

# Submerged vegetation and the variation in the autumn waterfowl community at Lake Tåkern, southern Sweden

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We analysed data from 25 years of standardised mid-September counts of waterfowl at eutrophic Lake Tåkern, southern Sweden. For eight species, counts were compared with a national index constructed from similar counts at numerous lakes and coastal sites. For Crested Grebes and Mute Swans there was a correlation between counts at Lake Tåkern and the national index, suggesting that they simultaneously vary in number over a large geographic area. Indirect gradient analysis (PCA) revealed a strong temporal trend in the data, which was covaried out in a partial PCA to expose residual patterns. This ordination separated Pochards and Tufted Ducks at one end of the first axis from Cormorants and Goosanders at the other. A direct gradient analysis, with biomass of submerged macrophytes (recorded for 14 of the 25 years) as the sole environmental variable, showed that bird species composition varied significantly with plant biomass. The piscivores, Cormorants and Goosanders, were abundant in years with small amounts of plant biomass, while several species were most abundant in years with large amounts. Our analyses suggest that the abundance of submerged macrophytes is an important determinant of the bird community composition in eutrophic lakes.

## 1. Introduction

The importance of a breeding or stopover site for birds may change over time due to large- or small-scale changes in land use, food availability and disturbance affecting both bird population size and their exploitation pattern (e.g. Gutzwiller &

Anderson 1999, Chamberlain *et al.* 2000, Kouki & Väänänen 2000, Donald *et al.* 2001, Kalejta-Summers *et al.* 2001, Vickery *et al.* 2001). Therefore, managing sites of importance for migrating or breeding birds will benefit from knowledge about the underlying causes for directional changes as well as fluctuations in bird numbers.

Conservation of wetlands that are important stopover sites for waterfowl is critical in regions where wetlands are scarce (Tucker & Evans 1997). Large numbers of ducks, geese and swans pass through southern Scandinavia each autumn on their way from breeding sites in the north to wintering areas in western and southern Europe and Africa. One of the most significant stopover sites in southern Sweden is Lake Tåkern. Recognised as an important breeding and resting site for waterfowl (e.g. Söderberg 1929, Ekstam 1975), Lake Tåkern is listed as an important site in the Ramsar convention (Naturvårdsverket 1989) and was established as a nature reserve in 1975 (Kärsgård 1987). The lake attracts large numbers of geese and ducks each autumn (e.g. Wallin & Milberg 1995, Gezelius 1998, Nilsson 2000). Biomass of submerged vegetation varies considerably in Lake Tåkern between years (Lohammar 1988, Blindow 1992). In fact, the lake has been suggested to alternate between two alternative stable states characterised either by clear water and high abundance of submerged macrophyte biomass, or turbid water, high phytoplankton biomass and only sparse occurrence of submerged macrophytes (Blindow 1992, Scheffer *et al.* 1993, Blindow *et al.* 1993, 1998).

Since the early 1970s, standardised counts at Lake Tåkern of around 20 wetland bird species, mainly ducks, have been conducted in mid-September. Here, we used these data in three different ways. First we compared counts from Lake Tåkern with data from numerous sites in southern Sweden recorded on the same days. This distinguished species that varies simultaneously in numbers over a large geographic area from those that respond to site-specific phenomena. Second, we used an indirect ordination technique, Principal Component Analysis (PCA), to structure the data from 25 years according to the birds recorded. To highlight the interannual variability in the bird community, we covaried out a strong temporal trend in a partial PCA (pPCA). Third, for 14 of the years under consideration, we had estimated the biomass of submerged macrophytes. We used these data in a direct gradient analysis to test whether plant biomass variation can 'explain' variation in the bird community.

