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Seabird-induced natural mortality of forage fish varies with fish abundance: Evidence from five ecosystems

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Abstract

Forage fish populations often undergo large and rapid fluctuations in abundance. However, most of their predators are buffered against such fluctuations owing to their slower pace of life, which allows them to maintain more stable populations, at least during short periods of food scarcity. In this study, we investigated top-down processes exerted by seabirds on forage fish stocks in five contrasted marine ecosystems, compiling numerous data sets on seabird counts, diets, energetic needs and prey energy content and abundance. Off Norway, South Africa, Peru, Sweden and Scotland, we found that predation pressure—estimated as the proportion of a fish stock consumed by seabirds—was generally low (median = 1%), but increased sharply at low levels of prey abundance. When prey biomass decreased below 15–18% of its maximum recorded value, predation by seabirds became a source of important additional pressure on prey stocks (~20% of prey biomass is consumed by seabirds). An earlier empirical study advocated for keeping forage stocks from falling below a threshold of 33% of long-term maximum prey biomass in order to safeguard seabird breeding success, but here we further suggest that a threshold of 18% should be considered as a limit not to be exceeded for the sake of the forage fish themselves, and below which extra cautious management of fisheries may be required. Nevertheless, despite exceptionally high rates of predation on some occasions, predation pressure was not correlated with prey dynamics, suggesting an absence of prey entrapment due to seabirds alone in these five ecosystems.

KEYWORDS

Benguela, Baltic Sea, Humboldt, predator–prey, prey consumption, Shetland

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1 | INTRODUCTION

Natural mortality (M) is an understudied aspect of fish population biology and fisheries science. In most fisheries' stock assessments, natural mortality is modelled as constant or as a function of size to account both for predation pressure and age (Gislason et al., 2010). However, a growing number of studies suggests that this assumption is incorrect, and that mortality could be density-dependent, or modulated by the environment (Dutil & Lambert, 2000; Fromentin et al., 2001; Pershing et al., 2015). Because fisheries' management often relies on stock assessments which compare fishing mortality (F) to natural mortality, understanding fluctuations in natural mortality is of primary importance. For example, a recent study found up to a 40% difference between estimates of spawning stock biomass (SSB), F and recruitment (R) in Atlantic cod (*Gadus morhua*, Gadidae) stock assessments, assuming a constant M versus a variable M linked to body condition (Casini et al., 2016). Here, we are interested in examining to what degree natural mortality rates of forage fish may be influenced by seabirds, which are widely distributed and abundant forage fish predators on all continental shelf ecosystems around the world (Cury et al., 2011). Additionally, on top of potential improvement of stock assessment, clarifying predator–prey functional relationships between forage fish and seabirds will also inform ecosystem-based management research, for example by better understanding how seabird diet relies on forage fish (Dickey-Collas et al., 2014; Peck et al., 2014), and the degree to which mass mortality of seabirds from starvation is exacerbated by low forage abundance and competition with large predatory groundfish for shared prey (Piatt et al., 2020).

Forage fish are consumed by a variety of upper trophic level species in marine ecosystems, including seabirds, marine mammals and larger piscivorous fish. Typically, and on regional scales, seabirds consume considerably less biomass than marine mammals or especially piscivorous fish (Gaichas et al., 2009), but seabirds can have significant impacts locally (Furness, 1978). In contrast to ectothermic groundfish that need to acquire only about 0.2%–1.2% of their body mass in food daily (Holsman & Aydin 2015), endothermic seabirds have high metabolic rates and need to consume upwards of 30%–80% of their mass in food daily (Ellis & Gabrielsen, 2002; Furness, 1990). Combined with the fact that seabirds gather to breed in very large colonies in the thousands to millions (Guinet et al., 1995), this results in a concentration of high energetic demands in a limited area. As central-place foragers, breeding birds return to breeding sites on land (or occasionally ice) to attend and provision offspring, which concentrates foraging areas closer to breeding locations. As a result, some studies have shown localized prey depletion in proximity to island-based colonies, and this may result in intraspecific competition among birds (Ainley et al., 2003; Birt et al., 1987; Lewis et al., 2001; but see Nur & Sydeman, 1999). Additionally, most of the forage fish of importance to seabirds are known to exhibit wide fluctuations in abundance in response to climate (e.g. Lluch-Belda et al., 1992) and are often subjected to high fishing mortality (Hilborn et al., 2017; Schwartzlose et al., 1999). Fish abundance often changes much faster than the abundance of predators, because many forage fish predators, including seabirds, have slower life-history characteristics such as high annual survival and delayed sexual maturity, which buffer their breeding populations from fluctuations in food supply (e.g. Hunt et al., 1996 and "canalization hypothesis" Gaillard & Yoccoz, 2003). Thus, the relative predation pressure exerted by seabirds should increase with declines in forage fish stocks, except under extreme conditions where adult seabirds are unable to obtain sufficient food for their own maintenance and survival (Cairns, 1988; Crawford et al., 2011; Erikstad et al., 1998). Therefore, seabird-induced natural mortality of forage fish could vary strongly with time.

If the proportion of a fish stock consumed by predators increases as biomass decreases, the stock in question may become entrapped, whereby populations cannot overcome predation pressures or easily return to previous levels of abundance (Smout et al., 2014). Bakun (2006) theoretically explored the functional responses of predators to biomass variation in small pelagic fish, and suggested that predation pressure should be nil when stocks are collapsed at very low levels of biomass (i.e. "refuge abundance"), but increase substantially when fish biomass reaches a level sufficient for predators to be interested in a population as prey. At low, but not collapsed biomass, Bakun predicted that "carnage predation" may hold the population at a relatively low biomass, and coined the term "predator pit" for this mechanism. Predator pits may be maintained until the forage fish population reaches a level sufficient to satiate predators and grow larger at the same time. The addition of human fishing pressure on small pelagic fish populations has been shown to increase the probability of stock collapse but not the duration of the collapse (Essington et al., 2015). Although fishing pressure after a collapse usually drops, or is even halted due to fisheries management and/or profitability, with no change, maintaining fishing effort at lower biomass would likely exacerbate the duration small pelagics are held in a predator pit. To date, fisheries' impacts and empirically estimated predation pressure have yet to be jointly addressed.

In this paper, we test the hypothesis of predator-pit dynamics for forage fish by examining (a) whether the proportion of forage fish stocks consumed by seabirds increases in response to drops in prey biomass, and (b) whether such increases in seabird-induced forage fish mortality affect forage fish population dynamics. To test this hypothesis, we model non-linear relationships between seabird consumption and fish biomass across five ecosystems, and determine the biomass thresholds at which seabirds might begin to exert top-down control on their prey populations. By determining such thresholds in five different ecosystems, this work also tests the generality of top-down control of seabirds on forage fish and identifies local differences, as suggested in (Peck et al., 2014).

2 | METHODS

To estimate seabird predation pressure on forage fish, we use long-term data collected in five contrasted ecosystems on: (a) Atlantic puffin (*Fratercula arctica*, Alcidae) and Atlantic herring (*Clupea harengus*, Clupeidae) at Røst off northwest Norway, (b) Cape gannet (*Morus capensis*, Sulidae) and sardine (*Sardinops sagax*, Clupeidae) and anchovy (*Engraulis encrasicolus*, Engraulidae) off western South Africa in the Southern Benguela ecosystem, (c) common murre (*Uria aalge*, Alcidae) and European sprat (*Sprattus sprattus*, Clupeidae) in the Baltic Sea, (d) twelve seabird species and lesser sandeel (*Ammodytes marinus*, Ammodytidae) off Shetland and (e) Peruvian booby (*Sula variegata*, Sulidae), Peruvian pelican (*Pelecanus thagus*, Pelecanidae) and Guanay cormorant (*Phalacrocorax bougainvillii*, Phalacrocoracidae) and anchovy (*Engraulis ringens*, Engraulidae) in the Northern Humboldt ecosystem (Figure 1). While the methodology used (see below) requires a large number of data and constrains the number of ecosystems on which we could test the hypothesis, these five ecosystems enabled investigation of predation pressure in contrasted environments, ranging from productive upwelling regions (Benguela, Humboldt) to the semi-closed Baltic Sea.

