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1 Waterbirds in the Baltic Sea are changing wintering patterns because of climate
2 warming. A study of selected species in the Odra River Estuary – a key
3 European wintering site.

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20 Abstract

21 Some species of birds react to climate change, by wintering in places closer to their
22 breeding areas. We investigated the responses of two groups of waterbirds to factors
23 associated with climate change. The Odra River Estuary (SW Baltic Sea) is of key importance
24 for wintering waterfowl. The most abundant birds here comprise two ecological groups:
25 benthic feeders and fish feeders. We showed that numbers of all benthivores, but not
26 piscivores, were negatively correlated with the presence of ice. We predicted that, with
27 ongoing global warming, this area would increase in importance for benthic feeders and
28 decrease for fish feeders. The maximum range of ice cover in the Baltic Sea has a weak and
29 negative effect on both groups of birds. Five of the seven target species are benthivores
30 (Greater Scaup *Aythya marila*, Tufted Duck *A. fuligula*, Common Pochard *A. ferina*, Common
31 Goldeneye *Bucephala clangula* and Eurasian Coot *Fulica atra*), and two are piscivores
32 (Smew *Mergellus albellus* and Goosander *Mergus merganser*). Local changes at the level of
33 particular species vary for different reasons. The local decline of Common Pochard may be a
34 reflection of the species' global decline. Climate change may be responsible for some of the
35 local changes in the study area; thereby increasing the importance of the area for Greater
36 Scaup and Tufted Duck while reducing it for Smew.

37

38 Introduction

39 Migration distance has declined in several species of aquatic (and other) birds as a
40 result of climate change (Musil et al. 2011; Lehikoinen et al. 2013; Meller 2016). The
41 distances that birds migrate from their breeding areas in northern and eastern Europe to their
42 central European wintering areas are shorter during mild winters (Lehikoinen et al. 2013;
43 Pavón-Jordan et al. 2015); conversely birds may change their wintering sites to warmer

44 regions during colder periods because they may perceive local manifestations of large-scale
45 atmospheric features (Newton 2008). Reducing migration distance can provide several
46 benefits associated with earlier arrival at the breeding grounds and greater survival (Coppack
47 and Both 2002; Jankowiak et al. 2015a; 2015b). Food resources of wintering sites may also
48 influence migration decisions (Cresswell 2014; Aharon-Rotman et al. 2016). Although winter
49 site fidelity is very high among waterfowl (Newton 2008), this can change in response to
50 weather, habitat and competition (Cresswell 2014). The changing of winter sites should thus
51 be seen as trade-off between the costs of finding a new site and the benefits it offers (Aharon-
52 Rotman et al. 2016). At sub-zero temperatures, shallow waters freeze over; birds therefore
53 expend more time and energy searching for food in deeper waters, with obvious consequences
54 for their energy balance. Shallow waters of offshore lagoons create ideal conditions for three
55 functional groups of waterbirds: piscivores, herbivores and benthivores. Our study area, the
56 Odra River Estuary (ORE), accommodates large numbers of waterbirds because of food
57 resources (Marchowski et al. 2015; Marchowski et al. 2016). Two groups of waterbirds – fish
58 feeders and benthic feeders – are among those most commonly wintering here. Because of its
59 position on the 0°C isotherm in winter (van Erden and de Leeuw 2010), the study area is
60 subject to significant variations in bird habitat conditions. Yet even relatively small variations
61 in temperature, causing ice cover to form or disappear, can lead to the displacement of
62 waterbirds. Changes in abundance and community structure in the ORE may reflect the
63 impact of climate change. Analysis of the dates of the appearance of ice-related phenomena in
64 the Szczecin Lagoon and of their frequency over time reveals a distinct pattern endorsing
65 recently observed trends in climate warming (Girjatowicz 2011). In this paper we test whether
66 abundance of some species in the ORE is changing in response to climate warming. We
67 predict that benthic feeding birds will be more sensitive and fish feeding birds less sensitive to
68 the factor related to climate, namely ice cover. If our prediction is correct, elevated

69 temperatures and the correspondingly shorter period of ice cover should provide relatively
70 better conditions for benthic feeders, which should increase in abundance. Feeding areas
71 where sedentary mussels are abundant tend to be in shallow waters (Marchowski et al. 2015),
72 so surface ice cover reduces food availability. Fish, on the other hand, remain available even
73 if the ice cover is considerable, since unfrozen, deeper, areas, located further from the shore,
74 may still be rich in fish. During cold winters the water in the ORE never freezes over entirely:
75 even during periods of sustained below-zero temperatures, patches of water remain free of ice,
76 where large aggregations of fish feeders (Smew and Goosander) have been observed
77 (Kaliciuk et al. 2003; Czeraszkiwicz et al. 2004; Marchowski and Ławicki 2011; Guentzel et
78 al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013).

