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

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

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Abstract

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22 migration. The Odra River Estuary in the Baltic Sea is important for wintering waterfowl and is

23 where we investigated how waterbirds respond to freezing surface waters. The most abundant

24 birds here comprise two ecological groups: bottom-feeders and piscivores. Numbers of all

25 bottom-feeders, but not piscivores, were negatively correlated with the presence of ice. With

26 ongoing global warming, this area is increasing in importance for bottom-feeders and decreasing

27 for piscivores. The maximum range of ice cover in the Baltic Sea has a weak and negative effect

28 on both groups of birds. Five of the seven target species are bottom-feeders (Greater Scaup

29 *Aythya marila*, Tufted Duck *A. fuligula*, Common Pochard *A. ferina*, Common Goldeneye

30 *Bucephala clangula* and Eurasian Coot *Fulica atra*), and two are piscivores (Smew *Mergellus*

31 *albellus* and Goosander *Mergus merganser*). Local changes at the level of particular species vary

32 for different reasons. A local decline of the Common Pochard may simply be a consequence of

33 its global decline. Climate change is responsible for some of the local changes in the study area,

34 disproportionately favoring some duck species while being detrimental to others.

Introduction

36 Migration distance has declined in several species of aquatic (and other) birds as a result

37 of climate change (Musil et al. 2011; Lehikoinen et al. 2013; Meller 2016). The distances that

38 birds migrate from their breeding areas in northern and eastern Europe to their central European

39 wintering areas are shorter during mild winters (Lehikoinen et al. 2013; Pavón-Jordan et al.

40 2015); conversely birds may change their wintering sites to warmer regions during colder

41   periods because they may perceive local manifestations of larger scale weather (Newton 2008).

42   Reducing migration distance can provide several benefits associated with earlier arrival at the

43   breeding grounds and greater survival (Coppack and Both 2002; Jankowiak et al. 2015a; 2015b).

44   Food resources of wintering sites may also influence migration decisions (Cresswell 2014;

45   Aharon-Rotman et al. 2016). Although winter site fidelity is usually very strong among

46   waterfowl (Newton 2008), this can change in response to weather, habitat, and competition

47   (Cresswell 2014). Changing winter sites may often be a trade-off between the costs of finding a

48   new site and the benefits it offers (Aharon-Rotman et al. 2016). At sub-zero temperatures,

49   shallow waters freeze over; forcing birds to expend more time and energy searching for food in

50   deeper, open waters. Three functional groups of waterbirds forage in the shallow waters of

51   offshore lagoons: piscivores, herbivores and bottom-feeders, for example, large numbers of

52   waterbirds gather to forage in the Odra River Estuary (hereafter ORE) (Marchowski et al. 2015;

53   Marchowski et al. 2016). Two groups of waterbirds – bottom-feeders and piscivores – are among

54   those most commonly wintering here. During winter, the study area is subject to wide variation

55   in temperatures, often making surface waters subject to freezing (van Erden and de Leeuw 2010).

56   Yet even relatively small variations in temperature, causing ice cover to form or disappear, can

57   lead to the displacement of waterbirds. Changes in abundance and community structure of birds

58   in the ORE may reflect the impact of climate change. Analysis of the dates of the appearance of

59   ice-related phenomena in the Szczecin Lagoon and of their frequency over time reveals a distinct

60   pattern illustrating recently observed trends in climate warming (Girjatowicz 2011). In this

61   paper, we are looking for how the abundance of some species in the ORE changes due to climate

62   warming. We are investigating whether climate change will differentially influence foraging

63   patterns, and consequently overwintering patterns, of these two groups of birds. Thus, increasing

64 temperatures due to climate change, and the shorter time interval with ice cover will result in

65 increasing numbers of bottom-feeders because they will then migrate shorter distances. Frosts in

66 the study area are never so severe that the water freezes completely to the bottom even in the

67 shallows. But even if ice does cover the surface of shallow water bottom-feeders have no access

68 to food and have to move to warmer areas because feeding areas where sedentary mussels are

69 abundant tend to be in shallow waters (Marchowski et al. 2015). Piscivores, on the other hand,

70 can still feed in such conditions (frozen surface of shallows, unfrozen deeper areas - further from

71 the shore, where there are no mussels but there are fish) and remain in the area, e.g. observation

72 of large aggregations of piscivores during harsh winters (Smew *Mergellus albellus* and

73 Goosander *Mergus merganser*) (Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004; Marchowski

74 and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012; Marchowski et al.

75 2013). This has consequences for conservation management plans in protected areas. Two

76 different groups of birds react differently to climate warming, showing different patterns of

77 moving closer to their breeding grounds, as a consequence in our area should be more bottom-

78 feeders. Thus, changes in the importance of wintering ground due to changing surface-water

79 freezing patterns expected under global warming regimes are likely to have important

80 consequences for very large numbers of these birds.

81 **Study area**

82   The study area in the south-western Baltic Sea forms the Polish part of the Odra River

83 Estuary system, which includes the Great Lagoon (the Polish part of the Szczecin Lagoon),

84 Świna Backward Delta, Kamień Lagoon, Dziwna Strait and Lake Dąbie (522.58 km2, Fig. 1).

