Breeding success and breeding population trends of waterfowl: implications for monitoring

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Traditional waterfowl monitoring includes only breeding or non-breeding population sizes, but the assessment of breeding success would provide valuable information for the interpretation of population trends, as well as for the early targeting of management measures and further studies. The relationship between breeding success and subsequent breeding population trends is not very well-known in particular for many waterfowl species. Using transfer function (TF) models, we analysed the relationship between breeding success measured as duckling numbers and post-breeding population sizes (i.e. the numbers of adults and ducklings in July), and subsequent breeding population trends for the mallard *Anas platyrhynchos*, common eider *Somateria mollissima*, common merganser *Mergus merganser* and goldeneye *Bucephala clangula* in Aasla, an island in southwestern Finland. In addition, we used data on the common eider in Söderskär, an island group in the Gulf of Finland, to analyse the extent to which fledgling numbers transform into recruitment and breeding population size. As a complement to the traditional methods of population monitoring, we present a simple and cost-effective method for the assessment of breeding success: the monitoring of post-breeding population sizes (including both adults and young). The breeding population sizes of the mallard, common eider and common merganser were positively related to their breeding success with a time lag corresponding to their recruitment age. For the common eider, the effect of the recruitment number on subsequent breeding population size seemed to last for up to three years after recruitment. There was a coupling between the post-breeding sizes and the subsequent breeding population sizes of the mallard, common eider and goldeneye with a lag corresponding to the recruitment age for the mallard and the common eider, but for goldeneye, one year later than the usual recruitment age. The chicks seem to recruit to the local breeding population to an extent that is sufficient for affecting local breeding population trends. Our results indicate that the annual breeding success of our target species can be assessed on the basis of their post-breeding population sizes. This easy and rapid monitoring method for breeding success is also suitable for voluntary bird watchers.

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There is an urgent need for insights into the population processes and reproductive success of waterbirds as 44% of the waterbird populations, for which there are data, have declined or become extinct, 34% are stable and only 17% are increasing (Wetlands International 2006). Concerning European waterbirds, for instance the north European populations of mallard *Anas platyrhynchos* have

been declining or stable, the Baltic breeding population of the common eider *Somateria mollissima* has decreased, the Baltic and Scandinavian populations of the common merganser *Mergus merganser* have probably decreased, and the populations of the goldeneye *Bucephala clangula* in northern and northwestern Europe have been stable (Wetlands International 2006).

Birds are considered useful biological and ecological indicators of e.g. ecosystem and ecological health, ecosystem changes, human-induced environmental effects and ecological risks (Bibby et al. 2000, Burger & Gochfeld 2001, Carignan & Villard 2002, Gregory et al. 2005, O'Connell et al. 2007). Coastal birds may have a potential as indicators of several aspects of the marine environment (Becker 1989, Oxynos et al. 1993, Furness & Camphuysen 1997, Diamond & Devlin 2003, Rönkä et al. 2005, Wanless et al. 2005, Boyd et al. 2006, Newman et al. 2007, Piatt et al. 2007, Wanless et al. 2007).

An early warning of environmental hazards is a prerequisite for identifying and implementing cost-effective management and conservation measures (Järvinen 1983). When bird population trends and demographic processes reflect environmental changes, bird monitoring can be used as a biological early-warning system of complex and unexpected environmental changes. The importance of monitoring the environment and investigating the reasons for population changes are widely recognised (Gregory et al. 2004, Sutherland et al. 2004, Gregory et al. 2005, Sutherland 2006, Hovestadt & Nowicki 2008). Recently, the focus, design and efficiency of monitoring programmes have invoked vivid discussion, and there has been an urge for targeted and adaptive monitoring frameworks and integration of monitoring programmes to conservation-oriented science and management (Nichols & Williams 2006, Lindenmayer & Likens 2009a, Wintle et al. 2010).

Birds are usually monitored by counting the number of pairs and densities of the breeding populations (e.g. O'Connor 1985). Waterbird population estimates can be derived from censuses made towards the end of the non-breeding season or from estimations of breeding pairs. Waterbird populations tend to be at their lowest and most stable sizes at these times (Wetlands International 2006). However, data on breeding population sizes and densities do not readily reveal the causes of population trends, neither do they help predicting future population changes (Elmberg et al. 2006),

even though plausible causes can be inferred by using time series on population trends jointly with environmental variables (e.g. Rönkä et al. 2005).

Breeding success is often a more rapid and direct indicator of environmental changes than is breeding population size. Many waterfowl species are relatively long-lived (Holmes et al. 2001). For instance, common eiders may become > 14 years (Öst & Steele 2010) and even 22 years old (Coulson 2010), and tufted ducks *Aythya fuligula* and pochards *Aythya ferina* may reach 14 years of age (Blums et al. 1996). In addition, many waterfowl species exhibit high site tenacity or philopatry (Grenquist 1965, Batt et al. 1992, Blums et al. 2002, Baldassarre & Bolen 2006), and some species have delayed recruitment (Batt et al. 1992, Holmes et al. 2001). For instance, common eiders usually recruit at 3-4 years of age (Hario & Selin 1987) and many other diving ducks at two years of age (Baldassarre & Bolen 2006).

Changes in breeding success may provide clues of the factors affecting breeding populations. It should be known, however, how breeding success affects the local recruit and breeding population trends. Furthermore, the interpretation of for instance human-induced environmental effects on breeding success requires knowledge on its natural variation. Breeding success can vary considerably owing to the weather (Hildén et al. 1982) and other factors not related to human activities (Batt et al. 1992), and may only reflect local and transient conditions.

