Ducks change wintering patterns due to changing climate in the important wintering waters of the Odra River Estuary

Dominik Marchowski Corresp., [1] , **Łukasz Jankowiak** [1] , **Dariusz Wysocki** [1] , **Łukasz Ławicki** [2] , **Józef Girjatowicz** [3]

[1] Department of Vertebrate Zoology and Anthropology, Institute for Research on Biodiversity, Faculty of Biology, University of Szczecin, Szczecin, Poland
[2] West- Pomeranian Nature Society, Szczecin, Polska
[3] Hydrography and Water Management Unit, Faculty of Earth Science, University of Szczecin, Szczecin, Poland

Corresponding Author: Dominik Marchowski
Email address: marchowskid@gmail.com

Some species of birds react to climate change by reducing the distance they travel during migration. The Odra River Estuary in the Baltic Sea is important for wintering waterfowl and is where we investigated how waterbirds respond to freezing surface waters. The most abundant birds here comprise two ecological groups: benthic feeders and fish feeders. We showed that numbers of all benthivores, but not piscivores, were negatively correlated with the presence of ice. We showed that, with ongoing global warming, this area is increasing in importance for benthic feeders and decreasing for fish feeders. The maximum range of ice cover in the Baltic Sea has a weak and negative effect on both groups of birds. Five of the seven target species are benthivores (Greater Scaup *Aythya marila*, Tufted Duck *A. fuligula*, Common Pochard *A. ferina*, Common Goldeneye *Bucephala clangula* and Eurasian Coot *Fulica atra*), and two are piscivores (Smew *Mergellus albellus* and Goosander *Mergus merganser*). Local changes at the level of particular species vary for different reasons. Local decline of the Common Pochard may simply be a consequence of its global decline. Climate change is responsible for some of the local changes in the study area, disproportionately favoring some duck species while being detrimental to others.

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[1]Department of Vertebrate Zoology and Anthropology, Institute for Research on Biodiversity, Faculty of Biology, University of Szczecin, Szczecin, Poland

[2]West-Pomeranian Nature Society, Szczecin, Poland

[3]Hydrography and Water Management Unit, Faculty of Earth Science, University of Szczecin, Szczecin, Poland

[*]Corresponding author: Dominik Marchowski marchowskid@gmail.com

Abstract

Some species of birds react to climate change by reducing the distance they travel during migration. The Odra River Estuary in the Baltic Sea is important for wintering waterfowl and is where we investigated how waterbirds respond to freezing surface waters. The most abundant birds here comprise two ecological groups: benthic feeders and fish feeders. We showed that numbers of all benthivores, but not piscivores, were negatively correlated with the presence of ice. We showed that, with ongoing global warming, this area is increasing in importance for benthic feeders and decreasing for fish feeders. The maximum range of ice cover in the Baltic Sea has a weak and negative effect on both groups of birds. Five of the seven target species are benthivores (Greater Scaup *Aythya marila*, Tufted Duck *A. fuligula*, Common Pochard *A. ferina*, Common Goldeneye *Bucephala clangula* and Eurasian Coot *Fulica atra*), and two are piscivores (Smew *Mergellus albellus* and Goosander *Mergus merganser*). Local changes at the level of particular species vary for different reasons. Local decline of the Common Pochard may simply be a consequence of its global decline. Climate change is responsible for some of the local changes in the study area, disproportionately favoring some duck species while being detrimental to others.

Introduction

Migration distance has declined in several species of aquatic (and other) birds as a result of climate change (Musil et al. 2011; Lehikoinen et al. 2013; Meller 2016). The distances that birds migrate from their breeding areas in northern and eastern Europe to their central European wintering areas are shorter during mild winters (Lehikoinen et al. 2013; Pavón-Jordan et al. 2015); conversely birds may change their wintering sites to warmer regions during colder periods because they may perceive local manifestations of larger scale weather (Newton 2008). Reducing migration distance can provide several benefits associated with earlier arrival at the breeding grounds and greater survival (Coppack and Both 2002; Jankowiak et al. 2015a; 2015b). Food resources of wintering sites may also influence migration decisions (Cresswell 2014; Aharon-Rotman et al. 2016). Although winter site fidelity is usually very strong among waterfowl (Newton 2008), this can change in response to weather, habitat and competition (Cresswell 2014). Changing winter sites may often be a trade-off between the costs of finding a new site and the benefits it offers (Aharon-Rotman et al. 2016). At sub-zero temperatures, shallow waters freeze over; forcing birds to expend more time and energy searching for food in deeper, open waters. Three functional groups of waterbirds forage in the shallow waters of offshore lagoons: piscivores, herbivores and benthivores, for example, large numbers of waterbirds gather to forage in the Odra River Estuary (hereafter ORE) (Marchowski et al. 2015; Marchowski et al. 2016). Two groups of waterbirds – bottom feeders and piscivores – are among those most commonly wintering here. During winter, the study area is subject to wide variation in temperatures, often making surface waters subject to freezing (van Erden and de Leeuw 2010). Yet even relatively small variations in temperature, causing ice cover to form or disappear, can lead to the displacement of waterbirds. Changes in abundance and community structure of birds in the ORE may reflect the impact of climate change. Analysis of the dates of the appearance of ice-related phenomena in the Szczecin Lagoon and of their frequency over time reveals a distinct pattern illustrating recently observed trends in climate warming (Girjatowicz 2011). In this paper we are looking for how abundance of some species in the ORE changes due to climate warming. We demonstrate that because of bottom feeding, benthivorous birds foraging patterns are impacted strongly by surface water freezing, in contrast to the fish feeding, piscivorous birds. Thus, climate change will differentially influence foraging patterns, and consequently overwintering patterns, of these two groups of birds. Thus, increasing temperatures due to climate change, and the shorter time interval with ice cover, will result in increasing numbers of benthivores because they will then migrate shorter distances. Frosts in the study area are never so severe that the water freezes completely to the bottom even in the shallows. But even if ice does cover the surface of shallow water benthic feeders have no access to food and have to move to warmer areas because feeding areas where sedentary mussels are abundant tend to be in shallow waters (Marchowski et al. 2015). Piscivores, on the other hand, can still feed in such conditions (frozen surface of shallows, unfrozen deeper areas - further from the shore, where there are no mussels but there are fish) and remain in the area, e.g. observation of large aggregations of fish feeders during harsh winters (Smew, *Mergellus albellus* and Goosander *Mergus merganser*) (Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013). This has consequences for conservation management plans in protected areas. Two different groups of birds react differently to climate warming, showing different patterns of moving closer to their breeding grounds, as a consequence in our area should be more benthivores.

