Environmental changes and population trends of breeding waterfowl in northern Baltic Sea

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Causes behind the changes in waterfowl populations in the Archipelago Sea, SW Finland, have until now not been quantitatively analysed. We modelled the impact of eutrophication, winter severity, weather conditions during breeding and water salinity on the breeding populations of ten waterfowl species (ducks, great crested grebe *Podiceps cristatus* and coot *Fulica atra*) using generalised linear models and the program TRIM (TRends and Indices in Monitoring data). The populations of the goldeneye *Bucephala clangula*, coot and velvet scoter *Melanitta fusca* decreased with increasing eutrophication. The populations of the goldeneye, coot, mallard *Anas platyrhynchos*, mute swan *Cygnus olor* and eider *Somateria mollissima* were most vulnerable to winter severity. We did not find evidence for impacts of weather conditions during breeding or water salinity on population trends. We also discuss alternative explanations to the observed population trends, such as predation and disturbance.

Introduction

The population sizes of birds are affected by food resources, availability of nesting sites, weather, predation, disease and disturbance (Newton 1998). Nowadays, environmental changes, such as those imposed by changes in land use and land management, are threatening the populations, range and diversity of European birds (Tucker & Heath 1994). Globally, 85% of threatened bird species are at risk as a result of habitat loss and degradation (BirdLife International 2000). Seabirds are an important part of marine ecosystems, usually as predators at the top of the food chain. They are also regarded as good indicators of environmental changes, especially contaminants (e.g. Becker 1989). Seabirds may, however, also serve as indicators of other aspects of the marine environment (Furness & Camphuysen 1997). They link into the marine ecosystem on a number of trophic levels (Tasker & Reid 1997). In addition, gulls, ducks and waders play an important role in the mass and energy fluxes of food webs, as well as food web control (Moreira 1997, Eybert *et al.* 2003). Thus, seabirds may provide means to monitor changes on lower trophic levels, and fill a part of the gap in our knowledge of marine ecosystems under stress.

Enclosed seas, such as the Baltic Sea, have specific environmental characteristics. However, the environmental problems of the Baltic Sea are to a great extent also faced by the other seas of the world. Since the 1960s, the main threat to the Baltic Sea is eutrophication, which is also recognised as one of the major threats to coastal marine ecosystems on a global scale (Nixon 1990). In the Baltic Sea, the increase of organic matter is largely caused by an increase of nutrient input followed by an increase in primary and secondary production (HELCOM 1993, Bonsdorff *et al.* 1997b).

Eutrophication mainly affects birds indirectly by increasing the primary production in the sea (Beukema & Cadée 1991, Pitkänen 1994, Bonsdorff *et al.* 1997a). If eutrophication leads to an increase in the food resources of birds, it may allow their populations to increase, which can lead to their spread into new habitats (von Haartman 1982, 1984). However, eutrophication may also change the species composition and function of aquatic animal communities (Leppäkoski 1975, Viitasalo *et al.* 1990, Bonsdorff 1992, Rumohr *et al.* 1996) or the vegetation structure in a way unbeneficial for birds. Thus, eutrophication may diminish the numbers and distribution of birds.

A major recent environmental change is climate change (IPCC 2001). There are few studies about the effects of climate change on seabirds, but it has been shown to affect oceanic seabirds by diminishing their food resources (Aebischer et al. 1990, Montevecchi & Myers 1997, Thompson & Ollason 2001, Croxall et al. 2002, Barbraud & Weimerskirch 2003). In the Baltic Sea, climate change may affect the breeding performance of waterfowl by altering the weather conditions during breeding or by affecting the condition of birds after the winter (Hildén 1964, Milne 1976). Weather, especially temperature, rainfall and wind, is important for the breeding success of several waterfowl species (Koskimies 1955, Hildén 1964, Koskimies & Lahti 1964, Koskinen et al. 2003). Many Baltic waterfowl migrate only as far as the western or southern Baltic Sea or the North Sea (Cramp & Simmons 1977, Pihl *et al.* 1995, Gilissen *et al.* 2002). Thus, winter severity in western Europe affects the non-breeding survival of several waterfowl species (Nilsson 1984, Koskinen *et al.* 2003).