The monitoring of breeding success would provide valuable information for the early targeting of management and conservation measures, as well as for further studies (Sutherland et al. 2004, Sutherland 2006). In particular, there is a need for reliable data on the recruitment and mortality of migratory European duck species, which are important quarry species in several countries (Elmberg et al. 2006).

Breeding success of waterfowl is already covered by monitoring programmes in e.g. Norway (Anker-Nilssen et al. 2007), Great Britain, Denmark and Finland (Oja & Pöysä 2007). Examples of the monitoring of the breeding success of other species groups of birds are for instance wildlife triangle censuses used for the monitoring of game species (Kangas & Kurki 2000, Ludwig et al. 2006) and the Constant Effort Sites (CES) ringing programme for passerines (Peach et al. 1998, Peakall 2000). In North America, a parallel to the CES programme is the Monitoring Avian Productivity and Survivorship (MAPS) programme (DeSante et al. 1995). An

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alert system for trends in population size and breeding success has been developed by e.g. the British Trust for Ornithology (Baillie et al. 2010).

Some monitoring schemes, such as the North American Waterfowl Breeding Population and Habitat survey (U.S. Fish and Wildlife Service 2010) and the Atlantic Flyway Breeding Waterfowl Survey (Heusmann & Sauer 2000, Costanzo & Hindman 2007), build on data collected by professional biologists. However, bird monitoring data are for the most part collected by voluntary bird watchers. Such schemes, including e.g. the North American Breeding Bird Survey (BBS), can be extremely useful (see e.g. Costanzo & Hindman 2007), but the data may also include noise and biases (Keller & Scallan 1999).

Simple and rapid one-visit methods that do not require extensive experience or special equipment are approachable for a wider range of bird watchers conducting monitoring than more labourious methods (Koskimies & Pöysä 1989). The availability of such undemanding methods is the prerequisite of cost-effective wide-scale monitoring that produces representative high-quality data (Greenwood 2007); a wide scale also makes the data less prone to noise and bias. Traditional methods for the monitoring of fledgling production are labourious and time-consuming and thus apply best to short-term studies.

In our study, we assess the relationship between breeding success and breeding population trends of waterfowl in two long-term bird monitoring areas on the Finnish coast of the Baltic Sea. We analyse the relationship between breeding success measured as either chick numbers or individual numbers in July (post-breeding population size including both adults and chicks) and breeding population trends for the mallard, common eider, goldeneye and common merganser in Aasla, an island in the Archipelago Sea, southwestern Finland. In addition, we address the relationship between recruitment number and subsequent breeding population size of the common eider in Söderskär, an island group in the Gulf of Finland. As a complement to the traditional methods of breeding population monitoring, we present a cost-effective method for the monitoring of breeding success comprising counts of fledging young and adults in July.

Our aims were to: 1) assess the relationship between different measures of breeding success (chick numbers, post-breeding population size and recruitment numbers) and subsequent breeding population trends, and 2) test the simple and cost-effective monitoring method of post-breeding population size.

Material and methods

Study areas

Aasla
The island of Aasla is situated on the fringe of the inner archipelago in Rymättylä in the Archipelago Sea, southwestern Finland (60°18'N, 21°57'E; Fig. 1). There were 20 study sites, which included bays, sounds and sea areas along the shore of the island, as well as small lakes. We used data from the whole area, because in this fine-scaled landscape, fledgling production on the lakes affects the pair numbers of several species in the sea areas. In addition, broods of many species move between lakes and the sea. The censused sea area totalled 24.4 km^2 and the land area of Aasla is 16 km^2.

Söderskär
Söderskär is a group of 27 islets in Porvoo in the central Gulf of Finland (60°07'N, 25°25'E; see Fig. 1). Söderskär is situated in the outer archipelago
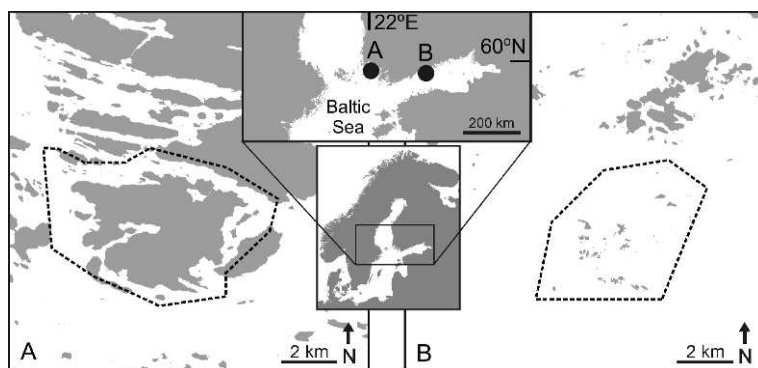

Figure 1. The study areas on the Finnish coast showing the island of Aasla (A; the smallest lakes are not depicted) and the island group of Söderskär (B).

and is exposed to wind and waves, even though the area is relatively closed. The islands of Söderskär are mainly treeless rocky islets, but there are some larger, wooded islands. The total land area covers 0.5 km^2, and the water area is 13.3 km^2 (Hario & Selin 1986). The island group is a bird sanctuary. The area is popular for recreational boating, but during 1 May-15 August, landing is prohibited.

