How do waterbirds respond to climate change? A study at a key wintering site in Europe.

Dominik Marchowski[1,2,*], 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, Szczecin University, ul. Wąska 13, 71-415 Szczecin, Poland

[2]West-Pomeranian Nature Society, ul. Wąska 13, 71-415 Szczecin, Poland

[3]Hydrography and Water Management Unit, Faculty of Earth Science, Szczecin University, ul. Mickiewicza 16, 70-383 Szczecin, Poland

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

Abstract

Many species of birds react to climate change, for example, by wintering in areas closer to their breeding areas. We investigated the responses of two different functional groups of waterbirds to factors associated with climate change. The Odra River Estuary (SW Baltic Sea) is of key importance to wintering waterfowl. The most numerous birds here belong to two ecological groups: benthic feeders and fish feeders. We showed that numbers of all benthivorous waterbirds were negatively correlated with the presence of ice, but failed to find such a relationship for piscivores. We anticipated that, with ongoing global warming, the significance of this area would increase for benthic feeders but decrease for fish feeders: our results bore this out. 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*), while the other two are piscivores (Smew *Mergellus albellus* and Goosander *Mergus merganser*). Local changes at the level of particular species vary for different reasons. The local decline of Common Pochard may be a reflection of the species' global decline. Climate change may be responsible for some of the local changes in the study area, namely, the significance of the area has increased for Greater Scaup and Tufted Duck but declined for Smew.

Key words: winter range shift; ice cover sensitivity; Greater Scaup; Tufted Duck; Common Pochard; Eurasian Coot; Smew; important bird areas; behaviour; Baltic Sea

Introduction

Climate change has caused the wintering ranges of many bird species to shift (Musil et al. 2011; Lehikoinen et al. 2013; Meller 2016). Knowing the behaviour of particular species, we can track changes in population numbers which may reflect changes in temperatures. 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; Pavon-Jordan et al. 2015). It is advantageous for populations to have short migration distances, since this means earlier arrival back at the breeding grounds, acquisition of higher quality territories, and probably greater survival (Coppack and Both 2002; Jankowiak et al. 2015a; 2015b). Bird may relocate their wintering sites to warmer regions during colder periods because they can sense local manifestations of large-scale atmospheric features (Newton 2008). For waterbirds wintering in the isothermal zone of about 0°C, there could be a more complex explanation: when the birds experience the freezing over of shallow water, they move to deeper water, but when that in turn starts to freeze, they abandon it and migrate south or west (Leif Nilsson pers. com.).

The food resources of wintering sites are also a factor informing decisions about staying at potential sites (Cresswell 2014; Aharon-Rotman et al. 2016). Although the level of winter site fidelity is known to be very high among waterfowl (Newton 2008), it can drop as a result of changes in weather, climate, habitat and competition (Cresswell 2014). The changing of winter sites should thus be seen as 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; birds therefore expend more time and energy searching for food in deeper waters, with obvious consequences for their energy balance. The shallow waters of offshore lagoons create ideal conditions for three functional ecological groups of waterbirds: piscivores, herbivores and benthivores. Our study area, the Odra River Estuary (ORE) accommodates large numbers of waterbirds because of its food resources (Marchowski et al. 2015; Marchowski et al. 2016). The study area has been designated an Important Bird Area (IBA) and also a Natura 2000 area (Wilk et al. 2010). Changes in the structure of species proportions and their numbers in the ORE over the years 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 that confirms and supports recently observed trends in climatic warming (Girjatowicz 2011). In this paper we examine whether the numbers of some species in the ORE are likely to change as a result of climate warming. We assume that benthic feeding birds will be more sensitive and fish feeding birds less sensitive to ice cover. If our assumptions hold true, elevated temperatures and the correspondingly shorter period of ice cover should provide better conditions for benthic feeders, the numbers of which ought to increase. Most feeding grounds rich in sedentary mussels lie in shallow water (Marchowski et al. 2015), so any ice cover significantly reduces food availability. Fish, on the other hand, remain available even if the ice cover is considerable, since unfrozen areas may still be rich in fish. During cold winters the water in the ORE never freezes over entirely: even during periods of sustained below-zero temperatures patches of water remain free of ice.

Study area

The study area lies in the south-western Baltic Sea and 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 with a total area of 522.58 km^2 (Fig. 1). 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). The waters of the Szczecin Lagoon, Kamień Lagoon and Lake Dąbie are brackish. The 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). Periodic backflows of water from the Pomeranian Bay (salinity ~7 psu) take place through the Świna Strait and, to a lesser extent, through the Dziwna and Peene Straits (the latter situated in the German part of the ORE). The average winter temperature is 0.3° C (Weatherbase 2016). The ORE is subject to strong anthropogenic pressure manifested by high levels of eutrophication (Radziejewska and Schernewski 2008). The 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) and appears to be fairly stable; in the early 2000s the estimated biomass was 94 280 metric tons (Marchowski et al. 2015). The distribution of the zebra mussel is highly uneven here: there are areas where it is abundant, but there are also large areas where there are hardly any (see the map in Marchowski et al. 2015). The average density of the zebra mussel in the ORE is 0.18 kg /m², but the vast majority of these resources occupies around 10% of the entire sea bed, where the mean density is 2.05 kg/m² (Stańczykowska et al. 2010). By comparison, other areas important for wintering benthos feeding birds, such as the adjacent Dutch lakes IJsselmeer and Markermeer, have an average density of 0.24 kg/m² (van Eerden & de Leeuw 2010). In contrast, the Vistula Lagoon in Poland has a much lower density of zebra mussels – 0.001 kg/m² (Stańczykowska et al. 2010) – and there are correspondingly smaller densities of benthivorous birds than in the Szczecin Lagoon (Neubauer et al. 2015). The fish consist mainly of 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 like smelt *Osmerus eperlanus* and occasionally marine fish like herring *Clupea harengus* (Wolnomiejski and Witek 2013).