Increasing eutrophication and climate change also affect the environmental conditions of the Archipelago Sea, which is a large archipelago in southwestern Finland in the northern Baltic Sea. The agricultural runoff to the Archipelago Sea is among the hotspots of HELCOM (1993). A part of the Archipelago Sea belongs to one of Finland's important bird areas (Leivo *et al.* 2002). During the past few decades, the species composition of the breeding bird communities in the Archipelago Sea has changed remarkably (von Haartman 1984, von Numers 1995).

Understanding the causes behind bird population changes requires that we link population trends with environmental monitoring data. Yet, most studies until now only document changes in bird populations without connecting them with environmental changes. To establish the link, the only option is to perform correlative analyses of time series of bird populations and environmental factors, which can be done using generalised linear models. However, the analyses are complicated by the fact that successive population indices are interdependent, as the population size is affected by the population processes of the previous years. The problem can partially be overcome using GEE (Generalised Estimating Equations) analyses (Liang & Zeger 1986). Autocorrelation of successive years' indices also affects the analyses since the impacts may only be evident with a lag (Minton 1968).

When studying environmental effects, it must be taken into account that many environmental changes do not affect birds directly, but instead via their predators, competitors or food resources (e.g. Morrison 1986). There may also be other factors, which fluctuate in a manner that is uncoupled with the observed environmental changes or may override their effects. In the case of waterfowl, these factors include predation (Grenquist 1965, Nordström *et al.* 2002), pathogens (Hollmén *et al.* 2002), parasites (Hollmén *et al.* 1996) and disturbance (Mikola *et al.* 1994). However, incorporation of these effects into the models is hampered by the lack of corresponding time series.

We modelled the impact of eutrophication, water salinity, winter severity and weather conditions during breeding on the breeding populations of ten waterfowl species (ducks, great crested grebe *Podiceps cristatus* and coot *Fulica atra*) in the Archipelago Sea. We also discuss the effects of predation pressure, disease and disturbance. This is the first attempt to quantitatively show the connection between waterfowl population changes and simultaneous environmental changes.

Materials and methods

Study area

The study area is situated around the island of Aasla in Rymättylä in the Archipelago Sea, southwestern Finland (Fig. 1). The average depth of the Archipelago Sea is 23 m. Therefore, the littoral shallow areas are very important for the functioning of the ecosystem (Bonsdorff & Blomqvist 1993), and are especially vulnerable (Cederwall & Elmgren 1990). The average annual salinity ranges between 3.5‰ and 7.0‰ (Viitasalo et al. 1990). The area is characterised by strong seasonality. During the winter months, there may be a permanent ice cover for over 100 days (Seinä & Peltola 1991). The Archipelago Sea can be divided into different zones (Bergman 1939, Andersson & Staav 1980, Granö 1981). The study area is situated on the fringe of the inner archipelago. Therefore, it is a suitable breeding area for most of the waterfowl species of the Finnish coast. The waterfowl species breeding in this area are mainly those of coastal estuaries and mainland wetlands.

Data

The bird data covered the years 1975–2003, but because most of the environmental data were from a shorter period, we restricted the statistical analyses to the period of 1984–2001.



Fig. 1. The study area in the surroundings of the island of Aasla in the Archipelago Sea, SW Finland. The bird census sites are numbered 1–11.

Waterfowl censuses

The waterfowl censuses were conducted by L. Saari. The data covered 11 study sites in the sea area surrounding the island of Aasla (60°18'N, 21°57'E) in Rymättylä (Fig. 1). The sites were bays, sounds and sea areas along the shore of the island. The data included ten species of waterfowl (ducks, great crested grebe and coot). The census method was a combination of point and round counts (Koskimies & Väisänen 1991). The sea areas were censused by walking (at one site rowing) standard routes along the shore around the island and stopping at standard sites. The census route was chosen so that all breeding birds in the area could be counted. Censuses were conducted only in good weather conditions. The censused sea area totalled 24.4 km².

