter countings (*line*). Species include herbivores: Mute Swan (*Cygnus olor*), Coot (*Fulica atra*), and Eurasian Wigeon (*Anas penelope*); invertebrate feeders: Goldeneye (*Buchepala clangula*) and tufted duck (*Aythia fuligula*); fish feeders: Great crested grebe (*Podiceps cristatus*) and Common merganser (*Mergus merganser*); and omnivorous species: (Common pochard (*Aythia ferina*)), as well as waterfowl, mainly feeding outside the lake including Mallard (*Anas platyrhynchos*) and Teal (*Anas crecca*)

submersed macrophytes to grow (Bergman et al., 1999). However, in some lakes, the shift between states is apparently initiated without direct human action, and several mechanisms have been suggested to cause such state shifts, including fish community dynamics (Hargeby et al., 1994), as well as abiotic factors (Hargeby et al., 2004, 2007; Moss et al., 2004). Our study lake, L. Krankesjön, has gone through several such state shifts, the latest one from turbid to clear water state occurring during the mid-1980s. From 1985, when the macrophytes covered only a few percent of the lake area, they increased to cover more than 45% within a few years (Blindow et al., 1993). Since then, the macrophyte cover has been relatively stable at between 30 and 50%.

Mallard (*Anas platyrhynchos*) and Teal (*Anas crecca*) showed no relation to macrophyte cover, but they showed a slight tendency for covariation with regional variations in abundances (Table 1). The absence of a relation with macrophyte cover is likely due to the fact that they mainly feed on land, i.e., they do not primarily rely on food in the submersed macrophyte beds. Invertebrate feeders, on the other hand, are visual feeders of invertebrates within the

Table 1 Stepwise multiple regressions using fluctuations in numbers of each waterfowl functional group (fish feeders, birds mainly feeding outside the lake, omnivores, invertebrate feeders, and herbivores) on a regional scale ("Reg#") and submersed macrophyte cover in L. Krankesjön ("Macrophytes") as independent variables and numbers of each functional waterfowl group as dependent variables

Independent	Dependent	*r*	*F*	*P*
(1) Reg# and Macrophytes	Fish feeders	0.82	8.16	0.012
(2) Macrophytes	Fish feeders	0.82	17.98	0.002
(1) Reg# and Macrophytes	Not feeding in the lake	0.42	0.88	NS
(2) Macrophytes	Not feeding in the lake	0.00	–	NS
(1) Reg# and Macrophytes	Omnivores	−0.52	1.53	NS
(2) Macrophytes	Omnivores	−0.50	3.05	NS
(1) Reg# and Macrophytes	Invertebrate feeders	0.73	4.62	0.046
(2) Macrophytes	Invertebrate feeders	0.68	7.67	0.022
(1) Reg# and Macrophytes	Herbivores	0.90	17.47	0.001
(2) Macrophytes	Herbivores	0.86	25.00	0.001

For each functional group, the partial correlation coefficients (*r*), *F*-statistics, and probability values (*P*) are given for both independent variables together (1) and for macrophyte cover (2). Criterion for the backward removal was *F*-to-remove $\geq$0.100. NS (non-significant) denotes $P > 0.05$

