Proceedings of the 5th International Conference on Modern Medicine and Global Health
DOI: 10.54254/2753-8818/2027.38439

Black-Legged Kittiwake Breeding Performance as an Indicator of Effective Forage Fish Availability

Yuhan Cui

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada
laura.cui@mail.utoronto.ca

Abstract. If seabird breeding metrics correlate with accessible food resources, breeding performance can serve as a contextual signal reflecting marine food supply status. This review synthesizes evidence linking black-legged kittiwake (Rissa tridactyla) breeding performance to effective forage fish availability, focusing on lesser sandeels within the North Sea. Synthesized findings from food supplementation trials, prey surveys, animal tracking datasets, long-term monitoring records, and fishery closure analyses demonstrate that prey abundance, age structure, and phenological synchrony between prey occurrence and bird breeding jointly shape reproductive outcomes. Fishing impacts depend on spatial overlap among fishing grounds, prey distributions, and colony foraging ranges. Predation and colony-local disturbances may also depress breeding success, creating ambiguity in causal inference. No universal prey density threshold can be derived to directly convert breeding performance into total fish biomass estimates. Standardized monitoring that separates breeding stages and integrates complementary datasets on prey, seabird diets, fisheries and predation is required to deploy this indicator reliably at local and regional scales.

Keywords: Black-legged kittiwake, breeding performance, forage-fish availability, lesser sandeel, ecological indicators

1. Introduction

Marine ecosystems are shaped by climate variability and human activities. Any assessment must consider interacting environmental and human pressures, not the effects of each one alone [1]. There is a need for biological indicators capable of integrating information about ecosystem conditions into measurable biological responses. Long-term monitoring of seabird reproduction can reveal marine ecosystem change, while representative colony networks strengthen spatial interpretation [2, 3]. However, not all seabird species respond to prey conditions in the same way, so the suitability of a particular species as an indicator depends on its foraging ecology and breeding constraints. In particular, the black-legged kittiwake, Rissa tridactyla, has the potential to serve as a sentinel of local food conditions because its surface-feeding ecology constrains access to prey [4]. Understanding links between prey conditions and breeding performance is also important for evaluating fisheries measures intended to benefit seabird conservation [4]. This sensitivity raises a central question: what aspect of food availability does kittiwake breeding performance represent?

© 2026 The Authors. This is an open access article distributed under the terms of the Creative Commons Attribution License 4.0 (https://creativecommons.org/licenses/by/4.0/).

DOI: 10.54254/2753-8818/2027.38439

For this paper, "breeding performance" includes hatching success, chick growth and survival, fledging success, and whole-season breeding success or productivity. Adult behavior and physiological condition are treated as supporting variables. Study-specific definitions and denominators are retained when comparing reproductive outcomes [5]. Here, kittiwake breeding performance is evaluated as an indicator of effective forage-fish availability during the breeding season, particularly lesser sandeel availability in the North Sea. Breeding performance is not treated as a direct measure of total fish biomass, marine productivity or climate change. The newly defined term "effective forage-fish availability" differs fundamentally from conventional prey abundance metrics. It describes prey resources accessible to adult kittiwakes within their foraging range during key reproductive phases.

This term considers not only prey abundance but also prey species composition, age and size structure, phenological overlap between prey availability and seabird breeding, spatial distribution relative to colony foraging ranges, and vertical accessibility. Climate and fisheries may alter these conditions and their relationship with breeding performance [4, 5]. Food-supplementation experiments show that increased food availability can improve kittiwake reproductive output [6]. However, sensitivity alone does not establish indicator reliability. Prey availability and timing during the breeding season affect breeding performance, while predation provides an alternative explanation for low breeding performance [5, 7].

Existing empirical studies have documented correlations between seabird productivity and forage fish stocks, yet many earlier works simplify prey resources as bulk biomass and overlook the dimensions of accessibility and phenology. A large body of regional monitoring work has confirmed kittiwakes' responsiveness to food limitation, but few syntheses systematically disentangle food signals from confounding local stressors. Current management frameworks frequently lack clear operational rules to translate seabird monitoring data into fishery decisions.

