Trends and population dynamics of a Velvet scoter population
(*Melanitta fusca*) - influence of density dependence and winter climate.

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Abstract

As many seaduck populations around the world have been reported to decline there is an increasing demand for knowledge about intrinsic and extrinsic factors determining population dynamics of these species.

In this study we analyzed long term dynamics of the summer population of velvet scoters (*Melanitta fusca*) breeding in the Åland archipelago in the Baltic Sea; in particular, we examined the influence of winter weather and density dependence on population change. The studied population exhibited substantial fluctuations but only a weak negative trend during the total period of 58 years (1949-2007) and no significant trend at all during the latter three decades of the study (1977-2007). We tested for density dependence and incorporated winter NAO-index into the model to test for effects of winter conditions. Our final model explained 56.3% of the variance of population growth of the studied population. Delayed density dependence explained 29.7%, pre-breeding climate 8.3% and post-breeding climate 18.3% of the variance. That breeding success is density dependent in a delayed manner is in accordance with the apprehension that velvet scoters breed at the age of two years. We conclude that density dependence and winter conditions must be taken into consideration when discussing population changes in seaducks in general and velvet scoter in particular.

Key words: PBLR, NAO, TRIM, seaducks, Baltic Sea

Introduction

During the last decades numbers of breeding pairs of velvet scoters (*Melanitta fusca*) have declined in several parts of the Baltic Sea (Andersson et al. 1978, Hario et al. 1986, Berndt and Hario 1997, Rintala and Tiainen 2004, Rönkä et al. 2005, Skov et al. 2011) and is classified as vulnerable according to the IUCN Red list. An exception to this trend is the population in the Swedish part of the Botnian bay, which increased substantially during the 1980s and 1990s (Svensson et al. 1999). Several different hypotheses concerning extrinsic as well as intrinsic factors explaining or contributing to the decline in numbers have been put forward: poor fledgling rates (Berndt and Hario 1997), eutrophication (Rönkä et al. 2005), predation (Hario et al. 1986, Nordström et al. 2002), and increased duckling mortality due to boating (Mikola et al. 1994). However, long-term surveys of the scoter population at the Åland archipelago (Nordberg 2002) exhibited substantial fluctuations in the number of breeding birds over time. This might indicate that other factors than the ones mentioned above influence scoter population dynamics in this area.

The effect of population density on vital rates of many species is an acknowledged fundament in population ecology (Newton 1998). In recent years, several studies of time-series of population counts concluded that density dependent processes influence population dynamics of waterfowl (Almaraz and Amat 2004, Viljugrein et al. 2005, Seavy et al. 2007, Murray et al. 2010). However, in this type of analysis it is difficult to assess which factors cause the observed density dependence. In some studies additional information on breeding success was included in the analysis (Elmberg et al. 2003, Nummi and Saari 2003, Hario and Rintala 2005). Examples of factors

that may cause density dependence are food limitation, nest-site limitation, predation, and disease (Newton 1998). Experimental studies with mallards (*Anas platyrhynchos*) have demonstrated density dependent nest-predation (Gunnarsson and Elmberg 2008, Elmberg et al. 2009), and duckling survival (Gunnarsson et al. 2006). There is also experimental evidence for the impact of food availability on survival of mallard ducklings (Gunnarson et al 2004).

It has been shown that winter weather conditions may influence waterfowl population dynamics (Blums et al. 2002, Lehikoinen et al. 2006, Jónsson et al. 2009). Adverse winter weather may entail increased energy costs and render difficulties in finding food. This may lead to starvation and subsequent increase in mortality (Blums et al. 2002) or poor pre-breeding body condition. Endogenous reserves deposited during winter affects breeding performance in waterfowl (Meijer and Drent 1999, Parker and Holm 1990) and poor pre-breeding body condition may result in e.g. decreased fledgling success (Lehikonen et al. 2006) or non-breeding (Coulson 2010).