Methods

Bird censusing

Our study covers two functional groups of waterbirds: 1) benthivores – 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); 2) piscivores – Smew *Mergellus albellus* and Goosander *Mergus merganser*. The study site is known to regularly host significant numbers of the biogeographic population of the above species (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) (see also Table 3). Here, by biogeographic population we mean that part of the global population associated with a specific flyway region. These subpopulations 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).

Censuses were conducted using standard methods for non-breeding season waterbird 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. From 1991/1992 to 1993/1994 three censuses were carried out per season in November, January, and March or April; in 2001/2002 only one mid-winter count in January was done. 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, stopping every few hundred metres or making observations from vantage points reachable by car. 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 solely aerial, whereas in 2009-2015 parallel aerial and ground counts were carried out. It was the aim of other research to determine the effectiveness of the two methods. The results show that in ice-free conditions almost all the species covered in this study can be assigned to a group with just a small error between methods (<6%). Only for one species – Coot – was the moderate error (16%): the numbers counted from the ground were higher than those from the aircraft. During periods with more than 70% ice cover, bird numbers counted from the aircraft were higher than those counted from the ground (Dominik Marchowski pers. com.). All counts were conducted in the same way using the same route and the same observation points. 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 allocated to either Scaup or Tufted Duck based on the mean ratio of these two species (1.0 Scaup : 0.8 Tufted Duck) obtained from other counts. This research involved observations of birds from a distance, which do not disturb the birds. In Poland, such studies do not need special permission or approval.

Statistical analysis

The dependent variable was the percentage of occurrence of a given species in relation to the total estimated population size in a given year. This approach was taken because the population sizes of the species covered by our study follow different trends. For example, the population of Scaup is decreasing, that of Smew is increasing and that of Goosander is more or less stable (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 entire population. Therefore, we indicate the numbers of a species by means of a coefficient calculated as the percentage of the biogeographic population present in the study area during a particular count. We obtained the data relating to the biogeographic populations 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 piscivore group (P) contained Smew and Goosander. We used the mean, maximum and 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 were gathered using the standard methods of the Baltic Sea ice information system. This partitions the Baltic into sectors, and the ice conditions in each sector are given in the "Monthly Ice Listing", a daily protocol supplying information on the degree of ice cover, position of the ice, the developmental stage of the ice, topography, ice type and the conditions for sailing across ice-covered water. For the calculations in this study, we used only the information on the number of days with total ice cover from one sector (Miroszewo). Observations of ice-related phenomena in this sector took place from a site on the shore of the Szczecin Lagoon (53.734 N, 14.331 E). Observations were conducted daily from 1 November to 30 April at 12:00 hrs UTC. The methodology for collecting ice cover data was the same throughout the study period. We compared the number of days with 100% ice cover in the period from 0 to 15 days prior to bird counts. The ice cover of 100% refers specifically to the observation point at Miroszewo (data from the Polish Institute of Meteorology and Water Management, which we used in our computations). This does not embrace the whole ORE, but is a good approximation of it. Our field observations during bird counts show that most of our study area is also nearly 100% frozen. In practice, however, the ORE is never completely covered by ice (Girjatowicz 1991; 2005; see also 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). These data were 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 the multicollinearity correlation between the above variables using the variation inflation factor (VIF). If VIFs were well above 2, the relevant variables were excluded from the analysis. Hence, we excluded the mean, maximum and minimal temperatures averaged over the 15 days prior to the count, as they were highly correlated. We used a general linear mixed model (GLMM) as a statistical solution to test the hypothesis relating to the different patterns of occurrence of benthivores and piscivores in the ORE. The percentage of numbers in relation to the species' whole population was used as a target variable and was treated with 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 hypotheses we assessed the following interactions: feeding group*season, feeding group*ice cover and feeding group*max ice. To demonstrate interactions at the level of particular species we produced another GLMM model (with month and method as random factors) and assessed the following interactions: species*season, species*ice cover and species*max ice. The parameters of this model are listed in Table S2 in the Supplementary material. The predicted values of this model for each species are shown on Figure 2. We used IBM SPSS Statistic version 20 software for the statistical analysis. $P < 0.05$ was considered statistically significant.

