

A mechanistic framework to inform the spatial management of conflicting fisheries and top predators

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Abstract

- Conflicts of interest between resource extraction and conservation are widespread, and negotiating such conflicts, or trade-offs, is a key issue for ecosystem managers. One such trade-off is resource competition between fisheries and marine top predators. Managing this trade-off has so far been difficult due to a lack of knowledge regarding the amount and distribution of prey required by top predators.
- Here, we develop a framework that can be used to address this gap: a bio-energetic model linking top predator breeding biology and foraging ecology with forage fish ecology and fisheries management.
- We apply the framework to a Baltic Sea colony of common guillemots *Uria aalge* and razorbills *Alca torda*, two seabird species sensitive to local prey depletion, and show that densities of forage fish (sprat *Sprattus sprattus* and herring *Clupea harengus*) corresponding to the current fisheries management target B_{MSY} are sufficient for successful breeding. A previously proposed fisheries management target for conserving seabirds, 1/3 of historical maximum prey biomass ($B_{1/3}$), was also sufficient.
- However, the results highlight the importance of maintaining sufficient prey densities in the vicinity of the colony, suggesting that fine-scale spatial fisheries management is necessary to maintain high seabird breeding success.
- Despite foraging on the same prey, razorbills could breed successfully at lower prey densities than guillemots but needed higher densities for self-maintenance, emphasizing the importance of considering species-specific traits when determining sustainable forage fish densities for top predators.

Abbreviations: $B_{1/3}$, Fish biomass at one-third of the historical maximum, sensu Cury et al. (2011); B_{lim} , Fish biomass limit under which there is a risk of fish recruitment impairment; B_{MSY} , Fish biomass corresponding to Maximum Sustainable Yield (MSY); B_{pa} , Fish biomass corresponding to a precautionary approach, typically lower than B_{MSY} as it includes estimation of uncertainty; CFP, The Common Fisheries Policy of the European Union; FMR, Field Metabolic Rate; FMR_{lim} , Physiological upper limit for daily energy consumption; t, metric tonne (106nonbreakingspaceg).

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6. *Synthesis and applications.* Our bio-energetic modelling framework provides spatially explicit top predator conservation targets that can be readily integrated with current fisheries management. The framework can be combined with existing management approaches such as dynamic ocean management, marine spatial planning and management strategy evaluation to inform ecosystem-based management of marine resources.

KEYWORDS

bio-energetic modelling, ecosystem-based management, fisheries, forage fish, seabirds, spatial dynamics, top predators

1 | INTRODUCTION

Conflicts between biodiversity conservation and human utilization of natural resources are widespread, with examples ranging from forestry and agriculture to fisheries (Cury et al., 2011; Henle et al., 2008; Hobday et al., 2015; Niemelä et al., 2005). Negotiating such conflicts or trade-offs is a key issue for ecosystem managers across continents and ecosystem types (Redpath et al., 2013; Rodríguez et al., 2006). The apparent competition for forage fish between industrial fisheries and marine top predators is one such conflict that has been difficult to resolve due to a lack of knowledge of the prey requirements for top predators and how they vary over time and space (Cury et al., 2011; Furness & Tasker, 2000; Grémillet et al., 2018; Hill et al., 2020; Sydeman et al., 2017). Despite the well-known fact that forage fish fisheries can affect reproduction and survival of marine top predators (Bertrand et al., 2012; Cook et al., 2014), management measures to protect their prey are relatively rare (but see for example North Sea: Frederiksen et al., 2008; Namibia: Ludynia et al., 2012; South Africa: Sherley et al., 2015). Furthermore, it is unknown whether targets commonly used to ensure sustainable exploitation of fish stocks, that is, maintaining biomasses (B) corresponding to Maximum Sustainable Yield (MSY) or a precautionary approach (PA; Jennings et al., 2001; List of Abbreviations), are compatible with top predator conservation (Cury et al., 2011). As several international and national policy frameworks call for comprehensive measures to protect populations of seabirds and marine mammals (EC, 2008; Pacific Fishery Management Council, 2019), this is an urgent question in the context of the general ongoing transition towards ecosystem-based management of the marine environment (Pikitch et al., 2004). A new generation of holistic policy frameworks to aid the implementation of ecosystem-based management such as Dynamic Ocean Management (Dunn et al., 2016) and Marine Spatial Planning (White et al., 2012) are specifically designed to handle conflicts by taking spatiotemporally explicit approaches. However, such approaches are difficult to apply without more detailed models of the underlying ecosystems.