In general, the velvet scoter is a seaduck breeding mainly by inland waters of the wooded tundra and taiga zones of northwestern Eurasia (Dementev and Gladkov 1952, Cramp and Simmons 1977). A substantial part of the Eurasian population overwinters in the southern parts of the Baltic Sea (Pomeranian Bay, coastal areas of Lithuania and Latvia, Gulf of Riga). A survey has estimated the Baltic winter population at 373, 000 birds (Skov et al. 2011). However, velvet scoters also breed in the Baltic Sea. This Baltic breeding population increased from the 1920's to the late 1950's (Merikallio 1958, Grenquist 1965). During the first decades of 20th century the occurrence of velvet scoter was confined to the inner zones of the archipelagos but during the increase the breeding range expanded to include also the outermost islets

and skerries (Grenquist 1951, 1952). This expansion is considered to be due to colonization along regular migration routes (Koskimies 1955), and stands in contrast to the recent decrease of the species.

Because of the availability of population counts over many decades, the breeding population of velvet scoters of the Åland archipelago in the Baltic is very well suited to study the interplay of different factors on population density. The aim of this study is to analyze the long-term dynamics of this population, concerning trends and possible influences of winter weather conditions and density dependence on population fluctuations.

Study area

The Åland islands constitute an autonomous province of Finland, situated between Sweden and Finland at the entrance of the Gulf of Bothnia in the Baltic Sea. They are separated from Sweden in the west by 40 km of open water and are more or less continuous with the Finnish archipelago in the east. Åland consists of a main island, nearly 300 smaller islands, roughly 6,000 skerries and 11,990 km² of brackish water. The islands' landmass occupies a total area of 1,527 km² of which the main island constitutes 1,010 km². About 58% of the land area is covered by forest and 13% by farmland. Mean annual temperature is 5-6°C, and mean annual precipitation is 5-600mm.

Seaduck males have traditionally been hunted during the spring at the Åland islands. In the period 1977 to 1994 the annual bag was estimated at 20-25,000 males. From 1995 hunting became strictly regulated and the annual bag decreased to 1,500-3,000 males. (Ålands landskapsstyrelse unpubl. data). Spring hunting of seaducks ceased altogether in 2005. The average number of breeding pairs of velvet scoters in Åland, 1991-2001, was estimated at 32,000 pairs (Nordberg 2002).

Methods

Survey

During breeding, male velvet scoters are found on the water in the vicinity of the nest sites (Cramp and Simmons 1977). We used surveys of such males as indicators of numbers of breeding pairs, collected and compiled by the Åland authorities. The surveys were conducted from boats following fixed routes along shorelines, and birds within 150-200 m of the boat were determined to species and sex. Boats were driven at slow speed, not to disturb the birds and so no birds were missed or counted double. Observations of velvet scoter males together with females, alone or in groups of maximum five individuals were counted and their positions were marked on a map. Surveys were conducted on clear and calm days in June, so weather conditions were kept optimal and constant between years. The method is a standard method and recommended by the Swedish Environmental Protection Agency (1978). It is widely used and considered to give reliable estimates of relative population size and density (Andersson et al. 1978). Data collected from the period 1949-2007 were used, including 15 different areas covering a total of 335 km². The size of areas varied from 1.5 to 156.7 km² with an average of 23.3 km². The number of areas contributing with data of a given year varied between 1 and 14 with an average of 3.5. The total area surveyed during a given year varied between 61 to 296 km² with an average of 148 km² (SD=66.5) and total counts ranged from 153 to 2,063 with an average of 1,005 (SD =495.8).

Trends

Common traits in large monitoring data sets are missing counts for individual site-year combinations. In these cases, trends based on index values by so called “chaining”, i.e. total number at time t_j divided by total number at time

t_{j-1} do not properly reflect population changes since they are influenced by the pattern of the missing values (Pannekoek and van Strien 2005).

Therefore, we analysed our data with the freeware program TRIM (version 3.53; Pannekoek and van Strien 2005). It uses loglinear models that make specific assumptions about the structure of the counts to obtain better trend estimates. The program interpolates missing counts from existing counts and can therefore be viewed as an advanced χ^2 test (Pannekoek and van Strien 2005).

