

**Fitness trade-offs from fishery-derived subsidies and  
bycatch mortality: modeling a compensatory ecological  
trap in seabirds**

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## DEDICATION

To Manuela Mege Quesney (*alias* Rebeka), whose unwavering support, patience, and love sustained me throughout this long and winding path.

*"if we are very careful and try very hard, we might not completely mislead ourselves"*

Richard McElreath

## BIOGRAPHICAL SUMMARY

I began my studies in marine biology, and in 2012 I met Alejandro Simeone, whose guidance would become central to my academic development. Alejandro introduced me to the world of seabirds and invited me to participate—between 2012 and 2019—in a systematic monthly monitoring program conducted in Valparaíso Bay, central Chile, aboard the *Fresia del Carmen*. During those years, I learned to identify and count seabirds at sea. I was fascinated by large feeding frenzies over zooplankton swarms and schools of pelagic fish—the most striking of which occurred in March 2015, when hundreds of dusky dolphins herded fish toward the surface while boobies, shearwaters, and pelicans plunged and dove to catch them, and a speckled smooth-hound shark circled the edges of the school. In 2013, after catching Alejandro's interest with some preliminary home-range analyses—following my first steps with R—he invited me to collaborate on my first scientific publication, focused on the abundance patterns of skuas and jaegers in Valparaíso Bay, which was later published in 2014 in the *Revista de Historia Natural de Chile*. Since then, I developed a strong interest in community ecology and completed my master's thesis—under Alejandro's guidance—on the dynamics of multi-species foraging associations in seabirds. Over time, my focus broadened to conservation issues, particularly the interaction between seabirds and fisheries. In parallel, I became increasingly interested in computation and modeling, which enabled me to collaborate with a range of researchers studying organisms ranging from bacteria and archaea to whales. In 2019, Alejandro encouraged me to contact Cristián Estades to pursue doctoral studies, with the aim of addressing seabird–fishery interactions from a population-level perspective. Fortunately, I followed his advice, and Cristián agreed to supervise me jointly with Alejandro. Since then, I have spent five years studying ecological traps between seabirds and fisheries—a process that has shaped my growth both as a scientist and as a person. I have refined my ability to formulate and investigate ecological questions in depth, with a focus on underlying mechanisms, using simulation modeling as a primary tool—an approach I inherited from Cristián. This perspective has expanded my research horizons and deepened my engagement with ecological theory.



## ACKNOWLEDGMENTS

I would like to thank my advisors for all their support and the time they devoted to the development of this thesis. I am especially grateful to Cristián, who spent many hours (perhaps too many) discussing the design and construction of the two individual-based models presented here, which I eventually managed to transcribe into nearly 160 pages of code (probably not in the most efficient way, but they work! see the appendix). It was a long and iterative process, during which he helped me avoid falling into despair and frustration through several divergences and failed iterations. I also appreciate his endless *subsidy* of ideas, which added substantial depth to the content of the thesis. I am also thankful to the *Laboratorio de Ecología de Vida Silvestre* (LEVS) and all its members for providing such a pleasant and supportive work environment. Finally, I want to thank Cristián G. Suazo for introducing me to the fascinating world of albatrosses on Gonzalo Island in the Diego Ramírez Archipelago.

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## ABSTRACT

Human-driven environmental change is occurring globally and at a pace that exceeds the adaptive capacity of most organisms, leading to the extinction of entire clades and reshaping the tree of life. Life-history strategies—species' schedules of development, reproduction, and survival—are key determinants of demographic responses to these changes, including immediate maladaptive behaviors such as ecological traps. Over the past five decades, ecological traps have gained prominence through theoretical advances and accumulating empirical evidence. However, most models have overlooked traps involving negative covariation among fitness components, limiting our ability to identify and manage them. This thesis addresses this gap by examining traps driven by fitness trade-offs, where increased benefits in one or more components (e.g., foraging success or reproduction) lead organisms to select habitats despite concurrent costs in another (e.g., survival), ultimately reducing lifetime reproductive success. Specifically, this work focuses on seabird–fishery interactions to assess how the interplay among bycatch mortality, fishery-derived trophic subsidies, and species' positions along the slow–fast life-history continuum contributes to the emergence and demographic consequences of ecological traps. Chapter 1 presents comparative evidence from 341 seabird species, showing that slow-lived species—such as albatrosses—are more likely to scavenge and are disproportionately threatened by bycatch. This highlights their susceptibility to compensatory ecological traps, where fishery-derived trophic subsidies fail to offset increased juvenile and adult mortality. Chapter 2 employs a spatially explicit individual-based model to evaluate how species with contrasting life histories respond

to compensatory traps across varying levels of bycatch and trophic subsidies. Results reveal nonlinear, species-specific, threshold-dependent dynamics: subsidies can buffer populations at low bycatch levels but exacerbate declines once mortality surpasses a critical threshold, reinforcing maladaptive behaviors. These findings suggest that compensatory traps may intensify the selective filtering of life-history strategies more strongly than previously anticipated. Chapter 3 applies this framework to evaluate whether interactions between Black-browed Albatrosses and demersal trawl fisheries in southern Chile give rise to ecological traps under contrasting bycatch and discard regimes (before and after 2019–2020 regulations), and assesses the potential for demographic compensation. Under pre-regulation conditions, high bycatch and discards ( $4,000 \text{ birds} \cdot \text{yr}^{-1}$  and  $11,000 \text{ t} \cdot \text{yr}^{-1}$ ) led to population decline, especially when cryptic mortality was included. In contrast, post-regulation scenarios ( $500 \text{ birds} \cdot \text{yr}^{-1}$  and  $3,000 \text{ t} \cdot \text{yr}^{-1}$ ) supported population persistence, highlighting the effectiveness of recent mitigation and regulatory measures. Overall, the findings confirm that, for slow-lived species, demographic trade-offs between fishery-derived subsidies and bycatch mortality resolve unfavorably under weak management, highlighting the need for strong and sustained mitigation policies. Together, the findings of this thesis advance our understanding of ecological traps by demonstrating that fitness trade-offs can give rise to nonlinear, threshold-dependent demographic responses in species exposed to human-altered environments. By introducing a framework previously overlooked in seabird–fishery systems, this work offers a novel basis for identifying sustainability thresholds, guiding discard and bycatch management, and informing ecosystem-based

fisheries policies aimed at reducing maladaptive behavior and strengthening the resilience of long-lived marine predators.

## RESUMEN

El cambio ambiental impulsado por el ser humano está ocurriendo globalmente y a un ritmo que excede la capacidad adaptativa de la mayoría de los organismos, llevando a la extinción de clados enteros y reconfigurando el árbol de la vida. Las estrategias de historia de vida —es decir, los cronogramas de desarrollo, reproducción y supervivencia de las especies— son determinantes clave de las respuestas demográficas frente a estos cambios, incluyendo conductas mal adaptativas inmediatas como las trampas ecológicas. En las últimas cinco décadas, las trampas ecológicas han cobrado relevancia gracias a avances teóricos y a una creciente evidencia empírica. Sin embargo, la mayoría de los modelos ha pasado por alto aquellas trampas que implican covariación negativa entre componentes de la adecuación biológica, lo que ha limitado nuestra capacidad para identificarlas y gestionarlas. Esta tesis aborda esa brecha examinando trampas impulsadas por compensaciones entre componentes de la adecuación, en las que beneficios en uno o más componentes (por ejemplo, éxito de forrajeo o reproducción) inducen a los organismos a seleccionar hábitats a pesar de costos concurrentes en otros (por ejemplo, la supervivencia), reduciendo, en última instancia, el éxito reproductivo a lo largo de la vida. En particular, este trabajo se centra en las interacciones entre aves marinas y pesquerías para evaluar cómo la interacción entre la mortalidad por captura incidental, los subsidios tróficos derivados de la pesca, y la posición de las especies a lo largo del continuo de historia de vida lento-rápido contribuye a la aparición y las consecuencias demográficas de las trampas ecológicas. El Capítulo 1 presenta evidencia comparativa de 341 especies de aves marinas, mostrando que las especies de vida lenta

—como los albatros— tienen mayor probabilidad de carroñear y están desproporcionadamente amenazadas por la captura incidental, lo que resalta su susceptibilidad a trampas ecológicas compensatorias, en las cuales los subsidios tróficos no logran compensar la mortalidad de juveniles y adultos. El Capítulo 2 utiliza un modelo individual basado en individuos y espacialmente explícito para evaluar cómo especies con historias de vida contrastantes responden a trampas compensatorias bajo distintos niveles de captura incidental y subsidios. Los resultados revelan dinámicas no lineales, dependientes de umbrales y específicas por especie: los subsidios pueden amortiguar las poblaciones cuando la captura incidental es baja, pero exacerbar los declives una vez que la mortalidad supera un umbral crítico, reforzando comportamientos mal adaptativos. Estos hallazgos sugieren que las trampas compensatorias podrían intensificar el filtro selectivo de las estrategias de historia de vida más fuertemente de lo que se había anticipado. El Capítulo 3 aplica este marco para evaluar si las interacciones entre albatros de ceja negra y pesquerías de arrastre demersal en el sur de Chile dan origen a trampas ecológicas bajo distintos regímenes de captura incidental y descarte (antes y después de las regulaciones de 2019–2020), y analiza el potencial de compensación demográfica. Bajo condiciones previas a la regulación, con altos niveles de captura incidental y descarte ( $4.000 \text{ aves}\cdot\text{año}^{-1}$  y  $11.000 \text{ t}\cdot\text{año}^{-1}$ ), se observó un declive poblacional, especialmente al incluir mortalidad críptica. En contraste, los escenarios posteriores a la regulación ( $500 \text{ aves}\cdot\text{año}^{-1}$  y  $3.000 \text{ t}\cdot\text{año}^{-1}$ ) permitieron la persistencia poblacional, destacando la efectividad de las medidas regulatorias y de mitigación recientes. En conjunto, los resultados confirman que, para especies de vida

lenta, las compensaciones demográficas entre subsidios tróficos y mortalidad por captura incidental se resuelven de manera desfavorable bajo una gestión inadecuada, subrayando la necesidad de políticas de mitigación fuertes y sostenidas. En su conjunto, esta tesis amplía nuestra comprensión de las trampas ecológicas al demostrar que las compensaciones entre los componentes de la adecuación biológica pueden generar respuestas demográficas no lineales y dependientes de umbrales en especies expuestas a ambientes alterados por el ser humano. Al introducir un marco previamente pasado por alto en los sistemas aves marinas–pesquerías, este trabajo ofrece una base novedosa para identificar umbrales de sostenibilidad, guiar la gestión de descartes y captura incidental, e informar políticas pesqueras basadas en el ecosistema orientadas a reducir comportamientos mal adaptativos y fortalecer la resiliencia de depredadores marinos de vida lenta.

## GENERAL INTRODUCTION

A large proportion of Earth's organisms inhabit ecosystems that have been modified by humans, primarily due to habitat loss, pollution, the introduction of exotic species, overexploitation, changes in the availability of predictable resources, 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 in many of these cases is that ecosystem changes have occurred at a much faster pace than the rate at which organisms evolved—a disparity known as HIREC (human-induced rapid environmental change) (Sih et al. 2011).

This temporal mismatch limits the development of adaptive behavioral responses and, in most cases, has negatively impacted species, reducing their populations and even driving some to extinction (Dirzo et al. 2014). These impacts have also occurred at broader taxonomic levels, including the extinction of two orders, ten families, and 73 genera of tetrapods (mammals, birds, reptiles, and amphibians) since the year 1500 (Ceballos and Ehrlich 2023). The current extinction rate is estimated to be 35 times higher than the background rate that prevailed over the past several million years (Ceballos and Ehrlich 2023). Despite this negative trend, some species and taxonomic groups have managed to thrive (Oro et al. 2013)—expanding their populations and ranges (Battey 2019) and, in some cases, rapidly adapting to HIREC (Reid et al. 2016, Alexandre et al. 2025). Understanding why some species are negatively affected while others thrive is essential for managing the profound changes that humans are imposing on the tree of life.

A key factor shaping species' responses to HIREC is their life-history strategy—that is, their schedules of development, reproduction and survival. Most organisms, if not all, are constrained by limited resources such as energy and time, which must be allocated across activities in a way that maximizes fitness. As a result, they face trade-offs in how these resources are distributed, such that greater investment in one function necessarily comes at the expense of another (Stearns 1992, Roff 2002). This zero-sum principle is a cornerstone of life-history theory and predicts that trade-offs should be universal (Stearns 1992). In the absence of such trade-offs, a "Darwinian demon"—a hypothetical organism capable of surviving and reproducing indefinitely—would emerge, violating the biological and ecological constraints that regulate natural populations.

In most species, life-history strategies are distributed along a principal axis defined by a trade-off between investment in development and reproduction versus investment in survival—known as the slow–fast continuum (Stearns 1983). At the fast end, species develop rapidly, reproduce prolifically, and live short lives; at the slow end, species develop slowly, have low reproductive potential, and live long lives (Gaillard et al. 2016). The slow–fast continuum is widely considered the dominant axis (though not the only one) structuring life-history variation (Stott et al. 2024). Although support varies depending on the traits analyzed and the methods used, this axis explains between 50% and 70% of life-history variation across broad taxonomic groups of vertebrates and invertebrates, after controlling for body size and phylogeny (Healy et al. 2019, Bakewell et al. 2020, Capdevila et al. 2020). Similar patterns have been found within diverse

taxonomic groups, including mammals (Gaillard et al. 1989, Oli and Dobson 2003), birds (Gaillard et al. 1989, Sibly and Brown 2007), insects (Bakewell et al. 2020), fish (Rochet et al. 2000), and plants (Salguero-Gómez et al. 2016, Rüger et al. 2018).

Species' positions along the slow–fast continuum profoundly influence their demographic processes and their ecological and evolutionary responses to HIREC. In general, fast-living species exhibit greater population growth potential (Saether and Bakke 2000), stronger density dependence (Herrando-Pérez et al. 2012), greater demographic stochasticity (Sæther et al. 2004), and a higher propensity for nonlinear or even chaotic population dynamics (Clark and Luis 2020, Munch et al. 2022, Rogers et al. 2022). These species are more sensitive to environmental variability and different components of climate change (Morris et al. 2008, Koons et al. 2009, Iles et al. 2019, Postuma et al. 2020, Compagnoni et al. 2021), and have the greatest potential to use demographic lability as an adaptive response to environmental fluctuations (Le Coeur et al. 2022). In contrast, slow-living species have evolved mechanisms to buffer environmental variability, stabilizing demographic rates under fluctuating conditions (Morris et al. 2008, Le Coeur et al. 2022). While this strategy reduces sensitivity to environmental variability—and potentially to climate change—it also limits their ability to respond to acute disturbances, resulting in lower compensation, resistance, and recovery capacity, as recently demonstrated for 162 populations of 69 animal species and 748 populations of 232 plant species (Capdevila et al. 2022). Consequently, organisms with slower life histories are generally at greater risk of extinction than faster

species, including plants, mammals, birds, reptiles, amphibians, and freshwater fish (Cooke et al. 2019, Carmona et al. 2021, Richards et al. 2021, 2024).

These findings underscore the importance of understanding the specific mechanisms through which HIREC can influence species' population dynamics, including its potential to impose life-history filters. In this regard, considering the most immediate responses of organisms—namely, their behavior—may play a crucial role in understanding, predicting, and mitigating the population-level consequences of HIREC and its effects on the tree of life. In this context, ecological traps—originally conceptualized by Dwernychuk and Boag (1972) and later developed by Gates and Gysel (1978)—offer a robust framework for examining maladaptive behavioral responses to anthropogenic environmental change.

An ecological trap occurs when an organism, through various mechanisms, finds a habitat equally or more attractive than other available options, despite experiencing reduced fitness having selected it (Schlaepfer et al. 2002, Robertson et al. 2013). Following, Robertson et al. (2013), three general mechanisms have been proposed through which HIRECs can generate ecological traps—by altering habitat quality, habitat preference, or both. 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 (Fletcher et al. 2012, Hale et al. 2015b). In addition, the impact of ecological traps tends to increase when they occupy a larger proportion of the available habitat (Delibes et al. 2001, Hale et al. 2015b) and when populations are small (through behaviorally mediated Allee effect) (Kokko and Sutherland 2001).

Ecological traps have been documented in terrestrial, urban, and, more recently, marine environments, and are commonly reported in invertebrates, birds, mammals, and reptiles (Robertson et al. 2013, Hale and Swearer 2016, Swearer et al. 2021). Theoretical models predict that slow-living species are more vulnerable to local extirpation due to traps (Kokko and Sutherland 2001, Hale et al. 2015b). These models typically assume that organisms prefer trapped habitats despite experiencing reduced survival and/or reproduction (Delibes et al. 2001, Kokko and Sutherland 2001, Donovan and Thompson 2001, Kristan et al. 2003, Fletcher et al. 2012, Hale et al. 2015b). However, in some cases, habitat preference may be driven by immediate benefits, such as increased foraging success. If sustained over time, these benefits can enhance reproductive traits, including greater breeder recruitment and breeding success. Yet, such scenarios may simultaneously entail a reduction in other fitness components, particularly survival, ultimately lowering individuals' lifetime reproductive success. When traps involve demographic trade-offs between key fitness components, their effects may deviate from current model predictions, potentially leading to nonlinear population responses over time and across the slow–fast life-history continuum, with unexpected consequences for population dynamics and long-term viability.

A key driver of such compensatory trap may by human-derived trophic subsidies, which offer abundant and predictable food resources that can enhance foraging success and reproduction (Oro et al. 2013). However, increased habitat preference can also elevate mortality risks from pollutants, predators, competition, parasitism, hunting, or accidental deaths, as has been observed in wide range of taxa, including birds, mammals, reptiles, and elasmobranchs (Morris 2005, Semeniuk and Rothley 2008, Rodewald et al. 2011, Lewison et al. 2014, Becker et al. 2015, Lamb et al. 2017, Sigaud et al. 2017, Tella et al. 2020, Simon and Fortin 2020, Singh et al. 2024).

A prominent case of these traps may arise from interactions between seabirds and fisheries. Fisheries are the most widespread industrial activity in marine ecosystems (Paolo et al. 2024) and supply approximately 8% of the world's protein (Boyd et al. 2022). Due to regulatory measures such as quota and size limits, a portion of catch (~12%) is discarded at sea (~7–16 million tons per year), generating a spatially and temporally predictable trophic subsidy (Gilman et al. 2020). Over half of all seabird species, across all families, consume these discards, which have shown positive effects at both individual and population levels (Bugoni et al. 2010, Bicknell et al. 2013, Oro et al. 2013, Real et al. 2017). These subsidies can improve foraging success and enhance reproductive traits such as earlier laying dates, larger clutch sizes, increased chick provisioning, and higher breeding success (Oro et al. 2013).

However, such subsidies represent a double-edged sword for seabirds. While they increase food availability and can provide individual benefits, they also intensify attraction to fishing vessels, thereby elevating the risk of incidental capture (bycatch).

Bycatch was first identified as a major threat to seabirds in the 1970s (Tull et al. 1972) and it is currently recognized as the leading cause of population decline and the second most prevalent threat by number of species affected—surpassed only by invasive species on islands (Dias et al. 2019). Conversely, fishery-derived food, primarily in the form of discards (Garthe et al. 1996, Votier et al. 2004, Bicknell et al. 2013, Sherley et al. 2019) can partially compensate for bycatch mortality by increasing recruitment in impacted populations (Rolland et al. 2008, 2009b, 2010, Barbraud et al. 2008, Genovart et al. 2016, Pardo et al. 2017). Although these studies provide evidence for compensatory mechanisms, they are limited in taxonomic scope, making it difficult to generalize their demographic effects across the slow–fast continuum. To fully understand these compensatory effects, it is essential to consider how they vary across species with different life-history traits.

Seabirds display remarkable variation in life-history traits across the slow–fast spectrum (Weimerskirch 2002, Dobson and Jouventin 2010, Sibly et al. 2012). At the fast end, for example, cormorants have an average generation time of 9 years and lay three eggs annually, whereas at the slow end, albatrosses have an average generation time of 27 years and produce a single egg every one or two years, as seen in the Wandering albatross (*Diomedea exulans*) and the Grey-headed albatross (*Thalassarche chrysostoma*) (Weimerskirch 2002, Jouventin and Dobson 2002, Sibly et al. 2012, Richards et al. 2021). Recent studies suggest that life-history traits are good predictors of vulnerability to anthropogenic threats—including bycatch—with slow-living species being the most susceptible (Richards et al. 2021, 2024). Moreover, the compensatory

effect of discards in offsetting bycatch is expected to be greater in fast-living species, as their population growth is more demographically sensitive to changes in reproductive parameters (Heppell et al. 2000, Saether and Bakke 2000). In contrast, slow-living species—whose population dynamics are more strongly influenced by survival—may experience weaker compensatory effects (Heppell et al. 2000, Saether and Bakke 2000). Yet, the extent to which the slow–fast continuum modulates interactions between trophic subsidies and bycatch remains unclear (Genovart et al. 2017, Votier et al. 2023). To date, neither conceptual frameworks nor formal ecological trap models have been applied to predict these effects in seabird populations representing a key opportunity to improve conservation and fisheries management strategies.

Albatrosses are long-lived seabirds with low reproductive output (Dobson and Jouventin 2010) and wide geographic ranges (Clay et al. 2019, Beal et al. 2021), making them particularly vulnerable to fishery-induced ecological traps (Dias et al. 2019). Among them, the Black-browed albatross (*Thalassarche melanophrys*) is one of the seabird species that most frequently interacts with global fisheries (Clay et al. 2019, Carneiro et al. 2020). In southern Chile—where approximately 20% of the global Black-browed Albatross population resides—these interactions are particularly intense due to the presence of the country’s largest trawl and longline fisheries (Adasme et al. 2019). Previous studies have shown that both trawl and longline fleets contributed to significant population declines in Black-browed albatross between 1993 and 2005 due to high levels of bycatch (Robertson et al. 2014). The implementation of mitigation measures in longline fisheries in 2005 led to partial recovery in the Diego Ramírez and Ildefonso

colonies. However, more recent estimates of bycatch from trawl fleets—particularly between 2013 and 2019—have revealed alarmingly high levels, far exceeding those reported in earlier assessments (Adasme et al. 2019). This renewed pressure, combined with consistently high discard rates from trawl vessels, poses a serious threat to Black-browed albatross conservation. These discards—especially during the breeding season—have been identified as a key food source for Black-browed albatross in Diego Ramírez (Arata and Xavier 2003), potentially enhancing recruitment, as has been documented in other populations such as those in the Kerguelen and South Georgia Islands (Rolland et al. 2008, 2009b, 2010, Pardo et al. 2017). However, this trophic subsidy comes at the cost of increased exposure to fishing vessels and, consequently, a higher risk of bycatch.

In light of these risks, a series of regulatory measures were implemented between 2019 and 2020 to reduce and control discards and seabird bycatch in Chilean trawl fisheries. These measures include the mandatory use of seabird bycatch mitigation devices, the enforcement of best fishing practices, and the installation of onboard image recording systems to improve monitoring and compliance (Resolutions No. 2110/2014, 2941/2019, and 2569/2021, see Cocas et al. 2024). Collectively, these efforts have led to a substantial reduction in both discards and bycatch in recent years (Cocas et al. 2024). Nevertheless, the extent to which these regulatory efforts have translated into demographic benefits for Black-browed albatross populations remains unclear, as no formal assessments have yet evaluated their population-level consequences.

Given the increasing human impact on ecosystems, ecological traps are likely to become more prevalent in the future. Expanding their theoretical framework and

improving our understanding of traps that produce negative covariation among fitness components—whose outcomes are often difficult to predict—will therefore be essential. In this context, analyzing the interaction between trophic subsidies, bycatch mortality, and seabird life-history traits represents an important first step toward developing mechanistic, predictive models to guide effective conservation and management. The Black-browed Albatross in Chile and its interaction with demersal trawl fisheries offers an ideal model system for evaluating compensatory ecological traps in seabirds, as it integrates all key components and processes involved. Insights gained from this system may inform research and management across a broader range of species, taxa, and fisheries. Strengthening management strategies based on this evidence will be critical not only for mitigating the impacts of fisheries on seabirds, but also for advancing ecosystem-based fisheries management.

## HYPOTHESIS

The population dynamics of seabirds interacting with fisheries are shaped by a demographic trade-off between increased mortality from bycatch and increased recruitment from fishery-derived trophic subsidies. The outcome of this trade-off is modulated by the interaction between species' life-history strategies and fisheries management.

## OBJECTIVES

General objective:

To analyze how the interactions among bycatch mortality, fishery-derived trophic subsidies, and species' positions along the slow–fast life-history continuum contributes to the emergence and demographic consequences of ecological traps in seabird populations exposed to fisheries.

Specific objectives:

1. 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.
2. To evaluate population-level responses to compensatory ecological traps in seabird species with different life-history strategies along the slow–fast continuum (i.e., slow, intermediate, and fast).

3. To assess whether interactions between Black-browed Albatrosses and demersal trawl fisheries in southern Chile give rise to ecological traps under contrasting bycatch and discard regimes—specifically before and after the implementation of fishery regulations—and whether trophic subsidies can compensate for bycatch-induced demographic costs.

## THESIS STRUCTURE

This thesis is composed of three chapters, each corresponding to one of the specific objectives. Chapter One examines how scavenging behavior influences seabird vulnerability to bycatch and explores the role of the slow–fast life-history continuum in modulating the occurrence and severity of ecological traps with fisheries. Chapter Two presents a theoretical, spatially explicit, individual-based simulation model designed to evaluate how species with different life histories (slow, intermediate, and fast) respond to a compensatory ecological trap, in which individuals preferentially select areas with elevated foraging success due to fishery subsidies. While this behavior can increase breeder and fledgling recruitment, it also elevates mortality risk from bycatch. Chapter Three applies this framework to a case study involving Black-browed Albatrosses interacting with industrial demersal trawl fisheries in southern Chile. It evaluates whether contrasting bycatch and discard regimes—specifically before and after the implementation of fishery regulations—generate conditions consistent with ecological traps and assesses the potential for discard-driven demographic compensation to buffer population-level impacts of bycatch. The thesis ends with a synthesis of findings across chapters, highlighting key insights and future research directions.

CHAPTER 1. The emergence of ecological traps in marine ecosystems: the case of seabirds and fisheries

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## **1. Abstract**

The unprecedented rate at which humans are altering ecosystems increasingly causes animals to select poor-quality habitats due to misleading cues. This phenomenon, known as an “ecological trap,” decreases population resilience and raises extinction risk. Nonetheless, the ecological trap framework has received little attention in marine environments, particularly in the context of seabird-fishery interactions. Seabird bycatch primarily occurs because seabirds are attracted to fishing vessels to feed on trophic subsidies, such as bait, discards, and catches. However, the concept of ecological traps has not been widely applied to frame this issue globally. In this study, we aimed to analyze the interaction between seabirds' scavenging behavior and bycatch in fisheries, as well as the effect of the slow-fast life history continuum on seabird vulnerability to ecological traps. Through a systematic literature review and Bayesian multilevel models accounting for phylogenetic relatedness (341 species), we demonstrate a clear preference–performance mismatch: slow-lived seabirds, such as albatrosses, are more likely to exploit trophic subsidies from fisheries and are consequently more threatened by bycatch (IUCN). 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 fishery management by highlighting the severity of these impacts, enhancing the effectiveness of management and conservation strategies, and supporting the enforcement of mitigation measures.