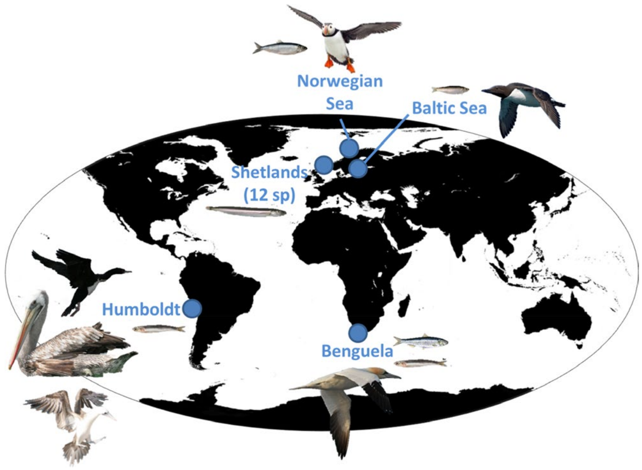

FIGURE 1 Ecosystems under study along with the studied seabird and fish species

2.1 | Estimates of seabird consumption and proportion of prey biomass consumed

To estimate seabird predation pressure, we combined several processes (estimation of bird numbers and population structure, bird energy requirements, bird diet and prey energetic values and abundance) based on a large number of data sets (see similar approaches in Queiros et al., 2018; Van Beveren et al., 2017). In particular, both the quantity consumed by seabirds and the prey stock size were evaluated. A schematic diagram of the general method used in this study is represented in Figure 2.

The main challenge of this study was to estimate the total quantity of a given prey that is extracted by seabirds C_t, meaning that all birds extracting prey should be included, that is both adults and chicks, as well as breeders and non-breeders that are present in the area and consume this prey. This was estimated using the formula below:

$$C_t = \frac{P_t}{AE * PreyNRJ} * \left(\begin{array}{l} DEE_B * N_{B,t} * Nbdays_{BS} \\ +DEE_{NB} * N_{B,t} * Nbdays_{NBS} \\ +DEE_{NB} * N_{NB,t} * Nbdays_{col} \end{array} \right) * \frac{1}{1,000} + C_{chick,t}$$

where

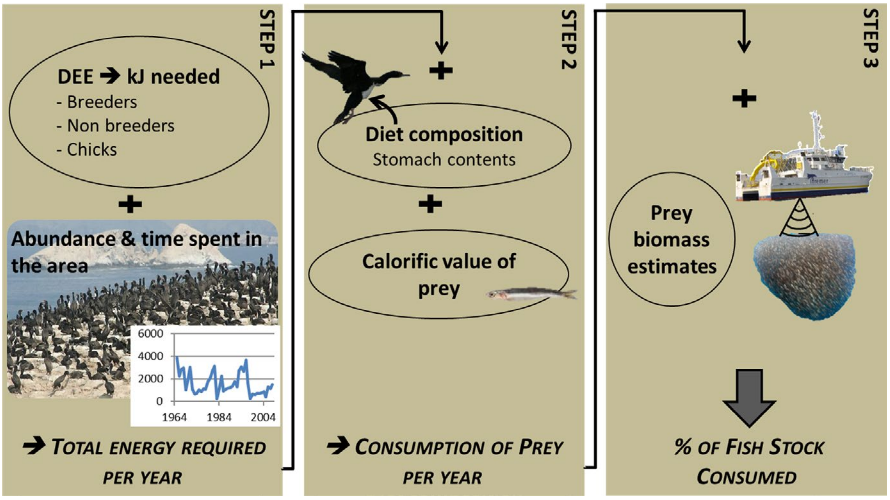

FIGURE 2 Schematics of the method used to quantify the proportion of a fish stock that is consumed by seabirds

TABLE 1 Main parameters and assumptions used in the estimation of seabird consumption in each ecosystem

	Proportion of prey in diet in terms of energy P_t	Assimilation Efficiency *AE*	Prey energetic value *PreyNRJ*	Daily Energy Expenditure *DEE*
Atlantic puffin in the Norwegian Sea	Chick = Adult diet Annual values (Anker-Nilssen & Aarvak, 2006; updated with www.seapop.no/en)	0.70 (Brekke & Gabrielsen, 1994)	3.7 kJ/g (Anker-Nilssen & Øyan, 1995)	Average body mass = 460 g (Barrett et al., 1995) DEE_B = 1.84 kJ g^{-1} day^{-1} (Ellis & Gabrielsen, 2002) DEE_{NB} = 2.25*BMR = 2.25*745.2 kJ/day (Ellis & Gabrielsen, 2002)
Cape gannet in the southern Benguela	Chick = Adult diet Annual values (average from all months and 2 localities) (Crawford et al., 2019)	0.74 (Crawford et al., 1991)	8.59 and 6.74 kJ/g for sardine and anchovy respectively (Batchelor & Ross, 1984)	DEE_B = 3,380 kJ/day (Adams et al., 1991; Berruti et al., 1993) DEE_{NB} = 2,767 kJ/day (Adams et al., 1991; Berruti et al., 1993)
Common murre in the Baltic Sea	Chick = Adult diet Annual values (Kadin et al., 2012)	0.78 (Hilton et al., 2000)	5.46 kJ/g (Enekvist, 2003)	DEE_B = 1,530 kJ/day (Roth et al., 2008) DEE_{NB} = 1,392 kJ/day (Roth et al., 2008)
Shetland Islands	Chick = Adult diet Period values (Furness, 1990; Furness & Tasker, 2000; Martin, 1989)	0.80 (Hilton et al., 2000)	6 kJ/g (Pedersen & Hislop, 2001)	DEE_B estimated from allometric equations per order (Ellis & Gabrielsen, 2002) DEE_{NB} = 2.25 BMR (Ellis & Gabrielsen, 2002)
Northern Humboldt	Chick = Adult diet Period values (Goya, 2000; Jahncke et al., 2004)	0.75 (Dunn, 1975; Laugksch & Duffy, 1984)	6.37 kJ/g (Cooper, 1978; Laugksch & Duffy, 1984)	DEE_B estimated from allometric equations of pelecaniform DEE_{NB} = 2.25 BMR (Ellis & Gabrielsen, 2002)

C_t is the consumption of the given prey (in tonnes). Note that the 1/1,000 in the equation is here only to convert from kg to tonnes.

P_t (unitless) corresponds to the proportion of the given prey in terms of energy in the diet in a given year *t*. Note that in each ecosystem, we assumed P_t to be independent of bird age class (chick and adult diet assumed to be the same) and breeding status (see Appendix S1 for more details and justifications).

AE (unitless) is the assimilation efficiency.

PreyNRJ (in kJ/g) is the calorific content of the prey

DEE (in kJ/day) is the daily energy expenditure of the birds. As breeding incurs an additional cost, two distinct DEEs were considered: one for breeding birds DEE_B and one for non-breeders or adults in the non-breeding season DEE_{NB}.

N_t (in thousands of birds) represents the number of birds present in the area in year *t*, either breeding $N_{B,t}$, or non-breeding $N_{NB,t}$.

Nbdays (in days) is the number of days during which the prey is consumed by the seabird species in the area. Three periods were distinguished: $Nbdays_{BS}$ corresponds to the number of days in the breeding season, $Nbdays_{NBS}$ the duration of the non-breeding season in which breeding birds are present in the colony and finally $Nbdays_{col}$ the duration in which non-breeding birds (immature or birds skipping reproduction) are present in the area. Note that for some ecosystems, birds are migratory and $Nbdays_{NBS}$ is zero.

