



## The emergence of ecological traps in marine ecosystems: The case of seabirds and fisheries

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### ABSTRACT

Human-induced rapid environmental change increasingly causes animals to select habitats of poor quality based on misleading cues, creating ecological traps that drive demographic decline and elevate extinction risk. Yet research on ecological traps has focused mainly on terrestrial and freshwater systems, while marine traps—particularly those linked to fisheries, the dominant marine industry and a potential source of traps for seabirds and other vertebrates—remain understudied. In this marine context, fisheries represent a double-edged sword for seabirds: the trophic subsidies they provide (bait, discards, and catches) offer predictable food but also attract birds to vessels, thereby increasing their risk of mortality from bycatch. Here, we analyze the interaction between seabirds' scavenging behavior and bycatch in fisheries, as well as the effect of the slow–fast life-history continuum on their vulnerability to ecological traps. Through a systematic literature review and Bayesian multilevel models accounting for phylogenetic relatedness (341 species), we show a clear preference–performance mismatch: slow-lived seabirds, such as albatrosses, are more likely to exploit fishery-derived trophic subsidies and are consequently more threatened by bycatch. Building on recent evidence that ecological traps are a common phenomenon in marine ecosystems, we propose that they should be recognized as a primary mechanism underlying seabird–fishery interactions. Moreover, incorporating ecological traps into theoretical frameworks could strengthen ecosystem-based fisheries management by clarifying the causes and consequences of fishery impacts on seabirds, enhancing the effectiveness of management and conservation strategies, and supporting the enforcement of mitigation measures.

### 1. Introduction

Most species on earth inhabit ecosystems that humans have modified through habitat loss, pollution, alien species, overexploitation, changes in resource availability, and more recently, climate change (Lewison et al., 2004; Parmesan, 2006; Butchart et al., 2010; Oro et al., 2013; Dirzo et al., 2014). A common feature to many of these cases is that such changes in ecosystems have occurred at rates faster than what organisms have experienced in their evolutionary past, often referred to as human-induced rapid environmental change (HIREC; Sih et al., 2011), hindering the development of adaptive behavioral responses. One of the consequences of HIREC is the appearance of ecological traps (Dwernychuk and Boag, 1972; Gates and Gysel, 1978; Schlaepfer et al., 2002).

An ecological trap refers to situations where organisms find a habitat equally or more attractive, despite their fitness being compromised (Robertson et al., 2013; Swearer et al., 2021). Three general mechanisms

have been proposed through which HIRECs can generate ecological traps: altering habitat quality, altering habitat preference, or both (Robertson et al., 2013). The first, known as the *degradation mechanism*, occurs when habitat quality declines without a corresponding decrease in habitat preference, leading organisms to continue selecting degraded environments. In contrast, the *attraction mechanism* involves increased attraction to and preference for habitats of low quality. Finally, *combined traps* result from the interaction of both mechanisms, whereby increased preference is directed toward degraded habitats—often leading to the most severe demographic consequences (Hale et al., 2015).

To prevent or mitigate ecological traps, it is important to identify their underlying causes and assess the vulnerability of taxa. In this regard, understanding the influence of behavioral and life history traits of species/populations is crucial for both the likelihood of trap selection by individuals and the consequences at the population level (Hale and Swearer, 2016). For instance, animals that use simple or single cues to

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select habitats, have a simple sensory system, or high mobility have been identified as more vulnerable to falling into traps (Hale and Swearer, 2016). As for fitness consequences, the ‘slow-fast’ continuum in life histories (Stearns, 1983; Gaillard et al., 2016; Capdevila et al., 2020) has been recognized as a key factor influencing the severity of traps (Kokko and Sutherland, 2001; Hale et al., 2015). Traps that greatly reduce survival are likely to have larger population-level impacts on species at the slow end of the continuum, which exhibit deferred maturity, low fecundity, and long generation times (Saether and Bakke, 2000; Capdevila et al., 2022).

Identifying anthropogenic activities that might drive the emergence of ecological traps could be useful for improving the management of marine ecosystems, where traps remain poorly studied despite their potential prevalence (Sherley et al., 2017; Teske et al., 2021; Swearer et al., 2021). Two HIRECs with major impacts on marine environments are derived from fisheries: incidental catch (bycatch) (Lewison et al., 2004) and food subsidies (Oro et al., 2013). Both HIRECs affect large marine vertebrates, including sea turtles, mammals, elasmobranchs (sharks and rays), and seabirds, which may severely compromise the sustainability of commercial fisheries (Lewison et al., 2014).

Fisheries subsidize seabirds by providing access to food that would otherwise be unavailable, including catch, bait, offal, and discards. Recent estimates indicate that fisheries discard between 7 and 16 million tons per year (Gilman et al., 2020), potentially sustaining large populations of scavenging seabirds worldwide (Garthe et al., 1996; Votier et al., 2004; Bicknell et al., 2013; Sherley et al., 2019). However, these subsidies have opposing effects. While they increase food availability and can offer individual benefits (e.g., improved foraging and breeding success; Oro et al., 2013), they also heighten the risk of bycatch by increasing attraction to fishing vessels (Sullivan et al., 2006; González-Zevallos and Yorio, 2006; Watkins et al., 2008; Favero et al., 2011; Zhou et al., 2019; Zhou and Brothers, 2022). As a consequence, seabirds are caught as bycatch in nets (e.g., purse seines, gillnets; Žydelis et al., 2013, Simeone et al., 2021), on hooks (e.g., longlines; Anderson et al., 2011), or by colliding with cables (e.g., trawls; Phillips et al., 2024). Bycatch is now recognized as the primary threat to seabirds at sea, causing severe population declines (Dias et al., 2019; Richards et al., 2021, 2024). This problem is particularly acute in the Southern Hemisphere, where many slow-lived seabird species occur, including albatrosses—90 % of which are currently threatened by bycatch (Richards et al., 2024).

Despite strong evidence that fishery-derived food subsidies elevate bycatch risk (Sullivan et al., 2006, González-Zevallos and Yorio, 2006, Watkins et al., 2008, Favero et al., 2011, Zhou et al., 2019, Zhou and Brothers, 2022), this phenomenon has not been formally examined using the theoretical and modeling framework of ecological traps to explain its underlying mechanisms, predict its demographic consequences, or evaluate potential management strategies. Nor has it been adequately considered in efforts to advance ecosystem-based fisheries management.