## 2. Materials and methods

### 2.1. Lake description

Lake Tåkern is a moderately eutrophic lake in an agricultural landscape dominated by large, open arable fields in south central Sweden (58°22'N, 14°49'E). The lake perimeter is 32 km and the lake surface is 44 km<sup>2</sup>. The average depth is 0.8 m and the difference between maximum (May) and minimum level (October) is 0.45 m. The zone between the arable fields and the lake itself is partly covered by forest (60%) and partly by open grazed areas (40%), all occurring on low-productive land gained when the water table was substantially lowered in the 1840s (Milberg 1991). Open water areas (about 29 km<sup>2</sup>) are surrounded by large stands of emergent and floating-leaved aquatic vegetation dominated by *Phragmites australis* with some *Carex pseudocyperus*, *Nuphar luteum*, *Scirpus lacustris* and *Typha angustifolia*. Charophytes (mainly *Chara tomentosa* and *Nitellopsis obtusa*) are the dominant submerged macrophytes; other common species are *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Potamogeton crispus* and *Ranunculus circinatus*. The lake is calcium-rich (about 40 µg Ca L<sup>-1</sup>), and mean summer concentrations of total phosphorus and total nitrogen are 30–55 µg L<sup>-1</sup> and 1400–1500 µg L<sup>-1</sup>, respectively. Important fish species are *Carassius carassius*, *Esox lucius*, *Perca fluviatilis*, *Rutilus rutilus*, *Scardinius erythrophthalmus* and *Tinca tinca*.

The shallow lake offers only limited opportunity for recreation. The boats in the lake are small and flat-bottomed (motor boats are prohibited) and are used for fishing and hunting, activities that are reserved for landowners only. The hunting season commences on 21 August, with very little hunting being conducted after the first 1–2 weeks. The general public has access to the lake mainly at four observation points designated by the conservation authorities, and is restricted to these places during the breeding season.

### 2.2. Estimation of submerged macrophyte biomass

An estimate of the average amount of submerged plant biomass per lake area (excluding reed belts)

was calculated per year by combining the average density of two types of plants (charophytes and angiosperms) with maps of their distribution. The distribution of submerged vegetation was mapped from a boat during July or August once a year from 1983 to 1994 (except for 1984, 1986 and 1993), as well as from aerial photographs (available for several years). Plant biomass was determined by means of a steel or sharpened plexiglass tube which was used to enclose a defined area of the lake bottom. Within the dense stands of charophytes, a small tube (diameter 100 mm) was used. Within the sparse and more scattered stands of angiosperms (mainly *Myriophyllum spicatum*), larger tubes were used (diameter 100 to 750 mm). Above- and below ground parts of the enclosed plants were collected with a rake and weighed, and average biomass was calculated from a larger number of samples.

In the years 1995–99 submerged plants were not visible from the boat due to high water turbidity. During those years, a rake was used to obtain an overview of the distribution of submerged plants in the lake. Biomass of submerged plants was determined by estimating a factor for reduction in plant density and/or height compared with previous years. Estimates for overall biomass of submerged macrophytes are therefore less precise, and likely overestimate the amounts for these years compared with the earlier years.

### 2.3. Bird counts in Lake Tåkern

In 1974 and 1976–99, simultaneous counts of wetland birds were conducted once in mid-September, around 0700–0900. This co-ordinated count took place on a Sunday or Saturday morning, and was undertaken as part of the International Waterfowl Counts (Nilsson 1995, 1999). Each count involved observations by 1–2 competent observers from each of ten fixed observation points around the lake perimeter. With the aid of telescopes, most of the open lake areas were covered in this way. Areas of large dense reedbeds were surveyed from a canoe.

### 2.4. Comparison with a national index

Since 1973, annual counts of waterbirds have been conducted on a large number of coastal and in-

land sites in southern Sweden during September (Nilsson 1995, 1999). Most counts occurred on the Sunday closest to September 15. Annual national September indices were calculated for eight species that had been recorded in sufficient numbers (for the present purpose) at Lake Tåkern. The indices were calculated by pair-wise comparisons of all sites, but excluding data from Lake Tåkern, counted in two consecutive years. The total for year 2 was expressed as per cent of the total for the same localities in year 1, this primary index being recalculated in relation to the index for year 1. Eventually the series was recalculated in relation to the mean index for the first ten years being equal to 100. The index was then correlated with the Tåkern counts, which had been transformed ( $\log [x + 1]$ ) before analyses.

