Research Paper

Identifying spatial drivers of long-term population growth in three large gull species: the importance of mink farms and urban areas

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ABSTRACT. Population growth generally shows extensive spatial variation within species, but the proximate and ultimate drivers of this variation are often poorly understood. For highly mobile colonial breeders, population growth is expected to be linked to resource availability within a considerable radius of the colony. We analyzed the relationship between population growth over the period 2000–2020 and resource availability for three large gull species in several hundred colonies in Denmark. Colony growth rates showed strong spatial autocorrelation for Herring Gull *Larus argentatus*, whereas no such relationship was apparent for the other two species (Great Black-backed Gull *L. marinus* and Lesser Black-backed Gull *L. fuscus*). Colony growth rates of Herring Gulls were correlated with relevant proxies of food availability within species-specific foraging ranges, including the extent of urban and subtidal foraging habitats, and the number of mink farms. No such correlations were found for the other two species. The positive relationships of Herring Gull colony growth with the number of mink farms and the extent of built-up area were particularly interesting, as they highlighted the strong dependency of this species on human-associated food sources. Furthermore, Denmark closed all mink farms in late 2020 because of concerns about the spread of SARS-CoV-2 virus between farms and between minks and humans, culling approximately 17 million minks. This dramatic change in food availability is expected to have a negative impact on the Danish Herring Gull population, which in recent years has fared better than in the neighboring countries.

Identification des éléments moteurs territoriaux liés à la croissance à long terme de la population de trois espèces de gros goélands : l'importance des visonnières et des zones urbaines

RÉSUMÉ. La croissance de la population présente généralement une variation spatiale importante au sein des espèces, mais les moteurs immédiats et globaux de ces variations restent souvent mal compris. Dans le cas de la reproduction coloniale hautement mobile, la croissance de la population semblerait liée à la disponibilité de ressources dans un rayon important de la colonie. Nous avons analysé la relation entre la croissance de la population au cours de la période 2000-2020 et la disponibilité des ressources pour trois espèces de gros goélands dans plusieurs centaines de colonies au Danemark. Le taux de croissance des colonies témoignait d'une forte auto corrélation spatiale chez les goélands argentés *Larus argentatus*, alors qu'aucune relation de cette nature n'était visible chez les deux autres espèces (goéland marin *L. marinus* et goéland brun *L. fuscus*). Le taux de croissance des colonies de goélands argentés était lié à des éléments pertinents comme la disponibilité de nourriture dans les aires d'alimentation spécifiques à l'espèce, y compris l'étendue des habitats d'alimentation urbains et infratidaux et le nombre de visonnières. Aucune corrélation semblable n'a été identifiée pour les deux autres espèces. Les relations positives entre la croissance des colonies de goélands argentés d'une part, et le nombre de visonnières et l'étendue des zones construites d'autre part, sont particulièrement intéressantes, car elles soulignent la forte dépendance de cette espèce vis-à-vis des sources d'alimentation d'origine humaine. En outre, le Danemark a fermé toutes ses visonnières à la fin 2020 en raison de préoccupations concernant la propagation du virus SARS-CoV-2 entre les élevages et entre les visons et les humains, abattant environ 17 millions de visons. Ce changement spectaculaire de la disponibilité de nourriture devrait avoir un impact négatif sur la population de goélands argentés au Danemark, qui ces dernières années, obtenait de meilleurs résultats que les pays voisins.

INTRODUCTION

Understanding the factors that drive patterns of avian distribution and abundance is a fundamental goal in ecology and conservation (Sutherland et al. 2009, 2013, Bolton et al. 2019). Spatial correlation in population growth rate may indicate a spatially correlated environment; this is known as the Moran effect (Moran 1953, Ringsby et al. 2002, Liebhold et al. 2004, O'Hanlon and Nager 2018). On the contrary, diverging population trends may indicate differences in local environmental

conditions. Factors influencing population dynamics are often identified using long-term data sets, but the generality of the findings can be compromised when studies are limited to a few sites, especially if the species in focus has a clumped distribution, like colonial waterbirds and seabirds, and are exposed to spatially highly variable environments. Alternatively, an array of study sites throughout the range of a species can be useful to complement single-site studies by providing a clearer picture of which drivers correlate with population growth (Sedinger et al. 2002,

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Frederiksen et al. 2005a, Robinson et al. 2013), and help understanding larger scale changes in species abundance (Liebhold et al. 2004, O'Hanlon and Nager 2018). Studying populations on a larger scale can increase the power of the study, as populations are likely to be exposed to a greater range of environmental conditions (Bairlein et al. 2013). Furthermore, such studies have been useful in identifying the drivers that influence variation in demographic parameters and how population size or density is regulated (Frederiksen et al. 2005a).

Seabirds are more threatened, and their conservation status has deteriorated faster over recent decades, than any other comparable avian group (Croxall et al. 2012). A high proportion of seabird species are classified as near threatened or threatened according to the Red List of the International Union for the Conservation of Nature (IUCN; BirdLife International 2015). Unfortunately, drivers behind spatial variation in population trends are generally poorly understood, although they have important implications for understanding changes in abundance across the range of species and for their population management. In the case of colonially breeding seabirds, there is evidence that they form spatially distinct populations and their demographic traits vary across different spatial scales, with inter-population differences found in parameters such as adult survival, productivity, and population growth rate (Frederiksen et al. 2005a, Harris et al. 2005, Cordes et al. 2015). As central place foragers during the breeding season, seabirds travel back and forth to the sea (or terrestrial habitats) constrained by the need to regularly provision and care for their offspring (Bolton et al. 2019), which radically affects their spatial ecology.

Seabird population growth is frequently affected by resource availability in their local environment (Davoren and Montevecchi 2003, Oro et al. 2004, O'Hanlon and Nager 2018). Most coastal ecosystems on which seabirds rely have been drastically altered by anthropogenic activities in the last decades, through overexploitation of resources, habitat destruction or modification, climate change, and introduction of invasive species (Grémillet and Boulinier 2009, Butchart et al. 2010, Cury et al. 2011). Such pressures are likely to influence species' population trends over different spatial scales (Brown et al. 1995), from disturbance and predation at a local level, to habitat change and severe or infrequent weather events that can act over local but also broader scales. At the same time, several species have benefitted from the increased availability of new food sources derived from anthropogenic activities (Oro et al. 2013). For example, populations of Northern Gannets (*Morus bassanus*) and Great Skuas (*Stercorarius skua*) are well known to rely on discards from the fishery activity (Votier et al. 2013, Church et al. 2019), while Yellow-legged Gulls (*Larus michahellis*) seem to be highly dependent on refuse dumps, urban-related subsidies, and fishery discards (Duhem et al. 2008, Karris et al. 2018, Méndez et al. 2020). Food availability is an important environmental factor that can be heavily affected by anthropogenic activities and directly influences the annual productivity and survival of seasonally breeding birds (Frederiksen et al. 2005b, O'Hanlon et al. 2020). Opportunistic foragers like gull species that can take advantage of both marine and terrestrial habitats, may be able to buffer themselves against changes in local food availability by switching to alternative food resources (Tyson et al. 2015, Sotillo et al. 2019,

Langley et al. 2021). However, the relative quality of these substitutes can have a significant impact on the outcome of such switches in diet (Österblom et al. 2008, White 2008), because, e.g., the energy content of consumed items has a direct influence on breeding success. This implies that population growth rates in gull species are likely to be influenced by the distribution of resources.

The principal objective of this study was to investigate the spatial variation of long-term population trends of the three large gull species, Great Black-backed Gull (*Larus marinus*), Lesser Black-backed Gull (*L. fuscus*), and Herring Gull (*L. argentatus*), breeding in Denmark from 2000 to 2020. The analysis was conducted across hundreds of colonies within a heterogeneous landscape of potential foraging habitats. Thus, as gulls generally use food sources within the vicinity of their colonies during the breeding season (Sotillo et al. 2019), we investigated whether trends in colony size were linked to resource availability around them. We expected that colonies located close together would show similar population trends, because birds exploit similar local resources and experience similar environmental conditions. Furthermore, because the analysis was conducted separately for each species, we explored whether the potential resources most closely linked to long-term population changes varied among species. This large-scale study, therefore, aimed to demonstrate the importance of both natural and anthropogenic food availability for the population dynamics of large gulls.