Study area

The study area in the south-western Baltic Sea forms the Polish part of the Odra River Estuary system, which includes the Great Lagoon (the Polish part of the Szczecin Lagoon), Świna Backward Delta, Kamień Lagoon, Dziwna Strait and Lake Dąbie (522.58 km^2, Fig. 1). The area comprises four interconnected Important Bird Areas (IBA) and also a Natura 2000 area (Wilk et al. 2010). The average and maximum depths of the estuary are 3.8 and 8.5 m, respectively; the dredged shipping lane passing through the estuary from the Baltic Sea to the port of Szczecin is 10.5 m deep (Radziejewska and Schernewski 2008). Waters of the Szczecin Lagoon, Kamień Lagoon and Lake Dąbie are brackish. Salinity in the central part of the estuary varies from 0.3 psu to 4.5 psu (mean = 1.4 psu) and declines with increasing distance from the sea (Radziejewska and Schernewski 2008). Average winter temperature is 0.3° C (Weatherbase 2016). The ORE is subject to high levels of eutrophication (Radziejewska and Schernewski 2008). Communities of benthic organisms are typical of freshwater bodies, and the fauna includes large populations of zebra mussels *Dreissena polymorpha*, which were introduced in the mid-19th century. By the 1960s, the biomass of zebra mussels in the Szczecin (Great) Lagoon was estimated at 110 000 metric tons (Wiktor 1969, Wolnomiejski and Woźniczka 2008). The distribution of the zebra mussel is extremely uneven (see the map in Marchowski et al. 2015). The average density of the zebra mussel in the ORE is 0.18 kg /m^2, but the vast majority occupies around 10% of the area, where the mean density is 2.05 kg/m^2 (Stańczykowska et al. 2010). Fish are mainly freshwater species such as roach *Rutilus rutilus*, bream *Abramis brama*, pike *Esox lucius*, perch *Perca fluviatilis* and ruff *Gymnocephalus cernua*; there are also anadromous fish including smelt *Osmerus eperlanus* and occasionally herring *Clupea harengus* among others (Wolnomiejski and Witek 2013).

Methods

Bird censusing

Our study covers two functional groups of waterbirds: benthivores (diving birds, bottom feeders, feeding on motionless type of food – mussels) – Greater Scaup (*Aythya marila* – hereafter Scaup), Tufted Duck (*A. fuligula*), Common Pochard (*A. ferina* – hereafter Pochard), Common Goldeneye (*Bucephala clangula* – hereafter Goldeneye) and Eurasian Coot (*Fulica atra* – hereafter Coot); piscivores (diving birds, fish feeders, feeding on mobile type of food – fish) – Smew and Goosander (Stempniewicz 1974; Johansgard 1978). Six of our target species belong to the order: Anseriformes, family: Anatidae, subfamily: Anatinae and Tribe: Mergini (Goldeneye, Smew and Goosander), Tribe: Aythyini (Scaup, Pochard and Tufted Duck); one species – Coot belongs to the order: Gruiformes, family: Rallidae (del Hoyo and Collar 2014). Although Coot is not closely related to the rest of our species, we included it into a common group of waterbirds and, due to its behavior and ecology, to the benthivores group (Stempniewicz 1974). These seven species are usually very abundant in the study area (Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004; Wilk et al. 2010; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013). These are important gathering areas for populations of these birds associated with regional migration flyways. These subpopulations (hereafter regional or flyway populations) are: Pochard – north-east Europe / north-west Europe; Tufted Duck – north-west Europe (wintering); Scaup – northern Europe / western Europe; Goldeneye – north-west and central Europe; Smew – north-west and central Europe (wintering); Goosander – north-west and central Europe (wintering); Coot – north-west Europe (wintering) (Wetlands International 2016). Thus, changes in the importance of this wintering ground due to changing surface-water freezing patterns expected under global warming regimes are likely to have important consequences for very large numbers of these birds.