Here, we present a spatiotemporally explicit mechanistic framework that can be used to determine the amount of prey required for central-place foraging top predators, and how this varies between species and depends on their population sizes. We build on existing work in bio-energetic modelling for colonial seabirds, which has previously been

used to investigate their responses to prey conditions, and how it may differ depending on species-specific characteristics (Elliott et al., 2013; Houston et al., 1996; Thaxter et al., 2013). Many predatory marine mammals and all seabirds are central-place foragers during the breeding season, which means that parents need to return to the colony regularly for breeding activities. As such, they are highly dependent on prey available close to the colony and within their maximum foraging depth (Boyd et al., 2017; Campbell et al., 2019; Matthiopoulos et al., 2008; Wanless et al., 2005). This may result in the top predators gradually depleting the prey around their colonies, potentially creating an 'Ashmole's halo' (lower prey density near the colony and within diving depth of the birds) (Ashmole, 1963; Birt et al., 2007; Jovani et al., 2016), an effect that will be stronger for large colonies (Ainley et al., 2004; Gaston et al., 2007; Lewis et al., 2001; Wakefield et al., 2013). While foraging further from the colony may partially compensate for local prey depletion, there is a limit to the distance that any top predator can travel without negative impacts on the breeding attempt, and this limit may be particularly low for species in which locomotion is slow and/or energetically costly (Elliott et al., 2013; Thaxter et al., 2010). Therefore, colony size and species-specific traits will both determine the area used by foraging top predators, and both will thus be important to consider when designing fisheries management approaches that aim to maintain sufficient prey resources.

As an example of how to apply our framework, we used two seabird species from the *Alcidae* family, the common guillemot *Uria aalge* (hereafter: guillemot) and the razorbill *Alca torda*, breeding sympatrically at a colony in the Baltic Sea and foraging on the same two forage fish species, sprat *Sprattus sprattus* and herring *Clupea harengus*. As wing-propelled pursuit-divers, the two seabird species have high flight costs (Elliott et al., 2013; Thaxter et al., 2010), which are reflected in their relatively short foraging ranges (Davoren & Montevecchi, 2003; Gaston et al., 2007). However, the razorbill, which has more energetically efficient flight, has been observed to spend relatively more time flying and less time diving, whereas guillemots are able to reach greater depths (Linnebjerg et al., 2015; Thaxter et al., 2010), suggesting that prey distribution effects are species-specific. The limited foraging range of the two study species makes them particularly sensitive to local prey declines, hence making them suitable as indicators of forage fish depletion (Cairns, 1988; Furness & Camphuysen, 1997; Piatt et al., 2007; Velarde et al., 2019). Apart from being the principal prey of both seabirds in this study system, the two forage fish species are also targeted by a large

industrial fishery that is regulated by annual quotas (ICES WGBFAS, 2019). To date, it has been unknown to what extent these quotas align with prey requirements for fish-eating top predators.

We investigated the following three questions: (a) What is the minimum density of prey fish required for successful breeding in the two seabird species and how does this depend on their population size? (b) How do species-specific traits, in particular diving and flying capabilities, influence this density? (c) Are current fisheries management targets sufficient for maintaining favourable conservation status of the two species?

The study provides a general framework for how bio-energetic modelling can be combined with commonly available data to design fishery management measures that maintain sufficient prey resources for top predators, thus contributing to the development of an ecosystem-based approach to fishery management.

2 | MATERIALS AND METHODS

2.1 | Bio-energetic model

Our framework is built around a bio-energetic model that simulates daily time and energy budgets for individual guillemots and razor-bills during the breeding season, building on a number of previous bio-energetic models for these species (Gaston et al., 2007, 2013; Houston et al., 1996; Langton et al., 2014; Thaxter et al., 2013). A key model assumption is that birds minimize foraging distance and time as they seek to lower daily energy expenditure while still covering their energetic needs. This assumes that the birds have perfect knowledge of fish distribution. The location and time spent foraging will then depend on forage fish distribution, breeding stage, metabolic cost for different activities as well as the energetic gain of foraging at different prey densities (Figure 1).