METHODS

Study area
The development of breeding colonies of the three gull species was investigated within Denmark. The study area consists of the peninsula Jutland, the two major islands Funen and Zealand, and about 407 smaller islands, which are dispersed between the North Sea and the Baltic Sea (Turner et al. 2014). These seas are connected through Skagerrak, Kattegat, and the Danish Straits, composing a system of extensive shallow waters. Agriculture has been the main industry for centuries in Denmark, and farming still plays a vital role in the economy. Denmark is the most intensively farmed country in Europe, with wheat, barley, rapeseed, maize, and grass and forages in rotation as the main crops. Animal husbandry includes a very large pig industry, as well as dairy cattle, mink, and chickens. Population density is moderately high (mean 136 inhabitants/km²), but highly spatially variable.

Study species
We studied the three species of large gulls that are common in northern Europe: Great Black-backed Gull, Lesser Black-backed Gull, and Herring Gull. Even though the three species are closely related, there are some differences in their foraging ecology and diet related to their relative size and subtle differences in morphology (Götmark 1982, 1984, Kim and Monaghan 2006). The populations of the three species have also developed differently in Denmark.

The Great Black-backed Gull is the world's largest gull, and it is sedentary or a short-distance migrant (Olsen 2010, Coulson 2019). As an opportunistic forager, its diet varies greatly (Götmark 1982, 1984, Garthe and Scherp 2003). Fish provided by human activities such as fishery discards or fish cleaning at ports, as well as caught

by shallow plunge dives offshore, constitutes an important food source. This species is also known to feed on waste in landfills, marine and terrestrial invertebrates, small mammals, and even some adult seabirds such as Atlantic Puffins (*Fratercula arctica*). In addition, during the breeding season it can eat large numbers of eggs and chicks of other breeding birds. The Great Black-backed Gull has been extending its breeding range in Europe for more than a century and started breeding in Denmark in 1930. Initially numbers increased fairly slowly reaching 330 pairs in the late 1960s. The population continued to grow to 1400 pairs in 1988, and had reached 3200 pairs by 2010, where after the population stabilized (T. Bregnballe, *unpublished data*). It is important to note that one-third of the population (1100 pairs) has been breeding in a single colony in northern Kattegat since 2013.

The Lesser Black-backed Gull is the smallest species studied here. Unlike the other two species, it is a long-distance migrant, travelling to the south of Europe and Africa in winter. Its lower wing loading, relative to the other species, means that it is better adapted for long-distance flight and has more maneuverability. The Lesser Black-backed Gull is mainly considered as a highly marine species, feeding on fish caught at sea by plunge diving or taken as waste at fishing boats (Kubetzki and Garthe 2003). Anthropogenic habitats such as agricultural lands, refuse dumps, and urban areas also provide important feeding opportunities, and the species has increased its terrestrial feeding in several parts of Europe (Coulson 2019). The species also feeds on small mammals, ducklings, earthworms, beetles, grain, and berries during the breeding period (Götmark 1982, 1984). The Lesser Black-backed Gull population in Denmark declined from approximately 2000 pairs in 1940 to approximately 1000 pairs in 1970, where after the trend reversed to a steady increase reaching 5400 pairs in 2001 (T. Bregnballe, *unpublished data*). Numbers have subsequently declined somewhat to 4900 pairs in 2020.

The Herring Gull is intermediate in size. Like the Great Black-backed Gull, it is sedentary or a short-distance migrant. More work has been conducted on the diet of Herring Gulls, concluding that food supplied by man is more important in their diet than for the other two species (Coulson 2019). These anthropogenic sources are mainly fish offal from harbors and fishing boats (Garthe and Scherp 2003), and waste from landfills and urban areas. Furthermore, they feed on earthworms and grain in agricultural fields, and on marine invertebrates such as crabs, mussels, and echinoderms in intertidal areas. Other common diet items are insects (mainly beetles), berries, freshwater fish, small mammals, and during the breeding season chicks of other pairs or other bird species (Götmark 1982, 1984). In the 1960s, the Herring Gull benefitted enormously from feeding on waste at landfills as well as fish offal, and the Danish breeding population increased more than 10-fold in just 20 years, from approximately 7000 pairs in 1950 (Møller 1978) to 76,000 pairs in 1970 (Bregnballe and Lyngs 2014). With the closure of landfills, together with the implementation of culling programs around the capital region of Denmark, numbers subsequently decreased to 58,000 pairs in 1988. However, with an expansion in the western part of the country overall numbers increased again, reaching 88,000 pairs in 2010 (Bregnballe and Lyngs 2014). Since then, numbers have been fairly stable (T. Bregnballe, *unpublished data*).

In contrast, Herring Gulls have decreased in most neighboring countries in recent decades (Hario and Rintala 2016, Nager and O'Hanlon 2016, van Roomen et al. 2018, Koffijberg et al. 2020).

Colony growth rates

The basic data were obtained through an unpublished database developed at Aarhus University, which contains the results of counts of breeding pairs of colonial coastal birds in Denmark during 1965–2021. Censuses have been conducted by professional staff as well as by volunteers. In some nature reserves, the development of gull populations has been followed through annual or almost annual counts, while other important sites have also been monitored on a regular basis. Larger colonies were typically counted more regularly, while smaller breeding sites tended to be counted less frequently, in some cases only a few times in the whole study period. Consequently, the coverage of counted colonies across the study area varied among years. The number of breeding pairs present at each locality were estimated following one or more of the following standardized methods: (1) direct counts of nests, (2) flush counts, (3) counts of incubating individuals from an elevated position (using binoculars and/or a telescope), or (4) counts of individuals (or incubating birds) on aerial photographs. Marked quadrate or transect counts of nests were conducted to extrapolate the numbers of breeding pairs in a few large colonies. The precision of counts varied because of a number of factors including (a) the timing of censuses of nests in relation to the phenology of the gulls, (b) how synchronously the gulls bred in the specific year, (c) the experience and counting skills of the observer, (d) the characteristics of the colony area, and (e) the exact value of the conversion factor used when estimating numbers of breeding pairs from numbers of individuals present in the colony area. Since 1996, the most widely used conversion factor has been 0.7 as recommended by Hälterlein et al. (1995). Recent comparisons of methods (partly by the use of unmanned aerial vehicles) have documented that observers tend to underestimate the size of large breeding colonies when trying to count the birds present in the colony area (T. Bregnballe, *unpublished data*).

In order to analyze changes in the abundance of breeding gulls over the period 2000–2020, colony growth rates (GR) were calculated from estimates of numbers of breeding pairs at each locality. Only colonies with three or more counts during the study period were considered for the analysis. GRs were quantified for each colony, using generalized linear models with log link and quasi-Poisson error to account for colonization and extinction events that occurred throughout the study period.

Resource availability

Local habitats

Large gulls are generalist foragers that rely on both marine and terrestrial habitats, therefore, in order to investigate any relationship between gull population changes and resource availability, information on proxies that reflect the availability of both marine and terrestrial potential-foraging habitats were included as covariates in the models. Spatial variation in potential resources referred to the period 2010–2019, because earlier habitat data were unavailable, or did not have sufficient spatial resolution for the analysis.

