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# Spatial patterns in age- and colony-specific survival in a long-lived seabird across 14 contrasting colonies

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Demographic rates such as recruitment and survival probability can vary considerably among populations of the same species due to variation in underlying environmental processes. If environmental processes are spatially correlated, nearby populations are expected to have more similar demographic rates than those further apart. Breeding populations and foraging ranges are spatially segregated in colonial seabirds, making them ideal for studying spatial patterns in demographic rates and their effects on local population dynamics. Here we explored variation in age-dependent survival probabilities across 14 colonies of Herring Gulls *Larus argentatus* breeding along the Dutch North Sea coast. We used long-term mark–recapture data of marked fledglings to estimate survival, and estimated spatial autocorrelation of survival probabilities. We assessed whether survival until recruitment age or until 10 years old (close to their expected lifespan) explained variation in population trajectories of each colony. Juvenile and adult survival showed a strong, but different, north-to-south gradient in survival probability, with lower juvenile but higher adult survival in northern colonies than southern colonies, whereas the spatial pattern of immature survival was less distinct. Neither recruitment nor the proportion of 10-year-old adults alive predicted whether a colony collapsed, declined, remained stable or increased. The distinct spatial pattern in survival suggests variation in regional food availability, which do not seem to drive local population dynamics. The absence of a link between survival and colony trajectories implies that connectivity between populations plays an important role affecting population dynamics.

**Keywords:** demography, *Larus*, Moran's *I*, population dynamics, spatially structured populations.

Assessing the levels and variability in vital rates such as fecundity, recruitment and annual survival is considered a crucial first step to start understanding the population dynamics of a species (Begon *et al.* 1990, Vandermeer & Goldberg 2013). Life history theory predicts that long-lived species, such as many seabirds, invest more in adult survival than in reproductive output (MacArthur & Wilson 1967, Stearns 1992), but different life stages or age groups face very different challenges affecting their survival probability.

Young individuals, exploring their surroundings or migratory pathways for the first time and whose foraging skills might not yet have been fully developed (Daunt *et al.* 2007), face other obstacles than for example recruits entering a breeding population, or established breeding adults provisioning a brood. As a result, post-fledging mortality in the juvenile stage is commonly expected to be higher than mortality in older age groups. Population change in long-lived species is often most affected by changes in adult survivorship (Pfister 1998, Doherty Jr. *et al.* 2004). Then again, adult survival is expected to vary less than juvenile survival (Gaillard & Yoccoz 2003). Gaston and Descamps (2011) found, for instance, that

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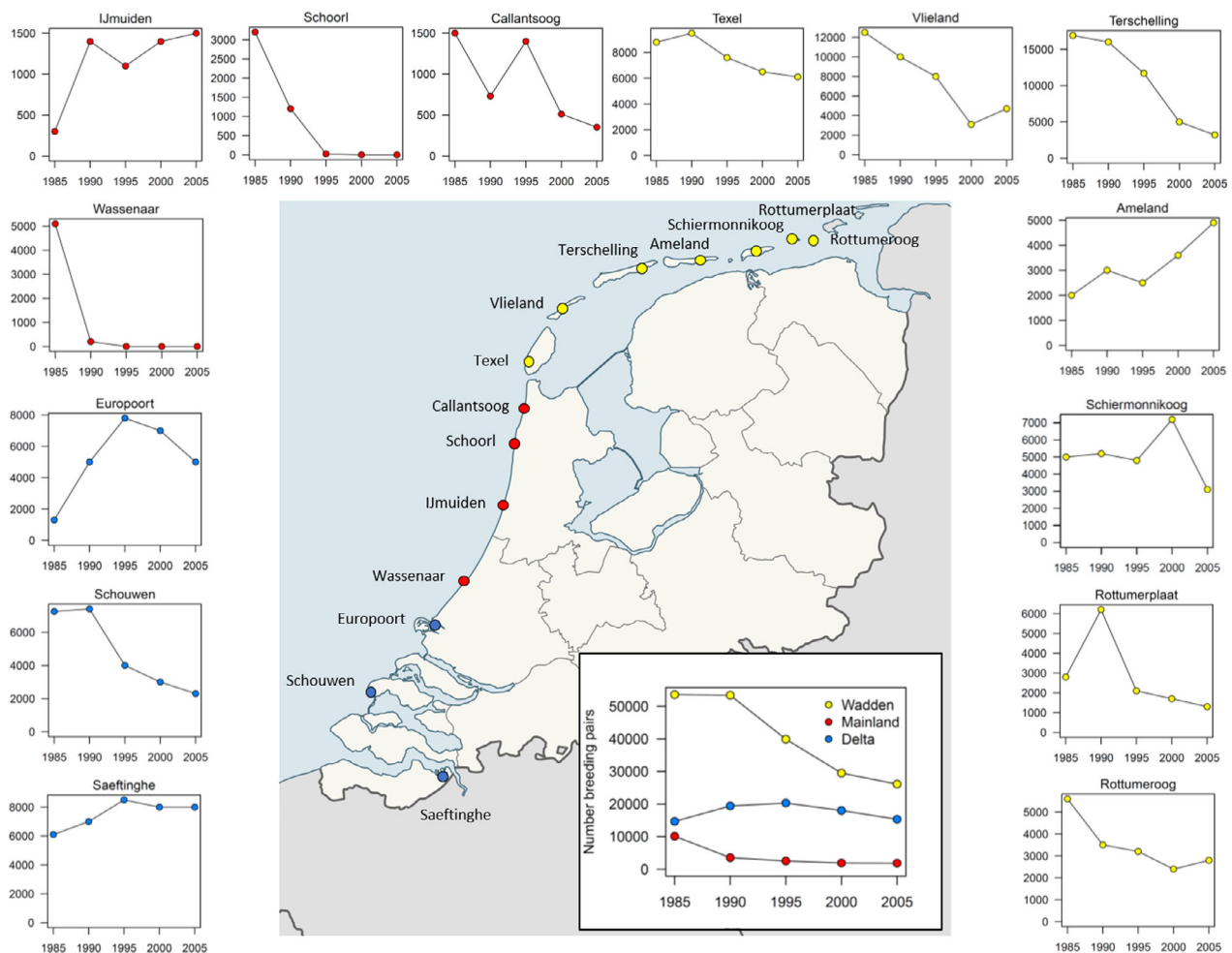
recruitment in Ancient Murrelet *Synthliboramphus antiquus* was driving population sizes. It is acknowledged that understanding what is driving population change in realistic settings is often more complicated and understudied (Beissinger & Westphal 1998, Mills *et al.* 1999, de Kroon *et al.* 2000).