Two of the 15 areas provided data for longer time periods, 1949-1975 and 1958-2007, respectively. The remaining 13 sites provided no data before 1993 and therefore generated many missing values when we analyzed the whole time period (1949-2007). This impaired model fit because of the deviation from a Poisson distribution, which is expected to impute counts and indices (Pannekoek and van Strien 2005). Serial correlation and overdispersion were both taken into account by TRIM to determine the best linear models used to calculate population trends. This was done in order to not underestimate the standard errors resulting from the deviation from the Poisson distribution that our data showed and to get rid of the confounding effects on autocorrelation for counts within sites. The stepwise procedure gradually progressed towards the smallest number of successive slope segments, i.e. the most parsimonious model. To decrease the standard errors we also tested 1993 as the base year since almost all sites had positive counts for this year, which in turn makes the imputed data more reliable. However, the number of individuals had a big impact on the imputed indices and was substantially larger in the two populations constituting most of the data up to 1993. Hence the decrease in standard errors did not alter the results. We also examined the data from 1977 to 2007. 1977 was recognized by TRIM as a breakpoint. This was also the year with the lowest number of individuals

throughout the time series and it seemed to divide the data set in two parts with different characteristics of the population trend.

Density dependence

To better understand what is driving the population dynamics of the studied velvet scoter population and how stability in their numbers may come about, we developed a simple population dynamics model. Exploring its properties we examined if population growth is regulated by direct or delayed density dependent mechanisms. For these analyses we only used the non-imputed data from the specific area of Kumlinge from 1977-2007.

According to a study on great snipe population regulation (Kölzsch et al. 2007), we tested for density dependence using the Parametric Bootstrap Likelihood Ratio (PBLR) test as proposed by Dennis and Taper (1994). It uses a stochastic form of the Ricker model to describe population growth

$$N_{t+1} = N_t \exp(a + b N_{t-i} + \sigma Z_t). \quad \text{eqn 1}$$

The population growth rate is therefore $r_t = a + b N_{t-i} + \sigma Z_t$. Model parameters are the constants a , b and σ , and the stochastic term Z_t is assumed to be an independent, standard normally distributed variable. The PBLR test would confirm direct ($i=0$) or delayed ($i>0$) density dependence if an incorporation of $b<0$ significantly increased the model's fit to the data. In this study direct as well as 1- and 2-year delayed density dependence ($i=1,2$) were tested for. Model selection was based on likelihood ratios and p-values of bootstrap samples as well as the for small sample size corrected Akaike's information criterion (AICc; Sugiura 1978). For each test we examined the regression plot, model fits, and determined the coefficient of determination $R^2(N_{t-i}) = b^2 \text{Var}(N_{t-i})/\text{Var}(r_t)$ that explains how much variation of the data is

explained by the respective density dependence. To account for the influence of small sample size, for each model we also examined the bias corrected $R^2_{adj} = 1 - (n-1)(1 - R^2)/(n-k-1)$, where k is the number of explanatory factors of the model and n the sample size.

Climate influence on population growth

Because winter conditions can influence breeding success, condition and survival of ducks (Blums et al. 2002, Lehikoinen et al. 2006, Jónsson et al. 2009), we further examined if the winter North Atlantic Oscillation index (NAO) related with changes in numbers of breeding scoters. The NAO accounts for general climatic conditions in Europe and has been used in several population studies (e.g. Hurrell and Deser 2010, Stenseth et al. 2003). However, it has been shown that the NAO index may be too crude a measure for local winter conditions to reveal climate effects on bird populations (Jónsson et al. 2009). Since we do not know which specific weather factors affect winter survival and body condition of velvet scoters, NAO was used as a general predictor in this study, even if it may be a weak one. We used the station-based winter NAO-index that characterises the climate conditions from December to March (www.cgd.ucar.edu/cas/jhurrell/indices.html). Climate factors like the NAO are often autocorrelated and its correlation to population growth rates may depend on the structure of possibly existing density dependence in population numbers (Royama 1992). Therefore, we directly incorporated NAO into our best model of the previous density dependence analysis. Because NAO may have an effect on female survival and/or body condition in the winter before breeding as well as on survival of young, we tested for the inclusion of NAO in the year of breeding (t) and the following year ($t+1$) to explain population growth r_t . The model can thus be written as

$$N_{t+1} = N_t \exp(a + bN_{t-i} + c_0W_t + c_1W_{t+1} + \sigma Z_t) \quad \text{eqn 2}$$

A certain proportion of environmental stochasticity is here explicitly attributed to the NAO, which is represented as W_{t+i} . Like in the previous section AICc and PBLR test results were calculated to decide if NAO during one of the two proposed years significantly improves the model fit.