One important foraging habitat for large gulls is the subtidal zone, which provides invertebrate prey such as bivalves, crustaceans, polychaetes, echinoderms, and small fish (O'Hanlon et al. 2017). According to Sibly and McCleery (1983), Herring Gulls are able to forage on invertebrates down to 3.1 m below the sea surface. Hence, as a proxy of resource availability in this habitat the area between the shoreline and 3 m depth was extracted from bathymetry data from the Danish Maritime Safety Administration (50 m grid), which was improved in the very shallow areas with transect depths from the Danish National Monitoring Database (ODA, https://odaforalle.au.dk; C. Göke, *unpublished data*). The tidal range in the study area is generally small and was not taken into account, except for the south-westernmost part of Jutland, where the tidal range can exceed 2 m (Ribergaard 2019). The potential subtidal zone in this region was defined as the area between the shoreline and 4 m depth (Appendix 1, Fig. A1.1). Large gulls commonly scavenge on fishery discards from fishing boats or ports (Tasker et al. 2000, Karris et al. 2018). Scavenging seabirds make extensive use of this fishery waste, especially of offal and roundfish, but also to some extent of flatfish, cephalopods, and benthic invertebrates (Camphuysen et al. 1995, Garthe et al. 1996). Thus, fishing activity could be a suitable index for foraging opportunities on fish provided by human activities, measured in this case as fishery landings because there are no publicly available data on discard quantities. Data on fishery landings were extracted from the national authorities (Danish Fisheries Agency 2020), and represented the total landings from vessels in Danish harbors between 2010 and 2019, excluding those from the fishmeal industry and from typical deep-sea fish species. The data contained the landings in tonnes of the following groups: gadoids, flatfish, freshwater fish, other fish (most importantly herring and mackerel), and invertebrates, which included shrimps, lobsters, deepwater prawns, squids, crabs, and sea urchins. Only the landings from the second quarter of the year (the main breeding period of the three gull species) were considered, and were averaged for each harbor for the period 2010–2019 in order to get a static variable (Appendix 1, Fig. A1.2).

Fur farms constitute another source of seafood for large gulls. Because fish waste and forage fish such as sandeels (*Ammodytidae*) are used as the principal feed for farmed American minks (*Neovison vison*), fur farms provide predictable foraging opportunities for gulls (Wilhelm et al. 2016, Juvaste et al. 2017, Shlepr et al. 2021). Hence, data on active mink farms were extracted from the national livestock register (Danish Veterinary and Food Administration 2020). The list of active mink farms in 2019 contained 1135 farms, which were used as an approximation of the distribution of mink farms between 2000 and 2020 (Appendix 1, Fig. A1.3). Other terrestrial resources that large gulls exploit are agricultural lands, where they collect earthworms, insects, and grain; and built-up areas, where they scavenge on waste (Coulson and Coulson 2008, Duhem et al. 2008). In Denmark, agricultural areas have decreased slightly since the 1960s, but they still make up approximately 60% of the total land area. However, permanent grassland provides more food resources for birds than intensively grown annual crops (McCracken and Tallowin 2004). Built-up areas (human settlements, buildings, facilities, etc.), on the other hand, have not stopped increasing since the 19th century and accounted for 10%

of the total land area in 2000 (Levin and Normander 2008). Grasslands and built-up areas were extracted from "basemap02," a public geodatabase that contains a nationwide map (10 m grid) of land use and land cover of Denmark for the year 2016 (Levin et al. 2017). Grassland was defined as the area covered by extensive-agricultural lands and semi-natural grasslands, and built-up area as the area covered by city centers, urban areas, buildings, and industries (Appendix 1, Figs. A1.4-5).

Foraging ranges

Potential maximum foraging distances differ between species of large gulls, most likely because of specific traits such as feeding behavior, wing loading, and flight speed (Götmark 1982, Camphuysen 1995, Jovani et al. 2016). Thaxter et al. (2012) reviewed studies of foraging ranges of many seabird species, including Lesser Black-backed and Herring Gull. The mean maximum foraging ranges of the two species were, respectively, 141.0 ± 50.8 km and 61.1 ± 44 km. For Great Black-backed Gull, few studies have estimated its foraging range, and according to the poor information available, the maximum is 60 km (Jovani et al. 2016, Maynard and Ronconi 2018). In a Danish colony, where a small sample of three individuals were tagged with GPS loggers, foraging trips of up to 61.9 km were recorded (J. F. Linnebjerg, *personal communication*). Therefore, foraging ranges were defined as 60 km buffers around colonies for Great Black-backed and Herring Gulls, and 140 km buffers for Lesser Black-backed Gulls.

We assumed that the distribution of the foraging gulls follows a gradient of decreasing density of foragers with increasing distance from the colony, reflecting the increasing travel costs associated with foraging at more remote locations. When resource variables were extracted from within the specific potential foraging ranges around each of the species' colonies, we attempted to represent this gradient by giving different weights to resources depending on the distance to the colony. The buffers were partitioned into rings with intervals of 5 km for Great Black-backed and Herring Gulls, and 10 km for Lesser Black-backed Gulls. The area or number of each resource variable was extracted for each of the rings using ArcMap 10.5.1. Then, the value for each variable in a ring was weighted by the inverse distance of that ring from the colony, and finally the values for all the rings were summed in order to get the definitive value of each resource variable for each colony of each species (Appendix 2, Fig. A2.1).

Statistical analysis

All statistical analyses were carried out in R, Version 3.6.3 (R Core Development Team 2019). In total, 197 colonies of Great Black-backed Gull, 105 colonies of Lesser Black-backed Gull, and 263 colonies of Herring Gull were used for the analysis, after colonies appearing in only one year of the study were excluded from the analysis. In order to investigate spatial clustering in colony GR, Moran's *I*, an index of spatial autocorrelation (Moran 1953, Overmars et al. 2003), was calculated for each species using the *ape* package (Paradis et al. 2004). This index is based on individual colony GRs and their location; if the observed *I* value is significantly greater than the expected *I*, GRs are positively autocorrelated (spatially clustered) and vice versa.

Spatial regression is a tool for robust statistical inference when response or predictor variables are spatially autocorrelated (Dormann et al. 2007, Rousset and Ferdy 2014). We used spatial

regression models to determine whether the variation in population GR was affected by resource availability in the landscape surrounding the colonies using the *spaMM* package (Rousset 2021). GR was the response variable, the different resources per colony (i.e., fishery landings, mink farms, subtidal zone, grassland, and built-up area) were the covariates, and the mean colony sizes in the study period were used as weights when regressing GR against the spatial predictors. Thus, GRs from bigger colonies were more influential than GRs from smaller colonies. Residual plots were inspected and all the predictor variables were log transformed in order to ensure normality, improve homogeneity of variances, and reduce the influence of outliers. Multi-collinearity between predictor variables was examined, variance inflation factor (VIF) > 10 suggesting severe collinearity when all the predictors were fitted together for each of the species (Appendix 3, Table A3.1). There was a strong positive correlation between grassland and built-up area for the three species (GBBG: r_s = 0.78, P < 0.001, n = 197; LBBG: r_s = 0.66, P < 0.001, n = 105; HG: r_s = 0.75, P < 0.001, n = 263). Because severe collinearity can have important and detrimental effects on the estimated regression parameters, the explanatory variable grassland was omitted from the analysis. We fitted all possible linear combinations of the four potential resource variables (i.e., fishery landings, mink farms, subtidal zone, and built-up area) for each species, and subsequently used the Akaike Information Criterion (AIC) to find the "best" fitting models. In addition, Akaike weights (w_i) were calculated in the *MuMIn* package (Bartoń 2020) and compared across candidate models. Finally, the top models were selected for each species based on AIC values (ΔAIC < 2), and the relative importance of each predictor variable was calculated by summing up all model Akaike weights in which the given parameter occurred. Residual plots and VIF values were inspected again for the best fitting models (Appendix 3, Table A3.2).
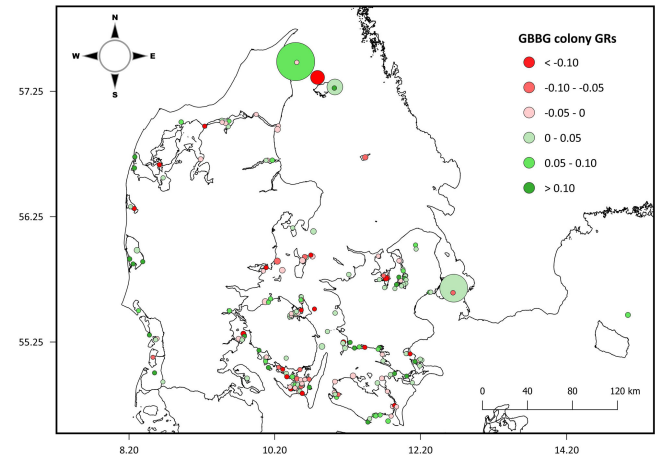
RESULTS