This paper will evaluate whether kittiwake breeding performance is a reliable and management-relevant indicator of forage-fish availability. It will examine the pathways through which oceanographic variability and fisheries affect prey availability and breeding performance. It will also compare data from food supplementation studies, direct measures of prey, regional comparisons, and changes in fishery activity. Emphasis is placed on whether the reliability of the indicator is affected by the age structure and phenology of the prey, temporal and spatial matching of prey measurements to colony foraging activity, and complementary information about alternative explanations for breeding failure. The review will then address the requirements for a proper interpretation, the limitations that affect the universal application, and the information needed prior to utilizing breeding performance in decision-making. The applied goal would be to determine what constitutes a useful warning signal versus information that validates the need for a certain management action.

2. Mechanistic basis: from ocean conditions to breeding performance

2.1. From environmental conditions to forage fish availability

Oceanographic conditions can affect kittiwake reproduction indirectly through effects transmitted across the food web. Temperature, circulation, and plankton phenology can affect forage fish and thus the timing, age structure, distribution and availability of prey for seabirds [5, 8]. Physical conditions should be considered as drivers of prey abundance but not substitutes for direct prey measurements [5, 8]. Climate indices can therefore suggest hypotheses related to environmental drivers, although the mechanism relevant to the current review remains forage-fish availability [9, 10]. Industrial forage-fish fisheries provide an additional driver. Commercial fishing can reduce prey

DOI: 10.54254/2753-8818/2027.38439

biomass, target certain age classes of forage fishes, and affect prey accessibility. The viability of this pathway depends on geographical overlaps between fishing areas, prey populations and colony foraging areas [4].

2.2. From forage-fish availability to kittiwake responses

As mentioned above, effective prey fish availability is not equivalent to prey biomass within a particular region. It depends on the availability of the prey fish of proper species, age, and size within the foraging range of the colony at the depth and time period for each breeding phase [4, 5, 11]. Breeding kittiwakes are central-place foragers that must return repeatedly to the colony, and their surface-feeding niche restricts their access to the deeper parts of the water column [4, 12]. Adults may increase foraging effort when prey availability decreases, but energetic constraints can limit compensation [6, 12].

The responses to food conditions differ across the breeding cycle [5]. Before and during incubation, food availability may affect adult energy allocation and reproductive investment [5, 6]. During chick rearing, it may affect adult foraging activity, prey delivery, chick growth, and survival [6]. A plausible sequence is that low prey abundance may require increased adult foraging activity. If compensation is insufficient, this may reduce food delivery rates during chick rearing, causing slow chick growth and eventually lower fledgling success and overall reproductive success [6, 12]. These behavioral shifts may precede or accompany reduced breeding success, yet they cannot be assumed to function as standalone monitoring indicators; empirical validation remains necessary. Breeding failure is not caused solely by food deprivation. Food availability and predation may both influence breeding outcomes [7].

Four predictions arise from this mechanistic model to be tested in the next section. Firstly, direct measures should be more informative than broad environmental proxies [4, 5, 9]. Secondly, prey abundance and age structure should jointly influence reproduction [5]. Thirdly, it is hypothesized that the association between prey availability and breeding success will be more predictable in colonies sharing the same prey sources [4, 11]. Finally, productivity alone cannot help determine the reason for reproductive failure [4, 7].

3. Empirical evidence: what has been demonstrated

3.1. Experimental evidence of food-supply effects

Experimental evidence of the direct influence of food supply on the breeding performance of black-legged kittiwakes comes from a supplemental-feeding study on Middleton Island, Alaska [6]. Monitoring in 2015, 2017 and 2018 used GPS-derived time-activity budgets to estimate energy expenditure [6]. Supplemented birds spent less time foraging, had lower estimated daily energy expenditure, and produced more fledglings than controls [6]. They spent approximately 25% of their time on foraging trips, compared with approximately 50% among controls [6]. However, there was no correlation found between energy expenditure and fledging success [6].

Because the tracked adults were already rearing chicks, these results do not rank indicator sensitivity throughout the breeding cycle [6]. In another tracking study, the lower variability of the trips by individuals correlated with a higher chance of chick fledging, but the characteristics of the trips did not explain annual breeding success [12]. Behavioural changes must therefore be interpreted together with reproductive output and prey availability rather than treated as independent markers of food shortage [6, 12]. Hence, experimental responses alone are not sufficient to conclude

DOI: 10.54254/2753-8818/2027.38439

that low breeding performance of the kittiwakes in nature is caused by low forage-fish availability [4, 6, 7].

