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RESEARCH ARTICLE

Top-down control of a marine mesopredator: Increase in native white-tailed eagles accelerates the extinction of an endangered seabird population

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Abstract

1. Bottom-up control is an important regulator of marine mesopredators such as seabirds. The prevalence of top-down control on these species is however less well understood. In particular, how native predators affect seabird populations has rarely been quantified.
2. Here, we investigate how an increase in white-tailed eagles in northern Norway, a stronghold for the species, affected a local population of 25,000 pairs of black-legged kittiwakes, a red-listed seabird, during a 42-year period ending with colony extinction. We use a natural experiment of two neighbouring colonies with/without eagle predation to disentangle the effects of eagles from local kittiwake foraging conditions (using size of young herring as a proxy).
3. At the colony where eagle predation occurred, and in contrast to the eagle-free colony, kittiwake breeding success and population size declined with increased eagle abundance, the latter more strongly under poor foraging conditions. Breeding success increased with improving foraging conditions at both colonies.
4. Simple population modelling shows that although conditions were insufficient to sustain the eagle-exposed colony, the increased abundance of eagles sped up its extirpation by many years.
5. *Policy implications*. Our study shows that top-down effects from avian predators can be significant regulators of seabird populations, challenging their conservation where native, often protected, predators are rising. Such effects, and their possible interaction with other factors, must also be accounted for when using seabird demographic traits as environmental indicators and when developing more flexible and effective management and action plans.

KEYWORDS
black-legged kittiwake, extinction rate, native predators, population dynamics, seabirds, top-down control, trophic interactions, white-tailed eagle

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1 | INTRODUCTION

The importance of bottom-up regulation of marine predators—through the abundance of plankton and forage fish—is well established (Beaugrand et al., 2003; Frederiksen et al., 2006; Piatt et al., 2020), and there is increasing evidence of the significance of top-down control (Baum & Worm, 2009; Frank et al., 2005). Often, small pelagic fish at an intermediate trophic level play a key role in the dynamics of marine food webs as 'wasp-waist' populations, by exerting both top-down control on zooplankton and bottom-up control on higher trophic levels such as seabirds and predatory fish (Cury et al., 2000; Fauchald et al., 2011). However, the importance of top-down control effects on these higher-level mesopredators remains poorly understood.

Seabirds are high-level marine predators and can play a key role in marine ecosystems as consumers of forage fish (Brooke, 2004; Saraux et al., 2021). Piscivorous seabirds are strongly regulated by bottom-up effects through the abundance of their main prey, which substantially affects their breeding success and mortality (Cury et al., 2011; Furness, 2007; Piatt et al., 2020; Suryan et al., 2021; Sydeman et al., 2021). Seabirds are currently one of the most endangered groups of birds on Earth, with populations declining worldwide (Croxall et al., 2012). Changes in resource availability, driven by overfishing and climate change, is one of their key threats (Dias et al., 2019). However, predation also ranks high, particularly by invasive alien species, but also by native animals. In fact, problematic native species are ranked as the 7th greatest impact of all threats and assessed to affect nearly 15% of all seabird species (Dias et al., 2019).

While there are numerous reports of native predators on seabirds (e.g. Blight et al., 1999; Hipfner et al., 2012; Millus et al., 2007), attempts to quantify their impact on demographic traits are scarce (Horswill et al., 2014; Paine et al., 1990; Phillips et al., 1999; Suryan et al., 2006), especially over the longer term (Morelli et al., 2021). This is nonetheless important for two reasons. First, understanding the magnitude of top-down effects of any predation on seabirds, especially on declining species, is necessary to inform conservation measures. Second, as top marine predators, seabirds can be useful indicators of marine ecosystem changes (Einoder, 2009; Piatt et al., 2007), but only if other effects on their ecology and demography are accounted for, such as predation by native species.

