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Age and sex ratios in the declining West Siberian/ North European population of Long-tailed Duck wintering in the Baltic Sea: Implications for conservation

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The West Siberian/North European population of Long-tailed Duck (*Clangula hyemalis*), which breeds in the Russian Arctic and northern Fennoscandia and winters in the Baltic Sea, has declined rapidly since the 1990s. To identify the causes of the decline and initiate effective conservation measures information on basic demographic parameters is needed. A photo survey method was used to estimate female age ratios and the proportion of males among adults in wintering Long-tailed Ducks at coastal and off-shore areas in the Baltic Sea. Female age ratios were defined as the number of first winter males, assumed equal to the number of first winter females, per adult female. Several thousand individuals were sampled each winter from 2008 to 2021. Female age ratios fluctuated between years and were consistently lower in the southern than in the central Baltic Sea. The proportion of males among wintering adults birds was male-biased, more so in the southern Baltic Sea than in other regions. A population model was used to analyse if low female age ratios between 2008 and 2021 has constrained population growth. Given that the estimated weighted mean female age ratio of 0.153 was representative at the population scale, an extremely high adult female mean annual survival rate of 0.872 would have been needed to maintain a stable population. Considering known sources of anthropogenic mortality in the Baltic Sea, and instead assuming a more realistic survival rate of *ca.* 0.80, a population decline of *ca.* 7.7% per year should have occurred during the study period.

1. Introduction

The Long-tailed Duck (*Clangula hyemalis*) is a sea duck species which breeds in Arctic tundra habitats and winters at sub-Arctic and temperate coastlines and at off-shore banks. Four larger populations are recognised: the West Siberian/ North European, the Iceland/Greenland, the North American, and the East Asian populations. At least the two largest populations, the West Siberian/North European and the North American populations have declined significantly in numbers since the 1990s and 1980s, respectively (Durinck *et al.* 1994, Skov *et al.*

2011, Bowman *et al.* 2015). Long-tailed Ducks belonging to the West Siberian/North European population breed in the Russian Arctic and in northern Fennoscandia and the vast majority of the birds winter in the Baltic Sea (Loshchagina *et al.* 2019, Karwinkel *et al.* 2020, Quillfeldt *et al.* 2021). Two Baltic wide surveys have shown that the number of wintering Long-tailed Ducks has decreased from approximately 4.3 million birds in 1992–1993 to approximately 1.5 million in 2007–2009 (Durinck *et al.* 1994, Skov *et al.* 2011). Winter surveys performed after 2009, which covered important parts of the Baltic Sea, have indicated a further decline (Nilsson 2012, 2016). Because of the rapid decline the species is globally classified as vulnerable on the IUCN Red List (Wetlands International 2021), and the West Siberian/North European population is classified as endangered on the HELCOM red list (HELCOM 2021). An International Single Species Action Plan for the conservation of the Long-tailed Duck has also been adopted by the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) with the objective to significantly reduce direct anthropogenic mortality and understand the wider drivers of the population decline (Hearn *et al.* 2015).

To better understand the population dynamics and the causes of the decline more information on basic demographic parameters, *i.e.*, juvenile production, survival rates and sex ratios, is needed. Such data are difficult to obtain in the Arctic because Long-tailed Ducks nest at low densities over vast often inaccessible tundra regions. Previous field studies of the species breeding biology in the Arctic, and population modelling, have shown that the reproductive success varies greatly between years and that population growth rates are highly sensitive to changes in adult female survival rates and to duckling survival (Alison 1975, Pehrsson 1986, Schamber *et al.* 2009, Flint 2015, Koneff *et al.* 2017). However, the demographic studies hitherto performed, including analyses of survival rates, return rates of marked individuals to nesting sites, nest and hatching success and duckling survival have, by necessity, been local in scale and may not be representative at the population level.

A complimentary way to obtain population wide information on basic demographic parameters is to analyse age and sex ratios at wintering sites where large number of Long-tailed Ducks from several breeding areas are aggregated. One method is to determine the sex and age of birds shot by hunters (Hario *et al.* 2009, Koneff *et al.* 2017, Aarhus University 2021, Rintala *et al.* 2022). Other samples, for example of by-caught birds in fishery, or of oil damaged birds, where dead bodies or wings can be examined, have also provided information (Hearn *et al.* 2015). In other species of sea ducks, with delayed plumage maturation, direct field observations of wintering birds have also been used to determine age and sex ratios (Smith *et al.* 2001, Rodway *et al.* 2003, 2015, Iverson *et al.* 2004, Robertson 2008).

Also the methods used in winter to estimate demographic parameters have constraints and may be more or less biased. For example, analyses of hunting bags might be significantly biased because juvenile birds may be more vulnerable to hunting than adults (Koneff *et al.* 2017). The willingness or opportunities to shoot males and females, respectively, may also differ. Samples of by-caught birds in fish nets might be biased because less experienced juveniles might be caught more often than adults (Stempniewicz 1994). In addition, the age and sex ratios obtained from analyses of collected dead birds or from direct observations in the field at specific sites during the non-breeding season, might not be representative for the whole population unless age and sex specific migration and spatial segregation patterns are corrected for.

The aim of this study was to use a novel photo survey method to estimate age and sex ratios of wintering Long-tailed Ducks in the Baltic Sea. By the photo survey method very large number of birds belonging to the West Siberian/North European population of Long-tailed Duck could be sampled at several different coastal and off-shore sea areas each winter season (Larsson 2022). A specific aim was to analyse the broad scale winter distribution of 6–10 months old juveniles, henceforth called first winter birds, and analyse if a too low production of first winter birds during the 14-year study period between 2008 and 2021 has constrained population growth and the possibility to obtain a stable Long-tailed Duck population.

2. Material and methods

2.1. Photo surveys

Flocks of wintering Long-tailed Ducks were surveyed from various boats, fishing and research vessels at offshore and coastal wintering and spring stopover sites in the Baltic Sea between 2008 and 2021 (Fig. 1). Surveys in the central and southern Baltic Proper, *i.e.*, at the main wintering sites, were performed between January and mid-April. Surveys more north in the Åland archipelago and in the northwestern Gulf of Finland, where Long-tailed Ducks aggregate in spring before they leave the Baltic Sea and migrate to their Arctic breeding grounds, were performed between mid-April and beginning of May. Long-tailed Ducks usually return to the Baltic Sea from their Arctic breeding grounds in October. Various surveys indicate that adult males, on average, in autumn arrive at the Gulf of Finland and northern Baltic Proper slightly earlier than females and juveniles (Lehikoinen *et al.* 2006). To avoid possible biases related to sex segregated migration patterns in autumn only results from photo surveys performed from January and onwards are included in the further analyses.