### 2.5. Community analyses

Indirect (unconstrained) ordination methods were initially used to summarise complex data and for data exploration leading to formulation of the hypothesis (Kauppinen & Väisänen 1993). With the advent of direct (constrained) ordination methods, hypothesis testing has become possible (e.g. Hallgren *et al.* 1999, Milberg *et al.* 2001). Here, we used both indirect and direct gradient analysis techniques to ordinate years according to the bird count data (including only the 14 most abundant species, recorded with a total of > 500 individuals). All analyses were conducted using default options in CANOCO 4.0 (ter Braak & Smilauer 1998) on log-transformed ( $\log [x + 1]$ ) count data.

Initially, a Detrended Correspondence Analysis (DCA) was conducted with the purpose of evaluating the length of gradients in the data. Since these were found to be short (< 0.7 SD) all subsequent analyses were done with methods based on linear relationships rather than unimodal ones.

We first conducted a PCA, an indirect gradient analysis method in which samples are arranged according to species composition and abundances alone. Important environmental gradients are then interpreted from trends in species abundances. Since we expected bird numbers to be negatively correlated with wind speed, we used wind recordings on the days of the count from the nearest meteorological station (Malmslätt; 35 km E of

Lake Tåkern) as a passive environmental variable in the DCA. We also used 'year' as a passive, continuous variable since we expected a linear temporal trend. This analysis (not reported) produced a high correlation between the scores for individual years in the first Principal Component (PC1) and the variable 'year', but a low correlation with the wind data (also low correlation with PC2). Therefore, we used 'year' as a covariable in the following partial PCA (pPCA), hence looking only at the residual variation after partialling out the temporal trend (see ter Braak 1988 for information on partial ordination analysis).

To describe how the bird community varied with the abundance of submerged macrophytes, we conducted a Redundancy Analysis (RDA). This direct gradient analysis technique explains community variation by detecting patterns of variation in species abundance that can best be explained by a set of environmental variables. We used estimates of the biomass of submerged macrophytes (log-transformed) as the sole environmental variable. The RDA included only data from the 14 years for which biomass estimates were available (1983, 1985, 1987–92, 1994–99). This analysis ranked

species according to their occurrence along the gradient from high to low plant biomass.

Finally, since a strong temporal trend in the data might confound the pattern related to plant biomass, we conducted a partial RDA (pRDA) where we covaried out the effect of 'year' to test the null hypothesis that the bird community is unrelated to the amount of submerged plant biomass.

### 3. Results

Thirty-two bird species were recorded at Lake Tåkern during the mid-September counts conducted between 1974 and 1999. Of these, 20 occurred in more than five years (Table 1). The most abundant bird species were the Coot, Mallard and Pochard (Table 1).

#### 3.1. Comparison with a national index

The national index and Lake Tåkern counts were correlated for two species of the eight tested: the Crested Grebe and Mute Swan (Table 2). However, the rela-

Table 1. Bird species recorded for more than five years during September counts at Lake Tåkern (1974, 1976–1999), the number of years a species was recorded, the total number of individuals recorded, and the coefficient of variation (CV) of annual counts.

	No. of years	Total No.	CV (%)
Coot ( <i>Fulica atra</i> )	25	198040	114
Mallard ( <i>Anas platyrhynchos</i> )	25	44734	68
Pochard ( <i>Aythya ferina</i> )	25	42310	98
Mute Swan ( <i>Cygnus olor</i> )	25	26588	41
Teal ( <i>Anas crecca</i> )	25	21091	87
Wigeon ( <i>Anas penelope</i> )	25	18834	83
Crested Grebe ( <i>Podiceps cristatus</i> )	25	6800	82
Goosander ( <i>Mergus merganser</i> )	25	2001	100
Gadwall ( <i>Anas strepera</i> )	25	1216	84
Goldeneye ( <i>Bucephala clangula</i> )	25	1061	84
Tufted Duck ( <i>Aythya fuligula</i> )	24	3121	112
Pintail ( <i>Anas acuta</i> )	24	1125	120
Shoveler ( <i>Anas clypeata</i> )	22	564	115
Garganey ( <i>Anas querquedula</i> )	13	38	
Red-necked Grebe ( <i>Podiceps grisegena</i> )	9	15	
Shelduck ( <i>Tadorna tadorna</i> )	8	18	
Slavonian Grebe ( <i>Podiceps auritus</i> )	8	12	
Red-breasted Merganser ( <i>Mergus serrator</i> )	7	140	
Cormorant ( <i>Phalacrocorax carbo</i> )	6	2491	
Whooper Swan ( <i>Cygnus cygnus</i> )	6	18	