We also tested the inclusion of a more specific estimate of winter weather in the model, by using data for maximum ice cover (Swedish Meterological and Hydrological Institute, <http://www.smhi.se/klimatdata/oceanografi/havsis/klimatindikator-havsis>).

Combining density dependence and climate influence in a final model

Based on previous results we tested a number of possible final models, step by step including additional factors that were only kept if the model fit significantly improved. Finally, we determined model structure, parameter estimates, goodness of fit and simulated trajectories of the best model. Coefficients of determination for the included factors show how much of the variance of population growth can be explained by each and the overall model. Rothery et al. (1997) have suggested that the inclusion of external factors in population models may increase the power to detect density dependence. We examined if this notion applied for the population dynamics of our velvet scooters. AICc and PBLR test statistics were calculated for the final model including and excluding the density dependence term.

Results

Trends

Due to an insufficient amount of data prior 1993 the model fits by TRIM were very poor and yielded high standard errors. Therefore, we could not draw any conclusions from trend indices of the particular years. However, the linear model using a stepwise procedure to select change points showed significant trends in some parts of the time series (Table 1). These trends were positive and negative without any obvious pattern.

The resulting imputed counts showed a deviation from the time effects model, but were still well within the confidence interval (Fig. 1a). TRIM also evaluated the general slope over the whole time series as a "moderate decline" (i.e. significant decline, but not significantly more than 5% per year: Overall slope imputed: Additive: -0.0034, SE: 0.0015, Multiplicative: 0.9966, SE: 0.0015, Moderate decline , $p < 0.05$).

It could be observed that there was a significant negative trend over 10 years towards 1977 and a significant positive trend 10 years after (Fig. 1b) This constituted 1/3 of the time series with relative stable decrease and increase, marking 1977 as a trend breaking year. We therefore chose this year as our base year for further analysis, omitting the years prior to it for increased precision. TRIM divided the dataset into nine time intervals of which three had significant slopes (Table 2). The imputed counts from the period 1977 to 2007 (Fig. 1c) revealed an overall stable population size during this selected period (i.e. no significant increase or decline) and it is certain that trends were less than 5% per year, (Overall slope imputed: Additive: 0.0023, SE: 0.0026, Multiplicative: 1.0023, SE: 0.0026, Stable).

Density dependence

Data from the survey area of Kumlinge (61.5 km²) was chosen for analysis of density dependence, because it provided the longest unbroken series of data.

Furthermore, it was large and thereby provided high population numbers resulting in a dominating impact on the TRIM analysis.

In accordance with previous results, the population dynamics model was developed only for the years 1977-2007. Density dependence test results (Table 3a) indicated that the velvet scoter population at Kumlinge was regulated by (1-year lagged) delayed density dependence. This means that the population size of year $t-1$ influenced population growth in year t , conforming to notions of delayed breeding in this species.

The delayed density dependence explained $R^2=26.6\%$ ($R^2_{adj}=23.8\%$) of the variation in population growth. It is negative, $\hat{b} = -0.0004$, and therefore down-regulated population growth (see also Fig 2a). This regulatory influence of density dependence became obvious when comparing model fits of the density-dependent model (Fig. 2c) with those of the null model (Fig. 2b).

Influence of winter weather on population growth

Winter weather seems to have influenced velvet scooter population growth (see Tab. 3b). Both the inclusion of winter conditions (as described by the NAO) of year t and $t+1$ significantly improved model fit. Model improvement was greater for NAO of year $t+1$. This notion was supported when 'maximum ice cover' (ICE) was included in the model, as ICE $t+1$ increased the impact of winter weather of year $t+1$ (Tab. 3e), even if not significantly. The impact of winter weather before breeding was better described by NAO of year t than ICE of year t . ICE and NAO were strongly correlated, $R = -0.6$ ($p < 0.001$), so that in our final model we chose to use only one variable for winter weather conditions; NAO.