In this study, we quantify the impact of white-tailed eagles *Haliaeetus albicilla* (hereafter eagles) on a population of black-legged kittiwakes *Rissa tridactyla* (hereafter kittiwakes) in the Norwegian Sea. Norway is hugely important for seabirds, with one in four European seabirds estimated to breed in Norwegian colonies until recently (Anker-Nilssen et al., 2015; Fauchald et al., 2015). However, many of these seabirds have experienced accelerating declines since the 1970s, with over a third estimated to have been lost only since 2010 (Anker-Nilssen et al., 2021). Many declines are driven by low prey availability causing poor breeding success (Durant et al., 2003; Fayet et al., 2021; Sandvik et al., 2014), but qualitative observations suggest predation by eagles may also play an increasingly important role, especially for open-nesting cliff-breeding species (Anker-Nilssen & Aarvak, 2009; Hipfner et al., 2012). Norway's population of white-tailed eagles declined drastically in the late 1800s and early 1900s and probably counted less than 500 breeding pairs in the 1950s (Haftorn, 1971). This was caused by targeted human persecution of eagles, which in some areas was intensified by offering a bounty (Hagen, 1952), and likely also reduced reproduction caused by pollutants such as DDE and PCBs (Helander et al., 2002). After national protection in 1968, the population increased substantially to an estimated 2787–4167 breeding pairs in 2013 (Heggøy & Øien, 2014). Central and north-western Norway, which also holds most of the largest seabird cliffs in mainland Norway (Sandvik et al., 2016), is the core area for the species in Europe. Since the late 1990s, an expanding population of immature eagles has been visiting the bird cliffs in summer and has been causing an increasing number of conflicts for the breeding performance of a variety of other seabird species (TAN, unpubl. data).

Here we take advantage of a unique system with two subpopulations of kittiwakes only 4 km apart experiencing contrasting eagle predation pressure within the Røst archipelago, one at a natural site with eagle predation ('cliff colony') and the other on a neighbouring inhabited island ('harbour colony') which eagles avoid due to human presence. This facilitates a natural experiment to disentangle effects of eagle predation pressure and kittiwake foraging conditions on kittiwake demographic traits, as the wide foraging range of kittiwakes, the closeness of the two subpopulations, and the lack of food from local sources in the diet of the harbour birds (TAN unpubl. data), mean they are very likely to share foraging grounds often spanning more than 100 km away from the colony (Christensen-Dalsgaard et al., 2018; Wakefield et al., 2017). The cliff colony, numbering 25,000 pairs in 1979, went extinct in 2020, while the harbour colony, with around 130 pairs in the early 1980s, increased by nearly 600% during that time. Using a dataset spanning 42 years on these two colonies and parallel observations of eagles in Røst, we investigate how kittiwake population size and breeding success at the two colonies is affected by eagle numbers—first low and then abruptly increasing since 1998—and by the kittiwakes' foraging conditions, including potentially interactive effects.

2 | MATERIALS AND METHODS

2.1 | Data collection

Apparently occupied nests (AONs) of kittiwakes were counted annually (except in 1985–1987) on 15 June (±1 day, hatching period) in designated study plots at two locations in Røst municipality, Nordland county; in 1979–2020 at the 'cliff colony' on Vedøy (67.480 N, 12.017 E) and in 1982–2020 at the 'harbour colony' on buildings at Kårøya (67.505 N, 12.078 E) in Røst harbour, following internationally standardized protocols (Walsh et al., 1995). Assuming plots were representative of the whole colony, the plot counts at Vedøy were later converted to total colony size by applying the total population estimate of 17,296 AONs counted nest-by-nest from detailed pictures covering the whole colony taken 15 June 1988 (SEAPOP, unpubl. data). In the same years except 1980 (Vedøy) and 1984 (Kårøya), breeding success (large chicks/nest, including empty nests that had been occupied in mid-June) was estimated from counting the number of large chicks in the same plots on 15 July (±1 day, early fledging period).

In parallel, the minimum number of individual eagles observed at any of the five highest (97–259 m) and largest bird cliffs in Røst was logged regularly (mean 45.5 ±1.54 days/year, range 28–61) in June and July when visited by the field crew. These islands, one of which is Vedøy, lie within 8 km of each other and have excellent conditions for soaring eagles. It was not possible to measure predation directly because the sudden and rapid nature of predation events would require almost constant surveillance by human observers, which on the timescale of our study is simply not possible. As our monitoring work was consistent over time, our data nevertheless provide an estimate of general eagle abundance around the largest bird cliffs in the archipelago, which we use as a proxy for eagle predation pressure on kittiwakes.

Analyses of regurgitates from kittiwakes at the harbour colony in 2006–2020 indicate they feed their chicks to a large extent on first-year (i.e. age 0) herring *Clupea harengus* (TAN, unpubl. data), the main prey of Atlantic puffin *Fratercula arctica* chicks in Røst whose diet has been monitored since 1979 (Saraux et al., 2021). As a proxy for food conditions experienced by the kittiwakes, we therefore used a weighted regression to calculate the average length of herring in the puffin diet on 1 July each year, which explains more of the variation in breeding success for puffins in Røst than herring abundance when back-calculated from year-class strength measured when the cohort recruits to the spawning stock several years later (Durant et al., 2003). This is most likely because the birds target herring larger than the average available (Anker-Nilssen & Lorentsen, 1990), which are more likely to appear in schools and more profitable for the birds in terms of time and effort per unit mass of fish taken.