tionships were not strong, especially not if we ‘correct’ for the multiple tests conducted (Table 2). Still, these two species seem to vary in number all over southern Sweden and do not seem greatly influenced by annual conditions at Lake Tåkern. For the other six species we conclude that the numbers at Lake Tåkern vary more or less independently of other sites. Hence, one or several site-specific conditions are likely to determine their numbers at Lake Tåkern.

**3.2. Indirect ordination analysis**

The pPCA, eliminating the strong temporal trend in the data, separated the Pochard and Tufted Duck at one end of the first axis from the Cormorant and Goosander at the other (Fig. 1).

Several of the most abundant species at Lake Tåkern feed on submerged macrophytes and others feed on macroinvertebrates associated with submerged vegetation, while a few are piscivores (Table 3). We therefore expected the abundance of submerged macrophytes (Fig. 2) to greatly influence the bird community composition as previously shown in some other lakes (Mitchell *et al.* 1988, Hanson & Butler 1994). Estimates of submerged macrophyte biomass (log transformed) for 14 of the 25 years correlated well ( $R = -0.908$ ;  $P < 0.001$ ) with the PC1 scores (from the ordination in Fig. 1B).

**3.3. Direct gradient analysis**

To further explore the importance of submerged macrophyte biomass, we conducted an RDA with

Table 2. Correlation between the National Index and counts at Lake Tåkern (log [x + 1]) 1976–1998.

	Correlation coefficient (R)	P
Crested Grebe	0.453	0.0303*
Mute Swan	0.437	0.0376*
Mallard	0.261	0.229
Coot	0.0811	0.713
Wigeon	0.0577	0.794
Teal	-0.0265	0.905
Goldeneye	-0.223	0.306
Tufted Duck	-0.256	0.238

\* ns when applying a Bonferroni correction for multiple tests ( $\alpha = 0.00625$ )

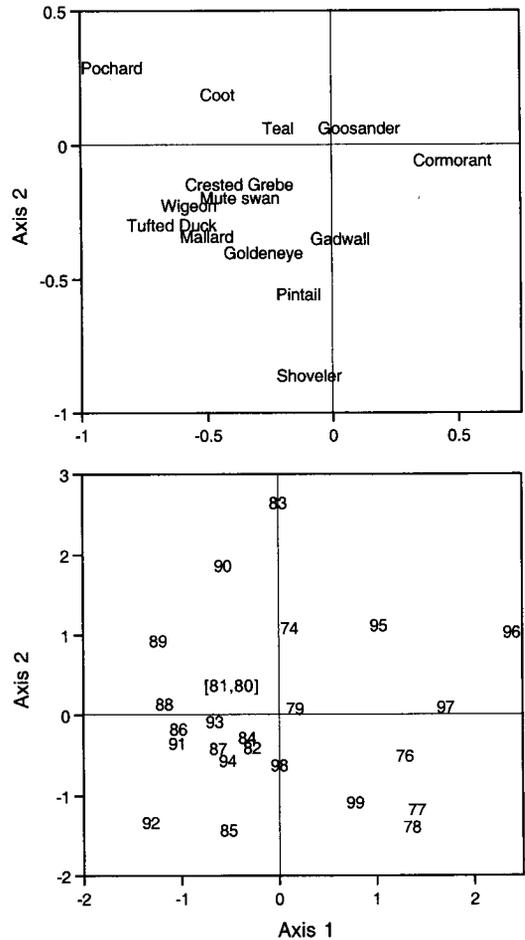


Figure 1. pPCA ordination diagram of (1A) the aquatic birds recorded in mid-September at Lake Tåkern and (1B) the study years. ‘Year’ was used as a continuous covariable to eliminate a strong temporal trend. Eigenvalues of PC1 and PC2 were 0.236 and 0.124, respectively.

