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# Natural regulation of the Baltic population of the Great Cormorant *Phalacrocorax carbo sinensis*: the interplay between winter severity and density dependence

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After a period of continuous increase and range expansion, the Baltic Great Cormorant population has stabilised in large parts of its range in recent years. Ringing recoveries reveal that considerable proportions of the population winter in areas that can be affected by prolonged frost periods. There is evidence that winter severity is an important density-dependent regulation factor: if the population is large, ice cover of coastal and inland water surfaces during harsh winters affects the population by reducing the availability of food resources. As long as the population remained small, however, it was not affected even by very cold winters, since the remaining accessible food resources were presumably still sufficient. The analysis presented here uses the average winter temperature in Germany as a proxy for winter severity in the frost-affected parts of the wintering areas of Baltic Cormorants. The Baltic Cormorant population in 1980–2016 is estimated from annual counts in Denmark, Schleswig-Holstein, Mecklenburg-Western Pomerania, Estonia, Finland and Gotland, which account for about 50% of the total population. The interplay between winter severity and density dependence is analysed using a linear and a non-linear regression model approach. The non-linear model gives a better description of the relationship between the size of the Baltic breeding population during the year ( $n$ ), the winter temperature  $T_n$ , and the population size during the previous year ( $n-1$ ). According to the model, a population of less than 41,400 breeding pairs would not suffer declines during even the coldest winters recorded since 1882. In 1989, the Baltic Cormorant population exceeded for the first time the threshold value for density-dependent regulation caused by severe winters. The winter 1995/96 was then the first one cold enough to cause a population decline. According to the model, during the years 2002/2003, 2005/06, 2008/09, 2009/10 and 2010/11 the winters have been cold enough to reduce population numbers. Furthermore, the model shows that the regulative winter effect is restricted to the low temperature range.

Key words: density-dependent regulation, winter mortality, population threshold

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As a consequence of decades of severe persecution, the Great Cormorant *Phalacrocorax carbo sinensis* had disappeared from much of its European range at the beginning of the 20th century. However, due to protection of the last colonies by landowners and also by sub-

sequent legal provisions in some countries (Herrmann 2011), the species not only survived, but even slightly increased up to the middle of the 20th century. It recolonised former breeding areas from where it had disappeared during the 19th century, such as Denmark

(1938) and Sweden (1948; Bregnballe & Gregersen 1995, Engström 2001). However, from the end of the 1950s until the end of the 1970s the Baltic Cormorant population remained relatively constant at a level of 2500–4000 breeding pairs. There are clear indications that the detrimental effects of chlororganic hydrocarbons, especially DDT and PCB, played a significant role in this stagnation (Herrmann 2012). With the reduction of application and later the complete ban of DDT in all European countries during the 1970s, together with reduced efforts to regulate colonies (Bregnballe 1996a), the Cormorant population started to recover. Simultaneously, it expanded its range towards the north-east, becoming a breeding bird in Estonia in 1983, on Gotland in 1992 and in Finland in 1996. In 2009, the Baltic population reached a level of about 165,500 to 167,000 breeding pairs. During the following years, the population decreased slightly (Bregnballe *et al.* 2014, Herrmann *et al.* 2014), but started to grow again in the most recent years (2014–2016; Figure 2).

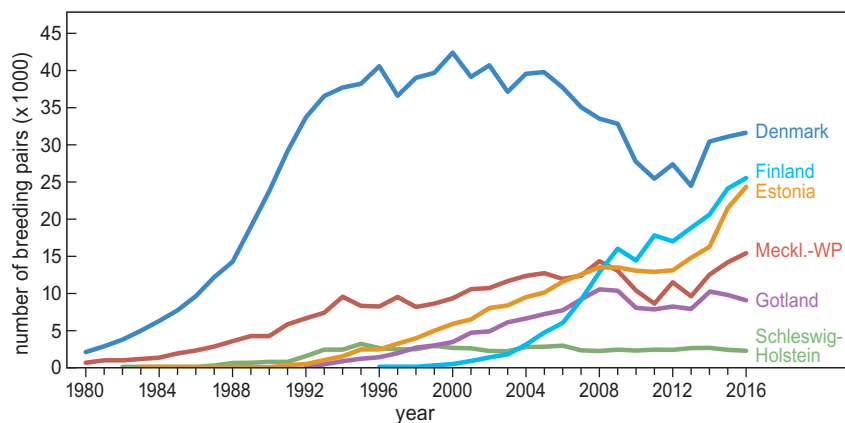
After any recovery phase, it is expected that a population will stabilise due to density-dependent effects. In population ecology, density dependence is seen as an essential feature for population regulation (Turchin 1995). Probably the most important (but not the only) mechanism of population regulation is competition for resources. Competition is strongly related to the number of individuals and resource availability that may be influenced by environmental factors such as meteorological conditions. The seasonal timing of density dependence, especially with reference to underlying mechanisms, is important for understanding the population ecology of a species and for the design of effective management and conservation strategies (Lok *et al.* 2013). This article explores the role of winter

severity in creating density-dependent regulation effects in the Baltic Great Cormorant population.