All research was conducted in accordance with relevant protocols, with ethical approval granted by the Norwegian Environment Agency (latest permit 2018/607), and with permission from the County Governor of Nordland (latest permit 161/2018).

2.2 | Analysis

Data processing and analysis was carried out in R 4.1.1 (R Core Team, 2021). Eagle number in each year was calculated as the average of the total daily numbers seen on the five main bird cliffs during the kittiwake chick-rearing period (defined as 1 June–31 July based on observations during the study period). Due to puffin breeding failure, average herring size could not be measured empirically in 15 years but was estimated from the linear relationship between herring year-class strength and herring size measured in the 26 other years (Supporting Information Section A).

We used negative binomial generalized linear models and linear models to test the effect of herring size and eagle numbers on kittiwake population size and breeding success across the two colonies, respectively. To control for differences in eagle observation effort, as some islands were visited less frequently in the early years of the study, we added 'yearly effort'—the total number of observation days across all islands during the kittiwake chick-rearing period each year—as a predictor to the full models of population size and breeding success. It explained <0.06% variance in the population size model so was removed from subsequent models, unlike in the breeding success model where it explained some variance so remained throughout (another approach using only data from the most visited island yielded similar results, see Supporting Information Section B). Temporal autocorrelation was only visible in the full cross-colony breeding success model and was successfully accounted for by adding an autocorrelation structure of order one. We started with the full model and dropped non-significant interactions until finding the best model based on AIC. To better understand the relationship between predictor and response variable in the presence of significant interactions between predictors, models were subsequently run on subsamples of the data (e.g. on each colony separately). The normality of residuals was checked for each model; breeding success was square-root-transformed to meet this assumption.

3 | RESULTS

The yearly average number of eagles seen daily during the kittiwake chick-rearing period ranged from 0.05 to 10.6 (the maximum in a given day ranging from 1 to 48), with a substantial increase from 1998 onwards (yearly mean 0.3±0.05 eagles before 1998 and 5.0±0.5 thereafter; Figure 1). During the study, the kittiwake cliff colony declined from approximately 25,000 pairs until it went extinct in 2020, while the harbour colony experienced an almost fivefold increase from 131 to 624 pairs. Breeding success before 1998 averaged 0.75±0.07 chicks/pair at the cliff colony and 0.79±0.05 in the harbour, versus 0.18±0.05 and 0.46±0.05 respectively thereafter.

3.1 | Effects on kittiwake population size

The best model of population size across the two colonies included interactions between all three predictors (colony, herring size and eagle numbers; ΔAIC = −2.7 and −58 with the models with one or no interactions), all of which were significant (Table S1). We therefore ran models separately for each colony. At the cliff colony, the interaction between herring size and eagle numbers remained just significant ($n = 38$, $z = 1.97$, $p = 0.048$), so we ran separate models again for years with below- and above-average herring size (43.3 mm), hereafter 'poor' and 'good' foraging conditions. In poor years, the negative relationship between eagle and kittiwake numbers was more pronounced than in good years (poor: $n = 22$, parameter