The census was repeated three times during the spring, and each species was counted during the census that best suited its breeding phenology, as recommended by Linkola (1959) for inland waters at the same latitude. The same methods were used every year. The annual phenology was taken into account in the timing of the censuses as well as possible. We tested the timing of the censuses in relation to the phenology of the spring migration for the goldeneye *Bucephala clangula* and the great crested grebe, which are transient migrants at the Jurmo ornithological station (59°50'N, 21°37'E) ca. 50 kilometres south of the study area. We correlated the time of the census with the time of the median migration of these species for the years 1975–2002. The correlations were positive and significant at p = 0.0744 (Pearson correlation coefficient = 0.34216, n = 28) for the goldeneye and at p = 0.0228 (Pearson correlation coefficient = 0.45348, n = 25) for the great crested grebe. For other species, valid independent data were unavailable.

The pair numbers were based on counted pairs (or equivalents, *see* Koskimies & Väisänen 1991), because searching for nests was unpractical due to the habitat structure. We only used data on breeding birds. For the mute swan *Cygnus olor*, however, the pair numbers include also non-breeding individuals because they were impossible to separate from the breeding population. The numbers of individuals were converted into pair numbers according to the method given by Linkola (1959) for each species either by dividing the individual number by two or by using the number of males or females as the pair number.

Measurement of eutrophication

Water quality data were collected and analysed by the Southwest Finland Regional Environment Centre and the Water Protection Association of Southwest Finland (Kirkkala *et al.* 1998, Suomela 2001). We chose ten monitoring stations within a radius of 15 km from Aasla. The samples were taken two or three (at one station four) times yearly in July–August. As measures of water quality, we used the surface water concentrations of total phosphorus (μ g l⁻¹) and chlorophyll α (μ g l⁻¹), as well as water transparency (Secchi depth, m) (Kirkkala *et al.* 1998).

We calculated means for the water quality measures for each station and each summer. We combined the variables into one variable by the principal component analysis (PCA) in the SAS statistical package (McCune & Grace 2002). Prior to running the PCA, we standardised each variable to mean = 0 and S.D. = 1. We chose to use the PCA because we needed one axis that summarises the water quality data, and wanted to know the values of the eigenvectors in order to interpret the axis. We identified the principal component as a variable indicating eutrophication. It consisted evenly of the three water quality variables: for water transparency, the value of the eigenvector was -0.570, for phosphorus 0.580 and for chlorophyll α 0.582.

At most of the monitoring stations, water quality is only measured in July-August. For one station, however, there are also data from June. In order to assess the relevance of the water quality in the late summer for the early breeding period of our target species, we calculated the correlation between the values in June and July-August for the principal component indicating eutrophication. We also calculated a partial correlation using "year" as the partial variable. There was a statistically significant correlation between the principal component for June and July-August (Pearson correlation coefficient = 0.75525, n =18, p < 0.0003), and the result was statistically significant even for the partial correlation (Pearson partial correlation coefficient = 0.58113, n = 18, p < 0.0144). Therefore, we felt justified to use the water quality data from July-August to represent the water quality during the summer months June-August.

Winter and breeding season weather

We measured winter severity initially with several variables: (1) average winter temperatures for November-February available at the Finnish Meteorological Institute (data for Turku 60°30'N, 22°16'E), (2) the yearly means of the North Atlantic Oscillation (NAO) index for December-March available at the Climatic Research Unit of the University of East Anglia, United Kingdom (http://www.cru.uea.ac.uk/), and (3) yearly maximum sea ice coverage (km²) of the Baltic Sea available at the Finnish Institute of Marine Research (Seinä & Peltola 1991). The maximum ice coverage is strongly correlated with regional November-February temperatures and the NAO index, but has the benefit of being directly and functionally connected with the wintering habits of several of our target species, and was therefore selected as the sole winter severity variable.

We calculated for each species the yearly mean temperature for the five first weeks of the breeding season. In order to estimate the start of breeding for each species in each year, we used the yearly median arrival time of each species, as recorded at the Jurmo ornithological station.

Water salinity

The water in the Baltic Sea is brackish. Its salinity is periodically increased by oceanic water pulses, between which the salinity gradually decreases. Water salinity influences the whole food web, and is therefore a potential factor that may affect the living conditions of the birds. The water salinity data were collected by the Finnish Institute of Marine Research at the Päiväluoto monitoring station (60°15′N, 21°58′E) in Nauvo, ca. two kilometres south of the study area. The samples were taken at the depth of 20 metres with an interval of ten days.