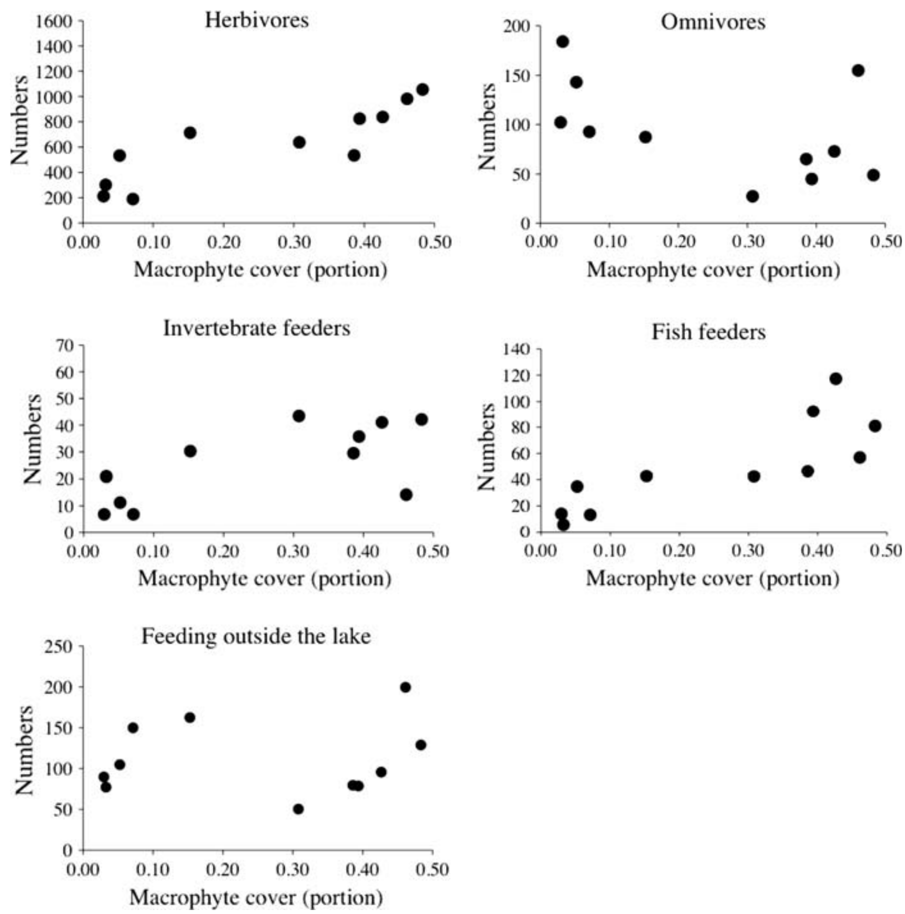

Fig. 3 The submersed macrophyte cover (%) related to functional groups of waterfowl during May–October, including herbivore species: Mute Swan (*Cygnus olor*), Coot (*Fulica atra*), and Eurasian Wigeon (*Anas penelope*); invertebrate feeders: Goldeneye (*Buchepala clangula*) and tufted duck (*Aythia fuligula*); fish feeders: Great crested grebe (*Podiceps cristatus*) and Common merganser (*Mergus merganser*); and omnivorous species (Common pochard (*Aythia ferina*), as well as waterfowl, mainly feeding outside the lake including Mallard (*Anas platyrhynchos*) and Teal (*Anas crecca*)

Table 2 Estimates of waterfowl consumption of submersed macrophytes in shallow lakes expressed as proportion (%) of macrophyte biomass

Main taxa	Consumption (%)	Source
Mute Swan and Coot	75	Reichholf (1973)
Mute Swan	Insignificant effect	Berglund et al. (1963)
Various taxa	1.6	Nienhuis (1978)
Mute Swan	15–60	Kiørboe (1980)
Mute Swan, Wigeon and Coot	3	This study
Mute Swan and Coot	25	Søndergaard et al. (1998)
Various taxa	13	Wollhead (1994)
Various taxa	15–100	Lodge et al. (1998)

submersed macrophyte beds. Therefore, they should be expected to respond more strongly to changes in macrophyte cover (Hanson & Butler, 1994). Our data partly supported this notion since population dynamics of this group showed a positive response to macrophyte cover (Fig. 3), whereas regional fluctuations had less of an influence (Table 1). Also, the fish-feeding Great Crested grebe and Common merganser showed a strong correlation to macrophyte cover (Fig. 3), which, with respect to Great Crested Grebe, has been previously expounded (Milberg et al., 2002).