## 2. 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 HIREC (“human-induced rapid environmental change”, Sih et al. 2011), hindering the development of adaptive behavioral responses. One of the consequences of HIREC is the appearance of ecological traps.

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). According to Robertson et al. (2013), three general mechanisms have been proposed through which HIRECs can generate ecological traps—by altering habitat quality, habitat preference, or both. 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 drivers and assess the vulnerability of the affected 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 select habitats, have a simple sensory system, or high mobility have been identified as more vulnerable to falling into ecological 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 and Swearer 2016). Traps that greatly reduce survival are likely to have larger impacts at the population level on that species at the slow end of the continuum, as such species are characterized by deferred sexual 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; Swearer et al., 2021; Teske 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, 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 of material per year (Gilman et al., 2020), potentially sustaining large populations of scavenging seabirds worldwide (Bicknell et al., 2013; Garthe et al., 1996; Sherley et al., 2019; Votier et al., 2004). However, these subsidies represent a double-edged sword. 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 (Favero et al., 2011; González-Zevallos and Yorio, 2006; Sullivan et al., 2006; Watkins et al., 2008; 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., 2024, 2021). 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 clear evidence that fishery-derived food subsidies elevate bycatch risk (Favero et al., 2011; González-Zevallos and Yorio, 2006; Sullivan et al., 2006; Watkins et al., 2008; 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, scavenging propensity should increase in slow-lived seabirds because these species prioritize survival over reproduction and, therefore, have more time available to explore and take advantage of new ecological opportunities (Sol et al. 2016). Second, under the "time-limited disperser model" (Ward 1987), scavenging propensity should be higher in fast-lived seabirds because these species prioritize current reproduction, leaving less time for searching which increases 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 generated an index of seabirds' use of trophic subsidies from fisheries (habitat and diet), referred to as "scavenging propensity", through a systematic review of the literature. We used the IUCN's Threats Classification Scheme (Salafsky et al. 2008) as an indicator of population-level consequences of bycatch. For both response variables, we compiled a global dataset for all 341 birds considered "seabirds" and used Bayesian multilevel models, integrating phylogenetic

relatedness, to infer the influence of the slow-fast continuum of life history on the occurrence of ecological traps on seabirds.

### **3. Methods**

#### **3.1. Systematic review protocol**

We generated an index of scavenging propensity using a systematic review protocol based on available literature as of July 2022. Through the ISI Web of Science Core Collection, and using relevant keywords (including: seabird\* OR penguin\* OR albatross\* OR petrel\* OR shearwater\* OR shag\* OR cormorant\* OR boobie\* OR gannet\* OR auk\* OR puffin\* OR skua\* OR gull OR gulls OR tern\* OR prion\* OR fulmar\* OR tropicbird\* OR frigatebird\* OR pelican\* AND fisher\* AND discard\* OR offal AND forag\* OR prefer\* OR attract\* OR feed\* OR diet), we developed a database with information extracted from published studies on seabird-fishery interactions. To be included in our study, an article had to meet the following criteria: (1) report original data (i.e., reviews were not included) on seabirds' use (habitat and diet) of trophic subsidies from fisheries, and (2) provide quantitative estimates at the species level of habitat use or diet related to fisheries. We defined an observation as one where habitat or diet use was studied at the species level. "Habitat use" included studies involving counts of scavenging birds during fishing operations (e.g., birds attending or interacting with vessels and/or consuming discards) and discard consumption experiments. Diet studies, typically conducted in colonies, included analyses of stomach samples, fatty acids, DNA, and isotope signatures.

Given the diversity of the response variables and varied reporting standards (e.g., absolute numbers, proportions, rates), we used a “vote counting” approach to quantitatively summarize the data across disparate studies (Koricheva and Gurevitch 2013). For each study, we recorded the species that used trophic subsidies from fisheries, the type of resource used (habitat, diet, or consumption experiments), the type of fishery involved, and the geographic location of the study. From the observation-level matrix, we generated a species-level matrix ( $n = 341$  species) that included the total number of observations per species, considering habitat and diet together (“scavenging propensity,” range = 0–50 observations).

### **3.2. Traits data and bycatch threat**

We considered seabirds to be species for which a substantial proportion of the population relies on the marine environment for at least part of the year (excluding marine ducks) (Croxall et al. 2012). Accordingly, 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. We used generation length (the mean age in years at which a cohort of individuals produce 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 ([datazone.birdlife.org](http://datazone.birdlife.org)). 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 et al. (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).

### **3.3. 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 2,000 trees for 329 seabird species and obtained an optimal consensus tree using the 50% majority-rule method (Holder et al., 2008), with the `consensus.edges` function from the `ape` package in R (Paradis and Schliep 2019). Polytomies were resolved using the function `multi2di` from `ape` package. The remaining twelve species that were not found on the platform were incorporated at a random position within their genus in the phylogeny, by using the `add.species.to.genus` function from the `ape` package in R. Simulation studies have shown that comparative regression models are robust to tree misspecifications in

both topology and branch lengths, especially if the misspecifications involves 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.

### **3.4. 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* package (Bürkner 2017) of R (R Core Team, 2023). The scavenging propensity index exhibited high overdispersion (as indicated by posterior predictive checks), which led to a poor fit for models suitable for count data, such as the negative binomial. Therefore, the “trap selection model” was fitted with a cumulative ordinal likelihood and a logistic link (Bürkner and Vuorre 2019). The ordinal scavenging index included five categories: no scavenging (0 obs.), low (1 to 5 obs.), medium (6 to 10 obs.), high (11 to 20 obs.), and very high scavenging propensity ( $\geq 21$  obs.).

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 (and thus the slow-fast continuum; 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 was included to account for the competitive potential of species, as larger (and slower) species tend to interact more frequently with fisheries (Zhou et al. 2019b). Geographic extent, habitat breadth, and migratory status were included to account for differences in encounter probability between seabirds and fisheries, as species with larger and more diverse habitats that migrate are likely to overlap more with large-scale fisheries. The foraging guild was included to account for the influence of foraging behaviors on the likelihood of interaction with specific gear (e.g., diving species, which are usually at the faster end of the slow-fast continuum, tend to interact less with large-scale gear that operates further from the coast). 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 (“random effect”) 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 set weakly informative priors for the intercepts (normal with a mean of zero and standard deviation of 5), fixed variables (normal with a mean of zero and standard deviation of 0.5), and for the standard deviation parameters (half-normal with a mean of zero and standard deviation of 0.5). Weakly informative priors assume that zeros represent the highest probabilities for the parameters, thus preventing the sampler from considering highly unlikely values and overfitting the model (McElreath 2020). When the posterior distributions of the parameters are centered on non-zero values, it indicates that the

empirical data provide contravening evidence to the weak priors. In contrast, when the data are not informative about the parameters, the model will default to the weak prior.

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. In addition, we adjusted for body mass as a fixed variable. As in the previous model, we incorporated the variance-covariance matrix as a varying intercept to account for phylogenetic relatedness, along with the genus to address uncertainty related to taxonomic biases. We set weakly informative priors for the intercept (normal with a mean of zero and a standard deviation of 1), fixed variables (normal with a mean of zero and a standard deviation of 0.5), and for the standard deviation parameters (half-normal with a mean of zero and a standard deviation of 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 8,000 iterations with a warm-up period of 4,000 iterations and a thinning rate of 1 iteration (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. Additionally, we ensured that each estimate had more than 400 effective samples and that the Gelman-Rubin statistic ( $R_{hat}$ ) values were below 1.01 (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.

#### 4. Results

We reviewed 275 peer-reviewed research articles selected through a literature search, of which 60% ( $n = 163$ ) met our inclusion criteria. From these articles, we extracted and compiled a total of 1,106 observations, with an average ( $\pm SD$ ) of  $6.7 \pm 11.4$  observations per study. Observations were skewed towards the southwestern and northeastern Atlantic Ocean (Figure 1A). Seventy-nine percent ( $n = 878$ ) of the observations came from “habitat use” studies (75% from count studies and 5% from consumption experiments), while 21% ( $n = 228$ ) were from diet studies (Figure 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 (Figure 1C). A total of 130 seabird species (38%) from 12 taxonomic families were identified as scavengers of fisheries (Figure 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 of the number of species from the reviewed articles 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 (Figure 1D).

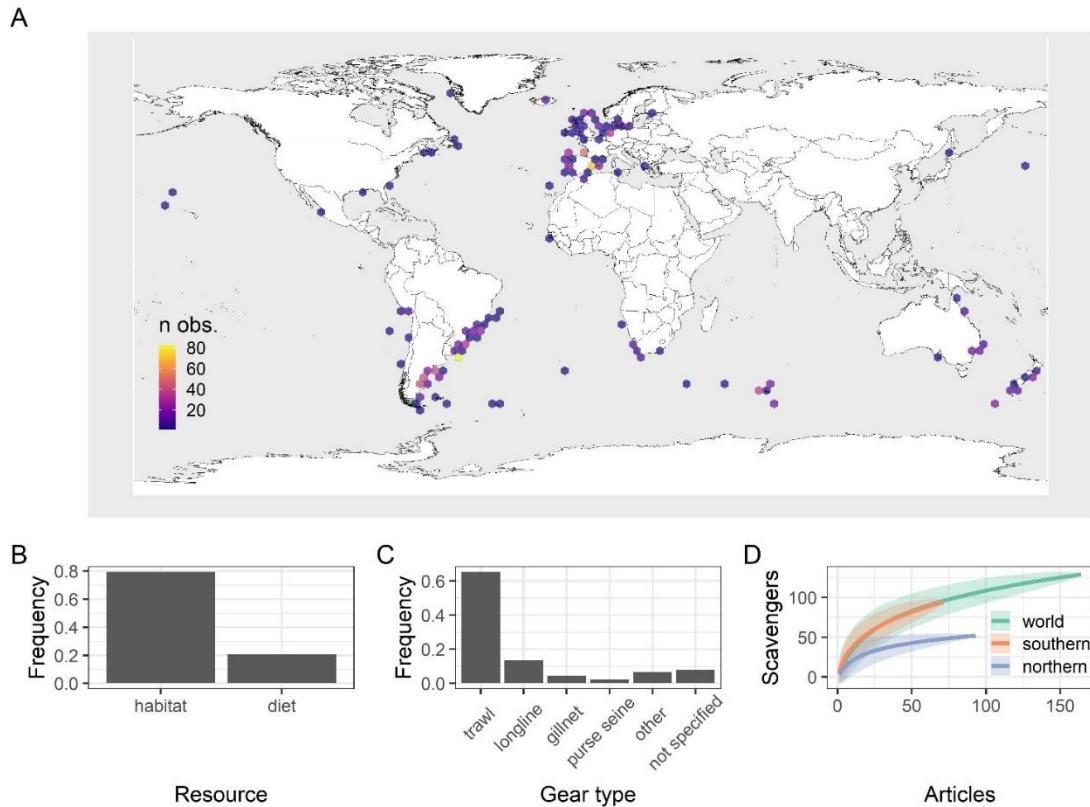


Figure 1. (A) Spatial variation of scavenging seabirds in fisheries compiled from a systematic review of the literature. Each observation ( $n=1106$ ) corresponds to a species that was recorded scavenging during fishing operations/consumption experiments (“habitat”) or that its diet contained trophic subsidies from fisheries. (B) Frequency of observations regarding the type of resource (“habitat” or diet). (C) Frequency of observations regarding the type of fishery (D) Cumulative curves of the total number of scavenging seabirds ( $\pm 2$  SE) for the reviewed articles ( $n= 163$  articles).

The “trap selection model” (Bayes  $R^2 = 37\%$ , 95% CI = 28 - 46%) showed that scavenging propensity was positively correlated with generation length ( $\beta = 0.58$ , 95% CI = 0.22 - 0.96,  $\beta(\text{pr} > 0) = 100\%$ , Figure 3A), 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 Figure 3B,C. The studied

seabirds exhibited a low phylogenetic signal for scavenging propensity ( $sd = 0.46$ , 95% CI =  $0.02 - 1.13$ , Table 1) and a comparatively higher variation associated with the genus of the species ( $sd = 0.64$ , 95% CI =  $0.08 - 1.14$ , Table 1).

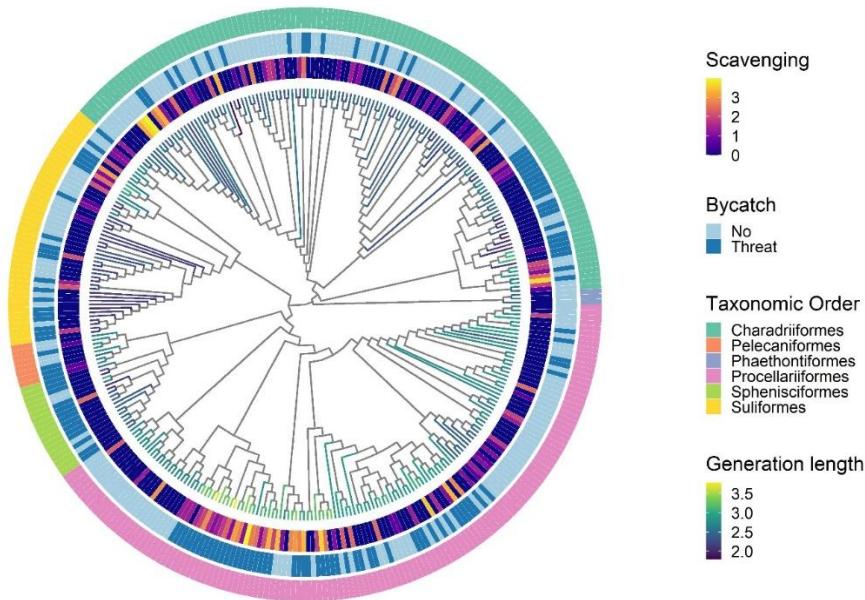


Figure 2. Patterns of variation in scavenging propensity (log scale), bycatch threat, and generation length (log scale) for the 341 seabird species examined. The consensus tree generated from two thousand trees using the 50% majority rule is shown.

A total of 134 seabird species have bycatch listed as a threat to their conservation, as reported by the IUCN threat classification scheme (Figure 2). The “trap consequences model” (Bayes  $R^2 = 0.44$ , 95% CI =  $0.35 - 0.52$ ) indicated a high probability of an interactive effect between scavenging propensity and generation length on the probability of being affected by bycatch ( $\beta$  interaction =  $0.38$ , 95% CI =  $0.05 - 0.73$ ,  $\beta(pr > 0) = 99\%$ , Figure 4A), while adjusting for body mass, phylogenetic relatedness ( $sd = 1.16$ , 95% CI =  $0.29 - 1.84$ , Table 2), and taxonomic genus as a varying intercept ( $sd =$

0.61, 95% CI = 0.04 - 1.34, Table 2). Posterior predictions showed that species with longer generation times and higher scavenging propensity had the highest probability of being affected by bycatch (Figure 4B-D). Species with shorter generation times and higher scavenging propensity showed the lowest probability of bycatch threat (Figure 4B-D).

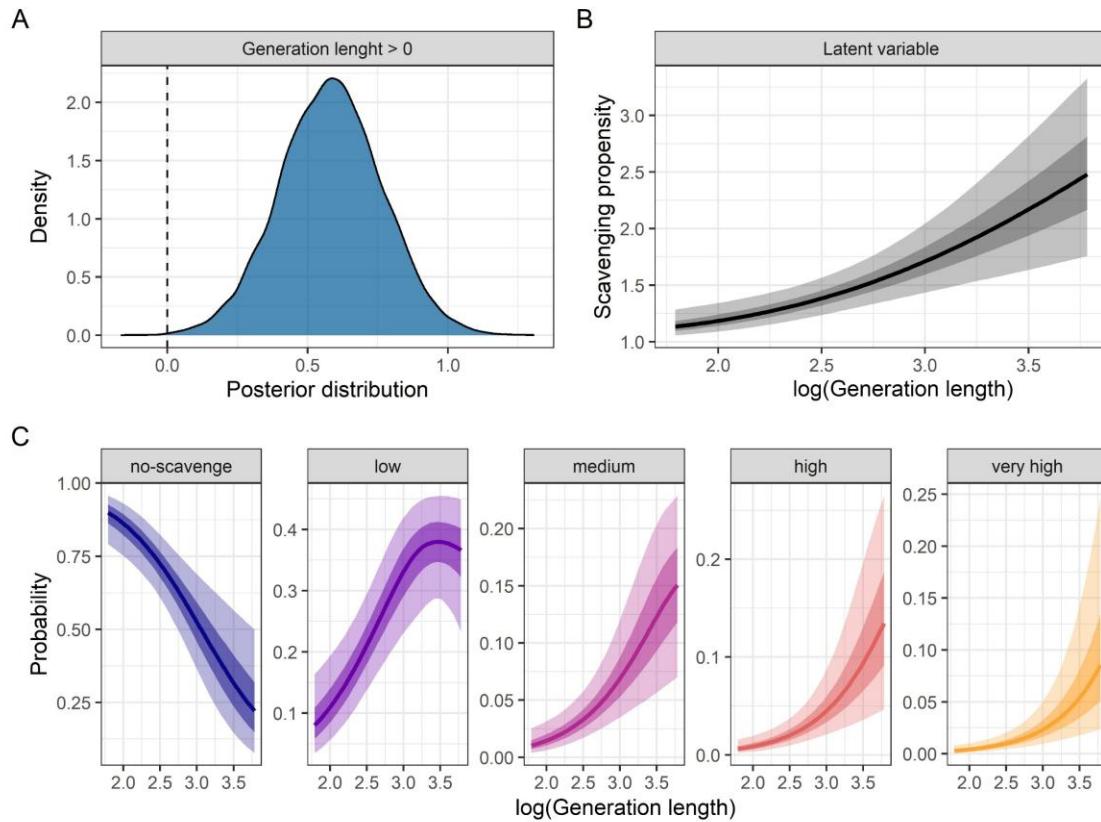


Figure 3. (A) Posterior distribution of the parameter from the generation length (log scale) on the scavenging propensity ( $\beta(\text{pr} > 0) = 100\%$ ) for 341 seabird species, adjusted for the body mass, geographic extent, habitat breath, migratory status, foraging guild, phylogenetic signal and uncertainty related to the taxonomic genus (Table 1). (B) Conditional effect (mean, 50% and 90% credible interval) of the generation length (in log scale) over the scavenging propensity in scale of the latent variable (level 1= no-scavenging, to, level 5= very high scavenging propensity). (C) Conditional effect (mean and 90% credible interval) of the generation length over each level of the scavenging propensity index. Continuous co-variables were conditionalized by their mean and all dummy variables (factors) were set to zero, which allows to make predictions about the grand mean.

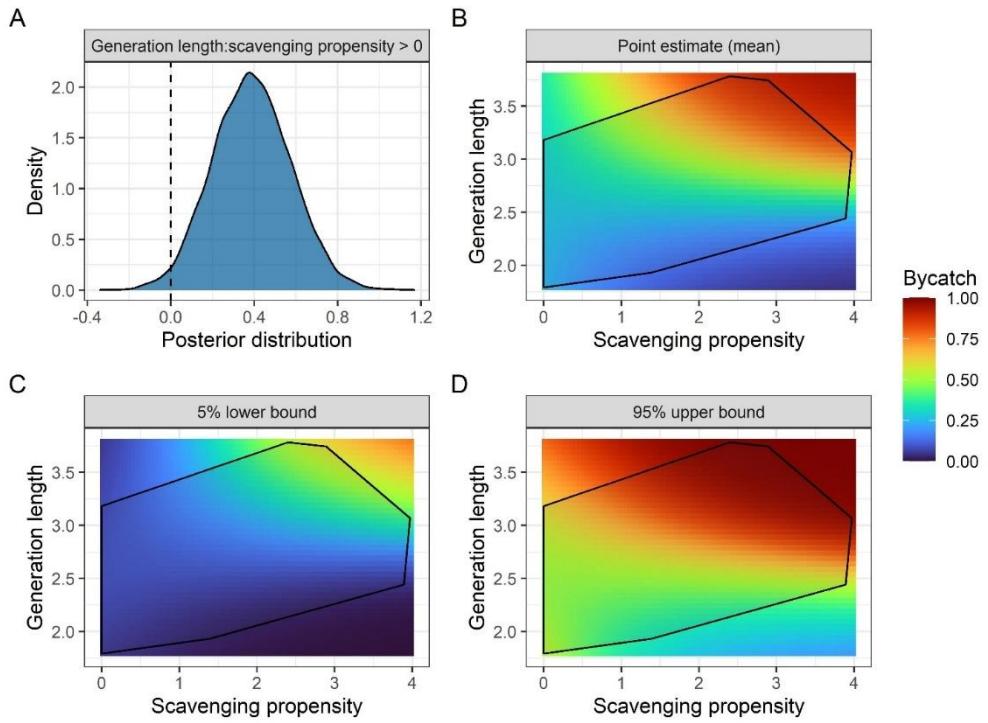


Figure 4. (A) Posterior distribution of the parameter from the interaction ( $\beta(\text{pr} > 0) = 98\%$ ) between the generation length (log scale) and the scavenging propensity (log scale) on the probability of bycatch threat for 341 seabird species, adjusted for the body mass, phylogenetic signal and uncertainty related to the taxonomic genus (Table 2). (B) Mean and 90% credible interval (C and D) of posterior predictions for the effect of the interaction between the generation length and the scavenging propensity (both in log scale) on bycatch threat probability, conditioned to the average size of seabirds. The black polygon shows the area containing all species of seabirds.

Table 1. Summary of regression coefficients from the “trap selection model”. See Figure 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	l-95% CI	u-95% CI	Rhat	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	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept[1]	0.92	0.33	0.31	1.61	1.00	11126	10089
Intercept[2]	2.63	0.37	1.96	3.42	1.00	11568	10557
Intercept[3]	3.41	0.4	2.69	4.25	1.00	11670	10311

Intercept[4]	4.54	0.46	3.7	5.5	1.00	12157	11574
Generation length	0.58	0.19	0.22	0.96	1.00	15200	11452
Body mass	0.49	0.18	0.14	0.85	1.00	12387	12073
Geographic extent	1.09	0.21	0.69	1.51	1.00	19380	12184
Habitat breadth	0.59	0.17	0.26	0.92	1.00	20388	12791
Full migrant	0.25	0.18	-0.11	0.62	1.00	21251	12341
guild1	-0.08	0.25	-0.57	0.42	1.00	12197	11405
guild2	0.23	0.23	-0.23	0.68	1.00	16751	11296
guild3	0.21	0.33	-0.44	0.85	1.00	15636	11095

Table 2. Summary of regression coefficients from the “trap consequences model”. See Figure 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	Rhat	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	Rhat	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	17049	12390
Scavenging propensity	0.07	0.17	-0.25	0.4	1.00	17026	12665
Body mass	1.03	0.23	0.58	1.5	1.00	14060	12252
Generation length: Scavenging propensity	0.38	0.18	0.05	0.73	1.00	21478	12382

## 5. Discussion

Our results showed that generation length influences the scavenging propensity of seabirds, and that the interaction of this behavior with generation length correlates with the bycatch probability for the analyzed species. Specifically, we show that slow-lived seabirds are most likely to use trophic subsidies from fisheries, and that these

species (the slowest and most prone to scavenging) have the highest likelihood of being affected by bycatch in fisheries. This was particularly clear for the slowest group of seabirds, the albatrosses (Diomedeidae), of which 21 out of 22 species are scavengers (to varying extents) and all species are threatened by bycatch (IUCN). This strongly suggests that ecological traps could be one of the main mechanisms underlying the interactions between seabirds and fisheries. Previous studies have briefly mentioned ecological traps (Le Bot et al. 2018) to frame “junk-food” scenarios, where fishing subsidies of low nutritional value decrease the reproductive success of seabirds (Grémillet et al. 2008). However, the concept of ecological traps has been absent in the literature describing the more common scenarios of equal or greater marine habitat preference due to trophic subsidies, where fitness decline is due to bycatch. Since these scenarios are triggered by an increased attraction of visual and olfactory cues from trophic subsidies, a combination of the “attraction” and “degradation” mechanisms through bycatch might be common among ecological traps involving seabirds and fisheries. This could partly explain the rapid global decline in seabird populations due to bycatch since the 1980s (59% of affected species have declining population trends, IUCN 2022), as combined traps tend to be most severe on populations (Robertson et al. 2013). Based on our results and previous work, we suggest that combined traps are most likely to arise in trawl fisheries from discards, in longlines from discards and mainly from baits, and in purse seines from discards and catches (Sullivan et al. 2006, González-Zevallos and Yorio 2006, Watkins et al. 2008, Favero et al. 2011, Zhou et al. 2019a, Zhou and Brothers 2022, Melvin et al. 2023, ACAP 2024).

In addition to these findings, we showed that the evolutionary history of seabird species plays a key role in determining their propensity for bycatch, but to a lesser extent for scavenging. A detailed examination of the evolutionary patterns of scavenging propensity and bycatch threat was beyond the scope of this study. However, our results support the long-standing idea that behavioral traits are more evolutionarily labile, exhibiting a weaker phylogenetic signal compared to morphological, life-history, or physiological traits (Blomberg et al. 2003). The strong phylogenetic signal observed for bycatch threat further supports recent evidence suggesting that demographic resilience to disturbances is more evolutionarily constrained in animals (Capdevila et al. 2022).

### **5.1. Likelihood of trap selection**

Our results show a positive correlation between generation time and seabird scavenging propensity, after adjusting for possible confounding effects of species competitive potential (body mass), probability of encounter (geographical extent, habitat breadth, and migration status), foraging guilds, phylogenetic relationships, 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, 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 have shown that animals at the “slow” end of the slow-fast continuum, which prioritize survival over reproduction and hence have a higher time budget, should explore more accurately the environment, and exhibit better performance in learning than those at the ‘fast’ extreme (Sol 2015, Sol and Maspens 2016). The latter should be facilitated by the fact that slow-lived species tend to be less constrained as they exhibit larger neural structures (Sol 2009). This has been particularly shown for land birds, including 385 species, where life histories that prioritize future over current reproduction have shown a greater tendency to consume novel food items (Sol et al. 2016). Taken together, the higher scavenging propensity for slow-lived seabirds observed in our study agreed with the hypothesis that innovativeness in the foraging domain could be more common in the slow end of the slow-fast continuum.