79

80 **Study area**

81 The study area lies in the south-western Baltic Sea and forms the Polish part of the
82 Odra River Estuary system, which includes the Great Lagoon (the Polish part of the Szczecin
83 Lagoon), Świna Backward Delta, Kamień Lagoon, Dziwna Strait and Lake Dąbie with a total
84 area of 522.58 km² (Fig. 1). The whole area has been designated as four interconnected
85 Important Bird Areas (IBA) and also a Natura 2000 area (Wilk et al. 2010). The average and
86 maximum depths of the estuary are 3.8 and 8.5 m, respectively; the dredged shipping lane
87 passing through the estuary from the Baltic Sea to the port of Szczecin is 10.5 m deep
88 (Radziejewska and Schernewski 2008). The waters of the Szczecin Lagoon, Kamień Lagoon
89 and Lake Dąbie are brackish. The salinity in the central part of the estuary varies from 0.3 psu
90 to 4.5 psu (mean = 1.4 psu) and declines with increasing distance from the sea (Radziejewska
91 and Schernewski 2008). Periodic backflows of water from the Pomeranian Bay (salinity ~7
92 psu) take place through the Świna Strait and, to a lesser extent, through the Dziwna and Peene

93 Straits (the latter situated in the German part of the ORE). The average winter temperature is
94 0.3° C (Weatherbase 2016). The ORE is subject to strong anthropogenic pressure manifested
95 by high levels of eutrophication (Radziejewska and Schernewski 2008). The communities of
96 benthic organisms are typical of freshwater bodies, and the fauna includes large populations
97 of zebra mussels *Dreissena polymorpha*, which were introduced in the mid-19th century. By
98 the 1960s, the biomass of zebra mussels in the Szczecin (Great) Lagoon was estimated at 110
99 000 metric tons (Wiktor 1969, Wolnomiejski and Woźniczka 2008). At present, this appears
100 to be fairly stable; in the early 2000s the estimated biomass was 94 280 metric tons
101 (Marchowski et al. 2015). The distribution of the zebra mussel is extremely uneven (see the
102 map in Marchowski et al. 2015). The average density of the zebra mussel in the ORE is 0.18
103 kg /m², but the vast majority of these resources occupies around 10% of the entire water body
104 bed, where the mean density is 2.05 kg/m² (Stańczykowska et al. 2010). The fish consist
105 mainly of freshwater species such as roach *Rutilus rutilus*, bream *Abramis brama*, pike *Esox*
106 *lucius*, perch *Perca fluviatilis* and ruff *Gymnocephalus cernua*; there are also anadromous fish
107 including smelt *Osmerus eperlanus* and occasionally herring *Clupea harengus* among others
108 (Wolnomiejski and Witek 2013).

109

110 **Methods**

111 ***Bird censusing***

112 Our study covers two functional groups of waterbirds: benthivores – Greater Scaup
113 (*Aythya marila* – hereafter Scaup), Tufted Duck (*A. fuligula*), Common Pochard (*A. ferina* –
114 hereafter Pochard), Common Goldeneye (*Bucephala clangula* – hereafter Goldeneye) and
115 Eurasian Coot (*Fulica atra* – hereafter Coot); piscivores – Smew *Mergellus albellus* and
116 Goosander *Mergus merganser*. The study site is known to regularly host large numbers of the

117 biogeographic populations of the above species (Kaliciuk et al. 2003; Czeraszewicz et al.
118 2004; Wilk et al. 2010; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and
119 Ławicki 2012; Marchowski et al. 2013) and meets the criteria for classification as a key site
120 for them (Wilk et al. 2010). Here, by biogeographic population we mean that part of the
121 global population associated with a specific flyway region. These subpopulations are: Pochard
122 – north-east Europe / north-west Europe; Tufted Duck – north-west Europe (wintering);
123 Scaup – northern Europe / western Europe; Goldeneye – north-west and central Europe;
124 Smew – north-west and central Europe (wintering); Goosander – north-west and central
125 Europe (wintering); Coot – north-west Europe (wintering) (Wetlands International 2016).

126 Censuses were conducted using standard methods for non-breeding season waterbird
127 counts (Komdeur et al. 1992; Wetlands International 2010). Birds were counted during 17
128 seasons (1991/1992 to 1993/1994 and 2001/2002 to 2015/2016) during the migration and
129 wintering periods between November and April. From 1991/1992 to 1993/1994 three
130 censuses were carried out per season in November, January, and March or April; there was
131 one midwinter count in January in 2001/2002. Altogether we analysed the results of 44
132 counts. Most counts were done on foot. Each observer was equipped with 10x binoculars and
133 tripod-mounted spotting scopes. Observers walked along the same routes, and the same
134 counting method was used during every census every year. Additionally, fourteen aerial
135 counts were made at an average speed of about 100 km/h and an altitude of about 80 m above
136 the water (see supplementary materials – S1 Table for the method of data collection: aerial or
137 ground). In the early 1990s counts were aerial, whereas in 2009-2015 parallel aerial and
138 ground counts were carried out (to compare methods). In ice-free conditions the species
139 covered in this study can be assigned to a group with just a small error between methods
140 (<6%), one species – Coot had a moderate error (16%), the ground method estimated greater
141 numbers than the aerial one. During periods with more than 70% ice cover, abundance from