Metapopulation trends, often assessed at national levels, are in fact the result of vital rates in individual populations and the connectivity between them (Pulliam 1988, Hanski 1998). Colonial species, including many seabird species, are typically patchily distributed. During the breeding period seabirds are central-place foragers, returning regularly to their breeding colony. Despite similar habitat preferences and foraging ranges (distances travelled from a colony), birds from neighbouring colonies often show strong spatial segregation (Wakefield *et al.* 2013, Corman *et al.* 2016, Bolton *et al.* 2018, Enners *et al.* 2018), which is suggested to reduce resource competition. Different foraging grounds, resources and the availability thereof may lead to variability in vital rates and population sizes between neighbouring colonies during the breeding season (O'Hanlon *et al.* 2017, O'Hanlon & Nager 2018). Nevertheless, if spatially correlated environmental conditions influence vital rates, then vital rates among closely situated colonies may be more similar to each other than distant sites (O'Hanlon & Nager 2018). Therefore, to understand population trends on regional, national or biogeographical scales, it would be best to evaluate vital rates and trajectories of multiple colonies or populations simultaneously (Holt 1997, Frederiksen *et al.* 2005, Ross-Smith *et al.* 2014). However, it takes large samples of marked birds and many years of data to provide reliable estimates of annual apparent survival for long-lived species (Lebreton *et al.* 1992). To estimate how different life stages and environments affect population growth, long-term datasets in multiple environmental conditions are required. Because of the difficulty of maintaining such long-term studies in multiple sites (Clutton-Brock & Sheldon 2010), these studies are scarce.

European Herring Gulls *Larus argentatus* are long-lived with a mean clutch size of two to three eggs (Glutz von Blotzheim & Bauer 1982), a maximum recorded age of ~35 years (Fransson *et al.* 2020) and an extended maturation as they

start breeding at, on average, 5 years old (Schreiber & Burger 2002). In the Netherlands, breeding numbers of this widespread colonial species increased between the 1960s until the mid-1980s, from just under 17 000 pairs to ~90 000 pairs (an 11.5% increase per year; Spaans 1998). Then, over a period of nearly 40 years, the Dutch Herring Gull population declined to ~32 000 pairs in 2018: a 64% decline overall (Spaans 1998, van Dijk *et al.* 2005, Boele *et al.* 2020). The trends in breeding numbers differed considerably between colonies and coastal regions (Fig. 1). In the south of the Netherlands (Delta area), numbers first stabilized and then increased again by 41% (2.8% per year) until 1996. In the north (Wadden Sea area), numbers stabilized and subsequently declined by 40% (-4.2% per year), while in between, along the mainland coast, most colonies collapsed: an overall decline of ~80% (-12.3% per year; Spaans 1998). In the early 21<sup>st</sup> century, the continuing decline was most pronounced in the Wadden Sea area (Boele *et al.* 2020). In the Delta area, colonies have recently either disappeared or dispersed into numerous smaller sites.

It was not until the mid-1980s, with the advent of the utilization of novel colour rings (individually unique and readable at distance), that an attempt was made to assess annual survival. A large-scale colour-ring scheme was set up, using 14 colonies of Herring Gulls, spread over the entire Dutch coastline (Spaans & de Wit 1985, Camphuysen *et al.* 2011). We used that unique colour ring dataset, operational between 1986 and 2020 (when the last known surviving individual was seen), to investigate the variation in survival probabilities between age groups and across colonies. Furthermore, we evaluated differences in chick condition during ringing and investigated the role of survival until recruitment and of breeding birds on local and regional population trends. We therefore asked: (1) What is the degree to which age classes differ in survival probability? (2) Does age-specific survival probability differ across colonies? (3) Did fledgling condition vary across colonies at the time of ringing? (4) Is there a spatial pattern in age-dependent survival between colonies? Using information gathered from questions 1–4, we qualitatively assessed whether (5) the observed variation in age- and colony-specific survival explains population trends of individual colonies?



**Figure 1.** Map of the Netherlands with Herring Gull study colonies and population trend graphs. The inset graph shows the population trends of the three regions. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## METHODS

### Data collection, ringing colonies

Around 100 Herring Gull fledglings were colour-ringed in each of 12 colonies in 1986 (1247 individuals), 13 colonies in 1987 (1353 individuals) and 14 colonies in 1988 (1395 individuals; Camphuysen *et al.* 2011). All 14 sites are distributed along the North Sea coast of the Netherlands, with distances ranging from 6 to 50 km between colonies (Fig. 1). Seven colonies were located on Wadden Sea islands (Rottumeroog-Texel), four colonies along the mainland coast of the provinces North and South Holland (Callantsoog-Wassenaar), and three colonies in the Delta area (Europoort, Schouwen and Saeftinghe). See

