

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

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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.

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19

## 20 **Abstract**

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 37 declined for Smew.

38

## 39 **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<sup>2</sup> (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

86 Szczecin Lagoon, Kamień Lagoon and Lake Dąbie are brackish. The salinity in the central part  
 87 of the estuary varies from 0.3 psu to 4.5 psu (mean = 1.4 psu) and declines with increasing  
 88 distance from the sea (Radziejewska and Schernewski 2008). Periodic backflows of water from  
 89 the Pomeranian Bay (salinity ~7 psu) take place through the Świna Strait and, to a lesser extent,  
 90 through the Dziwna and Peene Straits (the latter situated in the German part of the ORE). The  
 91 average winter temperature is 0.3° C (Weatherbase 2016). The ORE is subject to strong  
 92 anthropogenic pressure manifested by high levels of eutrophication (Radziejewska and  
 93 Schernewski 2008). The communities of benthic organisms are typical of freshwater bodies and  
 94 the fauna includes large populations of zebra mussels *Dreissena polymorpha*, which were  
 95 introduced in the mid-19<sup>th</sup> century. By the 1960s, the biomass of zebra mussels in the Szczecin  
 96 (Great) Lagoon was estimated at 110 000 metric tons (Wiktor 1969, Wolnomiejski and  
 97 Woźniczka 2008) and appears to be fairly stable; in the early 2000s the estimated biomass was  
 98 94 280 metric tons (Marchowski et al. 2015). The distribution of the zebra mussel is highly  
 99 ~~uneven here: there are areas where it is abundant, but there are also large areas where there are~~  
 100 ~~hardly any~~ (see the map in Marchowski et al. 2015). The average density of the zebra mussel in  
 101 the ORE is 0.18 kg /m<sup>2</sup>, but the vast majority of these resources occupies around 10% of the  
 102 entire sea bed, where the mean density is 2.05 kg/m<sup>2</sup> (Stańczykowska et al. 2010). By  
 103 comparison, other areas important for wintering benthos feeding birds, such as the adjacent  
 104 Dutch lakes IJsselmeer and Markermeer, have an average density of 0.24 kg/m<sup>2</sup> (van Eerden &  
 105 de Leeuw 2010). In contrast, the Vistula Lagoon in Poland has a much lower density of zebra  
 106 mussels – 0.001 kg/m<sup>2</sup> (Stańczykowska et al. 2010) – and there are correspondingly smaller  
 107 densities of benthivorous birds than in the Szczecin Lagoon (Neubauer et al. 2015). The fish  
 108 consist mainly of freshwater species such as roach *Rutilus rutilus*, bream *Abramis brama*, pike

109 *Esox lucius*, perch *Perca fluviatilis* and ruff *Gymnocephalus cernua*; there are also anadromous  
 110 fish like smelt *Osmerus eperlanus* and occasionally ~~marine fish like~~ herring *Clupea harengus*  
 111 (Wolnomiejski and Witek 2013).

## 112 **Methods**

### 113 ***Bird censusing***

114 Our study covers two functional groups of waterbirds: 1) benthivores – Greater Scaup  
 115 (*Aythya marila* – hereafter Scaup), Tufted Duck (*A. fuligula*), Common Pochard (*A. ferina* –  
 116 hereafter Pochard), Common Goldeneye (*Bucephala clangula* – hereafter Goldeneye) and  
 117 Eurasian Coot (*Fulica atra* – hereafter Coot); 2) piscivores – Smew *Mergellus albellus* and  
 118 Goosander *Mergus merganser*. The study site is known to regularly host significant numbers of  
 119 the biogeographic population of the above species (Kaliciuk et al. 2003; Czeraszkievicz et al.  
 120 2004; Wilk et al. 2010; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and  
 121 Ławicki 2012; Marchowski et al. 2013). Here, by biogeographic population we mean that part of  
 122 the global population associated with a specific flyway region. These subpopulations are:  
 123 Pochard – north-east Europe / north-west Europe; Tufted Duck – north-west Europe (wintering);  
 124 Scaup – northern Europe / western Europe; Goldeneye – north-west and central Europe; Smew –  
 125 north-west and central Europe (wintering); Goosander – north-west and central Europe  
 126 (wintering); Coot – north-west Europe (wintering) (Wetlands International 2016).