Results

We found that interactions between feeding group and season, feeding group and ice cover, feeding group and maximum ice extent on the Baltic sea were all significant. However, the strongest effects were exhibited by interaction with ice cover, then interaction with season. The effect of maximum ice extent was very small (Table 2).

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 fish feeding species did not change, regardless of the extent of ice cover (Tables 2, Fig. 2B).

Our results show changes in population number 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, Fig 2A).

Ice cover across the whole Baltic Sea had the same, though weak, impact on both ecological groups of birds. Numbers of birds in the ORE declined with expanding ice cover in the Baltic (Table 2, Fig 2C).

In the case of each particular species, the situation was more complex. The indices for Scaup and Tufted Duck increased in the ORE, despite the general decline in the numbers of species wintering in northern and western Europe, the negative impact of ice cover in the study area on abundance and the lack of any impact of ice cover on the Baltic Sea. Relative numbers of Pochard declined, both in our study area and in northern Europe in general, despite the negative impacts of ice cover in the study area on abundance and of ice cover in the Baltic as a whole. In the case of Goldeneye the index for the ORE did not change, but its European population increased; ice cover in the study area had negative impact and ice cover in the Baltic as a whole had any impact on abundance. Relative numbers of Coots did not change in the ORE, but European numbers did increase slightly; ice cover in the study area and in the Baltic as a whole had negative impact on abundance. The index for Smew decreased in the ORE whereas European numbers increased, but there was no impact of either ice cover in the study area or on the Baltic Sea as a whole on abundance. The relative numbers of Goosander did not change in the ORE, neither did those of the whole population wintering in north-western and central Europe; moreover, there was no impact of ice cover either in the study area or in the Baltic as a whole on its abundance. (see Tables 1 and 2, Fig. 2). Changes in the significance of the ORE for wintering populations of diving waterbirds in the last 25 years are shown in Table 3.

Discussion

As we had predicted, benthic feeding birds (Scaup, Tufted Duck, Pochard, Goldeneye and Coot) were more sensitive to the presence of ice cover in the study area. Benthivorous birds feed in the ORE mainly on mussels of the genus *Dreissena* (Marchowski et al. 2015, 2016), the best quality of food resources that are primarily found in water 1-2 m deep (Wolnomiejski and Witek 2013). Shallow water freezes over faster, displacing birds to deeper unfrozen areas where resources of food are hardly available. In addition, the food richness of unfrozen areas is declining owing to their greater exploitation. In the case of piscivorous birds we assumed that increasing ice cover would not affect their numbers: our results substantiate this assumption. Ice cover is never 100% here; the shipping lane between Świnoujście and Szczecin is kept free of ice (Girjatowicz 1991; 2005) and there are also always other areas free of ice, especially at the mouths of the small rivers flowing into the estuary. These areas free of ice may still abound in fish and provide food for fish feeders. In general, we have demonstrated the growing importance of the study area for all the benthivores. Considering this in relation to particular species, the two most numerous species have increased in numbers, while another three do not follow the general trend. In addition, we have shown that the study area is decreasing in importance to piscivores and that each species is decreasing in numbers, although the trend for Goosander is not significant.

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 (Fig. 2). This is unexpected, since our study area is 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 the 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 in the Odra basin. Consequently, the birds move to the south and west when there is thick ice cover in the northern Baltic, but they probably by-pass our study area. 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 still (EEA 2017). Nevertheless, if we consider the impact of ice cover of the whole Baltic within species, we can see the differences between them and the non-significant impact of this phenomenon on e.g. Smew and Goosander, which corresponds with the local results (Fig. 2).

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 discuss these for each species below.

Scaup

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 (Aunis 2013). At the same time we found that the significance of the ORE for this species was increasing. This had already been mentioned by Skov et al. (2011), who describe a threefold increase in Scaup numbers 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 areas like Wismar Bay and Traveförde supported much lower numbers than 15 years earlier. A similar trend has been found in Sweden, where Nilsson and Haas (2016) recorded a significant increase in the number of wintering Scaup between 1971 and 2015. But farther west still, 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

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 (Aunis 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).

Pochard

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 (Aunis 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 significant reduction in the importance of the estuary to this species (Table 3), corresponding with its global decline (Aunis 2013; Nagy et al. 2014; Wetlands International 2016) and operating factors other than climate change. 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.

Goldeneye

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 (Aunis 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. North of our study area, numbers at wintering sites have increased (Nilsson and Haas 2016) but to the south-west, e.g. in the Netherlands, they have declined (Hornman et al. 2012).

Coot

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 (Aunis 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.

Smew

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 (Aunis 2013). Although Smew cannot be classified as a piscivore in the same way as Goosander (and Red-breasted Merganser), it does feed on very small fish and on small invertebrates (Carboneras & 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 nowadays, the ORE is of less importance to Smew (Table 3). This statement is underpinned by the northward and eastward shift in wintering area boundaries due to climate warming, as already demonstrated by 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).