Combining density dependence and influence of weather in a final model

The best, final model explaining the dynamics of our velvet scooter population included by one year delayed density dependence, winter weather before breeding and winter weather after breeding.

$$N_{t+1} = N_t \exp (a + b N_{t-1} + c_0 W_t + c_1 W_{t+1} + \sigma Z_t). \quad \text{eqn 3}$$

Test results (Tab. 1c) and model fit trajectories (Fig. 2) revealed that this final model explains the rough outline of the population time series. The maximum likelihood estimates of the model parameters are $\hat{a} = 0.317$ (SE = 0.087), $\hat{b} = -0.0004$ (SE = 0.0001), $\hat{c}_0 = 0.022$ (SE = 0.007), $\hat{c}_1 = 0.015$ (SE = 0.007) and $\hat{\sigma} = 0.072$. The variance of r_t can thus be attributed to the different factors. Delayed density dependence explained $R^2(N_{t-1}) = 29.7\%$, pre-breeding weather $R^2(W_t) = 8.3\%$ and post-breeding weather explained $R^2(W_{t+1}) = 18.3\%$ of the variation in r_t . This means that our model explained 56.3% ($R^2_{\text{adj}} = 51.8\%$) of the variance of population growth of the velvet scooters in the area of Kumlinge. The remaining amount of variation can be accounted for by e.g. demographic stochasticity or environmental factors other than winter weather. Residuals were iid and normally distributed.

The additional test for density dependence using the model with influences of the NAO already included confirmed the notions of Rothery et al. (1997) that density dependence is more clearly detected than (see Tab. 3d). Density dependence emerged as the most important component of our population dynamics model.

Discussion

Trends

Although other studies and reports from various parts of the Baltic area have indicated declines in velvet scoter populations (Hario et al. 1986, Andersson et al. 1978, Berndt & Hario 1997, Rintala and Tiainen 2004, Rönkä et al. 2006), our results showed that the population of breeding velvet scoters at the Åland islands has not. It has exhibited substantial fluctuations over time but, somewhat unexpectedly, only a weak negative trend during the total period of 58 years (1949-2007) and no significant trend at all during the latter three decades of the study (1977-2007). The overall pattern indicates high numbers of velvet scoters during the 1950's, likely as a result of the population expansion and increase described by Koskimies, (1955), Merikallio (1958) and Grenquist (1965). This increase was followed by a decline that continued until the mid 1970's, after which the population has increased again, albeit showing fluctuations. Great fluctuations in local population numbers of coastal breeding velvet scoters were obviously common also during the first decades of the 20th century (Merikallio 1958).

There are several known cases where events of geographic expansion and population increase in mammals were followed by a population decrease (e.g. ungulates; Caughley 1970, 1976, beavers (*Castor spp*); Taylor 1970, Johnston and Naiman 1990, Hartman 1994, 2003, muskrats (*Ondatra zibethicus*); Hengeveld 1989). Similar patterns have also been observed in birds. The populations of black-headed gull (*Larus ridibundus*) in Sweden (Källander 1996) and Latvia (Viksne et al. 1996) have exhibited such a development during the 20th century. In the basic model of population irruption the factor causing post-peak population decline is overutilization of food resources (Caughley 1970, 1976). However, in most cases of observed irruption, e.g. in the case of black-headed gull, the actual factors causing the decline is unknown. The long-term population development of velvet scoters on Åland has the components of a population irruption; a population increase

and geographic expansion, a peak, and subsequent decrease to lower population numbers. However, it is not known what the factors causing the pattern were. Hunting could be an alternative explanation, but as there were no changes in hunting practices or intensity during the 1970's, the possible impact of hunting remains unclear.