Bird census data

Aasla

The waterfowl censuses in Aasla were conducted by L. Saari during 1975-2007. The census method was developed by L. Saari, and it corresponded to the methods presented by Linkola (1959) and Koskimies & Väisänen (1991). The method was a combination of point and round counts; the sea areas and lakes were censused from the shores on a standard route with fixed stopping sites. The route was chosen so that all breeding birds in the whole study area could be counted, and the stopping points were located so that there was a good visibility over each section. One of the sites was censused by boat. The route and the points stayed approximately the same each year, at least in terms of visual coverage. All birds in the open water were thus recorded. Some individuals staying in reed beds were probably not observed, but this bias was probably nearly constant over years.

The census of the breeding populations was repeated three times during spring: at the turn of April-May, in the middle of May and at the turn of May-June. The pair numbers of each species were based on the census that best suited its breeding phenology as recommended by Linkola (1959) for inland waters at the same latitude. For the study species in this paper, the pair numbers were based on the census at the turn of April-May. We took the annual phenology into account in the timing of the censuses. Censuses were only conducted in relatively calm and rainless weather with good visibility.

We based the size of the breeding population (i.e. pair numbers) on the number of adults (or equivalents, see Koskimies & Väisänen 1991), because searching for nests was impractical due to the habitat structure. We converted the numbers of individuals into pair numbers according to Linkola (1959). For the study species in this paper, the male numbers were used as the pair number. In these species, the sex ratio is close to 1:1, and as some females have already started incubating at the time

of the census, pair numbers can be estimated most accurately using male numbers.

The breeding success (i.e. chick numbers) and the age classes of chicks were assessed on the basis of brood counts in July. We estimated the age class of the chicks according to the classification given by Pirkola & Högmander (1974) for anatids. We used data on chicks in the age classes II-III (including small half-grown to almost fully-grown). The mortality of ducklings is largely concentrated into their first weeks (Hildén 1964, Hario & Selin 1991, Paasivaara & Pöysä 2007). The ducklings in the classes II-III have passed the most critical phases of development as to e.g. cold-sensitivity and predation (Koskimies & Lahti 1964, Hario & Selin 1989, Mikola et al. 1994, Paasivaara & Pöysä 2004).

In addition to the chick numbers, we collected data on the number of individuals in July (i.e. the post-breeding population size). We collected the data as described for the pair numbers and covered all the observed adults and juveniles. We chose to use the post-breeding population size of July, because later, the birds are less likely to belong to the local population due to post-breeding movements.

Our waterfowl censuses and brood counts covered all waterfowl species nesting in Aasla. Our four target species were chosen, because they are relatively abundant in the area, so that there were sufficient data on both population trends and breeding success.

Söderskär

For Söderskär, we used data on the common eider, which has been intensively studied in the area. The common eider censuses were conducted by M. Hario, R. Komu, J.T. Lehtonen, P. Muuronen, H. Selin and K. Selin during 1967-2007.

As pair numbers, we used the female numbers obtained in nest counts at the end of the brooding period in May and June. We searched the islands for the nests systematically according to the instructions of Koskimies & Väisänen (1991) for archipelago bird censuses. During the same period, we captured and ringed, or recaptured female common eiders on their nests, using a long-handled dip-net (Hario & Selin 1987, 2002). Females were caught no earlier than on the 20th day of the incubation period of the population (median date) to avoid nest desertion. We scored females captured for the first time (unringed) as recruits, and their share of the total catch was used as the annual recruitment rate.

We then used the annual recruitment rate in the catchable part of the population to calculate the total recruit number in the whole population.

Once recruited, females exhibited a high degree of breeding site fidelity. Only three out of 255 ringed females that had nested previously on Söderskär were captured on the adjacent archipelagos within a distance of 10-20 km, and there are no recoveries of established females from Söderskär breeding in the two other major colonies in the Gulf of Finland, 60 km (Rönnskär) and 125 km (Tvärminne) west of Söderskär (M. Hario & K. Selin, unpubl. data). There is no evidence of large-scale movements of recruits either. Of the 6,576 female nestlings ringed at Söderskär during 1977-2001, 236 recruited at Söderskär and only one outside Söderskär. The low rate of dispersal may be partly due to the detached location of the Söderskär archipelago, with 5-10 km open sea stretches to closest islands and 15-25 km to mainland peninsulas. The overall low recovery rate of recruits (3.6%) is due to heavy duckling mortality, a common feature in common eider studies (reviewed in Hario & Rintala 2006, 2009).

During 1965-2007, an average of 52.9% of incubating females (median: 53.3%) were captured, with the range of annual variation being comparatively small (SE = 1.8; 95% of capture proportions within in 49.2-56.6%). Not all females are equally catchable at nest. Hario et al. (2009) reported a constant difference in capture probability across years for individuals encountered the previous year and not encountered the previous year. This dichotomy stems from the different catchability of females, some being more difficult to trap at nest than others and thus more liable to remain undetected for longer periods. Yet, with our fairly constant catching effort in the entire population (we did not sample 'quotas'), we could not detect any change in the observed dichotomy across years. Therefore, we are confident that the catchable part of the population was representative of the whole population in terms of the recruitment rate.

We used the total fledgling number obtained in the brood count that was made 70 days after the median hatching date of the population, which is the average fledging time of common eider chicks (Hario & Selin 1989). We made our brood counts by censusing the feeding areas by boat in early morning (Hario & Selin 1989). We took the yearly timing of breeding into account in the timing of the brood counts. We imputed four annual missing fledgling number values by counting the average of two neighbouring values before and after the missing values.