In this study, we aimed to analyze the interaction between the scavenging behavior of seabirds and bycatch in fisheries, as well as the influence of the slow-fast continuum of life history on the occurrence and severity of ecological traps on seabirds. We examined two opposing hypotheses regarding the influence of the slow-fast continuum on the likelihood of trap selection by seabirds. First, slow-lived seabirds—prioritizing survival over reproduction—should show greater scavenging propensity because they have more time to explore and exploit new opportunities (Sol et al., 2016). Second, under the time-limited disperser model (Ward, 1987), fast-lived seabirds—prioritizing current reproduction—should show greater scavenging propensity because limited search time raises the cost of rejecting new opportunities. Regarding population-level consequences, we hypothesized that traps should be more severe for slow-lived scavengers due to their greater demographic sensitivity to adult and juvenile mortality compared to recruitment (Saether and Bakke, 2000). To test these hypotheses, we (i) generated a fisheries-associated scavenging-propensity index for

seabirds based on vessel association and/or diet via a systematic literature review, (ii) used the IUCN Threats Classification Scheme (Salafsky et al., 2008) as a proxy for population-level consequences of bycatch, (iii) compiled a global dataset covering 341 seabird species, and (iv) fit Bayesian multilevel models that accounted for phylogenetic relatedness.

## 2. Methods

### 2.1. Systematic review protocol

We systematically reviewed the literature through July 2022 to synthesize evidence on seabird scavenging and derive a fisheries-associated scavenging-propensity index. Because scavenging involves both searching for/associating with fishing activity and consuming fishery-derived subsidies, our search targeted (i) habitat association with fisheries and (ii) dietary evidence of subsidy consumption. Accordingly, we combined taxonomic terms for seabirds with terms reflecting interactions with fisheries and consumption, and searched the Web of Science Core Collection using a predefined search string (see Supplement S1 for the full search string). From this search, we compiled a database of primary studies (reviews excluded) reporting species-level quantitative estimates of scavenging via habitat association (e.g., counts of attendance/interaction with vessels during gear setting/hauling; discard-consumption trials) or diet (stomach contents, DNA metabarcoding, fatty acids, stable isotopes; typically at colonies). A flow diagram summarizing the identification, exclusion, and inclusion of studies is provided in Fig. S1.

A formal meta-analysis was infeasible because included studies reported heterogeneous, non-commensurable metrics (counts, rates, proportions) spanning occurrence, abundance, and multiple dietary tracers. We therefore adapted a vote-counting approach (Koricheva and Gurievitch, 2013), replacing ‘significant votes’ with occurrence records of fishery-related scavenging and aggregating them across independent studies to obtain a species-level index. We defined an observation as a species-level occurrence record assigned when a study reported (i) attendance or interaction with vessels during fishing operations, (ii) a positive discard-consumption experiment, or (iii) fishery-derived items in the diet. For each record, we noted species identity, evidence type (habitat association or diet), fishery type, and study location. A single article could contribute multiple records for a species if it reported distinct colonies, fisheries (e.g., different gears/targets), or geographically non-overlapping areas. In our dataset, 77.9 % of article–species combinations yielded one record, 14.1 % yielded two, and 7.8 % yielded three or more. We did not a priori exclude records occurring in similar habitats, populations, or seasons when they came from independent studies, as concordant observations across studies strengthen inference that the behavior is recurrent for a given species. Nevertheless, we formally assessed potential duplication: for each species, we quantified spatial and spatiotemporal overlap between studies as the share of records occurring in  $100 \times 100$  km grid cells ( $10,000 \text{ km}^2$ ; SO) and cell-year combinations (STO; using publication year as a proxy for sampling year) that contained  $\geq 2$  distinct studies. Mean SO and STO across species were 12.5 % and 1.8 %, respectively, indicating that, on average, spatial and spatiotemporal overlap between independent studies was low. Finally, we summed occurrence records across independent studies to generate the species-level scavenging propensity index (range: 0–52, Table S1). We interpret this index as a measure of species-level propensity to search for and/or consume fishery-derived subsidies.

We computed sample-based species accumulation curves using the function specaccum in the vegan package in R (Oksanen et al., 2022) based on 999 random permutations of study order. Curves were generated globally and separately for each hemisphere.

## 2.2. Traits data and bycatch threat

We compiled data for all 341 seabird species, including generation length, body mass, geographic extent ( $\text{km}^2$ ), habitat breadth (number of suitable habitats), migratory status, and foraging guild. Geographic extent was measured as the Extent of Occurrence (EOO) reported by BirdLife (BirdLife International, 2022a), defined as the area ( $\text{km}^2$ ) of the minimum convex polygon encompassing each species' mapped resident/breeding range. Although 26 species of *Anatidae* are considered sea-ducks (Harrison et al., 2021), we excluded this group from our analysis because they occur mainly on freshwater to brackish habitats, are exclusively coastal foragers with no pelagic species. We used generation length (the mean age in years at which a species produces offspring) because it is one of the best predictors of a species' position along the slow-fast continuum of life history (Gaillard et al., 2016). Its predictive power lies in the fact that this variable measures the strength of the trade-off between survival and fertility (Giaimo and Traulsen, 2019), two of the most basic components of biological fitness. Data on generation length, geographic extent, and habitat breadth were compiled from (Richards et al., 2021) and from BirdLife International (BirdLife International, 2022a). Original data on body mass (median body mass in grams) are sourced from (Cooke et al., 2019), while migratory status (full migrant/non-migrant) and foraging guilds (diver feeders, surface feeders, generalists, ground feeders) are from (Wilman and J. W., 2014). The bycatch threats for each species (binary variable) were obtained from the International Union for Conservation of Nature (IUCN) threat classification scheme (threats 5.4.3 & 5.4.4, <https://www.iucnredlist.org/resources/threat-classification-scheme>). These data were recently updated by a comprehensive review, which included more than 900 publications (Dias et al., 2019).

## 2.3. Phylogenetic relatedness

To account for phylogenetic relatedness in our analyses, we constructed a species-level phylogenetic tree using data from the BirdTree online platform (<http://www.birdtree.org>). This platform includes the phylogenetic trees from Jetz et al. (2012), and provides a complete tree of all extant species by combining time-calibrated trees. Specifically, the platform contains 10,000 post-burn-in trees from an ultrametric and fully resolved Markov chain Monte Carlo (MCMC) tree. We downloaded 2000 trees for 329 seabird species using the “Full trees (9,993 species), Ericson backbone” option (accessed in August 2022). We then obtained an optimal consensus tree using the 50 % majority-rule method (Holder et al., 2008), with the consensus.edges function from the ape package (version 5.6–2) in R (Paradis and Schliep, 2019). Polytomies were resolved using the function multi2di from ape package (same version). The remaining twelve species—most likely absent from the platform due to a lack of publicly available sequence data—were inserted at random within their respective genera in the phylogeny using the add.species.to.genus function from the ape package in R (same version). Simulation studies have shown that comparative regression models are robust to tree misspecifications in both topology and branch lengths, especially if the misspecifications involve small perturbations in the fine structure near the tips (Martins and Housworth, 2002; Stone, 2011). From the resulting consensus ultrametric-tree of 341 taxa, we obtained the variance-covariance matrix assuming a Brownian motion model of evolution for further analyses.