As mentioned earlier, our results for the period 1977-2007 differed from what has been observed in other parts of the Baltic Sea. It has been put forward that velvet scoters are poorly adapted to the conditions of the exposed outer archipelago (Koskimies 1955), which can result in poor fledgling rates (Berndt and Hario 1997). Data of fledgling rates are unfortunately lacking from Åland. If it could be shown that fledgling rates are higher at Åland than in other parts of the Baltic Sea it could help to explain why no substantial negative population trend could be observed as in studies from other areas (Hario et al. 1986, Andersson et al. 1978, Berndt & Hario 1997, Rintala and Tiainen 2004, Rönkä et al. 2006). It might also be that other factors that have been put forward as possible explanations to population declines, e.g. eutrophication (Rönkä et al. 2006), predation by mink (Nordström et al. 2002) and predation by gulls (Hario et al. 1986) have been less pronounced on Åland and therefore have had less impact on the population of velvet scoters.

Factors influencing population fluctuations

In our analysis of population fluctuations we found that 25-30% of the variation in population growth could be assigned to delayed density dependence. The breeding population size of one year (N_t) had a negative effect on the model value for population growth of the following year (N_{t+1}), which subsequently affects breeding population size the year after that (N_{t+2}). The most straightforward interpretation is that high density of breeding birds

has a negative effect on average breeding success. This results in lower recruitment, followed by lower numbers of breeding birds when the cohort hatched during a high density year is to breed for the first time, and velvet scoters breed for the first time at the age of two or three years (Cramp and Simmons 1977). Although density dependence on fledgling production has not yet been studied in velvet scoter it has been observed and shown to affect recruitment with a three year time lag in common eider (*Somateria mollissima*) in the Baltic Sea (Hario and Rintala 2006).

Our results do not allow for any profound conclusions about which factor(s) might cause the suggested density dependence. One possibility is intraspecific competition for food leading to decreased survival of young at high densities. Good examples of density dependent effects on reproduction in Baltic waterfowl include Larsson and Forslund 1994 (barnacle goose, *Branta leucopsis*) and Nummi and Saari 2003 (mute swan, *Cygnus olor*). In a field experiment Gunnarsson et al. 2004 showed that food abundance may have a profound effect on duckling survival in mallard (*Anas platyrhynchos*). That inadequate food supply affects duckling mortality in velvet scoter has been proposed by Koskimies and Lahti (1964). Another possibility is that apparent density dependence has been caused by fluctuations in some important food resources. Still another possibility is density dependent predation on nests and/or ducklings. Density-dependent nest predation has been observed for mallards (Elmberg et al. 2009). Gulls (*Larus spp.*) and feral mink (*Mustela vison*) are known to predate on scoter nests and ducklings in the Baltic (Koskimies 1955, Hario et al. 1986, Mikola et al. 1994, Nordström et al. 2002) and high densities may attract predators at a comparably higher level than at low densities. However, it could be questioned if variation in scoter numbers has sufficient impact on total prey availability for this to occur.

According to our model, winter weather conditions as expressed by winter NAO-index, affected the studied population in two ways. It seems to have affected not only the condition of breeding birds but also chick survival. The inclusion of winter weather conditions of year t and $t+1$ significantly improved model fit. Velvet scoters overwinter at sea in the southern parts of the Baltic Sea (Cramp and Simmons 1977, Durinck et al. 1993, Skov et al. 2011). Low air and water temperatures in combination with increased wind and wave action during winter entail increased energy costs and can be expected to render difficulties in search for food. Velvet scoter ducklings are considered to be more sensitive to adverse weather conditions than e.g. eider ducklings (Koskimies and Lahti 1964) and it is likely that during their first winter their hardiness is still below that of adults. Direct effects of weather on duckling survival have been reported for velvet scoter (Koskimies 1955) as well as for the closely related white-winged scoter (*Melanitta fusca deglandi*) in Canada (Traylor and Alisauskas 2006). Considering the substantial improvement of an inclusion of NAO_{t+1} to our model and its accounting for 18.3% of population growth variation, weather induced increase in winter mortality of young birds seems very reasonable.

The effect of weather conditions before breeding as indicated by the significant improvement of model fit by including NAO of year t , explained 8.3% of the variation in population growth. This may be caused by increased female winter mortality due to adverse winter weather. In diving ducks it has been shown that female survival is correlated with mean winter temperatures (Blums et al. 2002). However, Hario et al. (2009) found no correlation between survival of female eiders in the Baltic Sea and winter NAO.