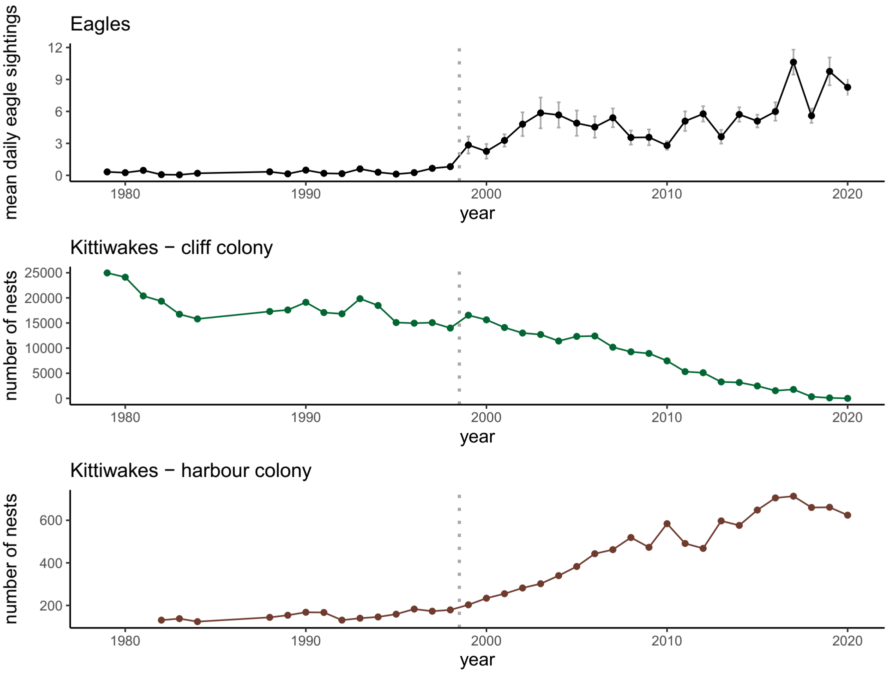

FIGURE 1 Trends in the average number of eagles seen daily in the bird cliffs in June–July (top, with standard errors) and the number of active kittiwake nests at the cliff (middle) and harbour (bottom) colonies over the study period. The dotted line indicates the year after which eagle numbers increased substantially.

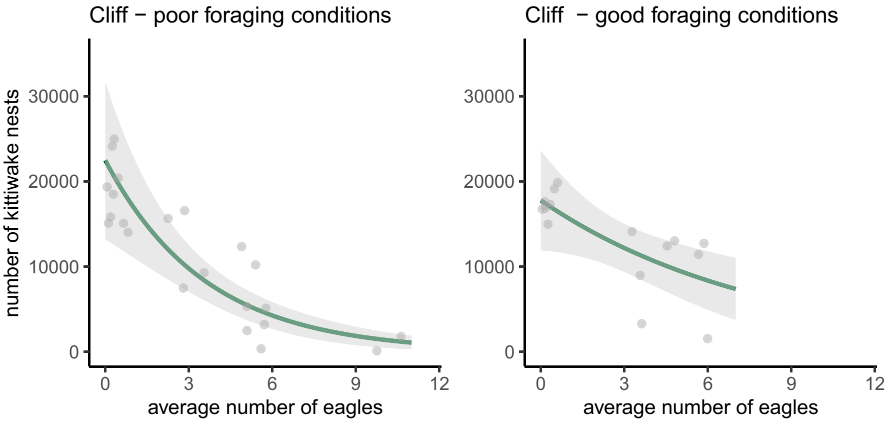

FIGURE 2 Marginal effect of eagle numbers on kittiwake population size at the cliff colony, under poor and good foraging conditions. The green lines indicate the predicted effect, the shaded areas the 95% confidence intervals and the dots the data.

estimate (p.e.) = −0.28 ± 0.05, $z = -6.06$, $p < 0.001$; good: $n = 16$, p.e. = −0.13 ± 0.05, $z = -2.58$, $p = 0.010$) (Figure 2), equivalent to a 24% drop in kittiwake population size following a one-unit increase in eagle numbers under poor foraging conditions, versus 12% under good conditions. Conversely, at the harbour colony, there was no significant interaction between the effects of eagle numbers and herring size on population size ($n = 35$, $z = 0.90$, $p = 0.420$). The additive model showed a positive relationship between eagle numbers and population size (p.e. = 0.19 ± 0.02, $z = 10.30$, $p < 0.001$, equivalent to a 21% increase in population size following a one-unit increase in eagle numbers) and no significant effect of herring size (p.e. = −0.008 ± 0.007, $z = -1.14$, $p = 0.253$).

3.2 | Effects on kittiwake breeding success

The best cross-colony model of breeding success included a significant interaction between colony and eagle numbers (Table S1) with herring size as an additive effect (ΔAIC = −29.5 compared to the full model). We therefore ran separate models for each colony (Figure 3). At the cliff colony, both eagle numbers and herring size were significant predictors of breeding success but acted in opposite directions ($n = 34$, eagle numbers: p.e. = −0.06 ± 0.02, $t = -2.78$, $p = 0.009$; herring size: p.e. = 0.013 ± 0.005, $t = 2.76$, $p = 0.009$). At the harbour colony, there was a similar positive relationship between herring size and breeding success but no effect of eagle numbers ($n = 32$, herring size: p.e. = 0.009 ± 0.003, $t = 2.64$, $p = 0.013$; eagle numbers: p.e. = 0.009 ± 0.015, $t = 0.62$, $p = 0.540$).