Supporting Information Appendix S1 for specifics per colony. Although fledglings were in general colour-ringed after they reached 30 days, when weights begin to level off, we compared measurements of wing length and body mass as well as a proxy for body condition (residuals of the linear relationship between body mass and squared wing length), during ringing to evaluate potential differences in ringing age between colonies. Body mass was recorded in seven colonies in 1988 (Rottumerplaat, Schiermonnikoog, Terschelling, Texel, Schoorl, Ijmuiden and Schouwen) and wing length in six of these colonies (excluding Schouwen). In subsequent years, colour rings were resighted mainly by citizen scientists and dedicated researchers. Resightings were collected until March 2020 ( $n = 87\,263$ ), when the last known survivor was

recorded for the last time at an age of 32 years. Colour-ringed individuals were resighted year-round in their entire expected flyway: from Denmark in the north to northern France in the south, Poland in the east and the UK in the west (Camphuysen *et al.* 2011). Of 3995 fledglings ringed between 1986 and 1988, 2134 birds (53.4%) were reported at least once as immatures (2–4 years of age) or adults, anywhere within that flyway. This ratio of resightings varied from 34.2% (Ameland,  $n = 310$ ) to 81.9% (IJmuiden,  $n = 105$ ) between ringing sites (average  $54.6 \pm 15.6\%$  se,  $n = 14$  colonies).

In survival studies based on colour-ring resightings, it is assumed that birds and their rings have a similar life expectancy. Particularly in long-lived birds, ring-loss can be a genuine problem (Nichols & Hines 1993). In the colour-ring project described here, individuals were marked with two darvic rings, one on either leg, engraved with a letter, number or symbol in a contrasting shade. Colours used were white, yellow, orange, red, blue, green and black in combinations that were characteristic for each site. Colour fading was an issue in white (turning yellowish), yellow (turning whitish) and orange (turning yellowish) rings, but this was soon recognized. The combination of two colours was unique for each of the ringing sites and the used colours overlapped between colonies. Only in Saeftinghe were two colours used that were not used in any other of the colonies (blue and red). Saeftinghe is also the colony where recent resightings ( $n > 2005$ ) were entirely lacking, suggesting the possibility of increased ring loss for red and blue rings.

The study colonies differed in several ways. Population size ranged from ~300 (IJmuiden) to 17 000 pairs (Terschelling) when the colour-ring project was set up (Fig. 1). Some colonies declined or even collapsed and disappeared, while others remained stable or increased in size, even only for some years. Some mainland colonies faced increasing pressure from mammalian predators, and others were situated on islands without predatory mammals. Key wintering areas of adult birds were mostly deep inland (Germany and the eastern half of the Netherlands) for birds originating from the six eastern Wadden Sea colonies, whereas birds from Texel and further to the south had a more coastal orientation reaching into the coastal zone of Belgium and northern France. For younger birds, the tendency to disperse in a SW direction

and share a common, coastal winter ground (France, Belgium and the Netherlands) was observed (Camphuysen *et al.* 2011). Some colonies were studied for several years at least (breeding success, recruitment rates), whereas others have never been visited since ringing.

## Data analysis

To estimate yearly survival probability, we used colour-ring resightings from 1986 to 2000 instead of until 2020, when the last known individual was reported to be alive. Ring loss became apparent after 10 years, and with an expected lifespan of 11 years (Coulson & Butterfield 1986), the majority of individuals were assumed to have died by 2000. Gulls were resighted year-round, and therefore we had to pool resightings. However, pooling lengthy resighting periods violates one of the assumptions of mark–recapture analyses; namely, that mortalities should happen during the intervals between resighting periods (Lebreton *et al.* 1992). We therefore pooled sightings between July and November, as this period yielded the largest potential for observing colour rings (Camphuysen *et al.* 2011), and discarded the sightings outside this period. If precision is increased by maximizing the sample size while leaving a long enough interval in which 50% of the mortalities happen, then pooling does not generate a bias in survival probabilities (Hargrove & Borland 1994, O'Brien *et al.* 2005). Because fledglings were ringed in July, first-year survival may be slightly biased downward because it is estimated over a longer period than 1 year; i.e. from July to September (midpoint of pooled resightings). We tested whether apparent survival probability differed with age and across colonies with a Cormack–Jolly–Seber mark–recapture analysis (White & Burnham 1999). The probability that a colour-ringed gull is sighted (resighting probability) could be affected by temporal and spatial variation in resighting effort of observers, in combination with behavioural differences of gulls, i.e. colony- and age-dependent wintering site choice (Camphuysen *et al.* 2011) and individual differences in foraging habitat choice (van Donk *et al.* 2020).

To limit the number of models and thereby prevent over-fitting, we used two steps with a set of *a priori* models. First, we tested how many ages (in years after fledging) showed differences in survival probability, by testing one to nine different

age classes, and included a model where survival could vary for juveniles (from ringing to 1 year old), immatures and adults (from 5 years and older). In this first step, resighting probability could vary across colony, between immatures and adults (from 5 years old and older), with observation year as an additional effect. In the second step, we tested whether survival probability differed between colonies and tested whether colony effects were age-dependent (using the number of ages from the first selection step). For that, we tested whether a colony effect occurred in different age groups: on juveniles, immatures, adults, juveniles and immatures, juveniles and adults, immatures and adults, or on each age class. In this step, we also tested model selection support for models without the interaction between colony and age class and without age class in resighting probability, while keeping colony and year in the structure in order to reduce the number of parameters to be estimated.

To test whether those survival probabilities, which we found to vary between colonies, were spatially correlated, we did a Moran's *I* spatial autocorrelation analysis (Moran 1950). A positive Moran's *I*-value indicates that survival probabilities of neighbouring colonies were more alike than those of colonies further apart. Distance between colonies was based on a straight-line between neighbouring colonies. To follow the curve of the coastline, the distances between non-neighbouring colonies are summed distances of neighbouring colonies in between.