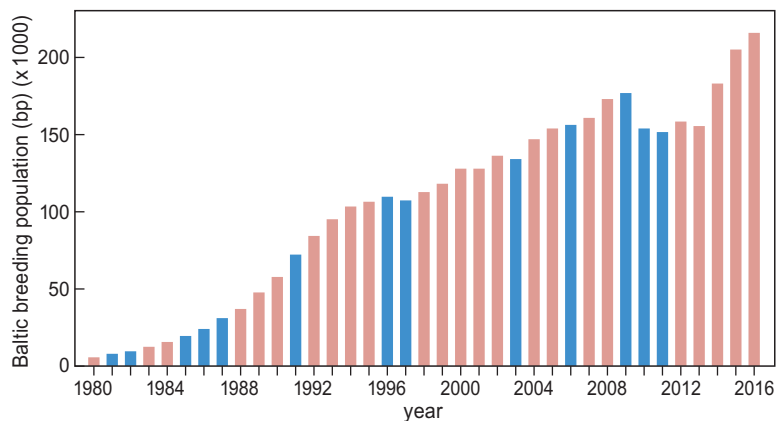
## METHODS

### Population data

In some of the Baltic countries Cormorant surveys have been performed annually for a long time, but annual counts have not been conducted for the entire Baltic Sea area. Complete numbers are available for 1980, 2006, 2009 and 2012 (Bregnballe *et al.* 2014, Herrmann *et al.* 2014). An index for the size of the Baltic breeding population can be obtained using population data from those regions for which continuous time series are available: Denmark, Germany (Baltic federal states Mecklenburg-Western Pomerania and Schleswig-Holstein), Estonia, Finland and the island Gotland (Sweden; Figure 1). These areas comprise about 50% of the Baltic breeding population (1980: 56.7%, 2006: 50.0%, 2009: 53.3%, 2012: 50.0%) and, as this is quite constant for the whole period, it is thus assumed that this sample is representative of the development of the Baltic Cormorant population. Multiplying the number of breeding pairs of the index areas by a factor of two is assumed to give a sufficiently precise estimate for the total Baltic breeding population (Figure 2). Here we use data from 1980 to 2016, as the year 1980 corresponds to the start of the recovery of the Baltic Cormorant population. It has to be noted that the estimation of Baltic Cormorant numbers may include some errors, for two reasons: (1) Counting errors: the counts are usually performed within a fixed time span at the time of maximum nest numbers. However, the period of maximum nest numbers may



**Figure 1.** Development of the breeding population of Great Cormorants in six Baltic regions where the breeding population has been surveyed annually.



**Figure 2.** Estimated development of the breeding population of Great Cormorants based on annual surveys in the six regions shown in Figure 1. These regions hold approximately 50% of the entire breeding population around the Baltic Sea; hence the total population is estimated by doubling the numbers counted in the index areas. The blue columns refer to population numbers after rather cold winters (average winter temperature in Germany below 0.0°C).

vary between the years, depending on the meteorological conditions during winter and spring. Hence, counting dates and the date of maximum nest numbers may deviate somewhat in some years. (2) The Baltic population numbers are calculated from annually counted sample areas that account for about half of the Baltic population. However, as shown above, this proportion varies slightly, which may also cause errors when estimating the size of the entire Baltic population.

#### Ringling recovery data

Ringling recovery data were used to analyse the winter distribution of Cormorants of Baltic origin, including recoveries of Cormorants ringed in northern Germany, Denmark, Sweden, Finland, the Russian part of the Gulf of Finland, Estonia, Latvia, Lithuania and Poland (numbers ringed and locations of ringling sites are given in Frederiksen *et al.* 2018). We used ringling and recovery data that had been obtained from the EURING database ([www.euring.org](http://www.euring.org)) and from the national ringling schemes for analyses conducted as part of CormoDist (Bregnballe *et al.* 2015), an EU-funded investigation of European Cormorant movements (see also Frederiksen *et al.* 2018). The analyses conducted for the present paper included Cormorants ringed in the Baltic Sea area between 1983 and 2013 and recovered dead between November 16 and February 15 during the winters 1983/84–2013/14 ( $n = 3688$ ). Migration movements of Great Cormorants within Europe may occur after mid-November and before mid-February (e.g. van Eerden & Munsterman 1986, 1995). However, analyses of the distance between ringling sites

and recovery sites suggest that the vast majority of birds have reached their wintering areas by mid-November and do not initiate spring migration before mid-February.

#### Climate data

We assume that winter severity affects Cormorants through a combination of low water temperatures and the development of ice cover on coastal and inland waters, which leads to reduced food availability for birds attempting to winter in northern and central Europe. However, data on ice cover are not available for the relevant areas. Hence, the average winter temperature in Germany is taken as a proxy for winter severity within the potentially frost-affected wintering