Goosander

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 (Aunis 2013). We found a slight decrease in the importance of the ORE to Goosander, but it was not significant, so 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

There is no doubt that the climate is changing: 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 has decreased on average by 50% over the last 36 years (Schröder 2015). There is evidence that the range and occurrence of migratory birds has 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 finding of Lehikoinen et al. (2013) in the case of Tufted Duck and of Pavon-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 the study area to these species is increasing, must therefore be due to their increased exposure to local dangers. The biggest threats to these species in the area include fishery bycatches (Žydelis et al. 2009; Bellebaum et al. 2013). The ecology of diving ducks makes this type of threat responsible for the extra mortality of all species covered by this study.

Acknowledgements

We thank all the people who took part in the fieldwork – mainly members of the West-Pomeranian Nature Society – but especially those who were the most active during the entire study period: Michał Barcz, Ryszard Czeraszkiewicz, Sebastian Guentzel, Michał Jasiński, Zbigniew Kajzer, Jacek Kaliciuk, Krzysztof Kordowski, Aneta Kozłowska, Wojciech Mrugowski, Arkadiusz Oleksiak, Bartosz Racławski, Tomasz Rek, Artur Staszewski, Marcin Sołowiej, Piotr Siuda, Paweł Stańczak, Maciej Przybysz. We are grateful to Leif Nilsson and the two anonymous reviewers for their valuable comments on the first version of the manuscript and Peter Senn who kindly improved our English.

References

Aharon-Rotman Y., Buchanan K.L., Clark N.J., Klaassen M., Buttemer W.A. 2016. Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds. Oecologia 182: 385-395.

Alerstam T. 1990. Bird migration. Cambridge University Press, Cambridge.

Aunins A., Nilsson L., Hario M., Garthe S., Dagys M., Pedersen I.K., et al. 2013. HELCOM Core Indicator Report. Online. Available: http://www.helcom.fi/.

Bellebaum, J., Schirmeister, B., Sonntag, N., Garthe, S., 2013. Decreasing but still high: bycatch of seabirds in gillnet fisheries along the German Baltic coast. Aquat. Conservat. Mar. Freshwat. Ecosyst. 23, 210–221.

BirdLife International 2004. Birds in Europe, population estimate, trends and conservation status. Cambridge UK: BirdLife Conservation Series No.12.

BirdLife International 2015 a. European Red List of Birds. Luxembourg: Office for Official Publications of the European Communities.

BirdLife International. 2015 b. *Aythya ferina*. The IUCN Red List of Threatened Species 2015:e.T22680358A82571892. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T22680358A82571892.en. Downloaded on 23 October 2016.

Blums P., Mednis A., Bauga I., Nichols J.D. & Hines J.E. 1996. Age-specific survival and philopatry in three species of European ducks: a long-term study. Condor 98**:** 61-74.

Carboneras C. & Kirwan G.M. 2016 a. Greater Scaup (*Aythya marila*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/52912 on 23 October 2016).

Carboneras, C. & Kirwan, G.M. 2016 b. Tufted Duck (*Aythya fuligula*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/52910 on 23 October 2016).

Carboneras, C. & Kirwan, G.M. 2016 c. Smew (*Mergellus albellus*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/52927 on 21 October 2016).

Carboneras, C. & Kirwan, G.M. 2016 d. Goosander (*Mergus merganser*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/52931 on 21 October 2016).

Carboneras, C., Christie, D.A. & Kirwan, G.M. 2016. Common Goldeneye (*Bucephala clangula*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.).

Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/52925 on 23 October 2016).
Coppack, T., Both, C., 2002. Predicting life-cycle adaptation of migratory birds to global climate change. Ardea 90: 369–378.
Cramp, S. & Simmons, K.E.L. eds. 1977. The Birds of the Western Palearctic. Vol. 1. Oxford University Press, Oxford.
Cresswell, W. 2014. Migratory connectivity of Palaearctic – African migratory birds and their responses to environmental change: the serial residency hypothesis. Ibis 156: 493–510. doi:10.1111/ibi.12168
Czeraszkiewicz R, Haferland HJ, Oleksiak A. 2004. The results of waterbirds count in the Western Pomerania in the season 2003/2004. In: Czeraszkiewicz R, Oleksiak A. Waterbirds in Western Pomerania. The results of counts in 2003/2004, ecology and conservation, ZTO–PZŁ, Szczecin. 2004. pp. 5–16. (in Polish with German summary).
Guentzel S., Ławicki Ł., Marchowski D., Kajzer Z., Barcz M., Racławski B., Sołowiej M., Staszewski A. 2012. The Szczecin Lagoon PLB320009. In: Ławicki Ł., Guentzel S. editors. Important Bird Areas in Poland – the inventory of non-breeding species in 2011/2012 season. ECO-EXPERT, Szczecin. (In Polish).
De Leeuw JJ. 1999. Food intake rates and habitat segregation of Tufted Duck *Aythya fuligula* and Scaup *Aythya marila* exploring Zebra Mussels *Dreissena polymorpha*. Ardea 87: 15–31.
Delany S.N., Reyes C., Hubert E., Phil S., Rees E., Haanstra L., van Strien A.1999. Results from the International Waterbird Census in the Western Palearctic and Southwest Asia 1995 and 1996. Wetland International Publ. Wageningen, The Netherlands.
Dillingham P.W., Fletcher D. 2008. Estimating the ability of birds to sustain additional human-caused mortalities using a simple detection rule and allometric relationship. Biological Conservation 141: 1783-1792.
EEA - The European Environment Agency data obtained from: http://www.eea.europa.eu/data-and-maps/figures/maximum-extents-of-ice-cover 10.02.2017
Ferreras P., Macdonald D. W. 1999. The impact of American mink *Mustela vison* on water birds in the upper Thames. J Appl Ecol 36: 701-708.
Finnish Meteorological Institute data obtained from: http://en.ilmatieteenlaitos.fi/ 10.02.2017
Girjatowicz J.P. 1990. Ice cover atlas for Polish Baltic Coastal waters. Akademia Rolnicza, Szczecin (in Polish).
Girjatowicz J.P. 2005. Ice conditions in Szczecin Lagoon and the Pomeranian Bay. In: Borówka R.K., Musielak S. (eds), Środowisko przyrodnicze wybrzeży Zatoki Pomorskiej i Zalewu Szczecińskiego. Uniwersytet Szczeciński, Szczecin, pp. 126-138 (in Polish).
Girjatowicz J.P. 2011. Ice Conditions on the Southern Baltic Sea Coast. J. Cold Reg. Eng.25:1-15.
Hornman M., van Roomen M., Hustings F., Koffijberg K., van Winden E., Soldaat L. 2012. Population trends in wintering and migrating waterbirds in The Netherlands in 1975-2010 (in Dutch with English summary). Limosa 85: 97-116
Jankowiak, Ł., Antczak, M., Kwieciński, Z., Szymański, P., Tobolka, M., Tryjanowski, P., 2015a. Diurnal raptor community wintering in an extensively used farmland. Ornis Fennica 92: 76-86.
Jankowiak, Ł., Polakowski, M., Kułakowski, T., Świętochowski, P., Tumiel, T., Broniszewska, M., Takács, V., 2015b. Habitat and weather requirements of diurnal raptors wintering in river valleys. Biologia (Bratisl). 70, 1136–1142.
Newton, I., 2008. The migration ecology of birds. Academic Press, London, United Kingdom.

Kaliciuk J, Oleksiak A, Czeraszkiewicz R. 2003. The results of counts of waterbirds in the Western Pomerania in the season 2002/2003. In: Czeraszkiewicz R, Oleksiak A. Waterbirds in Western Pomerania. The results of counts in 2002/2003, ecology and conservation. ZTO–PZŁ, Szczecin. 2003. pp. 14–25. (in Polish with German summary).

Kear, J. ed. (2005) Ducks, geese and swans. Oxford University Press, Oxford.

Lehikoinen A., Jaatinen K., Vahatalo A.V., Preben C., Crowe O., Deceuninck B., Hearn R., Holt C.A., Hornman M., Keller V., Nilsson L., Langendoen T., Tomankova I., Wahl J., Fox A.D. 2013. Rapid climate driven shifts in wintering distributions of three common waterbird species. Global Change Biology: 19, 2071–2081, doi: 10.1111/gcb.12200

Ludwichowski, I., Barker, R. & Bräger, S. (2002) Nesting area fidelity and survival of female Common Goldeneyes *Bucephala clangula*: are they density-dependent? Ibis 144**:** 452–460.

Ławicki Ł, Czeraszkiewicz R, Guentzel S, Jasiński M, Kajzer Z, Kaliciuk J, et al. 2008. Wintering of Waterbirds in the Western Pomerania in the years 2002-2008. Not. Orn. 49: 235–244. (in Polish with English summary).

Komdeur, J, Bertelsen J, Cracknell G. 1992. Manual for aeroplane and ship surveys of waterfowl and seabirds. IWRB Special Publication No.19. IWRB, Slimbridge, U.K.

Larsen K.1992. New figures of seaduck winter population in the Western Palearctic. IWRB Seaduck Bulletin No.1 Jan.1992.

Marchowski D, Ławicki Ł. 2011. Numbers of Waterfowl in Western Pomerania in the 2009/2010 season. Ptaki Pomorza 2: 159–166 (in Polish with English summary).

Marchowski D, Ławicki Ł. 2012. Numbers of Waterfowl in Western Pomerania in the season 2010/2011. Ptaki Pomorza 3: 129–134 (in Polish with English summary).

Marchowski D, Ławicki Ł, Guentzel S. 2013. Numbers of Waterfowl in Western Pomerania in the season 2010/2011. Ptaki Pomorza 4: 149–169. (in Polish with English summary).

Marchowski D., Neubauer G., Ławicki Ł., Woźniczka A., Wysocki D., Guentzel S., Jarzemski M. 2015. The importance of non-native prey, the Zebra Mussel *Dreissena polymorpha*, for the declining Greater Scaup *Aythya marila*: a case study at a key European staging and wintering site. PLoS ONE 10(12): e0145496.