Censuses were conducted using standard methods for non-breeding season waterbirds counts (Komdeur et al. 1992; Wetlands International 2010). Birds were counted during 17 seasons (1991/1992 to 1993/1994 and 2001/2002 to 2015/2016) during the migration and wintering periods between November and April. Three censuses were carried out per season in November, January, and March or April; there was one midwinter count in January in 2001/2002. Altogether we analysed the results of 44 counts. Most counts were done on foot. Each observer was equipped with 10x binoculars and tripod-mounted spotting scopes. Observers walked along the same routes, and the same counting method was used during every census every year. Additionally, fourteen aerial counts were made at an average speed of about 100 km/h and an altitude of about 80 m above the water (see supplementary materials – S1 Table for the method of data collection: aerial or ground). In the early 1990s counts were aerial, whereas in 2009-2015 parallel aerial and ground counts were carried out (to compare methods). In ice-free conditions the species covered in this study can be assigned to a group with just a small error between methods (<6%), one species – Coot had a moderate error (16%), the ground method estimated greater numbers than the aerial one. During periods with more than 70% ice cover, abundance estimated from the air was greater than that estimated from the ground (Dominik Marchowski pers. com.). Count method was treated as a random effect in the model. The detailed methodology and results of the counts are given elsewhere (Meissner and Kozakiewicz 1992; Meissner et al 1994; Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013). Where large numbers of unidentified *Aythya* species were counted – 26 000 ducks in November

2009, 13 000 in November 2010, 6 000 in January 2012, 3 300 in March 2012 and 13 500 in November 2015 – they were estimated to be in the ratio of 1:0.8 (scaup:tufted) based on observations in other studies. Observations were always at a distance that does not disturb the birds in any way, and in Poland, this research required no ethical or scientific permits.

Statistical analysis

Absolute numbers of birds can vary widely and independently, and so we use the proportion of the local population size (in our study area) in relation to flyway population for each species as our dependent variable (Nagy et al. 2014; Wetland International 2016). Thus, if we showed the trend of absolute numbers in our area, the resulting error would be the larger, the greater the changes in the size of the flyway population. Therefore, we indicate the numbers of a species by means of a coefficient calculated as the percentage of the regional population present in the study area during a particular count. We obtained the regional population size estimates from 1992 to 2012 from Nagy et al. (2014); for the period 2013-2016 we used the flat trend calculated by Nagy et al. (2014) (Table 1). Initially, we placed the different species in ecological groups. The benthivores (denoted by B) included Scaup, Tufted Duck, Pochard, Goldeneye and Coot, and the piscivores (P) contained Smew and Goosander. We used the minimum temperatures averaged over the 15 days leading up to the count day. The climate data were obtained from the Szczecin weather station (53.395 N, 14.6225 E, http://tutiempo.net). Another climate covariate was ice cover in the study area; data relating to this were published by the Polish Institute of Meteorology and Water Management. These data are from the observation point at Miroszewo on the shore of the Szczecin Lagoon (53.734 N, 14.331 E, http://www.imgw.pl/). We compared the number of days with 100% ice cover in the period from 0 to 15 days prior to the bird counts. The ice cover of 100% refers specifically to the Miroszewo observation point. This estimate is a good approximation for the region. In practice, however, the ORE is never completely covered by ice (Girjatowicz 1991; 2005; see the Discussion for an explanation) and birds are still present in such conditions. We also utilized the maximum ice extent in the Baltic Sea (max ice; data obtained from the website of The European Environment Agency; EEA 2017). Apart from climatic variables, we also wanted to test the changes in species occurrence during the survey years, so we used season as covariate. Prior to the final analysis, we checked multicollinearity between the above variables using the variation inflation factor (VIF). VIFs of all variables were in acceptable limits, minimum temperatures (VIF = 2.1), max ice (VIF = 1.03), ice cover (VIF = 2.07) and season (VIF = 1.04). However, we found a moderate linear significant relationship between minimum temperature and ice cover ($r = 0.52$, $p < 0.001$) and after exclusion of minimal temperature VIF showed no multicollinearity issue between variables – ice cover (VIF = 1.04), max ice (VIF = 1.03), season (VIF = 1.03) – and these were used in the subsequent analyses. Frozen water by definition impedes bottom-feeding duck foraging, we are testing whether that pattern is changing in association with climate change. We used a general linear mixed model (GLMM) to test above described relationship in our study area. The percentage of the flyway population present in the study area, estimated by species, was used as a target variable using the normal distribution response distribution and identity link function. Mixed models permitted repetition across survey months, methods (aerial and ground counts) and species (random intercept). Thus, to test our assumptions we included the following interactions: feeding group*season, feeding group*ice cover and feeding group*max ice. Selection of the best model structure for the dependent variable was based on the Akaike information criterion (AIC) (Zuur et al. 2009). All possible models were carried out (they are listed in Table S1 in Supplementary material). As the final models we assumed those in which

ΔAIC < 2 (Burnham & Anderson 2002) and in our case it was only a general model with all the tested variables. To test relationship between explanatory variables and particular species abundance we performed for each species GLMM model, where random effects were month and method. We checked also relationship between winter year and ice cover. To test it we used generalized linear model with negative binomial error distribution. We used IBM SPSS Statistic version 20 software for the statistical analysis. $P < 0.05$ was considered statistically significant.