Statistical methods

TRIM analyses

In order to assess the between-year changes in the population sizes of the study species and to investigate trends in these indices, we used the program TRIM (Trends & Indices for Monitoring Data) (Pannekoek & van Strien 2003). TRIM, which is based on log-linear models, can be used to analyse time series and estimate indices and trends (Hario 1998, Tiainen et al. 2001, Pannekoek & van Strien 2003). For each species, we chose the count sites, where the species had been observed at least in one year. TRIM used the data from the different count sites to calculate the overall population trend for each species. We used the linear trend model, which allows zero counts as long as there is one positive count for each year. The linear trend model also allows testing trends before and after particular change points. The indices were calculated with the year 1975 as the starting point. We started with a model, where all the years with positive counts were change points, used the Wald test to calculate the significance of the slope changes, and excluded nonsignificant change points. We used corrections for overdispersion and serial correlation, which are taken into account in TRIM by using a Generalised Estimating Equations (GEE) approach.

Generalised linear mixed model

We analysed the relationship between bird population sizes and the environmental variables using the GENMOD procedure in the SAS statistical package, release 8.2 (SAS Institute Inc. 2001). The GENMOD procedure fits generalised linear models to correlated responses using the Generalised Estimating Equations (GEE) method (SAS Institute Inc. 2001). In these models, we used the total pair numbers of Aasla because the environmental data were only available on a regional scale.

As the dependent variable, we used the yearly pair numbers of each species. We transformed the data using the log transformation because it fitted the data best according to the residuals. As independent variables, we used the yearly mean eutrophication, mean temperature of the early breeding period, mean water salinity and maximum ice coverage of the Baltic Sea. Because some environmental factors may affect bird populations with a lag, or a lag may result from delayed recruitment, we also used the independent variables with a time lag. We formed the lagged variables by calculating for each year the average of the values of the two preceding years. We used the variable as a general indicator of the circumstances in the past years in order to reduce the number of variables and to avoid overparameterisation. For the same reason, we built parallel models for effects with and without the time lag.

Because there was autocorrelation in our data between subsequent years, we included the term for "year" as a repeated subject. We simplified the models by excluding non-significant effects (water salinity) and interactions between effects. Finally, we obtained for each species a model without the time lag and a model with the time lag, both models including the population size as the dependent variable, and eutrophication, severity of winter and temperature of the early breeding season as independent variables. For each model, we checked the residuals for normality.



Fig. 2. Results of TRIM analyses of population sizes. Starting year was 1975 for all species (Population size index = 1). Change points indicate statistically significant trend shifts (Wald test). The results of TRIM analyses for the goosander and velvet scoter are not shown because there were no significant change points. For these species, only the pair numbers are presented. n = total sum of pair numbers.



Fig. 3. Environmental variables for the years 1984–2001. — **A**: Principal component values indicating eutrophication were formed using the principal component analysis (PCA) on total phosphorus (μ g \vdash^1), chlorophyll α (μ g \vdash^1) and water transparency (m) measured at ten monitoring stations in the Archipelago Sea, SW Finland. — **B**: Maximum total sea ice coverage (km²) of the Baltic Sea. — **C**: Variation in the daily temperature (°C) during the five first weeks of the breeding season in Turku, SW Finland, for the ten study species. The medians (line) and the 5% and 95% percentiles (whiskers) are depicted. — **D**: Sea water salinity (‰) at the Päiväluoto station in Nauvo. For illustrative purposes, a linear regression was fitted to every data set.

Results

Population trends

The breeding population trends of the study species in the sea area surrounding Aasla in 1975–2003 are presented in Fig. 2. For the mallard *Anas platyrhynchos*, tufted duck *Aythya fuligula*, eider *Somateria mollissima*, goldeneye and red-breasted merganser *Mergus serrator*, the populations were declining since the beginning or the middle of the 1990s. For the coot and great crested grebe, the population decline levelled off in the middle of the 1980s so that the populations were about stable but smaller than in 1975–1984. The mute swan was the only species that main-

tained a larger population in the end of the study period than in the beginning of the study period. For the goosander *Mergus merganser* and velvet scoter *Melanitta fusca*, no change point was statistically significant. The pair numbers of the goosander indicate that there was a decline since the year 1994, when the population was at its largest. The velvet scoter population crashed from 41 pairs in 1975 to 0–4 pairs since 1993.