142 the air was greater than abundance from the ground (Dominik Marchowski pers. com.). The
143 count method was treated as a random effect in the model. The detailed methodology and
144 results of the counts are given elsewhere (Meissner and Kozakiewicz 1992; Meissner et al
145 1994; Kaliciuk et al. 2003; Czeraszewicz et al. 2004; Marchowski and Ławicki 2011;
146 Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al. 2013). Where large
147 numbers of unidentified *Aythya* species were counted – 26 000 ducks in November 2009,
148 13 000 in November 2010, 6 000 in January 2012, 3 300 in March 2012 and 13 500 in
149 November 2015 – they were estimated to be in the ratio of 1:0.8 (scaup:tufted) based on
150 observations in other studies. This research involved observations of birds from a distance,
151 which do not disturb the birds. In Poland, such studies do not need special permission or
152 approval.

153 *Statistical analysis*

154 The dependent variable was the percentage occurrence of a given species in relation to
155 the total estimated population size in a given year. This approach was taken because the
156 population sizes of the species covered by our study follow different trends. For example, the
157 population of Scaup is decreasing, that of Smew is increasing and that of Goosander is more
158 or less stable (Nagy et al. 2014; Wetland International 2016). Thus, if we showed the trend of
159 absolute numbers in our area, the resulting error would be the larger, the greater the changes
160 in the size of the entire population. Therefore, we indicate the numbers of a species by means
161 of a coefficient calculated as the percentage of the biogeographic population present in the
162 study area during a particular count. We obtained the data relating to the biogeographic
163 populations from 1992 to 2012 from Nagy et al. (2014); for the period 2013-2016 we used the
164 flat trend calculated by Nagy et al. (2014) (Table 1). Initially, we placed the different species
165 in ecological groups. The benthivores (denoted by B) included Scaup, Tufted Duck, Pochard,
166 Goldeneye and Coot, and the piscivores (P) contained Smew and Goosander. We used the

167 minimum temperatures averaged over the 15 days leading up to the count day. The climate
168 data were obtained from the Szczecin weather station (53.395 N, 14.6225 E,
169 <http://tutiempo.net>). Another climate covariate was ice cover in the study area; data relating to
170 this were published by the Polish Institute of Meteorology and Water Management. These
171 data are from the observation point at Miroszewo on the shore of the Szczecin Lagoon
172 (53.734 N, 14.331 E, <http://www.imgw.pl/>). We compared the number of days with 100% ice
173 cover in the period from 0 to 15 days prior to the bird counts. The ice cover of 100% refers
174 specifically to the Miroszewo observation point. This estimate is a good approximation for the
175 region. In practice, however, the ORE is never completely covered by ice (Girjatowicz 1991;
176 2005; see the Discussion for an explanation) and birds are still present in such conditions. We
177 also utilized the maximum ice extent in the Baltic Sea (max ice) (data obtained from the
178 website of The European Environment Agency (EEA 2017)). Apart from climatic variables,
179 we also wanted to test the changes in species occurrence during the survey years, so we used
180 season as covariate. Prior to the final analysis, we checked the multicollinearity correlation
181 between the above variables using the variation inflation factor (VIF). If VIFs were high, the
182 relevant variables were excluded from the analysis. The VIFs of all variables were in
183 acceptable limits, minimal temperatures (VIF = 2.1), max ice (VIF = 1.03), ice cover (VIF =
184 2.07) and season (VIF = 1.04). However, we found a moderate linear significant relationship
185 between minimal temperature and ice cover ($r = 0.52$, $p < 0.001$) and after exclusion of
186 minimal temperature VIF showed no multicollinearity issue between variables – ice cover
187 (VIF = 1.04), max ice (VIF = 1.03), season (VIF = 1.03) – and these were used in the
188 subsequent analyses. We used a general linear mixed model (GLMM) to test the hypothesis
189 relating to the different patterns of occurrence of benthivores and piscivores in the ORE. The
190 percentage of the entire biogeographic population present in the study area, estimated by
191 species, was used as a target variable using the normal distribution response distribution and

192 identity link function. Mixed models permitted repetition across survey months, methods
193 (aerial and ground counts) and species (random intercept). Thus, to test our hypotheses we
194 included the following interactions: feeding group*season, feeding group*ice cover and
195 feeding group*max ice. Selection of the best model structure for the dependent variable was
196 based on the Akaike information criterion (AIC) (Zuur et al. 2009). All possible models were
197 carried out (they are listed in Table S1 in Supplementary material). As the final models we
198 assumed those in which $\Delta AIC < 2$ (Burnham & Anderson 2002) and in our case it was only a
199 general model with all the tested variables. To demonstrate interactions at the level of
200 particular species we produced another GLMM model (with month and method as random
201 factors) and assessed the following interactions: species*season, species*ice cover and
202 species*max ice. The parameters of this model are listed in Table S3 in the Supplementary
203 material. The predicted values of this model for each species are shown on Figure 2 and
204 predicted values were back-transformed. We used IBM SPSS Statistic version 20 software for
205 the statistical analysis. $P < 0.05$ was considered statistically significant.