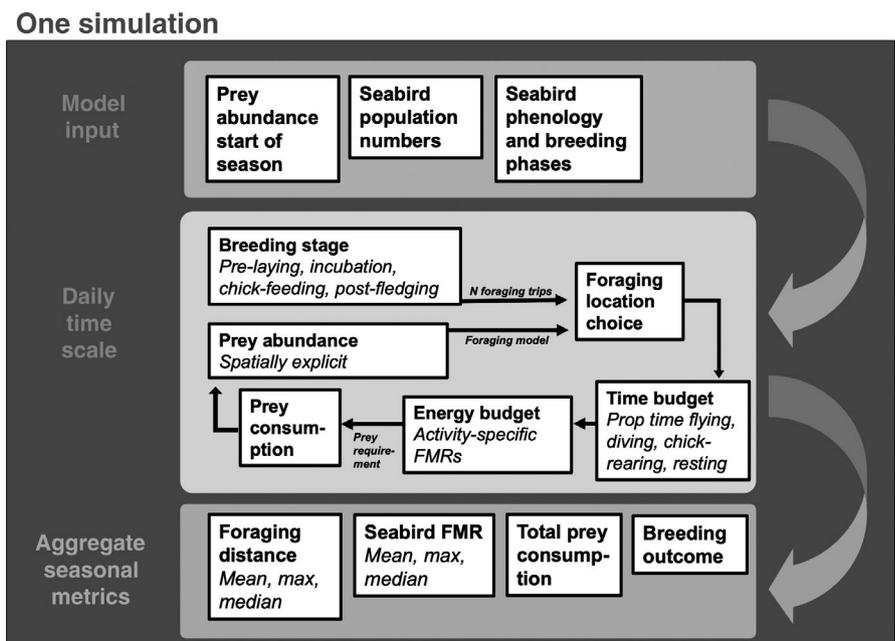
2.1.1 | Population structure and breeding stage dependence

The populations of both species were assumed to consist of two-thirds of breeding adults and one-third of non-breeding individuals, based on previous observations (Appendix S4 in Supporting Information). It was assumed that non-breeding individuals are present throughout the breeding season. Over the course of a breeding season, the breeding individuals go through four stages: pre-laying, incubation, chick-feeding and post-fledging, with stage-specific time and energy budgets. During the incubation and chick-feeding stages, each parent is bound to the colony for 12 hr each day to take turns in incubation/chick-guarding. In all stages but the chick-feeding stage each parent is assumed to make only one foraging trip per day, as this is the strategy that minimizes energy expenditure. The number of foraging trips during chick-feeding is species-specific, for details see Appendix S2 *Foraging trips*. We set a fixed chick-provisioning period of 21 days which is supported by previous observations in our colony.

2.1.2 | Activity-specific metabolic rates

Within a day, an individual breeding seabird can carry out four different activities: flying, foraging, incubating/brooding and resting. How much time they spend on each activity in a 24-hr cycle is an outcome of the model (Figure 1). Each activity has an associated metabolic rate through which daily time budgets are translated into energy budgets. We defined a physiological upper limit for daily energy consumption (Field Metabolic Rate, FMR_{lim}) as a multiplier of Basal Metabolic Rate (Table S3). If either species reached FMR_{lim} during a time-step of a simulation, it was defined as breeding failure and parents were assumed to abandon the chick in favour of self-maintenance (Regular et al., 2014; Wanless

FIGURE 1 Structure of the bio-energetic model with inputs, daily time steps and seasonal metrics. One simulation covers a full breeding season (Appendix S2 *Breeding phenology*). For each time step, the model simulates the distribution of seabird foraging locations and forage fish, time-activity budgets, energy expenditure and prey consumption for individual birds, which is scaled up to the population using population numbers of the two species



et al., 2005). However, we still let simulations continue until the end of the season to investigate the prey densities required for self-maintenance.

2.1.3 | Foraging submodel

To model prey capture of foraging seabirds, we calculated energy intake rates as a function of prey density, based on a simple foraging model previously used for foraging fish (e.g. Varpe & Fiksen, 2010). Prey capture Cr_i (number of prey s^{-1}) was calculated as follows:

$$Cr_i = Ss_i \times \pi Dd_i^2 \times Fdens \times Ddistr_i \times Cs_i \times DtPDI_i, \quad (1)$$

where Ss is swimming speed (ms^{-1}), Dd is the prey detection distance (m), $Fdens$ is the prey density (number of prey m^{-3}), $Ddistr$ is the proportion of prey available within diving depth, Cs is proportion of successful prey captures and $DtPDI$ is the proportion of time spent actively foraging during a dive cycle, that is, foraging time compensated for the pre- and post-dive intervals, and i is the index for the two species. See Appendix S2 for parameter values.

Energy gain ($ECapt$, [$kJ s^{-1}$]) was calculated as follows:

$$ECapt = Cr_i \times Fw \times Ef, \quad (2)$$

where Cr_i is from Equation (1), Fw is the prey weight (g) and Ef is the prey energy density (kJg^{-1}).