85 The area comprises four interconnected Important Bird Areas (IBA) and also a Natura 2000 area

86 (Wilk et al. 2010). The average and maximum depths of the estuary are 3.8 and 8.5 m,

87   respectively; the dredged shipping lane passing through the estuary from the Baltic Sea to the

88   port of Szczecin is 10.5 m deep (Radziejewska and Schernewski 2008). Waters of the Szczecin

89   Lagoon, Kamień Lagoon, and Lake Dąbie are brackish. Salinity in the central part of the estuary

90   varies from 0.3 psu to 4.5 psu (mean = 1.4 psu) and declines with increasing distance from the

91   sea (Radziejewska and Schernewski 2008). Average winter temperature is 0.3° C (Weatherbase

92   2016). The ORE is subject to high levels of eutrophication (Radziejewska and Schernewski

93   2008). Communities of benthic organisms are typical of freshwater bodies, and the fauna

94   includes large populations of zebra mussels Dreissena polymorpha, which was introduced in the

95   mid-19th century. By the 1960s, the biomass of zebra mussels in the Szczecin (Great) Lagoon

96   was estimated at 110 000 metric tons (Wiktor 1969, Wolnomiejski and Woźniczka 2008). The

97   distribution of the zebra mussel is extremely uneven (see the map in Marchowski et al. 2015).

98   The average density of the zebra mussel in the ORE is 0.18 kg /m², but the vast majority

99   occupies around 10% of the area, where the mean density is 2.05 kg/m² (Stańczykowska et al.

100 2010). Fish are mainly freshwater species such as roach *Rutilus rutilus*, bream *Abramis brama*,

101 pike *Esox lucius*, perch *Perca fluviatilis* and ruff *Gymnocephalus cernua*; there are also

102 anadromous fish including smelt *Osmerus eperlanus* and occasionally herring *Clupea harengus*

103 among others (Wolnomiejski and Witek 2013).

104 **Methods**

105 ***Bird censusing***

106   The study covers two functional groups of waterbirds: bottom-feeders (diving birds,

107 feeding on motionless type of food – mussels) –   Greater Scaup (*Aythya marila* – hereafter

108 Scaup), Tufted Duck (*A. fuligula*), Common Pochard (*A. ferina* – hereafter Pochard), Common

109 Goldeneye (*Bucephala clangula* – hereafter Goldeneye) and Eurasian Coot (*Fulica atra* –

110   hereafter Coot); piscivores (diving birds, feeding on mobile type of food – fish) – Smew and

111   Goosander (Stempniewicz 1974; Johansgard 1978). Six of our target species belong to the order:

112   Anseriformes, family: Anatidae, subfamily: Anatinae and Tribe: Mergini (Goldeneye, Smew and

113   Goosander), Tribe: Aythyini (Scaup, Pochard and Tufted Duck); one species – Coot belongs to

114   the order: Gruiformes, family: Rallidae (del Hoyo and Collar 2014). Although Coot is not closely

115   related to the rest of our species, we included it into a common group of waterbirds and, due to

116   its behavior and ecology, to the bottom-feeders group (Stempniewicz 1974). These seven species

117   are usually very abundant in the study area (Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004;

118   Wilk et al. 2010; Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki

119   2012; Marchowski et al. 2013). These are important gathering areas for populations of these

120   birds associated with regional migration flyways. These subpopulations (hereafter regional or

121   flyway populations) are: Pochard – north-east Europe / north-west Europe; Tufted Duck – north-

122   west Europe (wintering); Scaup – northern Europe / western Europe; Goldeneye – north-west

123   and central Europe; Smew – north-west and central Europe (wintering); Goosander – north-west

124   and central Europe (wintering); Coot – north-west Europe (wintering) (Wetlands International

125   2016).

126   Censuses were conducted using standard methods for non-breeding season waterbirds

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. Three censuses were carried out per season in

130   November, January, and March or April; there was one midwinter count in January in

131   2001/2002. Altogether we analyzed the results of 44 counts. Most counts were done on foot.

132   Each observer was equipped with 10x binoculars and tripod-mounted spotting scopes. Observers

133 walked along the same routes, and the same counting method was used during every census

134 every year. Additionally, fourteen aerial counts were made at an average speed of about 100

135 km/h and an altitude of about 80 m above the water (see supplementary materials – S1 Table for

136 the method of data collection: aerial or ground). In the early 1990s, counts were aerial, whereas

137 in 2009-2015 parallel aerial and ground counts were carried out (to compare methods). In ice-

138 free conditions, the species covered in this study can be assigned to a group with just a small

139 error between methods (<6%), one species – Coot had a moderate error (16%), the ground

140 method estimated greater numbers than the aerial one. During periods with more than 70% ice

141 cover, abundance estimated from the air was greater than that estimated from the ground

142 (Dominik Marchowski pers. com.). Count method was treated as a random effect in the model.