Statistical methods

We modelled the relations between breeding success and population trends using transfer function (TF) models, also called dynamic regressions (Box & Jenkins 1976, Yaffee & McGee 2000, Hänninen et al. 2003, Liu 2009).

As time series on bird populations and breeding success have an autocorrelated structure, standard regression or any other parametric analysis, may result in type II error, i.e. an increase in the test statistic and a risk to accept a false null hypothesis, and thus in ineffectual or incorrect models (Box & Newbold 1971). We introduced autoregressive integrated moving average (ARIMA) models to account for the autocorrelated structure of time series data (e.g. Box & Jenkins 1976). TF models merge the concepts of general regression models with those of ARIMA models (Box & Jenkins 1976, Yaffee & McGee 2000, Liu 2009).

Transfer functions are able to connect a time series with its own past values and with past and present values of other time series. The models can also include time lags between the modelled time series and the originator time series. The univariate ARIMA models are useful for the analysis of a single time series. In such a case, modelling is limited to the information contained in the series' own past.

The ARIMA time series analyses comprise an iterative procedure for modelling, encompassing three phases: identification of a time series, parameter estimation and diagnostic checking. Once an appropriate model is determined, it can be used to form a TF model, where the response of one time series is related to other time series.

The general form of the TF model is:

$$Y_t = C + \frac{\omega(B)}{\delta(B)} X_t + N_t,$$

where Y_t = output variable, X_t = input variable(s) and C = a constant term, which indicates a possible trend in the series. The parameter $\omega(B)$ = TF between Y_t and X_t, either in a linear form when $\delta(B) = 1$, or as a rational form when $\delta(B) \neq 1$. The value B represents the delay of the response.

The ω values ($\omega = \omega_0, \omega_1, \omega_2, \ldots$) are the TF weights for the input series X_t (Box & Jenkins 1976) and indicate how the input series affects the output series. Thus, the weight ω_0 is a measure of how the current response is affected by the current value of

the input series, whereas ω_1 is a measure of how the current response is affected by the value of the input series one period (in our case one year) ago. A negative value for the weighting factors is produced when the relationship between parameters is inverse. The sum of all weights (i.e. the steady-state gain) represents the total change in the mean level of the response variable. The software chooses weighting factors by minimising the deviations between estimated and observed values. The weighting factors' values and ranges depend on the features of the series (e.g. range of variation and existence of trends), and whether transformations have been used to produce stationarity. Therefore, the weighting factors only relate to the respective series and cannot be compared between models.

The variable N_t is a disturbance term, which is assumed not to be 'white noise', and is modelled as an ARIMA process. ARIMA modelling gives approximations that are more reasonable for N_t, resulting in more efficient estimates of the TF weights. At the beginning of modelling, the disturbance term is given a first-order autoregressive, AR(1), approximation, i.e.

$$N_t = \frac{1}{1 - \Phi\ B}\,a_t,$$

when there is no seasonality, as in our data. Here, a_t represents a sequence of random errors that are independently and identically distributed with normal distribution. B represents the backshift (or lag) operator, which refers to previous values in the data. The parameter Φ indicates the autoregressive (AR) operator in non-seasonal series. The disturbance term can also have a moving average (MA) operator, represented by θ in non-seasonal series. MA operator(s) are always placed in the denominator of the formula.

The TF test statistic for significance of the parameters is:

$$t = \frac{(\text{estimate}) - (\text{hypothesised value})}{(\text{estimated STD of estimate})},$$

where the t-value is associated with a one-sample t-test of the null hypothesis that 'parameter = 0'. This statistic is compared with a critical value of the t distribution with n - p degrees of freedom (n = number of observations, p = number of parameters estimated). Only significant parameters are included into the TF models, except for adjacent autoregressive (AR) operators, all of which are included.

We conducted the analyses using the ARIMA and TF models of the Scientific Computing Associates (SCA) Statistical System, release 8.0 (Liu 2009). For the target species in Aasla, we used the breeding pair numbers as the response (output) variable, and either chick numbers or post-breeding population sizes as the explanatory (input) variable in TF modelling. For the common eider in Söderskär, we built TF models with 1) the breeding pair number as the response variable and either the number of fledglings or recruits as the explanatory variable, and 2) the recruit number as the response variable and the fledgling number as the explanatory variable. We first built univariate ARIMA models for every series acting later as either output or input variables, which then were connected in TF models.

We evaluated the TF models on the basis of their coefficients of determination (r^2), residual standard errors and parsimony (for details, see Hänninen et al. 2003). We present the models showing 1) $r^2 > 0.5$, 2) the highest proportional decrease in error term when the TF model residual standard error was compared with those of the univariate ARIMA model of the same response variable (the decrease in error term was seen as due to the inclusion of convenient exploratory variables into the model) and 3) the lowest number of parameters.

A principal assumption concerning TF models is that the input series affects the output variable but not *vice versa*. There may be feedback from our output variable to our input variable, e.g. in the case of density dependence in breeding success (Nummi & Saari 2003). However, Liu & Hudak (1992) stated that although the assumption of a unidirectional relationship may not be strictly true, TF models can be used effectively. In the cases where the TF models fitted our data well, we are thus confident that possible violations against this assumption did not bias our results.