206

207 **Results**

208 Benthic feeding species in the study area were more sensitive to lower temperatures
209 and left sooner when colder weather increased ice cover, whereas numbers of fish feeding
210 species did not change, regardless of the extent of ice cover (Tables 2, Fig. 2B). According to
211 our most optimal model (Table S2), we found that interactions between feeding group and
212 season, feeding group and ice cover, and feeding group and maximum ice extent on the Baltic
213 sea were all significant. However, the strongest effects were interactions with ice cover, then
214 interaction with season. The effect of maximum ice extent was very small (Table 2). Our
215 results show changes in population indices in the ORE over the last 25 years. These indices
216 increased in the case of benthic feeding species but decreased for fish feeders (Table 2, Fig

217 2A). Ice cover across the whole Baltic Sea had the same, though weak, impact on both
218 functional groups of birds. Numbers of birds in the ORE declined with expanding ice cover in
219 the Baltic (Table 2, Fig 2C).

220 Where particular species are concerned, the situation is more complex. The population
221 indices of Scaup and Tufted Duck in the ORE exhibited an increasing trend, despite the
222 general decline in their entire northern and western European populations; numbers of both
223 species in the ORE were adversely affected by ice cover in that region but not by ice cover in
224 the whole Baltic. Relative numbers of Pochard in the ORE have declined, but so has the
225 whole northern European population; ice cover in the study area was detrimental to
226 abundance there, but ice cover in the whole Baltic had no effect. For Goldeneye, the index for
227 the ORE population was unchanged, despite the increase in the European population;
228 abundance was negatively impacted by ice cover in the study area, but not by ice cover in the
229 entire Baltic. Relative numbers of Coot in the ORE remained unchanged, despite the slight
230 increase in the European population; abundance was negatively impacted by ice cover in both
231 the study area and in the entire Baltic. The ORE population index for Smew decreased,
232 despite the increase in its biogeographic population; abundance in the ORE was unaffected by
233 ice cover either in the study area or in the Baltic as a whole. Finally, relative numbers of
234 Goosander in the ORE remained unchanged, like those of the whole population wintering in
235 north-western and central Europe; abundance in the ORE was unaffected by ice cover either
236 in the study area or in the Baltic as a whole. The details relating to all these species are listed
237 in Tables 1 and 2, Fig. 2 and Table S3. Table 3 summarizes the changes in the importance of
238 the ORE for wintering populations of diving waterbirds in the last 25 years.

239

240

241 **Discussion**

242 The phenomenon of freezing in our study area has decreased over time (Girjatowicz
243 2011), so that target birds species should tend to feed more recently more often than in the
244 past. However, two functional groups of waterbirds – benthivores and piscivores – react
245 differently to ice cover, a factor that is directly connected to climate change; this has
246 consequences for the wintering patterns of these species. Benthic feeding birds (Scaup, Tufted
247 Duck, Pochard, Goldeneye and Coot) tend to be more sensitive to ice cover in the study area
248 than fish feeders (Smew and Goosander). Benthivorous birds feed in the ORE mainly on
249 mussels of the genus *Dreissena* (Marchowski et al. 2015, 2016); the highest quality of this
250 food resource is found primarily in water 1-2 m deep (Wolnomiejski and Witek 2013).
251 Shallow water freezes over faster, displacing birds to deeper unfrozen areas where food is
252 accessible only with difficulty. In addition, when ice cover is present, the abundance of food
253 in unfrozen areas declines owing to its greater exploitation, because the birds congregate on a
254 limited area. In the case of piscivorous birds we predicted that increasing ice cover would not
255 affect their numbers: our results substantiate that prediction. The ORE is never completely
256 covered by ice: the shipping lane between Świnoujście and Szczecin is kept free of ice
257 (Girjatowicz 1991; 2005), and there are always other areas free of ice, especially at the
258 mouths of the small rivers flowing into the estuary. These ice-free areas may still abound in
259 fish and provide food for fish feeders. In general, we have demonstrated the growing
260 importance of the study area for all the benthivores. With respect to particular species, the two
261 most numerous ones have increased in numbers, whereas another three do not follow the
262 general trend. In addition, we have shown that the study area is decreasing in importance to
263 piscivores and that Smew is decreasing in numbers.