2.1.4 | Aggregate seasonal metrics

Our measures of seasonal individual fitness were as follows: (a) whether birds could breed successfully, that is, cover the energetic demands for

themselves and their chick over a whole breeding season and (b) whether adult birds could meet their own energetic demands without successfully raising a chick (referred to as 'self-maintenance' from hereon). We calculated the prey densities required for successful breeding at current population sizes by iteratively lowering initial densities until breeding would fail ($FMR > FMR_{lim}$) and denoted those densities B_{CG}^* and B_{RB}^* for guillemots and razorbills, respectively. Prey densities required for colony-based self-maintenance were estimated in a similar way by investigating the point where $FMR > FMR_{lim}$ in the non-breeding population. Population size limits at different prey densities were calculated by gradually increasing the population sizes until bird-driven prey depletion resulted in breeding failure ($FMR > FMR_{lim}$). These limits were calculated for one seabird species at a time while the other species' population size was kept constant.

2.2 | Uncertainty and sensitivity analyses

An uncertainty analysis was run to assess the confidence with which we could determine the prey densities required for successful breeding and self-maintenance. We also ran a sensitivity analysis to investigate the relative contribution of individual model parameters to the uncertainty in the results. For details, see Appendix S3.

2.3 | Study system and fisheries management targets

The model was parameterized for guillemots and razorbills at their largest colony in the Baltic Sea, the island of Stora Karlsö ($57^{\circ}17'N$, $17^{\circ}58'E$), with 15,700 and 12,000 breeding pairs, respectively (Olsson & Hentati-Sundberg, 2017; Figure 2). The two species feed almost exclusively on sprat and herring (Appendices

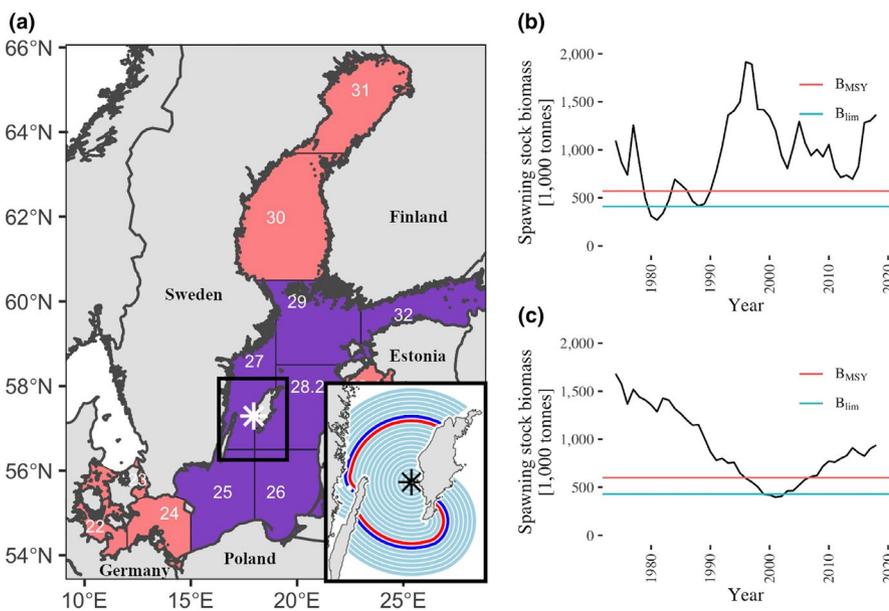


FIGURE 2 (a) Map of the Baltic Sea with fisheries management areas for sprat (area 22 – 32) and herring (area 25 – 29 + 32, purple coloured), map inset with Stora Karlsö (black star) and model foraging areas constructed as circular bands centred on the colony with a width of 5 km each, of which the red and blue are the observed maximum foraging distances for guillemots and razorbills, respectively. (b and c) Trends in biomass and management targets for (b) sprat and (c) herring

1 and 2), which are managed under the Common Fisheries Policy (CFP) of the European Union (EU), based on scientific advice from the International Council for Exploration of the Seas (ICES). ICES uses a multi-annual plan that specifies management targets for biomass to be conserved and fishing mortality for each fish species. Three biomass targets are currently defined for each species: B_{MSY} , B_{PA} and B_{lim} . B_{MSY} is the biomass level that is expected to produce Maximum Sustainable Yield for fisheries, which is the main management goal for all stocks managed under the CFP (EC, 2013), whereas B_{PA} and B_{lim} represent the PA and limit biomass reference points, respectively (see List of Abbreviations). A previous empirical study suggested prey biomass above 1/3 of the historical maximum as a seabird conservation target (Cury et al., 2011) and this level (denoted $B_{1/3}$) was also included in our analysis. The management strategy does not currently consider prey requirements of top predators. For further details on the management targets and how they were used in the analysis, see Appendix S1.