When wintering flocks were detected swimming on the water, the boat or the vessel approached the flock, and when the birds flew off, usually against the wind, photos were taken from the side. Photos were also taken on flying birds which were passing nearby when the boat or vessel was engaged in line transect surveys. The flocks that were approached varied in size from a few individuals to several hundred, sometimes several thousand birds. During the photo surveys, the aim was to take photos on specific flocks or individuals only once. When large flocks flew off the water or were passing the boat, photos were taken sequentially on parts of the flock to reduce the risk of taking photos

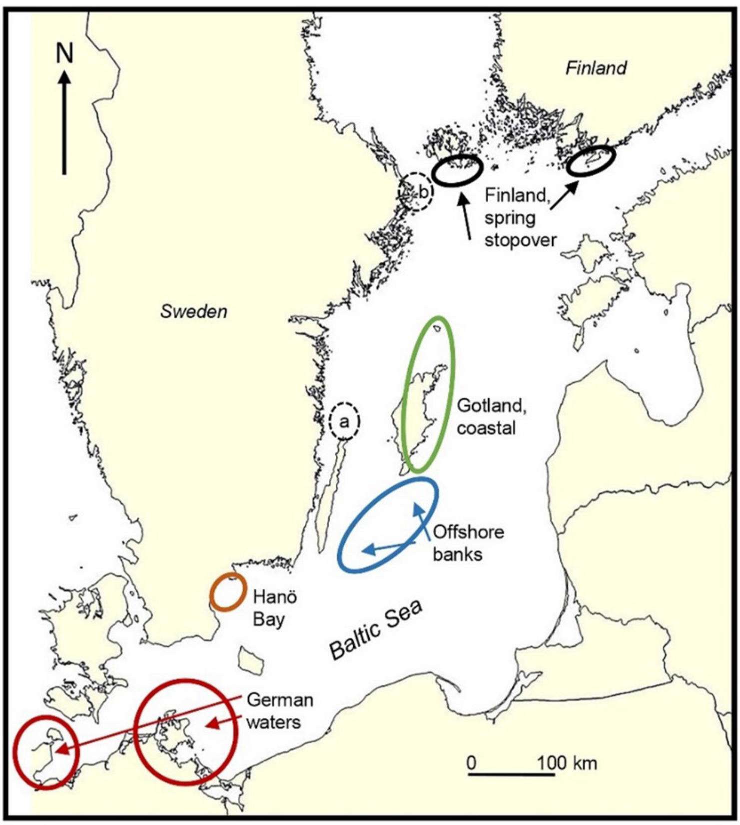

Fig 1. Map showing the five regions where photo surveys of wintering Long-tailed Ducks (*Clangula hyemalis*) were performed in the Baltic Sea between 2008 and 2021. Red, orange, blue and green circles show where photo surveys where performed in winter (January to mid-April). Black circles show where surveys were performed at spring stopover sites (mid-April to beginning of May). Dotted circles a, and b show where additional photo surveys were performed in winter 2017.

of the same birds more than once. Photos were taken with a high quality Nikon digital camera equipped with Nikon telephoto lenses between 200 and 500 mm. The photos, jpg image files, were viewed in Adobe Photoshop and analysed manually. All photos were taken and analysed by the author.

2.2. Plumage characteristics visible on photos of flying birds

In winter, between January and beginning of April, adult males have a complete black breast, well developed white scapulars, two fully elongated central tail feathers, a characteristic head feather pattern consisting of a large olive-grey patch from the bill base to around the eye and a large black oval patch on the lower cheeks. They also have a pink band on the bill. First winter males do not have a complete black breast and in most cases no elongated central tail feathers. Rarely, first winter males may have short central tail feathers, *i.e.*, visible but not fully elongated as in adult males. First winter males also have a pink band on the bill, although not always as bright as in adult males. The appearance of the white scapulars in first winter males varies from almost invisible to fully developed as in adult males. In first winter males the head patterns varies from female-like to fully adult male-like. Females appear brownish at a distance. Typically the sides of the head are whitish with a darker brownish cheek patch, crown and breast. The bill is dark grey and lack a distal pink band. Females lack elongated central tail feathers and white elongated scapulars. First winter females cannot be reliably distinguished from adult females on photos taken at a distance. Juvenile males can be distinguished from females by the presence of either a pale or pink distal band on the bill, white scapulars, an incomplete black breast band, or the typical male head feather pattern. In April the birds partly moult and the plumage becomes darker. The white scapulars in males are for example replaced by brown scapulars. A full description of plumage characteristics visible on photos of flying birds is presented in Larsson (2022).

2.3. Age and sex ratios

Individuals were classified from photos into three categories, that is, adult males, first winter males, and females, based on the plumage and bill characteristics. It was assumed that the overall sex ratio of first winter birds was equal during the time period when age ratio assessments were performed between January and mid-May. Hence, the sex ratio at hatching and the survival rate from hatching to first winter was assumed to be equal for males and females (Blums & Mednis 1996, Wood *et al.* 2021). By contrast, adult sex ratios were not assumed to be equal because mortality rates in ducks are often higher for adult females than for adult males during the breeding season.

The total numbers of adult males and first winter males observed on photos within a sampled area were counted directly. The total number of first winter females on photos within a sampled area was assumed to be equal to the total number of first winter males. The total number of adult females on photos within a sampled area was estimated as the total number of observed females minus the total number of observed first winter males. The total number of adults on photos was estimated as the sum of the observed total number of adult males and the estimated total number of adult females.

Female age ratios were estimated as the total number of observed first winter males, assumed equal to the number of first winter females, divided by the estimated total number of adult females. Female age ratios express the average number of first winter females, or first winter males, per adult female. Female age ratios are thus measures of the production of first winter birds in the population. The proportion of males among adults was estimated as the total number of adult males divided by the estimated total number of adults (see online only Supplementary Tables S1 and S2 for numerical calculations).

Lehikoinen *et al.* (2008) found in a study of Common Eiders (*Somateria mollissima*) that the sex ratio at hatching did not deviate from equal, but that female ducklings after hatching, but before fledging, had slightly higher mortality than male ducklings. They argued that sex differential mortality among hatchlings could be a cause for an observed male biased sex ratio among first-winter common eiders (~57% males) (Lehikoinen *et al.* 2008). If future studies will show that there is a biased sex ratio also among first winter Long-tailed Ducks the way to calculate female age ratios, as described above, should be adjusted. However, if existing, a slight deviation from unity in the sex ratio among first winter Long-tailed Ducks will not change the overall conclusions in the present study.

2.4. Surveyed regions

In total, 132 photo surveys were conducted between 2008 and 2021. The surveyed sites were grouped into five regions: (1) coastal waters east of the Swedish island of Gotland in the central Baltic Sea, (2) offshore banks in Swedish Exclusive Economic Zone in the central Baltic Sea, *i.e.*, Hoburgs Bank and Northern Midsjö Bank, (3) Hanö Bay, in Swedish waters in southern Baltic Sea, (4) German waters in the southern Baltic Sea at Fehmarn Belt and Pomeranian Bay including Adlerground, and (5) coastal Finnish spring stopover sites in the southern Åland archipelago and in the northwestern part of Gulf of Finland near Hanko (Fig. 1). Two previous Baltic wide surveys, in 1992–1993 and 2007–2009, respectively, and later surveys have shown that the surveyed regions 1 to 4 all are key wintering sites for Long-tailed Ducks in the Baltic Sea (Durinck *et al.* 1994, Skov *et al.* 2015, Nilsson 2016). Photo surveys in coastal waters east of Gotland were conducted between January and April, at offshore banks and at Hanö Bay in March and April and in German waters in the southern Baltic in January and February. In spring, wintering Long-tailed Ducks from the southern and central Baltic Sea move northward, mix and aggregate in the northern Baltic Proper, Åland archipelago, Gulf of Finland and Gulf of Riga before they leave the Baltic Sea for their Arctic breeding grounds. The photo surveys at the coastal Finnish spring stopover sites were therefore performed in the second half of April and beginning of May.