Spatial variation in GR

The autocorrelation analysis revealed that colony growth rates (GR) of Great Black-backed and Lesser Black-backed Gull colonies did not show any significant spatial clustering (GBBG: *Moran's I* = 0.014, P = 0.342, Fig. 1; LBBG: *Moran's I* = 0.029, P = 0.318, Fig. 2). On the contrary, GRs of Herring Gull colonies were spatially clustered (HG: *Moran's I* = 0.040, P = 0.005). Particularly, colonies located in the east of the study area mostly decreased, whereas the majority of colonies to the west increased (Fig. 3).
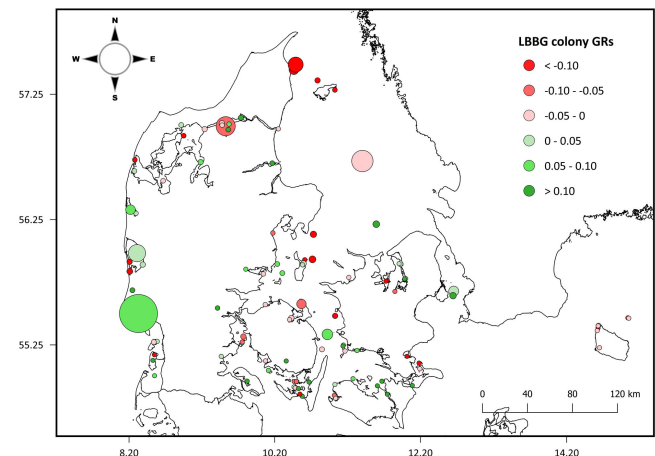
Spatial variation in resource availability

The most competitive spatial regression models explaining the variation in colony GR were identified for each species (Tables 1, 2, and 3). The best fitting model for the Great Black-backed Gull indicated that the size of the subtidal zone within the foraging range was the most relevant variable explaining such variation, but the 95% confidence intervals overlapped with zero (β = 0.0226, *%95 CI* = -0.0075–0.0536). Thus, we cannot assume that this variable had a significant effect driving the pattern of colony GR. For the Lesser Black-backed Gull, the top model included only the intercept, indicating that none of the variables succeeded in explaining the variation in colony GR. Finally, for the Herring

Fig. 1. Spatial variation in population growth rate (GR) by colonies in the period 2000–2020 for Great Black-backed Gull (*Larus marinus*). The color of the circle depicts the mean colony GR over the study period, while the size of the circle reflects the relative mean size of the colony.

Fig. 2. Spatial variation in population growth rate (GR) by colonies in the period 2000–2020 for Lesser Black-backed Gull (*Larus fuscus*). The color of the circle depicts the mean colony GR over the study period, while the size of the circle reflects the relative mean size of the colony.
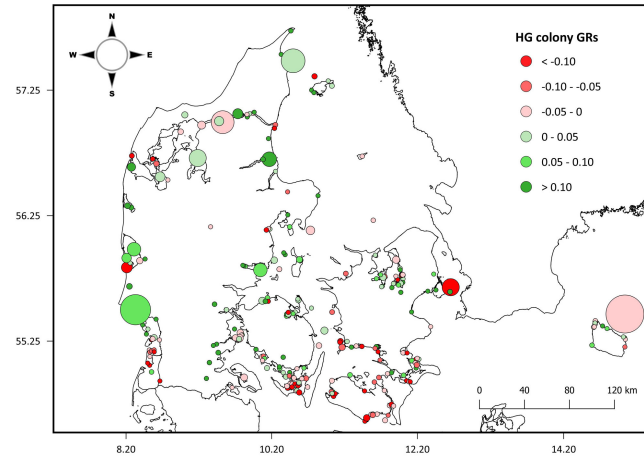

Gull, the best fitting model (w_i = 0.40, *ΔAIC to intercept-only model* = 21.79) showed that area of subtidal zone, number of mink farms and extent of built-up area were the most important variables explaining variation in colony GR, with all coefficients showing 95% confidence intervals that did not overlap with zero (Table 4). Colony GR was positively related to the abundance of mink farms and the extent of built-up area within the foraging range, but negatively to the extent of subtidal zone (Figs. 4A-C).

Fig. 3. Spatial variation in population growth rate (GR) by colonies in the period 2000–2020 for Herring Gull (*Larus argentatus*). The color of the circle depicts the mean colony GR over the study period, while the size of the circle reflects the relative mean size of the colony.

Table 1. Rank of spatial regression models explaining variation in Great Black-backed Gull (*Larus marinus*) colony growth rates by proxies of the availability of resources. K is the number of estimated parameters included, AIC is the Akaike Information Criterion value, ΔAIC is the AIC difference, and w_i is the Akaike weight.

Variables included within model	K	AIC	ΔAIC	w_i
Subtidal †	2	-372.38	0.00	0.206
Intercept only †	1	-372.01	0.37	0.171
Subtidal, built-up †	3	-370.64	1.74	0.087
Subtidal, fishery †	3	-370.59	1.78	0.085
Fishery †	2	-370.49	1.89	0.080
Subtidal, mink farms †	3	-370.39	1.99	0.076
Built-up	2	-369.65	2.73	0.053
Mink farms	2	-369.33	3.05	0.045
Fishery, mink farms	3	-368.81	3.57	0.035
Subtidal, fishery, mink farms	4	-368.69	3.69	0.033
Subtidal, fishery, built-up	4	-368.65	3.73	0.032
Fishery, built-up	3	-368.55	3.83	0.030
Subtidal, mink farms, built-up	4	-368.02	4.36	0.023
Built-up, mink farms	3	-367.68	4.70	0.020
Fishery, built-up, mink farms	4	-366.81	5.57	0.013
Subtidal, fishery, mink farms, built-up	5	-366.70	5.68	0.012

†Top-supported models (ΔAIC < 2)

Table 2. Rank of spatial regression models explaining variation in Lesser Black-backed Gull (*Larus fuscus*) colony growth rates by proxies of the availability of resources. K is the number of estimated parameters included, AIC is the Akaike Information Criterion value, ΔAIC is the AIC difference, and w_i is the Akaike weight.

Variables included within model	K	AIC	ΔAIC	w_i
Intercept only †	1	-62.03	0.00	0.383
Subtidal	2	-59.56	2.47	0.111
Built-up	2	-58.87	3.16	0.079
Fishery	2	-58.67	3.36	0.071
Mink farms	2	-58.10	3.93	0.054
Subtidal, fishery	3	-57.84	4.19	0.047
Subtidal, mink farms	3	-57.75	4.28	0.045
Subtidal, built-up	3	-57.57	4.46	0.041
Fishery, mink farms	3	-57.19	4.85	0.034
Fishery, built-up	3	-57.16	4.87	0.033
Built-up, mink farms	3	-57.01	5.02	0.031
Subtidal, fishery, built-up	4	-55.88	6.16	0.018
Subtidal, fishery, mink farms	4	-55.84	6.19	0.017
Subtidal, mink farms, built-up	4	-55.76	6.28	0.017
Fishery, mink farms, built-up	4	-55.21	6.82	0.013
Subtidal, fishery, built-up, mink farms	5	-53.89	8.14	0.007

† Top-supported models (ΔAIC < 2)

Table 3. Rank of spatial regression models explaining variation in Herring Gull (*Larus argentatus*) colony growth rates by proxies of the availability of resources. K is the number of estimated parameters included, AIC is the Akaike Information Criterion value, ΔAIC is the AIC difference, and w_i is the Akaike weight.