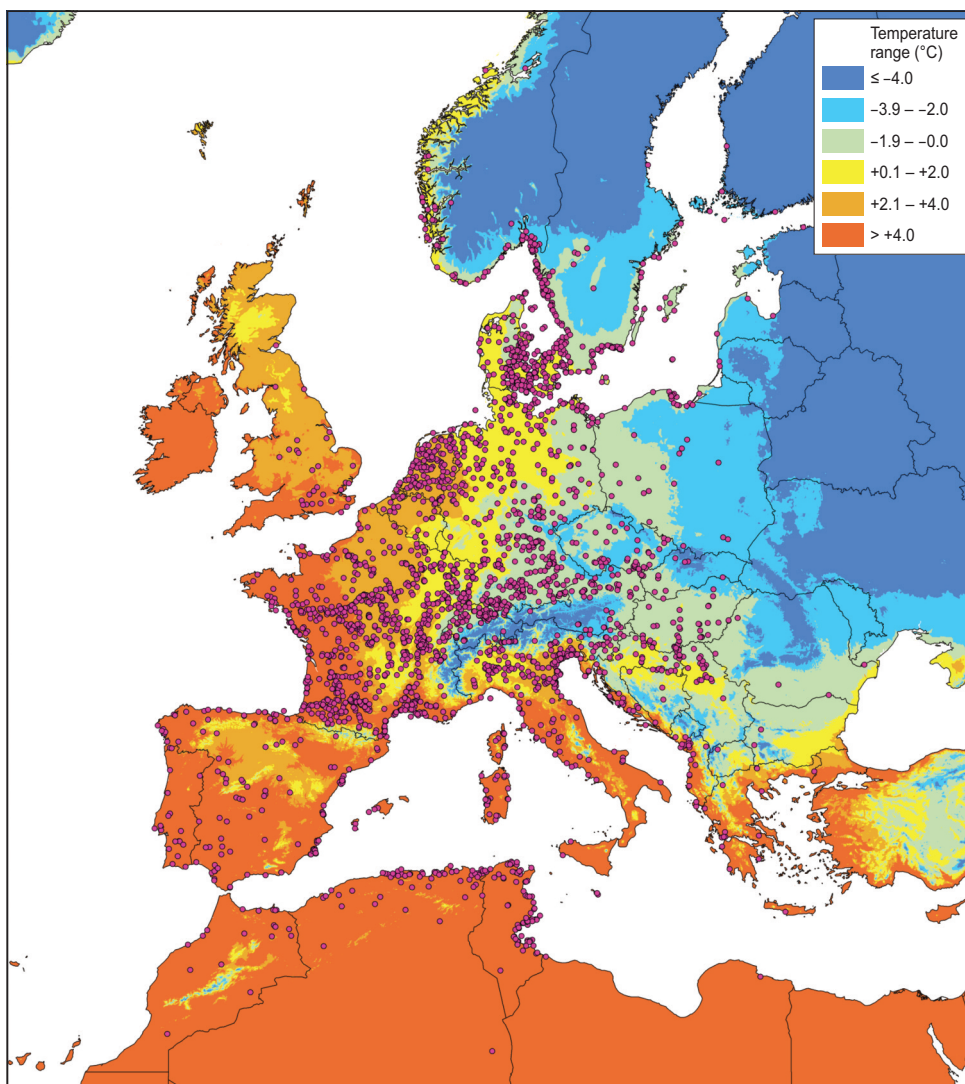
Cormorant foraging in extreme icy water (photo Steffen Ortmann, 16 January 2010).

areas of Baltic Cormorants. Temperature data are freely available at the Climate Data Centre of the German Meteorological Service (Deutscher Wetterdienst 2017). The meteorological winter is defined as the period from 1 December to 28 February. For the method of calculation of regional temperature averages see Deutscher Wetterdienst (2017).

The potentially frost-affected wintering areas of Cormorants are approximately delineated by the  $-2$  to  $+2^{\circ}\text{C}$  range of average January temperatures (Figure 3). We assume that this temperature zone is crucial for winter regulation of Cormorants. The colder areas are not relevant since they do not belong to the regular

wintering range of Cormorants, and the warmer areas do not play a role for temperature-related regulation since they are rarely frost affected. Germany covers a major proportion of the relevant temperature range and therefore is assumed to be a suitable descriptor for winter conditions within the potentially frost-affected wintering areas of Cormorants.

For constructing temperature zones in the wintering area of the Cormorants (Figure 3) we used data supplied by Fick & Hijmans (2017). They included monthly temperature (minimum, maximum and average) data and we modelled this on a  $1\text{-km}^2$  spatial resolution. The climate model used temperature data



**Figure 3.** Winter distribution of Great Cormorants breeding in the Baltic Sea area according to ringing recoveries during the period 1983/84–2013/14. The mapped temperature zones reflect modelled ‘averages’ of January temperatures 1979–2000 based on measures from meteorological stations located throughout Europe and parts of North Africa; see Fick & Hijmans (2017) for details.

collected throughout Europe and North Africa in December–February during 1979–2000. Weather station data were interpolated using thin-plate splines with covariates including elevation, distance to the coast and three satellite-derived covariates: maximum and minimum land surface temperature as well as cloud cover, obtained with the MODIS satellite platform; see Fick & Hijmans (2017) for further details.

### Statistical analysis

Our hypothesis is that severe winters cause extra mortality or poorer body condition among Cormorants wintering in potentially frost-affected areas. This will affect the number of breeding pairs around the Baltic Sea in subsequent years, since more birds than usual have either died or skip breeding because of poor body condition. To test this hypothesis, ordinary least square regression analyses are performed in order to describe the relationship between winter temperature of the year  $n$  ( $T_n$ ;  $n$  refers to the year of January–February, not that of December) and the relative population change ( $R_n$ ) from year  $n-1$  to year  $n$ . The relative population change  $R_n$  is given by the quotient of the population size during year  $n$  ( $P_n$ ) and the population size during the previous year ( $P_{n-1}$ ). The term  $b_0$  is the basic value of population change if the winter temperature is  $0^\circ\text{C}$ ;  $b_1$  to  $b_6$  are regression coefficients of the model functions.

For the analysis of effects of winter temperature on the population development of Baltic Cormorants we tested four different regression models. The models (1) and (2) assume a direct relationship between the winter temperature of the year  $n$  and the relative population change from year  $n-1$  to year  $n$ , without considering density dependence:

(1) Linear regression model:

$$R_n = P_n/P_{n-1} = b_0 + b_1 \times T_n$$

(2) Polynomial model:

$$R_n = P_n/P_{n-1} = b_0 + b_1 \times T_n + \dots + b_6 \times T_n^6$$

The models (3) and (4) include the total population size during the previous year ( $P_{n-1}$ ) as a second model parameter, thus introducing density dependence. These models assume a linear relationship between the population size  $P_n$ , the population size of the previous year  $P_{n-1}$ , and the winter temperature  $T_n$ . Model (4) additionally assumes a combined effect of  $T_n$  and  $P_{n-1}$  on the next-year breeding population  $P_n$ :

(3) Linear model:

$$P_n = b_0 + b_1 \times P_{n-1} + b_2 \times T_n$$

(4) Extended model:

$$P_n = b_0 + b_1 \times P_{n-1} + b_2 \times T_n + b_3 \times P_{n-1} \times T_n$$

For the regression analyses, we used the WinSTAT-Programme for Excel (R. Fitch Software, www.winstat.de).