143 The detailed methodology and results of the counts are given elsewhere (Meissner and

144 Kozakiewicz 1992; Meissner et al 1994; Kaliciuk et al. 2003; Czeraszkiewicz et al. 2004;

145 Marchowski and Ławicki 2011; Guentzel et al. 2012; Marchowski and Ławicki 2012;

146 Marchowski et al. 2013). Where large numbers of unidentified Aythya species were counted – 26

147 000 ducks in November 2009, 13 000 in November 2010, 6 000 in January 2012, 3 300 in March

148 2012 and 13 500 in November 2015 – they were estimated to be in the ratio of 1:0.8

149 (scaup:tufted) based on observations in other studies. Observations were always at a distance that

150 does not disturb the birds in any way, and in Poland, this research required no ethical or

151 scientific permits.

152 ***Statistical analysis***

153 Absolute numbers of birds can vary widely and independently, and so the proportion of

154 the local population size (in our study area) in relation to flyway population for each species was

155 used as our dependent variable (Nagy et al. 2014; Wetland International 2016). Thus, if we used

156   the trend of absolute numbers in our area, the resulting error would be the larger, the greater the

157   changes in the size of the flyway population. Therefore, we indicate the numbers of a species by

158   means of a coefficient calculated as the percentage of the flyway population present in the study

159   area during a particular count. We obtained the regional population size estimates from 1992 to

160   2012 from Nagy et al. (2014); for the period 2013-2016, we used the flat trend calculated by

161   Nagy et al. (2014) (Table 1). Initially, we placed the different species in ecological groups. The

162   bottom-feeders (denoted by B) included Scaup, Tufted Duck, Pochard, Goldeneye and Coot, and

163   the piscivores (P) contained Smew and Goosander. We used the minimum temperatures

164   averaged over the 15 days leading up to the count day. The climate data were obtained from the

165   Szczecin weather station (53.395 N, 14.6225 E, http://tutiempo.net). Another climate covariate

166   was ice cover in the study area; data relating to this were published by the Polish Institute of

167   Meteorology and Water Management. These data are from the observation point at Miroszewo

168   on the shore of the Szczecin Lagoon (53.734 N, 14.331 E, http://www.imgw.pl/). We compared

169   the number of days with 100% ice cover in the period from 0 to 15 days prior to the bird counts.

170   The ice cover of 100% refers specifically to the Miroszewo observation point. This estimate is a

171   good approximation for the region. In practice, however, the ORE is never completely covered

172   by ice (Girjatowicz 1991; 2005; see the Discussion for an explanation) and birds are still present

173   in such conditions. We also utilized the maximum ice extent in the Baltic Sea (max ice; data

174   obtained from the website of The European Environment Agency; EEA 2017). Apart from

175   climatic variables, we also tested the changes in species occurrence during the survey years, so

176   we used the season as a covariate. Prior to the final analysis, we checked multicollinearity

177   between the above variables using the variation inflation factor (VIF). VIFs of all variables were

178   in acceptable limits, minimum temperatures (VIF = 2.1), max ice (VIF = 1.03), ice cover (VIF =

179 2.07) and season (VIF = 1.04). However, we found a moderate linear significant relationship

180 between minimum temperature and ice cover (r = 0.52, p < 0.001) and after exclusion of minimal

181 temperature VIF showed no multicollinearity issue between variables – ice cover (VIF = 1.04),

182 max ice (VIF = 1.03), season (VIF = 1.03) – and these were used in the subsequent analyses.

183 Frozen water by definition impedes bottom-feeding duck foraging, we are testing whether that

184 pattern is changing in association with climate change. We used a general linear mixed model

185 (GLMM) to test above-described relationship. The percentage of the flyway population present

186 in the study area, estimated by species, was used as a target variable using the normal

187 distribution response distribution and identity link function. Mixed models permitted repetition

188 across survey months, methods (aerial and ground counts) and species (random intercept). Thus,

189 to test our assumptions we included the following interactions: feeding group*season, feeding

190 group*ice cover and feeding group*max ice. Selection of the best model structure for the

191 dependent variable was based on the Akaike information criterion (AIC) (Zuur et al. 2009). All

192 possible models were carried out (they are listed in Table S1 in Supplementary material). As the

193 final models, we assumed those in which ΔAIC < 2 (Burnham & Anderson 2002) and in our

194 case, it was only a general model with all the tested variables. To test the relationship between

195 explanatory variables and particular species abundance we performed for each species GLMM

196 model, where random effects were month and method. We checked also the relationship between

197 winter year and ice cover using a generalized linear model with negative binomial error

198 distribution. We used IBM SPSS Statistic version 20 software for the statistical analysis. P <

199 0.05 was considered statistically significant.

200 **Results**

201   Bellow, we present the results of our analyzes, the main one jointly examines two whole

202  groups - piscivores and bottom-feeders and the second one where each species were analyzed.