C_{chick} (in tonnes) corresponds to the consumption in tonnes made by chicks. This was either calculated through energy requirements and DEE (in the Benguela, Humboldt and Shetland),

Bird numbers N_t	**Number of days** *Nbdays*	**Chick consumption** C_{chick}	**Fish biomass**
Røst population $N_{B,t}$ estimated from counts (Anker-Nilssen & Aarvak, 2006; updated with www.seapop.no/en) $N_{NB,t}$ = nb of immature from 1 to 5 (estimated from number of fledglings and juvenile survival; Sandvik et al., 2008) + 25% of mature birds skipping reproduction	2 scenarios: (a) $Nbdays_B$ estimated annually equal to chick-rearing duration (b) $Nbdays_B = 152$ days $Nbdays_{NB} = 0$ $Nbdays_{col} = Nbdays_B$	Meal size = 108 g chick^{-1} day^{-1}, (Øyan & Anker-Nilssen, 1996) Nb of chicks estimated from counts $Nbdays_{chick}$ = chick-rearing duration estimated yearly	Age 0 fraction of the stock. Estimated using back-calculations from recruitment indices (i.e. age class 3) obtained through VPA (ICES, 2012; Toresen & Østvedt, 2000)
Lambert's Bay + Malgas Island populations (South Africa west coast) $N_{B,t}$ estimated from occupied breeding area sizes and densities of nests (Crawford et al., 2007 updated) $N_{NB,t}$ = nb of immature from 1 to 4 (estimated from number of chicks and age-dependent survival)	$Nbdays_B = 165$ (Jarvis, 1974) $Nbdays_{NB} = 140$ $Nbdays_{col}$ dependent on age class (Jarvis, 1974)	*Nb* of chicks = *nb* of breeding pairs * 0.45 DEE_{chick} = 2,236 kJ/day (Cooper, 1978) $Nbdays_{chick} = 97$ (Jarvis, 1974)	Spawning stock biomass West of Cape Agulhas Estimated based on hydro-acoustic surveys (Augustyn et al., 2018; Coetzee et al., 2008)
Entire Baltic Sea population $N_{B,t} = 100/65 * N_{B,t}$ at Stora Karlsö (Olsson & Hentati-Sundberg, 2017) from annual counts at Stora Karlsö $N_{NB,t} = 0.5 * N_{B,t}$	$Nbdays_B = 90$ (Hedgren, 1975) $Nbdays_{NB} = 275$ $Nbdays_{col} = 365$	Meal size = 4 * 10.26 = 41 g chick^{-1} day^{-1}, (Enekvist, 2003; Kadin et al., 2012) *Nb* of chicks = annual breeding success * *nb* of breeding pairs (Kadin et al., 2012) *Nbdayschick* = 18 days (Kadin et al., 2016)	Spawning Stock biomass Entire baltic Sea Estimated through XSA using acoustics and landings as inputs (ICES, 2018)
Shetland populations $N_{B,t}$ estimated from counts (Mitchell et al., 2004; Walsh et al., 1995) $N_{NB,t}$ = 25% of breeding birds	$Nbdays_B$ for each species (122 days for great skua, 106 for arctic skua, common murre and razorbill, 78 artic tern, 108 puffin, 136 kittiwake, great blacked-back gull, black guillemot, fulmar, shag and gannet) (Furness, 1990) $Nbdays_{NB} = 0$ $Nbdays_{col} = Nbdays_B$	*Nb* of chicks = Breeding success * *nb* of breeding pairs *DEE* from the same equation as non-breeding adult with $M_{chick} = 0.5\ M_{adult}$ $Nbdays_{chick}$ = chick-rearing duration estimated yearly	Total biomass Shetland stock Estimated from VPA using landings and experimental trawl surveys as inputs
Entire Northern Humboldt populations (31 islands) Monthly counts of total number of birds. $N_{B,t}$ and $N_{NB,t}$ derived from monthly average proportions of breeders versus non-breeders based on the 2003–2014 observations.	$Nbdays_{col} = 365$	DEE from the same equation as non-breeding adult with $M_{chick} = 0.5\ M_{adult}$ *Nb of* chicks = brood size * *nb* of breeding pairs $Nbdays_{chick}$ = 86, 133 and 110 days for cormorant, booby and pelican	Production biomass Northern Humboldt (7–18°S) from the coast to 100 km offshore Estimated from acoustic estimates and monthly length structure (Oliveros-Ramos & Peña, 2011)

that is $C_{chick} = \frac{P_t}{AE * PreyNRJ} * (DEE_{chick} * N_{chick} * Nbdays_{chickrearing})$ or directly from meal size given to the chicks (in Norwegian and Baltic Seas): $C_{chick} = P_{mass,t} * N_{chick} * Nbdays_{chickrearing} * Mealsize$

Once the consumption of a prey is estimated, it needs to be compared to the prey stock biomass to estimate the predation pressure. Fish biomass was estimated either through stock assessment models, or from direct acoustic biomass estimates, depending on the ecosystem (see Table 1). Only in the North Sea (case study Shetland Islands), did natural mortality (M) explicitly include bird consumption. Yet, while predator consumption included that of seabirds and marine mammals, the most important predators of sandeels by far are fish—especially mackerel, herring, cod, haddock, whiting, and gurnard, so that there should be little effect of seabird consumption on *M* (ICES-HAWG, 2020; ICES-WKSand, 2016). Further, stock biomass should represent the entire fish biomass present before seabird consumption occurred. Depending on the timing of stock biomass assessment and seabird consumption phenology, stock biomass had to be corrected. In the Humboldt, the production model estimates the biomass available each month, so that no correction was needed. Similarly, no corrections were applied in the Baltic, where stock assessment refers to the start of spawning (i.e. April), just before seabirds start consuming sprats and in the Norwegian Sea, where stock assessments refer to the first of January, that is before the predation events. By contrast, acoustic biomass estimates in the Benguela derive from November acoustic surveys and a stock assessment model in the Shetland estimates biomass on the 1st of July. In both cases, most of seabird consumption occurred beforehand, so that stock biomass was corrected by adding seabird consumption. Finally, the fish biomasses presented here represented annual estimates of the stock, and not fish availability within foraging range of the birds around the colonies, so that we are estimating the predation pressure on the stock and not local prey depletion. However, it has to be noted that in some large ecosystems, regional scales were used (e.g. we considered the southern subsystem of the Benguela, located off South Africa and not the entire Benguela ecosystem). Spatial scales can be found in Table 1 for each ecosystem.

Although the approach was the same everywhere, differences appeared in the estimation of these parameters because of species and ecosystem specificity. For instance, gannets in the Southern Benguela are resident seabirds and consumption outside of the breeding period had to be considered in order to estimate the entire predation pressure they exerted on sardine and anchovy stocks, while migrating Atlantic puffins are present in the eastern Norwegian Sea only for a few months in order to breed.

As some seabird data were not always available in each ecosystem, some assumptions had to be made (see summary in Table 1). While these were done to best fit our knowledge of the ecosystem or the species at play, they introduce uncertainty in our estimates of consumption and predation pressure. Nevertheless, we applied the same methodology through time within each ecosystem and among ecosystems. This allowed us to investigate temporal trends and compare among ecosystems, and to identify the magnitude of top-down effects. The main assumptions and parameters are summarized for each ecosystem in Table 1 and details about the specificities as well as monitoring methods are detailed in Appendix S1. Note that in the case of the Atlantic puffin in the Norwegian Sea, two different scenarios of consumption were run in the absence of diet data outside the chick-rearing period. The first assumed that puffins consumed herring during the entire time they are present at the colony while the minimum consumption scenario assumed herring consumption only during chick-rearing (see Appendix S1).

Predation pressure was then estimated as the percentage of the stock consumed by seabirds, calculated as: $Pred_t = 100 * \frac{C_t}{B_t}$.

2.2 | Relationships between consumption and biomass

In order to examine functional responses of seabird diet and aggregated prey consumption C_t to prey biomass, for each relationship we tested a selection of six a priori parametric models (null model assuming no link of seabird diet or consumption with prey biomass $y = a$; linear model assuming a constant increase of seabird diet or consumption with fish biomass $y = a * B + b$; second-order polynomial model assuming an optimum fish biomass for seabirds $y = a * B^2 + b * B + c$; as well as exponential, logarithmic and power models which all assume non-linearities and some sort of thresholds above or below which seabirds react differently to prey $y = a * e^{(-b * B)}$, $y = a^* \ln(B) + b$, $y = a^* B^b$). When looking at the relationship between seabird aggregated consumption and stock biomass, we also tested two additional models: type II and III functional responses: $C_t = \frac{a * B}{1 + b * B}$ and $C_t = \frac{a * B}{1 + b * B^2}$. Because data in the Shetland were only collected in 3 years, they are only presented as a qualitative indication and no model was performed for this ecosystem. Also, in the Humboldt, no model was performed for the diet data in the absence of annual estimated diet (diet was estimated by period in this ecosystem). All models were fitted using non-linear least square adjustment and the best fit was selected based on the lowest AICc values to avoid overparameterization (Piatt et al., 2007). When change in AICc (ΔAICc) was <2 between the two best models, the more parsimonious model was chosen. All models within a ΔAICc of 2 are presented along with the null model in Table 2. Once the numerical relationships between stock biomass and the percentage of the stock consumed by seabirds were established, we used a change-point analysis to identify thresholds within non-linear relationships (Andersen et al., 2009; Cury et al., 2011). The threshold in biomass was then expressed relatively to the maximum biomass observed in the time series (i.e. % threshold = 100 * (threshold/Max *B*)).