264 An interesting result is the negative effect of maximum ice cover in the entire Baltic
265 Sea on the numbers of all species in our study (Fig. 2). This is unexpected, since our study

266 area is in the warmer south-western Baltic, where one would anticipate an increase in the
267 number of waterbirds in such circumstances (Alerstam 1990). The explanation for this
268 relationship is not easy and certainly goes far beyond the scope of this work, but it may
269 inspire further research. However, we can speculate on possible scenarios. Maps showing the
270 maximum range of ice cover in the Baltic Sea show clearly that when the northern Baltic, i.e.
271 the Gulf of Bothnia and the Gulf of Finland, is completely frozen over, the entire Pomeranian
272 Bay (SW Baltic) (see the map – Fig.1) together with the ORE is also covered with ice
273 (Finnish Meteorological Institute 2017). These areas freeze over quickly because of their
274 shallowness and low salinity, the latter being due to the considerable influence of fresh water
275 from the Odra river basin. Consequently, during harsh winters, birds from northern Baltic
276 move to the south and west, but they by-pass our study area as it is covered by ice. Under
277 such circumstances there may sometimes be better conditions for waterbirds in areas farther
278 north, e.g. the southern coast of Sweden, where there is no ice cover (Finnish Meteorological
279 Institute 2017). Worth noting here, however, is that such cold weather causing the entire
280 Pomeranian Bay and Odra River Estuary to freeze over is rare and becoming rarer (EEA
281 2017). Nevertheless, if we consider the impact of ice cover of the whole Baltic within species,
282 we can see differences between them and the non-significant impact of this phenomenon on
283 e.g. Smew and Goosander, which corresponds with the local results (Fig. 2).

284 The global temperature has risen about 1°C over the last 130 years, and Northern
285 Hemisphere temperatures of the last 30 years have been the highest in over 800 years (Stocker
286 et al. 2013). The extent and duration of ice cover in the Baltic have decreased on average by
287 50% over the last 36 years (Schröder 2015). There is evidence that the range and occurrence
288 of migratory birds have changed in response to climate change and that some species have
289 shortened their migratory movements by wintering closer to their breeding areas (Musil et al.
290 2011; Lehikoinen et al. 2013; Pavon-Jordan et al. 2015; Meller 2016). Assuming continued

291 climate warming, the negative correlation between numbers of benthic feeding birds and the
292 number of days with ice cover indicates that the ORE is becoming more important for this
293 group of birds. Climate change seems to be the primary reason for increases (in the study
294 area) in numbers of Scaup and Tufted Duck and decreases in numbers of Smew; this
295 corresponds with the findings of Lehtikoinen et al. (2013) in the case of Tufted Duck and of
296 Pavón-Jordan et al. (2015) in the case of Smew. Our results are important for conservation
297 planning. Declines in the populations of species such as Scaup and Tufted Duck, even though
298 the importance of our study area to these species is increasing, but at the same time there is an
299 increase in exposure to locally emerging threats. The biggest threats to these species in the
300 area include fishery bycatches (Žydelis et al. 2009; Bellebaum et al. 2012). The ecology of
301 diving ducks makes this type of threat responsible for the extra mortality of all species
302 covered by this study. Comparison of a species' estimated total population numbers (Nagy et
303 al. 2014) with numbers for the ORE is interesting, since local trends and European trends do
304 not always concur. The different responses of particular species to the factors investigated are
305 also worth examining. We grouped the species by trends in the study area and discuss these
306 for each species below.

307 *Species with increasing population index in the study area*

308 Between the late 1980s and 2012, the population of Scaup wintering in northern and
309 western Europe declined at an annual rate of 3.57%/year (Nagy et al. 2014). Around 41% of
310 the Scaup from this population spent the winter in the Baltic Sea region (Skov et al. 2011),
311 and this, in turn, declined by 60% from 1991 to 2010 (Aunins et al. 2013). At the same time
312 we found that the importance of the ORE for this species was increasing. Scaup numbers
313 increased by 300% in the Szczecin Lagoon (the biggest part of Odra River Estuary – see the
314 map – Fig. 1) and the eastern coastal areas of Germany, as opposed to declines further west
315 along the German coast, where some areas (Wismar Bay and Travelförde) had fewer birds

316 than 15 years earlier (Skov et al. 2011). A similar trend was found in Sweden, where the
317 number of wintering Scaup increased between 1971 and 2015 (Nilsson and Haas 2016). But
318 farther west, in the Netherlands, Hornman et al. (2012) recorded decreases at the most
319 important wintering sites since 1980/1981. All of these studies confirm that Scaup is shifting
320 its wintering range northwards and eastwards, closer to its breeding areas: this is the reason
321 for the heightened importance to this species of the ORE, even as its overall population
322 wintering in northern and western Europe is declining.