Environmental changes

The environmental variables are presented in Fig. 3. The principal component values indicating eutrophication generally increased from the year



Fig. 4. The effects of eutrophication on the population sizes of the ten study species. The results of the variables with and without time lag are presented separately. — **A** and **B**: The estimates of the effect for all the species (box) together with the median (line) and confidence limits of 5% and 95% (whiskers). — **C** and **D**: The estimates of the effect for each species (line) together with the confidence limits of 5% and 95% (box). The species are the eider, great crested grebe, red-breasted merganser, goosander, velvet scoter, coot, mute swan, goldeneye, tufted duck and mallard. * = significant at p < 0.05.

1975 to the end of the 1990s. The yearly maximum ice coverage of the Baltic Sea decreased from 1984 to 1993, after which it slightly increased. The mean of the breeding period temperatures of each species differed between years, as did the variation in the temperatures. Sea water salinity decreased from 1984 to 2001.

Relationship between environmental variables and breeding bird populations

There were no species whose breeding population would have increased along with eutrophication in 1984–2001. On the contrary, the population sizes of the goldeneye, coot and velvet scoter decreased significantly. For the coot and velvet scoter, the effects were significant both in non-lag and lagged models (Fig. 4).

A severe winter seemed to diminish the populations of the mallard, goldeneye, mute swan, coot and eider in the following summer. The populations of the red-breasted merganser and goosander also expressed the same trend. The severity of the previous two winters seemed to diminish the populations of the tufted duck, coot and eider, and the same trend existed in the populations of the red-breasted merganser,



Fig. 5. The effects of winter severity on the population sizes of the ten study species. The results of the variables with and without time lag are presented separately. — **A** and **B**: The estimates of the effect for all the species (box) together with the median (line) and confidence limits of 5% and 95% (whiskers). — **C** and **D**: The estimates of the effect for each species (line) together with the confidence limits of 5% and 95% (box). The species are the eider, great crested grebe, red-breasted merganser, goosander, velvet scoter, coot, mute swan, goldeneye, tufted duck and mallard. * = significant at p < 0.05.

goosander and great crested grebe (Fig. 5).

The temperature of the breeding season appeared to have a negative impact on the breeding population sizes of the goosander and eider. The effect was visible in the lagged model for the tufted duck and eider (Fig. 6).

Discussion

Breeding bird population trends

The populations of nine species out of our ten study species declined when compared with the population sizes in the beginning of the study period (Fig. 2). For the mallard, tufted duck, eider, goldeneye and red-breasted merganser, the populations declined since the beginning or the middle of the 1990s, which may be in connection with increasing eutrophication in the 1990s or the harsh winters of 1994 and 1996 (Fig. 3). Disease may also have affected the eider population. Parasites may be involved in mass mortalities of eider ducklings in poor nutritional status (Hollmén *et al.* 1996). Furthermore, the eider duckling die-off in 1996 in the western Gulf of Finland was associated by Hollmén *et al.* (2002) with the outbreak of a viral disease. In 1996, the breeding success of the eider was poor also in Aasla (L. Saari unpubl. data). The decrease of the coot and great crested



Fig. 6. The effects of the temperature of the early breeding season on the population sizes of the ten study species. The results of the variables with and without time lag are presented separately. — **A** and **B**: The estimates of the effect for all the species (box) together with the median (line) and confidence limits of 5% and 95% (whiskers). — **C** and **D**: The estimates of the effect for each species (line) together with the confidence limits of 5% and 95% (box). The species are the eider, great crested grebe, red-breasted merganser, goosander, velvet scoter, coot, mute swan, goldeneye, tufted duck and mallard. * = significant at p < 0.05.

grebe levelled off since 1985, but the populations were not able to recover. The mute swan was the only species that maintained a larger population in the end than in the beginning of the study period, which may be due to its general increase and spread into new habitats.