## RESULTS

### Overall winter distribution of Baltic Cormorants

Figure 3 shows the distribution of winter recoveries (16 November – 15 February) of Baltic Cormorants during the period 1983/84–2013/14. It is evident that Cormorants belonging to this breeding population can be found wintering over most of Europe, ranging from Portugal in the west to Romania in the east and from Bergen (Norway) in the north to southern Tunisia in the south, i.e. covering distances of more than 3000 km in both directions. Although some of the birds obviously attempt to overwinter near to the breeding areas, the distribution of recoveries clearly suggests that the majority move to wintering areas located south and south-west of the breeding areas. Inland waterbodies such as lakes, ponds and rivers are winter habitats as well as coasts or coastal wetlands.

A very small proportion (1.4%) of the recoveries were obtained from areas with average January temperatures below  $-2^\circ\text{C}$  (Table 1). Areas with mean January temperatures between  $-2$  and  $+2^\circ\text{C}$  are potentially affected by longer frost periods. A proportion of 46.6% of the recoveries were obtained from these areas, whereas 52.0% were recovered from ‘frost-safe’ regions with a mean January temperature  $> 2^\circ\text{C}$ . It has to be emphasised that mortality and recovery probabilities of Cormorants are not equal across the entire wintering range in Europe and North Africa, and for this reason the distribution of ringing recoveries will

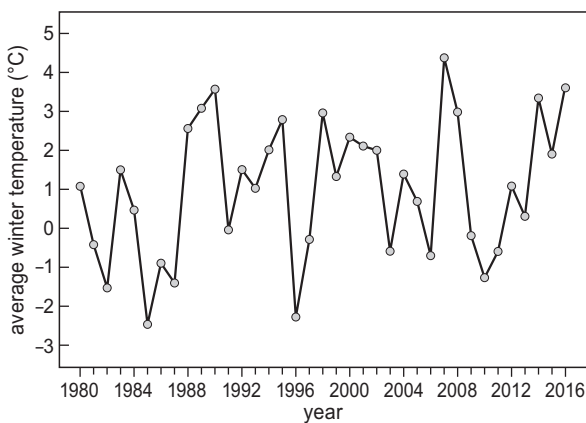
**Table 1.** Numbers and proportions of winter recoveries of Baltic Cormorants according to temperature zones.

Temperature range	Number	Proportion (%)
$\leq -4^\circ\text{C}$	5	0.1
$-3.9^\circ\text{C}$ to $-2^\circ\text{C}$	49	1.3
$-1.9^\circ\text{C}$ to $0^\circ\text{C}$	753	20.4
$+0.1^\circ\text{C}$ to $+2^\circ\text{C}$	965	26.2
$+2.1^\circ\text{C}$ to $+4^\circ\text{C}$	756	20.5
$> +4^\circ\text{C}$	1160	31.5
<b>Total</b>	<b>3688</b>	<b>100.0</b>

only approximately reflect the winter distribution of the population (see Frederiksen *et al.* 2018). However, the numbers provide evidence that a considerable proportion of Baltic Cormorants winter within potentially frost-affected regions and hence may suffer food shortage and other temperature-related impacts during severe winters.

### Winter conditions 1980–2016

The average winter temperatures in Germany during the study period ranged from  $-2.46^{\circ}\text{C}$  (1984/85) to  $4.38^{\circ}\text{C}$  (2006/07). Very cold winters with temperatures below  $-1^{\circ}\text{C}$  have been recorded in 1981/82 ( $-1.53^{\circ}\text{C}$ ), 1984/85 ( $-2.46^{\circ}\text{C}$ ), 1995/96 ( $-2.27^{\circ}\text{C}$ ) and 2009/10 ( $-1.27^{\circ}\text{C}$ ; Figure 4). Periods of consecutive cold winters with negative temperature values have been observed at the beginning and mid-1980s (1980/81–1981/82 and 1984/85–1986/87), at the mid-1990s (1995/96–1996/97), as well as from 2008/09 to 2010/11.



**Figure 4.** Average winter temperatures in Germany during the period 1979/80–2015/16. The year indicated on the x-axis refers to the year of the months January and February from the respective winter.

### Winter conditions and Cormorants

In the models (1) and (2) where the population size of the previous year was not taken into consideration, there was no significant relationship (significance level  $P = 0.05$ ) between the change in population size from year to year and the temperature in the winter between the two years (model 1:  $t_{36} = -0.255$ ; model 2:  $t_{36} = 1.15$ ), i.e. there was no direct influence of winter temperature on the development of the breeding population.

However, for the linear model (3) which included total population size during the previous year ( $P_{n-1}$ ) as

a second model parameter, i.e. introducing density dependence, the regression analysis showed a significant relationship between year-to-year changes in population size and winter temperature. The impact of both parameters ( $P_{n-1}$  and  $T_n$ ) was significant (all  $P < 0.05$ ) with the coefficient of determination  $R$  being 0.986 ( $b_0 = 2677.5$ ,  $b_1 = 0.9907$ ,  $b_2 = 1196.7$ ).

The temperature ( $T_{\text{const}}$ ), for which the population should remain constant ( $P_{n-1} = P_n$ ) is estimated as:

$$T_{\text{const}} = (0.0093 \times P_{n-1} - 2677.5)/1196.7$$

Lower temperatures, at a given population size  $P_{n-1}$ , according to the model, are expected to cause population declines, whereas higher temperatures do not prevent population growth.