## 2.4. Bayesian multilevel models

We used two Bayesian multilevel models with varying structures to address the main hypotheses of our work: the “trap selection model” and the “trap consequences model”. Both models were fitted using the brms (version 2.17.0) package (Bürkner, 2017) of R (R Core Team, 2021). We initially fit count models (e.g., negative binomial), for the “trap selection model” but posterior predictive checks showed systematic misfit driven

by the data's distribution: a heavy spike at zero (62 %) plus a long right tail (five species >35). We therefore adopted a more flexible ordinal specification, which uses category-specific intercepts/thresholds to capture both the zero spike and the uneven spacing at higher levels, yielding a substantially better fit. Specifically, the “trap selection model” was fitted with a cumulative ordinal likelihood and a logistic (logit) link (Bürkner and Vuorre, 2019). The ordinal index comprised five categories: no scavenging (0 obs.), low (1–5), medium (6–10), high (11–20), and very high scavenging propensity ( $\geq 21$ )—with upper thresholds increasing approximately geometrically to reflect near-doubling between levels while preserving adequate sample sizes per bin. Generation length was included as the main predictor of interest. Body mass, migratory status, and foraging guild were included as confounding variables, given their potential association with both generation length (Sibly et al., 2012) and scavenging propensity. In contrast, geographic extent and habitat breadth were incorporated to improve model precision by accounting for variation in the likelihood of encounter between seabirds and fisheries. Specifically, body mass captures life-history allometry (Gaillard et al., 2016) and competitive ability at discards—larger, slower-paced species tend to interact more frequently with fisheries (Zhou et al., 2019; Zhou and Brothers, 2022). Migratory status accounts for seasonal redistribution and potential overlap with large-scale fisheries across the annual cycle; migratory species—often slower-paced (Sibly et al., 2012)—may encounter offshore fleets more frequently. Foraging guild reflects behavioral strategies that shape both interaction with particular gear types and the likelihood of scavenging; for example, pursuit divers—generally faster-paced on the slow–fast continuum—typically interact less with offshore large-scale gear, whereas surface feeders, including slow-paced taxa such as albatrosses, are more prone to use discards. Although these covariates should control for much of the variation in reporting bias, we further included the genus of the species (76 genera) as a varying intercept to account for uncertainty related to taxonomic biases (e.g., genera that have been little studied). Finally, to account for the lack of independence among the analyzed species, we also incorporated the variance-covariance matrix derived from the phylogeny as a varying intercept. We used weakly informative priors to encode broad, plausible ranges for model parameters while letting the likelihood dominate when data are informative. Concretely, we placed zero-centered priors for the intercepts (Normal(0, 5)), fixed variables (Normal(0, 0.5)), and for the standard deviation parameters (Half-normal(0, 0.5)). These priors mildly shrink estimates toward reasonable values, improving regularization and sampler stability by ruling out implausible extremes (McElreath, 2020). When the data are informative, posterior means move away from zero, indicating that the likelihood overwhelms the prior; when data are weak, estimates remain closer to the prior (McElreath, 2020).

The “trap consequences model” estimated the probability of bycatch threat using a Bernoulli distribution with a logistic link. We included an interaction between generation length and the scavenging propensity index as our main fixed effects of interest. Similarly to the previous model, we adjusted for body mass as a fixed effect, added the variance-covariance matrix as a varying intercept to account for phylogenetic relatedness, and included genus as a varying intercept to address potential taxonomic biases. We set weakly informative priors for the intercept (Normal(0,1)), fixed variables (Normal(0, 5)), and for the standard deviation parameters (Half-normal(0, 0.5)). Prior to analyses, continuous variables were log-transformed and z-scaled due to their positive skewness (Richards et al., 2021). For both models, we ran four chains of 8000 iterations with a warm-up period of 4000 iterations (i.e., the total post-warm-up draws per model was 16,000). Convergence and mixing of chains were inspected visually using trace and density plots. We also used standard MCMC diagnostics and required a Gelman–Rubin statistic ( $R \leq 1.01$ ) and bulk- and tail-effective sample sizes (ESS)  $> 400$  for all parameters. Posterior predictive checks indicated adequate fit, and all models met these criteria with no divergent transitions (Gelman and Hill, 2006). Figures were produced using the ggplot2 (Wickham,

2016), ggtree (Yu et al., 2017), bayesplot (Gabry et al., 2019), and sf (Pebesma, 2018) packages in R.