2.3 | Effect of the predation pressure on prey dynamics

To investigate whether the predation pressure exerted by seabirds might impact prey dynamics, we examined the correlations between prey biomass and the number of avian predators or the percentage of

TABLE 2

Seabird diet and consumption according to prey biomass. Six a priori parametric models were fitted using non-linear least square adjustment (null model assuming no link of seabird diet or consumption with prey biomass, linear model assuming a constant increase of seabird diet or consumption with fish biomass, second-order polynomial models assuming an optimum fish biomass for seabirds, as well as exponential, logarithmic and power models which all assume non-linearities and some sort of thresholds above or below which seabirds react differently to prey). Additionally, functional responses of type II and III were also tested for the relationship between seabird consumption and prey biomass. Results of the most supported models (ΔAICc ≤ 2) are presented along with the null model. Selected models are indicated in bold (most parsimonious within a ΔAICc of 2 from the lowest AICc). Results are not presented in the Shetland system, where too few data points hindered quantitative analyses. Also, for the Humboldt, no model was performed on the diet data and consumption was estimated as the sum of the consumption made by the three seabird species.

Variables	Ecosystem/species	Model type	AICc	ΔAICc	*n*
Diet ~ stock biomass	Norwegian Sea—Puffins—Age 0 herring	**Null**	**211.1**	**0**	23
		Logarithmic	212.0	0.9	
		Power	212.3	1.2	
	Benguela—Gannets—Sardines	**Logarithmic**	**253.4**	**0**	37
		Power	254.0	0.6	
		Null	324.9	71.5	
	Benguela—Gannets—Anchovies	**Power**	**205.4**	**0**	37
		Logarithmic	205.8	0.4	
		Null	311.9	106.5	
	Baltic Sea—Murres—Sprats	**Null**	**64.1**	**0**	14
Consumption ~ Stock biomass	Norwegian Sea— Puffins—Age 0 herring	**Null**	**445.8**	**0**	22
		Type III functional response	447.0	1.2	
		Type II functional response	447.4	1.6	
	Benguela—Gannets—Sardines	**Type II functional response**	**590.8**	**0**	31
		Type III functional response	591.1	0.3	
		Logarithmic	591.4	0.6	
		Power	592.0	1.2	
		Null	615.3	24.5	
	Benguela—Gannets—Anchovies	**Type II functional response**	**503.0**	**0**	31
		Power	503.1	0.1	
		Type III functional response	504.1	1.1	
		Logarithmic	504.3	1.4	
		Linear	504.6	1.7	
		Null	589.5	86.5	
	Baltic Sea—Murres—Sprats	**Power**	**230.9**	**0**	14
		Logarithmic	231.1	0.2	
		Exponential	231.3	0.4	
		Linear	231.5	0.6	
		Null	234.0	3.1	
	Humboldt—All 3 species—Anchovies	Power	1,374.4	0	48
		Logarithmic	1,374.6	0.2	
		Type II functional response	1,374.8	0.4	
		Quadratic	1,374.9	0.5	
		Linear	1,374.9	0.5	
		Null	**1,375.6**	**1.2**	
		Exponential	1,375.6	1.2	
		Type III functional response	1,376.46	2.0	

(Continues)

TABLE 2 (Continued)

Variables	Ecosystem/species	Model type	AICc	ΔAICc	*n*
% consumed ~ stock biomass	Norwegian Sea—Puffins—Age 0 herring	**Power**	**196.9**	**0**	22
		Null	218.6	21.7	
	Benguela—Gannets—Sardines	**Power**	**135.8**	**0**	31
		Null	155.0	19.2	
	Benguela—Gannets -Anchovies	**Power**	**39.2**	**0**	31
		Null	74.3	35.2	
	Baltic Sea—Murres—Sprats	**Power**	**−22.7**	**0**	14
		Exponential	−21.6	1.1	
		Null	1.2	25.3	
	Humboldt—All 3 species—Anchovies	**Power**	**209.1**	**0**	48
		Null	254.7	45.6	

the stock that was consumed the previous year. Because stock biomass time series are often autocorrelated, residuals were checked for autocorrelation. While autocorrelation was never significant in the Baltic Sea, residuals from the models in the Humboldt and Benguela all displayed positive autocorrelation of order 1 (detected through the pacf function in R). To account for that, a one-year lagged time series of the stock biomass was added as an explanatory variable in the 6 models ($B_t \sim N_{t-1} + B_{t-1}$ and $B_t \sim Pred_{t-1} + B_{t-1}$ for sardine and anchovy in the Benguela and for anchovy in the Humboldt). Finally, we also studied the relationship between the change in prey biomass (i.e. $\Delta B = B_t - B_{t-1}$) and the percentage of the stock consumed at t−1 ($\Delta B \sim Pred_{t-1}$). These relationships were not investigated in Shetland due to too few data points and in the Norwegian Sea, where puffins consume age 0 herring that first recruit to the spawning stock at age 3. The relationship between this herring's spawning stock biomass and its recruitment three years later is weak (Sætre et al., 2002).

3 | RESULTS

3.1 | Diet

The percentage contributions of various prey species to the seabird predators included in our study are shown in Figure 3. For Atlantic puffins from 1982–2006, the contribution by mass of age 0 herring to the diet (Mean ± SD: 46 ± 22%, range: [13%–89%]) was not significantly related to the biomass of age 0 herring (Figure 4a, Table 2). For common murres, the mean contribution by mass of sprat to the diet from 2002–2012 was very high and stable across time (98 ± 2%, [93%–100%]), regardless of the biomass of sprat (Figure 4d). In the Humboldt ecosystem, the contribution of anchovy in the diet was usually quite high (81 ± 8%) but dropped significantly in El Niño years (55% for cormorants and 58% for boobies and pelicans; Figure 3b). For Cape gannets, the mean contribution by mass of sardine to the diet from 1978–2011 was 30 ± 19% [2%–61%] and that of anchovy 28 ± 16% ([3%–62%]; Figure 3e). The average combined contribution of these two prey species to the diet was 58 ± 14% ([16%–77%]; Figure 3e). In both cases, the percentage of fish in gannet diet increased with fish stock biomass, although the relationships differed (Table 2; Figure 4e,f). Finally, at Shetland the average contribution by mass of sandeel to the diet of 12 seabirds decreased from 88 ± 4% in 1977 and 83 ± 5% in 1986 to only 45 ± 10% in 2000 (Figure 3c).

3.2 | Consumption and proportion of prey stock consumed

The consumption of age 0 herring by Atlantic puffins at Røst (regardless of the scenario used) and the consumption of anchovy by boobies, cormorants and pelicans in the Humboldt ecosystem were not significantly related to the prey stock biomass (Figure 5a,b, Table 2). However, consumption of sardine and anchovy by Cape gannets in the southern Benguela ecosystem was significantly positively related to the biomasses of these prey species by a type II functional response (Figure 5e,f). Similarly, the consumption of sandeels by 12 seabird species at Shetland seemed to increase with the biomass of sandeels (Figure 5c). Finally, the consumption of sprats by common murres in the Baltic Sea decreased with sprat biomass following a power model (Figure 5d).

The predation pressure, as estimated by the percentage of the fish biomass consumed by seabirds, was generally low (median = 1% across all years and ecosystems; Figure 6). While this was true in most cases (≤20% in 95% of the cases), the predation pressure increased when fish abundance was low (Figure 6).

Further, in four ecosystems (it was not tested for Shetland due to few data points), all relationships were best fitted by power models. While the proportion of the stock consumed remained extremely low in the Baltic Sea (0.5%–1.2%; Figure 6d), it increased sharply in other ecosystems once fish biomass decreased below a certain threshold. This threshold was lower than the median biomass observed in the series (Figure 6) and varied between 15% and 18% of the maximum observed prey biomass (15% for herring in the Norwegian Sea regardless of the scenario Figure 6a, 16% for both anchovy and sardine in the Benguela Figure 6e,f and 18% for anchovy in the Humboldt Figure 6b).