The output from the linear model including population size shows increasing impacts of low temperatures with increasing size of the Baltic Cormorant population (Figure 5). According to this model, the winters 1984/85, 1995/96 and 2009/10 were sufficiently cold – and the population size large enough – to cause declines in the Baltic Cormorant population. These were three of the four coldest winters during the study period. The winter 1981/82 also was very cold, but according to this model it did not cause a population decline due to low Cormorant numbers.

In order to consider combined effects of the previous year's population size  $P_{n-1}$  and the mean winter temperature  $T_n$  on the population size  $P_n$ , we tested the extended model (4):

$$P_n = b_0 + b_1 \times P_{n-1} + b_2 \times T_n + b_3 \times P_{n-1} \times T_n$$

In this case, the linear component  $b_2 \times T_n$  was not significant, i.e.  $b_2 = 0$ . The significant model components (all  $P < 0.05$ ) were:

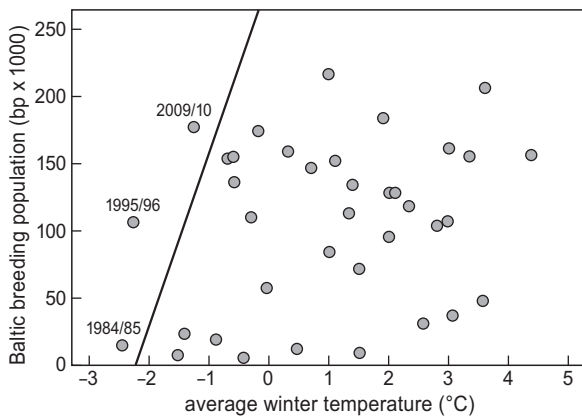
$$P_n = b_0 + b_1 \times P_{n-1} + b_3 \times P_{n-1} \times T_n = b_0 + (b_1 + b_3 \times T_n) \times P_{n-1}$$

The coefficient of determination of this model is  $R = 0.988$ , with  $b_0 = 6364.3$ ,  $b_1 = 0.9648$  and  $b_3 = 0.0237$ .

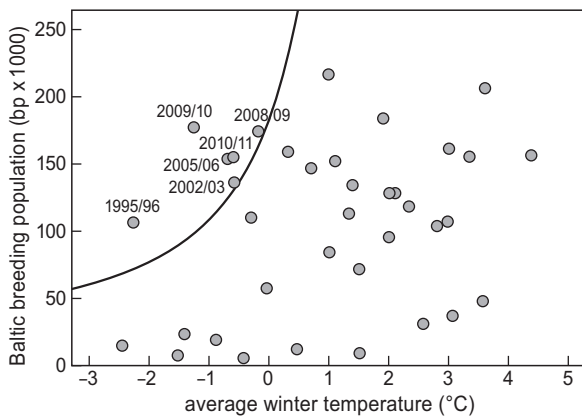
The temperature  $T_{\text{const}}$ , for which  $P_{n-1} = P_n$ , hence is calculated as:

$$T_{\text{const}} = ((P_{n-1} - b_0) / P_{n-1}) - b_1 / b_3$$

Similar to the linear model this model also shows an increasing  $T_{\text{const}}$  with increasing population size (Figure 6). The coefficient of determination is higher than that



**Figure 5.** Population size of Great Cormorants in the Baltic Sea in year  $n-1$  and temperature of the following winter ( $T_n$ ) during the period 1981–2017. The black line marks the temperature ( $T_{\text{const}}$ ) for which the population in year  $n$  will have the same size as in the previous year ( $P_n = P_{n-1}$ ) according to the linear model (3). The dots left of the line indicate those winters that are, according to this model, expected to cause a decline of the population in the following breeding season.



**Figure 6.** Population size of Great Cormorants in the Baltic Sea in year  $n-1$  and temperature of the following winter ( $T_n$ ) during the period 1981–2017. The black line marks the temperature ( $T_{\text{const}}$ ) for which the population in year  $n$  will have the same size as in the previous year ( $P_n = P_{n-1}$ ) according to the extended model (4). The dots left of the line indicate those years for which winter severity caused population declines.

of the linear model. According to this model, during the study period 1981–2017 the winters 1995/96, 2002/03, 2005/06, 2008/09, 2009/10 and 2010/11 should have caused population declines. The largest deviation from the equilibrium line is observed for the winter 2009/10. This winter caused the most pronounced decline of overall breeding pair numbers observed so far (Figures 1 and 2). The population size in 2009

was 177,700 breeding pairs, the mean winter temperature 2009/10 was  $-1.27^\circ\text{C}$ .

Extending the multiple regression model by additional components, such as relationships between exponential values of  $P_{n-1}$  and  $T_n$  or the population size  $P_{n-2}$ , does not improve the correlation. Hence, we consider the extended model (4) as the most appropriate one for describing the density-dependent effect of winter severity on the Baltic Cormorant population.

## DISCUSSION

### Winter distribution of Cormorants

The winter range of Great Cormorants from the Baltic Sea area stretches from the coasts of southern Norway across central, southern and western Europe to North Africa. This range covers a wide gradient of temperature zones (Figure 3). During cold winters, water surfaces of the north-eastern parts of the wintering area may become covered by ice. Van Eerden *et al.* (2012) analysed the winter distribution of Cormorants as obtained from the pan-European roost census in January 2003 considering 14 environmental factors (temperature, latitude, longitude, coastal and lake surface areas, surface areas of different river types). According to their results, the wintering range of Cormorants seems to be determined by temperature limits. Areas with an average winter temperature below  $-5^\circ\text{C}$  during the census year were not used by Cormorants. Within the appropriate ‘temperature window’, the birds were widely distributed, showing a strong tendency to be more abundant in the regions of the major river systems.