Results

In Aasla, the pair numbers of the mallard correlated with the chick numbers (N = 29, estimate = 1.83, P = 0.006; Table 1 and Fig. 2A) and the post-breeding population sizes (N = 29, estimate = 0.83, P < 0.001; see Table 1 and Fig. 2B) with a lag of one year. The pair numbers of the common eider correlated with the chick numbers (N = 24, estimate = 0.14, P = 0.006; see Table 1 and Fig. 2C) and the post-breeding population sizes (N = 24, estimate = 0.10,

Table 1. Identified transfer function (TF) models for the target species in Aasla with initial estimates of the parameters with standard errors, t- and p-values. Models with statistically insignificant estimates were excluded. Coefficients of determination for the models are calculated using $r^2 = 1 - ((n - 1)/(n - p))((\text{sum of squares}_{resid.})/(\text{sum of squares}_{total}))$, where n = number of observations and p = number of estimated parameters. The variables are PAIRS = pair numbers, CHICK = chick numbers and INDIV = individual bird numbers in July (i.e. post-breeding population size). The ω values are the TF weights for the input series and C is a constant term, which indicates a trend in the series. The value B represents the delay of the response. The parameter φ indicates an autoregressive (AR) operator, and the parameter θ indicates a moving average (MA) operator. The input parameter is significant when $|t| \geq 1.96$ (P < 0.05) and the disturbance term when $|t| \geq 1.64$ (P < 0.06). All the time series comprise yearly values.

A. *Anas platyrhynchos*
Pair number vs chick number $r^2 = 0.53$, N = 29

$$PAIRS_t = C + \omega_1 (B^1) CHICK_t + 1/(1 - \varphi_1 B^1) - \varphi_2 B^2 - \varphi_3 B^3)a_t$$

	C	ω_1	$1/(1 - \varphi_1 B^1)$	$\varphi_2 B^2$	$\varphi_3 B^3)a_t$
Estimate	87.75	1.83	0.75	0.03	-0.38
SE	10.64	0.61	0.17	0.22	0.18
t-value	8.24	3.00	4.39	0.16	-2.10
p-value	<0.001	0.006	<0.001	0.874	0.045

B. *Anas platyrhynchos*
Pair number vs individuals in July $r^2 = 0.61$, N = 29

$$PAIRS_t = C + \omega_1 (B^1) INDIV_t + 1/(1 - \varphi_1 B^1) - \varphi_2 B^2 - \varphi_3 B^3)a_t$$

	C	ω_1	$1/(1 - \varphi_1 B^1)$	$\varphi_2 B^2$	$\varphi_3 B^3)a_t$
Estimate	71.35	0.83	0.72	0.10	-0.36
SE	12.14	0.20	0.17	0.20	0.17
t-value	5.88	4.13	4.30	0.51	-2.16
p-value	<0.001	<0.001	<0.001	0.614	0.040

C. *Somateria mollissima*
Pair number vs chick number $r^2 = 0.93$, N = 24

$$(1 - B^1) PAIRS_t = \omega_2 B^2 + \omega_3 B^3 \omega_4 B^4 + \omega_5 B^5 (1 - B^1) CHICK_1 + 1/(1 - \varphi_1 B^1 - \varphi_2 B^2 - \varphi_3 B^3)a_t$$

	$\omega_2 B^2$	$\omega_3 B^3$	$\omega_4 B^4$	$\omega_5 B^5$	$(1-B^1)CHICK_1$	$\varphi_2 B^2$	$\varphi_3 B^3)a_t$
Estimate	0.10	0.11	0.14	0.14	-0.21	0.25	0.46
SE	0.04	0.05	0.05	0.05	0.18	0.18	0.19
t-value	2.22	2.19	2.73	3.05	-1.12	1.34	2.39
p-value	0.037	0.039	0.012	0.006	0.275	0.193	0.026

D. *Somateria mollissima*
Pair number vs individuals in July $r^2 = 0.95$, N = 24

$$(1 - B^1) PAIRS_t = \omega_2 B^2 + \omega_3 B^3 \omega_4 B^4 + \omega_5 B^5 (1 - B^1) INDIV_1 + 1/(1 - \varphi_1 B^1 - \varphi_2 B^2 - \varphi_3 B^3)a_t$$

	$\omega_2 B^2$	$\omega_3 B^3$	$\omega_4 B^4$	$\omega_5 B^5$	$(1-B^1)INDIV_1$	$\varphi_2 B^2$	$\varphi_3 B^3)a_t$
Estimate	0.11	0.12	0.11	0.10	-0.37	0.18	0.46
SE	0.03	0.03	0.03	0.03	0.19	0.20	0.19
t-value	3.71	3.74	3.55	3.32	-1.96	0.91	2.38
p-value	0.001	0.001	0.001	0.003	0.062	0.373	0.026

E. *Bucephala clangula*
Pair number vs individuals in July $r^2 = 0.67$, N = 29

$$(1 - B^1) PAIRS_t = \omega_3 B^3 (1 - B^1) INDIV_t + (1 - \theta_1 B^1)a_t$$

	$\omega_3 B^3$	$(1 - \theta_1 B^1)a_t$
Estimate	0.31	0.48
SE	0.10	0.18
t-value	3.21	2.71
p-value	0.003	0.012