3.3 | Effect of the predation pressure on prey dynamics

Autocorrelation in the residuals was positive and of order 1 in all models explaining prey stock biomass, except for the Baltic, where no autocorrelation was detected. Stock biomass at *t*−1 was thus added as an explanatory variable in the models (except for the Baltic) and had a significant positive effect on prey biomass at t in all relevant models (all $p < .009$). In the Humboldt, while prey biomass was positively related to the number of seabirds present at *t*−1, and negatively to the percentage of the stock consumed by seabirds at *t*−1, both relationships disappeared after accounting for autocorrelation (Figure 7a,d). In the Benguela, the sardine stock biomass was positively related to the number of birds present the previous year (regardless of the autocorrelation, Figure 7c), but not to the percentage of the stock consumed the year before (Figure 7f). The anchovy stock biomass in the Benguela was not related to either the number of gannets or the proportion of prey consumed by gannets in the previous year (Figure 7c,f). Sprat biomass was negatively related to both the number of murres the previous year and the proportion of stock that they consumed (Figure 7b,e).

Finally, the change in fish biomass from one year to another was not related to the percentage of the stock consumed the previous year in any of the ecosystems (Figure 7g–i).

4 | DISCUSSION

Many studies advocate that seabirds are good bioindicators of marine ecosystems (e.g. Cairns, 1988; Piatt et al., 2007), although an implied assumption and frequent observation is that these ecosystems are regulated by bottom-up processes (Aebischer et al., 1990; Frederiksen et al., 2006; Speckman et al., 2005). However, aquatic ecosystems are complex and may also be regulated by numerous biological interactions, including predation and competition. For instance, whole-lake experiments showed that trophic cascades could inhibit the response of primary producers to nutrient inputs (Carpenter et al., 2001). The existence of such top-down mechanisms or trophic cascades, which had previously been reported only from terrestrial ecosystems or lakes, has now been demonstrated in marine ecosystems (Ainley et al., 2006), especially after overfishing (Baum & Worm, 2009; Casini et al., 2009; Frank et al., 2005; Österblom et al., 2006). Further studies have proposed that marine ecosystems might be regulated by alternating bottom-up and top-down processes (Cury et al., 2008; Litzow & Ciannelli, 2007), or a "wasp-waist" interaction of the two (Fauchald et al., 2011), and that relative strength of bottom-up and top-down control may vary spatially (Frederiksen et al., 2007). For example, marine heatwaves

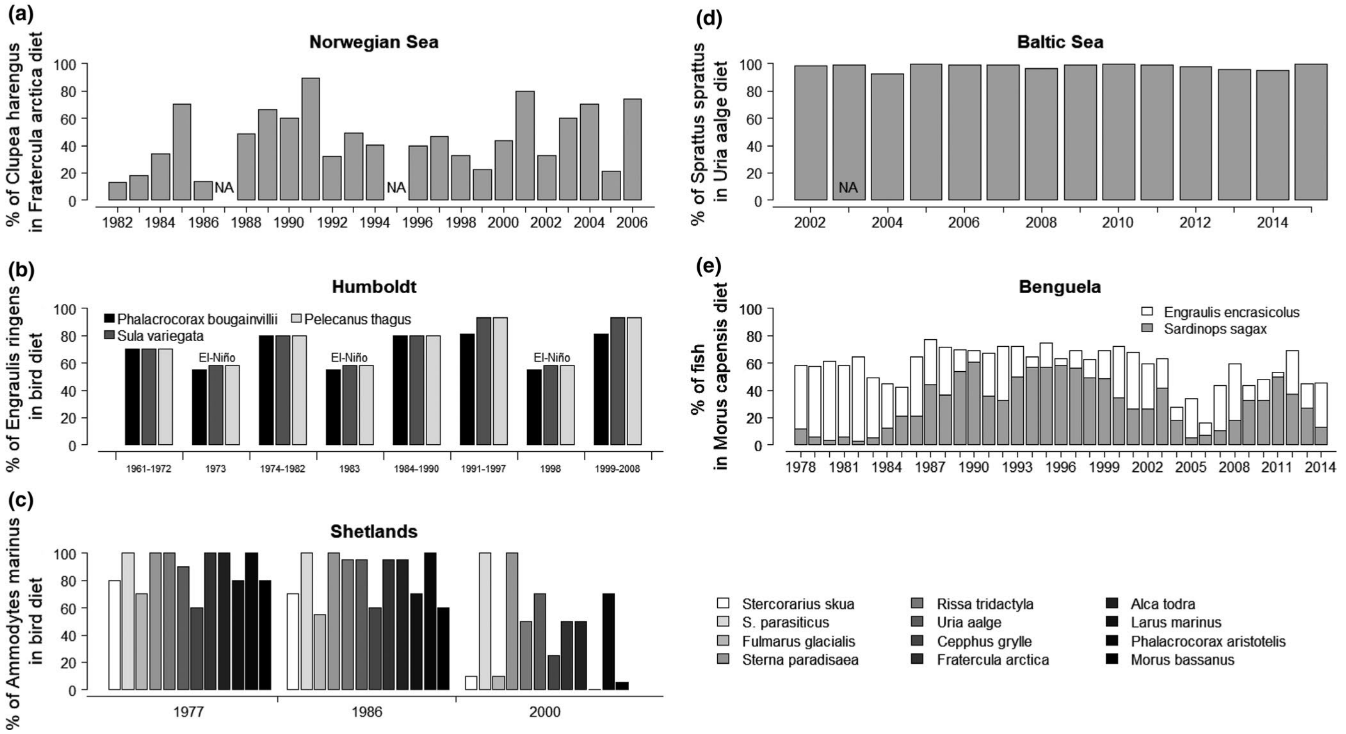

FIGURE 3 Trends in the annual contributions of the main fish prey to the diet of seabird species at Røst from 1982 to 2006 (Atlantic herring in puffin diet), in the Baltic Sea from 1985 to 1995 (sprat in murre diet), in the Northern Humboldt from 1961 to 2008 (anchovy in the diet of three bird species), on the west coast of South Africa from 1985 to 2011 (sardine and anchovy in gannet diet) and at Shetland in 1977, 1986 and 2000 (sandeel in the diet of 12 bird species)

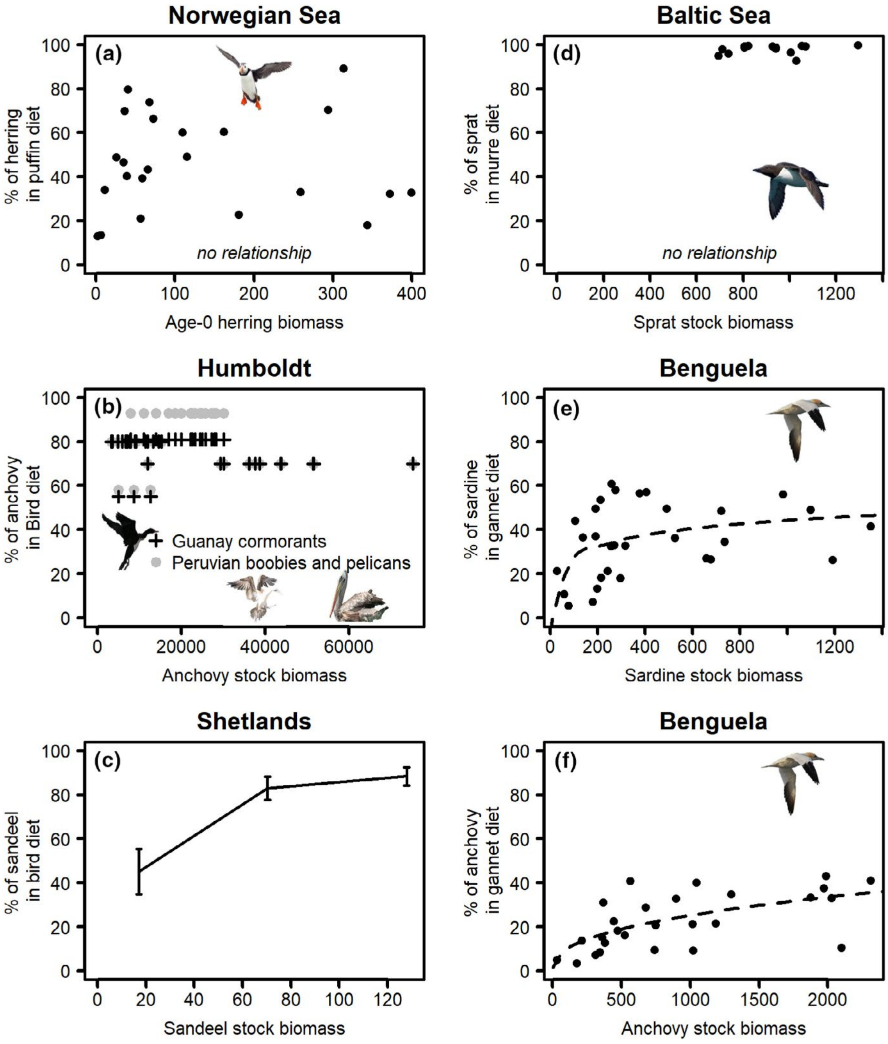

FIGURE 4 Relationships between the stock biomass of prey (thousand tonnes) and the percentage contribution of prey to the diet of seabirds for each of the five ecosystems. As 12 seabird species were considered at Shetland, we present the mean ± *SE* for that locality. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). Note that for the Benguela, the two candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes

can markedly increase metabolic rates and food demands of ectothermic groundfish and trigger temporary top-down control of prey populations and increased competition with seabirds for shared prey (Barbeaux et al., 2020; Piatt et al., 2020).

Here, we examined one component of top-down processes by estimating the predation pressure exerted by seabirds on forage fish in five different ecosystems. Because this requires a large quantity of data on both seabirds and forage fish, it was necessary to sometimes make assumptions that could have a marked effect on model outcomes. In the Norwegian Sea for instance, due to the absence of diet data outside of the chick-rearing period, we had to consider two extreme scenarios: that is, either puffins do not eat herring outside the chick-rearing season, or they consume herring during the entire breeding season. The latter scenario (i.e. maximum consumption) yielded some unrealistically high values (>100% of prey stock). However, such outcomes could also result from the uncertainty associated with calculating prey biomass in this ecosystem. Indeed, puffins eat age-0 herring, the biomass of which is not directly assessed (see the ESM for more details). Still, we believe the relationships we found likely reflect qualitatively the true relationship (in terms of shape) as we applied our methods consistently among years and among ecosystems but actual estimates under that scenario were less reliable.

With respect to seabird diets, we found that different species displayed marked differences in response to fluctuations in prey abundance. Seabird species have different locomotion and foraging strategies which limit the distance that they can forage from colonies, or the depth to which they can feed (e.g. Shealer, 2002). Large seabirds are, for instance, often less vulnerable to prey depletion due to greater travelling capacities and greater energetic efficiencies (Ellis & Gabrielsen, 2002; Furness & Tasker, 2000), which might explain the absence of seabird response to prey biomass decrease in the Humboldt system in typical (i.e. non-El Niño) conditions. The non-linear relationships between abundance of sardine and anchovy and the contribution of these species to the diet of Cape gannets off western South Africa suggest that gannets are able to maintain their intake of these species over a wide range of biomass variability. Cape gannets have indeed been shown to be flexible in their foraging effort and duration to track sardines and anchovies, their preferred prey even when abundance decreases or spatial distribution shifts (Green et al., 2015). However, below a certain threshold of prey biomass, gannets were not able to compensate anymore and had to shift

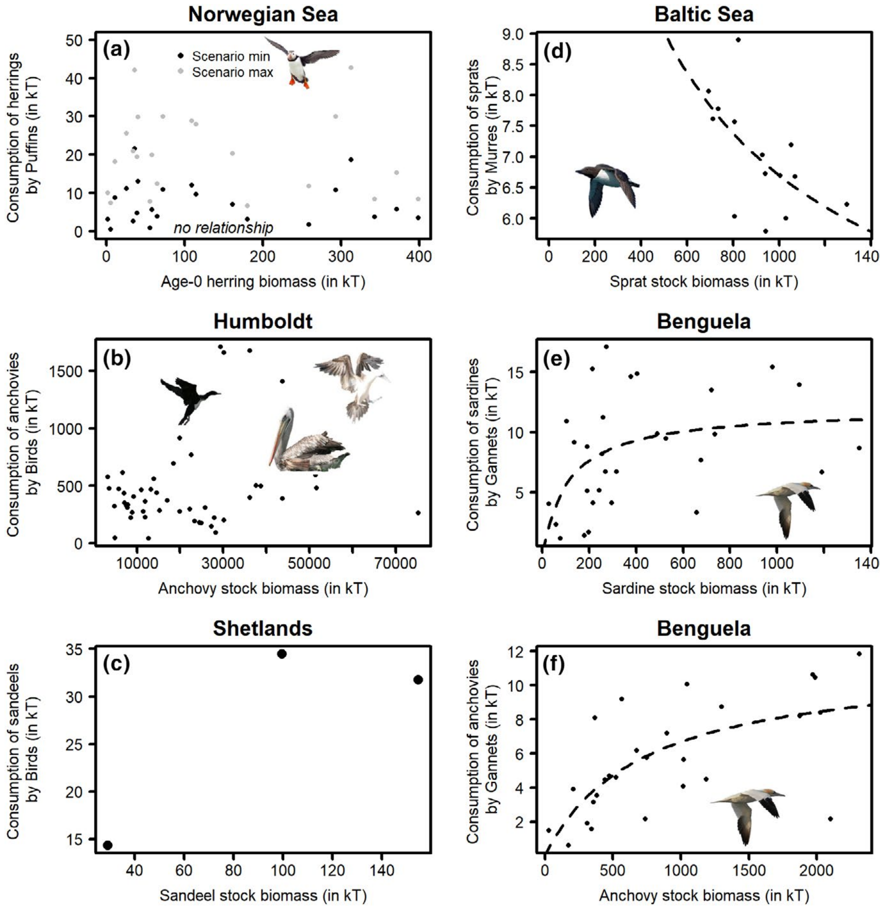

FIGURE 5 Relationships between the stock biomass of prey (thousand tonnes) and the consumption of prey (thousand tonnes) by seabirds. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). Note that for the Benguela and the Baltic, the different candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes

their diet towards other prey. Recent research off the south coast of South Africa has shown that in the postguard stage (>50 days) of chick-rearing, foraging range is extended and gannet diet may differ from that in the guard stage as a consequence of changes either in prey abundance and distribution, or in the energetic requirements of growing offspring (Botha & Pistorius, 2018). A similar relationship was evident for the average proportion of sandeel in the diets of seabirds at the Shetland Islands. Yet, this masks important differences between species, with Arctic skua (*Stercorarius parasiticus*, Stercorariidae) and Arctic tern (*Sterna paradisaea*, Laridae) maintaining 100% of their sandeel diet in all three periods of study, whereas the sandeel contribution to diet decreased from 70% to 80% to less than 10% in gannet (*Morus bassanus*, Sulidae), fulmar (*Fulmarus glacialis*, Procellariidae), great skua (*S. skua*, Stercorariidae) and great black-backed gull (*Larus marinus*, Laridae) between 1977 and 2000. Small surface-feeders, such as Arctic terns, are more constrained and, as such, more vulnerable to environmental changes than other species (Baird, 1990; Furness & Tasker, 2000; Shealer, 2002). Seabird diet, body size and the ability to switch to other prey when their favoured prey is depleted might then be important components of their sensitivity to environmental or fisheries-induced fluctuations in prey.

These results highlight the importance of forage fish accessibility for seabirds rather than just abundance. Indeed, a decrease in forage fish stock biomass does not automatically translate into a decrease in forage fish availability or catchability for seabirds, or at least not linearly, due to possible changes in spatial distribution. First, the shoaling behaviour of most forage fish means that predation, like fisheries catches, may be maintained even when prey abundance decreases (in fisheries known as hyperstability of catches, Hilborn & Walters, 1992). For example, as stock biomass decreases, forage fish may concentrate in their most suitable habitat (i.e. the basin hypothesis; MacCall, 1990), resulting in habitat contractions, but no decrease in fish density. In this study, the absence of relationships between seabird diet and forage fish abundance in the Humboldt system was in line with previous works which showed that except in the case of extreme El Niño events, seabird behaviour, breeding seasonality and population dynamics were affected by fish accessibility rather than fish abundance (Barbraud et al., 2017; Boyd et al., 2015, 2016, 2017; Passuni et al., 2015, 2018). Anchovy spatial distribution was shown to be strongly correlated with oxygen levels (Bertrand et al., 2010), so that when the oxycline goes up, anchovies are concentrated close to the surface, where they become accessible to shallow divers such as Peruvian boobies and Peruvian pelicans (Weimerskirch et al., 2012). This phenomenon may be apparent also in the Benguela with respect to anchovy accessibility to both purse-seine fishers as well as surface-diving predators, since unpublished evidence suggests that anchovy in recent periods are located closer to the sea bed given reduced stratification (and more homogenous oxygen levels) through the water column (SWG-PEL of Department of Environments, Forestry and Fisheries in South Africa 2019).