Results

Bellow, we present the results of our analyzes, the main one jointly examines two whole groups - piscivores and benthivores and the second one where each species were analyzed. The first analysis shows that bird numbers by feeding group were different in their relationships with ice cover, benthic feeding species in the study area were more sensitive to lower temperatures and left sooner when colder weather increased ice cover, whereas numbers of piscivorous species had higher tolerance to the extent of ice cover (Table 2). Interactions between feeding group and season, feeding group and ice cover, and feeding group and maximum ice extent on the Baltic sea were all important (Table 2). However, the strongest effects were interactions with ice cover, then interaction with season, this translates into increases of the importance of the site for benthivores. The effect of maximum ice extent was very small (Table 2). Our results show changes in population indices in the ORE over the last 25 years, these indices increased in the case of benthic feeding species but decreased for fish feeders (Table 2). Ice cover across the whole Baltic Sea had the same, though weak, impact on both functional groups of birds. Numbers of birds in the ORE declined with expanding ice cover in the Baltic (Table 2).

Where particular species are concerned, the situation is more complex. The population indices of Scaup and Tufted Duck in the ORE exhibited an increasing trend

(β_{Scaup}=0.026±0.010s.e.,p=0.011; however for Tufted Duck marginally insignificant β=0.008±0.004 s.e.,p=0.058), despite the general decline in their entire northern and western European populations; numbers of both species in the ORE were adversely affected by ice cover in that region (β_{Scaup}=-0.065±0.011s.e.,p<0.001; β_{Tufted}=0.032±0.005s.e.,p<0.001) but not by ice cover in the whole Baltic (β_{Scaup}=-0.099±0.074s.e.,p=0.186; β_{Tufted}=0.010±0.029s.e.,p=0.735). Relative numbers of Pochard in the ORE have declined (β=-0.009±0.003s.e.,p=0.005), but so has the whole northern European population, abundance was negatively impacted by ice cover in both the study area (β=-0.015±0.003s.e.,p<0.001); and in the entire Baltic (β=-0.053±0.023s.e.,p=0.023). For Goldeneye, the index for the ORE population was unchanged (β=-0.004±0.004s.e.,p=0.275), despite the increase in the European population, abundance was negatively impacted by ice cover in the study area (β=-0.016±0.004s.e.,p<0.001), but not by ice cover in the entire Baltic (β=-0.044±0.027s.e.,p=0.107). Relative numbers of Coot in the ORE remained unchanged (β<0.001±0.002s.e.,p=0.915), despite the slight increase in the European population, abundance was negatively impacted by ice cover in both the study area (β=-0.014±0.003s.e.,p<0.001), and in the entire Baltic (β=-0.038±0.016s.e.,p=0.019). The ORE population index for Smew decreased (β=-0.020±0.008s.e.,p=0.024), despite the increase in its flyway population, abundance in the ORE was unaffected by ice cover either in the study area (β=-0.013±0.010s.e.,p=0.183), or in the Baltic as a whole (β=-0.079±0.061s.e.,p=0.204). Finally, relative numbers of Goosander in the ORE remained unchanged (β=-0.005±0.008s.e.,p=0.572), like those of the whole population wintering in north-western and central Europe; abundance in the ORE was unaffected by ice cover either in the study area (β=0.018±0.009s.e.,p=0.063) or in the Baltic as a whole (β=-0.111±0.057s.e.,p=0.057). The details relating to all these species are listed in Table 1, showed in Fig. 2A and Table S3. Table 3 summarizes the changes in the importance of the ORE for wintering populations of diving waterbirds in the last 25 years. We also found positive relationship between year and winter ice (beta0 = 82.011, s.e. = 28.49, beta winter = -0.040, s.e. = 0.0142, Chi-square = 8.001, df = 1, p = 0.005; Figure 2B).