127 Censuses were conducted using standard methods for non-breeding season waterbird  
 128 counts (Komdeur et al. 1992; Wetlands International 2010). Birds were counted during 17  
 129 seasons (1991/1992 to 1993/1994 and 2001/2002 to 2015/2016) during the migration and  
 130 wintering periods between November and April. From 1991/1992 to 1993/1994 three censuses

131 were carried out per season in November, January, and March or April; in 2001/2002 ~~only one~~  
132 ~~mid winter count in January was done~~. Altogether we analysed the results of 44 counts. Most  
133 counts were done on foot. Each observer was equipped with 10x binoculars and tripod-mounted  
134 spotting scopes. ~~Observers walked along the same routes, stopping every few hundred metres or~~  
135 ~~making observations from vantage points reachable by car~~. Fourteen aerial counts were made at  
136 an average speed of about 100 km/h and an altitude of about 80 m above the water (see  
137 supplementary materials – S1 Table for the method of data collection: aerial or ground). In the  
138 early 1990s counts were ~~solely~~ aerial, whereas in 2009-2015 parallel aerial and ground counts  
139 were carried out. ~~It was the aim of other research to determine the effectiveness of the two~~  
140 ~~methods. The results show that in ice-free conditions almost all the species covered in this study~~  
141 can be assigned to a group with just a small error between methods (<6%). ~~Only for one species~~  
142 – Coot – ~~was the moderate error (16%); the numbers counted from the ground were higher than~~  
143 ~~those from the aircraft~~. During periods with more than 70% ice cover, ~~bird numbers counted~~  
144 ~~from the aircraft were higher than those counted from the ground~~ (Dominik Marchowski pers.  
145 com.). ~~All counts were conducted in the same way using the same route and the same~~  
146 ~~observation points~~. Count method was treated as a random effect in the model. The detailed  
147 methodology and results of the counts are given elsewhere (Meissner and Kozakiewicz 1992;  
148 Meissner et al 1994; Kaliciuk et al. 2003; Czeraszewicz et al. 2004; Marchowski and Ławicki  
149 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013). Where  
150 large numbers of unidentified *Aythya* species were counted – 26 000 ducks in November 2009,  
151 13 000 in November 2010, 6 000 in January 2012, 3 300 in March 2012 and 13 500 in November  
152 2015 – ~~they were allocated to either Scaup or Tufted Duck based on the mean ratio of these two~~  
153 ~~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](http://tutempo.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

176 standard methods of the Baltic Sea ice information system. This partitions the Baltic into sectors,  
 177 and the ice conditions in each sector are given in the "Monthly Ice Listing", a daily protocol  
 178 supplying information on the degree of ice cover, position of the ice, the developmental stage of  
 179 the ice, topography, ice type and the conditions for sailing across ice-covered water. For the  
 180 calculations in this study, we used only the information on the number of days with total ice  
 181 cover from one sector (Miroszewo). Observations of ice-related phenomena in this sector took  
 182 place from a site on the shore of the Szczecin Lagoon (53.734 N, 14.331 E). Observations were  
 183 conducted daily from 1 November to 30 April at 12:00 hrs UTC. The methodology for collecting  
 184 ice cover data was the same throughout the study period. We compared the number of days with  
 185 100% ice cover in the period from 0 to 15 days prior to bird counts. The ice cover of 100% refers  
 186 specifically to the observation point at Miroszewo (data from the Polish Institute of Meteorology  
 187 and Water Management, which we used in our computations). ~~This does not embrace the whole~~  
 188 ~~ORE, but is a good approximation of it.~~ Our field observations during bird counts show that most  
 189 of our study area is also nearly 100% frozen. In practice, however, the ORE is never completely  
 190 covered by ice (Girjatowicz 1991; 2005; see also the Discussion for an explanation) and birds are  
 191 still present in such conditions. We also utilized the maximum ice extent in the Baltic Sea (max  
 192 ice). These data were obtained from the website of The European Environment Agency (EEA  
 193 2017). Apart from climatic variables, we also wanted to test the changes in species occurrence  
 194 during the survey years, so we used season as covariate. Prior to the final analysis we checked  
 195 ~~the multicollinearity correlation~~ between the above variables using the variation inflation factor  
 196 (VIF). ~~If VIFs were well above 2, the relevant variables were excluded from the analysis.~~ Hence,  
 197 we excluded the mean, maximum and minimal temperatures averaged over the 15 days prior to  
 198 the count, as they were highly correlated. We used a general linear mixed model (GLMM) as a