Variables included within model	k	AIC	ΔAIC	w_i
Subtidal, mink farms, built-up †	4	-190.84	0.00	0.400
Subtidal, built-up, mink farms, fishery †	5	-190.32	0.52	0.308
Built-up, subtidal, fishery	4	-188.33	2.52	0.114
Mink farms, subtidal	3	-188.29	2.56	0.111
Mink farms, subtidal, fishery	4	-186.44	4.40	0.044
Built-up, subtidal	3	-182.73	8.11	0.007
Mink farms, built-up	3	-181.97	8.87	0.005
Mink farms	2	-181.90	8.94	0.005
Mink farms, built-up, fishery	4	-180.96	9.89	0.003
Mink farms, fishery	3	-179.92	10.93	0.002
Built-up, fishery	3	-179.36	11.49	0.001
Built-up	2	-175.43	15.42	0.000
Subtidal	2	-174.77	16.08	0.000
Subtidal, fishery	3	-173.60	17.24	0.000
Fishery	2	-170.38	20.46	0.000
Intercept only	1	-169.06	21.79	0.000

† Top-supported models (ΔAIC < 2)

DISCUSSION

Non-random spatial variation was found in GR of Herring Gull colonies over the study period across Denmark, but not for Great Black-backed and Lesser Black-backed Gull colonies. Herring Gulls showed positive autocorrelation in colony GR, meaning that colonies in close proximity had similar changes in size, most likely because they experienced similar ecological conditions (Ringsby et al. 2002, Liebhold et al. 2004). Populations of nearby colonies might have been affected similarly, either because they foraged in the same places or because food availability in the foraging habitats surrounding the colonies changed in the same direction. In any case, this suggests that the composition of potential resources was similar among neighboring colonies but different between colonies further away, which could lead to inter-population differences in parameters such as survival, reproduction, emigration, immigration, and consequently

Table 4. Parameter estimates of the best fitting model for Herring Gull (*Larus argentatus*), with standard error, 95% confidence interval, *t* value, and relative importance of each predictor variable.

Variable	Effect	SE	95% Confidence interval		*t*	Relative importance
			Lower	Upper		
Intercept	0,0111					
Subtidal	-0,0508	0,0150	-0,0818	-0,0209	-3,38	0,985
Mink farms	0,0374	0,0116	0,0145	0,0608	3,23	0,878
Built-up	0,0416	0,0194	0,0034	0,0810	2,15	0,838

Fig. 4. Scatterplots between colony growth rate (GR) and the predictor variables in the best fitting models for Herring Gull (*Larus argentatus*) (A, B, C). Each plot shows the relationship between GR and a predictor variable while holding the rest of predictors constant at their respective means, and the fitted slopes are the partial regression slopes of GR on its correspondent predictor variable from the full regression model of GR on all predictors. The shaded areas indicate the 95% confidence intervals of the predictions.

population growth rates (Frederiksen et al. 2005a, Harris et al. 2005, Cordes et al. 2015).

Spatial variation in colony GR only showed a relationship with the composition of resources available in the surrounding environment for one of the three species. The pattern of colony GR of Herring Gulls was strongly correlated with the extent of subtidal zone, built-up area, and the number of mink farms around the colonies. Hence, colonies located in areas with more built-up areas, more mink farms, and less subtidal zones showed greater increases in colony size. For Great Black-backed and Lesser Black-backed Gulls, no predictor variable succeeded in explaining the variation in colony GR.

The population trends of Herring Gulls in the study area seemed to be closely related to anthropogenic activities. It is well known that built-up areas offer breeding sites where large gulls can nest in safety from mammalian predators, and provide foraging opportunities in the form of waste in landfills, some industries, waste treatment plants, cities, and other urban areas (Coulson and Coulson 2008, Spelt et al. 2019, Méndez et al. 2020). Spärck (1951) already observed that the most common food ingested by Herring Gulls in Denmark was waste (in 32% of analyzed stomachs), and Andersson (1970) described the shift in diet of a population breeding in a colony in the south of Sweden between 1947 and 1965, from mainly fish and bivalves to refuse and earthworms. Gulls are increasingly using anthropogenic food sources including refuse dumps, fishery discards, and mink farms (Duhem et al. 2008, Tyson et al. 2015, Juvaste et al. 2017, Gutowsky et al. 2021), and the use of these resources may lead to increases in recruitment rates and therefore influence the distribution and population sizes of gull species (Cotter et al. 2012). Indeed, refuse dumps provide highly predictable food sources because of their daily availability and high abundance throughout the year (Duhem et al. 2008), although in Denmark this resource became very limited after the 1980s, when the large open dumps located near Copenhagen and Malmö were closed down (Bregnballe and Lyngs 2014). However, built-up areas can still provide foraging opportunities; for example, in a study of gulls breeding on rooftops in Aarhus (Denmark), Herring Gulls were observed feeding on waste from rubbish bins, restaurants, and shops (Lilleør 2000). In contrast, Great Black-backed and Lesser Black-backed Gulls of the study area are rarely observed foraging inside cities and industrial areas (T. Bregnballe, *unpublished data*).

Although few studies have addressed the effects of mink farms on large gulls, GPS tracking and direct observations indicate that at least Herring Gulls often feed at active fur farms (Frederiksen et al. 2020, Gutowsky et al. 2021, Shlepr et al. 2021). Mink farming was introduced in Denmark in the mid-1920s, and around 2000, the country became the world's leading producer and exporter responsible for about 40% of the world's annual mink production (Long 2003, Bonesi and Palazon 2007). Herring Gulls have taken advantage of this food source in the study area (Frederiksen et al. 2020) and this could explain the higher colony GRs in areas where mink farms were present nearby. The evolution of the ongoing coronavirus disease (COVID-19) pandemic, caused by the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), however, has dramatically changed this situation. Infection with SARS-CoV-2 occurred widely in farmed minks in

Jutland, spreading rapidly from farm to farm, and spilling back from mink to human (Xia et al. 2020, Hammer et al. 2021). The rapid accumulation of mutations in the spike protein gene could threaten public health and the effectiveness of anti-SARS-CoV-2 vaccines, so the Danish Government decided to cull all the approximately 17 million mink in Denmark (Frutos and Devaux 2020, Koopmans 2021). This unprecedented event caused rapid and dramatic changes in the gulls' foraging landscape, and further research is needed to evaluate the impact of the sudden disappearance of this food resource on gull communities.

The negative effect of subtidal zone in the best model for Herring Gulls was unexpected (Fig. 4A). There was no meaningful correlation between the predictor variables that could have affected the stability of the model, and the effect of subtidal zone was negative when it was regressed alone. Thus, there might be other underlying reasons explaining this negative relationship. Subtidal zones offer marine invertebrates as prey for large gulls, e.g., bivalves, crustaceans, polychaetes, and echinoderms (O'Hanlon et al. 2017). Our results show that greater extent of subtidal area was correlated with lower colony GRs, which could perhaps be related to a decrease in the food quality provided by this habitat over the study period (Lotze et al. 2005, Schückel and Kröncke 2013, Meyer et al. 2016). The population increases of Great Black-backed Gulls could also have displaced Herring Gulls in areas with large extents of subtidal zone, as Great Black-backed Gulls have been documented to outcompete Herring Gulls foraging on large crabs in the rocky intertidal along the coast of New England (Rome and Ellis 2004, Ellis and Good 2006), but a focused study would be needed to explore this in our study area. Another possibility is that the colonies surrounded by great extents of subtidal zone were already saturated by Herring Gulls at the beginning of the study period, and thus, other colonies with smaller subtidal zones might have shown higher GR, shaping the observed negative relationship. Similarly, locations colonized later in the study period would likely show steeper GRs than those that had been established earlier, so if these new colonies had small subtidal zones available within the foraging range, they could influence this negative correlation.