Discussion

The phenomenon of freezing in our study area has decreased over time (Girjatowicz 2011, Fig 2 B), so that target birds species should tend to feed more recently more often than in the past. However, two functional groups of waterbirds – benthivores and piscivores – react differently to ice cover, a factor that is directly connected to climate change; this has consequences for the wintering patterns of these species. Benthic feeding birds (Scaup, Tufted Duck, Pochard, Goldeneye and Coot) tend to be more sensitive to ice cover in the study area than fish feeders (Smew and Goosander). Piscivores can survive in colder areas, closer to their breeding ranges, but benthivores have to move further south and west. This phenomenon indicates that piscivores are declining in our study site because they are shifting further north and east in order to stay closer to their breeding areas. Benthivores are increasing their number for the same reason – they, too, are moving further north and east – but in their case the result is a greater number in our study area and a smaller one in areas further west and south. Benthivorous birds feed in the ORE mainly on mussels of the genus *Dreissena* (Marchowski et al. 2015, 2016); the highest quality of this food resource is found primarily in water 1-2 m deep (Wolnomiejski and Witek 2013). Shallow water freezes over faster, displacing birds to deeper unfrozen areas where food is accessible only with difficulty. In addition, when ice cover is present, the abundance of food in unfrozen areas declines owing to its greater exploitation, because the birds congregate on a limited area. In the case of piscivorous birds we predicted that increasing ice cover would not affect their numbers negatively: our results substantiate that prediction. The ORE is never completely covered by ice: the shipping lane between Świnoujście and Szczecin is kept free of ice (Girjatowicz 1991; 2005), and there are always other areas free of ice, especially at the mouths of the small rivers flowing into the estuary. These ice-free areas may still abound in fish and provide food for fish feeders. In general, we have demonstrated the growing importance of the study area for the benthivores. We made two analysis, the main one jointly examines two whole groups – piscivores and benthivores; the results of this analysis is the positive effect of not freezing for benthivores and negative effect for piscivores, also positive effect of season for benthivores, and negative effect for piscivores (see Table 2). In the other analysis, which examined each species separately, there are differences between them (see Fig. 2A). As far as the most numerous species – Scaup and Tufted Duck – are concerned, the results tally with those of the first analysis, i.e. their numbers are increasing (correlation with season). In the case of the less abundant species, the result of the second analysis is different: Pochard numbers, for example, are decreasing (negative effect). In the case of piscivores the first analysis showed the negative correlation between season and abundance among the fish-eaters. In the second analysis, where we assessed each species separately, Goosander showed no change (no correlation between season and abundance) whereas Smew did reveal a change (there was a correlation between season and abundance, tending towards a reduction in numbers). In fact, the strongest effect of the first years of the study relates to the fish-eaters, especially Smew, If we take the whole period from 1992 to 2016, we see a fall in numbers of this species (as shown in the model results), this was due to its very large numbers in the early 1990s. But if we take the period from 2002 to 2016 we find that its numbers are stable.

An interesting result is the negative effect of maximum ice cover in the entire Baltic Sea on the numbers of all species in our study. This is unexpected, since our study area is in the warmer south-western Baltic, where one would anticipate an increase in the number of waterbirds in such circumstances (Alerstam 1990). The explanation for this relationship is not easy and certainly goes far beyond the scope of this work, but it may inspire further research. However, we can speculate on possible scenarios. Maps showing the maximum range of ice cover in the Baltic Sea show clearly that when the northern Baltic, i.e. the Gulf of Bothnia and the Gulf of Finland, is completely frozen over, the entire Pomeranian Bay (SW Baltic) (see the map – Fig.1) together with the ORE is also covered with ice (Finnish Meteorological Institute 2017). These areas freeze over quickly because of their shallowness and low salinity, the latter being due to the considerable influence of fresh water from the Odra river basin. Consequently, during harsh winters, birds from northern Baltic move to the south and west, but they by-pass our study area as it is covered by ice. Under such circumstances there may sometimes be better conditions for waterbirds in areas farther north, e.g. the southern coast of Sweden, where there is no ice cover (Finnish Meteorological Institute 2017). Worth noting here, however, is that such cold weather causing the entire Pomeranian Bay and Odra River Estuary to freeze over is rare and becoming rarer (EEA 2017). Nevertheless, if we consider the impact of ice cover of the whole Baltic within species, we can see differences between them and the non-significant impact of this phenomenon on e.g. Smew and Goosander, which corresponds with the local results (Table S3).

The global temperature has risen about 1°C over the last 130 years, and Northern Hemisphere temperatures of the last 30 years have been the highest in over 800 years (Stocker et al. 2013). The extent and duration of ice cover in the Baltic have decreased on average by 50%

over the last 36 years (Schröder 2015). There is evidence that the range and occurrence of migratory birds have changed in response to climate change and that some species have shortened their migratory movements by wintering closer to their breeding areas (Musil at al. 2011; Lehikoinen et al. 2013; Pavon-Jordan et al. 2015; Meller 2016). Assuming continued climate warming, the negative correlation between numbers of benthic feeding birds and the number of days with ice cover indicates that the ORE is becoming more important for this group of birds. Climate change seems to be the primary reason for increases (in the study area) in numbers of Scaup and Tufted Duck and decreases in numbers of Smew; this corresponds with the findings of Lehikoinen et al. (2013) in the case of Tufted Duck and of Pavón-Jordan et al. (2015) in the case of Smew. Our results are important for conservation planning. Declines in the populations of species such as Scaup and Tufted Duck, even though the importance of our study area to these species is increasing, but at the same time there is an increase in exposure to locally emerging threats. The biggest threats to these species in the area include fishery bycatches (Žydelis et al. 2009; Bellebaum et al. 2012). The ecology of diving birds makes this type of threat responsible for the extra mortality of all species covered by this study. Comparison of a species' estimated total population numbers (Nagy et al. 2014) with numbers for the ORE is interesting, since local trends and European trends do not always concur. The different responses of particular species to the factors investigated are also worth examining. We grouped the species by trends in the study area and discuss these for each species below.

Species with increasing population index in the study area

Between the late 1980s and 2012, the population of Scaup wintering in northern and western Europe declined at an annual rate of 3.57%/year (Nagy et al. 2014). Around 41% of the Scaup from this population spent the winter in the Baltic Sea region (Skov et al. 2011), and this, in turn, declined by 60% from 1991 to 2010 (Aunins et al. 2013). At the same time we found that the importance of the ORE for this species was increasing. Scaup numbers increased by 300% in the Szczecin Lagoon (the biggest part of Odra River Estuary – see the map – Fig. 1) and the eastern coastal areas of Germany, as opposed to declines further west along the German coast, where some areas (Wismar Bay and Traveförde) had fewer birds than 15 years earlier (Skov et al. 2011). A similar trend was found in Sweden, where the number of wintering Scaup increased between 1971 and 2015 (Nilsson and Haas 2016). But farther west, in the Netherlands, Hornman et al. (2012) recorded decreases at the most important wintering sites since 1980/1981. All of these studies confirm that Scaup is shifting its wintering range northwards and eastwards, closer to its breeding areas: this is the reason for the heightened importance to this species of the ORE, even as its overall population wintering in northern and western Europe is declining.