Unfavourable weather during winter could also have a negative effect on female body condition and subsequently on breeding success. Effects on clutch size have been proposed for eider (Lehikoinen et al. 2006, Jónsson et al. 2009), but females of the more closely related white-winged scoter are not considered to be quite as dependent on endogenous body reserves for reproduction as eider (Brown and Fredrickson 1989), although females loose 25% of their peak body weight and have low body fat levels at the end of incubation (Brown 1981). In a study by Koskimies (1957) the average clutch size of individual female velvet scoters showed small variation between years. There are, however, several ways in how pre-breeding nutrient reserves may influence breeding success, e.g. by affecting hatch date (Traylor et al. 2004) and it has been speculated to influence recruitment in white-winged scoter (Alisauskas et al. 2004).

Poor pre-breeding condition is thought to be the reason for the high rate of non-breeding in common eider (Coulson 1984). In a study from northeast England each individual missed breeding, on average, once in five years (Coulson 2010). Scoters, like many other seaducks, have a long life span (Brown and Houston 1982, Kehoe et al. 1989) and it would not be surprising if they did not breed every year of their adulthood. Intermittent breeding has, however, never been documented in velvet scoter. In a study of clutch size and laying date by Koskimies (1957) the nesting of 17 marked individuals of female velvet scoters were monitored for 4 - 8 years (mean=6 years). There were 1-3 gaps in the presented data -series for 11 of these individuals, but unfortunately the author does not try to explain them. Failure to locate individual females in certain years is of course the most straightforward explanation, but as the author considered them to be “extremely site-tenacious”, intermittent breeding does not seem unlikely as an additional explanation.

The NAO-index is a rather crude measure of the weather factors that can directly affect survival and body condition of velvet scoters in the specific overwintering areas. In a study of eiders on Island, breeding numbers were significantly correlated to local winter weather conditions but not to winter NAO-index, although winter weather conditions were significantly correlated with winter NAO- index (Jónsson et al. 2009). This implies that winter weather conditions might have an even larger effect on the variation in breeding numbers of velvet scoters at Åland, than suggested by our results. However, considering that ‘maximum ice cover’(ICE) and NAO were strongly correlated, and that the replacement or inclusion of ICE into the model did not improve its explanatory power (Tab. 3e), we conclude that in our case NAO is a reasonably good index of winter weather conditions. In conclusion, we propose that there has been no trend in numbers of breeding scoters in the Åland archipelago during the last decades, and that annual variation in breeding numbers were to a large extent determined by density-dependent factors together with weather conditions in the overwintering areas. Future studies should try to pin-point which factors cause the observed density dependence, e.g. if it is intraspecific food competition or density dependent predation. Other questions needing answers are if winter weather conditions influence population dynamics by e.g. increased mortality or by inducing intermittent breeding.

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Figure 1. TRIM imputed counts for surveys of velvet scoter, at the Åland archipelago. (a) imputed counts and time effects model with confidence intervals for the years 1949-2007. (b) imputed counts for the years 1949-2007. (c) imputed counts for the years 1977-2007

Figure 2. Parametric Bootstrap Likelihood Ratio test results for density dependence of lag 1 year for Velvet scooter in Kumlinge. (a) shows a regression of the growth rate r_t and the population size N_{t-1} of the previous year. The density dependence model was parameterized with the parameters of this regression. Furthermore, we present the fit of some model trajectories (lines) for the density independent model (b) and the density dependent model with lag 1 year (c) on the population density data. Black dots represent yearly population counts, the dashed, bold lines indicate each model's deterministic fit ($\sigma=0$).

Figure 3. Final model fit on the population data from Kumlinge (black dots). It includes delayed density dependence, winter climate of year t and $t-1$. The lines represent different realizations of the model, each using a different stochastic variable $Z_t \sim N(0,1)$. Thus, a certain range of the model fit is presented. The dashed, bold lines indicate the model's deterministic fit with $\sigma=0$.

Fig 1

Fig 2

Fig 3

Table 1. TRIM slope for time intervals from 1949 to 2007 based on survey data on velvet scoter at the Åland archipelago.