203  Bird numbers by feeding group were different in their relationships with ice cover, bottom-

204  feeding species in the study area were more sensitive to lower temperatures and left sooner when

205  colder weather increased ice cover, whereas numbers of piscivorous species had a higher

206  tolerance to the extent of ice cover (Table 2). Interactions between feeding group and season,

207  feeding group and ice cover, and feeding group and maximum ice extent on the Baltic sea were

208  all important (Table 2). However, the strongest effects were interactions with ice cover, then

209  interaction with the season, this translates into increases in the importance of the site for bottom-

210  feeders. The effect of maximum ice extent was very small (Table 2). Population indices in the

211  ORE changed over the last 25 years, increased in the case of bottom-feeding species but

212  decreased for piscivorous species (Table 2). Ice cover across the whole Baltic Sea had the same,

213  though weak, impact on both functional groups of birds, numbers of birds in the ORE declined

214  with expanding ice cover in the Baltic (Table 2).

215   Where particular species are concerned, the situation is more complex. The population

216  indices of Scaup and Tufted Duck in the ORE exhibited an increasing trend

217  (β_{Scaup}=0.026±0.010s.e.,p=0.011; however for Tufted Duck marginally insignificant

218  β=0.008±0.004 s.e.,p=0.058), despite the general decline in their entire northern and western

219  European populations; numbers of both species in the ORE were adversely affected by ice cover

220  in that region (β_{Scaup}=-0.065±0.011s.e.,p<0.001; β_{Tufted}=0.032±0.005s.e.,p<0.001) but not by ice

221  cover in the whole Baltic (β_{Scaup}=-0.099±0.074s.e.,p=0.186; β_{Tufted}=0.010±0.029s.e.,p=0.735).

222  Relative numbers of Pochard in the ORE have declined (β=-0.009±0.003s.e.,p=0.005), but so has

223  the whole northern European population, abundance was negatively impacted by ice cover in

224 both the study area (β=-0.015±0.003s.e.,p<0.001); and in the entire Baltic (β=-

225 0.053±0.023s.e.,p=0.023). For Goldeneye, the index for the ORE population was unchanged (β=-

226 0.004±0.004s.e.,p=0.275), despite the increase in the European population, abundance was

227 negatively impacted by ice cover in the study area (β=-0.016±0.004s.e.,p<0.001), but not by ice

228 cover in the entire Baltic (β=-0.044±0.027s.e.,p=0.107). Relative numbers of Coot in the ORE

229 remained unchanged (β<0.001±0.002s.e.,p=0.915), despite the slight increase in the European

230 population, abundance was negatively impacted by ice cover in both the study area (β=-

231 0.014±0.003s.e.,p<0.001), and in the entire Baltic (β=-0.038±0.016s.e.,p=0.019). The ORE

232 population index for Smew decreased (β=-0.020±0.008s.e.,p=0.024), despite the increase in its

233 flyway population, abundance in the ORE was unaffected by ice cover either in the study area

234 (β=-0.013±0.010s.e.,p=0.183), or in the Baltic as a whole (β=-0.079±0.061s.e.,p=0.204). Finally,

235 relative numbers of Goosander in the ORE remained unchanged (β=-0.005±0.008s.e.,p=0.572),

236 like those of the whole population wintering in north-western and central Europe; abundance in

237 the ORE was unaffected by ice cover either in the study area (β=0.018±0.009s.e.,p=0.063) or in

238 the Baltic as a whole (β=-0.111±0.057s.e.,p=0.057). The details relating to all these species are

239 listed in Table 1, presented in Fig. 2A and Table S3. Table 3 summarizes the changes in the

240 importance of the ORE for wintering populations of diving waterbirds in the last 25 years. There

241 was positive relationship between year and winter ice (beta0=82.011, s.e.=28.49, beta winter=-

242 0.040, s.e.=0.0142, Chi-square=8.001, df=1, p=0.005; Figure 2B).

243

244 **Discussion**

245   The phenomenon of freezing in our study area has decreased over time (Girjatowicz

246 2011, Fig 2 B), so that target birds species should tend to feed more recently more often than in

247 the past. However, two functional groups of waterbirds – bottom-feeders and piscivores – react

248 differently to ice cover, a factor that is directly connected to climate change; this has

249 consequences for the wintering patterns of these species. Bottom-feeding birds (Scaup, Tufted

250 Duck, Pochard, Goldeneye, nd Coot) tend to be more sensitive to ice cover in the study area than

251 piscivores (Smew and Goosander). Piscivores can survive in colder areas, closer to their

252 breeding ranges, but bottom-feeders have to move further south and west. This phenomenon

253 indicates that piscivores are declining in our study site because they are shifting further north and

254 east in order to stay closer to their breeding areas. Bottom-feeders are increasing their number for

255 the same reason – they, too, are moving further north and east – but in their case, he result is a

256 greater number in our study area and a smaller one in areas further west and south. Bottom-

257 feeding birds forage in the ORE mainly on mussels of the genus Dreissena (Marchowski et al.