Several photo surveys were usually conducted at different sites and dates within the same region each season. In March 2017, surveys were also conducted at two additional Swedish sites outside the five defined regions, *i.e.*, (a) in coastal waters and offshore banks north of the island of Öland, and (b) in the Stockholm archipelago near Kapellskär in the northern Baltic Proper (Fig. 1).

Between 1,832 and 18,723 birds (mean = 8,857 birds) were photographed and analysed each winter season between 2009 and 2021. A smaller sample, photos of 471 birds, was obtained at spring stopover sites in the Åland archipelago in 2008. In 2020 and 2021, only the coastal waters east of the Swedish island of Gotland could be surveyed because of covid-19 travelling restrictions. The number of analysed photos from each region each year varied between 26 and 615 (mean = 269) (Supplementary Table S1).

The number of analysed photos and analysed birds varied between regions and years due to external factors such as weather conditions and the availability of ships and boats. The number of analysed birds were still very high at each region each year. The 95% confidence intervals of the estimated ratios and proportions of different bird categories were therefore generally low.

2.5. Standard errors of estimates

Since the aim of the study was to obtain broad scale Baltic wide estimates, female age ratios and the proportion of males among adults were estimated for each surveyed region and year from pooled samples. Possible age and sex specific segregation at smaller geographical and temporal scales were not considered. Standard errors and 95% confidence intervals of the estimated female age ratios and proportions of males were obtained by bootstrapping (Efron & Tibshirani 1994, Larsson 2022). The bootstrapping method is suitable to estimate standard errors when normality assumptions might not apply, for example when ratios are analysed. Photos taken in a region in specific years were resampled with replacement to produce one thousand resampled data sets. The number of photos in each resampled data set matched the number of photos in the original data set. The female age ratio and the proportion of males among adults were calculated for each of the resampled data sets to create sampling distributions of the two quantities. Standard errors were then estimated as the standard deviation of the sampling distributions of the female age ratio and the proportion of males among adults, respectively. For comparison, standard errors (SE) of the estimated proportions of males among adults were also calculated according to a general equation below (Eq. 1) applicable to proportions (Fowler *et al.* 1998),

$$\mathrm{SE} = \sqrt{\left(\frac{p(1-p)}{n-1}\right)} \quad (1)$$

where p is the proportion of adult males, and n is the number of all adults in the sample (Supplementary Table S2).

2.6. Population model

To analyse if the production of first winter birds between 2008 and 2021 has constrained the population growth and the possibility to obtain a stable Long-tailed Duck population a simplified matrix-based population model developed by Robertson (2008) was used. This population model has been specifically developed to allow the fecundity component, *i.e.*, the juvenile/adult ratio, here the female age ratio, to be measured in mid- to late winter. The population model is especially suitable for analyses of fecundity data from long-tailed ducks and other sea ducks with recognizable sub-adult plumages in winter (Robertson 2008).

Survival rates of juveniles or adults have not yet been measured in studies of Long-tailed Ducks belonging to the West Siberian/North European population. Population specific data on survival rates can therefore not be used as input values to the population model. However, Koneff *et al.* (2017) compiled information on annual survival rates of sea ducks, in the absence of harvest, from mark-recapture studies in North America, expert judgements, and allometric relationships with body weight. In their analyses they used a median annual survival rate of 0.81 for adult Long-tailed Ducks and 0.71 for subadults, *i.e.*, for the 2nd year survival rate. The estimated survival rate of Long-tailed Duck based on allometric relationships with body weight was higher (0.86, SD = 0.05) than the experts' estimates (Koneff *et al.* 2017). Here, in the further analyses annual survival rates between 0.75 and 0.87 are considered. Survival rates of first winter birds and older birds, *i.e.*, of all birds older than six month, are assumed equal.

To estimate the production of first winter birds needed to maintain a stable population equation (Eq. 2) was used, that is, equation 5 in Robertson (2008),

$$F = (1 - S\lambda^{-1}) / S^{4/3}\lambda^{-2} \quad (2)$$

where F in this case, under the assumption that all two-year old and older females have equal reproductive success, is the female age ratio in winter. S is the adult female annual survival rate and λ is the deterministic population growth rate, where $\lambda=1$ indicates a stable population, $\lambda<1$ population decline and $\lambda>1$ population increase.

3. Results

3.1. Female age ratios and distribution of first winter birds

Female age ratios of wintering Long-tailed Ducks, and hence the production of first winter birds, clearly differed between years (Fig. 2). Furthermore, female age ratios differed between surveyed wintering regions, which show that the winter distributions of first winter birds and adults were not identical at the broad scale level (Fig. 2). For example, female age ratios were consistently lower in the German waters in the southern Baltic Sea than in coastal waters east of Gotland and at offshore banks in the central Baltic Sea. Also at Hanö Bay in the southern Baltic Sea the female age ratios were low in the three winters when the region was surveyed. The female age ratios were also generally lower at offshore banks in the central Baltic Sea than at coastal waters east of Gotland in the ten winters when both regions were surveyed (Fig. 2).

Because wintering Long-tailed Ducks from the southern and central Baltic Sea aggregate at Finnish stopover sites in late April and May, the time-series of female age ratios obtained at Finnish stopover sites can be expected to covary with time-series obtained at the more southern wintering sites. Indeed, the annual estimates

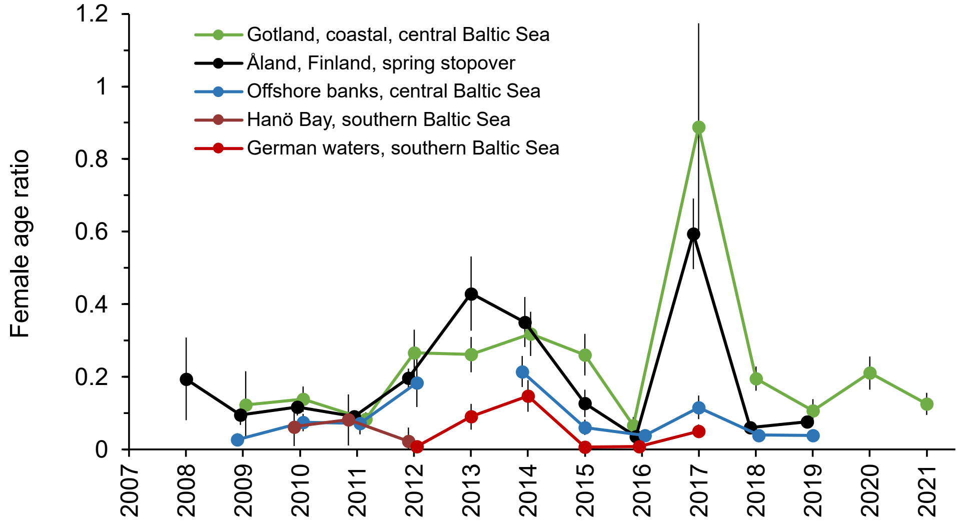

Fig. 2. Female age ratios of Long-tailed Ducks (*Clangula hyemalis*) in winter and spring, estimated as the number of first winter males, assumed equal to the number of first winter females, per adult female, in five different regions in the Baltic Sea between 2008 and 2021. Error bars indicate bootstrapped 95% confidence intervals. Sample sizes are given in Supplementary Tables S1 and S2. Non-overlapping 95% confidence intervals infer significant differences between specific estimates. In years when production of first winter birds was high, the winter distribution of first winter birds was to a large extent oriented towards coastal waters in the central and northern Baltic Proper. First winter birds observed between January and May hatched during the summer preceding the indicated calendar year.