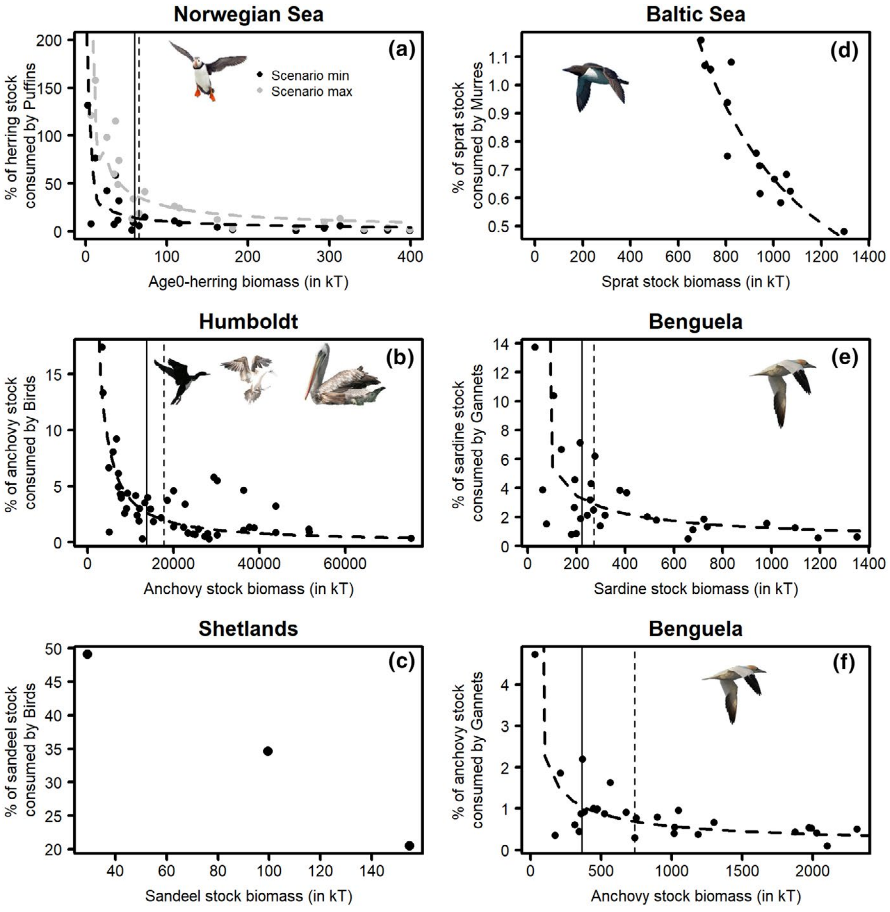

FIGURE 6 Relationships between the stock biomass of prey (thousand tonnes) and the percentage of the stock consumed by seabirds. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). The thresholds in the non-linear relationships between stock biomass and the percentage of the stock consumed by seabirds were calculated from change-point analyses and are indicated by vertical solid lines, while the median stock biomass is indicated by a dashed vertical line. Note that for the Baltic, the different candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes

Our results show that the predation pressure from seabirds, that is the proportion of the stock consumed by seabirds, was generally low (median = 1% and ≤20% of stock size in 95% of cases), confirming that bottom-up processes might be controlling seabird—forage fish interactions most of the time at the population scale. It is important to note that our analyses occurred at a regional or ecosystem scale, so that our results did not consider the potential for local prey depletion (Lewis et al., 2001) or the importance of top-down processes on spatial distribution at a fine scale. The broad scale used in this study might also explain why the estimated predation pressure was lower than that obtained by some previous studies (Furness, 1978). Nonetheless, when prey biomass decreased below a certain threshold (here estimated between 15% and 18% of the maximum biomass depending on the ecosystem and always lower than the median biomass), the predation pressure increased sharply as depicted by power relationships between prey biomass and the percentage of prey biomass consumed by seabirds. While it could not be tested in Shetland due to the small number of years monitored, this held true in the Norwegian Sea, in the Humboldt and in the Benguela. In contrast, the percentage of the sprat stock consumed by common murres in the Baltic Sea remained extremely low (≤1.2%) throughout the study. This could be explained by the high abundance and small variability in sprat biomass during the study period (Eero, 2012), which in fourteen years did not fall below 54% of its maximum value (a value well above the 15-18% threshold detected in other ecosystems). An increase in the proportion of prey that is consumed by predators when prey abundance is low was not unexpected, because predators need to satisfy their food requirements (Bakun, 2006) and even though some are able to switch their diet to alternative food sources, they may preferentially target energetically rewarding prey (Adams & Klages, 2010). Due to different life-histories between short-lived prey and long-lived predators, and the canalization of seabird adult survival, that is the key parameter buffering their population dynamics against temporal fluctuations (Gaillard & Yoccoz, 2003), the number of seabirds can still be high after a decrease in prey biomass, maintaining prey consumption at high levels. In some exceptional cases, the predation pressure we estimated became extremely high, such as in the Norwegian Sea, where this most likely reflected unrealistic survival rates for herring in the modelling for some of the poorest years (cf. ICES, 2012 and Appendix S1 for further details).

A rapid rise in the proportion of forage fish consumed, that is in predation mortality, once forage fish have been depleted below a certain threshold of abundance, might result in their entrapment in a predator pit (Bakun, 2006). This effect would be exacerbated if proportions of those prey taken by other predators in the ecosystem (e.g. other seabirds, seals, cetaceans, predatory fish, see Table S1) increase similarly and fishing mortality is also high. For several fish stocks in the North-West Atlantic, including Atlantic herring, chub mackerel (*Scomber colias*, Scombridae), haddock