An important factor that we did not explicitly consider in this study was the overlap of species distribution with fisheries (Clay et al. 2019). Greater overlap—and, therefore, a higher probability of encounter—with fisheries could be another cause of the higher scavenging propensity of slower species. However, this limitation should not substantially affect our results, as differences in encounter probabilities should have been captured by the geographic extent, habitat breadth, and migratory status of the examined species. Another limitation of our study relates to the incompleteness of the reported scavenger bird communities, as indicated by accumulation curves, which could bias our scavenging index. This issue was particularly noticeable in the southern

hemisphere and may be related to the lower level of research on small-scale fishing gear, such as gillnets and purse seines (Dias et al. 2019). These gears are commonly used in more coastal waters, where interactions with diving seabirds at the faster ends of the slow-fast continuum, such as cormorants and penguins, are expected to be more frequent (Žydelis et al. 2009, Crawford et al. 2017). Nevertheless, species at the slow end, such as petrels and shearwaters, also often interact with small-scale fisheries (Simeone et al. 2021). Therefore, it is unlikely that including the effects of small-scale gears would significantly affect our findings. In addition, this bias should have been partially accounted for by the foraging guilds and the taxonomic genus as varying intercepts in the “trap selection model.” Although these limitations increase the uncertainty about the causal mechanisms of scavenging behavior in seabirds, the correlation between generation length and scavenging propensity, as well as their interactive roles in determining bycatch risk, provides a basis for improving the management of fisheries through the ecological trap framework.

## **5.2. Population-level consequences of traps**

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 were 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. 2019a, 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. 2015b). 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, Battin 2004, Hale et al. 2015b).

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, 2009b, 2010, Tuck et al. 2015, Pardo et al. 2017). Pardo et al., (2017), demonstrated that bycatch in longline and trawl fisheries was one of the main factors driving a 40-60% population decline over 35 years among three albatross species in the South Georgia Islands. 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, suggesting 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 recent empirical evidence showing that demographic resilience in both animals and plants strongly correlates with life history traits along the slow-fast continuum (Capdevila et al. 2022). This study, which examined 162 populations of 69 animal species and 748

populations of 232 plant species, demonstrated that species with longer generation times require extended recovery periods after disturbance, whereas species with higher reproductive capacities exhibit greater resistance and compensatory responses.

In contrast to the main trend observed for slow-lived scavengers, their fast-lived counterparts showed the lowest probability of bycatch threat. Previous studies on fast-lived scavengers, such as seagulls, have shown that anthropogenic food subsidies tend to increase population growth rates and decrease variability in demographic parameters (Oro et al. 2013). Consequently, the explanation for our results may be related to the mediating role of the slow-fast continuum in the demographic compensation of trophic subsidies on bycatch. For fast-lived species, whose population growth depends primarily on reproductive rates (Saether and Bakke 2000), mortality from bycatch is more likely to be offset by trophic subsidies through increases in reproductive success and/or population recruitment (Genovart et al. 2017). Compensatory effects have also been described for slow-lived seabirds; however, the contribution of subsidies to population growth rates tends to be outweighed by mortality from bycatch (Pardo et al. 2017).

### **5.3. Incorporating ecological traps into the management of fisheries**

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, the theoretical foundations and modeling framework of ecological traps could help strengthen both current and future management initiatives—at the national level (e.g., National Plans of Action; NPOAs; Good et al., 2020) and in areas beyond national jurisdiction, such as Regional Fisheries Management Organizations (RFMOs), where the effectiveness of legal and regulatory frameworks to manage bycatch remains highly uncertain (Beal et al., 2021; Haas et al., 2021). In this context, mechanistic models of ecological traps (e.g., Sánchez-Clavijo et al., 2016; Simon and Fortin, 2020) could serve as valuable tools to improve population risk assessments and evaluate alternative management strategies, including bycatch mitigation and discard regulation. From a bottom-up perspective, the ecological trap framework could also promote greater compliance with mitigation measures and good practices on board (Melvin et al., 2023).

## 6. 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 demonstrate 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 framework can help raise awareness of the underlying causes and consequences of seabird–fishery interactions, guide more effective management through mechanistic models, and reinforce both the implementation of and compliance with mitigation measures.

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CHAPTER 2. When is the bait worth the risk? Modeling a compensatory ecological trap  
in seabirds

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## **1. Abstract**

Ecological traps occur when organisms find a habitat equally or more attractive than other available options, despite experiencing reduced fitness having selected it. In some cases, these traps involve trade-offs between fitness components, where gains in one offset losses in another. Such compensatory traps can generate complex population responses that vary depending on species' life-history strategies. A key driver of these traps is human-derived trophic subsidies, which increase habitat attractiveness by enhancing foraging success. Focusing on seabird–fishery interactions, we developed a spatially explicit simulation model to evaluate how species with different life histories (slow, intermediate, and fast) respond to a compensatory ecological trap, in which individuals preferentially select areas with elevated foraging success due to fishery subsidies. While this behavior can increase breeder and fledgling recruitment, it also elevates mortality risk from bycatch. Our results reveal nonlinear, threshold-dependent dynamics shaped by life-history traits. At low bycatch levels, subsidies had a net positive effect on population size. However, once bycatch mortality surpassed a species-specific threshold, the same subsidies intensified population declines by reinforcing maladaptive habitat preferences and increasing exposure to lethal risks. Under equivalent conditions, slow-lived species (albatrosses) were 1.4 times more likely to go extinct than intermediate-lived species (gulls) and 4.5 times more likely than fast-lived species (cormorants). By showing how trophic subsidies and mortality interact across the life-history continuum, our study demonstrates that compensatory ecological traps can influence community structure by selectively filtering species. We propose that

ecological traps offer a valuable framework for managing wildlife–subsidy interactions, particularly in systems where human-derived food sources are prevalent.

## 2. Introduction

A common assumption in ecology is that an organism's ability to survive and reproduce is closely linked to its habitat preferences, which have been shaped by natural selection. However, organisms do not always make adaptive choices and may find a habitat equally or more attractive than other available options, despite experiencing reduced fitness having selected it—a phenomenon known as 'ecological traps' (Dwernychuk and Boag 1972, Gates and Gysel 1978). Theoretical studies have shown that traps heighten the risk of extinction for local populations and spatially structured metapopulations (Delibes et al. 2001, Kokko and Sutherland 2001, Donovan and Thompson 2001, Kristan et al. 2003, Fletcher et al. 2012, Hale et al. 2015b). Empirical evidence further indicates that ecological traps are widespread in terrestrial and marine ecosystems and frequently result from rapid, human-driven environmental changes that outpace species' adaptive responses (Robertson et al. 2013, Hale and Swearer 2016, Swearer et al. 2021). As these changes persist, ecological traps are likely to become more frequent in the future.

Previous theoretical models of traps commonly assume maladaptive habitat selection in relation to survival or reproduction (Delibes et al. 2001, Kokko and Sutherland 2001, Donovan and Thompson 2001, Kristan et al. 2003, Fletcher et al. 2012, Hale et al. 2015b). However, ecological traps may involve trade-offs between different fitness components, whereby seemingly maladaptive behavior concerning one

component (e.g., survival) may be offset by gains in another (e.g., reproduction) (Battin 2004). Furthermore, ecological and evolutionary responses to these fitness trade-offs are expected to be influenced by species' life histories, particularly their position along the slow-fast continuum (Saether 1987, Stearns 1992). Species with a slower pace of life—characterized by longer lifespans, lower reproductive potential, and reduced maximum population growth rates—are anticipated to be more vulnerable to local extirpation due to ecological traps (Kokko and Sutherland 2001, Hale et al. 2015b). However, the introduction of traps involving demographic trade-offs and their interactions with life-history traits may lead to outcomes different from those predicted by previous models, both within populations and between species. This could potentially result in nonlinear responses, multiple equilibria, and even population growth, as well as contrasting responses along the slow-fast continuum (Sæther et al. 2004, Munch et al. 2005, Herrando-Pérez et al. 2012, Clark and Luis 2020). Therefore, understanding the specific mechanisms through which traps influence life histories is critical for preventing and effectively managing their consequences on populations (Robertson and Blumstein 2019, Swearer et al. 2021).

A key driver of compensatory traps may be human-derived trophic subsidies, which offer abundant and predictable food resources that can enhance foraging success and reproduction (Oro et al. 2013). However, increased habitat preference can also elevate mortality risks from pollutants, predators, competition, parasitism, hunting, or accidental deaths (Morris 2005, Semeniuk and Rothley 2008, Rodewald et al. 2011, Lewison et al. 2014, Becker et al. 2015, Lamb et al. 2017, Sigaud et al. 2017, Simon and

Fortin 2020). In this context, we define compensatory ecological traps as a specific form of ecological trap in which organisms preferentially select a habitat due to an increase in one or more components of fitness (e.g., foraging success and/or reproduction), even though another key component (e.g., survival) is simultaneously reduced. This trade-off can initially mask negative demographic outcomes, particularly when reproductive gains create the illusion of population-level benefits, even though lifetime reproductive success and long-term viability are ultimately reduced.

A potential example of such traps arises from interactions between seabirds and fisheries. Trophic subsidies provided by fishing vessels—such as bait, discards, and offal—attract seabirds and can enhance their foraging success (Oro et al., 2013). However, this attraction simultaneously increases the risk of bycatch through hooking (e.g., longline; Anderson et al. 2011), entanglement (e.g., purse seine, gillnets; Žydelis et al. 2013, Simeone et al. 2020), or collisions with gear (e.g., trawl; Phillips et al. 2024). Bycatch has recently been identified as the primary threat to seabirds at sea, contributing to population declines and raising extinction risk (Dias et al. 2019, Richards et al. 2021, 2024).

Conversely, food provided by fisheries—primarily through discards (Garthe et al. 1996, Votier et al. 2004, Bicknell et al. 2013, Sherley et al. 2019)—has the potential to mitigate the demographic costs of bycatch by improving breeder and fledgling recruitment (Rolland et al. 2008, 2010, Barbraud et al. 2008, Genovart et al. 2016, Pardo et al. 2017). This compensatory effect is expected to be more pronounced in fast-lived species due to their higher demographic sensitivity to reproduction compared to slow-

lived species, which are more sensitive to survival (Heppell et al., 2000; Saether and Bakke, 2000). However, the extent to which these compensatory effects are influenced by life history traits remains an open question (Genovart et al., 2017). Moreover, the ecological trap framework has been underutilized in explaining and predicting seabird-fisheries interactions and has not been applied to other large marine vertebrates affected by fisheries, including sea turtles, mammals, and elasmobranchs (Lewison et al. 2014). Furthermore, ecological traps remain relatively understudied in marine ecosystems (Swearer et al. 2021).

Despite strong evidence that fishery-derived food subsidies increase bycatch risk (Sullivan et al. 2006, González-Zevallos and Yorio 2006, Watkins et al. 2008, Favero et al. 2011) neither conceptual frameworks nor formal ecological trap models have been applied to predict how such subsidies—particularly discards—can generate compensatory traps. Moreover, it remains unclear how species' life-history strategies modulate demographic responses to these traps, especially when reproduction–survival trade-offs are involved. To address these gaps, we developed a spatially explicit, individual-based model (IBM)(Grimm and Railsback 2005) to evaluate how species with contrasting life histories (slow, intermediate, and fast) respond to a compensatory ecological trap in which individuals preferentially select areas with enhanced foraging success due to fishery subsidies. This behavior can increase both breeder and fledgling recruitment, but also elevates mortality risk from bycatch, resulting in demographic trade-offs that differ depending on life-history strategy. By integrating ecological trap theory with life-history theory, our study shows how such trade-offs can generate

nonlinear and dynamic population responses, thereby extending the classical ecological trap framework. It also provides novel insights for conservation and fisheries management in systems where bycatch and trophic subsidies co-occur.

### **3. Methods**

#### **3.1. The model**

The description of the model follows the protocol created by Grimm et al., (2006) to explain IBM within an ecological framework. Following the description of the model, we explain the experiments conducted in detail. The model was developed in R (R Core Team 2023) using the NetLogoR (Bauduin et al. 2019), dplyr (Wickham et al. 2023), and data.table (Barrett et al. 2024) packages. The code for the model can be found at: <https://github.com/cristobalanguita/Compensatory-ecological-trap>

#### **3.2. Model Purpose**

The model aims to simulate population responses of species with varying life-history strategies along the slow-fast continuum under compensatory ecological trap scenarios. In our simulation, the compensatory trap is established by introducing additional energy to a limited area of the habitat while simultaneously increasing mortality risk within the same region. This enhanced habitat increases foraging success by allowing individuals to remain longer in high-energy cells, increasing their chances of consuming energy over successive time steps before moving. This reduces the frequency of movement and the energetic costs of search. As a result, it can increase both breeder recruitment (i.e., the proportion of potential breeders that actually reproduce) and the

reproductive success of breeders (i.e., the number of chicks fledged per breeding individual). The level of mortality risk is determined by specific trap parameters. The base model is a spatially explicit simulation of the life cycle of a colonial bird. It integrates life-history traits, memory-based foraging behaviors, reproduction, and mortality in a patchy, energy-limited environment that changes dynamically as energy is depleted through foraging activity.

### 3.3. Entities, state variables, and scales

The model consists of four entities: (1) the population and its associated attributes, (2) an energy raster representing the environment and its attributes, (3) the colony, and (4) the trap raster and its associated attributes (Figure 1).

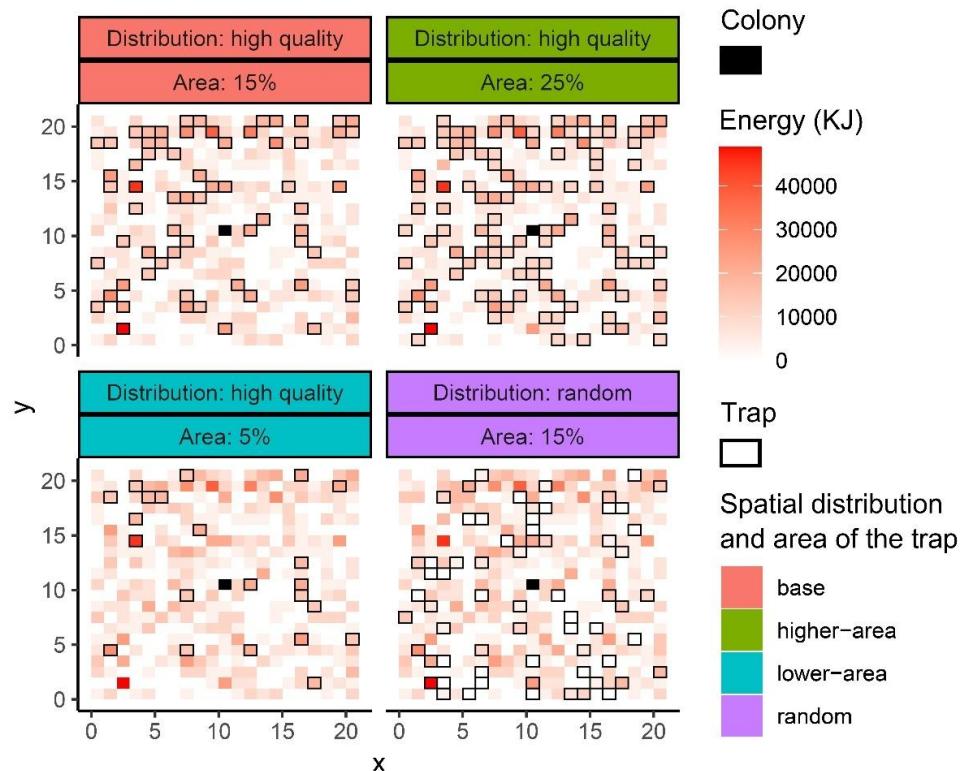


Figure 1. Model entities and spatial configuration of traps, showing variation in trap distribution (traps placed in high-quality habitat vs. randomly distributed traps) and trap area (5%, 15%, 25%). Each configuration was combined with three levels of bycatch mortality and three levels of trophic subsidies, resulting in 36 trap scenarios. Each scenario was simulated for the three life-history strategies and replicated seven times (see Figure 3). The energy raster represents the environment as a  $21 \times 21$  grid, with energy values generated using a zero-inflated negative binomial distribution. The environment has a toroidal (donut-shaped) topology, allowing individuals to move seamlessly across edges. The colony is located at the center of the grid ( $x = 10, y = 10$ ). The trap raster indicates the presence (black outline) or absence of a trap in each cell.

Each individual in the population is defined by five key state variables: identity code, spatial coordinates (both current and from the previous step), age, breeding state, and energy. The identity code is a unique identifier assigned to each individual at the start of the simulation or upon birth. Spatial coordinates represent the individual's position on the raster map, defined by the row and column numbers. The age of individuals ranges from zero (individuals less than one year old) to the maximum lifespan, which is determined by the life history traits of the species. The breeding-state variable includes three categories: non-breeder, breeder, and chick. Energy ( $E$ ) represents the energetic state of non-breeding and breeding individuals and is updated at each time step according to Equation 1 (Table 1). In this equation,  $C$  represents the energy consumption from foraging,  $B$  is the fixed energy lost through basal metabolism (denoted as  $\beta_{\text{basal}}$ ),  $M$  is the energy expended through movement (calculated as  $\beta_{\text{loss}} \times$  movement distance), and  $R$  is the energy allocated to reproduction. Reproductive energy ( $R$ ) includes the constant energy required for offspring production and its supply throughout the breeding season (denoted as  $\beta_{\text{supply}}$ ). For simplicity, chick energy expenditure is not modeled explicitly. Fledging probability is determined by parental provisioning, as described in the Reproduction sub-model.

Table 1. Summary of the equations used in the simulation model. Symbols and parameter definitions are provided in the main text.

	Equation	Sub model
Eq. 1	$E_{(t)} = E_{(t-1)} + C - B - M - R$	Movement and Foraging / Reproduction / Updates
Eq. 2	Energy[i,j] = Energy initial[i,j] × Prop(replenishment)[i,j]	Energy update
Eq. 3	Prop(replenishment)[i,j] $= \frac{1}{1 + e^{k(\text{replenishment steps}[i,j] - \beta \text{replenishment})}}$	Energy replenishment
Eq. 4	Consumption = $\beta \text{hunger} \times \frac{\text{energy}[i,j]}{\text{energy}[i,j] + \beta \text{holing}}$	Movement and Foraging
Eq. 5	diff = $180 -    \text{dire}_{\text{pref}} - \text{dire}_i   - 180  $	Movement and Foraging
Eq. 6	Cell weight = $\frac{1}{1 + e^{\beta k \text{dire}(\text{diff} - \beta \text{dire})}}$	Movement and Foraging
Eq. 7	$P(c_i) = \frac{\text{Cell weight}_i}{\sum_{j=1}^n P_j}$	Movement and Foraging
Eq. 8	[trap mortality] = $\begin{cases} 1, & \text{if } \beta \text{lethality} > U \\ 0, & \text{otherwise} \end{cases}$	Trap-mortality
Eq. 9	[successful winter] $= \begin{cases} 1, & \text{if } \frac{1}{1 + e^{k(\text{satiated steps} - \beta \text{reproduction})}} > U \\ 0, & \text{otherwise} \end{cases}$	Reproduction
Eq. 10	[fledgling] $= \begin{cases} 1, & \text{if } \frac{1}{1 + e^{k(\text{provisioning events} - \beta \text{fledge})}} > U \\ 0, & \text{otherwise} \end{cases}$	Reproduction
Eq. 11	[Starvation mortality] $= \begin{cases} 1, & \text{if } \frac{1}{1 + e^{k(\text{starving steps} - \beta \text{starvation})}} > U \\ 0, & \text{otherwise} \end{cases}$	Mortalities

Eq. 12	[Age mortality] $= \begin{cases} 1, & \text{if } [\beta_{\min} + (\beta_{\max} - \beta_{\min})e^{\frac{-\text{age}}{\beta_{\text{decay}}}}] > U \\ 0, & \text{otherwise} \end{cases}$	Mortalities
Eq. 13	[Constant mortality] = $\begin{cases} 1, & \text{if } \beta_{\text{constant}} > U \\ 0, & \text{otherwise} \end{cases}$	Mortalities

The energy raster representation of the environment consists of a  $21 \times 21$  grid, arranged with a toroidal (donut-shaped) topology. This means that when an individual crosses the grid's boundary, it reappears at the opposite edge, avoiding potential artifacts due to spurious edge effects. Each cell in the grid is assigned an energy value, expressed in kilojoules (kJ), and the cell's position is defined by its column and row numbers. Energy values are drawn from a zero-inflated negative binomial distribution (ZINBI; Rigby et al., 2019), providing variability in the energy content across the grid (Figure 1). The colony is positioned at the center of the grid, with coordinates (xcord, ycord) = (10,10) (Figure 1). The trap raster is defined by the presence or absence of a trap in each cell, with its layout also determined by the grid's column and row coordinates (Figure 1).

A year is represented as 365 days in the model, with each simulation step corresponding to 6 hours. As such, each day is composed of 4 steps, and a full year consists of 1460 steps. The model does not incorporate a circadian rhythm but includes seasonality, with distinct breeding and non-breeding periods. The breeding period is divided into two phases: the 'laying window,' during which individuals produce offspring within the colony, and the 'fledging period,' in which parents commute between the sea

and the colony to feed their chicks until they fledge or die. In our model, we represent a typical seabird phenology, with a breeding period lasting 146 days. This includes a 20-day 'laying window' for egg-laying and a 126-day 'fledging period,' which is consistent with the mean lengths of the incubation and fledging periods observed in seabird species (Schreiber and Burger 2001).

### **3.4. Process overview and scheduling**

The general schedule of the program is described in Figure 2. The program begins by defining the initial conditions, including the collection of individuals, their memory, and their state variables, the environment (energy raster), and the trap scenario. Afterward, the model begins to operate. Within each time step (6 hours), seven main sub-models or modules are processed in the following order: (1) Energy replenishment, (2) Movement, (3) Trap mortality, (4) Reproduction, (5) Mortalities, (6) Updates and (7) End simulation.

In the Energy update sub-model, the energy of the environment and the subsidy are replenished (see Energy update sub-model). Next, the Movement and Foraging sub-model operates, and birds rest, feed (consume energy), or move (random walk or 'oriented' random walk) based on their hunger level (i.e., energy level, see 'Movement and Foraging' sub-model). In the Trap Mortality module, deaths due to trap interactions are evaluated. Following this, the Reproduction sub-model operates. Satiated non-breeders who meet the breeding conditions during the laying window will go to the colony and produce offspring (see 'Reproduction' sub-model). During the fledging

period, satiated breeders return to the colony to feed their chicks and will continue to do so until the chick fledges or dies (see 'Reproduction' sub-model).

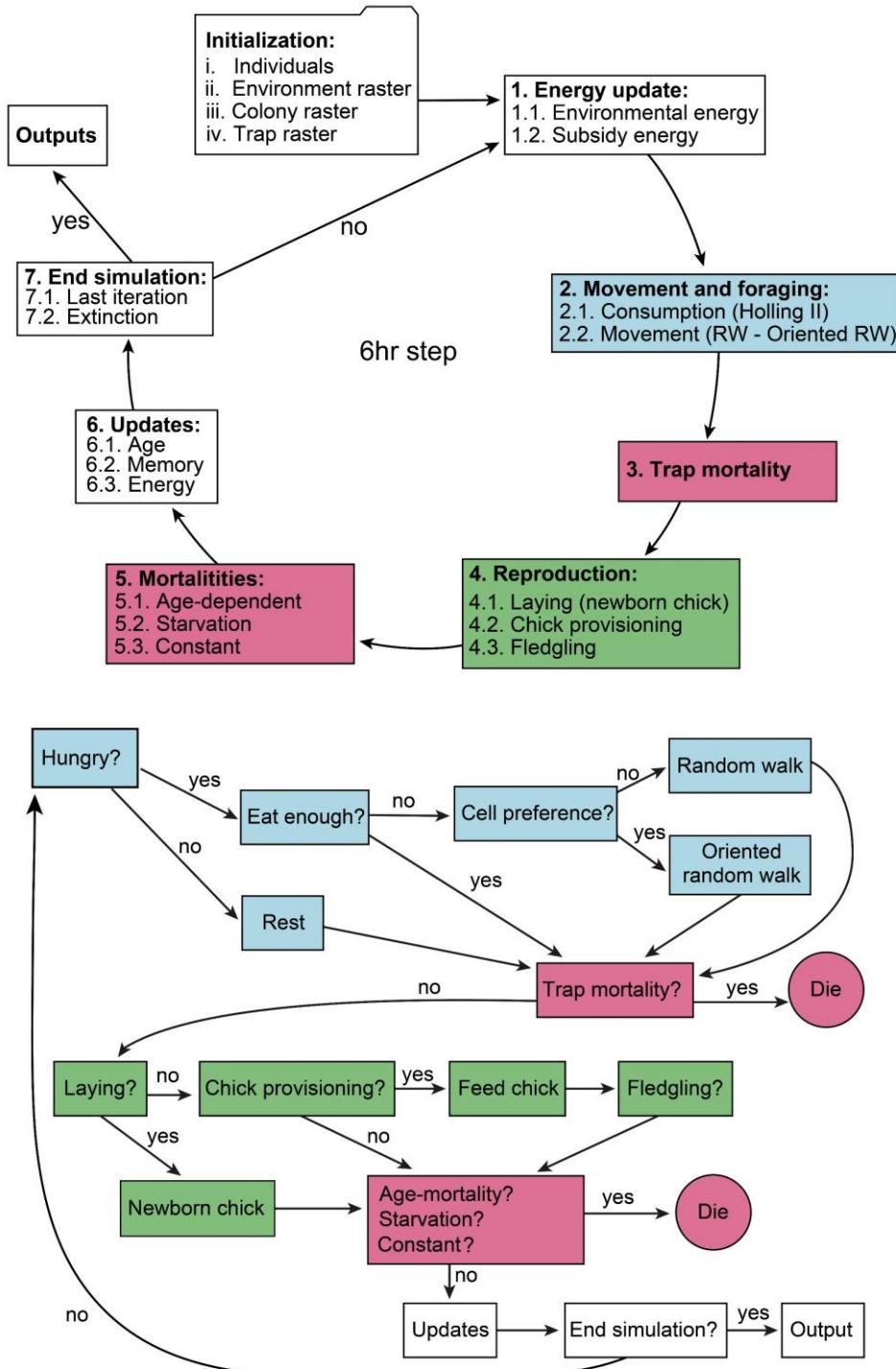


Figure 2. Overview of the program structure (top) and model components (bottom). The top panel illustrates the sequence of all modules within the program, while the bottom panel provides a detailed view of the model components.

panel provides a detailed view of the algorithms governing the Movement and Foraging, Reproduction, and Mortality sub-models, depicting the decision-making processes and actions performed by individuals throughout their life cycle. The Reproduction sub-model (in green) is executed only during the reproductive season.

In both cases, once this occurs, the breeders transition to non-breeder status. The same applies at the end of the fledging period for unsuccessful breeders (those whose chicks did not fledge). Next, the Mortalities sub-model operates, and death probabilities are assessed due to starvation, age, and other constant mortality factors (see 'Mortalities' sub-model). At the end of the algorithm, the age, energy, and memory of individuals are updated. The basal energy expenditure ( $\beta_{\text{basal}}$ ) and the energy lost due to movement ( $\beta_{\text{loss}} \times$  movement distance) are subtracted from the individuals' energy reserves.

The memory is then updated to store the coordinates and respective foraging success of each individual's current cell. Subsequently, for each individual, the cells in their memory are arranged from highest to lowest foraging success, and the first  $n = \beta_{\text{memory}}$  cells are stored. Individuals retain their memory throughout their lifetime. Lastly, the simulation stops either when the last iteration is reached or if the population becomes extinct. In both cases, the program saves the output.