According to our results from recoveries of ringed birds from the Baltic population during the period 1983/84–2013/14, the  $-2^\circ\text{C}$  isotherm of mean temperatures in January represents a suitable delineation of the wintering range of Cormorants. Regions with lower temperatures are almost not utilised. Regions with mean January temperatures between  $-2$  and  $+2^\circ\text{C}$ , however, are widely used by Cormorants. These regions have to be considered as frost-prone, i.e. Cormorants may suffer impacts of low temperatures and ice cover of water surfaces during severe winters. Regions with temperatures  $> 2^\circ\text{C}$  are rarely or never affected by longer lasting frost periods, therefore food shortage due to ice cover usually does not occur even during very cold winters. Almost 50% of the Cormorants have been recovered from potentially frost-affected areas, which indicates the potential vulnerability of Baltic Cormorants to harsh winters.



### Temperature effects on Cormorants

The main impact of low temperatures obviously has to be attributed to ice cover. If coastal lagoons, lakes or rivers are covered by ice, fish becomes inaccessible to the birds and, as a consequence, available food sources are reduced. Inland lakes and ponds freeze first, followed by coastal lagoons, whereas running waters are usually the last open water surfaces during cold spells. Hence, cold spells also cause a re-distribution of Cormorants, forcing them to concentrate at rivers. Cormorants are distributed in an irregular manner in areas with mountainous landscapes. Here, regularly occupied roosts persist in the valleys of larger rivers from which Cormorants exploit the still unfrozen waters nearby. Stable wintering numbers, as for instance documented for Bavaria since 1993/94 (Keller & Lanz 2003), suggest that the carrying capacity of these areas may have been reached. During periods of severe frost, birds are forced to move to ice-free regions, such as fast-flowing upstream areas. In these areas, the distribution of Cormorants thus changes rapidly according to weather conditions (van Eerden *et al.* 2012). The concentration of birds at the remaining open waters may lead to an overexploitation of local fish stocks and finally to food shortage. During the cold winter 2005/06, for instance, Görlach & Wagner (2008) and Wagner *et al.* (2008) recorded local depletion of fish stocks related to high Cormorant numbers at some small rivers in Thuringia. These are strong indications that increased competition for scarce resources is likely a main driver for density-dependent regulation in parts of the wintering areas.

Another aspect is the influence of water temperature on the energy budget and feeding strategy of Cormorants. Grémillet *et al.* (1999, 2001) found that Cormorants may manage their energy budget in a remarkably efficient way even in cold waters by minimising the time spent in water. Their substantial energy requirement is balanced by the highest predatory efficiency of any diving bird (White *et al.* 2011). However, the asset of high foraging efficiency is strongly related to high prey densities. Since heat loss in cold waters increases rapidly with decreasing prey density, Grémillet *et al.* (1999) anticipate that Cormorants are unable to utilise prey below a certain density during the winter period. Čech *et al.* (2008) studied Cormorant diet at two water reservoirs in the Czech Republic during summer, a mild and a cold winter. They showed that the average weight of fish taken by Great Cormorants increased significantly with decreasing air and water temperature. Whereas Cormorants at higher water temperatures are less selective, they

increase their foraging efficiency at low temperatures by taking bigger prey. Hence, during winter Cormorants not only need ice-free waterbodies, but also high prey densities and appropriate prey quality.

### Mean winter temperature as a proxy for winter severity

Frederiksen & Bregnballe (2000a) found that winter anomalies (deviation from long-term mean temperature) were highly correlated between Denmark and central Europe, as well as between Denmark and southern Germany, indicating that using Danish data was justified for the description of winter severity in the north-eastern wintering areas of Baltic Cormorants. It is assumed that the same is true for using German temperature data. Beside the mean temperature these authors also used the 'amount of cold' (absolute sum of temperature of all frost days) as another measure of winter severity. However, both measures were highly correlated; mean temperature was better to discriminate among mild winters. The mean winter temperature in Germany is thus assumed to be a suitable proxy for winter severity in the north-eastern parts of the wintering area of Baltic Cormorants. Water temperature is – with some delay – highly correlated with air temperature.

### Density-dependent population regulation of Baltic Cormorants

Density dependence is an essential feature of population regulation. Turchin (1995) argues that population regulation cannot occur in the absence of density dependence. Probably the most important (but not the only) mechanism of population regulation among Cormorants is competition. Competition can operate in many ways and is assumed to affect different life cycle parameters in Cormorants, such as mortality (Frederiksen & Bregnballe 2000a), reproductive performance (Bregnballe 1996b), age of first breeding (Frederiksen & Bregnballe 2001) and proportions of birds breeding.

For the Great Cormorant, Frederiksen *et al.* (2001) demonstrated how density dependence will lead to population regulation. In their model, the authors included density-dependent effects on adult survival and on the proportion of birds breeding. Model scenarios with moderate or strong levels of density dependence provided predictions that fitted to the observed numbers of breeding pairs, whereas scenarios without density dependence in survival overestimated population growth.