3.2. Calibration against direct prey measurements

A North Sea study examined the influence of sandeel abundance and seasonal overlap on various components of seabird breeding success [5]. The selected model of kittiwake fledging success had a pseudo-R^2 of 0.39 [5]. The interaction between log(age-0 sandeel abundance) and the temporal overlap between age-0 availability and chick rearing was also positive [5]. The negative interaction between log(age-0 sandeel abundance) and log(age-1 sandeel abundance) shows that their effects were not additive [5]. Therefore, age-0 abundance had the most beneficial impact when prey was available during chick rearing, and the contribution of one age class depended partly on the availability of the other [5]. Regional studies have similarly demonstrated positive associations between kittiwake breeding success and the abundance of age-0 sandeels, but negative associations between success and fishing activity; age-1 abundance and SST were not significant predictors in this analysis [4].

3.3. Food-web and spatial evidence

Information for bottom-up transmission comes from long-term plankton records. An analysis over six decades of Continuous Plankton Recorder found marked spatial variation in sandeel prey fields and a decline of more than 50% in estimated available prey energy in the western North Sea since the 1960s [8]. This result supports research that ties the presence of sandeels to breeding success but does not in itself prove the entire causal chain [5, 8]. GPS-based habitat-selection analyses at 15 colonies around the United Kingdom and Ireland found greater individual specialization in more heterogeneous environments [11].

3.4. Evidence that limits general interpretation

A 25-year analysis found that in colonies where foraging distributions overlap the fishing area, modelled breeding success, scaled to two potential fledglings per pair, decreased from 52% before the fishery to 23% during its operation [4]. After closure, the breeding success increased by approximately 10 percentage points through 2018 (95% confidence interval: 2–18) [4]. Control-colony comparisons strengthen the inference of fishery effects, although the before-after control-impact analysis remains observational [4].

However, the post-closure improvement is relatively small compared to the initial decrease and varies across colonies. There is no evidence of increased breeding success after closure for guillemots, razorbills, or puffins [4]. This divergence arises from interspecific differences in foraging depth, diet spectrum and foraging range; these species do not rely on sandeels to the same degree as kittiwakes. Data on the Faroe Shelf show that chick production peaks of seabirds correlate with primary production and juvenile fish indices. However, the increase in chick production after 2014, including kittiwakes' chick production, cannot be explained solely by changes in these indices [9]. Predation is another direct example of reduced indicator specificity. A 42-year study of two neighboring seabird colonies in Norway revealed that breeding success was negatively correlated with the population of white-tailed eagles in the exposed colony, while better foraging opportunities benefited both colonies [7].

DOI: 10.54254/2753-8818/2027.38439

3.5. Synthesis against the four mechanistic expectations

First, direct prey and diet data help interpret breeding performance, but the reviewed studies do not establish their general superiority over environmental proxies [4, 5, 9]. Second, abundance, phenology and age structure jointly influence breeding performance, yet no universal prey-density threshold has been identified [5]. Third, existing research does not directly test whether colonies sharing prey resources show synchronised breeding outcomes; habitat-selection evidence does not confirm cross-colony synchrony [11]. Fourth, Fisheries-related changes in prey availability and predation can both affect breeding performance, complicating causal attribution [4, 7]. Thus, the empirical evidence supports the conclusion that Black-legged kittiwake breeding performance is a potentially useful but context-dependent indicator of prey availability during the breeding season [4-7]. For the North Sea evidence considered, interpretation centres on lesser-sandeel availability at the local to regional scale relevant to colonies.

4. Indicator value, limitations and management use

Specific criteria are required when a sentinel is intended to represent a specific ecosystem component, such as a particular food resource. Namely, the response should have a predictable relationship with the target process, occur at the relevant scale, be repeatable enough, and provide information for management. This distinction is important because a species might be sensitive to ecological change without being a reliable indicator of its causes [3-5, 7]. Kittiwake breeding performance meets some of these criteria rather well. It is measurable at accessible breeding sites, can be repeated with standardized methodology, and may change in a single breeding season [3, 6].