### **3.5. Design concepts**

#### **3.5.1. Basic principles**

This model is built on the assumption that seabird populations are food-limited and energetically enriched habitats (trophic subsidies) generate benefits for foraging and reproduction, but they also increase the risk of mortality. Consequently, population vital

rates respond in opposite directions to habitat selection. The model is based on animals' ability to make behavioral and reproductive decisions using their previous foraging experience and current condition (energy). For instance, birds decide when to leave their present patch, in which direction to move, or when to go to reproduce in the colony.

### **3.5.2. Emergence**

Population size emerges as the result of individuals' foraging success, survival, and reproduction within a patchy and dynamic environment with limited resources. Movement is guided by a combination of experience and randomness. Reproduction is influenced by probabilities weighted by foraging success and life history traits. Mortality rates are determined by the combination of foraging success, age-specific mortality curves, and interactions with the environment (including trap mortality). As such, population growth is not directly modeled but emerges from the interplay of these factors within the simulation.

### **3.5.3. Adaptation**

Individuals follow spatially explicit movement rules, guided by their hunger (energy level) and previous foraging experience, to locate food patches.

### **3.5.4. Learning**

Individuals remember the locations of previously visited cells and the duration of successful foraging there (foraging success is defined as the cumulative time spent in a cell where consumption exceeds 95% of the maximum possible consumption, i.e.,  $\beta_{\text{hunger}}$ ). As individuals age, they accumulate foraging experience and, on average,

spend more time in higher-quality patches. Individuals do not learn from others' experiences, relying solely on their own interactions with the environment.

### **3.5.5. Prediction**

Individuals determine their movement direction based on the quality of habitats where they have previously foraged. These decisions are made without estimating future conditions or the consequences of their actions. As a result, individuals rely solely on past experiences to guide their foraging behavior.

### **3.5.6. Sensing**

Individuals know their present location, energy level, and memory. Based on these traits and seasonality, they can modify their behavior (as explained in the sub-model section). Individuals do not identify the habitat of their neighboring cells, nor do they recognize emergent properties of the population, such as its size (whether at sea or in the colony).

### **3.5.7. Interaction**

The model simulates an environment with limited energy, where exploitation competition is the primary form of indirect interaction. There are no hierarchical structures governing habitat selection or food consumption among individuals. Additionally, individuals do not assess the number of others in the same cell, nor can they predict the potential future locations of other individuals, which may influence their movement decisions.

### **3.5.8. Stochasticity**

Randomness in the model is incorporated through probabilities in individual movement decisions, reproduction, mortality, and energy renewal from the environment. Individuals without foraging experience follow a random walk pattern. Birds with prior experience in high-quality cells use weighted probabilities, based on their experience, to move towards those areas rather than following a straight-line path. Reproduction events (both laying and fledging) and mortality events (age-related, trap-related, starvation, and constant mortalities) are determined by weighted probabilities. The energy content of each cell changes dynamically over time, adding an additional layer of unpredictability.

### **3.5.9. Collectives**

Individuals do not form or belong to aggregations that influence each other's behavior or decisions. Each individual's actions are independent of others, and there are no social dynamics affecting habitat choice, foraging, or reproduction.

### **3.5.10. Observation**

At the end of each simulation, population-level variables were recorded, including total population size, number of newborns, recruits (breeders and chicks), and deaths, categorized by cause.

## **3.6. Initialization**

Prior to each simulation, 180 individuals were randomly distributed across the environment, all assigned a non-breeding status. The ages of individuals were randomly drawn from the age distribution of populations under stationary growth conditions (90–100 years in control conditions) for each life-history type, based on prior model runs. The individuals' energy levels followed a normal distribution with a mean of  $\beta_{\text{hunger}} \pm 10$  SD. At the beginning of the simulation, individuals had an 'empty' memory. The energy content of each cell was randomly sampled from a ZINBI distribution and scaled by the parameter  $\beta_{\text{food}}$  to reach the desired population size. The spatial configuration of the trap was defined by the corresponding trap parameters.

### **3.7. Sub models**

This section provides a detailed description of the sub-models for Energy update, Movement and Foraging, Trap Mortality, Reproduction, and Mortalities (Figure 3a).

#### **3.7.1. Energy update sub-model**

When the energy of a cell decreases to a minimum value due to consumption by individuals, it begins to increase proportionally to its initial value following a logistic replenishment function (see equations 2 and 3, Table 1). In this function, replenishment steps[i,j] denotes to the number of time steps elapsed since replenishment began for cell [i, j]. The parameter  $\beta_{\text{replenishment}}$  defines the midpoint (x-value) of the logistic curve, and k represents the steepness of the curve (with k = 1).

In this sub-model, the energy from the subsidy ( $\beta_{\text{subsidy}}$ ) is subsequently added to the cells where the trap is located. The amount of energy added depends on the trap parameters defined in the experiment.

### **3.7.2. Movement and Foraging sub-Model**

This sub-model simulates the movement and foraging behavior of individuals within a one-step period (6 hours), considering their energy levels and decision-making processes (Figure 3b). During each simulation step, birds either rest, feed, or move, depending on their hunger level. If a bird is not hungry (energy >  $\beta_{\text{hunger}}$ ), it remains in the same location and rests. If it is hungry (energy <  $\beta_{\text{hunger}}$ ), it attempts to consume energy in its current location. Energy consumption is modeled using a two-parameter Holling Type II response (Holling 1959), commonly applied to approximate feeding behaviors observed in nature (Sibly et al. 2013). The full equation is provided in Equation 4, Table 1. In this equation,  $\beta_{\text{hunger}}$  represents the maximum energy consumption in kilojoules (KJ),  $\text{energy}[i,j]$  is the amount of energy available in the current cell, and  $\beta_{\text{holling}}$  is the half-saturation constant that controls the rate at which energy consumption approaches its maximum as available energy increases. Energy consumption by individuals in the same cell occurs sequentially (using a for-loop) and in random order, with no hierarchical structure among individuals. Following the marginal value theorem, individuals leave the current cell when their consumption drops below a certain threshold (Charnov 1976). In contrast to the marginal value theorem, which defines this threshold relative to the habitat, our model assumes that individuals base this decision on their own energetic state. Specifically, they leave the current cell when

the energy they consume falls below or equals their basal energy expenditure (parameter  $\beta_{\text{basal}}$ ).

For modeling movement, birds follow a memory-biased random walk, directing their movement toward previously successful foraging locations. The only exception is recruits leaving the colony, who lack prior experience and thus follow an unbiased random walk. These naïve birds move to a neighboring cell within their movement radius ( $\beta_{\text{radius}}$ ), following a modified random walk pattern in which diagonal movement is penalized by a factor of 0.7 to maintain an isotropic movement pattern. All other birds (i.e., those with at least one memory cell), bias their movement toward the cell where they previously had the greatest foraging success. In these cases, the probability of moving to a given cell within their movement radius is determined by a logistic function that regulates the degree of directional stochasticity, based on the parameters  $\beta_{\text{kdire}}$  and  $\beta_{\text{dire}}$  (see Figure S1). This function allows birds to be guided toward a preferred direction while retaining flexibility to deviate from a straight-line path (see Figure S2).

To compute directionality, we first calculate the direction vector from the preferred cell to each candidate neighboring cell. We then calculate the direction vector from the current cell to each candidate cell. The absolute angular difference between these two vectors is computed (Equation 5, Table 1) and passed through a logistic function to assign weights to each candidate cell (Equation 6, Table 1). In this function,  $\beta_{\text{dire}}$  sets the midpoint and  $\beta_{\text{kdire}}$  the steepness of the curve, thus regulating how strongly birds are biased toward the preferred direction. Higher  $\beta_{\text{dire}}$  and lower  $\beta_{\text{kdire}}$  values result in more stochastic movement.

Finally, cell selection is implemented through weighted random sampling based on Equation 7 (Table 1), where Cell weight<sub>i</sub> is the weight assigned to cell *i*,  $\sum_{j=1}^n P_j$  is the total sum of weights across all candidate cells, and *n* is the total number of cells within the movement radius. For unbiased movement (i.e., naïve individuals), the same formula is applied, assigning an equal weight of 1 to all candidate cells—except diagonals, which are penalized with a weight of 0.7 to maintain isotropic movement.

### **3.7.3. Trap-mortality sub-model**

In this sub-model, the probability of mortality for individuals located in trap cells (trap raster) is assessed. The trap lethality parameter ( $\beta$  lethality) is compared to a random sample drawn from a uniform distribution between 0 and 1 (*U*). Mortality occurs when  $\beta$  lethality > *U* resulting in a probability of one. Otherwise, the probability is zero. The full equation is provided in Equation 5, Table 1. The same uniform random variable *U* is used consistently throughout the following sub-models to represent stochastic processes.

### **3.7.4. Reproduction sub-model**

This sub-model simulates the reproduction process of seabirds during the breeding season, including chick production during the ‘laying window’, provisioning by the parents, and the fledging of chicks. For simplicity, the model treats birds as asexual organisms. Reproduction depends on the age of first reproduction ( $\beta_{\text{firstbreed}}$ ) and the individual's current ( $\beta_{\text{hunger}}$ ) and wintering ( $\beta_{\text{reproduction}}$ ) energetic condition. The energetic condition during wintering is evaluated using a logistic function based on the

number of time steps in which the individual was satiated during the non-breeding season. If the output of this function exceeds a random value drawn from a uniform distribution ( $U$ ), the individual is considered to have wintered successfully. The full equation is presented in Equation 6, Table 1. In this equation,  $\beta_{reproduction}$  defines the midpoint (x-value) of the logistic function, and  $k$  represents the steepness of the curve ( $k = 1$ ). In addition to a successful wintering outcome, a bird can reproduce during the laying window if it meets two further conditions: it must be at or above reproductive age ( $age \geq \beta_{firstbreed}$ ) and its energy level must exceed the required threshold ( $energy > \beta_{hunger}$ ). If these conditions are met, the bird moves to the colony in a straight line over one time step and produces  $n = \beta_{clutch}$  number of chicks. When reproduction occurs, the 'mother' loses a fixed amount of energy ( $\beta_{supply}$ ), and the chick(s) gain the same amount of energy ( $\beta_{supply}$ ).

During the 'fledging period,' chick provisioning is based on the hunger parameter ( $\beta_{hunger}$ ). Once satiated, the breeder returns to the colony in a straight line over one time step, regardless of their location, to supply the chicks. For simplicity, the model does not explicitly simulate the various activities of birds during the reproductive stages, such as incubation, brood-guarding, or creches. Chicks are fed a fixed amount of energy throughout the reproductive stage, equivalent to the supply parameter ( $\beta_{supply}$ ), while the 'mother' loses a constant amount of energy ( $\beta_{supply}$ ). Chick fledging is modeled as a probabilistic event governed by a logistic function based on the number of times a chick was fed by its parent. If the output of this function exceeds a random value drawn from a uniform distribution ( $U$ ), the chick is considered to have successfully fledged. The full

equation is provided in Equation 7, Table 1. In this equation,  $\beta_{fledge}$  denotes the midpoint (x-value) of the logistic function and  $k$  determines the steepness of the curve (set to 1). Once fledging occurs, chicks transition to non-breeders and their energy is reset to the hunger parameter ( $\beta_{hunger}$ ).

### 3.7.5. Mortalities sub-model

In this sub-model non-trap related mortalities are evaluated, including starvation, age-dependent, and constant mortality.

*Starvation mortality:* Starvation mortality is evaluated at each time step using a logistic function based on the accumulated number of time steps during which an individual has not consumed energy—either through foraging (in the case of adults) or provisioning (in the case of chicks). If the output of this function exceeds a random value drawn from a uniform distribution ( $U$ ), the individual dies from starvation. The full equation is provided in Equation 8, Table 1. In this equation,  $\beta_{starvation}$  represents the midpoint (x-value) of the logistic function, and  $k$  controls its steepness (fixed at 1).

*Age-dependent mortality:* The probability of mortality due to age is assessed every five days and is estimated using a three-parameter exponential decay function based on the individual's age. If the output of this function exceeds a random value  $U$ , the individual dies. The full equation is provided in Equation 9, Table 1. In this equation,  $\beta_{min}$  is the minimum mortality rate,  $\beta_{max}$  is the maximum mortality rate, and  $\beta_{decay}$  controls the rate of exponential decline in mortality with age. By adjusting  $\beta_{min}$  and  $\beta_{max}$ , we define age-dependent mortality curves for each life history, using a consistent decay rate

( $\beta_{decay} = 5$ ). Additionally, individuals die when they reach the maximum age ( $\beta_{senescence}$ ) specific to their life history.

*Constant mortality:* This is a fixed probability of death, assessed once per year during the first step of each year. If the constant mortality parameter exceeds a random value U, the individual dies. The full equation is provided in equation 10 Table 1. In this equation,  $\beta_{constant}$  is the fixed mortality probability applied uniformly across all individuals during the annual mortality check.

### **3.8. Calibration and parameterization**

The parameters used in the model are presented in Table 2. We calibrated the parameters as follows: First, we set the basal expenditure parameter ( $\beta_{basal}$ ) according to the average ratio between the field metabolic rate (FMR) and the basal metabolic rate (BMR) in seabirds, i.e.,  $\beta_{hunger}/3.5$  (Schreiber and Burger 2001). Subsequently, we calibrated the  $\beta_{hunger}$  parameter so that, during the non-breeding season, individuals consumed an amount equivalent to the FMR of an average seabird.

Considering the energy replenishment parameter, individuals fed most frequently 1 or 2 times per day and consumed an average of 1200 KJ per day. Seabirds tend to increase their FMR throughout the breeding season, from incubation to brood to creche (Dunn et al. 2018). Accordingly, the parameter for energy loss from movement ( $\beta_{loss}$ ) was calibrated so that birds increased their average daily consumption by approximately 40% during the breeding season (~1600 KJ/day), due to the cost of commuting between the colony and the foraging grounds.

The movement radius was calibrated to allow individuals to reach the "edge" of the environment—used as a reference point in the toroidal landscape—within one day (four steps). The parameters regulating movement stochasticity ( $\beta_{\text{dire}}$  and  $\beta_{\text{kdire}}$ , Table 2) were adjusted to balance randomness in movement while minimizing the risk of frequent starvation-related mortality (see, Figure S1, S2).

We set the Holling type 2 constant ( $\beta_{\text{holling}}$ ) so that the function reaches half of its maximum value when the energy available to an individual equals the maximum consumption (i.e.,  $\beta_{\text{hunger}}$ ). The parameter for the energy cost of chick production and chick supply ( $\beta_{\text{supply}}$ ) was established at 10% of the  $\beta_{\text{hunger}}$  parameter. This represents an intermediate cost, considering that for most of the nestling period, seabird parents deliver meals weighing 5 to 35% of the adult body mass (Schreiber and Burger 2001).

Based on the parameters described above, chicks were fed most frequently one to two times per day. This feeding frequency falls within the range typical for seabirds provisioning their chicks, with variations ranging from several meals a day to one every one or two days. Consequently, we adjusted the fledging parameter to ensure that chicks fed at least once a day had a high probability of fledging. The parameter for starvation mortality was determined based on the allometric starvation model for an average seabird, following the approach of (Peters 1983).

We calibrated the energy distribution parameters of the raster (ZINBI distribution,  $\beta_{\mu}$ ,  $\beta_{\sigma}$ ,  $\beta_{\nu}$ ) to achieve a high degree of patchiness while minimizing

frequent deaths among individuals under control conditions (see above). The selected distribution included 40% zeros and ranged from 0 to 12 units (KJ).

We parameterized three life histories—slow, intermediate, and fast—based on typical reproduction and survival traits in seabirds following Schreiber and Burger, (2001), including mean clutch size, age at first reproduction, age-specific mortality, and senescence. As a reference, we used the parameters of an average albatross for the slow species, a seagull for the intermediate species, and a cormorant for the fast species (Table 2).

Table 2. List of parameters used in the model.

Abbreviation	Description (units)	Values
<b>Life cycle parameters</b>		
$\beta_{\text{hunger}}$	Hunger (KJ)	1000
$\beta_{\text{basal}}$	Basal energy expenditure (KJ)	$\beta_{\text{hunger}}/3.5$
$\beta_{\text{loss}}$	Energy loss from movement (KJ)	$\beta_{\text{basal}}/8$
$\beta_{\text{radius}}$	Radius of movement (cells)	5
$\beta_{\text{dire}}, \beta_{\text{kdire}}$	Parameters of movement directionality	$\beta_{\text{dire}} = 30^\circ, \beta_{\text{kdire}} = -0.2$
$\beta_{\text{hollling}}$	Constant in functional consumption	$\beta_{\text{hunger}} * 0.9$

$\beta_{reproduction}$	Energy of reproduction (satiated steps)	450 (~52% non-breeding season)
$\beta_{supply}$	Energy cost of chick production and supply (kJ)	$\beta_{hunger} * 0.1$
$\beta_{fledge}$	Number of provisioning events	110 (~once a day)
$\beta_{starvation}$	Starvation mortality (days without food)	10
$\beta_{constant}$	Annual constant mortality	1%
$\beta_{memory}$	Number of cells birds remember	30
<b>Life history parameters</b>		
$\beta_{clutch}$	Clutch size (number of offspring)	Slow = 1, intermediate = 2, fast = 3
$\beta_{firstbreed}$	Age of first reproduction (years)	Slow = 9, intermediate = 4, fast = 3
$\beta_{min}, \beta_{max}$	Age-mortality (min-max exponential function)	Slow = 5-25%, intermediate = 15-35%, fast = 20-40%
$\beta_{senescence}$	Max age (years)	Slow = 40, intermediate = 25, fast = 20
<b>Environmental parameters</b>		

$\beta_{mu}$ , $\beta_{sigma}$ , $\beta_{nu}$	Parameters of the energy raster (ZINBI)	$\beta_{mu} = 2$ , $\beta_{sigma} = 0.5$ , $\beta_{nu} = 0.2$
$\beta_{food}$	Food multiplicator	3500
$\beta_{replenishment}$	Energy replenishment time (steps)	12
<b>Trap parameters</b>		
$\beta_{proportion}$	Proportion of trapped area	5%, 15%, 25%
$\beta_{where}$	Energy percentile threshold used to place traps. Traps occur in cells with energy $\geq$ specified percentile	0.9 (high-quality), 0 (random)
$\beta_{subsidy}$	Subsidized energy per cell (kJ)	Low = 500, medium = 1500, high = 3500
$\beta_{lethality}$	Probability of mortality in trap- cells	Low = 2.50E-04, medium = 5.00E-04, high = 7.50E-04

### 3.9. Experiments

We first developed a base trap configuration to evaluate the effects of compensatory ecological traps on seabird populations. This model focused on a trap placed in the highest-quality habitat and served as the reference for all subsequent analyses (Figures 1 and 3). From this base, we implemented three additional trap

configuration variations to explore the influence of trap area and spatial distribution. Combining the four trap configurations with three levels of bycatch mortality and three levels of trophic subsidy resulted in a total of 36 unique simulation scenarios. Below, we detail the structure and assumptions of the base model, followed by a description of the additional configurations.

The base trap configuration featured a compensatory trap located in a high-quality area—randomly selected from cells within the 90th percentile of energy values. This trap occupied 15% of the habitat, remained present year-round, and added a daily trophic subsidy to the environment. Such traps may be common in marine predator-fishery interactions, as both predators and fisheries tend to co-occur in highly productive areas, including mesoscale frontal systems, eddies, upwelling zones, and continental shelves (Karpouzi et al. 2007, Scales et al. 2018, Welch et al. 2024). Simulations ran over a 100-year period, beginning with a 24-year initial phase during which populations were allowed to reach stable equilibrium (the 'control condition'). In year 25, the compensatory trap was introduced. We defined three levels for both mortality and subsidy—low, medium, and high. Preliminary analyses of population responses to a mortality gradient revealed that life histories tend to converge at both extremes of mortality. Therefore, we set intermediate, realistic values (with realized mortality ranging from 2% to 23%) where the differences among life histories were more pronounced (Table 1). We defined subsidy levels at which populations reached 1, 2, and 3 times the carrying capacity under control conditions without trap mortality.

Given the distinct life histories of the species and the sources of stochasticity, populations reached different equilibrium sizes (slow < intermediate < fast). To allow comparison across replicates, population sizes were standardized by their average equilibrium values. We then assessed short- and long-term population responses to the compensatory trap. The short-term response was measured as the average standardized population size during the first 10 years after the trap's introduction, while long-term response was measured as the average standardized population size over the last 10 years of the simulation.

To evaluate the effects of trap configuration, we modified the base configuration to include three additional variations (1) a larger-area trap, covering 25% of the habitat; (2) a smaller-area scenario trap, covering 5% of the habitat; and (3) a randomly distributed trap covering 15% of the habitat (Figure 3). For these variations, we analyzed only the long-term responses in comparison to the base model. Unless otherwise stated, results are expressed as means  $\pm$  one standard deviation (SD).

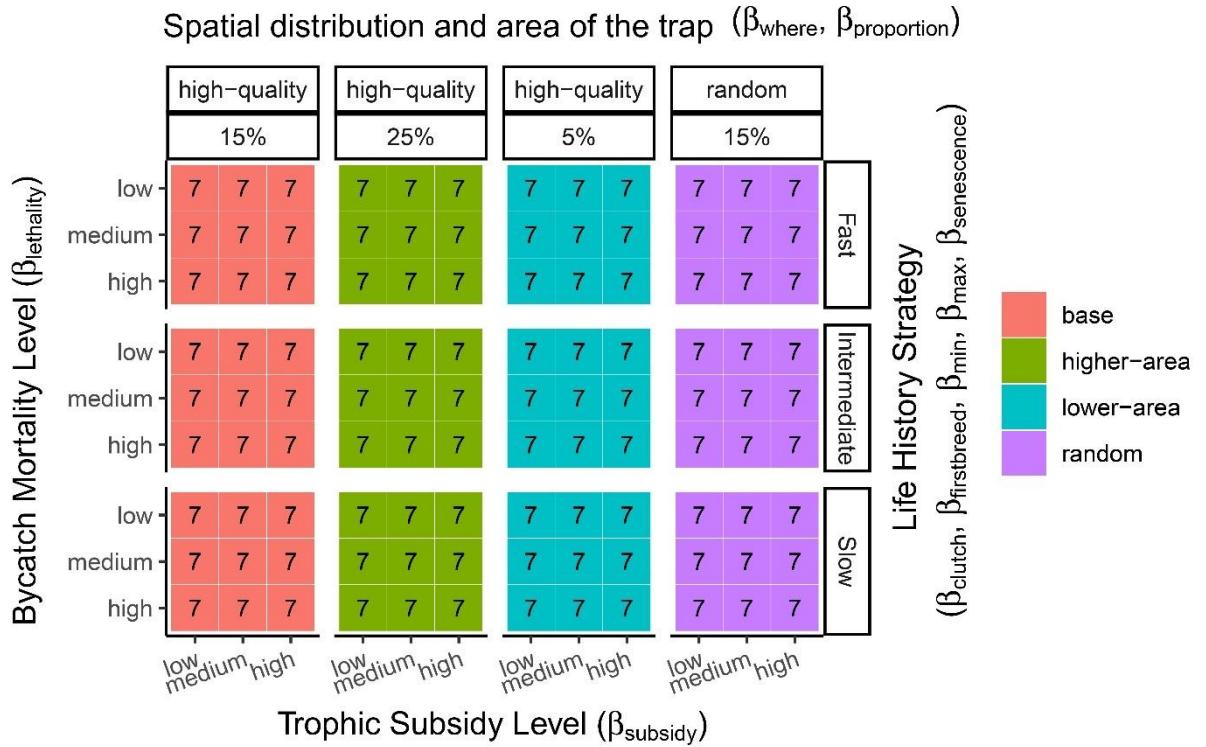
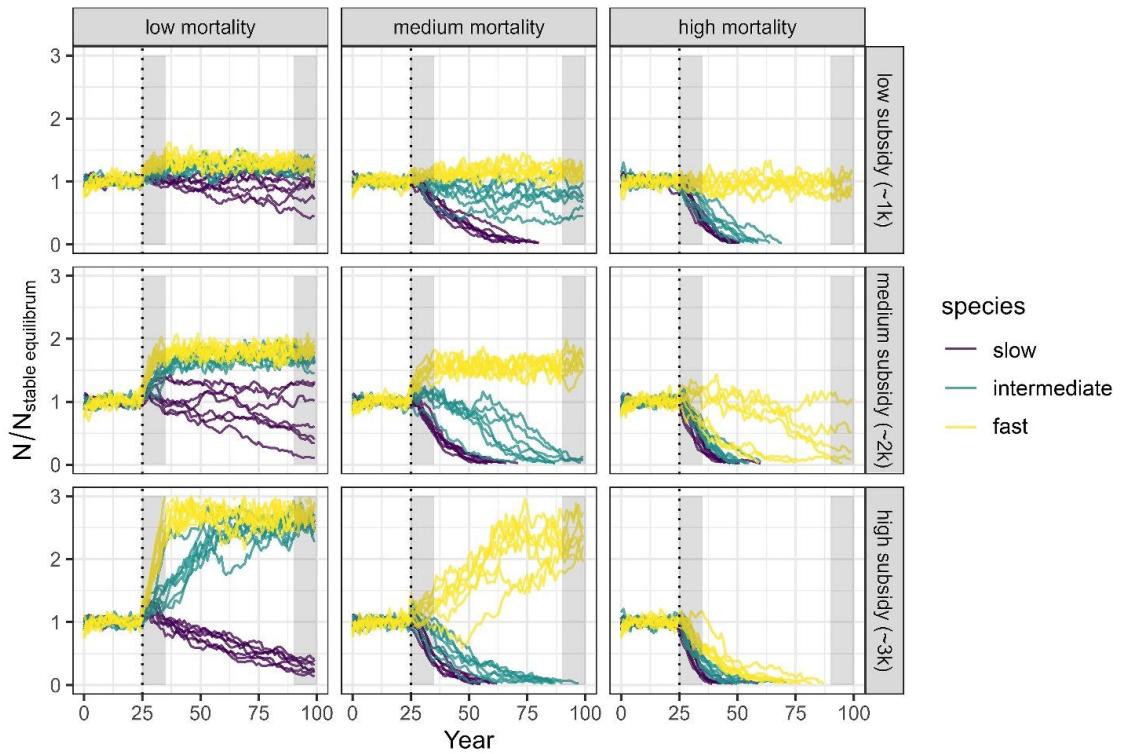


Figure 3. Diagram of all simulations evaluated across trap configurations. For each combination of trap distribution (high-quality vs. random) and trap area (5%, 15%, 25%), simulations were conducted under all combinations of bycatch mortality (3 levels), trophic subsidy (3 levels), and species' life-history strategies (3 types), resulting in a  $3 \times 3 \times 3$  matrix. The parameters (denoted with " $\beta$ ") associated with each variable are shown in parentheses (see Table 2). Each tile in the diagram represents a specific combination of these factors, with the number indicating the number of replicates. This design yielded a total of 756 simulations.