The two types of models tested in the present study suggest that the critical winter temperature for which

the population size will remain unchanged from year to year ( $T_{\text{const}}$ ) will increase with population size. However, the non-linear model not only offers a higher coefficient of correlation than the linear one, it also fits much better to the theoretical concept of density-dependent effects of winter severity. Assuming the model is valid beyond the range of observed data, it suggests a population size threshold for winter impacts of 41,400 breeding pairs for the lowest ever recorded mean winter temperature in Germany of  $-5^{\circ}\text{C}$ . For an indefinite population size, the theoretically highest value of  $T_{\text{const}}$  is  $1.485^{\circ}\text{C}$ . That means, the density-dependent effect of winter temperature is limited to low temperatures, higher temperatures do not have an effect. This fits well with the assumption that not the temperature as such, but ice cover related to low temperatures is the driving factor: ice-free winters, regardless of being mild or extremely mild, do not have an effect. At the same time, if the population size is small, the development of the population will not be affected even by the most severe winters. The lowest mean winter temperature in Germany ever recorded since 1882, during the winter 1940, was  $-5^{\circ}\text{C}$ . This winter temperature would, according to our calculations, correspond to 41,400 breeding pairs. Taking this as the lower limit of population size for which winter severity may cause declines, it can be concluded that until 1989 the Baltic Cormorant population was too small to suffer significant winter temperature related impacts. In fact, the very cold winters of the 1980s did not have any visible impact on the growth of the, at that time, still small population. Even the extremely cold winter 1984/85 did not reduce the population of c. 15,500 breeding pairs (Figure 2). The winter 1995/96 was the first very cold one with a breeding population sufficiently large enough to see population declines. After 1995/96, the winters 2002/2003, 2005/06, 2008/09, 2009/10 and 2010/11 were cold enough to cause population reductions. Figure 2 shows population declines after the winters 2002/03, 2009/10 and 2010/11, but not after the winters 1995/96, 2005/06 and 2008/09. The deviation of the predictions from the extended model and the observed development after the winters 1995/96, 2005/06 and 2008/09 may be linked to the possible inaccuracy of population estimates (see section 'Population data'). Furthermore, the mean winter temperature is a proximate, not an accurate measure for the meteorological conditions affecting Cormorants in the wintering areas during the respective year.

The most pronounced population effects are seen during the period 1995–1997 and, even stronger,

2010–2013. Both periods include very cold winters ( $-2.27^{\circ}\text{C}$  in 1995/96 and  $-1.27^{\circ}\text{C}$  in 2009/10), and they are characterised by two and three, respectively, consecutive cold winters. It has to be emphasised that extra mortality caused by cold winters may have both immediate as well as delayed population effects. Cormorants during their first year of life suffer especially high mortalities (Frederiksen & Bregnballe 2000b). A variable proportion of these birds would start breeding the year after at an age of two years (Frederiksen *et al.* 2001).

These results correspond nicely with the results of an analysis of adult survival done by Frederiksen & Bregnballe (2000a) for Danish Cormorants for the period 1978–1996. In their study, a combination of the European population size and winter severity explained 52–64% of the year-to-year variation in the survival of adult Cormorants. Survival was unusually low in 1995, the only occasion during the study period when a severe winter met a high population size, whereas the severe winters of the mid-1980s were not clearly associated with increased mortality.

The results of Frederiksen & Bregnballe (2000a) indicate that density-dependent regulation of Cormorant populations can occur through the effect of severe winters on adult mortality at high population densities. However, density-dependent regulation can also operate through other mechanisms. We consider it highly likely that some of the Cormorants that survive a severe winter will find it difficult to get into sufficiently good physical condition to initiate breeding, i.e. they may end up skipping the following breeding season. Hence, a decline in the breeding population following a severe winter could potentially reflect the combined effect of higher mortality and of poor body condition forcing some of the survivors to join the pool of non-breeders.

It has to be emphasised that competition for food resources during winter does not just mean competition among Baltic breeding birds. Baltic Cormorants share large parts of their wintering areas with the breeding populations of the North Sea coast (The Netherlands, Belgium, United Kingdom and southern Norway) or of the central European inland (non-Baltic Germany, France; Frederiksen *et al.* 2018). However, the significance of competition between the Baltic breeding population and non-Baltic breeding populations during winter has not yet been studied.

The interplay between winter severity and population size is obviously not the only way in which density-dependent population regulation of Cormorants occurs. Even in the case of a long sequence of warm winters the population will not grow indefinitely. For instance,

there are strong indications for density dependence on the reproductive performance in individual Cormorant colonies that are not limited in size by the availability of potential nesting sites. The reproductive success of the Danish colony on Vorskø remained constantly high during the period of colony growth, but decreased considerably when the colony stabilised and later declined (Frederiksen *et al.* 2001, Bregnballe & Gregersen 2003). The decline of breeding success in this colony was interpreted as a delayed response to increasing colony size, mediated through food availability (Bregnballe 1996b, Gienapp & Bregnballe 2012). Breeding success can have a direct impact on subsequent recruitment both on a local and a regional scale. An example of a local effect is the finding of a strong correlation between breeding success and recruitment in the following year in the Vorskø colony (Frederiksen & Bregnballe 2001). Their results indicated that recruitment could be indirectly density-dependent: when breeding success starts to decline because of decreasing food availability, it becomes less attractive for prospective breeders to settle and start breeding. These individuals may postpone the onset of breeding to a later year or choose another more attractive breeding colony, i.e. a mechanism whereby recruitment becomes density-dependent.