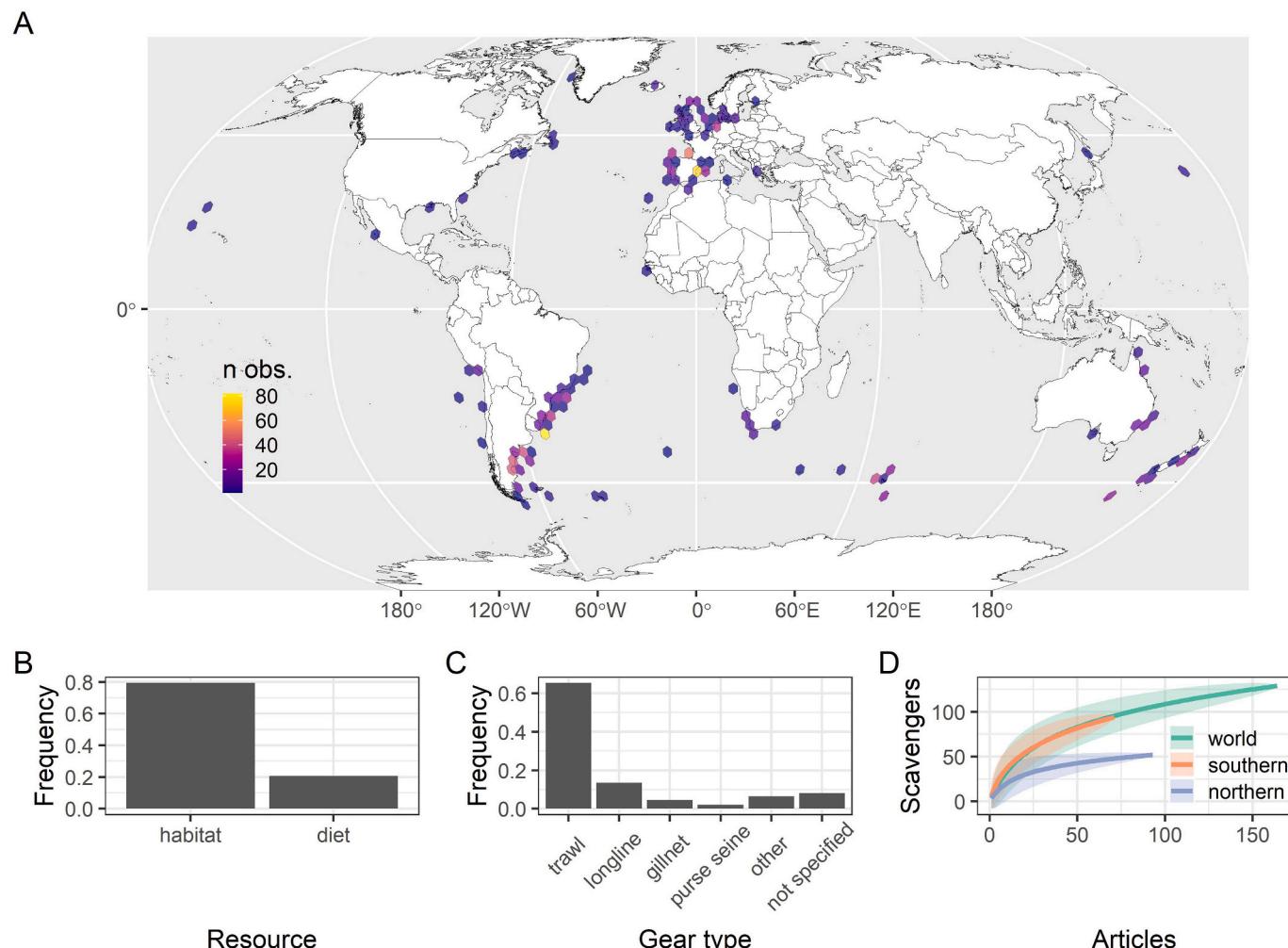
### 3. Results

We reviewed 275 peer-reviewed research articles selected through a literature search, of which 60 % ( $n = 163$ , Fig. S1) met our inclusion criteria. From these articles, we extracted and compiled a total of 1106 observations, with an average ( $\pm$  SD) of  $6.7 \pm 11.4$  observations per study. Publication years ranged from 1992 to 2022. After an initial increase in the number of studies during the early years, annual publication rates remained relatively stable, with some non-linear fluctuations, indicating sustained research interest in seabird–fishery scavenging over the past three decades (Fig. S2). Observations were skewed toward the southwestern and northeastern Atlantic Ocean (Fig. 1A, Table S2). Seventy-nine percent ( $n = 878$ ) of the observations came from habitat association studies (75 % from count studies and 5 % from consumption experiments), while 21 % ( $n = 228$ ) were from diet studies (Fig. 1B). Regarding the types of fisheries, 80 % of observations were from trawl, 15 % from longline, 4.5 % from gillnet, and 2 % from purse-seine gears (Fig. 1C). A total of 130 seabird species (38 % of the 341 species in our dataset) from 12 taxonomic families were identified as scavengers of fisheries (Fig. 2). The families with the greatest propensity for scavenging, on average, were *Diomedeidae* (albatrosses), *Stercorariidae*

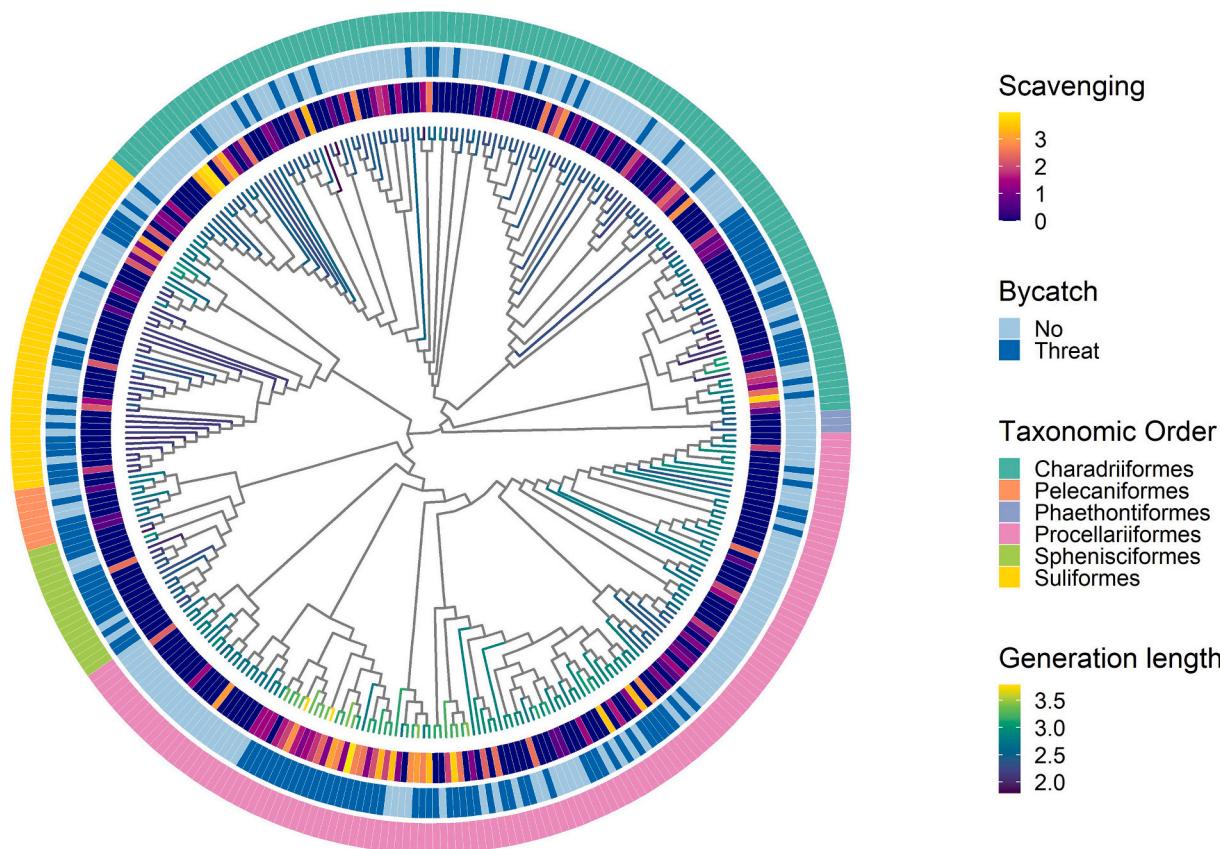
(skuas and jaegers), *Sulidae* (boobies), *Laridae* (gulls and terns), and *Procellariidae* (petrels and shearwaters). Accumulation curves from the reviewed articles, computed globally and separately for each hemisphere, showed that an asymptote was not reached, especially in the Southern Hemisphere, suggesting a larger scavenging community than what is reported in the published literature (Fig. 1D).

The “trap selection model” (Bayes  $R^2 = 37\%$ , 95 % CI = 28–46 %) showed that scavenging propensity was positively correlated with generation length (Fig. 3A,  $\beta = 0.58$ , 95 % CI = 0.22–0.96,  $\beta(\text{pr} > 0) = 100\%$ ), while adjusting for body mass, geographic extent, habitat breadth, migratory status, foraging guild, phylogenetic signal, and taxonomic genus as a varying intercept (Table 1). Posterior predictions of the effect of generation length on scavenging propensity are shown in Fig. 3B, C. The studied seabirds exhibited a low phylogenetic signal for scavenging propensity (Table 1,  $sd = 0.46$ , 95 % CI = 0.02–1.13) and a comparatively higher variation associated with the genus of the species (Table 1,  $sd = 0.64$ , 95 % CI = 0.08–1.14).