Relationship between eutrophication and breeding bird population sizes

Eutrophication has been assumed to benefit e.g. the eider, mute swan, great crested grebe and coot. As the primary production increases, the food resources of birds feeding on fish or benthos may increase (Cederwall & Elmgren 1980, Hario & Selin 1986, Laurila & Hario 1988, Elmgren 1989, Bonsdorff *et al.* 1997a). The great crested grebe and coot may profit from changes in shore vegetation (von Numers 1995). The food resources of herbivores are likely to increase in the beginning of the eutrophication process (Tenovuo 1975, Bonsdorff *et al.* 1997a), and some insect species have also increased along with eutrophication (von Haartman 1982). Some of our study species feed both on plants, insects and benthos, or use different resources in different seasons (e.g. Hildén 1964), but for most of them, chicks are dependent on insects (Hildén 1964). Eutrophication is also assumed to affect the bird distribution such that inner archipelago species may widen their distribution to the outer archipelago (Tenovuo 1976). Von Haartman (1984) suggested that an increase in food resources and changes in vegetation also allow some inland species to breed in the archipelago. Until present, the effects of the different impacts of eutrophication on birds have not, however, been thoroughly analysed.

In our study, the statistically significant effects of eutrophication were negative, but the range of the parameter estimates was larger than for the effects of the other variables (Fig. 4). While eutrophication increased, the breeding populations of the goldeneye, coot and velvet scoter decreased significantly. This may be due to a decrease in food resources, decrease in water transparency, overgrowth that makes swimming and nesting difficult, or other changes in the habitat structure.

According to our results, the effects of eutrophication on birds are probably more complex than what has been assumed. Each species responds to increasing eutrophication on the basis of its feeding and breeding ecology. Some species benefit from eutrophication in the beginning, but at a species-specific stage, the effects become negative. The effects may only be visible after a time lag because waterfowl are mainly long-lived, do not easily change breeding grounds and have better possibilities to change feeding areas than birds in many other taxonomic groups (Hildén 1964, Grenquist 1965).

In the long run, eutrophication may hamper birds e.g. by changing the structure of the food web in a way unfavourable for benthic feeders (Bonsdorff 1992, Rumohr et al. 1996). As the eutrophication process continues, the response of the benthic fauna changes from a structural response in terms of increased abundance to a functional response in terms of reduced complexity (Leppäkoski 1975, Pearson & Rosenberg 1978, Bonsdorff et al. 1991, O'Brien et al. 2003). Enrichment leads to increasing oxygen-consuming drift-algal mats, which cause anoxy at the sea bottom (Bonsdorff et al. 1997a) and reduce the diversity of littoral fauna (Rumohr et al. 1996, Norkko 1997). Benthic animals may also be damaged by algal blooms and overgrowth

(Bonsdorff 1992). Eutrophication contributes to a shift from suspension feeders to deposit feeders (Bonsdorff *et al.* 1997b, O'Brien *et al.* 2003), and changes the functions and processes at the sea bottom (Sandberg 1994).

As eutrophication exceeds a certain level, it may also lead to a change in fish communities and a decrease in fish stocks due to e.g. oxygen depletion (Rajasilta *et al.* 1989, Hansson & Rudstam 1990). In addition, decreasing seawater transparency makes it more difficult for birds to fish. Water transparency is especially important for the mergansers (Hildén 1964). Of our study species, particularly the goosander, red-breasted merganser and great crested grebe feed on fish. Even if increasing eutrophication increases their food resources, it may make feeding more difficult. It may be because of these opposite effects that we did not find any statistically significant impact of eutrophication on these species.

The eutrophication process in the inner archipelago may be at the stage at which its effects become negative for some bird species. The water quality in the Archipelago Sea was decreasing during the 1980s and 1990s (Jumppanen & Mattila 1994, Suomela 2001). Increasing areas were subjected to hypoxia in near-bottom water (Jumppanen & Mattila 1994). The quality of the sea bottom around Aasla was mainly semihealthy to semi-polluted following the classification of Leppäkoski (1975), and there were also polluted and dead sites (Räisänen 2003). The biomasses of benthic animals in the Aasla area declined in 1980-1993 (M. T. H. Rönkä, L. Saari, E. A. Lehikoinen, J. Suomela & K. Häkkilä unpubl. data). During 1997–2001, there was also a decline in the numbers of Monoporeia affinis, which is regarded as an indicator for healthy sea bottom (Räisänen 2003). This indicates that the quality of the sea bottom around Aasla is deteriorating.