Because we lack fertility rates, we could not use matrix modelling such as a Life Table Response Experiment (Caswell 2001) to test whether the observed variation in age- and colony-specific survival explained colony trajectories. Instead, we estimated per colony the proportion of fledglings that would survive until recruitment at the age of 5 years, and the proportion of fledglings that would survive until they are 10 years old (close to the expected lifespan of Herring Gulls). We calculated mean and 95% confidence intervals (95% CI) of both proportions by using a bootstrap approach where we drew 10 000 random samples from the beta distributions of the survival probabilities before multiplying age-dependent survival probabilities. The colony-specific proportions of recruits and 10-year-old birds were qualitatively compared with the population trajectory of the colony within the following 10 years (collapsed, declined, stable

or increased) (Fig. 1) to investigate whether survival probabilities could explain population trajectories.

Body mass, wing length and mass corrected for wing length were compared between colonies where these measures were taken during ringing. Wing length increments show less variation during growth than body mass (Camphuysen 2013) and the relationship between body mass was proportional to squared wing length ( $F_{1,419} = 66.67$ ,  $P < 0.001$ ). We therefore used the residuals of the linear model  $\text{body mass} \sim \text{wing length}^2$  as mass corrected for wing length.

We used RMark (Laake 2013) to run Cormack–Jolly–Seber (CJS) models in R (R Core Team 2017). Because our model structure included multiple age classes, goodness-of-fit could not be easily tested using regular analyses. We therefore used two approaches: (1) we estimated the median  $\hat{c}$  implemented in MARK (White & Burnham 1999) using the model where survival is dependent on age class and colony, and resighting probability is dependent on age class, colony and time, with an interaction between age class and colony; (2) we tested four common tests (Pradel *et al.* 2003) with R2UCare in R (Gimenez & Gaillard 2017) using all encounter histories, and using encounter histories where the first 4 years were removed to exclude the immature age class. We extensively discuss the results of the tests in Supporting Information Appendix S2, and we also examined the robustness of the model selection steps in Supporting Information Appendix S3. Model selection was based on Akaike's information criterion adjusted for small sample sizes and overdispersion (QAICc; Burnham & Anderson 2002). The confidence interval of the survival estimate for the colony where adult survival was close to 1 was re-estimated using a profile likelihood. Moran's *I* statistics were estimated with the permutation test of the package *spdep* (Bivand *et al.* 2013), using 10 000 permutations. To compare mass, wing length and the mass corrected for wing length at ringing between colonies, we used a Tukey HSD test.

## RESULTS

### Age-dependent survival

Apparent survival of Herring Gulls varied over six ages in the first model selection step as follows

(Supporting Information Appendix S3): lowest in the first year after ringing (survival probability 0.53, 95% CI 0.51–0.55), then increasing from 0.81 (95% CI 0.78–0.84) for 1-year-old birds to 0.87 for 2-year-old birds (95% CI 0.84–0.90), 3-year-old birds (95% CI 0.83–0.90) and 4-year-old birds (95% CI 0.83–0.90). Adult birds aged 5 years or older had on average a lower survival probability of 0.80 (95% CI 0.79–0.82). The overlap of confidence intervals of survival in birds between 1 and 4 years old and a competing model where the immature ages are grouped suggests that survival probability for gulls in immature ages are comparable (Appendix S3).

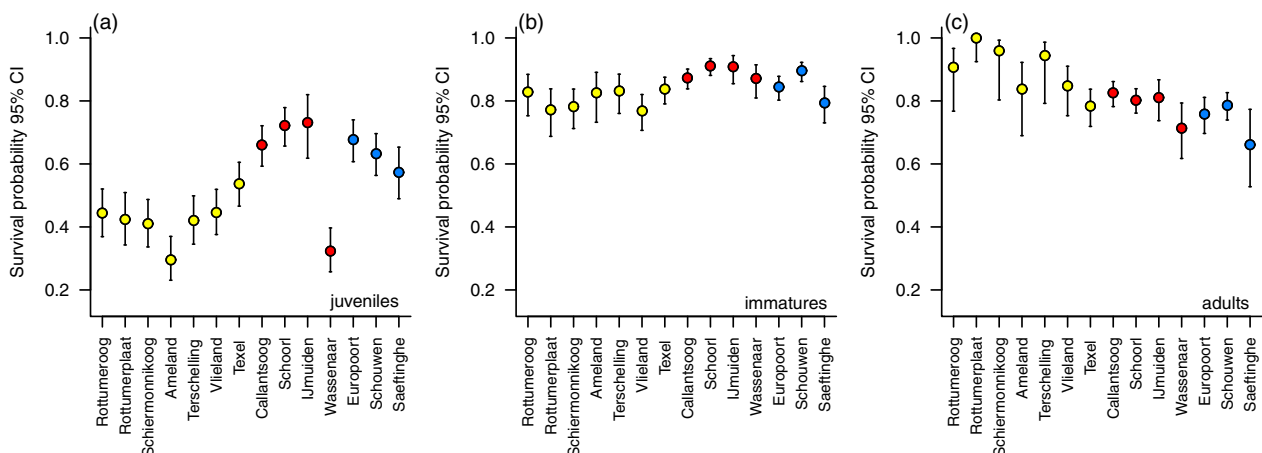
### Survival across colonies

In the second model selection step, the best supported model was a model where survival varied across colonies in the juvenile, immature and adult age classes (Appendix S3). In the first year after ringing, the juvenile age class, survival was lower in juveniles that were ringed in the Wadden Sea area (range 0.30–0.54) in comparison with juveniles from colonies along the mainland coast and in the Delta area (0.57–0.73), with as a notable exception and negative outlier the gulls that fledged near Wassenaar (apparent survival probability: 0.32, 95% CI 0.25–0.40; Fig. 2a). Yearly survival in immatures varied less: between 0.77 (95% CI 0.70–0.82) for birds fledged on Vlieland