Tufted Duck populations wintering in north-western Europe have recently been decreasing by 0.98%/year (Nagy et al. 2014). Lehikoinen et al. (2013) showed that the population estimated for the North-West Europe flyway remained relatively stable between 1987 and 2009, a situation confirmed by Wetlands International (2016). In the Baltic Sea region, too, there were no significant changes in numbers between 1991 and 2010 (Aunins et al 2013). We have found that our study area has increased in importance for this species, although not to the same extent as for Scaup. By comparison, Nilsson and Haas (2016) showed Swedish populations to have increased between 1971 and 2015, and Lehikoinen et al. (2013) reported a rapid increase in the last three decades for Finland. Tufted Ducks in the ORE behave in the same way as Scaup in that they form mixed flocks consuming the same type of food (Marchowski et al. 2016). At a larger scale, Tufted Ducks have a different migration and wintering strategy: Scaup concentrate in a few hot spots, moving jump-wise between them, whereas the distribution of Tufted Ducks is more diffuse (van Erden and de Leeuw 2010; Skov et al. 2011; Carboneras and Kirwan 2016a; Carboneras and Kirwan 2016b). This could cause Tufted Ducks to disperse to smaller water bodies outside our study area, e.g. the numerous lakes in the Pomeranian Lake District in northern Poland (~34 000 km²), whereas Scaup remain almost exclusively in the ORE (e.g. Marchowski and Ławicki 2011; Marchowski et al. 2013). The results of the Wintering Waterbird Monitoring programme also show the greater prevalence in Poland of Tufted Duck (29.5%) than Scaup (7.8%) (Neubauer et al. 2015). Scaup is known to concentrate in big flocks during migration and wintering, and the whole flyway population may be concentrated in a few hot-spots such the ORE (Marchowski et al. 2015): this is important in the context of species conservation planning. We have shown an increase in the importance of ORE for Scaup, but at the same time there is an increase in exposure to locally emerging threats such as bycatches in fishing nets (Bellebaum et al. 2012). Taking into account the above pattern of Scaup behaviour and our results, there is a justified fear that locally operating threats in the ORE may affect the entire flyway population of the species. This is one of the most important messages of our work.

Species with decreasing population index in the study area

Pochard populations from north-east / north-west Europe have declined rapidly at an annual rate of 3.35%/year (Nagy et al. 2014). Pochard numbers in the Baltic Sea region also declined by 70% between 1991 and 2010 (Aunins et al. 2013). In 1995 there were an estimated 300 000 Pochard in the north-east/north-west European population (Delany et al. 1999). With a constant decline of 3.35%/year, the total population should now be less than 150 000 (Nagy et al. 2014). Numbers of Pochard were expected to be higher in the ORE because of the reduced ice cover. However, we found a reduction in the importance of the estuary to this species (Table 3), corresponding with its global decline (Aunins et al. 2013; Nagy et al. 2014; Wetlands

International 2016). Pochard behaves more like Tufted Duck than Scaup over winter in being more dispersed and occurring on smaller bodies of water (e.g. Marchowski and Ławicki 2011; Marchowski et al. 2013; Neubauer et al. 2015). This implies that individuals may also be wintering outside the study area, e.g. on the numerous water bodies of the Pomeranian Lake District, like Tufted Duck. This local decline, however, seems to be driven by the species' global decline, despite the emergence of better conditions for wintering that might favour population growth.

Smew populations wintering in northern, western and central Europe increased at 1.97%/year between the late 1980s and 2012 (Nagy et al. 2014); in the Baltic Sea region numbers increased by 30% between 1991 and 2010 (Aunins et al. 2013). Although Smew cannot be classified as a piscivore in the same way as Goosander (and Red-breasted Merganser *M. serrator*), it does feed on very small fish and on small invertebrates (Carboneras and Kirwan 2016 c). Though more dependent on shallow water than Goosander, Smew generally forages on mobile types of food. So even if shallow waters freeze over, it may remain on site and search for food in deeper water, which is what we have observed. We found that today, the ORE is of less importance to Smew (Table 3) as illustrated by the northward and eastward shift in wintering area boundaries due to climate warming (Pavon-Jordan et al. 2015). Confirmation of this process is provided by the significant increase in numbers of Smew in 1971-2015 in places to the north of our study area, in Sweden (Nilsson and Haas 2016).