4 | DISCUSSION

Using a 42-year dataset on black-legged kittiwake, a seabird now endangered in Norway (Stokke et al., 2021), we quantify how a sudden return of an apex predator, the white-tailed eagle, affected kittiwake breeding success and population trend in two neighbouring colonies experiencing contrasting exposure to eagles. The eagles' effect on productivity is similar to that also reported in other species (Hipfner

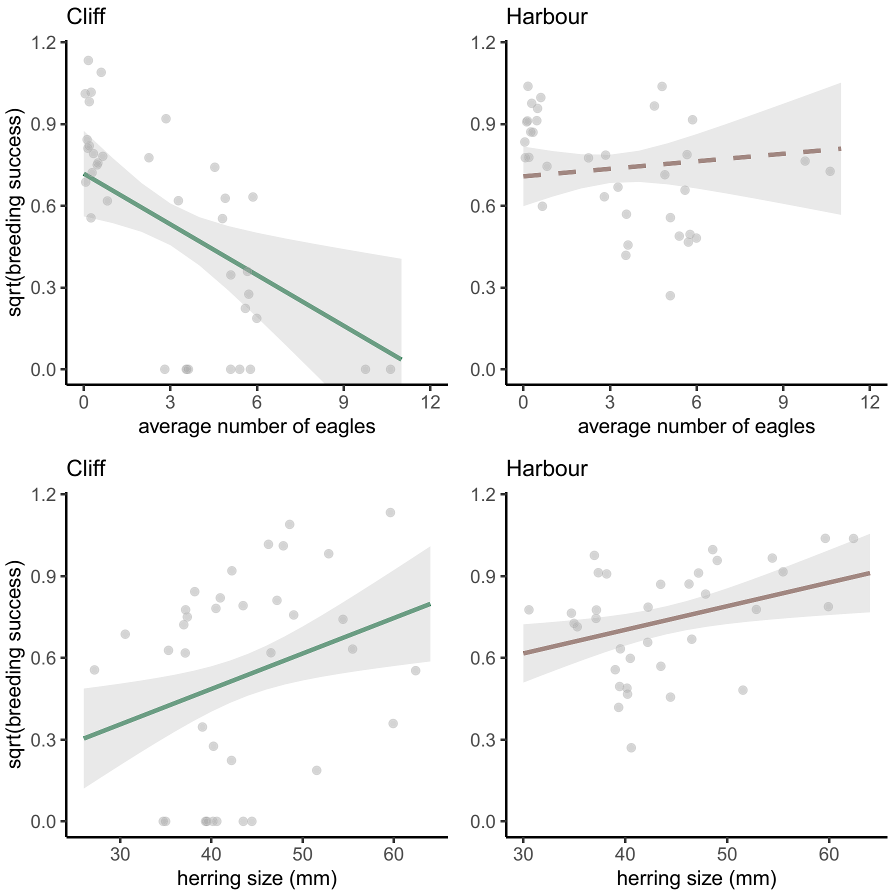

FIGURE 3 Marginal effect of eagle numbers (top) and herring size (bottom) on kittiwake breeding success at the cliff (left, green) and harbour (right, brown) colonies. The lines indicate the predicted effect (dashed = non-significant), the shaded areas the 95% confidence intervals and the dots the data.

et al., 2012) and recently quantified in common eiders *Somateria mollissima* (Morelli et al., 2021; Öst et al., 2022). Simple population modelling shows that although breeding conditions were insufficient to sustain the cliff colony even with low eagle presence (Supporting Information Section D), the increased abundance of eagles sped up the extinction of this iconic bird cliff in northern Norway by many years (Sandvik et al., 2014) (Figure S3). In addition, this effect was negatively correlated with kittiwakes' foraging conditions, likely because lower prey availability reduces the kittiwakes' ability (i.e. time available) to protect their offspring (Chivers et al., 2012). Kittiwake populations sharing their main prey with their predator (e.g. large gulls) can also experience higher predation under poor conditions (Regehr & Montevecchi, 1997).