## 4. Results

### 4.1. Base trap scenario

Population responses to the nine compensatory trap scenarios under the base configuration over a 100-year simulation period are shown in Figure 4. Below, we describe in detail the short- and long-term dynamics for each of the three life-history strategies (Figure 5).



**Figure 4.** Population responses of species with different life histories—slow (albatross), intermediate (gull), and fast (cormorant)—to a compensatory ecological trap involving a demographic trade-off between decreased survival and increased recruitment due to trophic subsidies ( $n = 189$  models; 3 life histories  $\times$  3 subsidy levels  $\times$  3 mortality levels  $\times$  7 replicates). Population sizes are standardized to the steady-state size observed in the first 24 years under control conditions. The ecological trap (base trap configuration) is introduced continuously from year 25 onward (indicated by the dashed line). Gray bars highlight short- and long-term responses (see Figure 5).

**Slow Species (e.g., albatross):** At low mortality, the slow species maintained a population size similar to the control under low subsidy (Figure 5a) and exhibited slight growth at medium ( $1.1 \pm 0.14$  times control) and high subsidy ( $1.1 \pm 0.09$  times control) levels in the short term (Figure 5a-c). However, in the long term, the population declined as subsidy levels increased (Figure 5a-c), reaching  $0.3 \pm 0.09$  times the control population under high subsidy (Figure 5c). At medium mortality, the slow species experienced a more pronounced short-term decline, which intensified with higher subsidy levels (from

$0.86 \pm 0.05$  times control at low subsidy to  $0.76 \pm 0.1$  times control at high subsidy, Figure 5d-f). Ultimately, this led to extinction across all subsidy levels in the long term (100% probability, Figure 5d-f). Under high mortality, the slow species showed an even steeper short-term decline as subsidy levels increased, resulting in a 100% probability of extinction (Figure 5g-i).

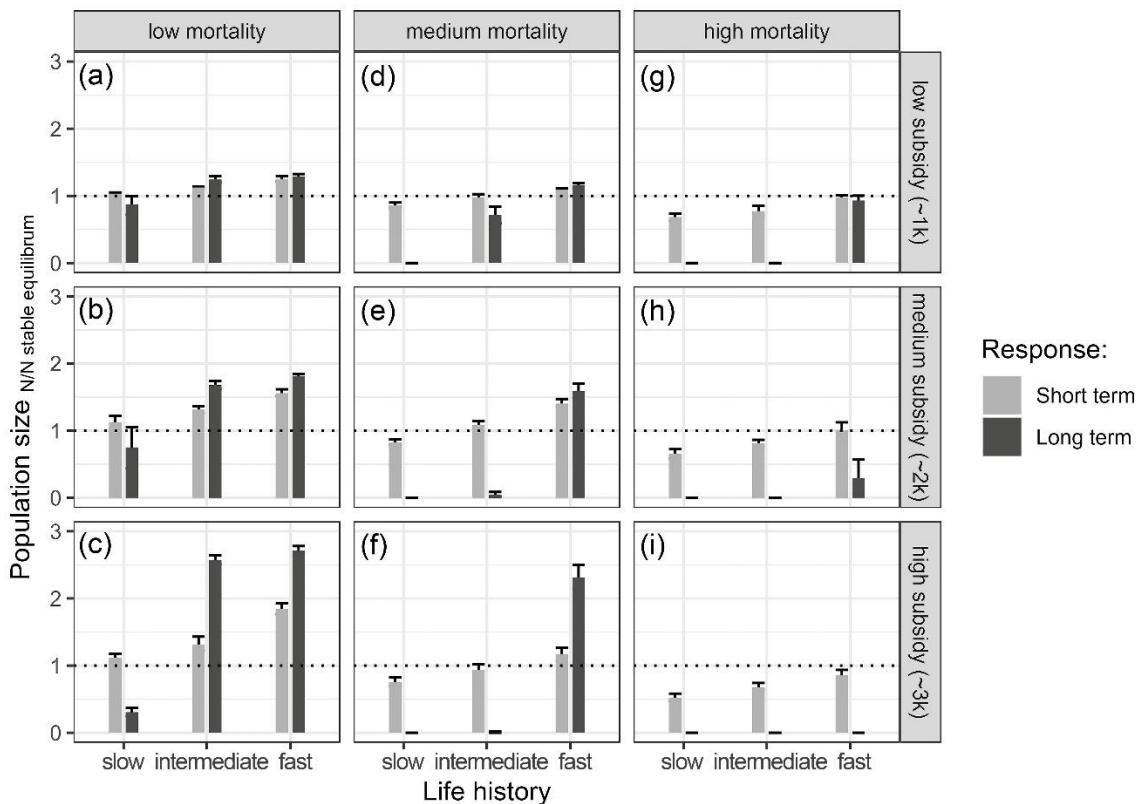


Figure 5. Short- and long-term population responses (mean  $\pm$  bootstrapped 95% confidence interval) of species with varying life histories—slow (albatross), intermediate (gull), and fast (cormorant)—to a compensatory ecological trap involving a demographic trade-off between decreased survival and increased recruitment due to trophic subsidies ( $n = 189$  models; 3 life histories  $\times$  3 subsidy levels  $\times$  3 mortality levels  $\times$  7 replicates). Population sizes are standardized to the steady-state size observed in the first 24 years under control conditions.

Intermediate Species (e.g., gull): At low mortality, the intermediate species achieved slightly higher asymptotic growth than the control in the long term ( $1.1 \pm 0.02$

times control, Figure 5a). At medium and high subsidy levels, it attained more substantial asymptotic growth, reaching  $1.7 \pm 0.09$  and  $2.6 \pm 0.1$  times the control, respectively (Figure 5b-c). Under medium mortality, the intermediate species exhibited a non-linear short-term response, peaking at medium subsidy levels ( $1.1 \pm 0.12$  times control, Figure 5e-f). However, in the long term, it showed lower asymptotic growth than the control at low subsidy ( $0.7 \pm 0.19$  times control, Figure 5d) and faced a tendency toward decline and eventual extinction at intermediate and high subsidy levels, with 43% and 71% probabilities of extinction, respectively (Figure 5e-f). Under high mortality, the intermediate species experienced sharp short-term declines and ultimately reached a 100% probability of extinction in the long term (Figure 5g-i).

**Fast Species (e.g., cormorant):** At low mortality, the fast species grew rapidly in the short term and reached asymptotic growth in the long term, attaining  $1.3 \pm 0.05$ ,  $1.8 \pm 0.04$ , and  $2.7 \pm 0.09$  times the control size as subsidy levels increased from low to high (Figure 5a-c). Under medium mortality, the fast species exhibited a non-linear short-term response similar to that of the intermediate species, with its highest population size observed at medium subsidy ( $1.4 \pm 0.09$  times control, Figure 5d-f). In the long term, it reached asymptotic growth at  $1.2 \pm 0.06$  and  $1.6 \pm 0.16$  times the control as subsidy levels increased from low to medium. At high subsidy, it grew to a larger size, but without reaching asymptotic growth ( $2.3 \pm 0.28$  times control, Figure 5f). Under high mortality, the fast species initially matched control population sizes at low and medium subsidy levels but experienced a short-term decline at high subsidy ( $0.8 \pm 0.11$  times control, Figure 5g-i). In the long term, it stabilized at sizes similar to the control under low subsidy

( $0.9 \pm 0.11$  times control, Figure 5g), while the likelihood of decline increased at medium and high subsidy levels, reaching 29% and 100% probabilities of extinction, respectively (Figure 5h-i).

#### 4.2. Trap variations

The smaller-area trap increased the resilience of declining populations compared to the base model and reduced the carrying capacity ( $K$ ) for growing populations (Figure 6).

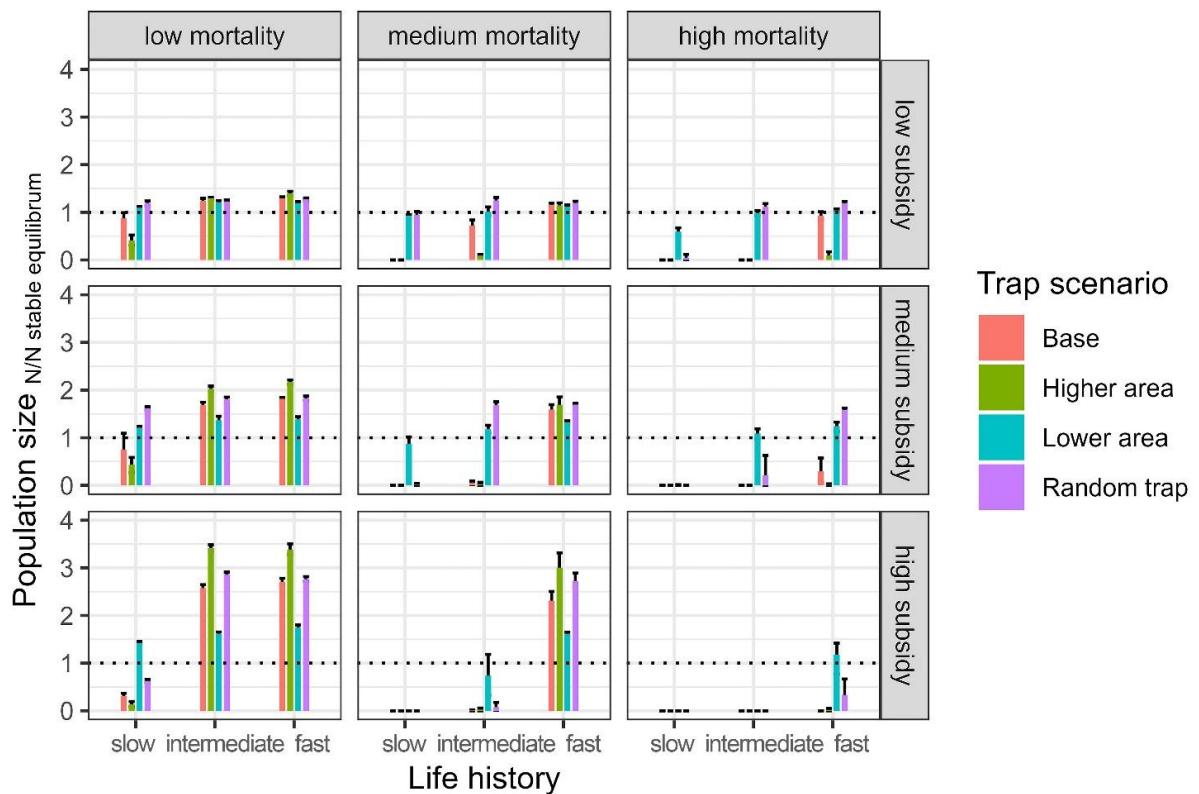


Figure 6. Long-term population responses (mean  $\pm$  bootstrapped 95% confidence interval) of species with varying life histories—slow (albatross), intermediate (gull), and fast (cormorant)—to the base trap configuration, a larger-area trap (25% of the habitat), a smaller-area trap (5% of the habitat), and a randomly distributed trap covering 15% of the habitat. Population sizes are standardized to the steady-state size observed during the first 24 years under control conditions.

In contrast, the larger-area trap generally had more severe impacts on declining populations and increased K for growing populations compared to the base model (Figure 6). Overall, the random trap scenario was less severe for declining populations and also increased K for growing populations in comparison to the base model (Figure 6).

## 5. Discussion

Understanding the mechanisms behind ecological traps is essential, especially given the rapid, human-induced environmental changes that present poorly known risks to populations. Previous ecological trap models have generally assumed reduced survival and/or reproduction among trapped populations (Battin 2004), leading to the conclusion that these traps inevitably decrease population sizes and heighten vulnerability to stochastic extinction. Our model introduces a novel trade-off: increased recruitment—driven by trophic subsidies—counterbalanced by a reduction in survival rates. While the model predicts similar results to previous models, it also reveals critical differences. As expected, the severity of trap impacts increases when traps occupy larger portions of available habitats or when they emerge in higher-quality habitats that attract greater preference (Delibes et al. 2001, Fletcher et al. 2012, Hale et al. 2015b). Below, we explore novel aspects of our model predictions, the assumptions underpinning them, areas for future refinement, and contrasts with existing evidence of seabird-fishery interactions. Finally, we discuss their implications for effective management and conservation strategies.

### 5.1. Fitness trade-offs within the ecological trap framework

Our model revealed a critical interaction between trophic subsidies and mortality, resulting in more complex population responses than anticipated by previous ecological trap models. These included non-linear responses both over time and across different levels of subsidy and mortality. All three life histories displayed non-linear temporal dynamics, where the initial positive effects of recruitment (breeders and fledging, Figure S3, S4) outweighed mortality (Figure S5). However, populations were unable to sustain growth in the long term, leading to eventual declines (e.g., the slow-lived species in scenario C, the intermediate-lived species in scenario E, and the fast-lived species in scenario G, Figure 4). This highlights the challenge of detecting a trap that appears advantageous in the short term but can lead to long-term population extinction. Overall, these responses are expected to be more common in fast-lived species, as they have greater potential for population growth, which also implies more pronounced density dependence (Herrando-Pérez et al. 2012), higher demographic stochasticity (Sæther et al. 2004) and a greater tendency toward nonlinear and chaotic dynamics (Clark and Luis 2020, Rogers et al. 2022).

Similarly, all three life histories exhibited non-linear responses across varying levels of mortality and subsidy. At lower mortality levels, trophic subsidies effectively compensated for mortality and promoted population growth. However, once mortality exceeded a critical threshold, subsidies amplified mortality impacts—specifically, increased habitat preference elevated effective mortality (Figure S5)—ultimately causing population declines and, in some cases, extinction. In contrast, simulations by Hale et al. (2015) showed that reductions in either fecundity or survival within traps individually

decreased metapopulation persistence, but their combined effects did not further amplify trap impacts. Our findings emphasize the importance of incorporating trade-offs among fitness components into ecological trap frameworks (Battin 2004), as habitat preference can cause fitness components to respond antagonistically or synergistically, resulting in more diverse responses than those anticipated by ecological trap models.

## **5.2. Influence of life history on compensatory ecological traps**

Additionally, our results demonstrate that the interplay between mortality and subsidies is heavily influenced by species' life history traits along the slow-fast continuum (Saether 1987)—the main axis of life history variation across several taxa, including mammals, birds, reptiles, fishes, insects, and plants (Sibly et al. 2012, Gaillard et al. 2016, Capdevila et al. 2020, Cooney et al. 2020). Considering the three habitat preference scenarios (base, higher, and lower area), our model predicts that the species with the slowest life history is 1.41 and 4.5 times more likely to face extinction compared to species with intermediate and fast life histories, respectively. These findings align with theoretical expectations, highlighting that 'slow' life-history species are particularly vulnerable to local extirpations caused by traps (Hale et al. 2015b). In contrast, faster species exhibit greater resilience and, under similar conditions, can thrive, with population sizes potentially increasing up to threefold compared to control groups. These results suggest that compensatory traps may amplify the selective filtering of life history more intensely than previously anticipated (Kokko and Sutherland 2001, Hale et al. 2015b).

Recent studies within a broader context agree with our findings, indicating that species with longer generation times require extended recovery periods following disturbances, while species with shorter generation times tend to exhibit greater resilience (Capdevila et al. 2022). Furthermore, animals with slower life histories are generally at greater risk of extinction compared to faster-reproducing species, including plants, mammals, birds, reptiles, amphibians, and freshwater fish. This could result in big shifts in ecological strategies across the tree of life (Cooke et al. 2019, Carmona et al. 2021, Richards et al. 2021, 2024). Integrating various trade-offs between fitness components into the theoretical framework of ecological traps is thus essential for identifying traps and clarifying their contribution to the global filtering of animal life histories.

### **5.3. The case of seabirds-fisheries interaction**

Model predictions agree with previous research documenting a variety of responses in seabirds across the slow-fast continuum in relation to fisheries discards and bycatch. For instance, studies on slow species such as albatross and shearwater suggest that while fisheries subsidies can enhance reproductive traits like recruitment and breeding success, these gains are offset by reduced survival rates due to bycatch, ultimately causing important population declines (Véran et al. 2007, Rolland et al. 2008, 2009b, 2010, Tuck et al. 2015, Genovart et al. 2016, 2017, Pardo et al. 2017, Cleeland et al. 2021). A well-documented case in South Georgia illustrates the impact of bycatch on the Wandering (*Diomedea exulans*), Gray-headed (*Thalassarche chrysostoma*), and Black-browed (*Thalassarche melanophrys*) albatrosses. Despite potential reproductive

and recruitment increases from fishery discards, bycatch has led to drastic declines in these populations, estimated at 40–60% over the past 35 years (Pardo et al. 2017). Similarly, the Balearic shearwater (*Puffinus mauretanicus*), Europe's most endangered seabird, has experienced substantial population declines due to bycatch. Projections suggest that, if bycatch rates remain unchanged, this species could face extinction within the next 61 years (Genovart et al. 2016). These findings are reinforced by recent studies that seabird life history traits predict extinction risk and vulnerability to anthropogenic threats, including bycatch (Richards et al. 2021, 2024).

In contrast, for species with fast life history traits our model predicts greater resilience and even potential for population growth in response to compensatory traps. Discards can positively influence various reproductive traits of faster seabirds (Oro et al. 2013), which often demonstrate greater phenotypic plasticity in reproduction compared to slower species. These species, which lay up to six eggs (Schreiber and Burger 2001), show earlier laying dates, increased clutch sizes, and improved hatching and breeding success. Notable examples include Audouin's gull (*Larus audouinii*), the Yellow-legged gull (*Larus cachinnans*), and the Lesser Black-backed gull (*Larus fuscus*) (Oro, 1996; Oro et al., 1996, 1995). Studies have shown a positive correlation between subsidy availability and population size, as well as a negative correlation with population variability in these gull species. This suggests that subsidies can mitigate the high demographic stochasticity inherent to fast life histories (Oro et al. 2013). Surprisingly, evidence for the positive effects of fishery discards on seabird population sizes remains largely circumstantial. Most such evidence stems from Northern Hemisphere seabirds,

including Black-backed gulls (*Larus marinus*), Herring gulls (*Larus argentatus*), Great skuas (*Stercorarius skua*), Northern gannets (*Morus bassanus*), and Northern fulmars (*Fulmarus glacialis*). These species experienced rapid population growth during the peak of discard production in the 20th century but have since stabilized or declined (Bicknell et al. 2013, Oro et al. 2013, Wilhelm et al. 2016, Langlois Lopez et al. 2023). While current fishery discards are approximately half of 1980s and 1990s levels, recent estimates suggest that global fisheries still discard between 7 and 16 million tons annually, with nearly 60% originating from trawl fisheries (Gilman et al. 2020). This substantial volume of discards likely continues to sustain large seabird populations. For instance, one extensive study found that despite a 48% decrease in North Sea discards from 1990 to 2010, these discards still supported an estimated 3.3 to 9.7 million seabirds annually (Sherley et al. 2019). These findings highlight the urgent need to reduce uncertainties surrounding global discard estimates and to investigate their role in driving compensatory traps for seabirds.

#### **5.4. Model assumptions, caveats, and future improvements**

Our model was based on two key assumptions. First, we assumed that populations were energetically limited. Second, we assumed that species with different life histories were approximately bioequivalent, meaning that they acquire and use energy in the same way, sharing all parameters except for life history. This assumption meets with the "energy equivalence rule," a central principle of the metabolic theory of ecology (Brown 2004, Robert Burger et al. 2021), which posits that energy partitioning among species in space is independent of body mass, due to compensatory variation in

metabolism-mass and abundance-mass relationships (Hatton et al. 2019). However, evidence from birds suggests that “population metabolism” (i.e., the total amount of basal energy used by a population per unit area) tends to be higher in larger species (Hatton et al. 2019), implying that compensatory effects may be smaller for slower species than predicted by our model. Nevertheless, if the assumption of bioequivalence does not hold, compensatory traps could lead to population responses that are difficult to predict. Such responses might include changes in habitat use, vital rates, population growth rates, and overall population sizes.

Additionally, to simplify our model, we assumed identical reproductive phenology across life histories. This assumption allowed us to evaluate traps with equal exposure for all life histories, but it may overlook critical aspects of life-history variation. For example, the duration of the developmental period is a fundamental axis of life-history variation (Cooney et al. 2020). Differences in developmental times, and consequently in the use of parental habitat, could influence species' responses to ecological traps, potentially leading to disparities in trap exposure and severity.

Finally, our model follows the principles of optimal foraging theory, which suggests that individuals make foraging decisions aimed at maximizing their fitness. Decisions about when and where to move are influenced by both hunger and previous foraging success. A valuable enhancement would be to incorporate trade-offs into these decisions (Railsback 2022), such as those between hunger and fear, or by using more direct fitness measures, including growth, survival, reproduction, and risk avoidance. Incorporating fear, in general terms, is expected to increase species resilience. However,

how fear emerges in response to the accumulated experiences of different life history strategies and its population-level consequences remain intriguing avenues for future research.

### **5.5. Management implications**

Our study suggests that compensatory trap models could be essential for understanding and predicting the impacts of anthropogenic food subsidies—such as crops, dumps, restaurants, offal, and fisheries discards—on scavenger species (Oro et al. 2013, Munstermann et al. 2022). These subsidies often come with major fitness costs, including increased risks of poisoning, pathogen infection (e.g., in birds: Becker et al., 2015), interference competition (e.g., in sharks: Semeniuk and Rothley, 2008), predation (e.g., in mammals and birds, Morris, 2005; Rodewald et al., 2011), hunting (e.g., mammals, Simon and Fortin, 2020), and incidental mortality (e.g., in seabirds, turtles, marine mammals and elasmobranchs: Lewison et al., 2014).

Ecological trap models have evolved from basic source-sink frameworks to realistic IBMs that incorporate habitat selection, individual learning or adaptive capacities, local interactions (both spatial and network-based), and dynamic, heterogeneous environments. These models are increasingly applied in terrestrial ecosystems to assess ecological traps, providing valuable insights for management and conservation strategies (Sánchez-Clavijo et al., 2016; Simon and Fortin, 2020). In contrast, the application of such models in marine ecosystems has remained notably absent, despite growing empirical evidence of their importance (Swearer et al., 2021).

For example, in seabird-fishery interactions, ecological trap frameworks have primarily focused on fitness declines driven by low-quality food sources, as described by the "junk food hypothesis" (Grémillet et al. 2008). Our findings, alongside existing evidence, emphasize the urgent need to recognize compensatory traps as an unintended consequence of fisheries activities, particularly when they are considered in the long term. These traps should be regarded as a cornerstone for advancing ecosystem-based fisheries management (EBFM) (Pikitch et al. 2004).

Integrating compensatory trap models into EBFM frameworks could substantially enhance conservation and management outcomes. These models could complement current population risk assessments—such as those endorsed by ACAP—which often overlook the interactive effects of trophic subsidies and bycatch. Parametrized using seabird movement and behavior ([www.seabirdtracking.org](http://www.seabirdtracking.org), Carneiro et al., 2024), metabolism (Dunn et al., 2018; Sibly et al., 2013), and demographic and fisheries data (e.g., bycatch rates and discard energy from observer programs), these models can help establish clear management objectives and fishery-specific thresholds. In doing so, they can identify sustainability tipping points—conditions under which subsidies shift from buffering to amplifying bycatch impacts—thus informing discard regulations and long-term mitigation strategies.

## 6. Conclusion

Our model reveals a critical interaction between trap subsidies and mortality, with distinct thresholds for species depending on their position across the slow-fast life history continuum. These thresholds mark the point at which subsidies shift from

providing demographic benefits to producing negative synergistic effects when combined with increased mortality, due to stronger habitat preference and exposure to lethal conditions. Our findings showed that, under similar behavioral and metabolic conditions, slow species are more vulnerable to extinction in compensatory traps—being 1.4 times more likely to go extinct than intermediate species and 4.5 times more likely than fast species. In contrast, fast species exhibit greater demographic resilience and even the potential for population growth in some scenarios. These results support and extend previous predictions about ecological traps, highlighting the need to broaden the conceptual framework to account for a wider range of fitness trade-offs. By elucidating how trophic subsidies and mortality interact across the life-history continuum, this work contributes to a broader understanding of the conditions under which ecological traps emerge and how they may influence community structure by selectively filtering life-history strategies. Importantly, our findings highlight the need to manage both bycatch and fishery discards in an integrated manner, as their demographic effects are not independent and may interact to reinforce maladaptive habitat selection and increase extinction risk. In these contexts, compensatory traps offer a critical conceptual and predictive framework for advancing EBFM, ultimately enhancing the effectiveness of conservation and management strategies.

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## 8. Supplementary material

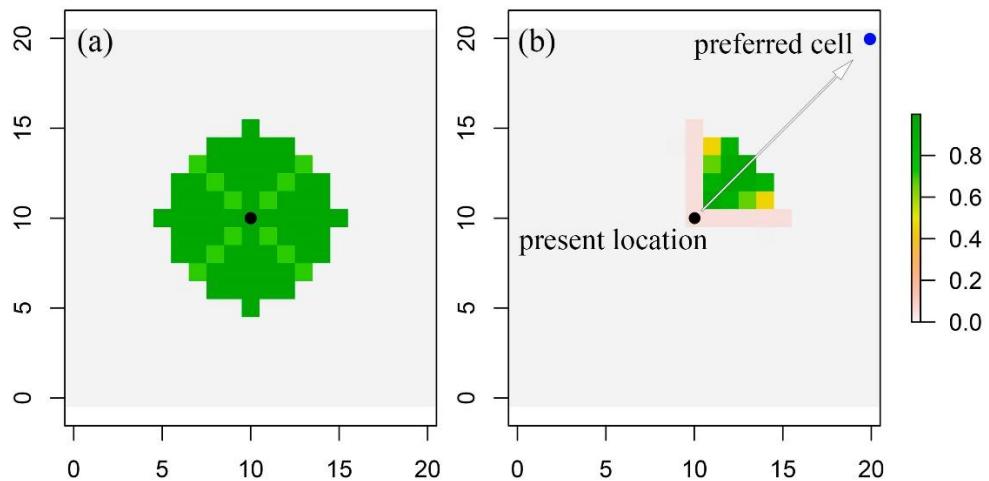


Figure S1. Diagram illustrating how movement probabilities are assigned to cells within the movement radius of an individual (located at the colony,  $x=10$ ,  $y=10$ , in the example), both without (a) and with (b) cell preference. In (a) all cells within the movement radius are assigned equal probability (1), except for diagonal cells, which are penalized (0.7) to maintain isotropic movement. In (b), higher probabilities are assigned to cells in the direction of the preferred cell (blue cell at  $x = 20$ ,  $y = 20$ , in the example). The figure illustrates the probabilities assigned using the chosen parameters ( $\beta_{dire}=30^\circ$  and  $\beta_{kdir}=-0.2$ , see Figure S2).