3 | RESULTS

3.1 | Seabird performance in relation to fisheries management targets

Forage fish density had a strong effect on breeding performance as well as time and energy budgets for both seabird species (Figures 3 and 4). At the lowest forage fish density considered (only herring at B_{lim}), breeding failed for both species due to prey depletion in the first week of the season, whereas in the highest prey density scenario (current biomass for both prey species), both species reproduced successfully

while foraging within a 25 km radius of the colony throughout the season (Figure 3). By examining a wide range of plausible values around the best estimates for all parameters in the uncertainty analysis, we concluded that these results are robust to parameter value uncertainties (Appendices S2 and S3). With a prey biomass corresponding to the main fisheries management target (B_{MSY}), successful reproduction occurred in 76% and 80% of model runs for guillemots and razorbills, respectively, which is sufficient for maintaining population sizes for these two seabirds in our system (Appendix S4). The results for $B_{1/3}$ were similar, that is, also sufficient for both species at current population levels and survival estimates (success in 68 and 73% of model runs, respectively). Numerical results for all scenarios are given in Appendix S3; Table S4.

The minimal forage fish densities required for successful breeding (B_{CG}^* and B_{RB}^*) were 56 and 55% of B_{MSY} , respectively. Interestingly, while razorbills could breed successfully at lower prey densities than guillemots, guillemots could self-maintain at slightly lower prey densities than razorbills by abandoning the chick and making only one trip per day (17% and 21% of B_{MSY} for guillemots and razorbills, respectively; Table S5). Guillemots' higher tolerance for colony-based self-maintenance and razorbills' higher tolerance for successful breeding was consistent across prey densities (Table S4). According to our model, the current fisheries management target can support substantially larger populations of the two seabird species (Figure 4).

The sensitivity analysis showed that maximum energy consumption, activity-specific metabolic rates and flight speed were the most influential parameters for guillemot model predictions, while metabolic rates, prey detection distance and number of trips were the most influential parameters for razorbills (Figure S4). The sensitivity analysis also showed that the parameter values for one species

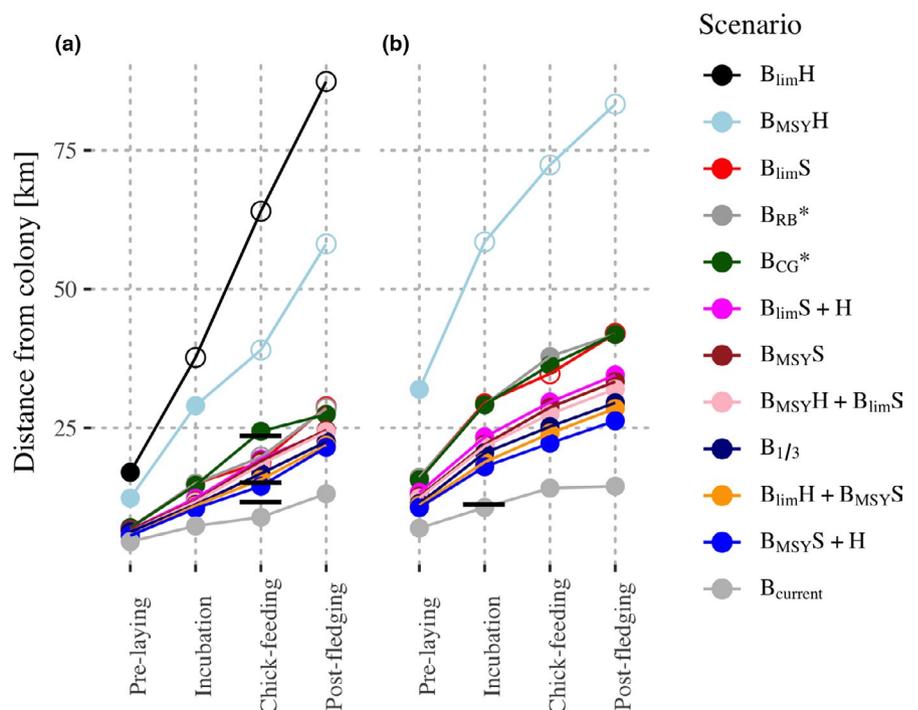


FIGURE 3 Foraging distance as a function of breeding stage and prey density for (a) guillemots and (b) razorbills. Open symbols indicate failed breeding at a given prey density and breeding stage. Missing data for razorbills at $B_{lim}H$ indicate that they cannot self-maintain at this prey density. Horizontal black lines indicate previously reported average foraging distances for different years obtained through GPS tracking (Appendix S2 *Foraging trips*). Prey densities in the legend are sorted from lowest on top to highest density (Appendix S1: Tables S1 and S2)