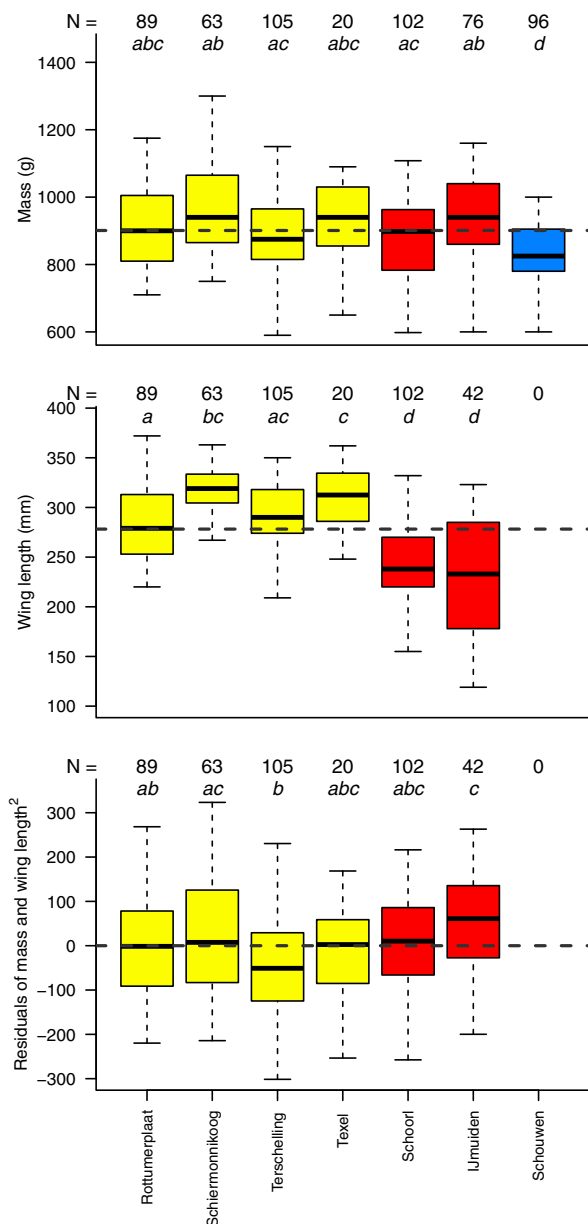
and 0.91 (95% CI 0.88–0.94) for birds fledged near Schoorl (Fig. 2b). Adult (5 years of age and older) yearly survival showed a north-east to south-west gradient in the annual apparent survival probability, with the highest survival for gulls from Rottumerplaat (1.00, 95% CI 0.92–1.00) and lowest survival for gulls from Saeftinghe (0.66, 95% CI 0.53–0.77; Fig. 2c). Adult survival at Saeftinghe (a stable colony for years following the ringing campaigns) was the only distinct outlier. Resighting probability varied across colonies, with the highest probability of those from mainland colonies (on average 0.66) and the lowest of those of Wadden Sea colonies on average (0.34), of which the resighting probability was often higher during the immature age class than during the adult age class. All resighting probabilities are listed in Appendix S3.

### Variation in juvenile condition between colonies

Mean fledgling body mass at ringing ranged between 834 and 969 g and differed significantly between colonies ( $F_{6,544} = 11.96$ ,  $P < 0.001$ ; Fig. 3). A Tukey posthoc test revealed that fledglings in Schouwen were lighter than in all other colonies, and the fledglings in Schiermonnikoog and IJmuiden were heavier than the fledglings in Terschelling and Schoorl. We also found differences between colonies for wing length



**Figure 2.** Age-class-dependent apparent survival of Herring Gulls marked in 1986–1988 in 14 colonies along the Dutch North Sea coast, ordered from north-east to south-west. Colours represent Wadden Sea colonies (yellow), mainland colonies (red) and Delta colonies (blue). (a) Juvenile survival probability per natal colony (from fledging until next summer). (b) Immature survival probability per natal colony, for birds from 1 to 5 years old. (c) Yearly adult survival probability per natal colony, for birds from 5 years old and older. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12023)]



**Figure 3.** Boxplots of mass (upper), wing length (middle) and mass corrected by wing length (the residuals of the relationship  $\text{mass} \sim \text{wing length}^2$ ) (lower) at ringing in 1988 in Herring Gull colonies where these measurements were recorded. Colours represent regions (yellow: Wadden Sea, red: mainland, blue: Delta). Horizontal hatched line shows the mean. Sample sizes are at the top, and the statistical differences between colonies are represented with letters a, b, c and d in such a way that overlapping letters indicate no statistical differences in mass, wing length and residual of  $\text{mass} \sim \text{wing length}^2$ , respectively. Box-and-whisker plots give the median (horizontal line inside the box), interquartile range (box) and range (bars). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

( $F_{5,415} = 57.54$ ,  $P < 0.001$ ) and mass to wing length ratio ( $F_{5,415} = 40.11$ ,  $P < 0.001$ ). In Schoorl and IJmuiden, wing length was statistically smaller than in the Wadden Sea colonies (Fig. 3), resulting in a relative high mass to wing length ratio (Fig. 3).