A total of 134 seabird species have bycatch listed as a threat to their conservation, as reported by the IUCN threat classification scheme (Fig. 2). The “trap consequences model” (Bayes  $R^2 = 0.44$ , 95 % CI = 0.35–0.52) provided strong evidence for an interaction between scavenging propensity and generation length in predicting bycatch risk (Fig. 4A,  $\beta$  interaction = 0.38, 95 % CI = 0.05–0.73,  $\beta(\text{pr} > 0) = 99\%$ ), while adjusting for body mass, phylogenetic relatedness (Table 2,  $sd =$



**Fig. 1.** Evidence base used to characterize seabirds' scavenging behavior and to derive a fisheries-associated scavenging propensity index from a systematic review of the literature. (A) Global distribution of observations ( $n = 1106$ ), each corresponding to a species-level record of scavenging during fishing operations/consumption experiments (“habitat”) or consumption of fishery-derived subsidies documented in diet studies. (B) Frequency of records by evidence type (“habitat” vs. diet). (C) Frequency of records by fishery type. (D) Cumulative number of scavenging seabird species detected across reviewed articles ( $n = 163$ ; mean  $\pm$  2 SE).



**Fig. 2.** Phylogenetic visualization of variation in seabird scavenging propensity, bycatch threat, and generation length across 341 species. Scavenging propensity and generation length are shown on the log scale. The phylogeny is a 50 % majority-rule consensus derived from 2000 trees.

1.16, 95 % CI = 0.29–1.84), and taxonomic genus as a varying intercept (Table 2,  $sd = 0.61$ , 95 % CI = 0.04–1.34). Posterior predictions showed that species with longer generation times and higher scavenging propensity had the highest probability of being affected by bycatch (Fig. 4B–D). Species with shorter generation times and higher scavenging propensity showed the lowest probability of bycatch threat (Fig. 4B–D).

#### 4. Discussion

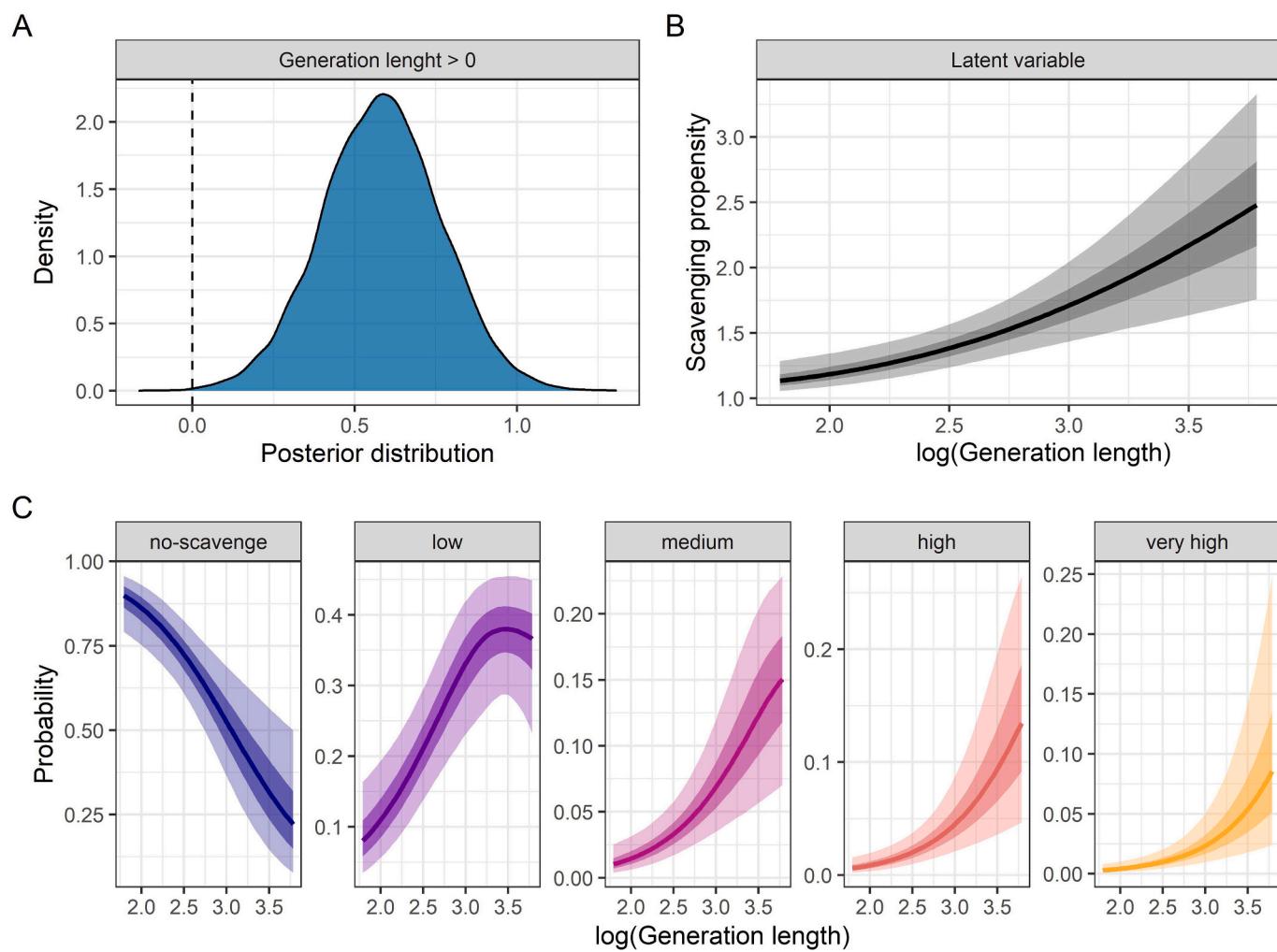
Our results show that generation length influences seabirds' scavenging propensity, and that the interaction between this behavior and generation length correlates with bycatch probability across species. Specifically, slow-lived seabirds are the most likely to exploit fishery-derived trophic subsidies, and these species—the slowest and most prone to scavenging—have the highest likelihood of being affected by bycatch. This pattern is particularly evident in albatrosses (*Diomedaeidae*), the slowest group of seabirds: 21 of 22 species scavenge to varying degrees, and all are threatened by bycatch (IUCN). Our results suggest that ecological traps may be a key mechanism underlying seabird–fishery interactions. While the concept has been briefly used to describe ‘junk-food’ scenarios—where low-quality fishery subsidies reduce reproductive success (Grémillet et al., 2008)—it remains largely absent from studies addressing more common situations in which trophic subsidies increase habitat preference yet reduce fitness via bycatch. In such cases, cueing on visual and olfactory signals can simultaneously increase habitat preference ('attraction') while elevating mortality risk ('degradation'), consistent with combined traps, which are often the most harmful (Robertson et al., 2013). This mechanism could help explain the global decline in seabird populations affected by bycatch, 59 % of which are decreasing (BirdLife International, 2022b). Building on our findings and prior evidence, we propose a general two-stage

pathway by which different gears generate combined ecological traps: (1) fishery-derived subsidies elevate attraction and attendance around vessels; and (2) fitness costs arise primarily via bycatch. Specifically, trawls attract through batched discards/offal, with losses from warp/gear strikes and net entanglement; longlines attract with bait (and any discharged discards/offal), with losses from hooking and drowning; purse seines attract by aggregating birds around targeted schools and released/discarded catch during sets and processing, with losses from encirclement/entrapment and collisions.