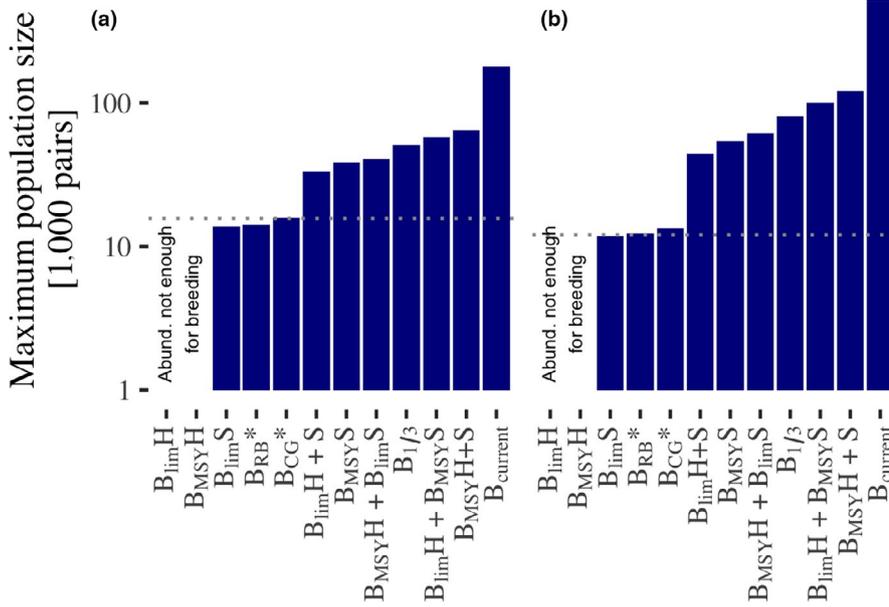


FIGURE 4 Upper limits to seabird population size (number of breeding pairs) at different forage fish densities for (a) guillemot and (b) razorbill. Dotted horizontal lines denote current population sizes. Note logarithmic scale on y-axis. For a description of forage fish density scenarios, see Table S2