As a partial explanation, fish feeders also use vision to detect prey, and water clarity generally relates positively to macrophyte cover (Blindow et al., 1993; Hargeby et al., 1994), enhancing prey detection (Eriksson, 1985). Hence, although some waterfowl groups have shown regional fluctuations in abundances, macrophyte cover seems to have stronger effects on abundances in L. Krankesjön. During fall, from late August to October, mainly migratory individuals comprise the waterfowl in the lake. The strong relation between macrophyte cover and waterfowl abundances implies that waterfowl may actually adjust their migratory routes as a result of the present macrophyte cover in lakes.

Reductions in waterfowl abundances are generally seen as consequences of deteriorating habitat quality, whereas the possibility that waterfowl may instead be a driving force behind changes in the lake or wetland habitat is rarely discussed, even though many bird species have the potential to affect their habitat (van Donk & Otte, 1996; Marklund et al., 2002). For example, Coot (*Fulica atra*), which is a dominant waterfowl species in many shallow lakes, including L. Krankesjön, may consume between 43 and 45 g DW of macrophytes tissue per individual per day (Kiørboe, 1980; van Donk & Otte, 1996), and Mute Swan 104 g DW day^{-1} (Kiørboe, 1980; Mitchell & Wass, 1995). Feeding rate of the third herbivorous species included in our study, Eurasian Wigeon, is unfortunately not available with us. In L. Krankesjön, the number of bird days per year is about 460,000 for Coot and 35,000 for Mute Swan. Hence, these two herbivores would, theoretically, consume 19,675 and 3,590 kg DW of macrophytes per year, respectively. Submersed macrophytes cover about 35% (1.5×10^6 m^2) of the lake area and have an approximate biomass of 600 g m^{-2} (Blindow et al., 2002), which correspond to a total macrophyte biomass in the lake of about 900,000 kg (DW). This means that Coot and Mute Swan have the potential to consume about 2.6% of the macrophyte biomass in L. Krankesjön.

These calculations, although somewhat crude, still illustrate that the feeding rate by the main herbivorous bird species may not affect the total standing stock of submersed macrophytes in this specific lake. Accordingly, our long-term data set shows no negative effects on macrophytes from waterfowl, but shows, instead, a positive relation, suggesting that the level of herbivory, at least on *Chara* spp. in L. Krankesjön, is of minor concern. Besides direct consumption, herbivorous birds may also detach macrophytes from the sediment (van Donk & Otte, 1996; Nolet et al., 2001) and also make nutrients flow from sediments to water (Chaichana et al., 2009). Waterfowl herbivory on macrophyte resting stages has also been documented, although the effects on the aboveground macrophyte biomass in subsequent years may be low (Sponberg & Lodge, 2005).

Although waterfowl may affect macrophytes in several ways, presently the effects of waterfowl in L. Krankesjön remain negligible, mainly due to the extremely high biomass of the macrophytes covering a major part of the lake area and reaching from bottom to the water surface from May to late October. However, during periods of lower macrophyte biomass, or when the lake is in transition between alternative stable states, the consumption rate of waterfowl may indeed have a negative effect on the macrophytes. This may also be the reason for the highly variable estimates of waterfowl effects on macrophytes reported in the literature (Table 2), ranging from a few percent to almost complete eradication of the macrophytes (Lodge et al., 1998).

From our study, we may conclude that macrophytes have a strong positive effect on waterfowl abundances, whereas waterfowl herbivory seems to have limited effects on the macrophyte cover. Although the overall effect of macrophytes is positive, not all waterfowl groups respond to changes in macrophyte abundances. For example, species not mainly feeding in the lake, such as Mallard, Teal, and Common Pochard will not respond to changes in macrophyte cover. On the other hand, the population dynamics of waterfowl feeding on macrophytes, invertebrates, as well as fish, are strongly regulated by macrophytes. Hence, restoration efforts directed toward increasing macrophyte cover will stimulate different bird species in different ways. It may also be noted that if migrating waterfowl are selecting lakes based on lake water quality, then migratory routes may change over time as a result of lake management efforts or spontaneous shifts between turbid and clearwater states.

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