vegetation biomass as the sole environmental variable (Fig. 3). With only one environmental variable, this type of analysis constrains this variable to the first axis while the second axis displays most of the residual variation. Since the pattern was partly confounded by the long-term changes in the bird fauna in 1983–1999, we conducted a pRDA, using ‘year’ as a continuous covariable, with the sole purpose of achieving a more rigid statistical test of the strength of the relationship between bird community and plant biomass. This test showed that the relationship, even after eliminating variation explained by ‘year’, was highly

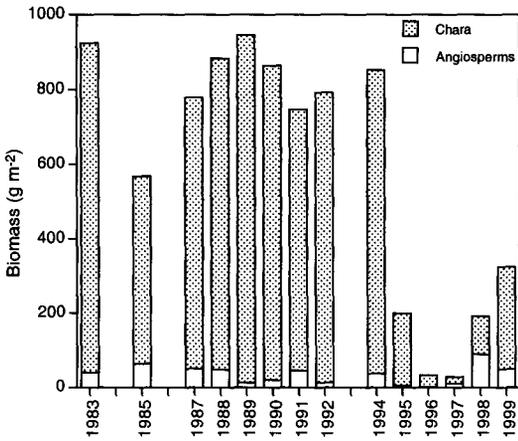


Figure 2. Biomass (g fresh weight m<sup>-2</sup> of lake surface outside the reed belts) of angiosperms (white) and charophytes (hatched) in Lake Tåkern.

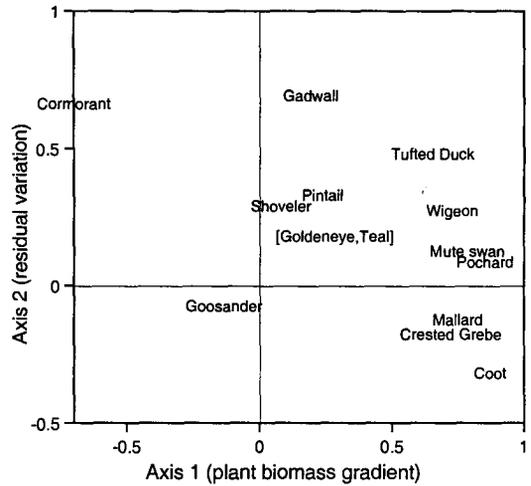


Figure 3. RDA ordination diagram of mid-September bird counts from 14 years. Biomass of submerged macrophytes (log transformed) was used as the only environmental variable, hence the x-axis represents a gradient of years from little (-) to large (+) amounts of biomass. Eigenvalues of axis 1 and 2 were 0.387 and 0.212, respectively.

significant ( $P = 0.0025$  in a Monte Carlo permutation test with 1999 permutations,  $F = 4.14$ ; eigenvalue of the first axis was 0.174).

Cormorants and Goosanders were most abundant in years with low plant biomass (i.e. they were located far to the left in Fig. 3 and had low RDA and pRDA scores in Table 3). Many spe-

cies were associated with conditions of high plant biomass (i.e. they were located far to the right in

Table 3. Ordination scores for bird species recorded during September counts at Lake Tåkern (1983, 1985, 1987–92, 1994–99) along the first ordination axis, constrained by submerged plant biomass gradient, in RDA and pRDA (using 'year' as covariabel). The number within parentheses is the amount of variance in a species 'explained' by plant biomass. Food preference according to Cramp and Simmons (1977, 1980), Krapu and Reinecke (1992), Nummi and Väänänen (2001).