258 2015, 2016); the highest quality of this food resource is found in water 1-2 m deep

259 (Wolnomiejski and Witek 2013). Shallow water freezes over faster, displacing birds to deeper

260 unfrozen areas where food is accessible only with difficulty. In addition, when ice cover is

261 present, the abundance of food in unfrozen areas declines owing to its greater exploitation,

262 because the birds congregate on a limited area. In the case of piscivorous birds increasing ice

263 cover not affect their numbers negatively. The ORE is never completely covered by ice: the

264 shipping lane between Świnoujście and Szczecin is kept free of ice (Girjatowicz 1991; 2005),

265 and there are always other areas free of ice, especially at the mouths of the small rivers flowing

266 into the estuary. These ice-free areas may still abound in fish and provide food for piscivores. In

267 general, there is growing importance of the study area for the bottom-feeders. The main analysis

268 jointly examines two whole groups – piscivores and bottom-feeders; the results of it are the

269 positive effect of not freezing for bottom-feeders and negative effect for piscivores, and also a

270   positive effect of the season for bottom-feeders, and negative effect for piscivores (see Table 2).

271   In the other analysis, which examined each species separately, there are differences between

272   them (see Fig. 2A). As far as the most numerous species – Scaup and Tufted Duck – are

273   concerned, the results tally with those of the first analysis, i.e. their numbers are increasing

274   (correlation with season). For the less abundant species, the result of the second analysis is

275   different: Pochard numbers, for example, are decreasing (negative effect). In the first analysis,

276   abundance and season were negatively correlated in piscivores. In the second analysis, in which

277   we examined species separately, abundance and season were independent in the Goosander,

278   while abundance and season were negatively correlated in the Smew. In fact, the strongest effect

279   of the first years of the study relates to the piscivores, especially Smew. If we take the entire

280   period (1992 - 2016), the Smew declines in numbers (confer with model results), which was due

281   to their being very abundant in the early 1990s. From 2002 - 2016, Smew numbers are stable.

282   An interesting result is the negative effect of maximum ice cover in the entire Baltic Sea

283   on the numbers of all species in our study. This is unexpected since our study area is in the

284   warmer south-western Baltic, where one would anticipate an increase in the number of

285   waterbirds in such circumstances (Alerstam 1990). The explanation for this relationship is not

286   easy and certainly goes far beyond the scope of this work, but we can speculate on possible

287   scenarios. On maps with the maximum range of ice cover in the Baltic Sea we can see clearly

288   that when the northern Baltic, i.e. the Gulf of Bothnia and the Gulf of Finland, is completely

289   frozen over, the entire Pomeranian Bay (SW Baltic) (see the map – Fig.1) together with the ORE

290   is also covered with ice (Finnish Meteorological Institute 2017). These areas freeze over quickly

291   because of their shallowness and low salinity, the latter being due to the considerable influence

292   of fresh water from the Odra river basin. Consequently, during harsh winters, birds from

293   northern Baltic move to the south and west, but they by-pass our study area as it is covered by

294   ice. Under such circumstances, there may sometimes be better conditions for waterbirds in areas

295   farther north, e.g. the southern coast of Sweden, where there is no ice cover (Finnish

296   Meteorological Institute 2017). Worth noting here, however, is that such cold weather causing

297   the entire Pomeranian Bay and Odra River Estuary to freeze over is rare and becoming rarer

298   (EEA 2017).

299   The global temperature has risen about 1°C over the last 130 years, and Northern

300   Hemisphere temperatures of the last 30 years have been the highest in over 800 years (Stocker et

301   al. 2013). The extent and duration of ice cover in the Baltic have decreased on average by 50%

302   over the last 36 years (Schröder 2015). There is evidence that the range and occurrence of

303   migratory birds have changed in response to climate change and that some species have

304   shortened their migratory movements by wintering closer to their breeding areas (Musil at al.

305   2011; Lehikoinen et al. 2013; Pavon-Jordan et al. 2015; Meller 2016). Assuming continued

306   climate warming, the negative correlation between numbers of bottom-feeding birds and the

307   number of days with ice cover indicates that the ORE is becoming more important for this group

308   of birds. Climate change seems to be the primary reason for increases (in the study area) in

309   numbers of Scaup and Tufted Duck and decreases in numbers of Smew; this corresponds with

310   the findings of Lehikoinen et al. (2013) in the case of Tufted Duck and of Pavón-Jordan et al.

311   (2015) in the case of Smew. Our results are important for conservation planning. Declines in the

312   flyway populations of species such as Scaup and Tufted Duck, even though the importance of

313   our study area to these species is increasing, but at the same time, there is an increase in exposure

314   to locally emerging threats. The biggest threats to these species in the area include fishery

315   bycatches (Žydelis et al. 2009; Bellebaum et al. 2012). The ecology of diving birds makes this

316 type of threat responsible for the extra mortality of all species covered by this study. Comparison

317 of a species' estimated total population numbers (Nagy et al. 2014) with numbers for the ORE is

318 interesting, since local trends and European trends do not always concur. The different responses

319 of particular species to the factors investigated are also worth examining. We grouped the

320 species by trends in the study area and discuss these for each species below.