Relationship between weather and breeding bird population sizes

Most of the study species overwinter primarily in the southern Baltic Sea, the Danish sounds or Kattegat (Cramp & Simmons 1977, Pihl *et al.* 1995, Gilissen *et al.* 2002). A small part of the

Finnish population of some waterfowl winters in Finland (Gilissen et al. 2002). Therefore, winter severity and ice conditions in the Baltic Sea are crucial for most Finnish waterfowl. In addition to mortality due to starvation and cold, severe winters may force birds to migrate further than normal, which includes extra risks. Furthermore, if the Baltic Sea is largely covered by ice, birds have to feed in small areas, which leads to increased competition for food and possibly elevated risk for disease (Grenquist 1965, but see Hario et al. 1995). Severe winters have been proposed to influence the populations of the great crested grebe and coot (von Haartman 1945), tufted duck (Hildén 1966) and mute swan (Minton 1968, Koskinen et al. 2003).

Winter severity in the Baltic Sea also reflects winter severity in the North Sea and further off the coast of western Europe, as well as in central Europe (Hurrell 1995). The occurrence of severe winters in western Europe is synchronised over about ten degrees latitude extending from the Atlantic coast of France to the northern Baltic Sea (Beukema *et al.* 1996). However, a part of the Finnish population of e.g. the great crested grebe, red-breasted merganser and coot migrates to the Mediterranean, Africa or the Black Sea, and is therefore not affected by winter severity in the Baltic Sea (Cramp & Simmons 1977).

In our study, the statistically significant effects of winter severity were negative, and the range of the parameter estimates was quite small (Fig. 5). After severe winters, the breeding populations of the mute swan, mallard, eider, goldeneye and coot diminished, and the redbreasted merganser and goosander populations expressed the same trend. This could be expected because of the wintering distribution of these species. The severity of the previous two winters seemed to diminish the breeding populations of the tufted duck, coot and eider, and the same trend was seen in the red-breasted merganser and goosander populations. This indicates that the effects of longer periods of cold winters could be additive, and it may take time for these species to recover from hard winters.

It is surprising, however, that there was no relationship between winter severity and the population size of the velvet scoter, which largely overwinters in the same area as the mute swan and eider. However, the velvet scoter feeds in deeper waters than the mute swan, and is thus less dependent on the ice situation on the coast. The breeding success of the mute swan may also be lower after a hard winter, when a part of the population may give up breeding (Nummi & Saari 2003). The chicks of the mute swan develop slowly and are dependent on ice-free waters until late in the autumn (Tenovuo 1975). The wintering grounds of the velvet scoter extend further south along the coast of western Europe than those of the eider (Cramp & Simmons 1977). Furthermore, the velvet scoter is a late breeder and arriver and is thus less exposed to cold springs.

Weather, especially temperature, rainfall and wind, is important for the breeding success of the eider, the velvet scoter and the mute swan (Koskimies 1955, Koskimies & Lahti 1964, Koskinen et al. 2003). Even though the temperature of the breeding season is important for the breeding success of birds, its effects on population sizes are not self-evident because the survival of adult birds is rarely affected by poor weather and even a severe crash in fledgling production may not be carried over to the size of the future local breeding population. In addition, the impacts of weather on the breeding population are difficult to analyse because of the effects of weather on the detectability of birds. In our study, high temperature in the early breeding season seemed to have a slightly negative impact on the breeding population sizes (Fig. 6). All the statistically significant effects were negative (Fig. 6). The negative effects may, however, be an artefact due to the better detectability of the birds in cold springs, as they gather or stay longer in larger flocks during the prebreeding and early breeding period.