### Spatial patterns of survival

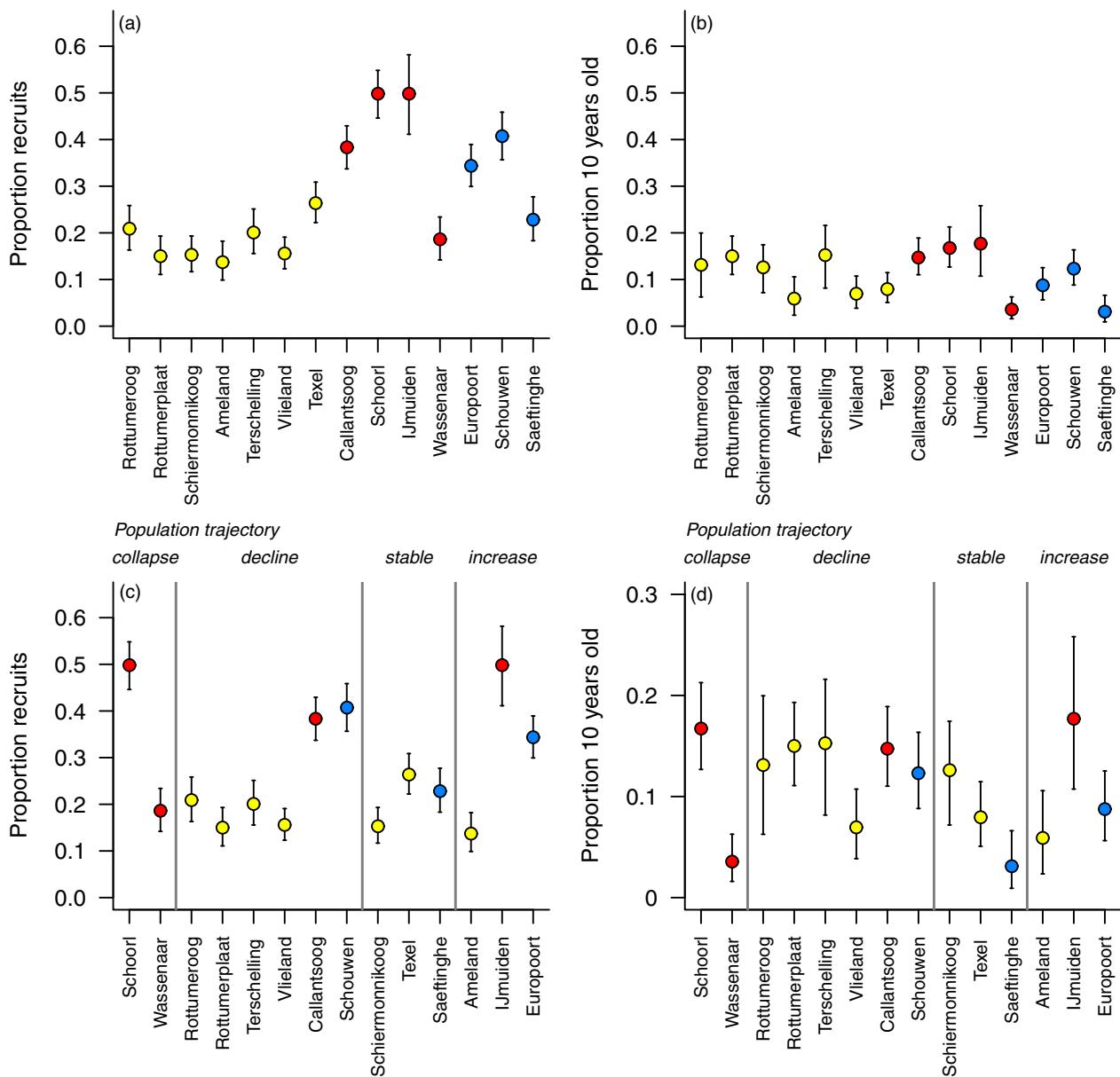
We found evidence for positive spatial autocorrelation of juvenile survival probabilities (Moran's  $I$  statistics = 0.195,  $P = 0.02$ ), immature survival probabilities (Moran's  $I$  statistics = 0.201,  $P = 0.02$ ) and yearly survival of adults (Moran's  $I$  statistics = 0.373,  $P < 0.001$ ), indicating that survival probabilities of gulls in nearby colonies were more similar than those of further colonies. This effect was strongest for adults.

### Can variation in recruitment rate and proportion survived until 10 years of age explain population trends?

The proportion of fledglings surviving until the age of recruitment (at 5 years old) ranged from 0.14 (95% CI 0.10–0.18) for gulls fledged in Ameland to 0.50 (95% CI 0.45–0.55) for gulls fledged in Schoorl (Fig. 4a). Gulls breeding in colonies on the mainland and in the Delta area produced generally more recruits than those from the Wadden Sea area, with the exception of relatively low recruitment in Wassenaar (0.19, 95% CI 0.14–0.23) and Saeftinghe (0.23, 95% CI 0.18–0.28). Yet, the proportion of ringed birds that survived until 10 years old showed considerably less variation (Fig. 4b), ranging between 0.03 (95% CI 0.01–0.07) for gulls fledged in Saeftinghe and 0.18 (95% CI 0.11–0.26) for gulls fledged in IJmuiden.

However, the proportion of juveniles reaching the age of recruitment (Fig. 4c) and the age of 10 years (Fig. 4d) did not relate to the trajectory of each of the natal colonies in the decade following ringing. Two mainland colonies that collapsed during (Wassenaar) or shortly after (Schoorl) the ringing campaigns produced one of the lowest and the highest proportions of recruits, respectively. Similarly, Ameland, a site in the Wadden Sea experiencing a strong population increase, had the lowest proportion of juveniles surviving to breeding age, and IJmuiden, another successful and





**Figure 4.** Proportion of Herring Gull fledglings that survived until (a, c) recruitment age of 5 years and (b, d) until an age of 10 years. (a, b) The proportion of recruits and of those becoming 10 years old in spatial order. (c, d) The proportion of recruits and those becoming 10 years old in order of population trajectory (collapsed, declined, remained stable, increased) in the 10 years after ringing. Colours represent regions (yellow: Wadden Sea, red: mainland, blue: Delta). Bars show the 95% confidence intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12023)]

developing site along the mainland coast, had one of the highest proportions of juveniles surviving to breeding age.