### **Shifting the wintering areas towards the north: an opportunity turns into a risk**

The traditional wintering areas of Baltic Cormorants are the Mediterranean Sea, including the Adriatic Sea, and the coasts of the North Sea, British Channel and Atlantic Ocean from France to Portugal and Spain (Bregnballe *et al.* 1997, Bønløkke *et al.* 2006, Köppen 2007, Heinicke & Köppen 2007, Herrmann *et al.* 2015). Ringing results from the 1930s show a clear coastal affiliation of wintering locations, but since the 1950s inland areas are used as well (Herrmann *et al.* 2015). With the expansion of the breeding range of Cormorants to the eastern and northern Baltic Sea, a re-distribution of wintering sites took place. The south-eastern areas (Adriatic Sea) were now occupied by Cormorants from the eastern and northern Baltic, whereas simultaneously south-western Baltic Cormorants disappeared from that region, while at the same time, Cormorants expanded their wintering areas towards the north: starting at the beginning of the 1980s, the south-western Baltic Sea was occupied as a wintering area (Herrmann *et al.* 2015, Bregnballe *et al.* 2021, Frederiksen *et al.* 2018). Furthermore, migration distances became shorter. An increasing proportion of Cormorants spent winter in areas closer to the breeding

sites: for Cormorants ringed in north-east Germany, it could be shown that winter recoveries within a distance of 500 km were exceptional before the 1990s, but increased during the 1990s and finally made up a proportion of c. 32% of the recoveries after 2000 (Herrmann *et al.* 2015). Similarly, Danish ringing data show that the mean geographical position of Cormorants recovered during winter moved north starting from the early 1990s (Bønløkke *et al.* 2006, Bregnballe *et al.* 2021).

There is some evidence to suggest that a shift of wintering areas closer to the breeding sites may give an advantage for breeding performance and breeding success. On the basis of ringing recoveries, Bregnballe *et al.* (2006) found that males and females wintering at distances < 300 km arrived 2–3 weeks earlier at the breeding site than those birds migrating longer distances; males and females that arrived early produced more fledglings than those that arrived later. Females that arrived early could breed across more seasons and hence had higher lifetime reproductive success. However, distance reductions in migration from long to intermediate obviously did not bring an advantage: intermediate distance migrants did not arrive earlier and did not breed with more success or more frequently than those wintering at long distances.

Shifting the wintering areas towards the north, closer to the breeding sites, has probably been an advantage for the birds with respect to breeding performance, and the risk of this strategy had apparently been low as long as the Baltic breeding population was small. This situation changed with increasing population size: in mild winters short-distance migration may still be an advantage, but in severe winters it will turn into a risk. Birds that try to stay in the northern wintering areas may suffer very high mortality, as was observed in January–February 2010 (Koop & Kieckbusch 2010, T. Bregnballe unpubl. data). But also those birds that survived probably suffered a decreased physical condition, which should influence breeding performance. Surprisingly, after the cold winters 2009/10 and 2010/11 the numbers of Cormorants wintering in the south-western Baltic did not recover to previous numbers, even though the winters were rather mild (Herrmann *et al.* 2015, unpubl. data). At the same time, the Baltic breeding pair numbers did recover, indicating that the lower numbers wintering in the Baltic Sea were not the result of lower population numbers but rather an adaptive behaviour of the birds to ‘catastrophic events’, possibly combined with increased mortality among birds having developed the strategy of wintering close to the breeding areas.

Since Cormorants may cause conflicts with fishery and aquaculture as well as with angling interests, there have been strong demands for population control on a European level (e.g. Decision of the European Parliament of 4 December 2008, see European Commission 2013). However, in light of density-dependent regulation, population control by culling must have limited effects: culling reduces the number of birds and hence the competition, which in turn will reduce the strength of natural density-dependent regulation. Hence, anthropogenic regulation efforts are counter-balanced by natural density-dependent mechanisms. The interplay between culling and density dependence has been studied theoretically by Frederiksen *et al.* (2001). The authors showed that culls with the intensity practised at that time had limited effects on population development. Culling at very high intensities is required in order to achieve population control. However, even if a reduction in the number of Cormorants was achieved, it may not lead to a similar reduction in conflicts. Hence, actions to control damage rather than Cormorant populations are likely to be more cost-effective. The recommendations given later by the European Commission (2013) are in line with these findings.

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## SAMENVATTING

In het Oostzegebied is de populatie van de Aalscholver *Phalacrocorax carbo sinensis* sterk in aantal toegenomen en heeft de soort zijn verspreidingsgebied sterk uitgebreid. Inmiddels is hieraan een eind gekomen. Uit ringonderzoek blijkt dat veel vogels de winter doorbrengen in gebieden met aanhoudende strenge vorst. De strengheid van de winter zou bij toenemende aantallen kunnen doorwerken op de voedselbeschikbaarheid en zo op de aantalsregulatie van de populatie. In het hier beschreven onderzoek is de gemiddelde wintertemperatuur in Duitsland als maat genomen voor de strengheid van de winter in het overwinteringsgebied van de Baltische Aalscholvers. In 1980–2016 is de Baltische populatie bepaald door tellingen vanuit een vliegtuig in Denemarken, Sleeswijk-Holstein, Mecklenburg-Vorpommern, Estland, Finland en Gotland (50% van de totale Baltische populatie). Voor de analyse van de gegevens zijn zowel lineaire als niet-lineaire regressiemodellen gebruikt. Het niet-lineaire model gaf de beste verklaring voor het verband tussen de broedpopulatie in het jaar  $n$ , de wintertemperatuur  $T_n$  en de broedpopulatie in het jaar ervoor ( $n-1$ ). Het model voorspelt dat bij een populatie van minder dan 41.400 broedparen er geen effect is van de temperatuur in de winter op de grootte van de broedpopulatie in het jaar erna, zelfs niet bij strenge winters. In 1989 kwam de Baltische populatie boven deze grens uit, die als drempelwaarde wordt gezien waarboven er effecten optreden van strenge winters op de aantallen. De winter van 1995/96 was daarna de eerste winter die streng genoeg was voor een meetbaar effect op de populatieomvang. Volgens het model zouden de winters 2002/03, 2005/06, 2008/09, 2009/10 en 2010/11 ook koud genoeg zijn geweest om een negatief effect te sorteren.