	RDA score	pRDA score	Plant material	Invertebrates	Fish
Coot	0.87 (76)	0.51 (26)	**	*	
Pochard	0.85 (73)	0.67 (44)	**	*	
Mute Swan	0.79 (62)	0.67 (45)	***		
Mallard	0.75 (56)	0.54 (29)	**	*	
Wigeon	0.73 (53)	0.76 (58)	***		
Crested Grebe	0.73 (53)	0.35 (12)		*	**
Tufted Duck	0.65 (42)	0.65 (42)	*	**	
Teal	0.31 (10)	0.49 (24)	**	*	
Goldeneye	0.28 (8)	0.24 (6)	*	**	
Pintail	0.24 (6)	0.25 (6)	**	*	
Gadwall	0.20 (4)	0.62 (39)	**	*	
Shoveler	0.085 (1)	0.18 (3)	*	**	
Goosander	-0.13 (2)	-0.042 (0)			***
Cormorant	-0.70 (49)	-0.15 (2)			***

\*\*\* Practically sole food item;

\*\* More than half of the food intake but still supplemented by other types;

\* A substantial food item, but less than half of the intake.

Fig. 3 and had high scores in Table 3): Wigeon, Pochard, Mute Swan, Tufted Duck, Gadwall, Mallard, Coot and Teal.

#### 4. Discussion

Birds in transit during autumn are likely to select a stopover site depending on both food availability and level of disturbance (Tuite *et al.* 1984). Birds at Lake Tåkern are only subject to co-ordinated human disturbance for a few days at the beginning of the hunting season. For most of the year, human disturbance will be highly localised and there are always parts of this large lake where birds are relatively undisturbed. Therefore, we expected food availability to be more important than disturbance in determining its suitability as a stopover site. Several of the most abundant species at Lake Tåkern feed on submerged macrophytes and others feed on macroinvertebrates associated with submerged vegetation, while a few are piscivores (Table 3). Hence, we expected at least some species to respond to the abundance of submerged plant biomass. This assumption was confirmed in the present study. First, there was a significant correlation between the ordination scores for years in the indirect gradient analysis (Fig. 1B) with submerged plant biomass (Fig. 2). Second, the direct gradient analysis (Fig. 3) allowed a strict test of this assumption to be conducted showing that plant biomass 'explained' a significant part of the variation in species composition, even after covarying out the long-term change in data.

Data from single bird counts during the migration season are crude estimates of an intrinsically volatile parameter. Therefore, it is perhaps surprising that so clear and interpretable patterns emerged from our analysis. On the other hand, birds have no reason to remain at a lake with poor food availability during autumn migration, even in the absence of human disturbance (Väänänen 2001). Instead, birds will aggregate and remain a long time at a suitable site. Autumn count data might therefore be a very sensitive proxy for food availability. Consequently, the interannual variation was much larger during autumn at Lake Tåkern than that reported in studies of breeding

waterfowl populations (CV in Table 1 compared with Nudds 1983 and Kauppinen & Väänänen 1999).

Cormorants and Goosanders were most abundant in years with low plant biomass. As both are piscivores (Cramp & Simmons 1977), we speculate that sparse submerged plants offer better conditions for these birds than dense vegetation, which may act as a mechanical obstacle. The Cormorant has expanded greatly in range and number in northern Europe in the latter part of the time period under consideration (van Eerden & Gregersen 1995). Therefore, its ordination must be interpreted with care since it occurred in only six years out of the 14 analysed in the RDA and pRDA.