Meanwhile, despite their protection from eagles, the parallel increase in numbers of kittiwakes breeding in the nearby human settlement can only be explained by immigration (Supporting Information Section E), most likely from the declining cliff colony, the main source population in our remote study area. This is further substantiated by numerous local reports of similar problems for kittiwakes in most other cliff colonies along the Norwegian coastline and their increasing numbers breeding in/near human settlements and on offshore oil rigs (Christensen-Dalsgaard et al., 2019), away from such predation. However, this increase only represents ~2% of the lost breeders at the cliff colony, and with the latter now extinct and non-sustainable productivity levels, the harbour colony has already started and will likely continue to decline. Nevertheless, this shows that adult kittiwakes can maximize their own breeding success by moving nesting location. Although in our study this was not sufficient to offset the declines at the main colony, this mechanism may help with protecting declining colonies elsewhere, if a sufficiently good alternative nesting location is provided. A key question is whether other birds dispersed to new colonies, prospering for areas where eagles are less abundant or deterred. Further research should aim to independently quantify the effects of natal and breeding dispersal and uncover the mechanisms that trigger such responses over adaptation to local conditions, while also addressing potential density-dependent effects (Supporting Information Section F).

Although direct predation of kittiwake chicks—and sometimes adults—was observed, usually in the last part of the chick-rearing period, eagles also likely reduced kittiwake breeding success through facilitating predation from corvids and large gulls by flushing adults away from their nests (Myran, 2021). This was observed irregularly, most often involving ravens *Corvus corax*, during monitoring of common guillemots *Uria aalge* in the same cliffs around noon at on average 6 (range 3–10) different days in late June and early July each year. Detailed knowledge of such predator–prey interactions over time is essential to identify and refine possible management measures for this complex system where both predator and prey are protected species. This is especially important as white-tailed eagles are increasing along the Norwegian coast and throughout the northern hemisphere, which may intensify their impact on seabirds (Hipfner et al., 2012), while kittiwakes—and other seabirds eagles can target—continue to decline rapidly (Croxall et al., 2012; Dias et al., 2019; Sandvik et al., 2014).

When additional pressures are induced by management actions, such as the protection of a conflicting species or when reducing its access to other food sources (e.g. fisheries offal) which may affect their numbers, distribution or behaviour, extra care should be taken to minimize the negative effects on other species of special conservation concern. In a constantly changing environment, there is an urgent need to develop and test a variety of possible actions that can make seabird management plans sufficiently dynamic and effective to buffer unintended consequences. For kittiwakes breeding along the Norwegian mainland this is no easy task, given that it is the highly mobile population of immature eagles that constitutes the extra burden—during a long period of poor food conditions.

In light of our findings, targeted conservation actions for kittiwakes would need to address two key questions: first and foremost, how to increase food abundance during breeding, while simultaneously decreasing disturbance and predation from eagles. Depending on location-specific drivers of decreased food availability, the former may be achieved through protecting important foraging areas (Pichegru et al., 2010), managing key stocks of forage fish with a wider ecosystem perspective than securing fisheries (Cury et al., 2011) and reducing the impact of climate change, which will require concerted global action (Clairbaux et al., 2021). In parallel, kittiwakes may be protected from eagles by creating refuges, for example, nesting structures built in locations close to existing colonies but less likely to be subject to high predation, such as close to human habitations, under bridges or on other constructions, including even offshore structures (Christensen-Dalsgaard et al., 2019) where predators have limited access or are kept away by human presence. This can help regional populations survive periods when food conditions are insufficient to secure an adequate breeding success, as documented to regularly affect auks during the cyclic decadal and longer-lasting temperature regimes typical of higher latitudes (Hansen et al., 2021; Irons et al., 2008).

Altogether, our results support findings in other species that prospering apex predators, for example, after cessation of population control, reduced pollutant levels or increased anthropogenic subsidies (Elmhagen et al., 2017; Oro et al., 2013; Roos et al., 2012), can have significant consequences for seabird populations (Ekroos et al., 2012; Scopel & Diamond, 2017), and shed light on the importance of top-down control of some seabird species. Our study also provides new evidence that the resulting increase in nest predation varies with the foraging conditions for the targeted populations. With seabirds declining worldwide, improving our understanding of the impact of both native and alien predators on seabird populations under deteriorating environmental conditions will be essential to inform future conservation.

AUTHOR CONTRIBUTIONS

Tycho Anker-Nilssen conceived the ideas and approach, collected and processed the data and led the writing of the manuscript together with Annette L. Fayet who conducted the data analysis. Tomas Aarvak helped collecting data and contributed critically to article drafts. All authors gave final approval for publication and agree to be held accountable for the content.

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CONFLICT OF INTEREST

We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available through the SEAPOP database and open access reports posted on the websites of NINA (https://www.nina.no/english/Home) and SEAPOP (https://seapop.no/en/), and from the Dryad Digital Repository https://doi.org/10.5061/dryad.b8gtht7f9 (Anker-Nilssen et al., 2022).

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SUPPORTING INFORMATION

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

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