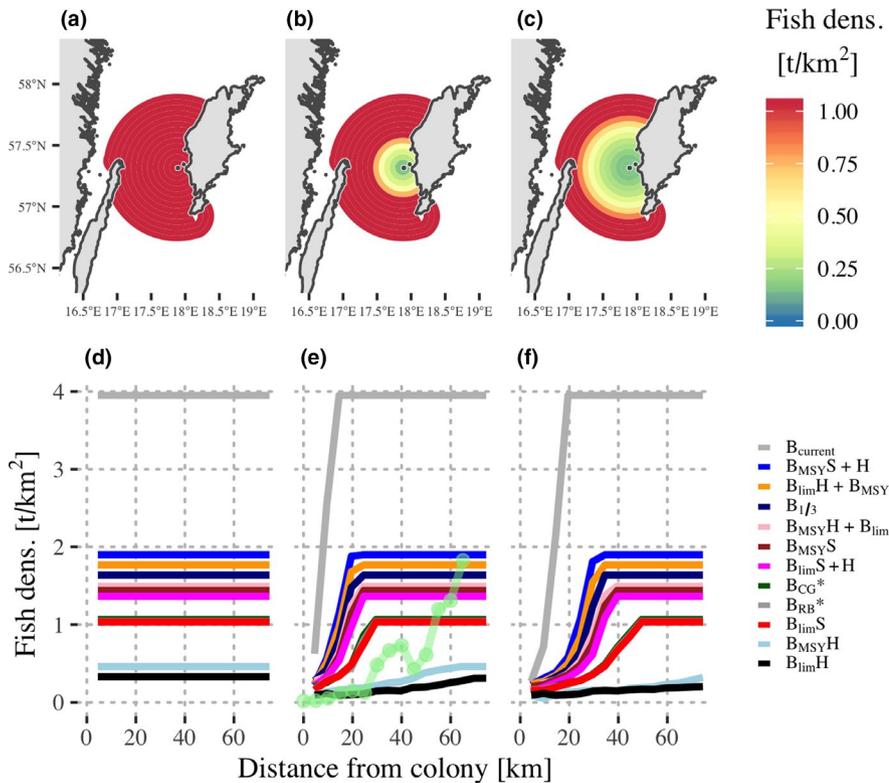


FIGURE 5 Gradients of fish density with increasing distance from the colony in the beginning, middle and end of the breeding season, based on initial densities B_{RB}^* (a–c), that is, the prey density scenario with the most far-reaching depletion effect, and at all prey densities (d–f). Although the model allowed birds to forage up to 110 km over-sea distance from the colony, no foraging took place beyond 55 km, that is, the maximum foraging distance which makes energetic sense for these two species in this system. In (e) empirical data for the prey gradient observed in 2014 are shown as a green semi-transparent line

affected the energetics of other species (through their effect on consumption).

3.2 | Species-specific and stage-dependent foraging patterns

The model predicted different foraging patterns for the two species in relation to prey density. Guillemots were predicted to forage

closer to the colony than razorbills and both species were predicted to forage at an increasing distance from the colony over the course of the breeding season (Figure 3). Average foraging distance also varied strongly as a function of initial prey densities—in razorbills the mean foraging distance in the chick-rearing period varied between 14 and 47 km in $B_{current}$ and B_{RB}^* , respectively. The modelled difference between species in foraging distance corresponds qualitatively to earlier observed differences between the two species (Hentati-Sundberg et al., 2018) and the foraging distances

predicted by the model agree with data obtained from GPS tracking at the colony (Evans et al., 2013; Isaksson et al., 2019; Figure 3; Appendix S2).

3.3 | Prey depletion by foraging seabirds

The increase in foraging distance over the season reflects the gradually declining prey densities close to the colony (Figure 5). An Ashmole's halo emerged at all prey densities but its size varied from 15 to 55 km in B_{current} and B_{RB}^* , respectively. The total size of the foraging area in the successful breeding scenarios varied between 700 and 7,400 km². The near-colony fish density at the end of the season varied between 0.05 and 0.28 tkm⁻², which corresponds to 7%–15% of the densities in the unaffected areas far from the colony. This steep gradient in prey density agrees with a previously estimated fish density of 0.018 tkm⁻² close to Stora Karlsö in the middle of the breeding season, that is, an even lower number than suggested by the model (Figure 5e). The total seabird consumption over one breeding season varied between 1659 and 2020 t and showed a negative relationship with initial prey densities, meaning that seabirds consumed more at lower prey densities. This reflects the higher foraging costs (flying and diving) of birds facing prey shortages, which requires a greater energy intake. Our consumption estimates largely agree with results from other colonies (Appendix S4).

4 | DISCUSSION

Mitigating conflicts in ecosystem management requires frameworks for evaluating and reconciling targets from different spheres, such as resource use management and environmental conservation. To that end, we developed a mechanistic bio-energetic model linking seabird breeding biology and foraging ecology with forage fish and fisheries management targets. Our model shows that densities of forage fish corresponding to currently used fisheries management targets are sufficient for successful breeding of guillemots and razorbills at the largest colony in the Baltic Sea. A previously proposed target for conserving seabirds, 1/3 of historical maximum prey biomass (Cury et al., 2011) was also found sufficient. However, the large size of the fishery management area (>100,000 km²) compared to the size of the seabird foraging area during the breeding season (<3,000 km² when successful) highlights the need for a spatially explicit approach, which could mitigate local conflicts between top predator conservation and industrial fishing.

4.1 | Seabird traits and prey availability

At low prey densities, guillemots had a competitive advantage for self-maintenance, whereas razorbills were better at breeding successfully, something that is in line with earlier empirical findings

and model results for these species (Linnebjerg et al., 2015; Thaxter et al., 2010, 2013). In contrast with many other study systems, razorbills at Stora Karlsö often bring only one prey item to their chick per trip (Appendix S2), which indicates that high-quality prey is available to razorbills during chick-feeding despite their more limited diving capacity (Figure S2). The Atlantic biogeographical population of guillemots is substantially larger than that of razorbills, suggesting that the superior diving capacity of guillemots is a competitive advantage in deep, well-oxygenated waters (Berglund & Hentati-Sundberg, 2014). More generally, our findings highlight that species-specific traits of top predators determine how fish biomass (the unit used in fisheries management) translates into prey availability.