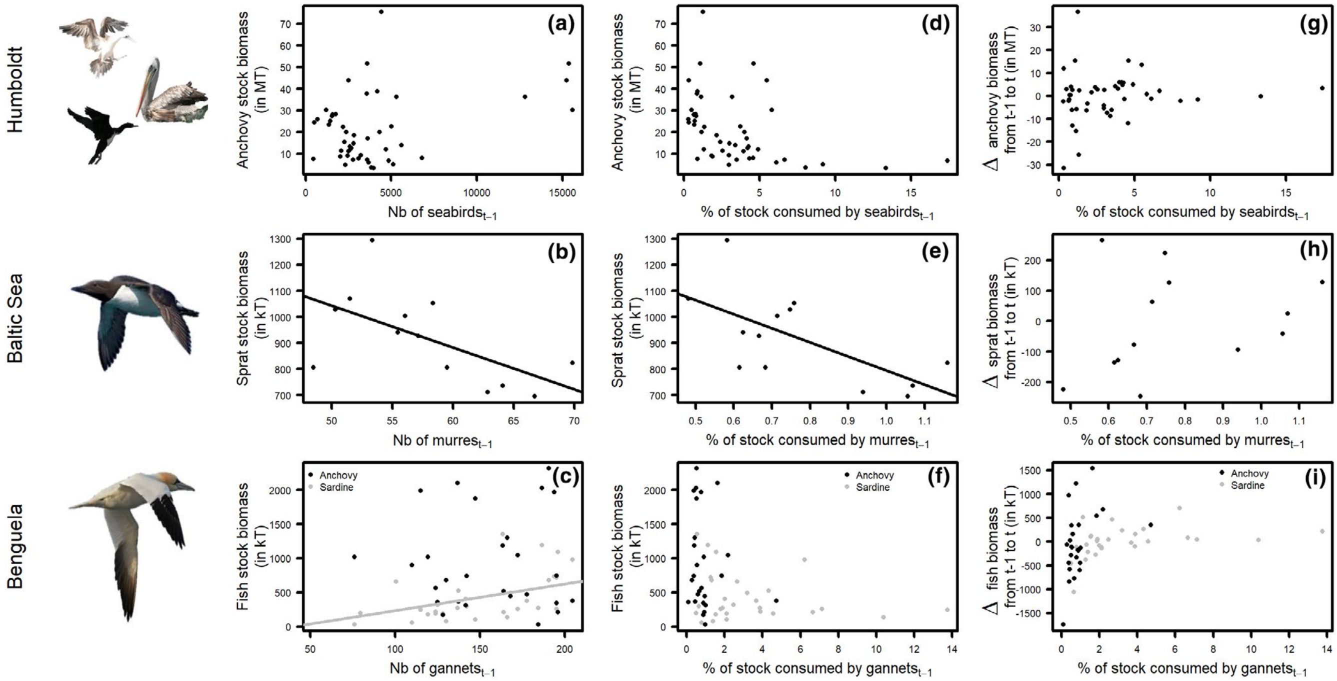

FIGURE 7 Relationships between fish stock biomass at year *t* and the number of seabirds (in thousands) present at year*t*−1 (left) or the percentage of the stock consumed by seabirds at year*t*−1 (middle). To account for autocorrelation in the Benguela and Humboldt ecosystems, the stock biomass at *t*−1 was added as an explanatory variable in all 6 models run for these two ecosystems. Lines depicting the relationships are drawn in the case of significant relations (linear model with the stock biomass at *t*−1 as a co-variable). On the right are represented the relationships between the change in fish stock biomass from year*t*−1 to year *t* and the percentage of the stock consumed by seabirds at year*t*−1. Such analyses were not considered for the Norwegian Sea ecosystem, as puffins there consume age 0 herring, which reach maturity at age 3, nor for Shetland where seabirds were not monitored on an annual basis

(*Melanogrammus aeglefinus*, Gadidae) and silver hake (*Merluccius bilinearis*, Merlucciidae) empirical evidence suggested that recruitment remained poor when stocks were reduced to 10% of pristine levels, but that good year-classes were experienced, and stock rebuilding took place when biomass was above about 20% of peak levels of abundance (Brown et al., 1983). Here, we found that predation pressure increased sharply when the stock biomass decreased below 15%–18% of its maximum abundance. These observations raise the question as to whether such predation pressure might constrain prey stocks and keep them at very low levels.

First, positive correlations between prey biomass and the number of seabirds the year before were highlighted in both the Benguela and Humboldt ecosystems. While this might appear surprising, it could be due to temporal autocorrelation in prey biomass time series, that is the fact that a high prey biomass in a given year is likely to be followed by another high prey biomass the next year and vice versa (Fréon et al., 2005). If the ecosystem is indeed under bottom-up control, or both prey and predators react the same way to other external variables, then both would endure similar favourable or unfavourable periods, explaining the positive relationship between prey at $t + 1$ and predator at *t*. Indeed, a partial temporal autocorrelation of lag 1 was present in the residuals of the models in the Benguela and the Humboldt. Once we removed the autocorrelation by adding a 1-year lagged time series of the prey biomass as a covariate in the model, both relationships between prey biomass and predator abundance or consumption disappeared in the Humboldt. Further, a negative temporal correlation of predator and prey abundance, despite being the most commonly used approach to investigate predation (e.g. Frank et al., 2005; Worm & Myers, 2003), does not allow one to distinguish between predators driving prey dynamics and both populations responding in opposite directions to an external environmental driver (Hunt & McKinnell, 2006; Oken & Essington, 2015). When looking at the effect of the predation pressure, instead of the number of predators, on the prey biomass a year later, no relationship was detected in the Humboldt or Benguela ecosystems. In contrast, a significant negative relationship between prey biomass and the number of birds or the percentage of the stock consumed by seabirds the year before was found in the Baltic Sea. Given the very low predation pressure (<1.2%) estimated in this ecosystem, we suggest that this might be due to a spurious correlation, perhaps attributable to a third variable to which sprat and murres might react differently. Finally, looking at how predation pressure affects the change in prey biomass from one year to another, rather than the absolute value of biomass, should remove the variance explained by temporal autocorrelation and enable an investigation of the immediate effects of predation, whereas the effect on absolute biomass might be delayed (Oken & Essington, 2015). Importantly, no relationships were highlighted between these two variables, suggesting that seabird predation pressure did not drive changes in forage fish abundance.

However, it should be borne in mind that we only estimated a portion, often small (e.g. Shannon et al., 2004), of the overall natural mortality, as consumption by other predators present in the area (large predatory fish, marine mammals, other seabirds) was not included. Further, predators do not target the entire population, but rather focus on given length- (or age-) classes, making the effect of predation harder to detect (Oken & Essington, 2015). Hence, in years when prey biomass is low and corresponding seabird consumption requires a significant part of the forage fish stock, strong competition might arise between predators and fisheries. During such intense competition, as created in the North Pacific by the massive biennial fluctuations in predatory adult pink salmon (Ruggerone et al., 2019; Springer & Van Vliet, 2014) or during the 2014–2016 marine heatwave when all forage fish stocks crashed simultaneously (von Biela et al., 2019; Jones et al., 2018; Piatt et al., 2020), it is increasingly apparent that seabirds may take the brunt of competitive displacement from food supplies (e.g. 10%–20% of the NE Pacific population of common murres died en masse from starvation during the heatwave; Piatt et al., 2020). In the California current, seabirds whose diet is mainly forage fish, especially anchovy, respond negatively to forage fisheries (Koehn et al., 2017). While economic consequences of fishing forage fish are unclear for piscivorous fisheries (Engelhard et al., 2014), the impact on conservation of seabirds and marine mammals might tip the scales towards keeping forage fish at sea being more valuable than fishing them out (Koehn et al., 2017). Many seabirds have an unfavourable conservation status. Seabirds are more threatened, and declining faster, than other groups of birds (Dias et al., 2019). For example, nine of 15 seabird species (60%) that breed in the Benguela ecosystem are classified, in terms of criteria of the International Union for the Conservation of Nature (IUCN), as Endangered, Vulnerable or Near-threatened; these include three that feed mainly on sardine and anchovy, whereas several seabirds that do not compete with fisheries for food have a Red List status of Least Concern (Crawford, 2013; IUCN, 2019). Cury et al. (2011) identified a threshold of approximately one-third of maximum prey biomass below which seabird breeding success was consistently reduced and more variable. Similarly, when the biomass of sardine spawners fell below c. 25% of its maximum observed value, survival of adult African penguins (*Spheniscus demersus*, Spheniscidae) decreased markedly (Robinson et al., 2015) and survival and numbers breeding decreased for three Benguela seabirds when a forage availability index reached low values (Crawford et al., 2019). There may be a still lower ecological threshold (15%–18% according to our study) where prey species, or at least spatial components of prey stocks (e.g. west coast versus south coast in the Benguela), suffer high rates of natural and fishing mortality. Interestingly, 20% of maximum biomass is often used in fishery management as a limit biomass (B_{lim}) below which a stock should not fall or a recovery plan should be put in place. Here, we confirm a similar threshold and advise fishery managers to exercise due care in allocating allowable catches or fishing licences, etc., at low levels of abundance.

To conclude, our study is important as it contributes to the growing literature in support of an ecosystem approach to fisheries (EAF; Dickey-Collas et al., 2014; Hill et al., 2020; Koehn et al., 2017; Pikitch et al., 2004). While top-down processes due to predation of forage fish by seabirds did not seem to control forage fish dynamics in any of the five ecosystems we considered, the predation pressure sometimes attained high levels, which signals the need for fisheries management to account for ecosystem constraints when setting catch limits in periods of low forage fish biomass. Finally, our results (and in particular the differences of sensitivity of seabird diet to prey biomass among species) also suggest that forage fish accessibility might be more important than forage fish abundance depending on the ecophysiological constraints that apply to seabirds (e.g. depth to which they can dive). As a consequence, fish stock management should not only ensure a safe level of fish biomass for the stock to be sustainable and the predators to feed (Cury et al., 2011), but also focus on safeguarding predator foraging grounds. Measures such as spatial enclosure around breeding sites have for instance been used in different areas (see Sydeman et al., 2017 for more on the subject). Spatial planning is thus an extremely important component of human activity (and especially fishery) management in order to safeguard all components of the ecosystem.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Mendeley data at http://dx.doi.org/10.17632/5bb8nhb6hr.1

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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