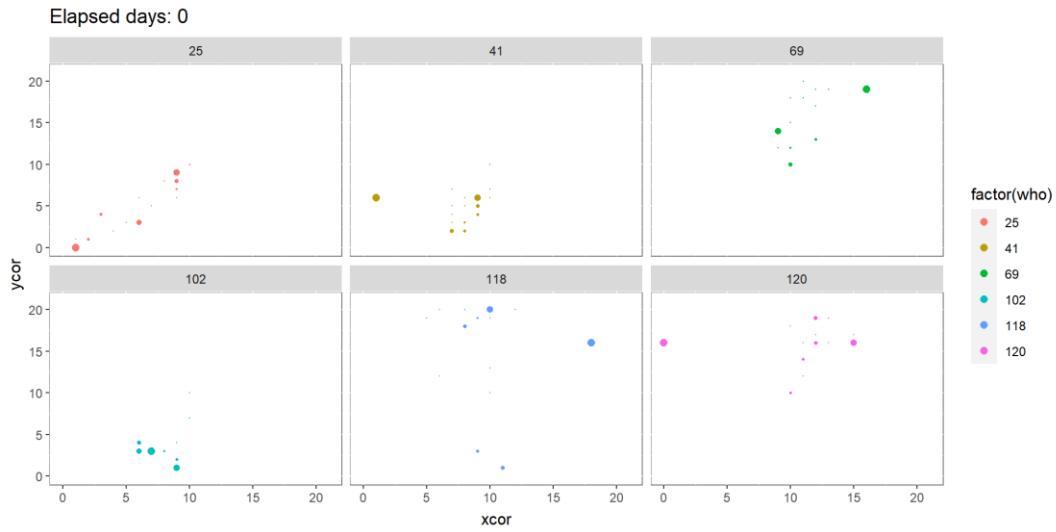


Figure S2. Animation illustrating the movement of individuals with habitat preference across cells. The annual cycle of six randomly selected individuals in the base model is displayed, with a fade effect applied to their locations to enhance visualization. On day 219, the reproductive season begins, and the individuals return to the colony at the center of the raster ( $x = 10, y = 10$ ) to feed their chick.

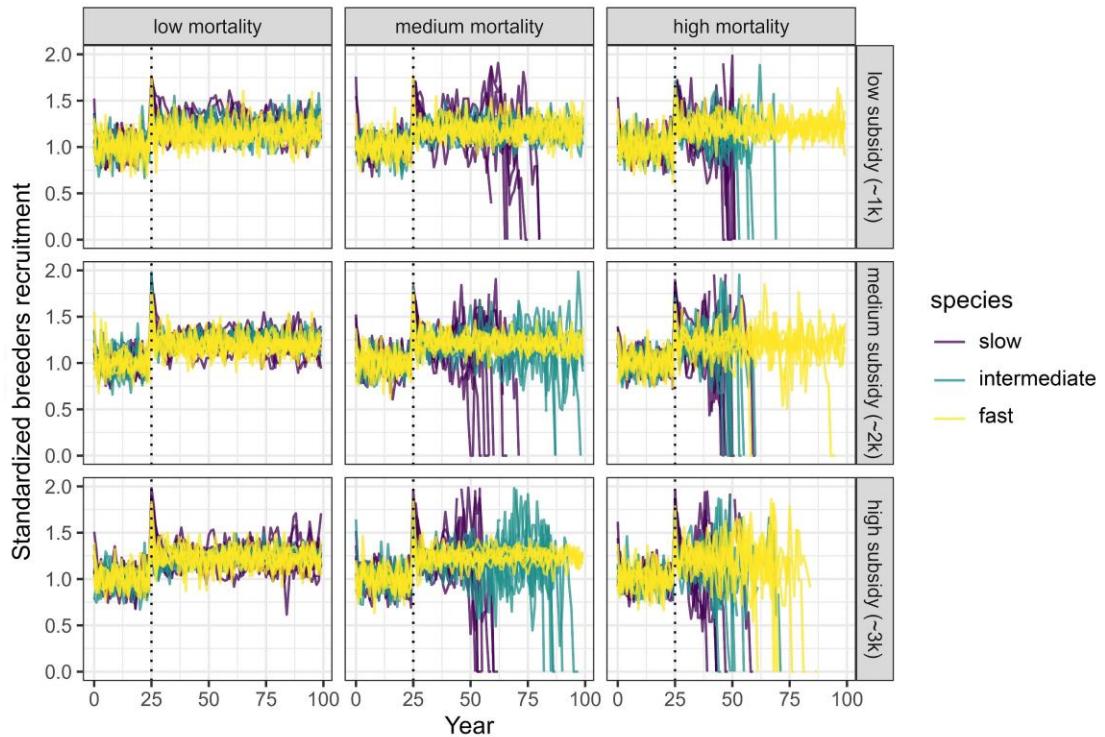


Figure S3. Breeders recruitment in species with varying life histories—slow (albatross), intermediate (gull), and fast (cormorant)—in the base trap configuration ( $n = 189$  models; 3 life histories  $\times$  3 subsidy levels  $\times$  3 mortality levels  $\times$  7 replicates). The dashed line indicates the start of the trap. The proportion of breeders relative to the total number of potential breeders is shown, standardized to the average values observed during the first 24 years under control conditions.

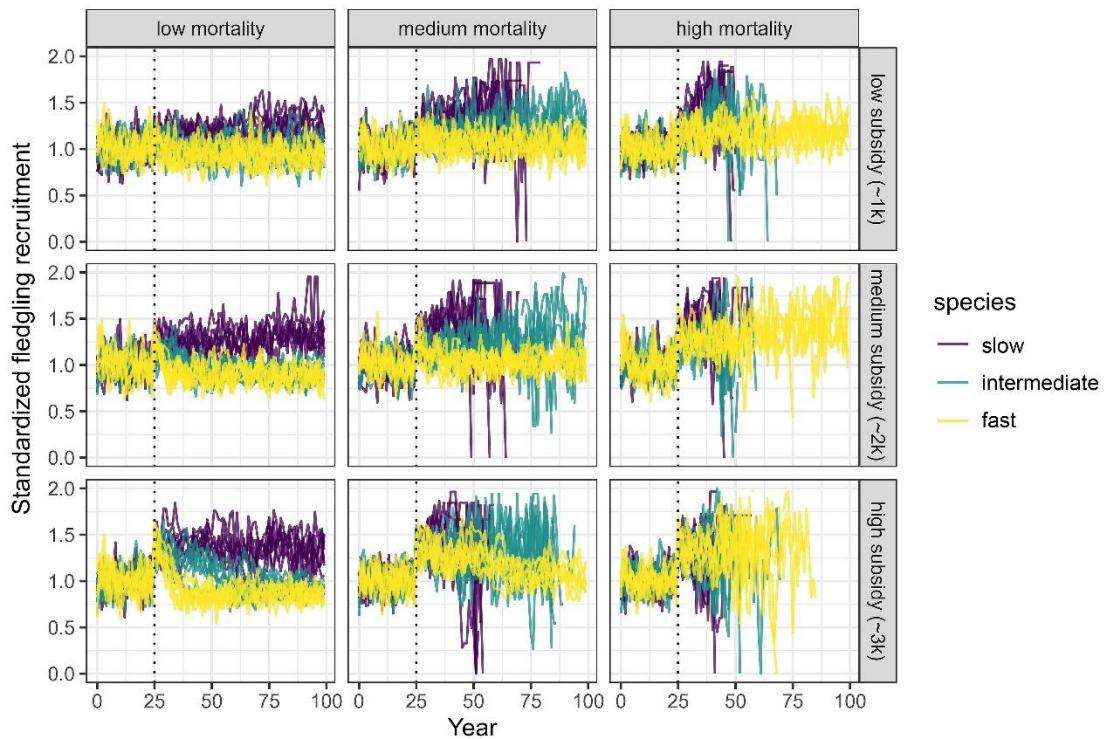


Figure S4. Fledgling recruitment in species with varying life histories—slow (albatross), intermediate (gull), and fast (cormorant)—in the base trap configuration ( $n = 189$  models; 3 life histories  $\times$  3 subsidy levels  $\times$  3 mortality levels  $\times$  7 replicates). The dashed line indicates the start of the trap. Recruitment is expressed as the number of fledglings per breeder, standardized to the average values observed during the first 24 years under control conditions.

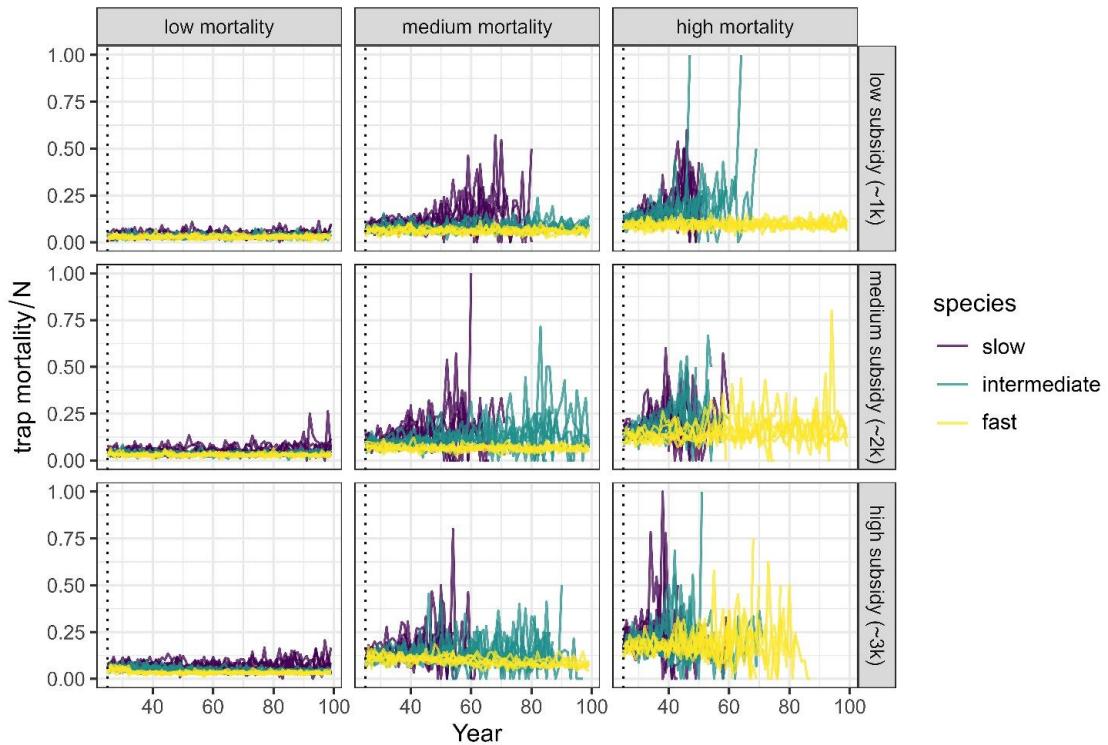


Figure S5. Effective trap mortality of species with varying life histories—slow (albatross), intermediate (gull), and fast (cormorant)—in the base trap configuration ( $n = 189$  models; 3 life histories  $\times$  3 subsidy levels  $\times$  3 mortality levels  $\times$  7 replicates).

CHAPTER 3. Risky Rewards: Modeling a Compensatory Ecological Trap Between the Black-Browed Albatross and Trawl Fisheries

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## **1. Abstract**

Ecological traps occur when organisms find a habitat equally or more attractive than other available options, despite experiencing reduced fitness having selected it, often as a result of human-induced environmental change. In marine ecosystems, fisheries can generate compensatory ecological traps by providing trophic subsidies (e.g., discards) that enhance habitat attractiveness and potentially increase recruitment, while simultaneously elevating bycatch risk. We evaluated whether interactions between Black-browed Albatrosses and demersal trawl fisheries in southern Chile give rise to ecological traps under contrasting bycatch and discard regimes, and evaluated the potential for demographic compensation. Using a spatially explicit, individual-based bioenergetics model, we simulated population dynamics at Chile's four largest colonies under a no-fishing scenario (no-trap) and three ecological trap scenarios reflecting varying levels of bycatch and discards before and after the implementation of mitigation measures in 2019–2020: pre-regulation trap, pre-regulation with cryptic mortality (i.e., unobserved bycatch), and post-regulation. Under pre-regulation conditions—characterized by an estimated annual mortality of 4,000 birds and 11,000 t of discards—the model predicted divergent outcomes: Diego Ramírez expanded beyond no-trap levels, whereas Ildefonso and Diego de Almagro declined, with the cryptic mortality scenario—assuming bycatch levels three times higher than observed—ultimately driving populations to extinction. Although recruitment increased in some colonies, these gains were primarily driven by density-dependent relaxation of competition following elevated mortality, rather than energetic benefits from discards. Thus, while trophic

subsidies contributed to trap formation by attracting individuals, they were insufficient to offset the demographic costs of bycatch. In contrast, the post-regulation scenario—with substantially reduced bycatch (400 birds) and discards (3,000 t)—produced population trajectories resembling the no-trap scenario, supporting long-term persistence in most colonies. Evangelistas, however, declined toward extinction across all scenarios, suggesting it functions as a demographic sink. Finally, our findings underscore the critical role of bycatch mitigation (mostly Bird Scaring lines) and discard reduction in supporting the long-term viability of Black-browed Albatross populations. Regulatory measures implemented in Chile since 2019 markedly improved demographic outcomes, highlighting the importance of sustaining and strengthening these efforts. More broadly, ecological trap theory offers a valuable framework for understanding maladaptive habitat selection and guiding ecosystem-based fisheries management.

## **2. Introduction**

Ecological traps occur when organisms find a habitat equally or more attractive than other available options, despite experiencing reduced fitness having selected it. Such maladaptive choices can elevate the risk of population extinction (Dwernychuk and Boag 1972, Gates and Gysel 1978, Kokko and Sutherland 2001). These phenomena are closely linked to human activities that alter habitats faster than organisms can adapt—a process known as "human-induced rapid environmental change (Sih et al. 2011). A well-known example involves the attraction of invertebrate and vertebrate species to artificial lights or window reflections, which can lead to injury, mortality, or impaired reproduction (Schlaepfer et al. 2002). Over recent decades, evidence for ecological traps

has grown across terrestrial, urban, and, more recently, marine environments (Robertson et al. 2013, Hale et al. 2015a, Swearer et al. 2021). This trend, coupled with expanding human pressures on natural ecosystems, suggests that the prevalence of ecological traps is likely to increase.

Most ecological trap models assume that individual survival or reproduction is compromised due to poor habitat selection (Delibes et al. 2001, Kokko and Sutherland 2001, Donovan and Thompson 2001, Kristan et al. 2003, Fletcher et al. 2012, Hale et al. 2015b). However, because habitat selection often involves trade-offs among fitness components, compensatory traps—where increases in one vital rate (e.g., reproduction) mask reductions in another (e.g., survival)—may be more common than currently assumed (Battin 2004, Chapter 1,2). A key driver of such traps is the availability of human-derived trophic subsidies (Oro et al. 2013). These subsidies offer abundant and predictable food sources and have been documented in 20% of bird and 30% of mammal orders, where they may enhance foraging success and reproduction (Oro et al. 2013). Yet, increased habitat preference from subsidies can also elevate mortality risks from pollutants, predators, competition, parasitism, hunting, or accidental deaths (Morris 2005, Semeniuk and Rothley 2008, Rodewald et al. 2011, Lewison et al. 2014, Becker et al. 2015, Lamb et al. 2017, Sigaoud et al. 2017, Simon and Fortin 2020). These trade-offs between survival and reproduction can yield complex, nonlinear population outcomes (Chapter 2), and may be especially relevant in systems where anthropogenic food sources attract animals into risky environments.

A particularly relevant context in which ecological traps involving such trade-offs may emerge is the interaction between seabirds and fisheries. Seabirds are attracted to artisanal and industrial fishing vessels due to the trophic subsidies they provide, including bait, catches, and, most notably, discards (Chapter 1). Global fisheries discard an estimated 7 to 16 million tons of biomass annually, with approximately 60% originating from trawl operations (Gilman et al. 2020). This attraction exposes seabirds to elevated bycatch risk through hooking (e.g., longline; Anderson et al. 2011), entanglement (e.g., purse seine, gillnets; Źydelis et al. 2013, Simeone et al. 2020), or collisions with gear (e.g., trawl; Phillips et al. 2024). Bycatch is currently the leading marine threat to seabird conservation, affecting nearly 30% of species globally, with well-documented negative effects on both adult and juvenile survival (Dias et al. 2019). At the same time, some studies suggest that fishery discards—capable of subsidizing millions of birds (Garthe et al. 1996, Sherley et al. 2019)—can enhance breeding success and increase recruitment (Rolland et al. 2008, 2009b, 2010, Pardo et al. 2017, Cleland et al. 2021). These dual pressures can generate contrasting demographic effects that may vary across species, fisheries, and management regimes (Chapter 2). However, despite increasing recognition that fisheries may create ecological traps through trophic subsidies (Chapters 1-2), the demographic trade-offs driving such traps—and their long-term population consequences—remain poorly understood.

Albatrosses—among the seabird groups most affected by these interactions—exemplify this issue. Of the 22 species, 21 exhibit some degree of scavenging behavior, and all are threatened by bycatch (Dias et al. 2019, Phillips et al. 2024, Chapter 1). Their

strong reliance on fishery discards as a food source (Chapter 1), combined with slow life histories—characterized by delayed reproduction, single-egg clutches, and high adult survival (Sibly et al. 2012, Richards et al. 2021)—and wide-ranging movements across ocean basins (Clay et al. 2019, Beal et al. 2021), make them particularly vulnerable to fishery-induced ecological traps (Chapter 2). Although some populations have shown recruitment increases associated with discards (Rolland et al. 2008, 2009b, 2010, Pardo et al. 2017, Cleland et al. 2021), the joint demographic effects of bycatch and trophic subsidies remain difficult to disentangle through correlative models—especially across spatially structured populations. Mechanistic models are thus essential for assessing the conditions under which ecological traps may emerge and persist, as they allow explicit representation of trade-offs among vital rates and the integration of spatial dynamics.

Within this group, the Black-browed Albatross (*Thalassarche melanophrys*) is one of the species that interacts most frequently with global fisheries (Clay et al. 2019, Carneiro et al. 2020). Nearly 20% of the global Black-browed Albatross population inhabits southern Chile, which also supports the country's largest trawl fisheries (Adasme et al. 2019). The industrial central-south trawl fleet targeting South Pacific hake (*Merluccius gayi*) has operated off central Chile since the 1930s, while southern fleets (41–57°S) targeting *Merluccius australis*, *Macruronus magellanicus*, and *Micromesistius australis* began operations in the late 1970s. Previous studies linked trawl and longline fisheries to significant albatross declines between 1993 and 2005 (Robertson et al. 2014), while subsequent mitigation in longline fleets facilitated recovery in colonies on Diego Ramírez and Ildefonso.

More recent estimates, however, indicate alarmingly high bycatch levels in trawl fisheries between 2013 and 2019—far exceeding earlier assessments (Richard and Adasme 2019, Adasme et al. 2019). These impacts also involved high discard rates, which have been identified as a key foraging resource during the breeding season in Diego Ramírez (Arata and Xavier 2003), potentially enhancing recruitment, as has been observed for this and other albatross species in the Kerguelen and South Georgia Islands (Rolland et al. 2008, 2009b, 2010, Pardo et al. 2017). However, these energetic benefits come at the cost of increased exposure to fishing vessels and, consequently, a higher risk of bycatch. This trade-off raises serious concerns about the long-term sustainability of both fisheries and albatross populations.

In response, Chile introduced regulatory measures between 2019 and 2020, including mandatory seabird bycatch mitigation (primarily bird-scaring lines), best fishing practices, and onboard electronic monitoring systems with image recording devices (Resolutions No. 2110/2014, 2941/2019, and 2569/2021; see Cucas et al. 2024). These actions have led to substantial reductions in bycatch and discards in recent years (Cucas et al. 2024). Still, the effects of these measures on Black-browed Albatross populations remain unknown.

To address this gap, we evaluated whether interactions between Black-browed Albatrosses and demersal trawl fisheries in southern Chile give rise to ecological traps under contrasting bycatch and discard regimes—specifically before and after the implementation of fishery regulations—and whether trophic subsidies can compensate for bycatch-induced demographic costs. To this end, we developed a spatially explicit,

individual-based bioenergetics model to simulate population-level dynamics under varying bycatch and discard conditions. The model incorporates the four largest Chilean colonies—home to 99.6% of the national Black-browed Albatross population—and is parameterized with species-specific data on habitat use, metabolic demands, movement behavior, and life-history traits. This framework allows us to project population trajectories under alternative management scenarios shaped by recent regulatory changes and to evaluate the effectiveness of these measures in guiding ecosystem-based fisheries management and long-term conservation planning.

### **3. Methods**

Figure 1 illustrates the study framework, which integrates an individual-based model (IBM) parameterized with a species distribution model (SDM) and empirical estimates of fishing bycatch and discards derived from an on-board observation program. Foraging track data was used to predict the habitat of Black-browed albatrosses during the breeding season (September to April/May) through the SDM, while fisheries data informed monthly bycatch rates and the weekly energetic contribution of discards in trap scenarios.

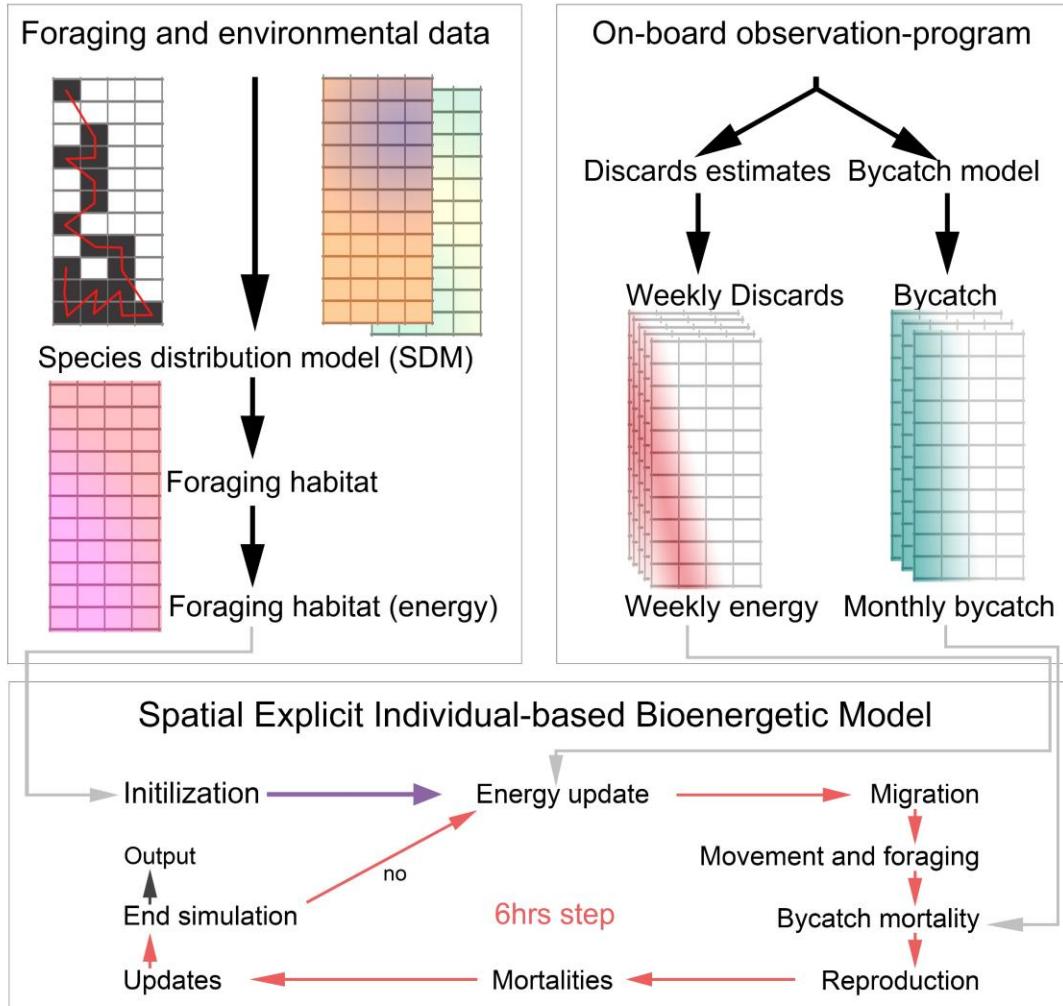


Figure 1. Study framework integrating a species distribution model (SDM), empirical fisheries data, and an individual-based model (IBM) to simulate compensatory ecological trap scenarios involving Black-browed Albatrosses and trawl fisheries in Chile. The colored palettes of the rasters do not represent any real variable; they are intended to be illustrative only.

### 3.1. Black-browed albatross distribution

We modeled the foraging distributions of Black-browed albatrosses during the breeding season using a random forest algorithm (Breiman 2001) implemented in the biomod2 R package (Thuiller et al. 2021), with a spatial resolution of 20x20 km. Tracking data from 163 individuals across three colonies—Diego Ramirez, Ildefonso, and Diego de

Almagro—were utilized, spanning five breeding seasons (incubation, brood/guard, and post-brood/guard) between 1997 and 2012 (Table S1, see, Robertson et al., 2014). After filtering to retain only one presence point per grid cell, 2,477 presences remained. To fit and evaluate the model, we generated pseudo-absence data, as required by the algorithm. Following recommendations for random forest models, we selected an equal number of pseudo-absence points to presence points to optimize performance (Barbet-Massin et al. 2012). We used 10 replicates of pseudo-absences, randomly distributed across the study area ( $88^{\circ}\text{S}$  to  $55^{\circ}\text{S}$ ,  $73.1^{\circ}\text{W}$  to  $32.5^{\circ}\text{W}$ ), excluding cells where presence was recorded.

We incorporated six environmental proxies that directly or indirectly could influence the distribution of Black-browed albatross prey, along with two factors related to habitat accessibility and intraspecific competition. The environmental proxies included chlorophyll-a, sea surface temperature, sea water velocity, wind speed, bathymetry, and topographic slope. These environmental predictors have been successfully used in previous studies to model the distributions of top predators, including albatrosses (Wakefield et al. 2011, Oppel et al. 2012, Scales et al. 2014). These data, sourced from Bio-ORACLE at a spatial resolution of 0.05 degrees, represent average conditions for the period 2000–2010 (Assis et al. 2024).

During the breeding season, birds are constrained by the need to return regularly to their nesting sites—a central-place foraging constraint—which makes some habitats more costly to access than others (Orians and Pearson, 1979). Because the energetic cost of accessing foraging areas increases with distance from the colony (Matthiopoulos

2003), we used the distance to the nearest colony as a proxy for habitat accessibility. Additionally, seabird habitat use is shaped by competition driven by niche overlap (Wakefield et al., 2011, 2013). Competition among conspecifics tends to be more intense than interspecific competition (Simberloff and Dayan 1991) and it is typically influenced by conspecific density. To account for this, we used the distance to the “Falkland super colonies” (including Steeple Jason and Beauchêne Islands, which account for ~50% of the global population) as a proxy for parapatric competition (Wakefield et al. 2011). Both layers were calculated using the gridDistance function in the raster package (Hijmans and van Etten 2010).