of female age ratios at Finnish spring stopover sites correlated significantly with the estimates obtained at the coastal waters east of Gotland ($r=0.87$, $p<0.01$, $n=11$ years). Correlations between estimates of female age ratios at Finnish waters and offshore banks ($r=0.61$, $0.05<p<0.1$, $n=10$ years) and German waters ($r=0.56$, $p>0.05$, $n=6$ years), respectively, were also positive but not significantly so.

In years when female age ratios were low at the Finnish spring stopover sites, indicating low production of first winter birds, as observed in 2009, 2010, 2011, 2016, 2018 and 2019, the estimated female age ratios were low also in other regions that were surveyed earlier in the same winter (Fig. 2). However, in years when female age ratios were high at Finnish spring stopover sites and at coastal waters east of Gotland, indicating high production of first winter birds, as in 2013, 2014 and 2017, the female age ratios in German waters in southern Baltic Sea, and at offshore banks in the central Baltic proper, were considerably lower. In 2017, female age ratios at two additional coastal sites in the central and northern Baltic Proper were also found to be high (0.53 and 0.27 at sites a and b, respectively) (Fig. 1). Thus, in years when production of first winter birds was high, the winter distribution of first winter birds was to a large extent oriented towards coastal waters in the central and northern Baltic Proper.

3.2. Proportion males among adults

The proportion of males among adults was male biased (Fig. 3 and 4). The male bias was more pronounced in the southern Baltic Sea, that is, in German waters and at Hanö Bay, than in other regions. The proportion of males among adults was also slightly more male biased at offshore banks in the central Baltic Sea than at coastal waters east of Gotland and at Finnish spring stopover sites. Non-overlapping 95% confidence intervals can be used to identify significant differences between specific estimates (Fig. 3). No significant long-term trend of adult sex ratios was observed in any of the five surveyed regions over the study period (all $p>0.10$, linear regressions).

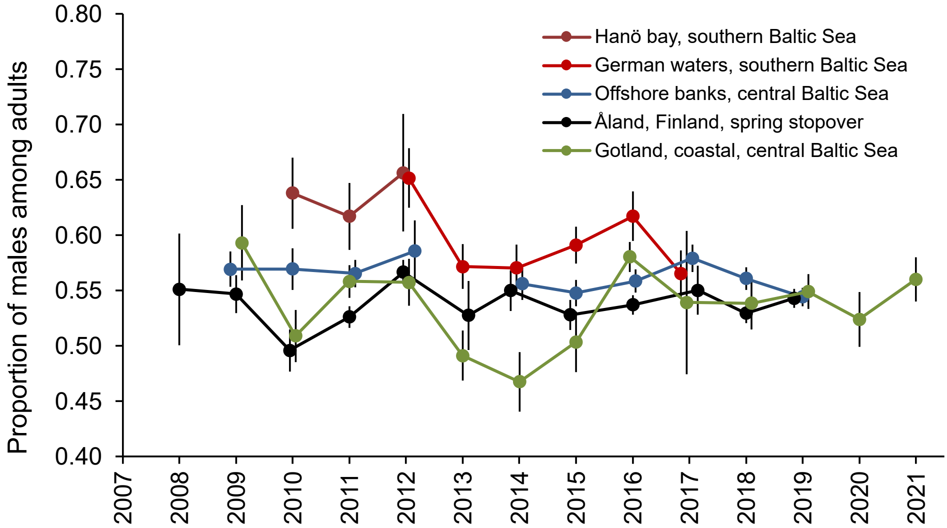

Fig. 3. Adult sex ratios of wintering Long-tailed Ducks (*Clangula hyemalis*), estimated as the total number of adult males divided by the total number of adults, differed between regions in the Baltic Sea. The overall adult sex ratio was male biased. The adult sex ratio in winter was more male biased in the southern parts of the Baltic Sea. Error bars indicate bootstrapped 95% confidence intervals. Non-overlapping 95% confidence intervals infer significant differences between specific estimates. Sample sizes are given in Supplementary Tables S1 and S2.

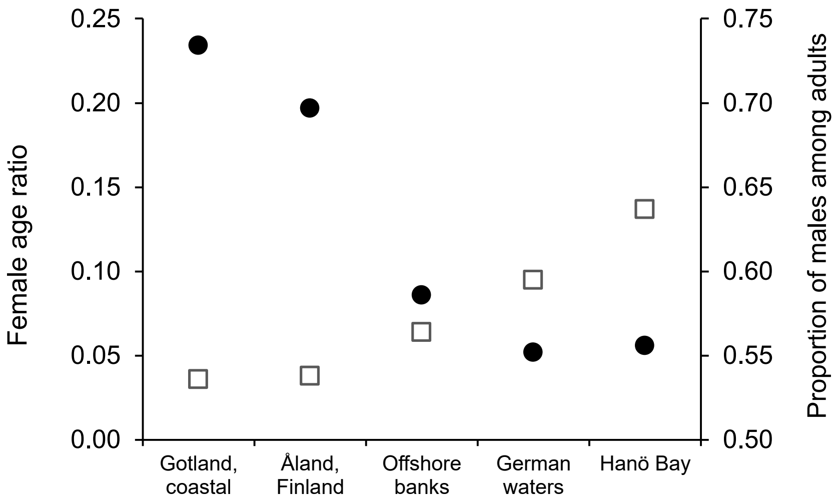

Fig. 4. Mean age and sex ratios of wintering Long-tailed Ducks (*Clangula hyemalis*) in five different regions in the Baltic Sea between 2008 and 2021. Black dots show means of yearly estimates of female age ratios. Open squares show means of yearly estimates of the proportion of males among adults. Sample sizes are given in Supplementary Table S2.