It is perhaps surprising that the Crested Grebe, the third piscivore in our data set (Cramp & Simmons 1977), was not associated with sparse submerged macrophytes but was located in the middle of the species swarm in Fig. 3 (some distance away from the Cormorant and Goosander). Since there has been a general decline of this species in Sweden, as well as at Lake Tåkern during this time period, coinciding with a reduction in submerged vegetation (Fig. 2), the pRDA score for this species is relevant. Covarying out 'year' revealed a clear association of this species with abundance of submerged macrophytes (Table 3). Invertebrates can be an important food item for the Crested Grebe, particularly in summer, and can even be the dominant food in some areas (Il'icev *et al.* 1985). Macroinvertebrates are abundant in dense vegetation (Krull 1970, Pöysä 1992, Hargeby *et al.* 1994, Marklund 2000), where they are probably protected from predation by fish. Hence, we suggest that the Crested Grebe might rely, to a large extent, on invertebrates during the autumn at Lake Tåkern, which would explain its ranking in the plant biomass gradient in Fig. 3.

Many species were associated with conditions of high plant biomass (Fig. 3, Table 3): Wigeon, Pochard, Mute Swan, Tufted Duck, Gadwall, Mallard, Coot and Teal. This group contains omnivores, plant eaters and those primarily eating small invertebrates (Olney 1968, Nilsson 1972, Cramp & Simmons 1977, 1980, Pöysä 1982, Suter 1982, Krapu & Reinecke 1992, Nummi & Väänänen 2001). As explained above, macro-

invertebrate abundance is likely to peak in years with extensive stands of submerged plants leading to ample and diverse food sources for all three feeding guilds.

Our data show that submerged plant biomass is a key factor, explaining a major part of the fluctuations of birds at Lake Tåkern during the autumn. Unfortunately, our understanding of the mechanisms causing changes in submerged macrophyte biomass is limited, and we can therefore not give any recommendations to enhance plant biomass in order to stabilise the lake's value for waterfowl. Several factors like nutrient loading, fish abundance, water level fluctuations and some weather conditions may affect submerged plants, and the picture is complicated by possible interactions between these factors (Blindow *et al.* 1998).

Bird count data are gathered along coasts and at lakes and wetlands around the world mainly to enable the detection of temporal trends in population size (Bautista *et al.* 1992, Prys-Jones *et al.* 1994, Link & Sauer 1998, Siriwardena *et al.* 1998, Duncan *et al.* 1999). Such data can also be used to examine other questions such as possible causes for fluctuations in numbers. We believe ordination methods, especially direct gradient analysis, to be powerful tools in analysing bird count data (see Petersen 1998, Boren *et al.* 1999 and Chamberlain *et al.* 2000 for other examples). This is not only because they summarise complex data but also because of their strength in detecting underlying gradients in data. Species are unlikely to respond independently to changes in the environment, i.e. several species might respond to the same environmental change (although not necessarily in the same way), so a 'community perspective' makes sense. Another strength in direct gradient analysis methods is the possibility to conduct a single statistical test, rather than numerous species-wise tests, thereby reducing the risk for Type I error (i.e. rejecting a null hypothesis that is true).

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## Sammanfattning: Undervattensvegetation och variationen i höstrastande sjöfågel i Tåkern, södra Sverige

Vi analyserade data från standardiserade sjöfågelräkningar i den måttligt eutrofa sjön Tåkern i södra Sverige. Hos åtta arter jämfördes räkningarna med ett nationellt index konstruerat från likande räkningar vid åtskilliga lokaler. För skäggdopping och knölsvan fanns en korrelation mellan räkningarna vid Tåkern och index, vilket tyder på att dessa arter varierar simultant över ett stort geografisk område. Enligt en indirekt gradientanalys (PCA) fanns en tydlig förändring över tiden i data, och denna eliminerades i en partiell PCA för att avslöja mönster i resterande variation. I denna ordination fördelades arterna längs första ordinationsaxeln från brunand och vigg till storskarv och storskrak. En direkt gradientanalys, i vilken biomassa av undervattensväxter (beräknat för 14 av de 25 åren) var den enda miljövariabeln, visade att fågelfaunan varierande signifikant med växtbiomassan. Fiskätande arter (storskrak och storskarv) var vanligast under år med små mängder växter medan flera andra arter var vanligast under år med mycket växter. Vår analys tyder på att mängden undervattensväxter är mycket betydelsefull för fågelfaunans sammansättning i eutrofa sjöar.

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