Our results also show that evolutionary history influences seabird vulnerability to bycatch more than their scavenging behavior. While a full evolutionary analysis was beyond the scope of this study, our findings support the view that behavioral traits are more evolutionarily labile than life-history traits (Blomberg et al., 2003), and align with recent evidence suggesting that demographic resilience to disturbances is strongly constrained by evolutionary history in animals (Capdevila et al., 2022).

##### 4.1. Trap selection

Our results show a positive correlation between generation time and seabird scavenging propensity, after adjusting for body mass, migratory status, and foraging guild as potential confounders; geographic extent and habitat breadth as precision covariates; and accounting for phylogenetic relatedness and taxonomic uncertainty at the genus level. This suggests a relevant influence of the slow-fast continuum of life history on the probability of trap selection for seabirds that interact with fisheries. A plausible explanation for this lies in the behavioral innovations associated with life histories. To forage on trophic subsidies that are otherwise unavailable, seabirds need to sample and explore the fishing environment, solve how to take advantage of subsidies (from catch,



**Fig. 3.** Effect of generation length on seabird scavenging propensity across 341 species. (A) Posterior distribution of the generation-length coefficient (log scale), showing  $P(\beta > 0) = 1.00$ . Estimates adjust for body mass, geographic extent, habitat breadth, migratory status, foraging guild, and account for phylogenetic signal and genus-level taxonomic uncertainty (see Table 1). (B) Model-predicted conditional effect of generation length on the latent ordinal response (1 = no scavenging; 5 = very high propensity), with mean, 50 % and 90 % credible intervals. (C) Conditional effects for each observed level of the scavenging index (mean, 50 % and 90 % credible intervals). Continuous co-variables were conditionalized by their mean and all dummy variables (factors) were set to zero, yielding predictions at the grand mean.

**Table 1**

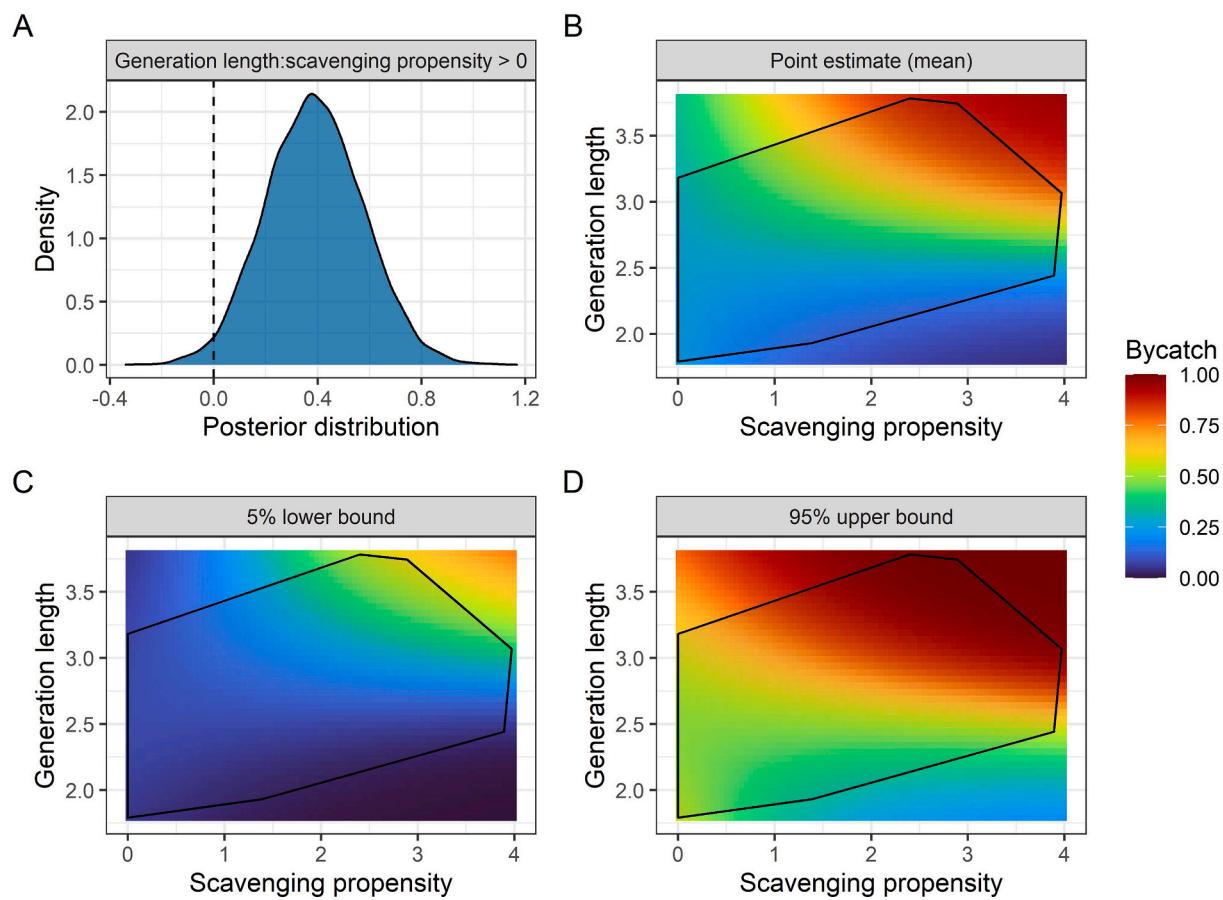
Summary of regression coefficients from the “trap selection model”. See Fig. 3 for the full posterior distribution of the generation length and its conditional effect over the scavenging propensity in seabirds.