F. *Mergus merganser*
Pair number vs chick number $r^2 = 0.65$, N = 30

$$PAIRS_t = C + \omega_2 (B^2) CHICK_t + 1/(1 - \varphi_1 B^1)a_t$$

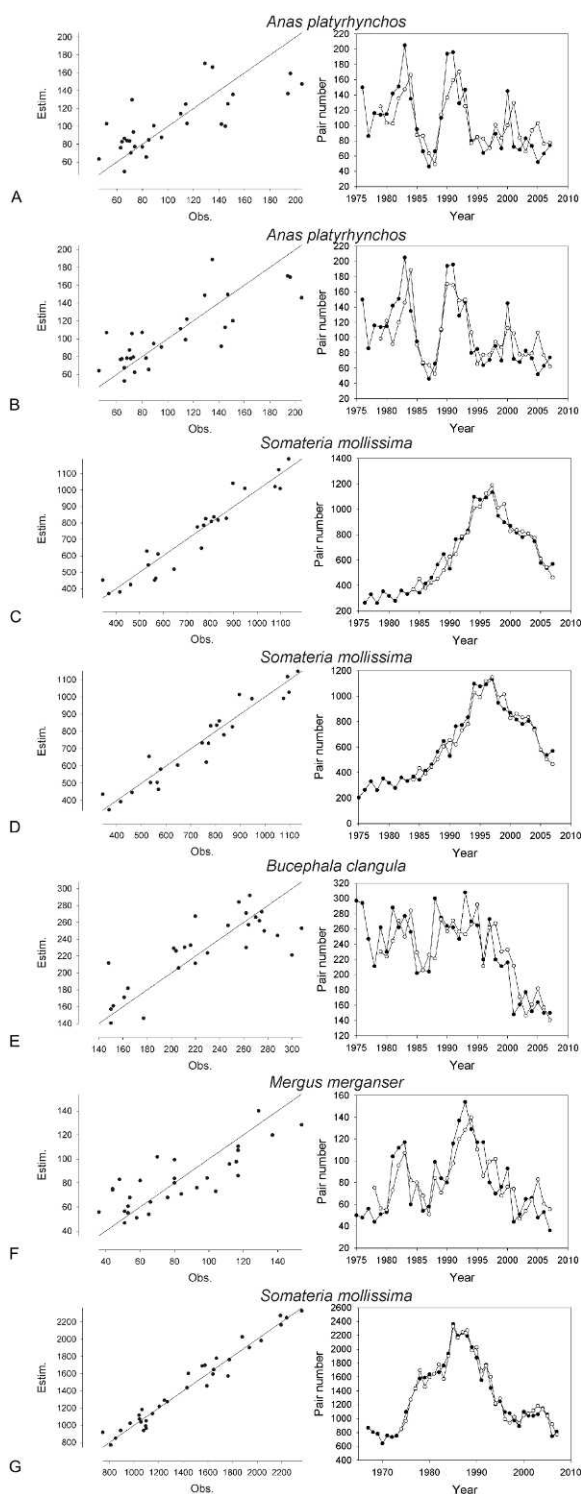|	C	$\omega_2 (B^2)$	$1/(1 - \varphi_1 B^1)a_t$
Estimate	61.82	1.41	0.74
SE	12.69	0.39	0.14
t-value	4.87	3.63	5.40
p-value	<0.001	0.001	<0.001

Figure. 2. The time series studied for each significant transfer function model. The left panels include model fit scatterplots (observed values on X-axis and estimated values on Y-axis). In the right panels, the observed (•) and modelled (○) changes in the time series are presented. The A-G refer to corresponding models in Table 1 (A-F) and Table 2 (G).

P = 0.003; see Table 1 and Fig. 2D) with a time lag of 2-5 years.

The pair numbers of goldeneye correlated with the post-breeding population sizes with a lag of three years (N = 29, estimate = 0.31, P = 0.003; see Table 1 and Fig. 2E). The pair numbers of the common merganser correlated with the chick numbers with a lag of two years (N = 30, estimate = 1.41, P = 0.001; see Table 1 and Fig. 2F). We did not find an interpretable relationship between neither the post-breeding population sizes and the pair numbers for common merganser nor between the chick numbers and the pair numbers of goldeneye.

In Söderskär, the pair number of the common eider correlated with the number of recruits with a lag of 0-3 years (N = 34, estimate = 0.56, P < 0.001; Table 2 and see Fig. 2G). We did not find an interpretable relationship between fledgling and recruit numbers, and neither between fledgling and pair numbers.

Discussion

Relationship between reproductive success, recruit and breeding population trends

Our results imply that the chicks recruit to the local breeding population to an extent sufficient for affecting the local population trend. Among our target species in Aasla, the breeding populations of mallard, common merganser and common eider followed their chick numbers with a time lag that corresponds well with their recruitment age, which is one year for mallard, two years for common merganser and on the average 3-4 years for common eider (Cramp & Simmons 1977, Hario & Selin 1987). The effect of breeding success on population trends is even more pronounced when fledgling production is correlated over larger areas which seems to be the case for instance on the Finnish coast (Desholm et al. 2002).

The relationship between post-breeding and subsequent breeding population sizes was for mallard and common eider similar to the relationship between chick numbers and subsequent breeding population sizes, with time lags that correspond to their recruitment ages. In contrast, we did not find a coupling between post-breeding and subsequent breeding population sizes of common merganser, and for goldeneye there was a coupling between post-breeding and subsequent breeding population sizes but not between chick numbers and

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Table 2. Identified transfer function (TF) model for the common eider in Söderskär with initial estimates of the parameters with standard errors, t- and p-values. Only the significant model is presented. Coefficient of determination for the model is calculated using $r^2 = 1 - ((n-1)/(n-p))((\text{sum of squares}_{resid.})/(\text{sum of squares}_{total}))$, where n = number of observations and p = number of estimated parameters. The variables are PAIRS = pair number and RECR = recruit number. The ω values are the TF weights for the input series. The value B represents the delay of the response. The parameter φ indicates an autoregressive (AR) operator. The input parameter is significant when $|t| \geq 1.96$ (P < 0.05) and the disturbance term when $|t| \geq 1.64$ (P < 0.06). All the time series comprise yearly values.