Relative importance of environmental factors, and future directions

We found a significant relationship between eutrophication and winter severity, and waterfowl breeding population sizes. The effects of eutrophication and winter severity on bird populations were negative. In addition to the variables analysed here, there are, however, other factors that may affect waterfowl populations. These factors could not be incorporated in our models because decent time series are lacking for e.g. disturbance, predation, pathogens and parasites. Viruses and other diseases may have significant effects on the survival and breeding success of e.g. the eider (Hildén 1964, Grenquist 1965, Hollmén *et al.* 1996, Hollmén *et al.* 2002), but they have not been subjected to long-term monitoring. Studies of the relationship between changes in benthos abundance and bird populations are also impaired by the shortage of long-term monitoring data.

During our study period, summer housing and leisure boating have increased in the Archipelago Sea. However, the summer cottages in the Aasla area were mainly built before the beginning of the study period, and after the year 1975, there have been no major changes in the number of houses. Freetime boating has increased in the Aasla area, and the decline of the velvet scoter started first in a sound that was most exposed to boating. However, freetime boating has not been systematically monitored.

Disturbance may expose ducklings to bad weather if they become separated from the female (Koskimies 1957), but it is particularly harmful to ducks because it increases the vulnerability of the broods to predation by gulls (Åhlund & Götmark 1989, Laurila 1989, Mikola et al. 1994). Especially the great black-backed gull Larus marinus and the herring gull Larus argentatus catch ducklings (Mikola et al. 1994), even though the predation of healthy broods is not very effective (Hario & Selin 1989). In addition to direct predation, the gull risk causes indirect impacts on the productivity of bird populations, as escaping and diving leave less time for feeding and may exhaust the chicks. The numbers of the great black-backed gull and herring gull in Aasla were rising through the 1970s and 1980s (L. Saari unpubl. data). The largest numbers were observed in 1989 for the herring gull and in 1994 for the great black-backed gull. Since 1994, both of these species have been declining. Generally, an increase of great gulls may affect particularly the eider and velvet scoter, but in this case it does not seem probable.

In addition to predation by gulls, predation by other birds and mammals is important both for adult survival and breeding success (e.g. Grenquist 1959, Hildén 1964), as well as population sizes of seabirds (Nordström *et al.* 2002). The predators present in the Aasla area include e.g. the American mink *Mustela vison*, red fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides*, pine marten *Martes martes*, goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*, whitetailed sea eagle *Haliaetus albicilla*, and hooded crow *Corvus corone*.

Nordström et al. (2002) concluded that predation by the American mink affects the populations of the tufted duck, velvet scoter and red-breasted merganser because they increased in mink removal areas. However, the populations of the mute swan, eider and goosander did not increase after mink removal. Therefore, there is a possibility that mink predation would have affected the decline of the tufted duck, velvet scoter and red-breasted merganser in Aasla. However, we do not find it likely because the mink population in Aasla has not changed during the study period. The white-tailed sea eagle is a rare visitor in Aasla, even though one pair has been nesting at a distance of three kilometres from Aasla since 2003. Even the populations of most of the other predators in Aasla have been so small or remained so stable that it is unlikely that they have affected the population changes of our study species. It is probable, however, that predation by the pine marten has affected the goldeneye population in Aasla.

Our results suggest that increasing eutrophication and severe winters may affect waterfowl population trends. It is evident that the quality of several components of the waterfowl habitats around Aasla is deteriorating due to eutrophication. Nine out of our ten study species have declined either during the whole study period or since the mid-1990s. However, when using correlative environmental data, the results must be interpreted with caution because it is difficult to verify causalities.

Even though eutrophication and winter severity probably affect the population trends of many of our study species, they do not explain the population changes of all of them. More attention should thus be paid to food resources, disturbance, disease, predation and availability of nesting sites. Environmental changes, including eutrophication and climate change, may widely affect ecological patterns and processes (Bjørnstad & Grenfell 2001, Stenseth et al. 2002) and thereby, e.g., the feeding ecology and reproductive success of seabirds (Montevecchi & Myers 1997). These effects may first be visible near the limits of seabird ranges (Barrett & Krasnov 1996, Montevecchi & Myers 1997). In order to understand changes in seabird populations, there is a need for long-term environmental data, as well as data on regional bird population dynamics, such as breeding success, recruitment and migration. More should also be known about the dynamics of northern marine ecosystems and the interactions between seabirds, their food resources and the environment.

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