323 Tufted Duck populations wintering in north-western Europe have recently been
324 decreasing by 0.98%/year (Nagy et al. 2014). Lehtikoinen et al. (2013) showed that the
325 population estimated for the North-West Europe flyway remained relatively stable between
326 1987 and 2009, a situation confirmed by Wetlands International (2016). In the Baltic Sea
327 region, too, there were no significant changes in numbers between 1991 and 2010 (Aunins et
328 al 2013). We have found that our study area has increased in importance for this species,
329 although not to the same extent as for Scaup. By comparison, Nilsson and Haas (2016)
330 showed Swedish populations to have increased between 1971 and 2015, and Lehtikoinen et al.
331 (2013) reported a rapid increase in the last three decades for Finland. Tufted Ducks in the
332 ORE behave in the same way as Scaup in that they form mixed flocks consuming the same
333 type of food (Marchowski et al. 2016). At a larger scale, Tufted Ducks have a different
334 migration and wintering strategy: Scaup concentrate in a few hot spots, moving jump-wise
335 between them, whereas the distribution of Tufted Ducks is more diffuse (van Erden and de
336 Leeuw 2010; Skov et al. 2011; Carboneras and Kirwan 2016a; Carboneras and Kirwan
337 2016b). This could cause Tufted Ducks to disperse to smaller water bodies outside our study
338 area, e.g. the numerous lakes in the Pomeranian Lake District in northern Poland (~34 000
339 km²), whereas Scaup remain almost exclusively in the ORE (e.g. Marchowski and Ławicki
340 2011; Marchowski et al. 2013). The results of the Wintering Waterbird Monitoring

341 programme also show the greater prevalence in Poland of Tufted Duck (29.5%) than Scaup
342 (7.8%) (Neubauer et al. 2015). Scaup is known to concentrate in big flocks during migration
343 and wintering, and the whole biogeographic population may be concentrated in a few hot-
344 spots such the ORE (Marchowski et al. 2015): this is important in the context of species
345 conservation planning. We have shown an increase in the importance of ORE for Scaup, but
346 at the same time there is an increase in exposure to locally emerging threats such as bycatches
347 in fishing nets (Bellebaum et al. 2012). Taking into account the above pattern of Scaup
348 behaviour and our results, there is a justified fear that locally operating threats in the ORE
349 may affect the entire biogeographic population of the species. This is one of the most
350 important messages of our work.

351 ***Species with decreasing population index in the study area***

352 Pochard populations from north-east / north-west Europe have declined rapidly at an
353 annual rate of 3.35%/year (Nagy et al. 2014). Pochard numbers in the Baltic Sea region also
354 declined by 70% between 1991 and 2010 (Aunins et al. 2013). In 1995 there were an
355 estimated 300 000 Pochard in the north-east/north-west European population (Delany et al.
356 1999). With a constant decline of 3.35%/year, the total population should now be less than
357 150 000 (Nagy et al. 2014). Numbers of Pochard were expected to be higher in the ORE
358 because of the reduced ice cover. However, we found a significant reduction in the
359 importance of the estuary to this species (Table 3), corresponding with its global decline
360 (Aunins et al. 2013; Nagy et al. 2014; Wetlands International 2016). Pochard behaves more
361 like Tufted Duck than Scaup over winter in being more dispersed and occurring on smaller
362 bodies of water (e.g. Marchowski and Ławicki 2011; Marchowski et al. 2013; Neubauer et al.
363 2015). This implies that individuals may also be wintering outside the study area, e.g. on the
364 numerous water bodies of the Pomeranian Lake District, like Tufted Duck. This local decline,

365 however, seems to be driven by the species' global decline, despite the emergence of better
366 conditions for wintering that might favour population growth.

367 Smew populations wintering in northern, western and central Europe increased at
368 1.97%/year between the late 1980s and 2012 (Nagy et al. 2014); in the Baltic Sea region
369 numbers increased by 30% between 1991 and 2010 (Aunins et al. 2013). Although Smew
370 cannot be classified as a piscivore in the same way as Goosander (and Red-breasted
371 Merganser), it does feed on very small fish and on small invertebrates (Carboneras & Kirwan
372 2016 c). Though more dependent on shallow water than Goosander, Smew generally forages
373 on mobile types of food. So even if shallow waters freeze over, it may remain on site and
374 search for food in deeper water, which is what we have observed. We found that nowadays,
375 the ORE is of less importance to Smew (Table 3). This statement is underpinned by the
376 northward and eastward shift in wintering area boundaries due to climate warming, as already
377 demonstrated by Pavon-Jordan et al. (2015). Confirmation of this process is provided by the
378 significant increase in numbers of Smew in 1971-2015 in places to the north of our study
379 area, in Sweden (Nilsson and Haas 2016).

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

381 Coot populations wintering in north-west Europe increased by 0.19%/year between the
382 late 1980s and 2012 (Nagy et al. 2014), but in the Baltic region there was a 60% decline
383 between 1991 and 2010 (Aunins et al. 2013). We have found no changes in Coot numbers in
384 the ORE over the last 25 years (Table 3). Likewise, no changes in numbers were recorded
385 between 1975 and 2010 at wintering sites in warmer areas to the south-west (the Netherlands)
386 (Hornman et al. 2012). Long-term figures for Sweden (1971-2015), while not revealing any
387 distinct increase, do show that Coot populations fluctuated, rising during mild periods and
388 falling during cold periods (Nilsson and Haas 2016). The expected increase in numbers due to
389 improvements in habitat quality did not happen. Factors such as pressure from American

390 mink *Neovison vison*, which are responsible for the decline of Coot in many places (e.g.
391 Ferreras and Macdonald 1999), may have held back potential increases. Moreover, compared
392 to the bottom-diving ducks, Coot is more sensitive to cold weather: a study by Fredrickson
393 (1969) demonstrated high mortality after periods of severe weather (also reflected in the
394 results of Swedish breeding bird surveys – Leif Nilsson pers. com.) but that the population
395 recovered during mild winters. This factor may also be the reason for the different reactions of
396 Coot and diving ducks to the cold.