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

322 Between the late 1980s and 2012, the population of Scaup wintering in northern and

323 western Europe declined at an annual rate of 3.57%/year (Nagy et al. 2014). Around 41% of the

324 Scaup from this population spent the winter in the Baltic Sea region (Skov et al. 2011), and this,

325 in turn, declined by 60% from 1991 to 2010 (Aunins et al. 2013). At the same time, we found

326 that the importance of the ORE for this species was increasing. Scaup numbers increased by

327 300% in the Szczecin Lagoon (the biggest part of Odra River Estuary – see the map – Fig. 1) and

328 the eastern coastal areas of Germany, as opposed to declines further west along the German

329 coast, where some areas (Wismar Bay and Traveförde) had fewer birds than 15 years earlier

330 (Skov et al. 2011). A similar trend was found in Sweden, where the number of wintering Scaup

331 increased between 1971 and 2015 (Nilsson and Haas 2016). But farther west, in the Netherlands,

332 Hornman et al. (2012) recorded decreases at the most important wintering sites since 1980/1981.

333 All of these studies confirm that Scaup is shifting its wintering range northwards and eastwards,

334 closer to its breeding areas: this is the reason for the heightened importance to this species of the

335 ORE, even as its overall population wintering in northern and western Europe is declining.

336 Tufted Duck populations wintering in north-western Europe have recently been

337 decreasing by 0.98%/year (Nagy et al. 2014). The population estimated for the North-West

338 Europe flyway remained relatively stable between 1987 and 2009 (Lehikoinen et al. 2013), a

339 situation confirmed by Wetlands International (2016). In the Baltic Sea region, too, there were

340 no significant changes in numbers between 1991 and 2010 (Aunins et al 2013). We have found

341 that our study area has increased in importance for this species, although not to the same extent

342 as for Scaup. Swedish populations, by comparison, have increased between 1971 and 2015

343 (Nilsson and Haas 2016), and Lehikoinen et al. (2013) reported a rapid increase in the last three

344 decades for Finland. Tufted Ducks in the ORE behave in the same way as Scaup in that they

345 form mixed flocks consuming the same type of food (Marchowski et al. 2016). At a larger scale,

346 Tufted Ducks have a different migration and wintering strategy: Scaup concentrate in a few hot

347 spots, moving jump-wise between them, whereas the distribution of Tufted Ducks is more

348 diffuse (van Erden and de Leeuw 2010; Skov et al. 2011; Neubauer et al. 2015; Carboneras and

349 Kirwan 2016a; Carboneras and Kirwan 2016b). This could cause Tufted Ducks to disperse to

350 smaller water bodies outside our study area, e.g. the numerous lakes in the Pomeranian Lake

351 District in northern Poland (~34 000 km²), whereas Scaup remains almost exclusively in the

352 ORE (e.g. Marchowski and Ławicki 2011; Marchowski et al. 2013). Scaup is known to

353 concentrate in big flocks during migration and wintering, and the whole flyway population may

354 be concentrated in a few hot-spots such the ORE (Marchowski et al. 2015): this is important in

355 the context of species conservation planning. There is an increase in the importance of the ORE

356 for Scaup, but at the same time, there is an increase in exposure to locally emerging threats such

357 as bycatches in fishing nets (Bellebaum et al. 2012). Taking into account the above pattern of

358 Scaup behavior and our results, there is a justified fear that locally operating threats in the ORE

359 may affect the entire flyway population of the species. This is one of the most important

360 messages of our work.

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

362   Pochard populations from north-east/north-west Europe have declined rapidly at an

363   annual rate of 3.35%/year (Nagy et al. 2014). Pochard numbers in the Baltic Sea region also

364   declined by 70% between 1991 and 2010 (Aunins et al. 2013). In 1995 there were an estimated

365   300 000 Pochard in the north-east/north-west European population (Delany et al. 1999). With a

366   constant decline of 3.35%/year, the total population should now be less than 150 000 (Nagy et al.

367   2014). Numbers of Pochard were expected to be higher in the ORE because of the reduced ice

368   cover. However, we found a reduction in the importance of the estuary to this species (Table 3),

369   corresponding with its global decline (Aunins et al. 2013; Nagy et al. 2014; Wetlands

370   International 2016). Pochard behaves more like Tufted Duck than Scaup over winter in being

371   more dispersed and occurring on smaller bodies of water (e.g. Marchowski and Ławicki 2011;

372   Marchowski et al. 2013; Neubauer et al. 2015). This implies that individuals may also be

373   wintering outside the study area, e.g. on the numerous water bodies of the Pomeranian Lake

374   District, like Tufted Duck. This local decline, however, seems to be driven by the species' global

375   decline, despite the emergence of better conditions for wintering that might favor population

376   growth.

377   Smew populations wintering in northern, western and central Europe increased at

378   1.97%/year between the late 1980s and 2012 (Nagy et al. 2014); in the Baltic Sea region

379   numbers increased by 30% between 1991 and 2010 (Aunins et al. 2013). Although Smew cannot

380   be classified as a piscivore in the same way as Goosander (and Red-breasted Merganser M.