## DISCUSSION

We found age- and colony-specific differences in apparent survival probabilities of Herring Gulls

from 14 colonies along the Dutch coast that fledged between 1986 and 1988. As expected, when not taking colony effects into account, survival probability was lowest in their first year of life. It then rapidly increased in the immature stage and reached its peak for individuals between 2 and 5 years old. Survival probability of adult gulls (5 years old and older) was lower and did

not change with age any further. Studies on immature survival of seabirds are rare and, compared with adult survival, immature survival is often lower (i.e. Fay *et al.* 2015) or equal (i.e. Sandvik *et al.* 2008). That immature Herring Gulls have a high survival probability compared with adults could be explained by: (1) a higher mortality risk for breeders compared with non-breeders, (2) senescence, which may start to play a role in the adult stage, or (3) colour-ring fading or loss, causing a downward bias in adult survival. However, individuals with faded colour-rings could still be identified and we used resighting data up until 2000, after which colour-ring loss became apparent. Survival probability of the juvenile, immature and adult age classes varied across colonies. Yet, the survival probability of immatures, a category of birds that is not yet strictly bound to any colony and its hinterland in summer, varied least and did not have a clear large-scale regional pattern.

### Colony-specific juvenile survival

Colony-specific juvenile survival probabilities were spatially related, i.e. survival was more similar in neighbouring colonies than in colonies at greater distances. Differences across colonies were large and juvenile survival was in general lower in the north (Wadden Sea islands) than along the mainland coast and the Delta area in the south, showing a clear gradient. Assuming at least partially overlapping hinterlands during breeding (Enners *et al.* 2018) and perhaps even overlapping wintering grounds for juveniles originating from neighbouring breeding colonies (Camphuysen *et al.* 2011), the explanation may be related to region-specific differences in resource bases in summer or winter. Fledging mass could provide an indication of resource quality and availability during the chick-rearing period. For example, chicks of Yellow-legged Gulls *Larus michahellis* that fledged in a better condition and Herring Gull chicks with higher pre-fledging growth rates had higher survival probabilities after fledging (Arizaga *et al.* 2015, Bosman *et al.* 2016). We found that, during ringing, mass corrected for wing length was highest in IJmuiden (the mainland colony with highest juvenile survival) and lowest in Terschelling (a Wadden Sea colony), suggesting that juveniles from colonies with the highest juvenile survival may have been in better condition than those from colonies with low juvenile survival.

Understanding when and where in the first year after ringing most mortality occurs might be an important next step to unravel the regional pattern of juvenile survival.

Regional differences in fledgling condition could be caused by food quality and food availability. Gulls breeding in colonies at the mainland coast and Delta area had easier access to landfill sites, which were widely available in the late 1980s, in comparison with the Wadden Sea colonies (Spaans 1998). Food from landfill sites is only a profitable resource if available reasonably close to the breeding colony (van Donk *et al.* 2017, 2019), which might explain higher juvenile survival in mainland colonies. Pons and Migot (1995) found that the number of Herring Gull fledglings per pair decreased after closure of a nearby landfill. Due to national and international legislation, the availability of landfills for our study populations has decreased over the last decades (Camphuysen 2013), which may have consequences for present juvenile survival in mainland colonies as well.

There was a notable outlier in the juvenile survival gradient: the colony at Wassenaar, where survival probabilities of juveniles were less than a third of that in neighbouring colonies. This colony collapsed the year after the ringing campaign ended; in fact, it was increasingly difficult to find enough fledglings for ringing in the final year of the campaign (40 fledglings captured and ringed instead of the ~100 in the preceding years). Of these ringed fledglings, the percentage that was sighted within the first year after ringing decreased (79% in 1986, 11% in 1987 and 5% in 1988), suggesting many never left the colony in 1987 and 1988. Wassenaar was the first mainland colony to disappear following the introduction of Red Fox *Vulpes vulpes* in the area (Bouman *et al.* 1991) and fledglings commonly fell prey to foxes frequenting the colony in these later years. Schoorl and Calantsoog followed the same fate in later years (Woutersen 1992, Camphuysen 2013). It is assumed that, following the initial losses, surviving birds that lost their breeding colonies joined colonies on buildings, in industrial areas or in Fox-free colonies in Europoort (Delta), IJmuiden (mainland) and on Texel (Wadden Sea).

### Colony-specific adult survival

Adult survival probabilities ranged from 0.96 to 0.66 following a trajectory that was the opposite

of that found for survival of juveniles: adult survival was higher in the north (Wadden Sea islands) than along the mainland coast and Delta area. One explanation for this opposite trend is that life-history strategies may differ per colony (Kentie *et al.* 2020); when environmental conditions are more unfavourable, individuals put a higher effort in their own survival than in their reproductive success. Another explanation is perhaps that under unfavourable conditions, only high-quality individuals survive until adulthood. Adult survival for individuals originating from Wassenaar, the colony that was by then collapsed, was comparable to that of neighbouring colonies. The distinct outlier in adult survival probability was for birds from Saeftinghe. These birds were ringed with a blue–red ring combination, two colours not used in any of the other colonies. We assume that the red and/or blue rings were made from a different type of plastic and were prone to more rapid wear and earlier losses, thereby resulting in seemingly lower apparent survival probabilities.

For the mainland and Delta colonies and the colony on Texel, adult survival probability was lower than expected. In long-lived gull species, which have a long period of immaturity, adult annual survival is expected to be ~0.9 (Chabrzyk & Coulson 1976, Glutz von Blotzheim & Bauer 1982). Other studies usually reported adult survival probabilities of Herring Gulls in the same order of magnitude that we found for the Wadden Sea colonies, although these estimates were either from before our study period (Brown 1967, Chabrzyk & Coulson 1976, Coulson & Butterfield 1986) or from populations breeding in Canada (Allard *et al.* 2006, Breton *et al.* 2008), with the exception of the study of Wanless *et al.* (1996), which found a relatively high survival estimate of 0.88 for the period 1990–1994. Pons and Migot (1995) found lower survival probabilities in the second half of their study period between 1983 and 1989 in a Herring Gull colony in France, and Rock and Vaughan (2013) also found declining survival estimates during their study period from 1992 to 2006 in an urban Herring Gull population. Other, more recent studies found adult survival probabilities that were more comparable to the lower survival probabilities along the mainland coast in our study (Camphuysen & Gronert 2012, Dierschke *et al.* 2021). Overall, these estimates

suggest that survival probabilities for the European Herring Gull populations are declining, which may contribute to their declining population size.