Somateria mollissima

Pair number vs recruit number $r^2 = 0.97$, N = 34

$(1 - B^1)$ PAIRS$_t$ =	ω_0	+ $\omega_1 B^1$	+ $\omega_2 B^2$	+ $\omega_3 B^3$	$(1 - B^1)$ RECR$_t$ +	$1/(1 - \varphi_1 B^1$	- $\varphi_2 B^2$	- $\varphi_3 B^3)a_t$
Estimate	0.88	0.24	0.22	0.56		0.05	0.03	0.50
SE	0.11	0.11	0.11	0.11		0.15	0.16	0.16
t-value	8.30	2.29	2.07	5.21		0.31	0.18	3.12
p-value	<0.001	0.029	0.047	<0.001		0.759	0.858	0.004

breeding population sizes. The breeding population size of goldeneye followed its post-breeding population size with a lag of three years, whereas its recruitment age usually is two years (Cramp & Simmons 1977).

The effect of the recruitment number on the pair numbers of common eider in Söderskär probably reflects the importance of the recruitment to the breeding population size in the year of recruitment, lasting to the three following years.

The relationship between reproductive success and breeding population trends depends on juvenile mortality, natal dispersal and recruitment age, and is thus affected by events in both breeding and wintering grounds as well as by events along the migration route. The post-breeding population size reflects the current breeding success and the breeding population size, and is affected by reproductive success, natal dispersal of potential recruits and the number of adults staying in the breeding area after breeding (for many duck species mainly females). The local post-breeding population size may differ significantly from the population size in the early breeding period, depending on the movements of the birds into feeding, moulting and flocking areas (Hario & Selin 1989, Haig et al. 1998).

Different processes occurring in the duckling and recruitment phases may affect the relationship between breeding success and subsequent population size. For instance, in our results, the effects that were not ecologically interpretable (see section Results) may be due to anomalies in the variation of the breeding success, e.g. total breeding failures. The occurrence of second broods and replacement clutches might also bias the results. However, in our study area, second broods are very rare as are replacement clutches, because the breeding season is short and anatid males leave the breeding sites early.

In addition, the pre- and post-fledging movements of ducklings may affect the extent to which the ducklings observed in a given area recruit to the local population. Common eider broods stay in shallow waters close to their nest sites in the first days after leaving the nest but soon move to deeper waters (Hario & Selin 1989). The common merganser may also lead its brood long distances to rearing areas (Cramp & Simmons 1977). If ducklings move to a greater extent to and from the study area before the count in July, the relationship between local fledgling production and subsequent breeding population trends may become obscured. The effect of this factor probably does not differ between years and therefore does not bias our results, but its importance is likely to differ between species. In addition, as it seems probable that the fledgling production is correlated over larger areas in the Archipelago Sea and in the Gulf of Finland (Desholm et al. 2002), the breeding success in our study area is likely to reflect the breeding success in adjacent areas.

In the recruitment phase, the degree of natal philopatry is essential for the relationship between local fledgling production and subsequent population trends. Mallard, common merganser and common eider females show high site fidelity (Cramp & Simmons 1977, Batt et al. 1992, Baldassarre & Bolen 2006, Hario & Rintala 2006). Especially among anatids, females return to their birth areas and former nesting sites to breed, whereas males pair with any female in the common wintering grounds and follow the female to her breeding grounds next spring (Batt et al. 1992, Clarke et al. 1997). Therefore, the site choice of

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females may affect local breeding population trends more than the choice of males. However, a recent analysis has shown that, for instance, male mallards are more philopatric than previously thought (Doherty et al. 2002).

Concerning species showing lower site fidelity, juveniles may recruit into the population of their autumn area instead of the area of their natal site. In our study, this may at least partly explain the fact that we found a relationship between the post-breeding population sizes and subsequent breeding population sizes of the goldeneye but not between its chick numbers and subsequent breeding population sizes.

In local studies, the issue of scale and range has to be taken into account. In our study, this applies especially to the area of Aasla that may not be as closed as the area of Söderskär in terms of the recruitment of local fledglings. Concerning common eider, common merganser, goldeneye and mallard in Aasla, our study area does probably not cover the whole area to which the young recruit. This might have contributed to the fact that our models did not fit equally well for all studied species. Further research is needed to know the extent to which the chicks represent the local fledgling production. However, the ideal is spatially comprehensive monitoring of breeding success. In large monitoring areas, more fledglings are likely to stay within the target areas.

Our results indicate that the common eider breeding population in Söderskär is highly dependent on the yearly recruitment to the breeding population, which has also been found in earlier studies (Hario et al. 2005, Hario & Rintala 2006). The mortality of female common eiders in Söderskär has remained fairly constant (Hario & Selin 2002, Hario et al. 2009), but local fledgling production does not suffice to sustain the breeding population (Hario & Selin 1991). The breeding populations of Aasla and Söderskär may be in different phases of decline, where the population of Söderskär would need more immigration in order to subsist than the population of Aasla. The common eider breeding population started to decline in 1986-1987 in Söderskär (Hario et al. 2005, Hario & Rintala 2006), but not until the middle of the 1990s in Aasla (Rönkä et al. 2005). Earlier studies in Söderskär have shown a coupling between the fledgling number and recruitment with a time lag of three years (Hario et al. 2005, Hario & Rintala 2006).