To train and evaluate the model, we used 75% of the occurrence points for calibration and the remaining 25% for validation. Model performance was assessed using the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS) over the sensitivity (rate of correctly identifying presence/habitat) and specificity (rate of correctly identifying absence/unsuitable habitat) of models. From the 10 replicates, we selected the best-performing models ( $TSS > 0.75$ ) to construct an ensemble distribution model. This ensemble was created by averaging the raw model outputs, weighted by their respective TSS scores, to produce a single distribution map scaled from 0 to 1. This raster was used to simulate the habitat quality of the Black-browed albatross in the individual-based model.

### **3.2. Bycatch and discard estimates**

Bycatch and fishing data from the three trawl fisheries operating between 33°S and 57°S were provided by Chile's Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP). This dataset was collected by scientific observers from IFOP and includes 24,700 monitored hauls conducted between 2015 and 2022. It contains detailed information on the date and location of each haul, total catch, total discards, the number of Black-browed Albatrosses caught as bycatch, and the type of mitigation measures used, if any. Based on these records, we classified mitigation use as a binary variable (yes/no), indicating whether at least one of the following systems was implemented during the haul: tori lines, snatch blocks, or “bird buffers”. On average, IFOP on-board observers monitored 44% of fishing trips by the central-south fleet, 36% by freezer stern trawlers, and 52% by factory stern trawlers annually.

The observed data were aggregated into a  $20 \times 20$  km grid to calculate the total number of Black-browed Albatrosses caught as bycatch, the total volume of discards (in tons), the percentage of hauls where mitigation measures were used, and the total trawl time per haul within each grid cell, stratified by year, month, and fishery. Based on this aggregated dataset, we fitted two models using Generalized Additive Model for Location, Scale, and Shape (GAMLSS, Stasinopoulos et al., 2017). Specifically, bycatch in fishery  $f$  during year  $y$ , month  $m$ , and in grid cell  $c$  was assumed to follow a Negative Binomial distribution:

$$Bycatch_{fymc} \sim NBI(\mu_{fymc}, \sigma_{ym})$$

In the first model (“bycatch model”), the logarithm of the mean was modeled as:

$$\log(\mu_{fymc}) = \text{fishery}_f + f(\text{lat}_c, \text{long}_c) + (1|\text{cell}_c) + \text{year}_y + \text{month}_m \\ + \sqrt{\text{discards}_{fymc}} + \log(E_{fymc})$$

Where, fishery, year, and month were included as fixed effects, while discards were included using a square root transformation to improve model fit. The latitude and longitude of the cell center were modeled non-linearly using a thin plate spline. A random effect for the grid cell ID was incorporated to account for extra residual spatial variation. Fishing effort (logarithmic of the total trawl time, hrs.) was included as an offset term. In addition, to improve the model fit, the logarithm of the dispersion parameter was modeled as a function of year and month, treated as fixed effects:

$$\log(\sigma_{ym}) = \text{year}_y + \text{month}_m$$

Additionally, we fitted a second model (“mitigation model”) to evaluate the effects of mitigation measures implemented to reduce bird bycatch. We estimated this effect using a separate model that excluded year as a fixed effect on the  $\mu$  parameter, as year was highly collinear with the mitigation variable and absorbed most of the variation. Therefore, we used the same model formula as before but removed year as a fixed effect and included the percentage of sets with mitigation measures as a continuous predictor (% mitigation use<sub>fymc</sub>).

To estimate the total number of bycatch events that would have occurred if 100% of fishing hauls had been monitored, we used a random resampling approach. Specifically, we resampled the observed haul matrix—stratified by year and fleet—to simulate unobserved hauls, using the estimated total number of hauls for each fishery

as a reference (IFOP 2022). As with the observed hauls used to fit the bycatch model, the simulated hauls were aggregated into a  $20 \times 20$  km grid to calculate total trawl time and discards (in tons) within each grid cell, stratified by year, month, and fishery. We then applied the bycatch model to predict bycatch in the resampled unobserved hauls. Predicted values were subsequently added to the observed values to obtain an estimate of total annual mortality. Finally, we estimated average annual mortality for the two analyzed time periods (2016–2019 and 2020–2022; see below).

In addition, we used the bycatch model to estimate the average monthly probability of bycatch,  $P(Y > 0)$ , for each grid cell, based on the fully completed matrix (including both observed and simulated hauls), by applying the cumulative distribution function of the Negative Binomial distribution (pNBI). This was done for both analyzed time periods, and the resulting set of probability rasters was used as spatial input for the individual-based model (IBM). A bycatch dilution parameter within the IBM was then calibrated to match the total annual mortality predicted for each simulated scenario.

### **3.3. Energy from discards**

Using IFOP data, we generated weekly rasters of energy (measured in kilojoules, kJ) derived from fisheries discards. Following the same random resampling approach used for bycatch estimation, we reconstructed total fishing effort under the assumption that 100% of hauls had been monitored. Specifically, we completed the haul matrix by resampling the observed hauls—stratified by year and fleet—to simulate the unobserved portion, using the estimated total number of hauls for each fishery as a reference (IFOP,

2022). From this completed matrix, we used the spatial location and discard biomass of each (observed and simulated) haul to estimate the total amount of discarded energy per  $20 \times 20$  km grid cell, stratified by year and week, from which we derived weekly energy rasters using the following equation:

$$\text{Discarded energy}_{[i,j],y,w} = \sum_{f=1}^F (B_{f,y,w} \times C_f)$$

where Discarded Energy<sub>[i,j],y,w</sub> is the total amount of energy subsidized in the cell [i,j], during the year y and week w (in kilojoules), F is the total number of fisheries considered, f represents each fishery (central-south, factory and freezer trawl),  $B_{f,y,w}$  is the total biomass discarded by fishery f in the year y and week w (in grams) and  $C_f$  is the specific calorific value of the discards from fishery f (measured in KJ per gram). The calorific values for each fishery ( $C_f$ ) were drawn from a Gamma distribution:

$$C_f \sim \text{Gamma}(\alpha_f, \beta_f)$$

with shape ( $\alpha_f$ ) and scale ( $\beta_f$ ) parameters based on the mean and standard deviation, respectively, of the energy density of the main discarded species in each fishery (see Supplementary Material S2). The resulting weekly rasters were then averaged across years to obtain the mean spatial distribution of discarded energy for each study period (2016–2019 and 2020–2022; see below) and were used as spatial input for the individual-based model (IBM).

### **3.4. Individual-based model**

The base model described in Chapter 2 was adapted to simulate the population dynamics of the Black-browed Albatross under a scenario without fisheries and three ecological trap scenarios driven by trawl fisheries in southern Chile. The model tracks population dynamics in an energy-limited, patchy environment that changes dynamically as resources are progressively depleted. A compensatory ecological trap emerges when fishery discards (represented as weekly rasters) introduce additional energy into the environment, potentially enhancing foraging success by allowing individuals to remain longer in high-energy cells. This increases their chances of acquiring energy across successive time steps before moving, thereby reducing movement frequency and the energetic costs associated with searching. As a result, this can boost both breeder recruitment (i.e., the proportion of potential breeders that actually reproduce) and reproductive success (i.e., fledgling probability). However, these potential benefits are counterbalanced by a simultaneous increase in mortality risk (represented as monthly rasters) within the same areas. The base model is a spatially explicit simulation of the Black-browed Albatross life cycle, incorporating metabolic demands (energetic requirements and expenditures), movement patterns, life-history traits, and memory-based foraging behavior. The following section highlights the main differences between this model and that presented in Chapter 2, following the protocol proposed by Grimm et al. (2006) for describing individual-based models in ecological research. The model was developed in R (R Core Team 2023) using the NetLogoR (Bauduin et al. 2019), dplyr (Wickham et al. 2023), and data.table (Barrett et al. 2024) packages. The code for the

model can be found at: <https://github.com/cristobalanguita/Compensatory-ecological-trap>

### 3.4.1. Entities, state variables, and scales

The model incorporates four main entities: (1) individuals and their attributes, (2) the environmental raster, (3) energy rasters derived from fishery discards, and (4) mortality rasters representing bycatch risk (Figure 2).

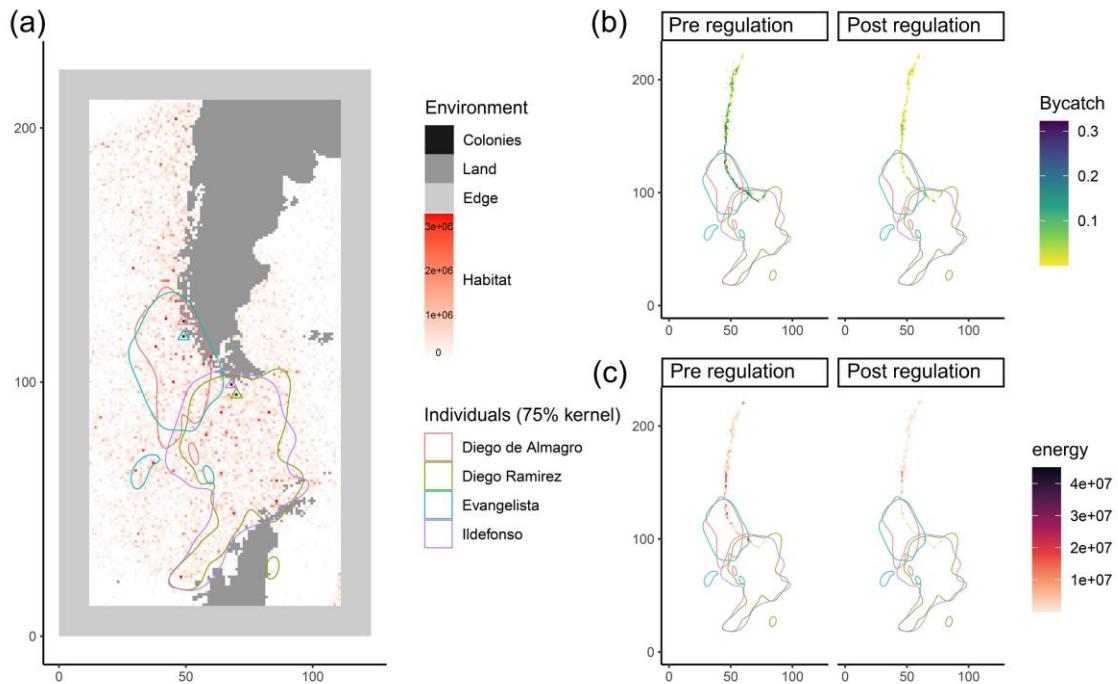


Figure 2. The four entities of the individual-based model (IBM) are shown: the environment raster (a); individuals; mortality rasters representing bycatch risk (b); and energy rasters derived from fishery discards (c). The environment consists of four cell types: colonies, land, edge cells, and habitat. Habitat cells serve as movement and foraging areas for individuals and are characterized by an energy value (in kJ, ranging from zero to a maximum). Individuals are represented by density contours for each colony (triangles). Panels (b) and (c) illustrate the average bycatch probability and discard-derived energy before and after the implementation of regulatory measures, respectively. However, the rasters used in the model are dynamic, varying monthly for bycatch risk and weekly for energy availability.

The state variables of individuals include an identity code, colony code, family code, spatial coordinates (current and previous), age, breeding state, and energy level. Due to the large population sizes of Black-browed Albatrosses, we used super-individuals to reduce computational demand, with each super-individual representing 200 actual individuals. Rather than scaling metabolic or demographic parameters, we preserved individual-level bioenergetic processes. Instead, energy inputs from fisheries (i.e., trophic subsidies) and bycatch mortality were scaled proportionally to the number of super-individuals. This approach simplified model implementation while maintaining demographic and energetic realism.

The environmental raster spans from 32.3°S to 73.7°S latitude and from 106.6°W to 36.3°W longitude, comprising 224 rows (y-coordinates) and 124 columns (x-coordinates), with each cell measuring 20 × 20 km—totaling 27,776 cells. This area encompasses the entire breeding range of the Black-browed albatross and the full operational range of demersal trawl fleets in southern Chile. The wintering habitat (extending from central-south Chile to Peru) was not explicitly modeled. All rasters were projected using a Lambert Equal-Area Azimuthal projection centered at 53.49°S, 71.57°W—the midpoint of all foraging locations—to ensure spatial accuracy.

The environment is divided into four cell types: habitat, colony, land, and edge cells (Figure 2a). Habitat cells serve as movement areas for individuals and are characterized by an energy value (ranging from zero to a maximum, in kJ) that reflects habitat quality for Black-browed albatrosses. Energy availability is spatially distributed across habitat cells and is updated at the beginning of each winter to account for

interannual variation. It then changes dynamically over time in response to consumption by individuals and subsequent replenishment. Specifically, the annual energy distribution is generated using a pseudo-random sample from a Poisson distribution. The rate parameter of this distribution is defined by three components: habitat predicted by the SDM, a scaling parameter that controls spatial patchiness, and a temporally correlated term that allows the modeling of positive, negative, or neutral temporal correlation in each grid cell (see supplementary material S3).

Colony cells represent the geographic locations of breeding colonies, including the four main Black-browed albatross colonies in Chile (from north to south): Diego de Almagro Island, Evangelistas Islets, the Ildefonso Archipelago and the Diego Ramírez Archipelago (Figure 2a). These colonies are accessible to individuals only during the breeding season. Land cells, representing South America and Antarctica, are inaccessible to individuals. Similarly, edge cells, located at the periphery of the environment, cannot be selected. Although these boundaries are simplified, the modeled area is sufficiently large to encompass all habitat predicted by the SDM. This approach provides a simple and efficient way to define the spatial extent of the model and reduce the computational cost of simulating a larger area.

Mortality rasters represent the probability of mortality (Figure 2b), ranging from 0 to 1, while Subsidy rasters (Figure 2c), derived from fishery discards, are expressed in kilojoules (kJ).

In the model, a year is represented as 365 days, with each simulation step corresponding to 6 hours (resulting in 1,460 steps per year). The model does not incorporate a circadian rhythm but includes seasonality, with distinct non-breeding and breeding periods. During the non-breeding season, we simulated an implicit migration where individuals "migrate" to a "wintering room" and then return to the simulated habitat (see Migration sub-model). The breeding period is divided into two phases: the laying window, during which individuals lay eggs in the colony, and the fledging period, during which parents alternate between foraging at sea and attending the colony to feed their chicks until they fledge or die. The year cycle is represented by 113 days of non-breeding season (11 May–August), a 30-day laying window (September), and a 252-day supply period (October 1–10 May) (CG Suazo, unpublished data).

### **3.4.2. Process overview and scheduling**

The general schedule of the program is described in Figure 3. The program begins by defining the initial conditions, including the entities and their state variables. Within each time step (6 hours), eight main sub-models or modules are processed in the following order: (1) Energy replenishment, (2) Migration, (3) Movement, (4) Trap mortality, (5) Reproduction, (6) Mortalities, (7) Updates and (8) End simulation.

### **3.4.3. Sub models**

#### **3.4.3.1. Migration**

For simplicity, we model the migration implicitly, where the migratory population enters a temporary state referred to as the "wintering room" during the winter and later

re-enters the habitat that we model explicitly. The departure of individuals to the wintering room followed a logistic function. The full equation is presented in equation 1, Table 1. In this equation,  $\beta_{\text{day\_departure}}$  defines the midpoint (x-value) of the logistic function, and  $k$  represents the steepness of the curve ( $\beta_{\text{slope\_day\_departure}}$ , Table 2). When the condition is met (i.e.,  $[\text{probability of departure}] > U$ ), the individuals enter the wintering room. Individuals in the wintering room remain on standby, where their energy remains unchanged, but they are subject to age-related mortality.

Once a specific date is reached, the individuals start their breeding migration and re-enter the modeled habitat following the same procedure as in the winter migration ( $\beta_{\text{day\_return}}$  and  $\beta_{\text{slope\_day\_return}}$  parameters, Table 2). When individuals return to the modeled habitat, their energy status is updated to the average energy level prior to leaving the system. Additionally, they are given a wintering condition (number of successful foraging events) based on the day they return and the population size. This value is assigned based on Equation 2, Table 1. In this linear equation,  $\beta_{\text{return}}$  is the coefficient of the return day,  $\beta_{\text{popu}}$  of the population size and represents the intensity of negative density dependence (see Discussion), and  $\epsilon \sim N(0, \sigma_{\text{return}})$  is an error term from a Gaussian distribution with mean 0 and standard deviation  $\sigma_{\text{return}}$ . While this linear model assigns average wintering conditions to migrants, the reproduction of reproductively active individuals (see reproductive sub-model) also depends on their foraging success in the modeled habitat during the days prior to the winter migration and the remaining days before the start of the laying window

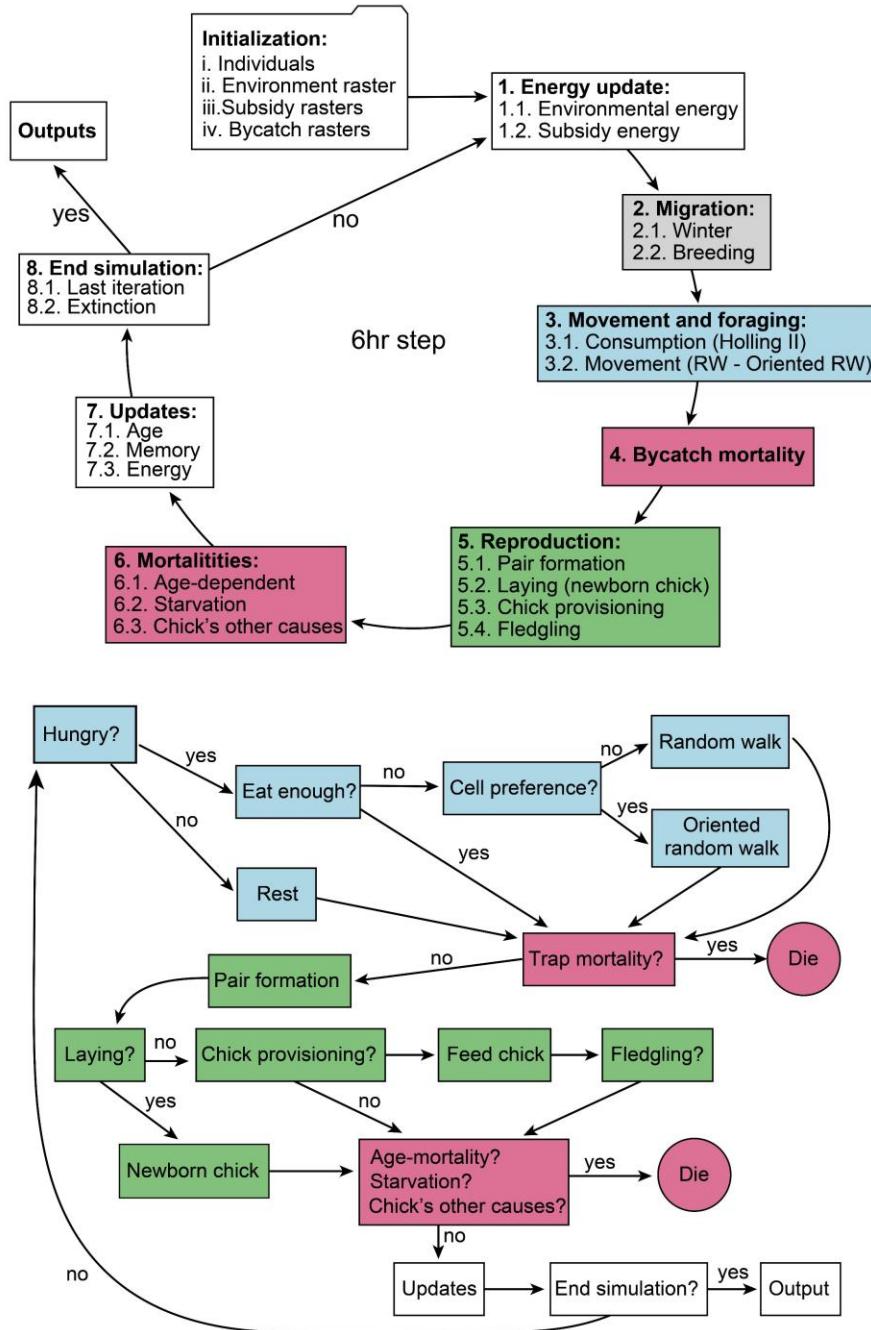


Figure 3. Overview of the program structure (top) and model components (bottom). The top panel illustrates the sequence of all modules within the program, while the bottom panel provides a detailed view of the algorithms governing the Movement and Foraging, Reproduction, and Mortality sub-models, depicting the decision-making processes and actions performed by individuals throughout their life cycle. The Reproduction sub-model (in green) is executed only during the reproductive season.

Table 1. Summary of the equations used in the simulation model. Symbols and parameter definitions are provided in the main text.

	Equation	Sub model
Eq. 1	[Probability of departure]  $= \begin{cases} 1, & \text{if } \frac{1}{1 + e^{k(\text{day of the year} - \beta \text{day\_departure})}} > U \\ 0, & \text{otherwise} \end{cases}$	Migration
Eq. 2	Wintering condition  $= (\alpha_{\text{return}} + \beta_{\text{return}} \cdot \text{day of the year} - \beta_{\text{popu}} \cdot \text{popu\_year}) + \epsilon$	Migration
Eq. 3	Assimilable energy <sub>[i,j]</sub>  $= \frac{\text{Discarded Energy}_{[i,j]} \cdot A_{\text{efficiency}} \cdot E_{\text{competition}}}{\beta_{\text{super\_individuals}}}$	Energy updates
Eq. 4	$A_{\text{efficiency}} \sim \text{Beta}(\beta_{\mu\_ssimulation}, \beta_{\sigma\_ssimulation})$	Energy updates
Eq. 5	$E_{\text{competition}} \sim \text{Beta}(\beta_{\mu\_competition}, \beta_{\sigma\_competition})$	Energy updates
Eq. 6	Subsidized energy  $= [\beta_{\min} + (\beta_{\natural} - \beta_{\min}) e^{\frac{-\text{time step}}{\beta_{\text{subsidy\_decay}}}}]$	Energy updates
Eq. 7	[Age – breeding probability]  $= \begin{cases} 1, & \text{if } \frac{1}{1 + e^{k(\text{age} - \beta \text{age\_first\_breed})}} > U \\ 0, & \text{otherwise} \end{cases}$	Reproduction

### 3.4.3.2. Energy update sub-models

In this sub-model, at the beginning of each winter, the energy distribution is updated based on the energy matrix generated during the model's initialization phase.

Additionally, once the trap is activated, the weekly assimilable energy from fishing discards is allocated to the corresponding grid cells once per week. Specifically, before entering the albatross habitat, the energy derived from discards is adjusted for assimilation efficiency and exploitative interspecific competition according to the Equation 3, Table 1. In this equation, Discarded Energy<sub>[I,j]</sub> is the total amount of energy (kJ) subsidized in the cell [I,j], A<sub>efficiency</sub> is the assimilation efficiency estimated for the Black-browed albatross, and E<sub>competition</sub> represents the proportion of energy available to Black-browed albatrosses relative to other species frequenting fisheries and βsuper\_individuals scales the energy to match the number of super-individuals in the model. Assimilation efficiency values (A<sub>efficiency</sub>) were drawn from a Beta distribution (Equation 4, Table 1), with a mean βmu\_assimilation and a dispersion parameter of βsigma\_assimilation (Table 2). Similarly, E<sub>competition</sub> representing the availability of discards to Black-browed albatrosses, was also drawn from a Beta distribution (Equation 5, Table 1), with a mean of mu\_competition and a dispersion parameter of βsigma\_competition. Finally, the resulting assimilable energy is divided by βsuper\_individuals to ensure the energy content is appropriately scaled to the model's use of super-individuals (Equation 3, Table 1).

Beyond the energy replenishment process described in Chapter 2, we incorporated a dilution function for the energy subsidized by fishing discards using an exponential decay function (Equation 6, Table 1). Once the subsidy is added to each cell, the energy decays exponentially over time (measured in simulation steps) until it matches the baseline energy level of the base model (βnatural in Equation 6, Table 1).

The parameter  $\beta_{\text{subsidy\_decay}}$  (Equation 6, Table 1) determines the slope of this decay, thereby controlling the duration for which the subsidies remain available to the Black-browed albatross.

#### **3.4.3.3. Movements and foraging sub-model**

Similarly to the previous model, this sub-model simulates the movement and foraging behavior of individuals within a one-step period (6 hours), considering their energy levels and decision-making processes. During each simulation step, birds either rest, feed, or move, depending on their hunger level. In the previous model (Chapter 2), individuals abandoned a cell when they were unable to consume more than their basal metabolic rate. The destination cell was always the top-ranked cell in their memory. In the new model, however, destination cells are selected using a weighted probability based on each cell's foraging success in memory. This modification introduces greater stochasticity and ecological realism into movement decisions, as higher-quality cells have a higher—but not guaranteed—probability of being selected.

#### **3.4.3.4. Trap-mortality sub-model**

Trap mortality is modeled as a probabilistic event, determined by the value of each cell in the monthly bycatch probability rasters generated by the bycatch model. These rasters are scaled by the lethality parameter depending on each trap scenario ( $\beta_{\text{lethality}}$ , Table 2), which was calibrated to match the total mortality estimated under the different scenarios.

#### **3.4.3.5. Reproduction sub-model**

Similarly to Chapter 2, the reproduction of individuals depends on the age of first reproduction, as well as the individual's current and wintering energetic conditions. However, unlike in Chapter 2, the probability of breeding in relation to the age of individuals is modeled using a logistic function. The full equation is presented in equation 7, Table 1. In this equation,  $\beta_{age\_first\_breed}$  defines the midpoint (x-value) of the logistic function, and  $k$  represents the steepness of the curve ( $\beta_{slope\_first\_breed}$ , Table 2). Therefore, during the 'laying window,' a bird can reproduce if it is satiated (energy >  $\beta_{hunger}$ ), had a successful winter (successful winter = 1) and has an age-breeding probability = 1. If these conditions are met, the bird moves to the colony in a straight line over one time step. Once individuals arrive at the colony, a logistic function determines whether breeding habitat is available. The inflection point of this function corresponds to the 90% of the carrying capacity ( $\beta_{k\_prop}$ , Table 2) of each colony ( $\beta_{K\_colony}$ , Table 2). As population size approaches this threshold, birds are increasingly unable to reproduce. Conversely, when the population size is below the carrying capacity, pairs are randomly assigned a "family" code, and each pair "lays" one egg. However, there is also a probability of pair failure, determined by a model parameter that reflects the likelihood of successful pair formation ( $\beta_{failure\_pair}$ , Table 2).

During the 'fledging period,' chick provisioning is determined by the hunger parameter ( $\beta_{hunger}$ ). Once satiated, parents return to the colony in a straight line within one time step—regardless of their location—to feed the chick. This process is independent for each parent, meaning both individuals can return and provision the chick during the same time step. For simplicity, the model does not explicitly simulate

the different reproductive stages, such as incubation, guard, and post-guard (see, calibration). Chicks receive a fixed amount of energy throughout the reproductive stage, equivalent to the supply parameter ( $\beta_{\text{supply}}$ ). Fledging is determined by a logistic function (as in Chapter 2) based on the number of feedings provided by both parents ( $\beta_{\text{fledge}}$  and  $\beta_{\text{slope\_fledge}}$ , Table 2). Once fledging occurs, chicks become non-breeders, their energy is reset to the hunger parameter ( $\beta_{\text{hunger}}$ ), and their family code is erased. Each bird then continues its life independently.