Marchowski D., Jankowiak Ł., Wysocki D. 2016. Newly demonstrated foraging method of Herring Gulls and Mew Gulls with benthivorous diving ducks during the nonbreeding period. Auk 133: 31–40.

Meller K. 2016. The impacts of temperature on the long-term variation in migration and breeding performance of birds. PhD dissertation. The Helsinki Lab of Ornithology The Finnish Museum of Natural History Luomus Zoology Unit University of Helsinki Finland. Available at: https://helda.helsinki.fi/bitstream/handle/10138/160724/The_impa.pdf?sequence=1

Musil, P., Musilová, Z., Fuchs, R. & Poláková, S. 2011. Long-term changes in numbers and distribution of wintering waterbirds in the Czech Republic, 1966– 2008. Bird Study 58: 450–460.

Nagy S., Flink S., Langendoen T. 2014. Waterbird trends 1988-2012. Results of trend analyses of data from the International Waterbird Census in the African-Eurasian Flyway. Wetlands International. Ede, the Netherlands.

Neubauer G., Meissner W., Chylarecki P., Chodkiewicz T., Sikora A., Pietrasz K., Cenian Z., Betleja J., Gaszewski K., Kajtoch Ł., Lenkiewicz W., Ławicki Ł., Rohde Z., Rubacha S., Smyk B., Wieloch M., Wylegała P. Zieliński P. 2015. Monitoring of Birds in Poland in years 2013-2015. Newsletter of Nature Monitoring 13: 1-92.

Nilsson L., Haas F. 2016. Distribution and numbers of wintering waterbirds in Sweden in 2015 and changes during the last fifty years. Ornis Svecica 26:3–54.

Pavon-Jordan D., Fox A., D., Clausen P., Dagys M., Deceuninck B., Devos K., Hearn R. D., Holt C. A., Hornman M., Keller V., Langendoen T., Ławicki Ł., Lorentsen S., H., Luiguj L., Meissner W., Musil P., Nilsson L., Paquet J. Y., Stipniece A., Stroud D. A., Wahl J., Zenatello M., Lehikoinen A. 2015. Climate-driven changes in winter abundance of a migratory waterbird in relation to EU protected areas. Diversity Distrib. 21: 571-582.
Pearce J.M., Reed J.A., Flint P.L. 2005. Geographic variation in survival and migratory tendency among North American Common Merganser. Journal of Field Ornithology 76: 109-118.
Perdeck A. C. 1998. Poisson regression as a flexible alternative in the analysis of ring-recovery data. Euring Newsletter 2: 37-42.
Radziejewska T, Schernewski G. 2008. The Szczecin (Oder) Lagoon. In: Schiewer U, editor. Ecology of Baltic Coastal Waters. Berlin Heidelberg: Springer,. pp. 116–117.
Runge M. C., Sauer J.R., Avery M.L., Blackwell B.F., Koneff M.D. 2009. Assessing allowable take of migratory birds. Journal of Wildlife Management. 73: 556-565.
Skov H, Heinänen S, Žydelis R, Bellebaum J, Bzoma S, Dagys M, et al. Waterbird 2011. Populations and Pressures in the Baltic Sea. Nordic Council of Ministers, Copenhagen.
Schröder J. 2015. Does ice coverage in the Baltic Sea affect numbers of diving ducks wintering in the Netherlands? Limosa 88: 22-30.
Stańczykowska A, Lewandowski K, Czarnoleski M. 2010. Distribution and densities of *Dreissena polymorpha* in Poland – past and present. In: Van der Velde G, Rajagopal S, Bij de Vaate A, editors. The Zebra Mussel in Europe. Margraf Publishers, Weikersheim: pp. 119-132.
Stempniewicz L, Meissner W. 1999. Assessment of the zoobenthos biomass consumed yearly by diving ducks wintering in the Gulf of Gdańsk (southern Baltic Sea). Ornis Svecica 9: 143–154.
Stocker T.F., Qin D., Plattner G.K., Tignor M., Allen S.K., Boschung J., et al., editors 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.
Taylor, B. & Kirwan, G.M. 2016. Common Coot (*Fulica atra*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/53695 on 21 October 2016).
van Erden M. R., de Leeuw J.J. 2010. How *Dreissena* sets the winter scene for water birds: dynamic interaction between diving ducks and zebra mussels. In: van der Velde G., Rajagopal S., bij de Vaate A. The Zebra Mussel in Europe. 2010. Backhuys Publ., Leiden, The Netherlands.
Wacker A. 2010. Careless youth? Food in the early life-stages of zebra mussels. In: Van der Velde G., Rajagopal S., bij de Vaate A. The Zebra Mussel in Europe. 2010. Backhuys Publishers, Leiden, The Netherlands.
Weatherbase. 2016.: Historical Weather for Szczecin, Poland. (access: 29.01.2016), available at: http://www.weatherbase.com/.
Wetlands International. Guidance on waterbird monitoring methodology: Field Protocol for waterbird counting. Wetlands International, Wageningen. 2010. Available from: http://www.wetlands.org.
Wetlands International 2016. *"Waterbird Population Estimates"*. Retrieved from wpe.wetlands.org on Tuesday 11 Oct 2016
Wiktor J. 1969. Biology of *Dreissena polymorpha* (Pall.) and its importance on Szczecin Lagoon. Stud. Mater. Mor. Inst. Ryb., Gdynia. (in Polish).