Colony GR of Great Black-backed and Lesser Black-backed Gulls did not show any significant correlation with any of the predictor variables. These species are considered to rely more on marine resources like fishery discards and offal than Herring Gulls (Camphuysen 1995, Kubetzki and Garthe 2003, Lato et al. 2021), so a relationship with fishery activity was expected. However, the proxy that we used, i.e., fishery landings in Danish harbors, may not have represented accurately the distribution and availability of this food source, as offal is mainly discarded offshore far from the harbors. It would be preferable to use real data on the spatial distribution of fishery discards or, failing that, fishery activity. In the 1990s, it was estimated that discards in the North Sea accounted for around 22% of landings (Garthe et al. 1996), and the total amount of discarded biomass could potentially support an average scavenger-seabird community of 5.66 (3.33–9.74) million birds (Sherley et al. 2020). After the Common Fisheries Policy (CFP) was reformed in 2013 introducing a ban on fishery discards (Zeller et al. 2011, Feekings et al. 2012), this resource has become more limited for scavenging large gulls in Europe. Therefore, although this resource could have boosted large gull population trends and distributions in the past, it is unlikely to

have been an important driver in the second half of the study period (Wilhelm et al. 2016, Foster et al. 2017, Karris et al. 2018). Thus, it is more likely that other factors not included in this study have influenced the observed between-colony variation in colony GR of these two species. Such factors could include spatiotemporal variation in the availability of natural food items, as well as changes in the local breeding environment due to increasing or decreasing predation and/or competition. Some studies have documented that Lesser Black-backed Gulls may suffer from nest site competition and predation of chicks by Herring Gulls (Kilpi 1983, Hario 1994, Hario and Rudbäck 1996). Because of its size and early arrival at breeding grounds, the Great Black-backed Gull is unlikely to be negatively affected by the other species at the breeding site. However, it may compete with the two other species for access to discards from fishing boats. Further analyses and more focused studies would be required to unravel how the three study species interact (Garthe et al. 1999). On the other hand, it is possible that predictors simply failed to explain the variation in colony GRs because of the high individual specialization in foraging behavior shown by these two species (Juvaste et al. 2017, Maynard and Ronconi 2018, Lato et al. 2021).

Variation in colony GR may have been influenced by local food depletion and density-dependent processes. Ashmole (1963) suggested that food availability is the main regulator of seabird populations, as colony members preferentially forage close to their colony in order to minimize travel costs, gradually depleting food nearby, and consequently creating a "halo" with low food availability. Seabirds from colonies with bigger breeding populations or from colonies with naturally few or lower-quality resources nearby, often have to travel longer distances to find suitable foraging grounds (Gaston et al. 2007, Elliott et al. 2009). This means that seabirds from such colonies are affected by higher travel costs and consequently reduced net gains, which can eventually be reflected in the breeding success (Jovani et al. 2016). Unfortunately, foraging ranges are often estimated from insufficient samples of tracked individuals, as is the case of the Great Black-backed Gull in this study, leading to uncertainties in the extent of foraging areas actually available to birds in a given colony (Soanes et al. 2013, Lascelles et al. 2016). In addition, several studies of multiple seabird colonies have concluded that neighboring colonies frequently do not overlap in their foraging areas (Masello et al. 2010, Wakefield et al. 2013, Jovani et al. 2016), and thus estimated foraging ranges can overestimate the real availability of foraging areas per colony. For instance, in the study by Corman et al. (2016) in the German Wadden Sea, Lesser Black-backed Gulls showed colony-specific segregation in foraging areas during the breeding period, thus avoiding inter-colony competition. Furthermore, in many situations resources are aggregated in patches rather than being uniformly distributed (Wakefield et al. 2009), modifying the distribution of foraging areas and consequently the levels of inter-colony competition. Therefore, because there is often considerable intraspecific inter-colony variation in foraging ranges, the application of generic species-level foraging radii might be prone to considerable error (Bolton et al. 2019). Beyond that, within-colony segregation has also been documented among sexes, often linked to size dimorphism, and among age-classes (Phillips et al. 2011, Cleasby et al. 2015, Borrmann et al. 2019), further increasing the variation in foraging ranges.

Another factor that could affect our results is the uncertainty derived from the proxies utilized to represent the availability of potential resources for gulls. Some potential food sources were not included in the analysis because of lack of data, e.g., rubbish dumps, aquaculture facilities, density of fish and invertebrates at sea. Moreover, studies on the ecology of large gulls during the non-breeding season are rare, but essential to better understand the development of populations (Kim and Monaghan 2006, Nager and O'Hanlon 2016). Spatial variation in population trends is not only driven by variation in food availability, because there are other factors that constrain colony growth. Potentially important external factors include competition, predation, pollution, and diseases; while other factors related to species-specific traits (e.g., diet preferences, feeding behaviors, and digestive capabilities) are also likely to be important (Brown et al. 1995, Crespin et al. 2006, Nager and O'Hanlon 2016). Therefore, in general there is not only one cause of population change, but most likely a combination of species-specific factors influencing the development of populations, which can vary spatially at the same time.

CONCLUSION

This study analyzed the population developments of Great Black-backed, Lesser Black-backed, and Herring Gulls breeding in Denmark in the last two decades. The results obtained suggest that changes in Herring Gull colony size were sensitive to the distribution of resources in the coastal environment, highlighting the importance of food availability within the foraging range of gull colonies during the breeding season. For the other two species, no such patterns were identified. Furthermore, Herring Gull colonies in close proximity and exploiting similar local resources tended to show similar population growth, in agreement with the theoretical Moran effect. Hence, this study highlights the potential of monitoring multiple colonies, as it allows identifying the effects of key environmental drivers of population dynamics over space and time. Two of the potential resources that explained the distribution and population dynamics of Herring Gulls (i.e., mink farms and built-up areas) were derived from anthropogenic activities, demonstrating the close relationship between this species and humans. Based on the current study, we anticipate that the Danish Herring Gull breeding population, which in recent decades has fared better than in the neighboring countries, will decline in the coming years after the recent closure of all mink farms in Denmark.

Responses to this article can be read online at:
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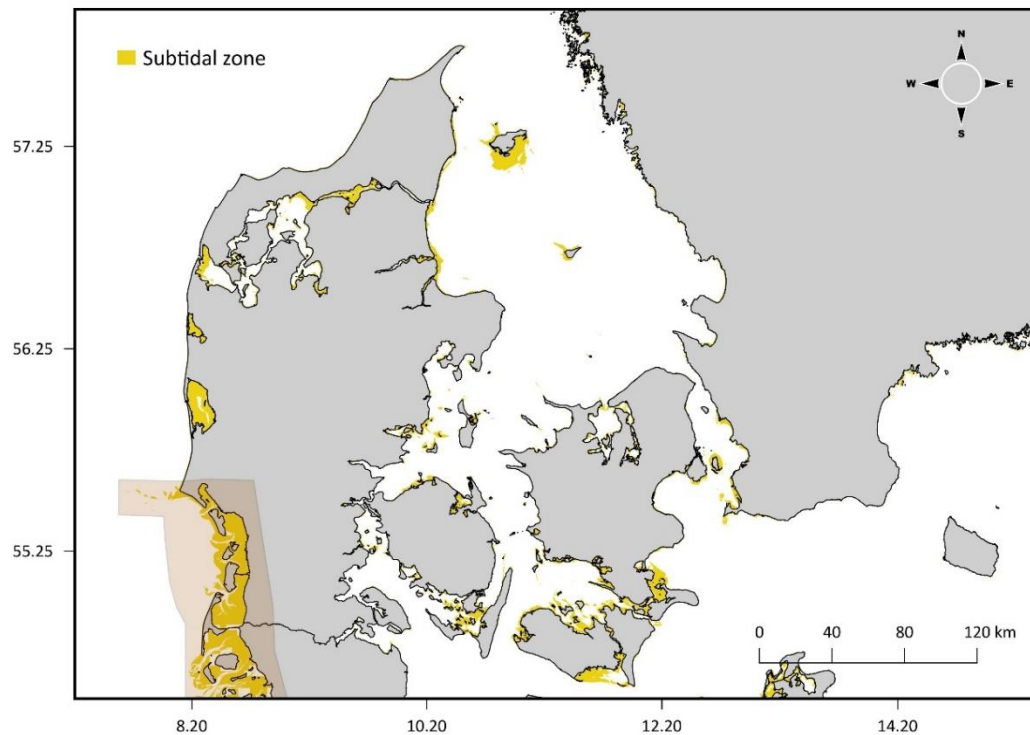(*Larus marinus*) relative to reduced fishing activities in Southeastern Canada. Waterbirds 39(sp1):136-142. https://doi.org/10.1675/063.039.sp104