3.3. Population growth model

Relationships between female age ratios observed in winter, survival rates and population growth, based on a simplified deterministic matrix-based population model developed by Robertson (2008), are visualised in Fig. 5 and 6. Two alternative input values to the model for the fecundity component were chosen. As a first alternative, a weighted mean female age ratio, based on the mean female age ratios observed in winter in regions 1 to 4, was used to represent a population wide value (Supplementary Tabel S2). The weights given to the four mean female age ratios were chosen to approximately reflect the number of wintering individuals in different parts of the Baltic Sea, as presented in Skov *et al.* (2011). The mean female age ratio observed in German waters (0.052) was given a weight of 0.24 reflecting the proportion of the population estimated to winter in the southern Baltic Sea, that is, in Danish, German, and Polish waters. Similarly, the mean female age ratio observed at Hoburgs bank and Northern Midsjö banks (0.086) was given a weight of 0.24 reflecting the proportion of the population estimated to winter at these two offshore banks and at the closely situated Southern Midsjö bank. The mean female age ratio observed in coastal waters east of Gotland (0.234) was given a weight of 0.51 reflecting the proportion of the population estimated to winter along the coasts of the central Baltic Sea, that is, along the coasts of Lithuania, Latvia, Estonia, mainland Sweden north of Hanö Bay, and in other residual areas in the Baltic Sea (Skov *et al.* 2011). Lastly, the mean female age ratio observed at Hanö Bay (0.056) was given a weight of 0.01 reflecting the proportion estimated to winter at Hanö Bay and along the southernmost coast of Sweden. Thus, the weighted mean female age ratio used as input to the population model was (0.052*0.24) + (0.086*0.24) + (0.234*0.51) + (0.056*0.01) = 0.153.

As a second alternative, the mean female age ratio observed at Finnish spring stopover sites was used. The rationale for this choice was that previous surveys indicate that only a small

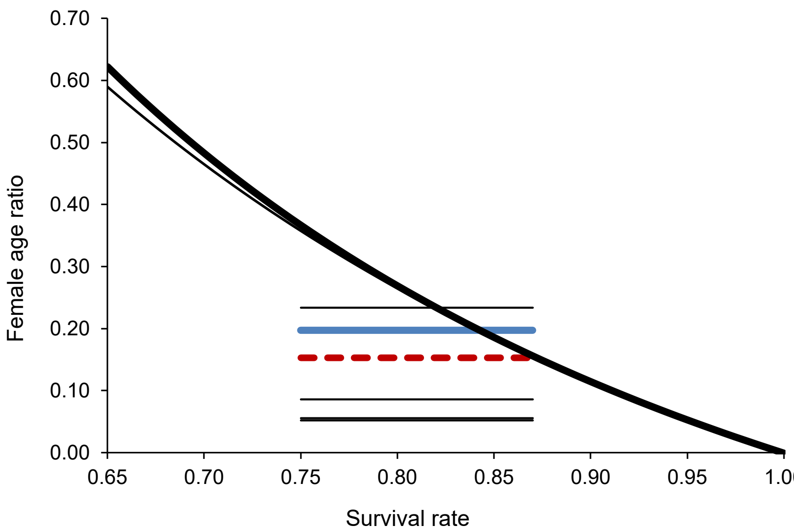

Fig. 5. Relationships between female age ratios observed in winter, adult female annual survival rates and population growth rates based on a deterministic matrix-based population model developed by Robertson (2008). The black thick curve shows the combinations of female age ratios and survival rates that will result in a stable population (λ=1), when age of first reproduction is two years. The black thin curve, only slightly deviating from the thick curve, shows the corresponding combinations when age of first reproduction is three years. Horizontal thin lines show the mean female age ratios observed in winter at four regions in the Baltic Sea. The thick blue horizontal line shows the female age ratio observed at spring stopover sites in Finland. The thick red dotted line shows the weighted mean female age ratio. The width of the horizontal lines represents possible adult female survival rates. Combinations of female age ratios and survival rates below the curved line will result in population declines.

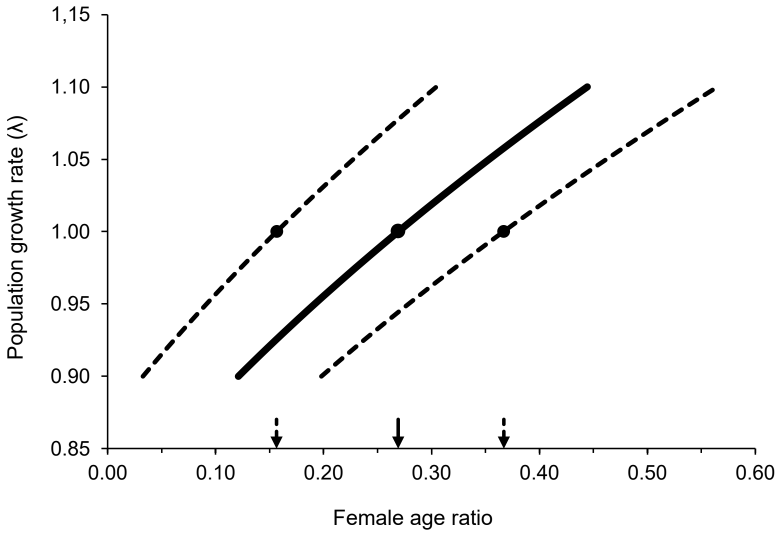

Fig. 6. Relationships between female age ratios observed in winter, adult female annual survival rates and population growth rates based on a deterministic matrix-based population model developed by Robertson (2008). The black thick curve shows the relationship between female age ratios and population growth rates (λ) when adult female annual survival rate is set to 0.80. The dotted curves above and below the solid curve show the corresponding relationships when adult female annual survival rate is set to 0.87 and 0.75, respectively. Arrows indicate the female age ratios, 0.156, 0.269 and 0.367, that are needed to obtain a stable population (λ=1) when survival rates is set 0.87, 0.80 and 0.75, respectively.

number of birds stay at the spring stopover sites in mid-winter, partly because of ice cover, and, hence, that the vast majority of the birds observed in the Finnish waters in late spring must consist of a mixture of birds from several wintering regions further south. The observed yearly female age ratios at the Finnish stopover sites between 2008 and 2019 varied from 0.036 to 0.594 and the overall mean female age ratio was 0.197 (n=12 years) (Fig. 5 and Supplementary Table S2).

Given that the weighted mean female age ratio of 0.153 was representative for the whole wintering population in the Baltic Sea, an extremely high adult female mean survival rate of 0.872 would have been needed to maintain a stable population (Fig. 5 and 6). If one instead assume that a female survival rate of approximately 0.80 is more realistic, and combine that value with the weighted mean female age ratio of 0.153, a population decline of approximately 7.7% per year (λ=0.923) should have occurred during the study period.

If the slightly higher mean female age ratio of 0.197 observed at spring stopover sites in Finland better represent the population wide value, an adult female mean survival rate of 0.843 would have been needed to maintain a stable population. Again, given a more realistic female survival rate of approximately 0.80, and the observed female age ratio of 0.197, a population decline should have occurred during the study period, in this case, of approximately 4.6% per year (λ=0.954) (Fig. 5 and 6).

4. Discussion

To better understand the dynamics of the West Siberian/North European population of Long-tailed Duck, and by conservation measures to stop and reverse the recent rapid population decline, accurate and non-biased data on basic demographic parameters are needed. Because Long-tailed Ducks breed at low densities over large tundra areas, studies of the reproductive output and survival rates at the Arctic Russian and northern Fennoscandian nesting grounds will for logistic reasons be local in scale and the data obtained might not be representative on a broad population scale. A complementary way to obtain demographic information is to conduct broad scale studies of a selected set of demographic parameters at wintering sites. In this 14-year study a novel photo survey method was successfully used at some of the most important coastal and offshore wintering and spring stopover sites for Long-tailed Ducks in the Baltic Sea. By the photo survey method it was possible to annually survey very large number of birds and estimate the yearly variation in female age ratios, *i.e.*, the variation in the production of first winter birds, as well as the proportion of males among adults and the spatial segregation of sex and age groups of wintering Long-tailed Ducks.