199 ~~statistical solution~~ to test ~~the~~ hypothesis relating to the different patterns of occurrence of  
 200 benthivores and piscivores in the ORE. The percentage of ~~numbers in relation to the species'~~  
 201 ~~whole population~~ was used as a target variable and was treated with normal distribution response  
 202 distribution and identity link function. Mixed models permitted repetition across survey months,  
 203 methods (aerial and ground counts) and species (random intercept). Thus to test our hypotheses  
 204 we ~~assessed~~ the following interactions: feeding group\*season, feeding group\*ice cover and  
 205 feeding group\*max ice. To demonstrate interactions at the level of particular species we  
 206 produced another GLMM model (with month and method as random factors) and assessed the  
 207 following interactions: species\*season, species\*ice cover and species\*max ice. The parameters  
 208 of this model are listed in Table S2 in the Supplementary material. The predicted values of this  
 209 model for each species are shown on Figure 2. We used IBM SPSS Statistic version 20 software  
 210 for the statistical analysis.  $P < 0.05$  was considered statistically significant.

211

## 212 Results

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

217 Benthic feeding species in the study area were more sensitive to lower temperatures and  
 218 left sooner when colder weather increased ice cover, whereas numbers of fish feeding species did  
 219 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.

## 243 Discussion

244 ~~As we had predicted,~~ benthic feeding birds (Scaup, Tufted Duck, Pochard, Goldeneye and  
 245 Coot) ~~were~~ more sensitive to ~~the presence of~~ ice cover in the study area. Benthivorous birds feed  
 246 in the ORE mainly on mussels of the genus *Dreissena* (Marchowski et al. 2015, 2016), the best  
 247 quality of food resources that are primarily found in water 1-2 m deep (Wolnomiejski and Witek  
 248 2013). Shallow water freezes over faster, displacing birds to deeper unfrozen areas where  
 249 resources of food are hardly available.  In addition, the food richness of unfrozen areas is  
 250 declining owing to their greater exploitation. In the case of piscivorous birds we ~~assumed~~ that  
 251 increasing ice cover would not affect their numbers: ~~our results substantiate this assumption.~~ Ice  
 252 cover is never 100% here; the shipping lane between Świnoujście and Szczecin is kept free of ice  
 253 (Girjatowicz 1991; 2005) and there are also always other areas free of ice, especially at the  
 254 mouths of the small rivers flowing into the estuary. These areas free of ice may still abound in  
 255 fish and provide food for fish feeders. In general, we have demonstrated the growing importance  
 256 of the study area for all the benthivores. Considering this in relation to particular species, the two  
 257 most numerous species have increased in numbers, while another three do not follow the general  
 258 trend. In addition, we have shown that the study area is decreasing in importance to piscivores  
 259 and that each species is decreasing in numbers, although the trend for Goosander is not  
 260 significant.

261  An interesting result is the negative effect of maximum ice cover in the entire Baltic Sea on the  
 262 numbers of all species in our study (Fig. 2). This is unexpected, since our study area is the  
 263 warmer south-western Baltic, where one would anticipate an increase in the number of  
 264 waterbirds in such circumstances (Alerstam 1990). The explanation for this relationship is not  
 265 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 Travemünde** 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). Lehtikoinen 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 Lehtikoinen 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 km<sup>2</sup>), 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, 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 Lehtikoinen 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 Lehtikoinen 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**, 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 et 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 Lehtikoinen 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.

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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<sup>2</sup>] 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  | <b>0.018</b>     |
| Season            | -0.013      | 0.006     | -2.204 | <b>0.028</b>     |
| Max ice           | -0.001      | 0.000     | -2.824 | <b>0.005</b>     |
| Feed[B]           | -38.751     | 11.959    | -3.240 | <b>0.001</b>     |
| Season*Feed[B]    | 0.019       | 0.006     | 3.212  | <b>0.001</b>     |
| Ice cover*Feed[B] | -0.044      | 0.007     | -6.623 | <b>&lt;0.001</b> |
| Max ice*Feed[B]   | 0.001       | <0.001    | 2.071  | <b>0.039</b>     |
| Species (r)       | 0.074       | 0.048     |        |                  |
| Method (r)        | 0.015       | 0.020     |        |                  |

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| Month (r) | 0.001 | 0.002 |
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|-----------|-------|-------|

635 Table 3. ~~Changes in the significance~~ of the Odra River Estuary (ORE) for the biogeographic population  
 636 (b.p) of diving waterbirds showing: the percentage of the biogeographic population in 1992; the  
 637 percentage of the biogeographic population in 2016; the mean percentage of the biogeographic population  
 638 in the period 1992 – 2016  $\pm$  standard error; and the trend ~~in changes of the area's significance to the~~  
 639 ~~species~~ in the period 1992 – 2016.

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

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



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

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