Species with no changes in the population index in the study area

Coot populations wintering in north-west Europe increased by 0.19%/year between the late 1980s and 2012 (Nagy et al. 2014), but in the Baltic region there was a 60% decline between 1991 and 2010 (Aunins et al. 2013). We have found no changes in Coot numbers in the ORE over the last 25 years (Table 3). Likewise, no changes in numbers were recorded between 1975 and 2010 at wintering sites in warmer areas to the south-west (the Netherlands) (Hornman et al. 2012). Long-term figures for Sweden (1971-2015), while not revealing any distinct increase, do show that Coot populations fluctuated, rising during mild periods and falling during cold periods (Nilsson and Haas 2016). The expected increase in numbers due to improvements in habitat quality did not happen. Factors such as pressure from American mink *Neovison vison*, which are responsible for the decline of Coot in many places (e.g. Ferreras and Macdonald 1999), may have held back potential increases. Moreover, compared to the bottom-diving ducks, Coot is more sensitive to cold weather: a study by Fredrickson (1969) demonstrated high mortality after periods of severe weather (also reflected in the results of Swedish breeding bird surveys – Leif Nilsson pers. com.) but that the population recovered during mild winters. This factor may also be the reason for the different reactions of Coot and diving ducks to the cold.

Goldeneye populations wintering in north-west and central Europe increased at 0.26%/year between the late 1980s and 2012 (Nagy et al. 2014) and increased in the Baltic Sea region by 50% between 1991 and 2010 (Aunins et al. 2013). This corresponds to the data provided by Lehikoinen et al (2013), which show an increase in numbers in the northern Baltic wintering area (Finland and N Sweden), but a decline in the southern part of its wintering range (Switzerland, France). In our work we found the relative number of Goldeneye in the ORE to be stable in the period 1992-2016 (Table 3). This again tallies with the findings of Lehikoinen et al. (2013) that duck abundances are independent of temperature in the central part of the flyway. This is probably why the shift in wintering range is not perceptible in our study area but is more pronounced at other, e.g. Swedish wintering sites, where numbers have increased (Nilsson and Haas 2016) but not in the Netherlands, where they have declined (Hornman et al. 2012).

Goosander populations wintering in north-west and central Europe have been stable since the early 1990s (Nagy et al. 2014); moreover, numbers in the Baltic Sea between 1991 and 2010 did not change significantly (Aunins et al. 2013). We also found non-significant changes in the ORE, so it must be regarded as stable (Table 3). As in the case of Goldeneye, the explanation is that in the central part of the flyway, species abundances are independent of temperature. In other areas, observations indicate a shift farther to the north and east in the wintering range as a result of climate warming (Hornman et al. 2012; Lehikoinen et al. 2013; Nilsson and Haas 2016).

Conclusion

Our study shows that climate change can influence distribution of overwintering waterbirds. Apart from climate changes, however, feeding ecology, interspecific competition, fishery and other human-related disturbance may be also important and should be taken into consideration (Quan et al. 2002, Žydelis et al. 2009, Clavero et al., 2011; Eglington & Pearce-Higgins, 2012). We show that the protected areas covered by our study will be more important for some species (Scaup and Tufted Duck) but less so for others (Smew). Taking into account the large abundance of the target species regularly present in the ORE, conservation measures applied here will have a large impact on whole populations and will be particularly important for Scaup. Shifts in species distributions should be accounted for in future management plans for Special Protection Areas of the European Natura 2000 network. We believe that our results add new insight to the problem of wintering waterbirds protection and can help to shape conservation policy in the southern Baltic.

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Table 1. Regional flyway populations and annual trends (after Nagy et al. 2014) for seven species of waterbirds using the Odra River Estuary.

(1) Target species. (2) Functional group: B – benthivores, P – piscivores. (3) Estimated number of individuals from regional flyway population in 1992, the numbers are presented in thousands. (4) Estimated number of individuals from regional flyway population in 2012, the numbers are presented in thousands. (5) Population trend % per annum - long term assessment. (6) Significances of changes.

Species (1)	Functional group (2)	Number of individuals (1992) (3)	Number of individuals (2012) (4)	Population trend % p.a. (5)	Significance of changes (6)
Greater Scaup	B	300	150	-3.57	Large decline
Common Pochard	B	280	150	-3.35	Large decline
Tufted Duck	B	1,100	820	-0.98	Large decline
Goosander	P	130	100	-0.09	Stable
Eurasian Coot	B	990	950	+0.19	Moderate increase
Common Goldeneye	B	210	240	+0.26	Moderate increase
Smew	P	13	24	+1.97	Large increase

Table 2. Results of general linear mixed models for seven species showing the influence of ice cover, maximum ice extent [km^2] in the Baltic Sea (max ice) and season on the percentage of occurrence of benthivores (denoted by B, Scaup, Tufted Duck, Pochard, Goldeneye, Coot) and piscivores (denoted by P, Smew, Goosander) in the Odra River Estuary. Species, method and month were treated as random effects.

Model Term	Coefficient	Std. Error	t	*P*
Intercept	26.553	11.619		
Ice cover	0.014	0.006	2.375	**0.018**
Season	-0.013	0.006	-2.204	**0.028**
Max ice	-0.114	0.040	-2.824	**0.005**
Feed[B]	-38.751	11.959	-3.240	**0.001**
Season*Feed[B]	0.019	0.006	3.212	**0.001**
Ice cover*Feed[B]	-0.044	0.007	-6.623	**<0.001**
Max ice*Feed[B]	0.094	0.046	2.071	**0.039**
Species (r)	0.074	0.048		
Method (r)	0.015	0.020		

Month (r)	0.001	0.002

Table 3. Population index trends in the Odra River Estuary (ORE) for the regional biogeographic (flyway) population (b.p.) of diving waterbirds showing the percentage of the flyway population in 1992; the percentage of the flyway population in 2016; the mean percentage of the flyway population in the period 1992 – 2016 ± standard error; and the trend in the period 1992 – 2016.