4.1. Spatial segregation patterns

Female age ratios differed between regions within the Baltic Sea (Fig. 2). Female age ratios were consistently lower in the German waters in the southern Baltic Sea than at offshore banks and coastal waters in the central and northern Baltic Proper. Hence, the winter distributions of first winter birds and adults were not identical at the broad Baltic wide level. The partial segregation of age groups, with a higher proportion of first winter birds wintering more north, was also more pronounced in years with high production of first winter birds.

The proportion of males among adults also differed between the studied regions (Fig. 3 and 4). The observed overall broad scale pattern was a male biased adult sex ratio. This result is consistent with observations from several other sea duck populations, and with the finding that the mortality rate of adult female sea ducks during the breeding season usually is higher than that of adult males (Flint 2015). In this study, the proportion of males among adults in winter was clearly more male biased in the German waters and at Hanö Bay in the southern Baltic Sea than in other regions. The proportion of males among adults was also slightly more male biased at the offshore banks than in coastal waters east of Gotland and at Finnish spring stopover sites. Similar spatial and temporal segregation between adult males and adult females at wintering and stop-over sites has previously also been reported in several other sea ducks (Petersen & Savard 2015). No significant long-term trend of adult sex ratios was observed over the study period.

There is a possibility that different age and sex ratios at different wintering regions to some extent could be an effect of that birds from different parts of the breeding range, and which experience different conditions in summer, have different centres of distribution in the Baltic Sea. However, the studies that exist on migration movements do not support such a segregation pattern. For example, Quillfeldt *et al.* (2021) found that Long-tailed Ducks marked with implanted satellite transmitters at breeding sites on Kolguev Island in northwestern Russia spent the winter in different parts of the Baltic Sea, including in the regions surveyed in the present study. Furthermore, by studying marked Long-tailed Ducks breeding in Alaska, Petersen *et al.* (2003) concluded that wintering populations would be expected to contain a mix of birds from different breeding areas, and breeding populations would include birds from different wintering areas. It should be noted that here, in the present study, segregation patters of age and sex groups of Long-tailed Ducks were analysed on a large Baltic wide scale. Additional small scale spatial and temporal segregation patterns, related to habitat use and environmental variables, cannot be excluded and warrants further studies. Irrespective of the causes for segregation patters in winter, knowledge about the patterns is necessary to interpret result from any type of surveys monitoring age and sex ratios or population size.

4.2. Population trajectories

Baltic wide surveys have shown that the West Siberian/North European population of Long-tailed Ducks declined by approximately 65% between 1992–1993 and 2007–2009 (Durinck *et al.* 1994, Skov *et al.* 2011) and regional surveys in parts of the Baltic Sea performed after 2009 have indicated further declines (Nilsson 2016). It is therefore of interest to analyse if the decline has been caused by low reproductive success, or low survival rates, for example because of additional anthropogenic mortality.

In this study it was found that the production of first winter birds, measured as the female age ratios in winter, clearly fluctuated between years. Furthermore, positive correlations between time-series also showed that female age ratios observed in different wintering regions fluctuated in a similar way. This indicates that monitoring efforts with the photo survey method, at a relatively few key wintering and spring stopover sites, can capture large scale population processes and provide reliable demographic information to further analyses.

The overall mean female age ratio was low during the study period between 2008 and 2021. Regardless of whether the weighted mean female age ratio of 0.153, or the slightly higher mean female age ratio of 0.197 observed at the Finnish stopover sites, was closest to the true population value, very high mean female survival rates of 0.872 and 0.843, respectively, would have been needed to balance the low female age ratios and maintain a stable population.

Results from this study as well as from other more elaborated sea duck population models all show that even very small changes in female adult survival rates will have large effects on predicted population trajectories (Flint 2015). No field studies have hitherto produced any estimates of the natural adult survival rates of birds from the West Siberian/North European Long-tailed Duck population. However, it is known that anthropogenic mortality of wintering Long-tailed Ducks can be considerable in the Baltic Sea region, because of recurrent spills of oil and chemicals from ships at important wintering sites (Larsson & Tydén 2005, Larsson 2016), by-catches in fishery (Bellebaum *et al.* 2012, Žydelis *et al.* 2009) and hunting (Hearn *et al.* 2015). In the International Single Species Action Plan for the Conservation of the Long-tailed Duck, Hearn *et al.* (2015) emphasised the difficulties to obtain good background statistics to quantify anthropogenic mortality rates for the West Siberian/North European population. However, they estimated that anthropogenic mortality from oil spills, by-catch and hunting accounted for an additional mortality of approximately 2–5% per year. Furthermore, Koneff *et al.* (2017), in their evaluation of risk of overharvest of sea ducks in North America, used a median adult survival rate in the absence of harvest of 0.81 for adult Long-tailed Ducks and 0.71 for subadults. It is therefore reasonable to assume that the true survival rate of 6 months old and older Long-tailed Ducks wintering in the Baltic Sea, when natural and anthropogenic mortality rates have been added, was 0.80 or lower during the study period. If so, then the total Baltic wintering population should have declined by an alarming rate of about 4% to 8% per year from 2008 to 2021.

4.3. Causes for fluctuating juvenile production

In this study, and in many other studies of arctic breeding sea ducks, geese and waders, the juvenile production has been observed to fluctuate markedly between years (Fig. 2) (Pehrsson 1986, Schamber *et al.* 2009, Nolet *et al.* 2013, Aharon-Rotman *et al.* 2015, Flint 2015). Breeding propensity, nest and hatching success and duckling survival at the Arctic breeding grounds may vary due to varying predation pressures and to varying climatic factors affecting the condition of breeding birds and their offspring. Arctic voles and lemmings are known to exhibit population cycles with peaks every 3–5 years. Generalist predators like the Arctic fox, and several species of avian predators, feed to a large extent on voles and lemmings but may shift to alternative prey, for example, eggs and chicks of waterfowl and waders, in years when rodents are scarce (Summers & Underhill 1987, Aharon-Rotman *et al.* 2015). In a recent study Rintala *et al.* (2022) argued that the reproductive success of Long-tailed ducks was related to lemming abundances in the previous year but also to direct and indirect effects of temperature and precipitation. Similarly, in a study of Dark-bellied Brent Geese (*Branta bernicla bernicla*) which breeds on coastal arctic tundra at the Taimyr Peninsula in northern Russia, Nolet *et al.* (2013) found that breeding success was dependent on lemming abundance, temperature at the breeding sites, *i.e.*, onset of spring, and population size. They also concluded that low juvenile production and the levelling off of the brent goose population from the 1990s and onwards was mainly the result of faltering lemming cycles (Ims *et al.* 2008, Nolet *et al.* 2013). Thus, although it seems very likely that the fluctuating reproductive success of Long-tailed Ducks, in general terms, to a large extent is affected by Arctic generalist predators switching between prey species in different years, additional important interactions related to weather and climate change at the breeding and wintering sites remains to be elucidated. For example, it cannot be excluded that carry-over effects are present, *i.e.*, that varying environmental conditions at the wintering and spring stopover sites affects the condition of spring migrating Long-tailed Ducks and their subsequent reproductive success in the Arctic (Waldeck & Larsson 2013, Larsson *et al.* 2014, Rintala *et al.* 2022). The variable production of first winter birds observed in the present study does not follow a strict 3–5 year cycle which indicates that also other factors than vole and lemming abundances are affecting juvenile production (Fig 2). Further analyses of temporal and spatial predation patterns as well as analyses of effects of climate change and other environmental factors at the breeding and wintering grounds are therefore needed.