Time intervals	Additive	SE	Multi-plicative	SE	CI	Significance and slope
1949-1952	0.210	0.082	1.234	0.010	0.198	Positive
1952-1957	0.009	0.041	1.01	0.041	0.081	NS
1957-1958	-0.248	0.148	0.78	0.115	0.226	NS
1958-1961	0.062	0.035	1.064	0.037	0.072	NS
1961-1962	-0.245	0.085	0.782	0.066	0.13	Negative
1962-1967	-0.019	0.022	0.981	0.021	0.042	NS
1967-1968	-0.151	0.086	0.859	0.074	0.146	NS
1968-1977	-0.021	0.011	0.979	0.011	0.021	Negative
1977-1986	0.057	0.011	1.058	0.011	0.022	Positive
1986-1987	-0.344	0.095	0.709	0.067	0.132	Negative
1987-1992	0.089	0.022	1.093	0.024	0.048	Positive
1992-1995	-0.023	0.029	0.978	0.028	0.056	NS
1995-1997	-0.171	0.041	0.843	0.034	0.067	Negative
1997-2001	0.036	0.021	1.037	0.021	0.042	NS
2001-2007	-0.026	0.014	0.974	0.014	0.027	NS

Table 2. TRIM slope for time intervals from 1977 to 2007 based on survey data on velvet scoter at the Åland archipelago.

Time intervals	Additive	SE	Multi-plicative	SE	CI	Significance and slope
1977-1983	0.041	0.023	1.042	0.024	0.048	NS
1983-1984	0.2	0.110	1.221	0.135	0.264	NS
1984-1986	-0.008	0.064	0.992	0.064	0.125	NS
1986-1987	-0.341	0.12	0.711	0.085	0.167	Negative
1987-1990	0.126	0.043	1.134	0.048	0.095	Positive
1990-1995	0.015	0.02	1.015	0.021	0.04	NS
1995-1997	-0.192	0.042	0.825	0.035	0.068	Negative
1997-2001	0.035	0.022	1.036	0.023	0.045	NS
2001-2007	-0.027	0.015	0.973	0.015	0.029	NS

Table 3. Model selection and Parametric Bootstrap Likelihood Ratio (PBLR) test results of the population dynamics model. AICc-values (Akaike's Information Criterion corrected for small sample size) correspond to the stated H_1 -model. Sample likelihood ratios $LR = L(H_0)/L(H_1)$ and P -values are presented with the respective null model (H_0) that H_1 was nested in. Bold highlighting indicates important results. Model abbreviations are: DID, density independent model; DD, direct density dependent term included; DD_1 , delayed density dependence of lag 1 year included; DD_2 , density dependence of lag 3 years included; NAO_t , North Atlantic Oscillation Index of breeding year included; NAO_{t+1} , NAO Index of first year juveniles included, ICE_{t+1} , maximum ice cover of first year juveniles included.

Model (H_1)		<u>PBLR test results</u>			
		AICc	H_0	LR	P
(a)	DID	-46.00			
	DD	-49.30	DID	0.06	0.144
	DD_1	-52.92	DID	0.01	0.018
	DD_2	-46.65	DID	0.07	0.102
(b)	$DD_1 + NAO_t$	-55.87	DD_1	0.07	0.028
	$DD_1 + NAO_{t+1}$	-61.02	DD_1	< 0.01	0.002
(c)	$DD_1 + NAO_{t+1} + NAO_t$	-63.20	$DD_1 + NAO_{t+1}$	0.09	0.023
(d)	$NAO_{t+1} + NAO_t$	-50.95			
	$DD_1 + NAO_{t+1} + NAO_t$	-63.20	$NAO_{t+1} + NAO_t$	< 0.01	0.001
(e)	$DD_1 + NAO_{t+1} + NAO_t + ICE_t$	-65.47	$DD_1 + NAO_{t+1} + NAO_t$	0.803	0.998
	$DD_1 + NAO_{t+1} + NAO_t + ICE_{t+1}$	-64.97	$DD_1 + NAO_{t+1} + NAO_t$	0.117	0.894
	$DD_1 + ICE_{t+1} + ICE_t$	-60.37	$DD_1 + NAO_{t+1} + NAO_t$	0.713	0.476