Wilk T., Jujka M., Krogulec J., Chylarecki P. (eds) 2010. Important Bird Areas of international importance in Poland. OTOP, Marki.
Wolnomiejski N, Witek Z. 2013. The Szczecin Lagoon Ecosystem: The Biotic Community of the Great Lagoon and its Food Web Model. Versita Ltd. London.
Wolnomiejski N., Woźniczka A. 1008. A drastic reduction in abundance of *Dreissena polymorpha* Pall. in the Skoszewska Cove (Szczecin Lagoon, River Odra estuary): effects in the population and habitat. Ecological Questions 9: 103–111.
Żydelis, R., Bellebaum, J., Österblom, H., Vetemaa, M., Schirmeister, B., Stipniece, A., et al., 2009. Bycatch in gillnet fisheries – An overlooked threat to waterbird populations. Biol. Conserv. 142, 1269–1281.

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

Species	Number of individuals (1992)	Number of individuals (2012)	Population trend % p.a.
Common Pochard	280,000	150,000	-3.35
Tufted Duck	1,100,000	820,000	-0.98
Greater Scaup	300,000	150,000	-3.57
Common Goldeneye	210,000	240,000	+0.26
Smew	13,000	24,000	+1.97
Goosander	130,000	100,000	-0.09
Eurasian Coot	990,000	950,000	+0.19

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) species in the Odra River Estuary. Species, method and month were treated as random effects in relation to their regional breeding population.

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	-0.001	0.000	-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]	0.001	<0.001	2.071	**0.039**
Species (r)	0.074	0.048		
Method (r)	0.015	0.020		
Month (r)	0.001	0.002		

Table 3. Changes in the significance of the Odra River Estuary (ORE) for the biogeographic population (b.p) of diving waterbirds showing: the percentage of the biogeographic population in 1992; the percentage of the biogeographic population in 2016; the mean percentage of the biogeographic population in the period 1992 – 2016 ± standard error; and the trend in changes of the area's significance to the species 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 Pochard	1.84	0.20	0.62±0.09	↓
Common Goldeneye	4.48	0.63	1.21±0.14	→
Eurasian Coot	0.86	0.68	0.61±0.07	→
Smew	7.04	2.76	7.01±1.27	↓
Goosander	12.59	1.80	6.85±1.01	→