5. Conclusions

The photo survey method used in this study is an effective method to obtain yearly values of basic demographic parameters of wintering Long-tailed Ducks. Compared to other methods, for example analyses of hunting bags, the photo survey has the great advantage that it does not suffer from the problem with small sample sizes and differential vulnerability of different sex and age groups. The results from this and previous studies clearly indicate that a combination of a too low average production of juveniles, and a too high anthropogenic mortality rate, has caused, and is still causing, a rapid decline of the West Siberian/North European Long-tailed Duck population. To be able to halt and reverse the ongoing population decline one urgently need management actions that reduce the direct anthropogenic mortality at the most important wintering sites in the Baltic Sea, as well as ensure the availability of high quality feeding conditions in networks of marine protected areas. It will be more feasible in the short term to affect the further population trajectory by implementing management actions that reduce anthropogenic mortality at the wintering sites than management actions that intend to increase the overall reproductive output in the Arctic.

Ålders- och könskvoter i den minskande Västsibiriska/Nordeuropeiska populationen av alfågel som övervintrar i Östersjön: konsekvenser för bevarandet

Den västsibiriska/nordeuropeiska populationen av alfågel (*Clangula hyemalis*) som häckar i arktiska Ryssland och norra Fennoscandia och övervintrar i Östersjön, har minskat snabbt i antal sedan 1990-talet. För att identifiera orsakerna till minskningen och initiera effektiva bevarande-åtgärder behövs information om grundläggande demografiska parametrar. En fotoinventerings-metod användes för att skatta ungproduktion och adult könskvot hos övervintrande alfåglar i kust-områden och på utsjöbankar i Östersjön. Flera tusen individer analyserades varje vinter från 2008 till 2021. Antalet unga honor, dvs. 6–10 månader gamla individer, antogs vara lika som antalet ungar hanar. En honlig ålderskvot beräknades som antalet unga honor per vuxen hona. Denna ålderskvot varierade mellan år men var konsekvent lägre bland övervintrande individer i södra än i centrala Östersjön. Könskvoten hos övervintrande adulta individer var skev, med ett överskott av adulta hanar. Överskottet av adulta hanar var större i södra Östersjön än i andra regioner. En populationsmodell användes för att analysera om en låg produktion av 6-10 månader gamla ungfåglar mellan 2008 och 2021 har begränsat populationstillväxten. Givet att den skattade genomsnittliga vägda honliga ålderskvoten på 0.153 var representativ på populationsnivå, så skulle en extremt hög adult årlig överlevnadsgrad för honor om 0.872 ha behövts för att upprätthålla en stabil population. Med hänsyn till kända mänskliga faktorer som påverkar alfåglars överlevnad, bland annat utsläpp av olja och kemikalier från fartyg, bifångst vid nätfiske och jakt, är det mer rimligt att anta en årlig överlevnadsgrad på ca 0,80 och därmed att den i Östersjön övervintrande alfågelpopulationen minskade i en alarmerande takt om cirka 7.7% per år mellan 2008 och 2021.

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References

Aarhus University 2021: Danish Wing Survey. — Available at https://fauna.au.dk/en/hunting-and-game-management/wing-survey (accessed 16.10.2022).

Aharon-Rotman, Y., Soloviev, M., Minton, C., Tomkovich, P., Hassell, C. & Klaasen, M. 2015: Loss of periodicity in breeding success of waders links to changes in lemming cycles in Arctic ecosystems. — Oikos 124: 861–870. https://doi.org/10.1111/oik.01730

Alison, R. M. 1975: Breeding biology and behaviour of the oldsquaw (*Clangula hyemalis* L.). — Ornithological Monographs 18: i–52.

Bellebaum, J., Schirmeister, B., Sonntag, N. & Garthe, S. 2012: Decreasing but still high: bycatch of seabirds in gillnet fisheries along the German Baltic coast. — Aquatic Conservation Marine and Freshwater Ecosystems 23: 210–221

Blums, P. & Mednis, A. 1996: Secondary sex ratio in Anatinae. — Auk 113: 505–511.

Bowman, T.D, Silverman, E.D., Gilliland, S.G., & Leirness, J.B. 2015: Status and trends of North American sea ducks: Reinforcing the need for better monitoring. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 1–28. CRC Press, Boca Raton, FL.

Durinck, J., Skov, H., Jensen, F. P. & Pihl, S. 1994: Important marine areas for wintering birds in the Baltic Sea. — EU DG XI Research Contract no. 2242/90-09-01. Ornis Consult Report.

Efron, B. & Tibshirani, R.J. 1994: An Introduction to the Bootstrap. — Chapman and Hall/CRC.

Flint, P.L. 2015: Population dynamics of sea ducks: Using models to understand the causes, consequences, evolution, and management of variation in life history characteristics. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 63–96. CRC Press, Boca Raton, FL.

Fowler, J., Cohen, L. & Jarvis, P. 1998: Practical Statistics for Field Biology, second edition. — Wiley, Chichester.

Hario, M., Rintala, J. & Nordenswan, G. 2009: Dynamics of wintering Long-tailed Ducks in the Baltic Sea – the connection with lemming cycles, oil disasters, and hunting. — Suomen Riista 55: 83–96. (In Finnish, with English summary).

Hearn, R.D., Harrison, A.L. & Cranswick, P.A. 2015: International Single Species Action Plan for the Conservation of the Long-tailed Duck *Clangula hyemalis*, 2016–2025. — AEWA Technical Series. No. 57. Bonn, Germany

HELCOM 2021: HELCOM Red List of Birds – *Clangula hyemalis*. — Available at https://helcom.fi/baltic-sea-trends/biodiversity/red-list-of-baltic-species/red-list-of-birds/ (accessed 16.10.2022).

Ims, R.A., Henden, J.-A. & Killengreen, S.T. 2008: Collapsing population cycles. — Trends in Ecology and Evolution 23: 79–86. https://doi.org/10.1016/j.tree.2007.10.010

Iverson, S.A., Smith, B.D. & Cooke, F. 2004: Age and sex distributions of wintering surf scoters: implications for the use of age ratios as an index of recruitment. — Condor 106: 252–262.