397 Goldeneye populations wintering in north-west and central Europe increased at
398 0.26%/year between the late 1980s and 2012 (Nagy et al. 2014) and increased in the Baltic
399 Sea region by 50% between 1991 and 2010 (Aunins et al. 2013). This corresponds to the data
400 provided by Lehikoinen et al (2013), which show an increase in numbers in the northern
401 Baltic wintering area (Finland and N Sweden), but a decline in the southern part of its
402 wintering range (Switzerland, France). In our work we found the relative number of
403 Goldeneye in the ORE to be stable in the period 1992-2016 (Table 3). This again tallies with
404 the findings of Lehikoinen et al. (2013) that duck abundances are independent of temperature
405 in the central part of the flyway. This is probably why the shift in wintering range is not
406 perceptible in our study area but is more pronounced at other, e.g. Swedish wintering sites,
407 where numbers have increased (Nilsson and Haas 2016) but not in the Netherlands, where
408 they have declined (Hornman et al. 2012).

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

415 wintering range as a result of climate warming (Hornman et al. 2012; Lehtikoinen et al. 2013;
416 Nilsson and Haas 2016).

417 **Conclusion**

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

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

687 (1) Target species. (2) Functional group: B – benthivores, P – piscivores. (3) Estimated number of
688 individuals from biogeographic population in 1992, the numbers are presented in thousands. (4)
689 Estimated number of individuals from biogeographic population in 2012, the numbers are presented in
690 thousands. (5) Population trend % per annum - long term assessment. (6) Significances of changes.
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Species (1)	Functional group (2)	Number of individuals (1992) (3)	Number of individuals (2012) (4)	Population trend % p.a. (5)	Significance of changes (6)
Greater Scaup	B	300	150	-3.57	Large decline
Common Pochard	B	280	150	-3.35	Large decline
Tufted Duck	B	1,100	820	-0.98	Large decline
Goosander	P	130	100	-0.09	Stable
Eurasian Coot	B	990	950	+0.19	Moderate increase
Common Goldeneye	B	210	240	+0.26	Moderate increase
Smew	P	13	24	+1.97	Large increase

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718 Table 2. Results of general linear mixed models for seven species showing the influence of ice cover,
 719 maximum ice extent [km²] in the Baltic Sea (max ice) and season on the percentage of occurrence of
 720 benthivores (denoted by B, Scaup, Tufted Duck, Pochard, Goldeneye, Coot) and piscivores (denoted
 721 by P, Smew, Goosander) in the Odra River Estuary. Species, method and month were treated as
 722 random effects in relation to their regional breeding populations.