Group-level effects	Estimate	Est.Error	1-95 % CI	u-95 % CI	R	Bulk_ESS	Tail_ESS
sd (taxonomic genus)	0.64	0.27	0.08	1.14	1.00	2478	2483
sd(phylogenetic)	0.46	0.31	0.02	1.13	1.00	2447	5807
Population-Level Effects	Estimate	Est.Error	1-95 % CI	u-95 % CI	R	Bulk_ESS	Tail_ESS
Intercept[1]	0.92	0.33	0.31	1.61	1.00	11,126	10,089
Intercept[2]	2.63	0.37	1.96	3.42	1.00	11,568	10,557
Intercept[3]	3.41	0.4	2.69	4.25	1.00	11,670	10,311
Intercept[4]	4.54	0.46	3.7	5.5	1.00	12,157	11,574
Generation length	0.58	0.19	0.22	0.96	1.00	15,200	11,452
Body mass	0.49	0.18	0.14	0.85	1.00	12,387	12,073
Geographic extent	1.09	0.21	0.69	1.51	1.00	19,380	12,184
Habitat breadth	0.59	0.17	0.26	0.92	1.00	20,388	12,791
Full migrant	0.25	0.18	-0.11	0.62	1.00	21,251	12,341
guild1	-0.08	0.25	-0.57	0.42	1.00	12,197	11,405
guild2	0.23	0.23	-0.23	0.68	1.00	16,751	11,296
guild3	0.21	0.33	-0.44	0.85	1.00	15,636	11,095

baits, offal, and discards), and learn to incorporate the new behaviors into their repertoire. Such innovations in the foraging domain should be constrained by time, and thus it is not surprising that they have

previously been linked to life histories in other taxonomic groups (Sol, 2015).

Theoretical and empirical evidence has shown that animals at the



**Fig. 4.** Effect of the interaction between generation length and seabird scavenging propensity on bycatch-threat probability across 341 species. (A) Posterior distribution of the interaction coefficient (both predictors log-scaled), with  $P(\beta > 0) = 0.98$ ; estimates control for body mass and account for phylogenetic signal and genus-level taxonomic uncertainty (Table 2). (B-D) Posterior predictions of bycatch-threat probability over the joint gradient of generation length and scavenging propensity (both log-scaled), showing the mean (B) and 90 % credible intervals (C, D), conditional on mean body mass. The black polygon delineates the covariate space occupied by the 341 species.

**Table 2**

Summary of regression coefficients from the “trap consequences model”. See Fig. 4 for the full posterior distribution and the conditional effect of the interaction between the generation length and the scavenging propensity over the probability of bycatch threat for seabirds.

Group-level effects	Estimate	Est.Error	l-95 % CI	u-95 % CI	R	Bulk_ESS	Tail_ESS
sd(taxonomic genus)	0.61	0.35	0.04	1.34	1.00	2395	5241
sd(phylogenetic)	1.16	0.37	0.29	1.84	1.00	2731	1997
Population-Level Effects	Estimate	Est.Error	l-95 % CI	u-95 % CI	R	Bulk_ESS	Tail_ESS
Intercept	-0.82	0.5	-1.88	0.1	1.00	8014	9829
Generation length	0.33	0.22	-0.12	0.77	1.00	17,049	12,390
Scavenging propensity	0.07	0.17	-0.25	0.4	1.00	17,026	12,665
Body mass	1.03	0.23	0.58	1.5	1.00	14,060	12,252
Generation length: Scavenging propensity	0.38	0.18	0.05	0.73	1.00	21,478	12,382

“slow” end of the slow-fast continuum, which prioritize survival over reproduction and hence have a larger time budget, should explore more accurately the environment, and exhibit better performance in learning than those at the ‘fast’ extreme (Sol, 2015; Sol and Maspons, 2016). This pattern may be facilitated by larger neural structures in slow-lived species (Sol, 2009). Consistent with evidence from 385 land-bird species showing that taxa prioritizing future over current reproduction are more prone to consume novel foods (Sol et al., 2016), the higher scavenging propensity of slow-lived seabirds in our study supports the idea that foraging innovativeness is more prevalent at the slow end of the slow–fast continuum.

#### 4.2. Population-level consequences

Understanding the consequences of ecological traps at the population level is one of the most important requirements for managing this conflict. We provide evidence showing that slow-lived scavengers, such as albatrosses, have the highest probability of bycatch among seabirds, strongly suggesting more severe population-level effects of ecological traps for these species. These results are adjusted for body size and therefore should not simply be attributed to the higher bycatch rates of larger (and slower) species due to their greater competitive ability (Zhou et al., 2019; Zhou and Brothers, 2022) and much reduced maneuverability (Heswall et al., 2021). These findings are consistent with theoretical studies that show that life-history traits are an important determinant of population responses to ecological traps (Kokko and

Sutherland, 2001; Hale et al., 2015). These studies have shown that slow-lived species, which have a greater demographic sensitivity to mortality, should have higher long-term vulnerability and a greater likelihood of experiencing local extirpation from ecological traps, especially when these traps reduce survival (Kokko and Sutherland, 2001; Hale et al., 2015).

Slow-lived seabirds, such as petrels, shearwaters, and albatrosses, are particularly susceptible to population declines due to bycatch, which reduces survival rates both in juveniles and adults (Véran et al., 2007; Rolland et al., 2008, 2009, 2010; Tuck et al., 2015; Pardo et al., 2017). Recent research further identifies clutch size and generation time as key predictors of seabirds' extinction risk and vulnerability to anthropogenic threats, including bycatch (Richards et al., 2021, 2024). Our results align with these findings and suggest that ecological traps may be one of the main mechanisms driving the increased bycatch risk and extinction threat faced by slow-lived species (Richards et al., 2024). Our findings are also consistent with the evidence showing the influence of the slow–fast continuum on the demographic resilience of both animals and plants (Capdevila et al., 2022).

In contrast to the pattern observed in slow-lived scavengers, fast-lived counterparts exhibited the lowest probability of being threatened by bycatch. Previous studies on fast-lived scavengers, such as seagulls, have shown that anthropogenic food subsidies tend to boost population growth rates and reduce variability in demographic parameters (Oro et al., 2013). This suggests that the differences observed in our results may stem from the influence of the slow–fast continuum in shaping how trophic subsidies compensate for bycatch mortality. In fast-lived species—whose population growth is primarily driven by reproductive output (Saether and Bakke, 2000)—trophic subsidies are more likely to offset bycatch through increased reproductive success and/or recruitment (Genovart et al., 2017). While some compensatory effects have also been documented in slow-lived seabirds, the demographic benefits of subsidies in these species are often outweighed by the negative impacts of bycatch mortality (Rolland et al., 2009, 2010; Pardo et al., 2017).

#### 4.3. Limitations and future directions

Our scavenging propensity index is literature-derived and therefore sensitive to research effort. Uneven sampling—across taxa, space, fisheries and seasons—can bias the index: concentrated effort yields more records, whereas sparse effort depresses them. Several regions remain undersampled despite substantial discarding (in rates or total biomass; Gilman et al., 2020)—notably the Northwest Pacific, Western Central Pacific (Southeast Asia), the Indian Ocean, and the Eastern Central Atlantic (West Africa). Because species composition along the slow–fast continuum is not uniform, underrepresentation can bias the index differently by region: gaps in the Indian Ocean and Western Central Pacific may miss faster-paced assemblages (Richards et al., 2024), whereas our species accumulation curves indicate the largest overall shortfall in the Southern Hemisphere (see Fig. 1), where assemblages are slower-paced on average (Richards et al., 2024). Because these biases pull in opposing directions, their net effect on estimates and generalizability is a priori uncertain.