Karwinkel, T., Pollet, I.L., Vardeh, S., Kruckenberg, H., Glazov, P., Loshchagina, J., Kondratyev, A., Merkel, B., Bellebaum, J. & Quillfeldt, P. 2020: Year-round spatiotemporal distribution pattern of a threatened sea duck species breeding on Kolguev Island, south-eastern Barents Sea. — BMC Ecology 20:31. https://doi.org/10.1186/s12898-020-00299-2

Koneff, M.D., Zimmerman, G.S., Dwyer, C.P., Fleming, K.K., Padding, P.I., Devers, P.K., Johnson, F.A., Runge, M.C. & Roberts, A.J. 2017: Evaluation of harvest and information needs for North American sea ducks. — PLoS ONE 12(4): e0175411. https://doi.org/10.1371/journal.pone.0175411

Larsson, K. 2016: Sjöfart och naturvärden vid utsjöbankar i centrala Östersjön – Havsplanering kan reducera konflikter. — Havs- och vattenmyndighetens rapport 2016: 24. (In Swedish).

Larsson, K. 2022: Age and sex ratios of wintering Long-tailed Ducks can be determined by analysis of photos of flying flocks at sea: A method description. — Ornis Svecica 32, 00–00 (in press).

Larsson, K. & Tydén, L. 2005: Effects of oil spills on wintering Long-tailed Ducks *Clangula hyemalis* at Hoburgs bank in central Baltic Sea between 1996/97 and 2003/04. — Ornis Svecica 15: 161–171.

Larsson, K., Hajdu, S., Kilpi, M., Larsson, R., Leito, A. & Lyngs, P. 2014: Effects of an extensive *Prymnesium polylepis* bloom on breeding eiders in the Baltic Sea. — Journal of Sea Research 88: 21–28. https://doi.org/10.1016/j.seares.2013.12.017

Lehikoinen, A, Kondratyev, A.V., Asanti, T., Gustafsson, E., Lamminsalo, O., Lapshin, N.V., Pessa, J & Rusanen, P. 2006: Survey of arctic bird migration and staging areas at the White Sea, in the autumns of 1999 and 2004. —The Finnish Environment 25. Finnish Environment Institute.

Helsinki. http://hdl.handle.net/10138/38722
Lehikoinen, A., Öst, M., Hollmén, T. & Kilpi, M. 2008: Does sex-specific duckling mortality contribute to male bias in adult common eiders? — Condor 110: 574–578. http://dx.doi.org/10.1525/cond.2008.8574
Loshchagina, J., Vardeh, S., Glazov, P., Pollet, I.L. & Quillfeldt, P. 2019: Long-tailed Duck (*Clangula hyemalis*) ecology: insights from the Russian literature. Part 2: European part of the Russian breeding range. — Polar Biology 42: 2277–2297. https://doi.org/10.1007/s00300-019-02595-0
Nilsson, L. 2012: Distribution and numbers of wintering sea ducks in Swedish offshore waters. — Ornis Svecica 22: 39–60.
Nilsson, L. 2016: Changes in numbers and distribution of wintering Long-tailed Ducks *Clangula hyemalis* in Swedish waters during the last fifty years. — Ornis Svecica 26: 162–176. https://doi.org/10.34080/os.v26.21855
Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y. & Ebbinge, B.S. 2013: Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. — Journal of Animal Ecology 82: 804–813. https://doi.org/10.1111/1365-2656.12060
Pehrsson, O. 1986: Duckling production of the Oldsquaw in relation to spring weather and small-rodent fluctuations. — Canadian Journal of Zoology 64: 1835–1841.
Petersen, M.R., McCaffery, B.J. & Flint, P.L. 2003: Post-breeding distribution of Long-tailed Ducks *Clangula hyemalis* from the Yukon-Kuskokwim Delta. — Wildfowl 54: 129–139.
Petersen, M.R. & Savard J.-P.L. 2015: Variation in migration strategies of North American sea ducks. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 267–304. CRC Press, Boca Raton, FL.
Quillfeldt, P., Morkūnas, J., Kruckenberg, H., Kondratyev, A., Loshchagina, J., Aarvak, T., Øien, I.J., Bellebaum, J. & Glazov, P. 2021: Year-round movements of Long-tailed Ducks *Clangula hyemalis* from Kolguev Island, Barents Sea. — Polar Biology 45: 71–87. https://doi.org/10.1007/s00300-021-02973-7
Rintala, J., Hario, M., Laursen, K. & Møller, A.P. 2022: Large-scale changes in marine and terrestrial environments drive the population dynamics of long-tailed ducks breeding in Siberia. — Scientifc Reports 12:12355. https://doi.org/10.1038/s41598-022-16166-7
Robertson, G.J. 2008: Using winter juvenile/adult ratios as indices of recruitment in population models. — Waterbirds 31: 152–158.
Rodway, M.S., Regehr, H.M., Boyd, W.S. & Iverson S.A. 2015: Age and sex ratios of sea ducks wintering in the Strait of Georgia, British Columbia: Implications for monitoring. — Marine Ornithology 43: 141–150.
Rodway, M.S., Regehr, H.M. & Cooke, F. 2003: Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks – implications for conservation and estimating recruitment rates. — Canadian Journal of Zoology 81: 492–503.
Schamber, J.L., Flint, P.L., Grand, J.B., Wilson, H.M. & Morse, J.A. 2009: Population Dynamics of Long-tailed Ducks Breeding on the Yukon-Kuskokwim Delta, Alaska. — Arctic 62: 190–200.
Skov, H., Heinänen, S., Žydelis, R., Bellebaum, J., Bzoma, S., Dagys, M, Durinck, J., Garthe, S., Grishanov, G., Hario, M., Kieckbusch, J.J., Kube, J., Kuresoo, A., Larsson, K., Luigujoe, L., Meissner, W., Nehls, H.W., Nilsson, L., Krag Petersen, I., Mikkola Roos, M., Pihl, S., Sonntag, N., Stock, A. & Stipniece, A. 2011: Waterbird Populations and Pressures in the Baltic Sea. — TemaNord 2011:550. Nordic Council of Ministers, Copenhagen 2011.
Smith, C.M., Goudie, R.I. & Cooke, F. 2001: Winter age ratios and the assessment of recruitment of Harlequin Ducks. — Waterbirds 24: 39–44.
Stempniewicz, L. 1994: Marine birds drowning in fishing nets in the Gulf of Gdansk (southern Baltic): numbers, species composition, age and sex structure. — Ornis Svecica 4: 123–132.
Summers, R.W. & Underhill, L.G. 1987: Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (*Charadrii*) on the Taymyr Peninsula. — Bird Study 34: 161–171.
Waldeck, P., & Larsson, K. 2013: Effects of winter water temperature on mass loss in Baltic blue mussels: implications for foraging sea ducks. — Journal of Experimental Marine Biology and Ecology 444: 24–30.
Wetlands International 2021: Waterbirds Populations Portal. — Available at https://wpp.wetlands.org/ (accessed 16.10.2022).
Wood, K.A., Brides, K., Durham, M.E. & Hearn, R.D. 2021: Adults have more male-biased sex ratios than first-winter juveniles in wintering duck populations. — Avian Research 12: 51. https://doi.org/10.1186/s40657-021-00286-1
Žydelis, R., Bellebaum, J. Österblom, H. Vetemaa, M., Schirmeister, B., Stipniece, A., Dagys, M., van Eerden, M. & Garthe, S. 2009: Bycatch in gillnet fisheries – An overlooked threat to waterbird populations. — Biological Conservation 142: 1269–1281.

Online supplementary material

Supplementary material available in the online version includes Tables S1 and S2.