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		

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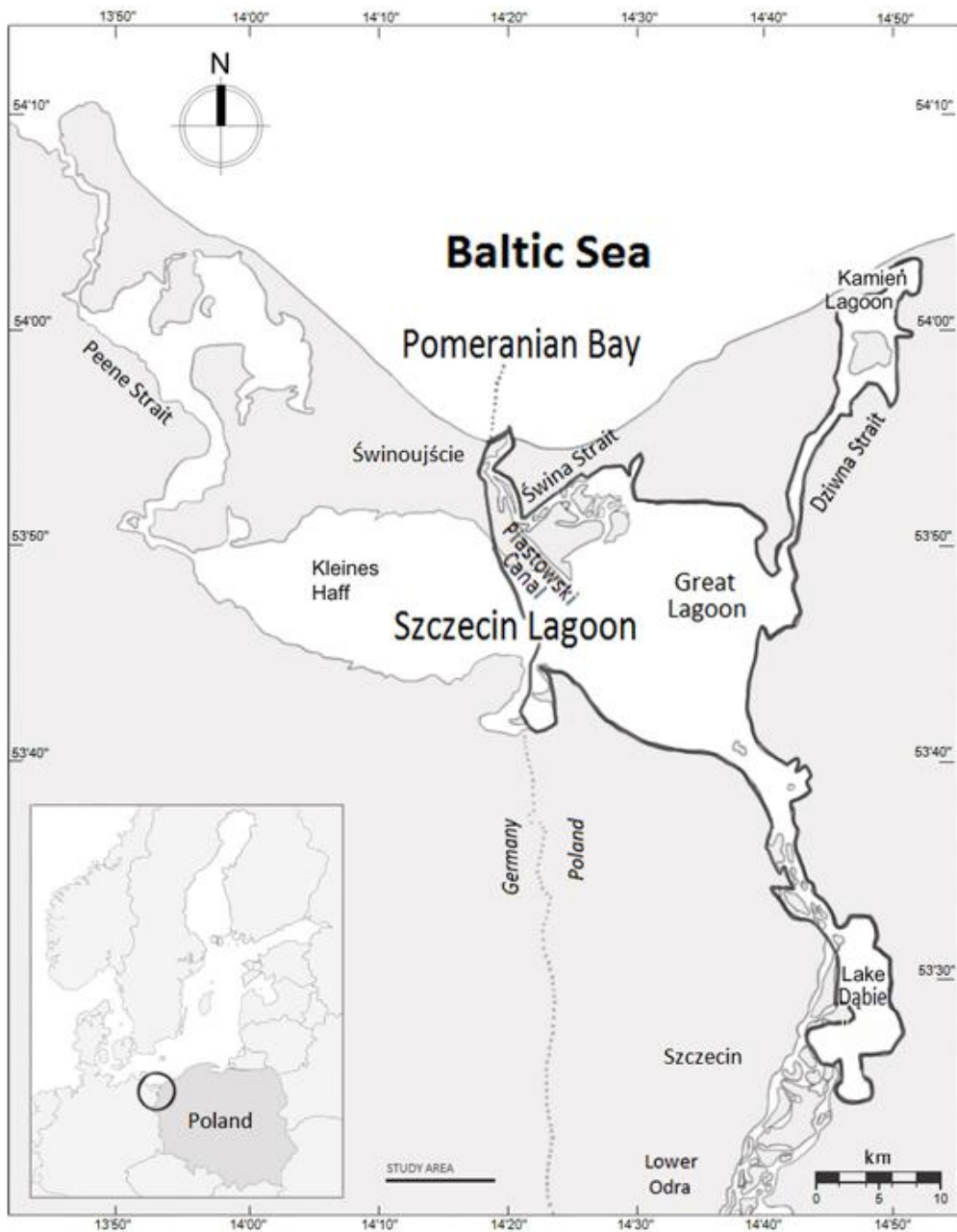
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729 Table 3. Population index trends in the Odra River Estuary (ORE) for the biogeographic population
 730 (b.p.) of diving waterbirds showing the percentage of the biogeographic population in 1992; the
 731 percentage of the biogeographic population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

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

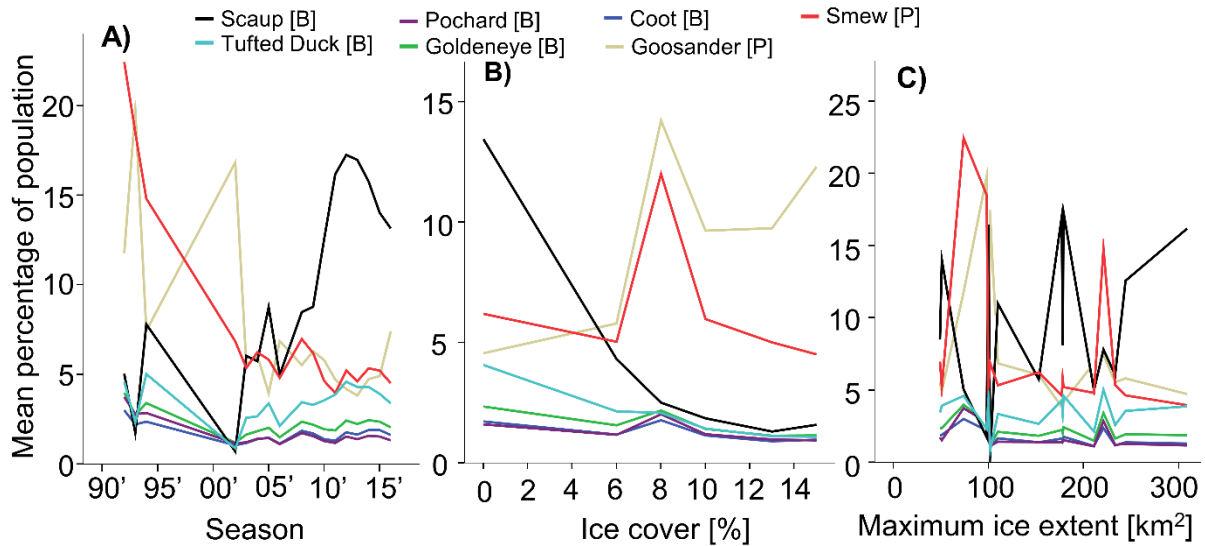
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769 Figure 1. The Odra River Estuary, north-western Poland.



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783 Figure 2 A-C. Predicted results of the general linear mixed model showing the influence of season, ice
784 cover and maximum ice extent [km²] in the Baltic Sea (max ice) on the percentage of the population of
785 the target species in the Odra River Estuary. The predicted values were obtained from the model
786 where we added species as a fixed variable. The model's parameters are listed in Table S1 in the
787 Supplementary material.



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