4.1. Limitations of reliable interpretation

First, the same breeding-performance outcome can arise through multiple causal pathways [6, 7]. Low overall productivity does not distinguish whether the failure occurs in the incubation, chick-rearing, or both. However, additional evidence is needed to determine its cause [5, 7]. Second, environmental proxies are not always stable. Climate indices can provide ecological context and generate hypotheses but should not be used as equivalent to direct prey information unless the intermediate pathway is established [8, 9]. Third, prey effects may be non-additive and depend on age composition and seasonal overlap [5]. Adults may increase foraging effort or allocate time differently in response to food shortage, but compensation is constrained [6, 12]. The studies reviewed here do not establish a continuous conversion from breeding success to prey biomass or a universal management threshold [4, 5].

4.2. Spatial and temporal limitations

Estimates of impacts due to fisheries relied upon the spatial overlap of fishing, the distribution of sandeels, and the foraging range of each colony [4]. Thus, regional interpretation is possible, but using the information from a single colony to make a regional conclusion is not justified [4, 11]. Temporal interpretation is also affected by the reproductive stage. The overall breeding productivity considers multiple stages but might conceal when failure occurred [5].

Thus, the time period should be defined depending on the reproductive parameter analyzed, rather than assuming that an annual breeding-performance value represents prey conditions throughout the entire calendar year. Prey effects may also depend on phenological matching. The

DOI: 10.54254/2753-8818/2027.38439

effect of sandeels on reproductive success of seabirds depends on age class, abundance, and temporal overlap with reproductive phases [5]. Thus, an annual prey abundance estimate might be less useful if the prey is absent during the time period of maximum energetic demands [5].

4.3. Choice of breeding parameters and integrated monitoring approach

Overall breeding productivity should remain a key summary parameter because it can be monitored over long periods and compared across years and colonies [3]. Nevertheless, within each monitoring program it should be calculated using one fixed and explicitly reported denominator. Statistics on occupied nests, active nests, breeding pairs, breeding attempts, eggs laid, and chicks hatched cannot be considered equivalent to one another.

Hatching success and fledging success should be reported separately whenever possible to isolate reproductive failure at different stages, although they do not by themselves establish its cause [5, 7]. Other variables can help interpret breeding outcomes but should not be considered as equivalent measures of breeding performance [6, 12]. The monitoring framework should include ecologically representative colonies and regular measurements of prey abundance or density, age composition, phenology, and spatial accessibility [3, 5, 11]. Diet measurements can show whether the kittiwakes continue to feed on the focal forage-fish species or shift to alternative prey [4]. Information on fishing activity and predation is also needed to evaluate alternative explanations for reproductive failure [4, 7].

4.4. From the ecological signal to management action

The main management significance of kittiwake breeding performance lies in its utility as a warning signal that generates testable hypotheses. Marine assessments should consider cumulative stressor effects before attributing change to a particular pressure [1]. The following cautious operational sequence can be based on the evidence synthesized above. First, investigators should establish whether the change is biologically significant, persistent, and unusual against the background of long-term trend. Second, identify affected reproductive stages and whether changes are shared by ecologically comparable colonies. The next step is to compare prey abundance, age composition, phenology, spatial accessibility, and diet measurements, along with fishing and predation [4, 5, 7]. This operational framework is a synthesis constructed within this review; it has not been validated as a formal decision system in any single empirical investigation.

Precautionary action may be justified under uncertainty, but its rationale and expected benefits should be explicit. Thus, the amount and consistency of supporting evidence should determine the degree of confidence in the causal explanation and specificity of the response [1]. Thus, breeding performance can help in the evaluation of the spatial fishery measures, but conclusions should not be based on a single colony, annual value, or species. Long-term trends, spatial differences, prey measurements, and specific foraging ecology of the species remain necessary [4].