381   serrator), it does feed on very small fish and on small invertebrates (Carboneras and Kirwan

382   2016 c). Though more dependent on shallow water than Goosander, Smew generally forages on

383   mobile types of food. So even if shallow waters freeze over, it may remain on site and search for

384 food in deeper water, which is what we have observed. We found that today, the ORE is of less

385 importance to Smew (Table 3) as illustrated by the northward and eastward shift in wintering

386 area boundaries due to climate warming (Pavon-Jordan et al. 2015; Nilsson and Haas 2016).

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

388 Coot populations wintering in north-west Europe increased by 0.19%/year between the

389 late 1980s and 2012 (Nagy et al. 2014), but in the Baltic region, there was a 60% decline

390 between 1991 and 2010 (Aunins et al. 2013). We have found no changes in Coot numbers in the

391 ORE over the last 25 years (Table 3). Likewise, no changes in numbers were recorded between

392 1975 and 2010 at wintering sites in warmer areas to the south-west (the Netherlands) (Hornman

393 et al. 2012). Long-term figures for Sweden (1971-2015), while not revealing any distinct

394 increase, do show that Coot populations fluctuated, rising during mild periods and falling during

395 cold periods (Nilsson and Haas 2016). The expected increase in numbers due to improvements in

396 habitat quality did not happen. Factors such as pressure from American mink *Neovison vison*,

397 which is responsible for the decline of Coot in many places (e.g. Ferreras and Macdonald 1999),

398 may have held back potential increases. Moreover, compared to the bottom-diving Ducks, Coot

399 is more sensitive to cold weather: a study by Fredrickson (1969) demonstrated high mortality

400 after periods of severe weather (also reflected in the results of Swedish breeding bird surveys –

401 Leif Nilsson pers. com.) but that the population recovered during mild winters. This factor may

402 also be the reason for the different reactions of Coot and diving ducks to the cold.

403 Goldeneye populations wintering in north-west and central Europe increased at

404 0.26%/year between the late 1980s and 2012 (Nagy et al. 2014) and increased in the Baltic Sea

405 region by 50% between 1991 and 2010 (Aunins et al. 2013). This corresponds to the data

406 provided by Lehikoinen et al (2013), an increase in numbers in the northern Baltic wintering area

407 (Finland and N Sweden), but a decline in the southern part of its wintering range (Switzerland,

408 France). In our work, we found the relative number of Goldeneye in the ORE to be stable in the

409 period 1992-2016 (Table 3). This again tallies with the findings of Lehikoinen et al. (2013) that

410 duck abundances are independent of temperature in the central part of the flyway. This is

411 probably why the shift in wintering range is not perceptible in our study area but is more

412 pronounced at other, e.g. Swedish wintering sites, where numbers have increased (Nilsson and

413 Haas 2016) but not in the Netherlands, where they have declined (Hornman et al. 2012).

414   Goosander populations wintering in north-west and central Europe have been stable since

415 the early 1990s (Nagy et al. 2014); moreover, numbers in the Baltic Sea between 1991 and 2010

416 did not change significantly (Aunins et al. 2013); we also found non-significant changes in the

417 ORE.(Table 3). As in the case of Goldeneye, the explanation is that in the central part of the

418 flyway, species abundances are independent of temperature. In other areas, observations indicate

419 a shift farther to the north and east in the wintering range as a result of climate warming

420 (Hornman et al. 2012; Lehikoinen et al. 2013; Nilsson and Haas 2016).

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424

425 **Conclusion**

426   Climate change can influence the distribution of overwintering waterbirds. Apart from

427 climate changes, however, feeding ecology, interspecific competition, fishery and other human-

428   related disturbance may be also important and should be taken into consideration (Quan et al.

429   2002, Žydelis et al. 2009, Clavero et al., 2011; Eglington & Pearce-Higgins, 2012). Protected

430   areas covered by our study will be more important for some species (Scaup and Tufted Duck) but

431   less so for others (Smew). Taking into account the large abundance of the target species regularly

432   present in the ORE, conservation measures applied here will have a large impact on entire

433   populations and will be particularly important for Scaup. Shifts in species distributions should be

434   accounted for in future management plans for Special Protection Areas of the European Natura

435   2000 network. Our results add new insight to the problem of wintering waterbirds protection and

436   can help to shape conservation policy in the southern Baltic.

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

690 (1)   Target species. (2) Functional group: B – bottom-feeders, P – piscivores. (3) Estimated number of
691 individuals from regional flyway population in 1992, the numbers are presented in thousands. (4)
692 Estimated number of individuals from regional flyway population in 2012, the numbers are presented in
693 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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721 Table 2. Results of general linear mixed models for seven species showing the influence of ice cover,
722 maximum ice extent [km^2] in the Baltic Sea (max ice) and season on the percentage of occurrence of
723 bottom-feeders (denoted by B, Scaup, Tufted Duck, Pochard, Goldeneye, Coot) and piscivores (denoted
724 by P, Smew, Goosander) in the Odra River Estuary. Species, method and month were treated as random
725 effects.