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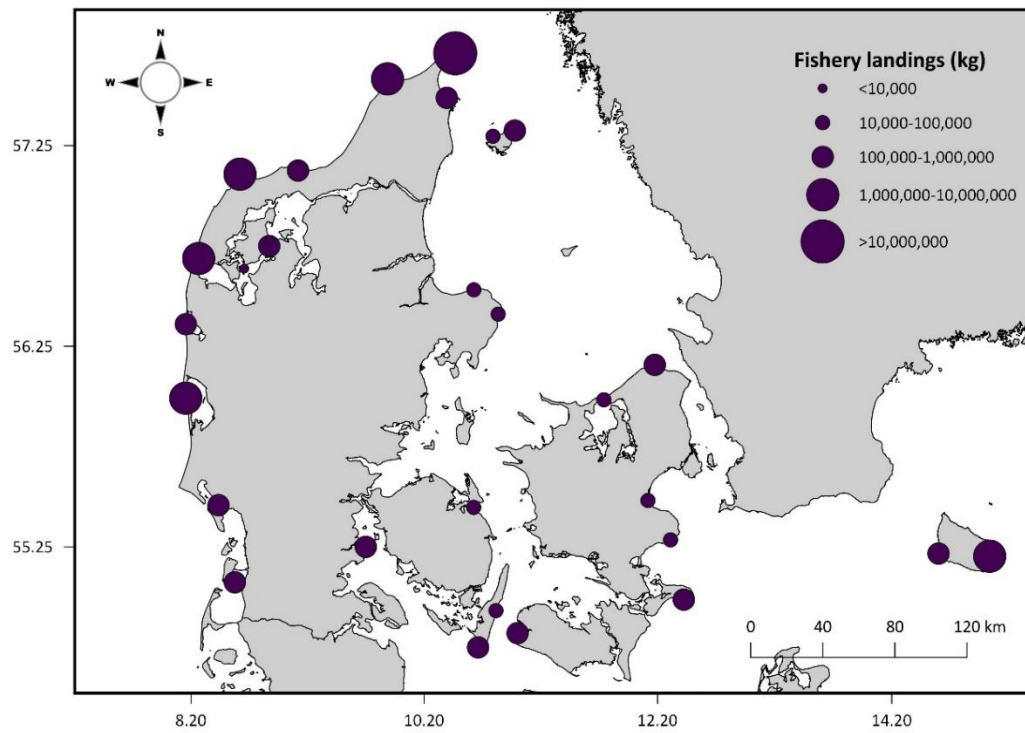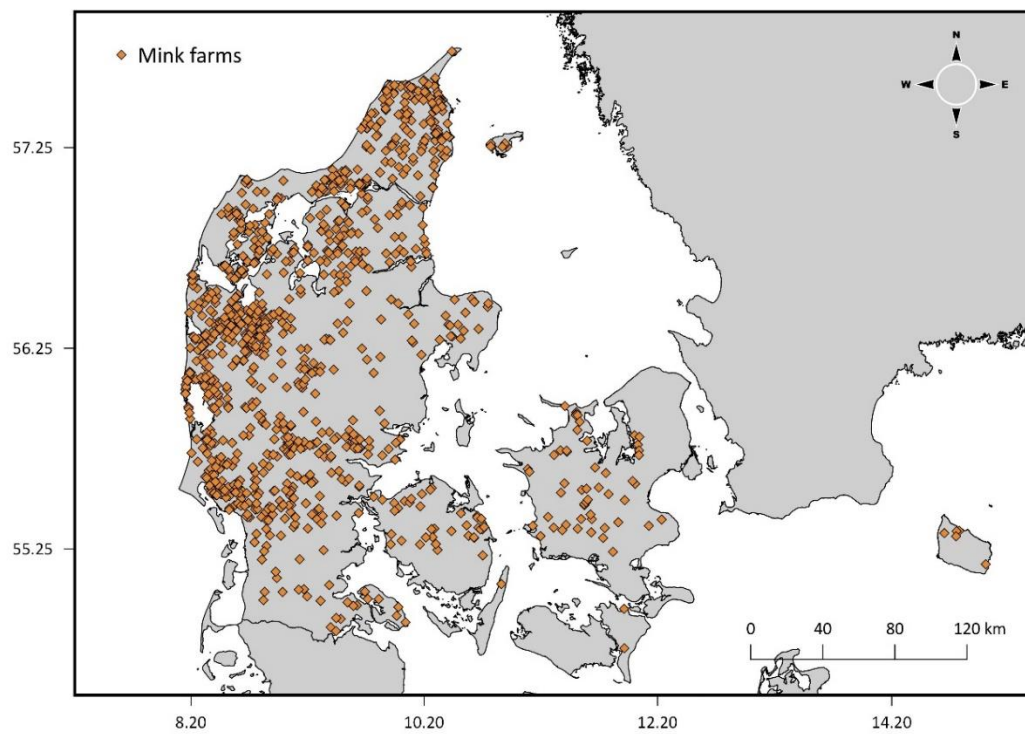
Appendix 1

We extracted information on proxies that reflect the availability of potential-foraging habitats in order to investigate the relationship between gull population changes and resource availability. All the maps in this study were developed in QGIS 3.4.15.