5. Conclusion

Kittiwake breeding performance functions as a conditional local-to-regional indicator reflecting effective forage-fish availability during breeding seasons. Synthesized evidence shows prey abundance, age composition and phenological synchrony jointly regulate kittiwake reproductive output, and fishery impacts only emerge when fisheries overlap spatially with prey fields and colony foraging zones. Behavioral adjustments such as extended foraging trips can partially offset food

DOI: 10.54254/2753-8818/2027.38439

limitation, though such compensation has clear energetic boundaries. Predation and colony-scale disturbances can independently reduce breeding productivity, introducing uncertainty in causal attribution. No universal conversion function exists to translate breeding metrics directly into absolute prey biomass or set fixed ecological thresholds. This indicator delivers practical value for marine ecosystem monitoring and supports precautionary fisheries management by providing early warning signals of degraded prey conditions. Its application requires standardized multi-metric monitoring protocols and complementary datasets to separate food limitation from confounding environmental pressures. This synthesis has several notable limitations. Most empirical evidence comes from the North Sea and focuses heavily on lesser sandeels, so findings may not transfer straightforwardly to other ocean regions with different prey communities. The proposed stepwise assessment framework has not been field-tested in operational fishery governance. Future research should test this indicator across broader geographic contexts, quantify the relative weighting of multiple co-occurring stressors, and develop quantitative decision thresholds to translate seabird monitoring signals into actionable conservation policies.

References

[1] Hollarsmith, J. A., Therriault, T. W., & Côté, I. M. (2022). Practical implementation of cumulative-effects management of marine ecosystems in western North America. *Conservation Biology, 36*(1), e13841. DOI: 10.1111/cobi.13841

[2] Sydeman, W. J., Schoeman, D. S., Thompson, S. A., et al. (2021). Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels. *Science, 372*(6545), 980–983. DOI: 10.1126/science.abf1772

[3] Clairbaux, M., Rönkä, M., Anker-Nilssen, T., et al. (2024). An ecologically sound and participatory monitoring network for pan-Arctic seabirds. *Conservation Biology, 38*, e14287. DOI: 10.1111/cobi.14287

[4] Searle, K. R., Regan, C. E., Perrow, M. R., et al. (2023). Effects of a fishery closure and prey abundance on seabird diet and breeding success: Implications for strategic fisheries management and seabird conservation. *Biological Conservation, 281*, 109990. DOI: 10.1016/j.biocon.2023.109990

[5] Régnier, T., Wright, P. J., Harris, M. P., et al. (2024). Effect of timing and abundance of lesser sandeel on the breeding success of a North Sea seabird community. *Marine Ecology Progress Series, 727*, 1–17. DOI: 10.3354/meps14520

[6] Kahane-Rapport, S. R., Whelan, S., Ammendolia, J., et al. (2022). Food supply and individual quality influence seabird energy expenditure and reproductive success. *Oecologia, 199*, 367–376. DOI: 10.1007/s00442-022-05191-y

[7] Anker-Nilssen, T., Fayet, A. L., & Aarvak, T. (2023). Top-down control of a marine mesopredator: Increase in native white-tailed eagles accelerates the extinction of an endangered seabird population. *Journal of Applied Ecology, 60*, 445–452. DOI: 10.1111/1365-2664.14343

[8] Olin, A. B., Banas, N. S., Johns, D. G., et al. (2022). Spatio-temporal variation in the zooplankton prey of lesser sandeels: Species and community trait patterns from the Continuous Plankton Recorder. *ICES Journal of Marine Science, 79*, 1649–1661. DOI: 10.1093/icesjms/fsac101

[9] Olsen, B., Anker-Nilssen, T., Danielsen, J., et al. (2025). Half a century of environmental variability and seabird trends on the Faroe Shelf in the North Atlantic Ocean. *Frontiers in Marine Science, 12*, 1544866. DOI: 10.3389/fmars.2025.1544866

[10] Votier, S. C., Sherley, R. B., Scales, K. L., et al. (2023). An overview of the impacts of fishing on seabirds, including identifying future research directions. *ICES Journal of Marine Science, 80*(9), 2380–2392. DOI: 10.1093/icesjms/fsad173

[11] Trevail, A. M., Green, J. A., Bolton, M., et al. (2021). Environmental heterogeneity promotes individual specialisation in habitat selection in a widely distributed seabird. *Journal of Animal Ecology, 90*, 2875–2887. DOI: 10.1111/1365-2656.13588

[12] Schlener, J., Whelan, S., Hatch, S., et al. (2024). If it ain't broke, don't fix it: Variable foraging behaviour is associated with low kittiwake reproductive success. *Animal Behaviour, 209*, 155–167. DOI: 10.1016/j.anbehav.2023.12.015