Within undersampled Southern Hemisphere countries—especially Chile, Peru, and Ecuador, which host large artisanal fleets (Arriaga and Martinez, 2002; Alfaro-Shigueto et al., 2010; Vega et al., 2018)—bias is likely driven primarily by the underrepresentation of small-scale/coastal fisheries (e.g., gillnets, purse seines). This can bias the index toward offshore fleets and surface-feeding, slow-lived taxa, while underdetecting interactions involving faster-lived divers (e.g., cormorants, penguins) (Žydelis et al., 2009; Crawford et al., 2017). Nevertheless, slow-lived species (e.g., petrels, shearwaters) also frequently interact with small-scale fleets (Simeone et al., 2021), so expanding coverage of these gears is unlikely to overturn our main findings. We partially account for these biases by including foraging guild and

taxonomic genus as varying intercepts in the trap-selection model. A related unmodeled factor is explicit spatial overlap between species' distributions and fishing effort (Clay et al., 2019): greater overlap—and thus higher encounter probability—could contribute to the higher observed scavenging propensity of slow-lived species; however, we expect much of this variation to be partially absorbed by covariates such as geographic extent, habitat breadth, and migratory status.

Another limitation concerns breeding-season and near-colony biases, as much of the diet evidence comes from colony-based sampling during reproduction, when seabirds act as central-place foragers, restricting ranges toward colony-proximate waters. While these biases are partly mitigated because most observations in our review are habitat-based (~79 %), we acknowledge possible underdetection of offshore and non-breeding interactions; expanding integrated datasets that link individual tracking with vessel activity and observer/electronic-monitoring records should be a priority to refine species-level estimates of scavenging propensity. Such efforts would also help reduce underreporting in small-scale/artisanal fisheries, improving coverage of coastal interactions and faster-lived taxa.

Although these limitations increase uncertainty about the causal mechanisms underlying seabird scavenging, the strong correlation between generation length and scavenging propensity—and their interactive role in shaping bycatch risk—provides a robust foundation for improving fisheries management within an ecological-trap framework. Importantly, any bias or underreporting of fast-lived species in our index would likely inflate, not diminish, the conservation relevance of this issue: underdetected interactions in small-scale/coastal contexts imply that true exposure and trap likelihood may be higher than our estimates suggest.

Future work should rigorously test for ecological traps by: (1) demonstrating preference for vessel-associated habitats (or equal preference across habitats); (2) quantifying fitness differences among habitats; and (3) showing reduced fitness in the (equally) preferred habitat (Robertson and Hutto, 2006). In addition, research should evaluate how among-individual differences (Barbraud et al., 2013; Tuck et al., 2015; Weimerskirch et al., 2023)—age, sex, personality, energetic state, experience, spatial memory, and social learning—shape both the emergence of traps and their population-level consequences. Individual-based models (Grimm and Railsback, 2005; Railsback and Grimm, 2019) provide a promising framework for propagating state-dependent behavior and individual heterogeneity (Le Scornec et al., 2025) into decision-relevant demographic predictions. Such models can be parameterized with data on seabird movement and behavior (e.g., [seabirdtracking.org](#); Carneiro et al., 2024), personality; (Weimerskirch et al., 2023), metabolic requirements (Sibly et al., 2013; Dunn et al., 2018) and demographic and fisheries information—such as bycatch rates and discard-derived energy—collected through onboard observer programs, yielding decision-relevant outputs including measurable objectives and fishery-specific risk thresholds (see Management Implications).

#### 4.4. Management implications

The need for ecosystem-based fisheries management (EBFM) has emerged from the recognition of the major unintended consequences that fisheries can have on ecosystems, including evolutionary changes in populations, cascading effects, and bycatch (Pikitch et al., 2004). Our findings suggest that ecological traps offer a valuable conceptual and modeling framework to enhance EBFM by clarifying how trophic subsidies from fisheries can increase seabird extinction risk. This perspective may help raise awareness among stakeholders and inform regulatory efforts to improve fisheries management.

From a top-down perspective, ecological-trap theory and its mechanistic modeling framework could strengthen both current and future management initiatives—at the national level (e.g., National Plans of Action; Good et al., 2020) and in areas beyond national jurisdiction

overseen by Regional Fisheries Management Organizations (RFMOs), where the effectiveness of legal and regulatory tools to manage bycatch remains uncertain (Beal et al., 2021; Haas et al., 2021; Baker et al., 2024). In this context, mechanistic models of ecological traps (Sánchez-Clavijo et al., 2016; Simon and Fortin, 2020) could enhance population risk assessments and the evaluation of alternative management scenarios by setting measurable targets and fishery-specific reference points (e.g., BPUE, discard rates/biomass). In doing so, they could identify thresholds (tipping points) at which fishery-derived subsidies shift from conferring net demographic benefits to generating negative synergistic effects when combined with elevated bycatch mortality—via stronger habitat preference and increased exposure to lethal conditions. By pinpointing these tipping points, the models could inform the selection and implementation of bycatch-mitigation and discard best practices recommended by the Agreement on the Conservation of Albatrosses and Petrels (ACAP, 2024a, 2024b, 2024c). From a bottom-up perspective, the ecological trap framework could also improve communication with stakeholders and foster compliance with onboard good practices and mitigation measures (Melvin et al., 2023).

## 5. Conclusion

Bycatch is one of the leading causes of vertebrate loss in marine ecosystems and represents the most critical threat to seabird conservation at sea. For seabirds, bycatch risk is largely driven by their attraction to fishing vessels offering trophic subsidies. Yet, the ecological trap mechanism has rarely been used to frame this issue at a global scale. In this article, we showed a clear preference–performance mismatch: slow-lived seabirds—particularly scavengers such as albatrosses—are more likely to exploit fishery-derived subsidies and are disproportionately threatened by bycatch. Building on recent evidence highlighting ecological traps as a relevant phenomenon in marine systems, we propose that ecological traps offer a powerful framework to understand and predict seabird–fishery interactions and to advance ecosystem-based fisheries management. This approach is broadly applicable beyond seabirds, extending to other vertebrates—including marine mammals, sea turtles, and elasmobranchs (sharks and rays)—where analogous trap dynamics may arise. Such a framework can clarify the causes and consequences of vertebrate–fishery interactions, guide more effective management through mechanistic models, and reinforce both the implementation of and compliance with mitigation measures.

## CRediT authorship contribution statement

**Cristóbal Anguita:** Visualization, Methodology, Investigation, Formal analysis, Data curation, Writing – review & editing, Writing – original draft, Conceptualization. **Alejandro Simeone:** Conceptualization, Writing – review & editing, Supervision. **Cristián F. Estades:** Supervision, Conceptualization, Writing – review & editing.

## Declaration of competing interest

The authors declare no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111674>.

## Data availability

Data will be made available on request.

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