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

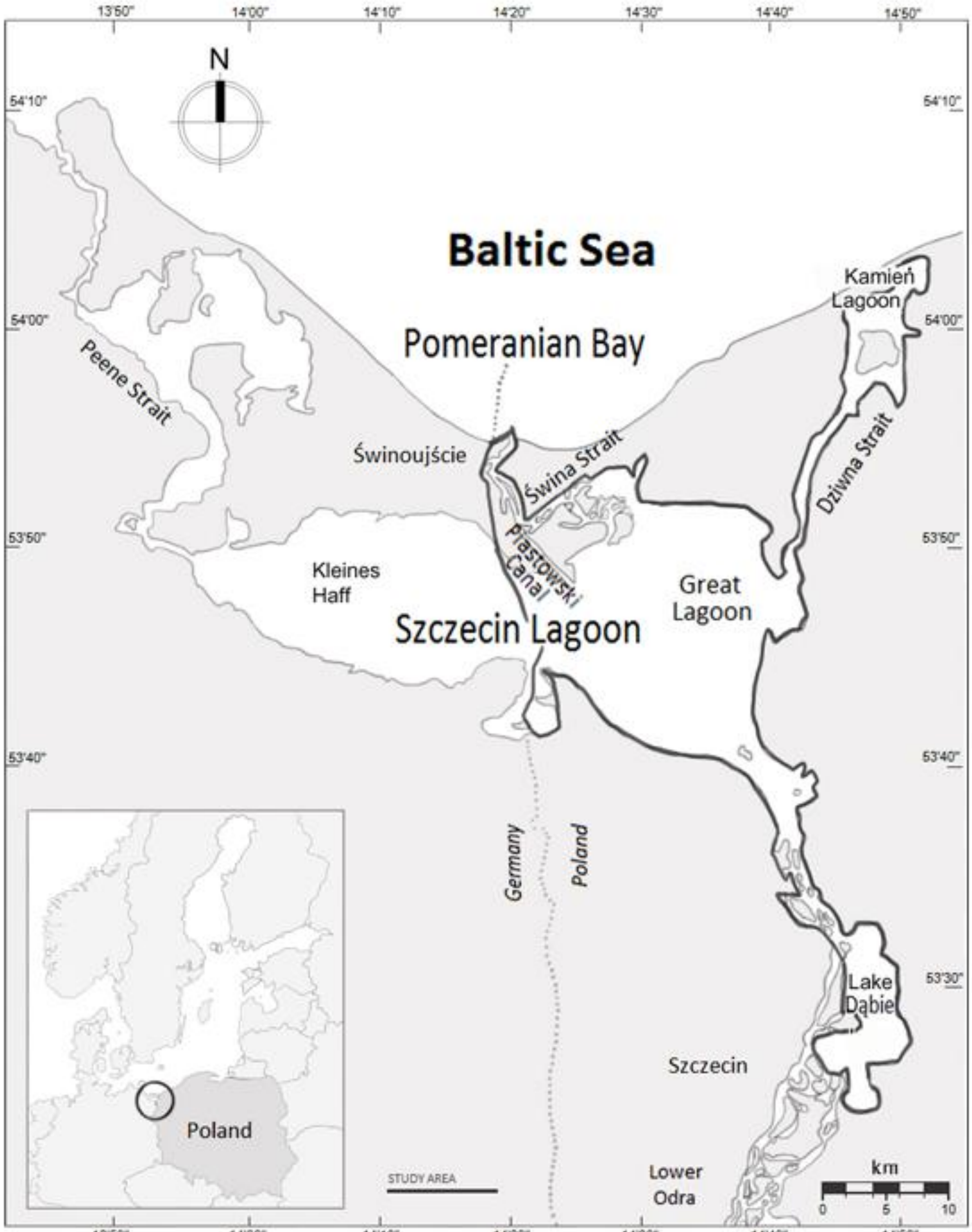
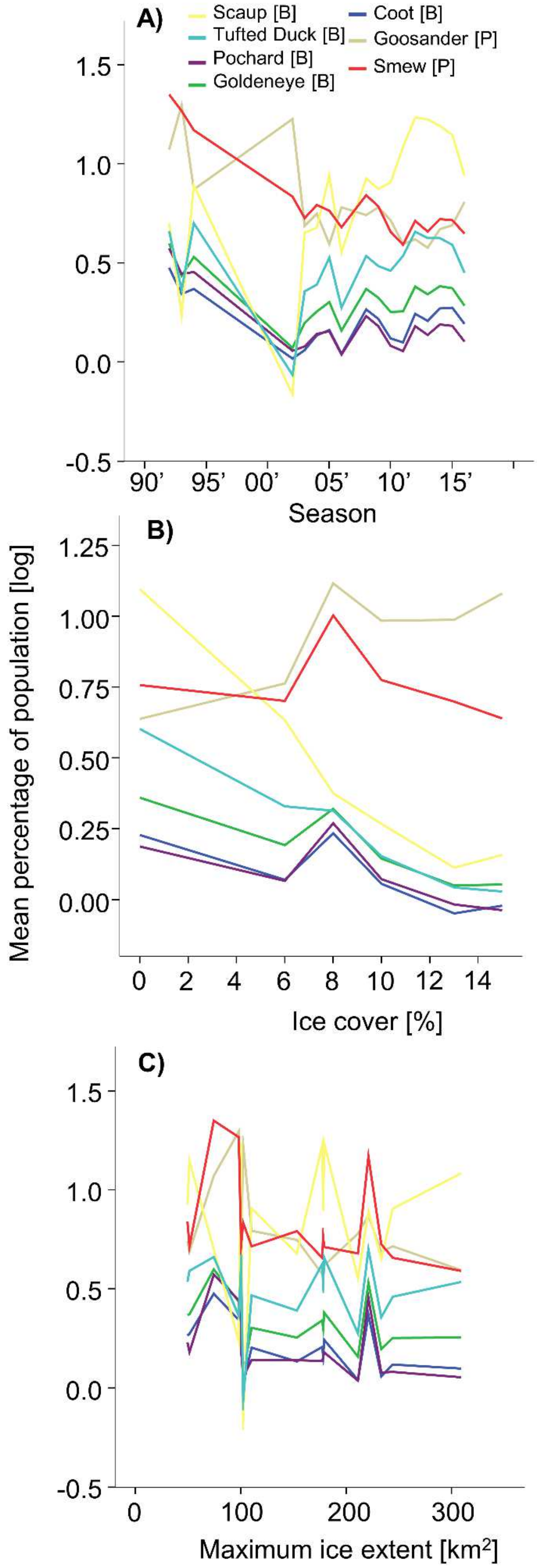


Figure 2 A-C. Predicted results of the general linear mixed model showing the influence of season, ice cover and maximum ice extent [km^2] in the Baltic Sea (max ice) on the percentage of the population of the target species in the Odra River Estuary. The predicted values were obtained from the model where we added species as a fixed variable. The model's parameters are listed in Table S1 in the Supplementary material.


A)
Scaup [B]
Tufted Duck [B]
Pochard [B]
Goldeneye [B]
Coot [B]
Goosander [P]
Smew [P]
1.5
1.0
0.5
0.0
-0.5
90'
95'
00'
05'
10'
15'
Season
B)
Mean percentage of population [log]
1.25
1.00
0.75
0.50
0.25
0.00
0
2
4
6
8
10
12
14
Ice cover [%]
C)
1.5
1.0
0.5
0.0
-0.5
0
100
200
300
Maximum ice extent [km2]

713
714