Implications for monitoring

To detect bird population changes and to understand their causes, a coherent monitoring system is needed. The measurements of regional population dynamics should be as thorough as possible, covering the population processes that are affected by environmental change (Tiainen 1985). An ideal monitoring system would address breeding population size, reproductive success and mortality (Järvinen 1983, Kilpi 1985, O'Connor 1985, Tiainen 1985, Sutherland 2006). Monitoring methods should be as simple as possible but reliable and efficient (Koskimies & Pöysä 1989).

Our results indicate that breeding success is carried over to the post-breeding population size to an extent that allows the assessment of breeding success on the basis of post-breeding population size. Our method is systematic and cost-effective in the sense that the breeding success can be assessed with one count without extensive monitoring of the broods during the breeding season. In addition, in traditional brood counts, individual adults, individual chicks as well as adults with chicks are counted and recorded separately, and the chicks are aged (e.g. Koskimies & Väisänen 1991). This requires expertise and takes time during field work. In contrast, the method of counting all individual birds is simple and rapid, which makes it applicable to bird watchers.

The reliability and accuracy of the monitoring method that we present here requires further study in different surroundings and using different species. We had the privilege of using data collected by a constant set of monitors in relatively stable environments. In Aasla, the data were collected by a single monitor, and in the open Söderskär area, it is easy to find all common eider nests and observe broods. With multiple monitors and in changing habitats, however, detectability has to be considered (Royle & Dorazio 2008). This is an issue common to all monitoring and not specific to our method. However, when constant methods are used, censuses conducted during the breeding and fledgling periods produce abundance indices that are unlikely to host trends or other effects that would affect the usability of the data.

To ensure the spatial representativeness of the data, we need several monitoring areas. With multiple monitoring areas, the annual differences between the areas can be taken into account and used to identify factors that influence breeding population status and breeding performance (Suther-

land et al. 2004). In addition, as for any one-visit census, annual differences in phenology have to be accounted for (Sutherland 2006). Furthermore, for quarry species, hunting pressure may differ between sexes (Merkel 2004, Guillemain et al. 2007, Mitchell et al. 2008) and vary between years, which is important to consider when planning waterfowl monitoring and interpreting monitoring results.

Waterfowl breeding areas may be too remote, unapproachable or extensive to be covered by bird watchers even using simple and rapid methods. Aerial surveys are used in the monitoring of some waterfowl breeding populations for instance in North America (e.g. Béchet et al. 2004). The method of monitoring post-breeding population sizes including both adults and young is more cost-effective and better suited for aerial monitoring than methods that include aging the birds and require multiple visits. It must be noted, though, that aerial monitoring is only applicable in open habitats and for conspicuous species.

In order to interpret monitoring results and infer causalities between environmental factors and bird populations, further studies are needed on the mortality of waterfowl species as well as their movements during and after the breeding season (Haig et al. 1998). Conditions, both in breeding areas, along the migration route and in wintering grounds should be taken into consideration. For migratory species, carry-over effects of conditions during the non-breeding period are increasingly recognised as crucial to consider (e.g. Faaborg et al. 2010). Programmes such as the North American Waterfowl Banding Program increase our knowledge on the migration pathways, annual harvest rates (Balkcom et al. 2010) and even annual survival rates (Pearce et al. 2005) of waterfowl and would be welcome on a wider scale around the world.

On the basis of the information on breeding success provided by the monitoring of post-breeding population sizes, it is possible to gain a better understanding of breeding population trends and the relationship between breeding success in a given year and the subsequent breeding populations. Furthermore, to improve our knowledge on bird population trends, integrated approaches can be created that combine long-term data sets (Wernham et al. 2002) or extract common signals from intercorrelated time series such as the productivity of several seabird species in a given area (Frederiksen et al. 2007).

Well-designed monitoring has been seen as a critical basis for research, management and decision making (Lindenmayer & Likens 2009a). There is a growing view that ecological monitoring should be hypothesis-driven and targeted to address management issues (Wintle et al. 2010). This kind of focused monitoring has been opposed to surveillance monitoring that is not guided by *a priori* hypotheses (Nichols & Williams 2006). Some long-term research and monitoring programmes can be criticised as inefficient, poorly planned and lacking focus (Nichols & Williams 2006, Lindenmayer & Likens 2009a,b).

Among waterfowl monitoring programmes, there are both targeted and surveillance approaches. One of the main applications of waterfowl monitoring is harvest management, and there are several programmes that serve this purpose, including e.g. U.S. Fish and Wildlife Service's Adaptive Harvest Management Program (Nichols et al. 2007), the Wing Survey conducted by the National Environmental Research Institute in Denmark (Clausager 2003) and the duck wing collection conducted by the Finnish Game and Fisheries Research Institute (Alhainen et al. 2010). Even with no prior hypothesis or target, data on waterfowl population trends and breeding success can be used in designing nature reserve networks and species conservation measures, assessing the effects of management and conservation efforts, and prioritising measures in case of oil spills or other environmental hazards.

At its most valuable, monitoring data can serve as an early warning signal for unexpected change in environmental conditions and population status, and for long-lived species such as many waterfowl species, this requires information on breeding success. With too narrow monitoring schemes, we may not be able to respond to new information needs arising from unforeseen future management and conservation challenges (e.g. Wintle et al. 2010). As resources are limited, monitoring and conservation funds and effort should be used efficiently. The method presented in our paper is cost-efficient compared to multi-visit methods including aging the chicks, and it allows the participation of voluntary bird watchers as an important resource.

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