To better capture the interaction between seabirds and their prey, possible model improvements include to consider: seasonal prey movements (Durant et al., 2007), prey patchiness (Fauchald, 2009), prey depth distribution (Boyd et al., 2017; Shoji et al., 2014), costs of thermoregulation (Ellis & Gabrielsen, 2002) and seabirds' knowledge of the prey field (Ward & Zahavi, 1973). Interspecific competition and/or local enhancement may also be relevant to consider, for example, surface-feeders that depend on fish being chased to the surface by other predators (Thiebault et al., 2014). It would also be interesting to apply the framework to species with longer foraging ranges (e.g. Carneiro et al., 2020).

4.2 | Spatial scales of seabird foraging and fisheries management

Competition with fisheries for prey has been identified as one of the main threats to seabird populations globally (Dias et al., 2019). Still, most fisheries are managed without consideration for potential impacts on seabirds (Hill et al., 2020; Sydeman et al., 2017). We find that B_{MSY} are enough to maintain the populations of guillemots and razorbills at current sizes at our study colony, but this requires a fish density within the seabirds' foraging area that corresponds to the average level for a much larger area. Forage fish management in the Baltic Sea today is on a scale (>100,000 km²) that is more than one order of magnitude larger than the foraging range of any top predators breeding in the region (e.g. Isaksson et al., 2016; Oksanen et al., 2014). Among the 14 sprat and herring stocks currently managed with advice from ICES (www.ices.dk/advice), the mean size of the management area is 720,000 km², suggesting that this type of spatial mismatch is a general pattern. This indicates a need for protection of important foraging areas of seabirds at appropriate spatial scales in addition to general fisheries management practices. While the estimated seabird consumption in our system is small compared to commercial fisheries (around 2,000 t for this colony during the breeding period and approximately 25,000 t for all seabirds throughout the Baltic Sea annually, in contrast to >500,000 t for fisheries; Hansson et al., 2017) the effect is still significant for ecological processes at a seasonal and local scale.

Our framework can be extended to any central-place foraging top predator to calculate spatiotemporally explicit prey requirements. The

resulting numbers can be used directly as top predator targets within ecosystem-based fisheries management, taking an appropriately PA in setting these targets given the inherent uncertainties in parameter estimates within the bio-energetic modelling. There are several possible ways to integrate such targets within the present quota-based fisheries management. The most straightforward and precautionary way would be to define the whole seabird foraging area as a Marine Protected Area and use Marine Spatial Planning to distribute fishing effort to other areas (Frederiksen et al., 2008). Voluntary commitments from the fishing sector to avoid key areas for top predators, especially during breeding seasons, would be another alternative (Abbott & Wilen, 2010). A third and more data-intensive and dynamic approach would be to set up continuous fish stock monitoring around seabird colonies and regulate fishing effort in real time based on the state of the prey resources, in the spirit of Dynamic Ocean Management (Dunn et al., 2016). Novel technologies such as drones for fish data collection could be useful tools in this transition (Mordy et al., 2017).

In our case, the fishery losses for avoiding seabird foraging areas are relatively moderate, but in areas where top predator consumption is greater and/or the overlap between top predator foraging areas and important fishery grounds is greater, the trade-off between fisheries and conservation may be stronger. In such cases, our framework can be integrated with Management Strategy Evaluation to identify and negotiate balanced strategies for fisheries and conservation (Dichmont et al., 2013).

5 | CONCLUSIONS

Mechanistic models of top predator breeding and foraging ecology, such as the one introduced here, improve our ability to manage the trade-off between fisheries and conservation. While our results suggest that current fisheries targets are sufficient to ensure successful breeding of both guillemots and razorbills in our study system, they also point to the strong dependence on local prey resources, suggesting a need for fisheries management at a much finer scale than what is applied today. The study also highlights the importance of a multi-species approach, as sensitivity analyses revealed that changing parameter values in one top predator had an effect on prey requirements of the other, which reflects the complexity and interactions inherent to marine ecosystems. As animal tracking data become increasingly available, the presented framework can be a useful tool for making ecosystem-based management decisions that minimizes conflict between marine wildlife and fisheries.

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AUTHORS' CONTRIBUTIONS

J.H.S., A.B.O. and O.O. conceived the ideas, designed methodology and analysed data; T.J.E., N.I. and P.-A.B. provided and analysed data; J.H.S. led the writing of the manuscript; all authors contributed to writing. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.0p2ngf1z7> (Hentati-Sundberg, 2020).

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SUPPORTING INFORMATION

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