Survival can be affected by natural factors such as ageing and disease, and nutritional stress resulting from natural fluctuations in resources or inter- or intraspecific competition. Survival can also be affected by anthropogenic factors, such as hunting, persecution, toxic stress (chemical pollutants), collisions with traffic or wind turbines, or human-made changes in food availability (Vauk & Prüter 1986, Spear *et al.* 1987, Bradbury *et al.* 2014). These factors can vary between age groups (given differences in life-history status and age-specific life experience) as well as between cohorts and regions (environmental factors, levels of protection or persecution). Besides low overlap in foraging regions between colonies during the breeding period (Enners *et al.* 2018), a link was found between the region of the breeding colony and the wintering region in our study populations (Camphuysen *et al.* 2011). Such ‘migratory linkage’ has also been found in Herring Gulls in the UK (O’Hanlon *et al.* 2022) and in American Herring Gulls *Larus smithsonianus* (Anderson *et al.* 2019). These differences in wintering areas and consequently habitats in American Herring Gulls have been suggested to be the cause of differing survival rates between those breeding in the Atlantic region (from 0.80 to 0.83) and those breeding in the Great Lakes and the Arctic area (0.87 and 0.91, respectively; Anderson *et al.* 2019). Kralj *et al.* (2018) also suggested that survival of Yellow-legged Gulls breeding along the Adriatic coast was dependent on colony and food supplies in wintering areas.

Sudden and strong declines in annual survival probabilities in earlier studies have sometimes been related to declines in the availability or quality or the resource base (Breton *et al.* 2008, Rock & Vaughan 2013). Yet, after closure of a heavily used landfill site close to a Herring Gull colony, Pons and Migot (1995) could not detect a direct change in survival probability, despite a decline in adult mass. The spatial relationship of adult survival across colonies we found suggests some common environmental factors among neighbouring colonies that is influencing adult survival; the source, however, is unclear.

### Can survival explain population trends of individual colonies?

Each of our study colonies differed remarkably in their fate. Understanding variation in demographic parameters could help understanding of the drivers behind this decline (Oro *et al.* 2004, Genovart *et al.* 2018), yet whether or not a colony declined or increased in population size in the following decade was not reflected in the proportion of fledged gulls surviving until recruitment age or in the proportion that reached 10 years of age. Similarly, Juez *et al.* (2015) tested whether Yellow-legged Gulls in northern Spain that hatched in colonies with decreasing population trends had lower survival rates than those from stable or increasing colonies, but they failed to find a link between survival probability and colony trends. These missing links between population trends and survival probability suggest that it is likely that juveniles dispersed from declining populations to populations which increased in breeding pairs, or to fragmented breeding populations in industrial or urban areas (Rock & Vaughan 2013). The proportion of recruits that breed in their natal colony (natal philopatry) in Herring Gulls has been estimated to be between 39% (Spaans 1971) and 77% (Chabryk & Coulson 1976). These rates of recruitment are estimates from colonies where gulls were culled and therefore may be underestimates, yet it shows their capability to disperse to other colonies. Although our dataset is limited because some colonies were not revisited after marking, of those that were seen in a colony during the breeding months, ~60% were seen in their natal colony, and those individuals that seem to have dispersed moved to a nearby colony. The fact that the immature and adult survival probabilities of gulls originating from collapsed or declining colonies were similar to those of gulls from adjacent colonies supports the importance of natal dispersal for population regulation. Another explanation of why we did not find a link between survival and population growth could be that the three birth cohorts (1986–1988) that were marked deviated in survival probabilities from other birth cohorts of which the population was made up. However, this deviation would have to be quite large.

Assuming that the survival of the three birth cohorts was representative, the absence of a link

between survival and colony trajectories may point towards a source–sink metapopulation structure of breeding Herring Gulls (Pulliam 1988, Runge *et al.* 2006). Connectivity between breeding populations often forms an important role in maintaining population sizes in a fragmented population (Kentie *et al.* 2014, Reichert *et al.* 2021). However, the Herring Gull metapopulation continued to decline, suggesting a lack of sufficient source populations which can maintain sink colonies. As Newton (1998) pointed out, to understand ultimately what is causing population developments, additional to studies of reproductive and mortality rates, knowledge of external limiting factors are required, such as whether resource levels or other factors differ between areas.

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### AUTHOR CONTRIBUTIONS

**Rosemarie Kentie:** Formal analysis (lead); methodology (lead); software (lead); writing – original draft (lead); writing – review and editing (equal). **Judy Shamoun-Baranes:** Funding acquisition (equal); methodology (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Arie L. Spaans:** Conceptualization (lead); data curation (equal); funding acquisition (equal); investigation (lead); project administration (lead); resources (lead); writing – review and editing (equal). **C. J. Camphuysen:** Data curation (equal); formal analysis (supporting);

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## CONFLICT OF INTEREST

There is no conflict of interest.

## ETHICAL NOTE

Bird ringing was permitted and the ringers were licensed by the Dutch Centre for Avian Migration & Demography.

## Data Availability Statement

Data associated with this manuscript are archived in the Data Archive System (DAS) of NIOZ Netherlands Institute for Sea Research and publicly available at <https://doi.org/10.25850/nioz/7b.b.gc>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1** Characteristics per colony (no. of ringed, no. resighted, location, colony fate).

**Appendix S2** Goodness-of-fit tests of mark–recapture models.

**Appendix S3** Model selection procedure, and parameter estimates of the best supported model.