Species	%b.p.1992	%b.p.2016	Mean1992–2016±SE	Trend in ORE
Greater Scaup	5.68	12.60	14.17±2.84	↑
Tufted Duck	2.87	4.79	2.61±0.25	↑
Common Goldeneye	4.48	0.63	1.21±0.14	→
Eurasian Coot	0.86	0.68	0.61±0.07	→
Goosander	12.59	1.80	6.85±1.01	→
Smew	7.04	2.76	7.01±1.27	↓
Common Pochard	1.84	0.20	0.62±0.09	↓

Figure 1. The Odra River Estuary, north-western Poland.

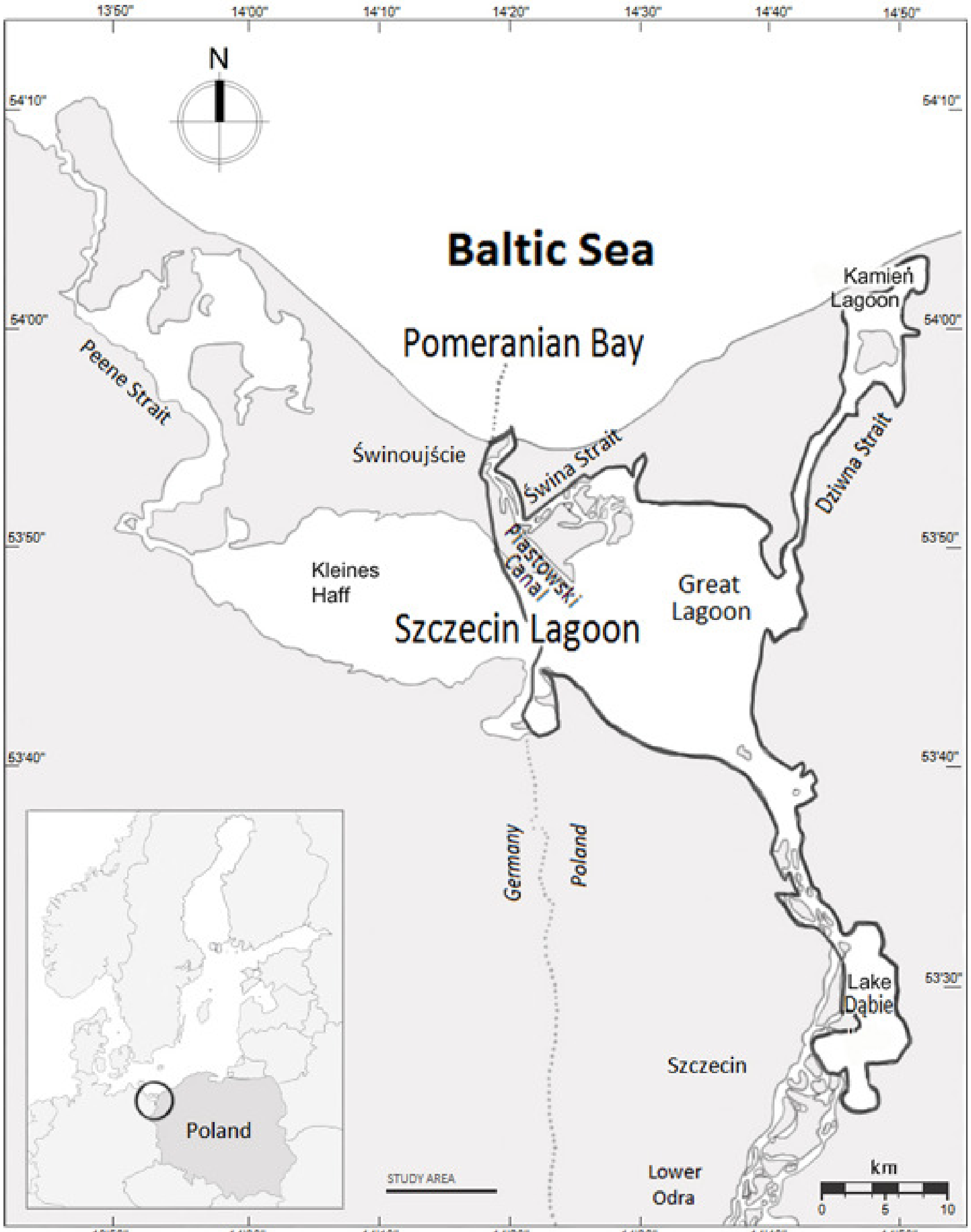

Figure 2 A. Predicted results of the general linear mixed model showing the changes of the percentage of the target species population in the Odra River Estuary during years 1992 - 2016. The predicted values were obtained from the model where we added species as a fixed variable. The model's parameters are listed in Table S3 in the Supplementary material. Dashed lines – the gap with birds data. B) Changes in the ice cover duration in the Odra River Estuary during years 1992 – 2016. Results of a generalized linear model (with negative binomial error distribution) - correlation between year and winter ice. Dotted lines show 95% confidence intervals bounds.