Model Term	Coefficient	Std. Error	t	*P*
Intercept	26.553	11.619		
Ice cover	0.014	0.006	2.375	**0.018**
Season	-0.013	0.006	-2.204	**0.028**
Max ice	-0.114	0.040	-2.824	**0.005**
Feed[B]	-38.751	11.959	-3.240	**0.001**
Season*Feed[B]	0.019	0.006	3.212	**0.001**
Ice cover*Feed[B]	-0.044	0.007	-6.623	**<0.001**
Max ice*Feed[B]	0.094	0.046	2.071	**0.039**
Species (r)	0.074	0.048		
Method (r)	0.015	0.020		
Month (r)	0.001	0.002		

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732 Table 3. Population index trends in the Odra River Estuary (ORE) for the regional biogeographic (flyway)
733 population (b.p.) of diving waterbirds showing the percentage of the flyway population in 1992; the
734 percentage of the flyway population in 2016; the mean percentage of the flyway population in the period
735 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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772   Figure 1. The Odra River Estuary, north-western Poland.

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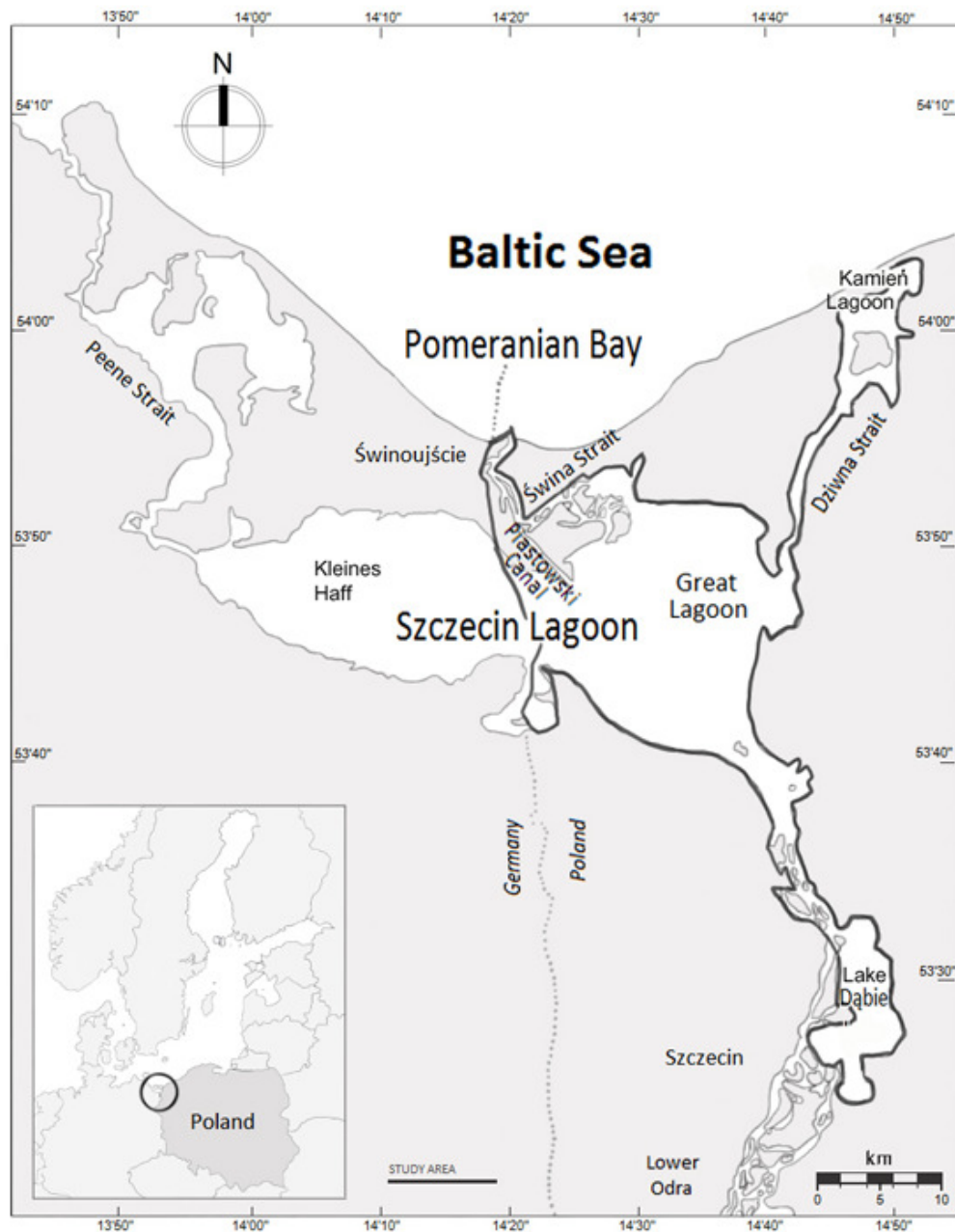
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786   Figure 2 A. Predicted results of the general linear mixed model showing the changes of the percentage of
787   the target species population in the Odra River Estuary during years 1992 - 2016. The predicted values
788   were obtained from the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

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