Fig. A1.1. Spatial distribution of subtidal zones in the study area. Subtidal zone was defined as the area between the shoreline and 3 m depth, except in the most south-western region of Jutland, where the maximum depth was set in 4 m (the shaded area in the map).
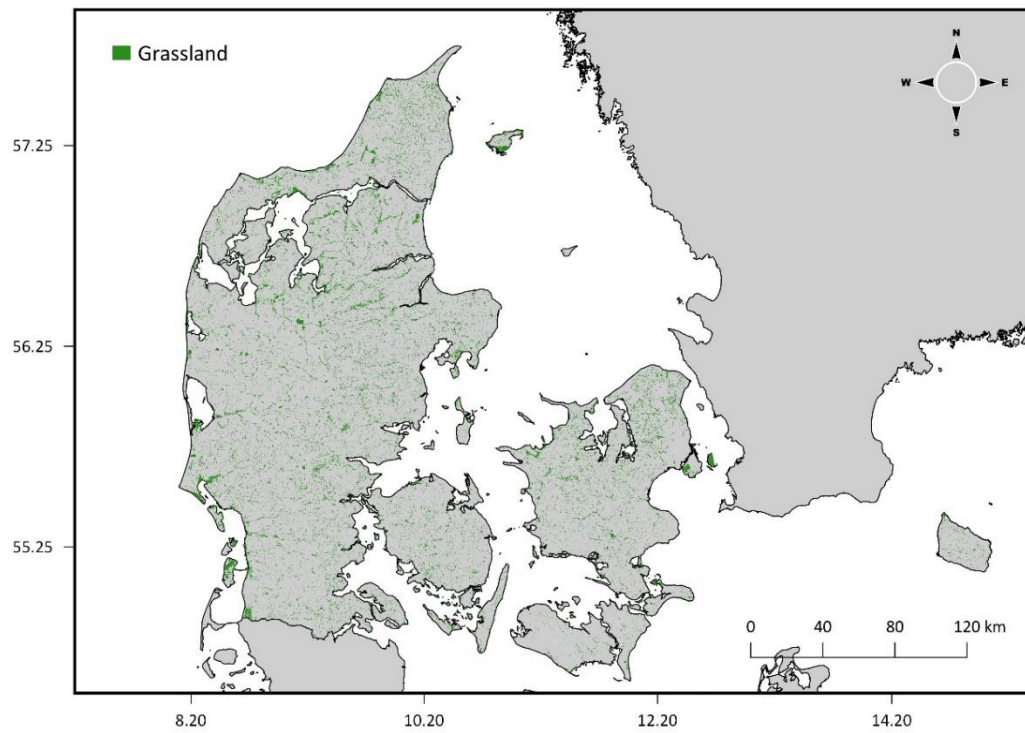
Fig. A1.2. Spatial distribution of harbors with commercial fisheries in the study area. The size of the circle reflects the average weight of landings from the 2nd quarter of the year for the period 2010-2019.
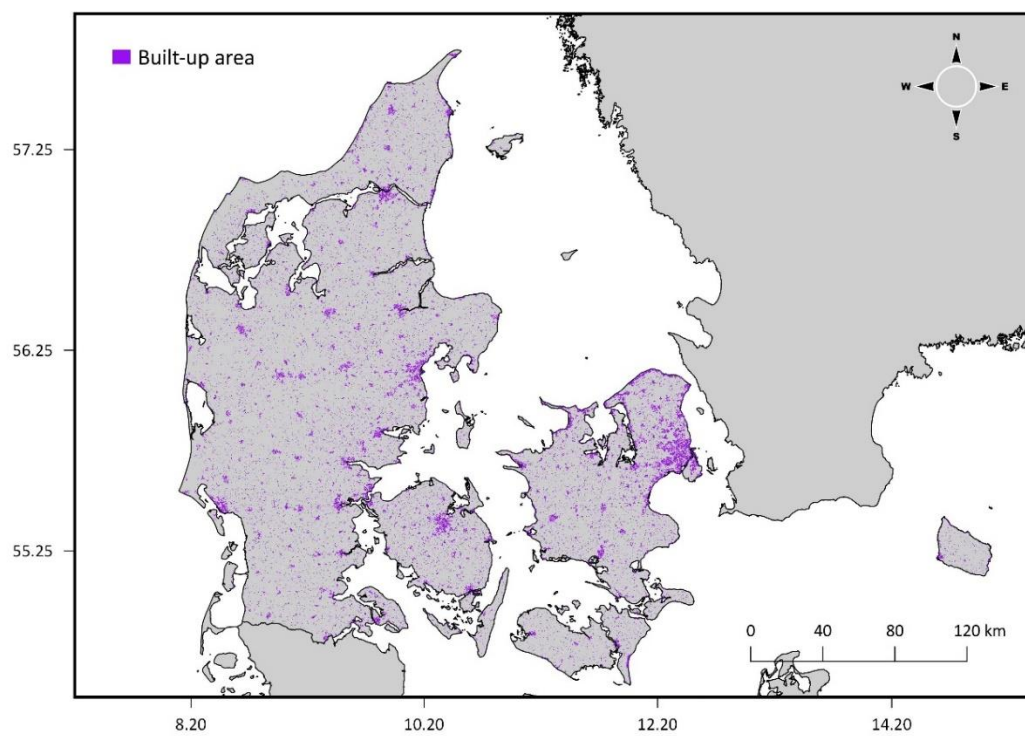

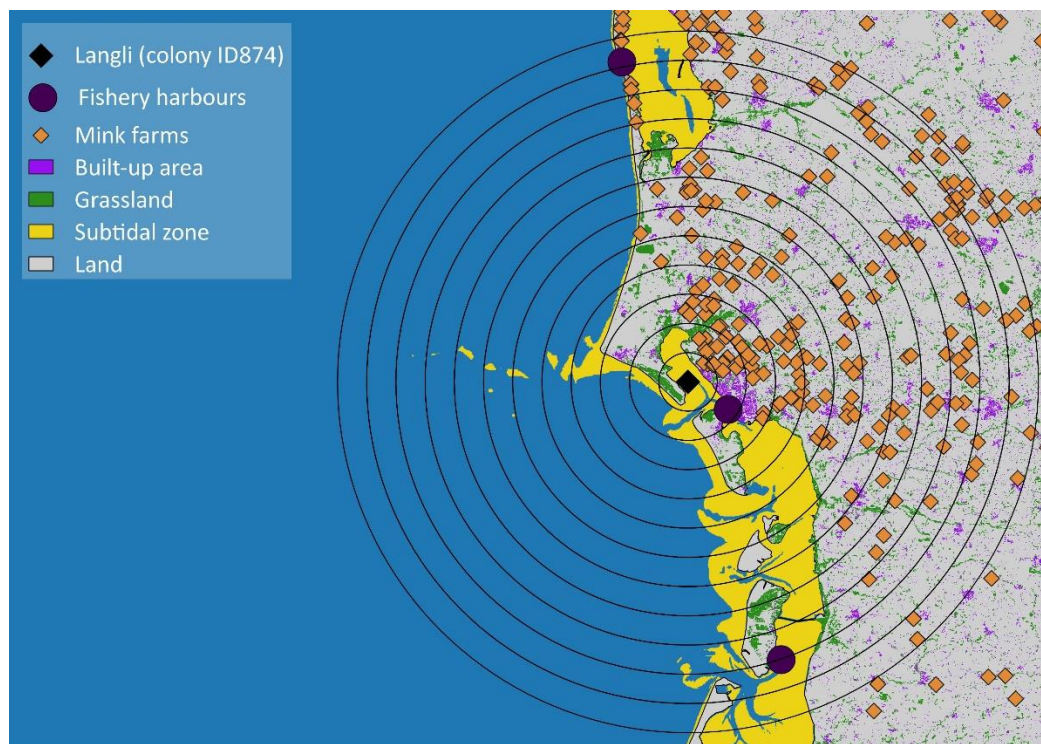**Fig. A1.3.** Spatial distribution of active mink farms in the study area in 2019.

Fig. A1.4. Spatial distribution of grasslands in the study area.

Fig. A1.5. Spatial distribution of built-up areas in the study area.

Appendix 2

This representation of the foraging range of a Great Black-backed Gull breeding in Langli (colony ID874) has been prepared to enlighten how resource variables were extracted for one colony and species, representing the increasing travel costs of gulls associated with foraging at more remote locations. In this case, the maximum foraging range was set as 60 km around the colony, and the interval between rings was 5 km. The extension or quantity of each resource variable was calculated for each ring, and the value of each ring was weighted depending on the distance to the colony. Finally, the values for all the weighted rings were summed in order to get a total value for the colony. This same process was followed to calculate the availability of each resource variable in every colony.

Fig. A2.1. Representation of the different resources available for a single colony of Great Black-backed Gull in the coast of Jutland, Denmark.

Appendix 3

Detecting collinearity in the spatial regression models of the three *Larus* species. Tolerance and VIF values were calculated using the *olsrr* package in R (Hebbali 2020).

Table A3.1. Tolerance and Variance Inflation Factor (VIF) values from the models fitting together all the predictor variables. VIF > 10 suggests important collinearity issues, while VIF > 5 requires to be investigated.

Species	Predictor variable	Tolerance	VIF
	Fishery landings	0.585	1.71
	Mink farms	0.158	6.34
GBBG	Subtidal	0.673	1.48
	Grassland	0.060	16.54
	Built-up	0.106	9.46
	Fishery landings	0.195	5.14
	Mink farms	0.020	50.80
LBBG	Subtidal	0.142	7.07
	Grassland	0.003	307.08
	Built-up	0.008	128.63
	Fishery landings	0.541	1.85
	Mink farms	0.134	7.45
HG	Subtidal	0.499	2.00
	Grassland	0.044	22.78
	Built-up	0.102	9.82

Table A3.2. Tolerance and Variance Inflation Factor (VIF) values from the best fitting model for Herring Gulls (*L. argentatus*).

Species	Predictor variable	Tolerance	VIF
	Subtidal	0.918	1.09
HG	Mink farms	0.870	1.15
	Built-up	0.818	1.22

Hebbali, A. 2020. *OLSRR: Tools for building OLS regression models (Version 0.5.3)*. [online] URL: https://cran.r-project.org/web/packages/olsrr/index.html