#### **3.4.3.6. Mortalities sub-model**

Unlike the model presented in Chapter 2, this version does not include constant mortality. Instead, mortality is modeled as a combination of age-dependent and starvation-related mortality (Table 2). In addition, chicks face a probabilistic risk of mortality due to factors unrelated to parental provisioning (e.g., weather conditions, predation).

#### **3.4.3.7. Updates sub-model**

The previous model simulated high habitat fidelity, as individuals remembered their highest foraging success in each cell by ranking success values from highest to lowest at the end of each time step. In the current model, individuals update their memory by averaging their current foraging success with previously stored values. This results in more dynamic memory and foraging behavior, as preferred cells shift in response to energy depletion.

### **3.4.4. Initialization**

We initialized the model by assigning each colony a number of individuals—implemented as super-individuals for computational efficiency—scaled to represent the total population size estimated from the most recent census data: Diego de Almagro = 400, Evangelistas = 150, Ildefonso = 1,450, and Diego Ramírez = 1,450 (Table S4). Individuals were spatially distributed using coordinates randomly drawn from individuals of their respective colonies in prior model runs under stationary growth conditions in the no-trap scenario (after 100 years). Likewise, individual ages were sampled from the corresponding age distributions generated in those same simulations. Initial energy levels followed a normal distribution with a mean of  $\beta_{\text{hunger}}$  and a standard deviation of 10. At the beginning of the simulation, all individuals had an empty memory. The energy content of each grid cell, generated from Poisson-distributed values, was scaled using the parameter  $\beta_{\text{food}}$  to allow colonies to reach their maximum population sizes under food-limited conditions (see, No-trap scenario in section 2.5.). All simulations began with a 15-year initialization phase during which individuals became familiar with their environment and the population reached a stable age distribution. During this phase, carrying capacity was set equal to the initial population size. At year 16, carrying capacities were updated to the maximum values estimated based on breeding habitat availability. In trap scenarios, the ecological trap was introduced at that point. The spatial configuration of the trap was defined by discard and bycatch rasters, along with additional trap-related parameters (Table 2).

### **3.4.5. Parameterization and calibration**

The parameters used in the model are presented in Table 2. Below, we describe them in the order in which they appear in the model's program components.

Table 2. List of parameters used in the model.

Model component	Parameter/s	Description	value
Initialization	$\beta_{super\_individuals}$	Number of super-individuals used to scale fishery-derived energy inputs and bycatch mortality, while maintaining individual-level metabolic and demographic processes.	200
	$\beta_{years}$	Simulation duration (years)	150
	$\beta_{start\_trap}$	Start of the trap (year)	16
	$\beta_{lambda\_habitat}$	Poisson parameter for initial energy distribution	1.2
	$\beta_{rho}$	Temporal autocorrelation in energy availability across years	0.9
	$\beta_{food}$	Scalar multiplier for total available food	165000
	$\beta_{replenishment}$	Midpoint of the energy replenishment function (steps)	80
Energy updates	$\beta_{replenishment\_slope}$	Slope of the energy replenishment function	1
	$\beta_{mu\_assimilation}$	Assimilation efficiency (mean)	0.780
	$\beta_{sigma\_assimilation}$	Assimilation efficiency (variation)	0.083
	$\beta_{mu\_competition}$	Competition parameter (mean)	0.85
	$\beta_{sigma\_competition}$	Competition parameter (variation)	0.1
Migration	$\beta_{subsidy\_decay}$	Decay of subsidy (steps)	10
	$\beta_{migratory\_prop}$	Proportion of population that migrate	0.8
	$\beta_{day\_departure}$	Midpoint day of winter migration function	15 of Jun

	$\beta$ slope_day_departure	Slope of the winter migration function	0.2
	$\beta$ day_return	Midpoint day of breeding migration function	20 of August
	$\beta$ slope_day_return	Slope of the breeding migration function	0.2
	$\alpha$ return, $\beta$ return, $\beta$ popu, $\sigma$ return	Parameters for assigning wintering conditions for migrants	267, 2.08, -0.00375, 4
Movement and foraging	$\beta$ hunger	Hunger (KJ)	1000
	$\beta$ holling	Constant in functional consumption (KJ)	1000
	$\beta$ radius	Radius of movement (cells)	12
	$\beta$ dire, $\beta$ kdire	Parameters from movement stochasticity function	30°,-0.2
Bycatch mortality	$\beta$ lethality	Scaling bycatch mortality	pre-regulation trap=1400, pre-regulation cryptic trap=300, post-regulation trap=2500
Reproduction	$\beta$ age_first_breed	Midpoint of the first breed function (years)	9
	$\beta$ slope_first_breed	Slope of the first breed function	1
	$\beta$ reproduction	Midpoint of reproduction function (satiated steps)	260
	$\beta$ slope_reproduction	Slope of the reproduction function	0.1
	$\beta$ failure_pair	Failure of pair formation	0.005
	$\beta$ k_prop	Midpoint of the carrying capacity function	0.9
	$\beta$ slope_k_prop	Slope of the carrying capacity function	-0.5
	$\beta$ K_colony	Vector of the breeding carrying capacity of each colony (number of super-breeders)	Diego Ramirez=1800, Ildefonso= 600, Evangelista=50, Diego de Almagro=300
	$\beta$ clutch	Clutch size	1

	$\beta_{\text{supply}}$	Cost of chick provision (KJ)	850
	$\beta_{\text{fledge}}$	Midpoint of the fledgling function (provisioning events)	270
	$\beta_{\text{slope\_fledge}}$	Slope of the fledgling function	0.05
Mortality	$\beta_{\text{age\_mortality}}$	Vector of age-specific mortality	see Table S7
	$\beta_{\text{senescence}}$	Senescence age	40
	$\beta_{\text{adult\_starv}}$	Midpoint of the starvation function (steps)	120
	$\beta_{\text{adult\_slope\_starv}}$	Slope of the starvation function (steps)	1
	$\beta_{\text{chick\_starv}}$	Midpoint of the starvation function of chicks (steps)	40
	$\beta_{\text{chick\_slope\_starv}}$	Slope of the starvation function of chicks (steps)	1
	$\beta_{\text{other\_causes}}$	Other cause of chick mortality	0.003
Updates	$\beta_{\text{basal}}$	Basal energy expenditure (KJ)	$\beta_{\text{hunger}}/2.2$
	$\beta_{\text{loss}}$	Energy loss from movement (KJ)	40
	$\beta_{\text{memory}}$	Number of cells that birds remember	5

**Initialization module:** Because empirical information on habitat energy distribution and replenishment dynamics is lacking, we applied a pattern-oriented modeling (POM; Grimm et al. 2005) approach to calibrate these parameters so that the model would reproduce expected demographic patterns. Specifically, the spatial patchiness of energy availability ( $\beta_{\text{lambda\_habitat}}$ ; Table 2) and its replenishment rate ( $\beta_{\text{replenishment}}$ ) were adjusted to match demographic parameters observed in other populations of Black-browed Albatrosses, including breeder and fledgling recruitment, average provisioning rates, and fledging timing (see above). For example, lower values of

$\beta_{lambda\_habitat}$  or  $\beta\_replenishment$  resulted in reduced reproductive success, whereas higher values caused parents to invest less effort in chick provisioning, leading to earlier-than-expected fledging.

For both theoretical and practical reasons, we incorporated a positive interannual autocorrelation structure ( $\rho_{interannual}$ ; Table 2). Although we selected a high value for  $\rho_{interannual}$ , the stochastic nature of the energy generation process resulted in an effective correlation of approximately 0.65 between the first and second years, declining to around 0.45 by the third year. This interannual autocorrelation helped buffer the effects of demographic stochasticity arising from interannual variation (see Discussion).

**Energy updates sub-model:** The parameters used to estimate assimilation efficiency for the Black-browed Albatross ( $\beta_{mu\_assimilation}$  and  $\beta_{sigma\_assimilation}$ , Table 2) were based on a beta regression analysis derived from 46 observations across 23 seabird species consuming various fish and invertebrate diets (see Supplementary Material S5) (for a similar approach see, Shearley et al. 2019).

The parameters estimating the proportion of fishery subsidies available to Black-browed Albatrosses—after accounting for competition with other species ( $\beta_{mu\_competition}$  and  $\beta_{sigma\_competition}$ , Table 2)—were based on the relative abundance of this species in the bycatch (Adasme et al. 2019). These values are considered conservative, as Black-browed Albatrosses are the most abundant seabird species interacting with trawl fisheries, accounting for approximately 90% of seabird bycatch in these fleets (Adasme et al. 2019).

Although empirical data on the persistence of discards from these fisheries are lacking, we assumed an exponential decline over approximately two days ( $\beta_{\text{subsidy\_decay}}$ , Table 2). This assumption appears justified, given that discards are typically rapidly consumed by scavengers, dispersed by ocean currents, or sink due to oceanographic processes (Garthe et al. 1996, González-Zevallos and Yorio 2006, Sherley et al. 2019).

**Migration sub-model:** The Black-browed Albatross is a migratory species that moves northward during the winter. Although we lack data on the proportion of the population that remains at higher latitudes, we assume this fraction is likely small ( $\beta_{\text{migratory\_prop}}$ , Table 2), given the substantially higher numbers observed in central Chile during the winter compared to the summer months (Figure S6). The parameters defining the winter migration function ( $\beta_{\text{day\_departure}}$  and  $\beta_{\text{slope\_day\_departure}}$ , Table 2) were calibrated so that individuals would begin to migrate (i.e., move to the “wintering room”) in late May to early June, following the end of the breeding season. In contrast, the parameters defining the breeding migration ( $\beta_{\text{day\_return}}$  and  $\beta_{\text{slope\_day\_return}}$ , Table 2) were calibrated so that birds would begin returning to the breeding habitat (i.e., leave the waiting area) in August ( $\beta_{\text{day\_return}}$ , Table 2).

The parameters defining foraging success during the winter (i.e., upon exiting the “wintering room”) were calibrated to produce a negative density-dependent effect on breeder recruitment ( $\alpha_{\text{return}}$ ,  $\beta_{\text{return}}$ ,  $\beta_{\text{popu}}$ , and  $\sigma_{\text{return}}$ , Table 2). Although negative density dependence is biologically expected, no empirical data is available to inform its strength (see Discussion). To guide the calibration, we first ran preliminary

simulations of the model without migration, in which density dependence emerged from habitat saturation at the breeding site. We then used the output from these runs to fit a linear model of wintering condition (accumulated foraging success) as a function of the day of the year and population size. The resulting coefficients ( $\alpha_{\text{return}}$ ,  $\beta_{\text{return}}$ ,  $\beta_{\text{popu}}$ , and  $\sigma_{\text{return}}$ ) were subsequently used to assign wintering conditions in the full model with migration. While this linear model determines the average wintering condition of returning individuals ( $\pm$  and error  $\sigma_{\text{return}}$ ), reproduction also depends on foraging success within the breeding habitat in the days before departure and between return and the onset of the laying window.

**Movement and foraging sub-model:** The hunger parameter ( $\beta_{\text{hunger}}$ , Table 2) was calibrated so that, on average, individuals consumed the equivalent of their daily field metabolic rate (FMR, in kilojoules) during both the non-breeding and breeding seasons, accounting for their basal metabolic rate ( $\beta_{\text{basal}}$ , Table 2) and the energy costs associated with movement ( $\beta_{\text{loss}}$ , Table 2). Specifically, we used the Seabird FMR Calculator, based on a meta-analysis of seabird FMRs during the breeding season (Dunn et al., 2018), to estimate the FMR for the breeding period. This tool requires inputs such as species, body mass, and colony latitude, and provides daily FMR estimates for each of the three breeding phases: incubation, guard, and post-guard. Using this calculator, we estimated the FMR of an average 3,570 g Black-browed Albatross (mean of male and female) breeding at 56°S (latitude of the Diego Ramírez archipelago). We then computed a weighted average FMR across the three phases, using the duration of each phase as weights, and used this value as the representative FMR for the breeding season

(FMR=2700 kJ·day<sup>-1</sup>). Because the FMR of Black-browed Albatrosses during the non-breeding season is unknown, we calibrated  $\beta_{\text{hunger}}$  so that daily consumption matched the FMR estimated for the incubation phase (FMR=2070 kJ·day<sup>-1</sup>, for a similar approach, see Sherley et al., 2019). To match the desired FMR for the breeding season, we further calibrated the energy loss due to movement ( $\beta_{\text{loss}}$ , Table 2) to reflect the approximate 30% increase in energy expenditure, accounting for the additional costs of commuting between the colony and foraging grounds to provision chicks.

The Holling type 2 constant ( $\beta_{\text{holling}}$ , Table 2) was set so that the function reaches half of its maximum value when the energy available to an individual equals the maximum consumption ( $\beta_{\text{hunger}}$ , Table 2).

The movement radius ( $\beta_{\text{radius}}$ ) was calibrated so that birds moved an average distance of 150 km per time step (6 hours), consistent with foraging distances recorded for Black-browed Albatrosses during the breeding season in Chile (Figure S7). Parameters controlling movement stochasticity ( $\beta_{\text{dire}}$  and  $\beta_{\text{kdire}}$ ; Table 2) were adjusted to balance directional randomness while minimizing the risk of starvation-related mortality.

**Bycatch mortality sub-model:** This parameter ( $\beta_{\text{lethality}}$ , Table 2), which scales the probability of mortality in each cell of the monthly bycatch rasters, was calibrated to produce an average mortality rate equivalent to that estimated for each ecological trap scenario.

**Reproduction sub-model:** The parameters governing the age at first reproduction ( $\beta_{\text{age\_first\_breed}}$  and  $\beta_{\text{slope\_first\_breed}}$ ; Table 2) were calibrated based on (Nevoux et

al. 2010), with reproduction beginning at a low probability at age 5 and averaging around 8.9 years (Weimerskirch et al. 1987). The parameters of the reproduction function, which is based on accumulated foraging success during the winter ( $\beta_{reproduction}$  and  $\beta_{slope\_reproduction}$ ; Table 2), were calibrated to yield an average breeder recruitment rate of approximately 90% across colonies. This value closely approximates the average of observed breeding probabilities reported for Kerguelen (mean = 0.96 for experienced breeders; Pardo et al. 2013), the Falkland Islands (mean = 0.88; Ventura et al. 2021), and South Georgia (mean = 0.78; Pardo et al. 2017). It also accounts for the fact that breeders face a probability of pairing failure, which was calibrated to average 1% ( $\beta_{failure\_pair}$ ; Table 2).

The parameters of the carrying capacity function ( $\beta_k\_prop$  and  $\beta_{slope\_k\_prop}$ ; Table 2) were calibrated to smooth the population's approach to carrying capacity. The estimation of colony-specific carrying capacities is described in the Experiments section ( $\beta_K\_colony$ , Table 2).

Clutch size ( $\beta_{clutch}$ ) was set to 1, consistent with all Procellariiformes species (Schreiber and Burger, 2001). The energetic cost of provisioning was set at 850 kJ per meal, consistent with the expected energy intake of Black-browed Albatross chicks. This value is based on a 250 g (dry weight) meal (Mills et al. 2020), assumed for simplicity to consist primarily of squid (Arata and Xavier 2003), with an average caloric density of 3.4 kJ/g (Croxall and Prince 1982).

Although fledging success also depends on the spatial and temporal distribution of energy, the parameters of the fledging function ( $\beta_{\text{supply}}$  and  $\beta_{\text{slope\_fledge}}$ ; Table 2) were calibrated so that, on average, chicks became independent in April (C.G. Suazo, unpubl. data) after receiving approximately 170 meals from both parents. This expected number of meals was derived from empirical estimates of foraging trip duration and breeding phase length (Table S8). While reproductive success varied across colonies and population sizes, this calibration resulted in an overall average fledging success of approximately 75%, accounting for additional sources of chick mortality (see above). This value is consistent with observed breeding success in Black-browed Albatrosses at Kerguelen, where experienced breeders achieve an average success rate of 75% (Rolland et al. 2009b, Pardo et al. 2013). The same value was previously used to model the populations of Diego Ramírez and Ildefonso (Robertson et al. 2014).

**Mortality sub-model:** For age-specific mortality parameters ( $\beta_{\text{age\_mortality}}$ ; Table S9), we used a combined approach based on Nevoux et al. (2010) and Pardo et al. (2013). Specifically, we assigned a mortality rate of 0.224 for individuals under one year of age—excluding chicks, which are subject to separate mortality sources (see above)—based on Nevoux et al. (2010). For ages 1 to 5, we implemented a linear decline in mortality, reaching the value estimated by (Pardo et al. 2013) at age 5. From that point onward, we followed the mortality estimates from (Pardo et al. 2013), which indicate a linear decrease in mortality between ages 5 (0.198) and 8 (0.066), a constant mortality rate of 0.066 between ages 8 and 30, and a linear increase in mortality beyond age 30 (Table S9). The senescence parameter ( $\beta_{\text{senescence}}$ ) was set at 40. The parameter for the

starvation functions (adult and chick) were determined based on the allometric starvation model following Peters, (1983). Additionally, considering that albatross chicks may die not only due to parental care failure but also from external factors—such as storms, predation, or flooding—we calibrated the parameter representing other sources of mortality to yield an average chick mortality rate of approximately 12%.

**Updates sub-model:** For the basal metabolic rate ( $\beta_{\text{basal}}$ ; Table 2), we used a value equivalent to  $\beta_{\text{hunger}} / 2.2$ , based on the observed FMR-to-BMR ratio in Black-browed Albatrosses (Kroeger et al., 2020). Finally, as noted above, we calibrated the parameter of energy loss due to movement ( $\beta_{\text{loss}}$ ; Table 2) to produce an increase in energy consumption equivalent to the field metabolic rate (FMR) during the breeding season.

### 3.5. Experiments

We simulated four scenarios: a fishery-free environment (no-trap scenario) and three compensatory traps (pre-regulation, pre-regulation with cryptic bycatch, and post-regulation, Table 3). These scenarios represent conditions before and after the implementation of regulatory measures, introduced between 2019 and 2020, aimed at reducing and controlling discards and bycatch in national trawl fisheries. Simulations ran over a 165-year period, beginning with the 15-year initialization phase. At simulation year 16, the compensatory trap became active. We ran nine replicates per scenario, resulting in a total of 36 simulations, with an average runtime of 40 hours per simulation—equivalent to 1,440 total computing hours.

**No-trap scenario:** The no-trap scenario represents a fishery-free environment in which populations can reach their maximum potential size. Colony-limiting factors and maximum population sizes were determined based on quantitative estimates of habitat availability (Supplementary Material S10), and evaluated against the hypothesis that Black-browed albatross populations are food-limited (Wakefield et al. 2014). Based on these estimates, we assume that population sizes in the Ildefonso Archipelago, Diego de Almagro Island, and the Evangelistas Islets are primarily limited by breeding habitat rather than food (Table S8). In contrast, for the Diego Ramírez Archipelago, we considered that food availability would be insufficient to sustain the population size estimated from breeding habitat availability alone (180,000 pairs, see Discussion). Given that both populations are at the upper limit predicted by Wakefield et al. (2014)—we adopt a conservative approach and assume that the maximum population size at Diego Ramírez, limited by food availability, is 50% higher than the last census in 2002 (i.e., 82500 pairs).

**Pre-regulation trap:** This scenario represents the high bycatch–subsidy conditions observed between 2015 and 2019, prior to the implementation of regulatory measures aimed at reducing and controlling discards (Table 3). Monthly and weekly rasters of bycatch and discard-derived energy were generated using the methodology described in Sections 2.2 and 2.3.

**Pre-regulation cryptic trap:** This scenario represents a case with the same subsidy level as the previous scenario but includes cryptic bycatch. This is mortality that is largely unobservable and can be considered to include all birds killed or seriously injured in

interactions with fishing gear that are not landed or counted (Bartle, 1991, Melvin et al. 2011, Richard et al. 2017, Tamini et al. 2015). There is considerable uncertainty about the extent of cryptic mortality in trawl fisheries (Phillips et al. 2024), with estimates reaching up to eight times the observed mortality (Richard and Adasme 2019). In this study, we adopt a more conservative approach and apply a multiplier of three to the bycatch in the high bycatch–subsidy scenario (Table 3). The energy from discards remained the same as in the previous scenario.

**Post-regulation trap:** This scenario represents the low bycatch–subsidy conditions observed between 2020 and the present, following the implementation of regulatory measures aimed at reducing and controlling discards and bycatch (Table 3). Monthly and weekly rasters of bycatch and discard-derived energy were generated using the methodology described in Sections 2.2 and 2.3.

Finally, we summarized the population response for each scenario—using means and 95% bootstrap-based confidence intervals—across replicates over four 20-year time windows centered on simulation years 10, 50, 100, and 150 (i.e., 10 years before and after each focal year), for the number of pairs, breeder recruitment, and fledgling recruitment.

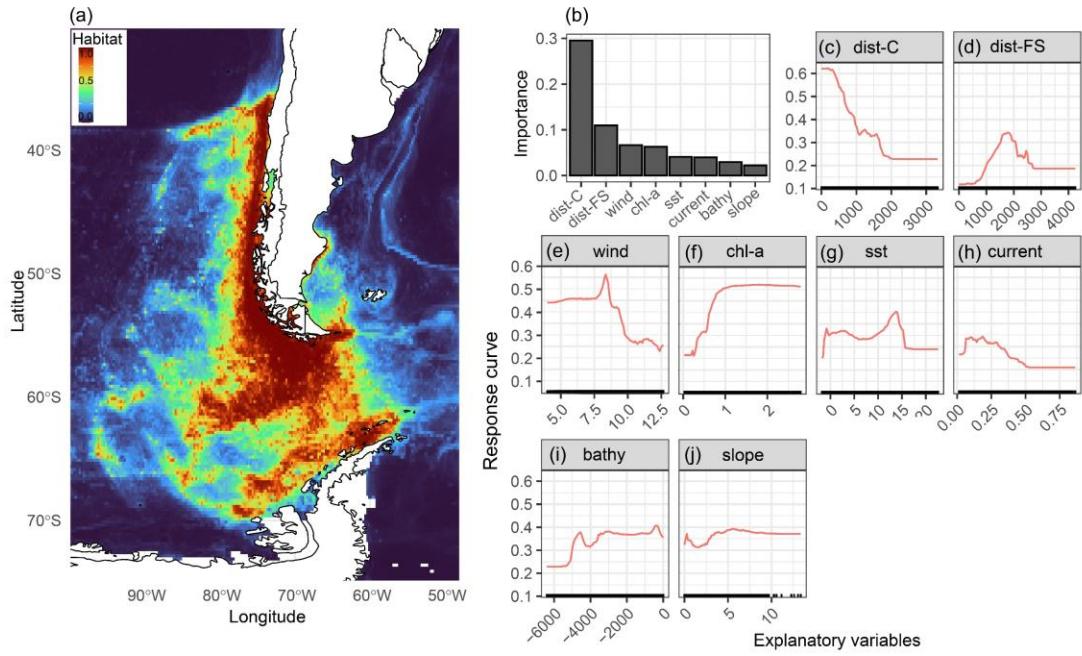
Table 3. Description of the evaluated scenarios, including a fishery-free environment (no-trap) and three ecological trap scenarios. Trap scenarios are characterized by the average annual bycatch ( $\text{birds}\cdot\text{yr}^{-1}$ ) and the average annual food subsidy from fisheries—expressed in both biomass ( $\text{t}\cdot\text{yr}^{-1}$ ) and energy ( $\text{kJ}\cdot\text{yr}^{-1}$ )—calculated over the corresponding time periods based on total fishing effort and data from the national onboard observer program. Values of bycatch and food subsidy in biomass were rounded to the nearest 1,000.

Scenario	bycatch (birds·yr <sup>-1</sup> )	subsidy biomass (t·yr <sup>-1</sup> )	subsidy energy (kJ·yr <sup>-1</sup> )	Time period
No-trap	–	–	–	–
Pre-regulation trap	4,000	11,000	5.9E+10	2015-2019
Pre-regulation cryptic trap	12,000	11,000	5.9E+10	2015-2019
Post-regulation trap	500	3,000	1.7E+10	2020-2022

#### 4. Results

##### 4.1. Predicted Foraging Habitat of the Black-browed Albatross During the Breeding Season

The ensemble model (SDM) showed good fit and predictive performance (TSS and AUC > 0.92). The most important variables explaining the distribution of the Black-browed albatross were the distance to the nearest colony and the distance to the Falkland super colonies, chlorophyll-a and wind speed (Figure 4). The remaining predictor variables had a lower relative effect, each contributing less than 5% (Figure 4). Response curves indicated a higher probability of occurrence in waters near the colony, farther from the super-colony of the Falkland Islands, characterized by high chlorophyll-a concentrations and wind speed of intermediate intensity (Figure 4). Overall, the assembled model predicted a wide distribution from 36°S to 77°S, concentrated along the continental edge within 200 km of the South American Pacific coast (Figure 4). Habitat increased towards more oceanic areas (>1,000 km from the coast) in the southernmost part of its range (60°S) and in the surrounding waters of northwest Antarctica (Figure 4).



**Figure 4.** (a) Predicted foraging habitat during the breeding season of Black-browed Albatrosses from Chile (foraging tracks from birds breeding in Diego Ramírez, Ildefonso, and Diego de Almagro, Table S1), based on a random forest (SDM). (b) Variable importance plot. (c-j) Average response curves for each predictor included in the model: dist-C (distance to the nearest colony), dist-FS (distance to the “super colony” in the Falkland Islands), wind (wind velocity), chl-a (chlorophyll-a), sst (sea surface temperature), current (current velocity), bathy (bathymetry), and slope (sea floor slope).

#### 4.2. Bycatch of Black-browed Albatrosses and Energy Subsidies from Trawl Fisheries

The “bycatch model” (GAMLSS) explained 35% of the variation in Black-browed Albatross bycatch in demersal trawl fisheries between 2015 and 2022. Bycatch rates showed strong seasonal variation, peaking in winter (June–August) and remaining elevated during spring (September–November) (Figure 5). Mortality rates were notably high prior to the implementation of fisheries regulations (2015–2019), peaking in 2016, and showed a marked decline between 2020 and 2022 following the adoption of regulatory measures (Figure 5, Figure 6). Overall, bycatch rates increased sharply toward the extreme south, with the highest values observed between 50°S and 57°S (Figure 5),

except during winter (July-August), when fishing activity was concentrated at lower latitudes (Figure 6). Total discard volume was positively correlated with bycatch rate ( $\beta = 0.19$ , 95% CI: 0.15–0.23,  $t = 8.72$ ,  $P < 0.001$ , Figure 5, Figure 6, Figure 7). Among fleets, the factory fleet reported the highest bycatch rates, followed by the freezer fleet and the central-southern fleet (Figure 5). The random effect of grid cell showed minimal variation ( $SD = 0.002$ ), suggesting that there is little to no residual spatial variation unaccounted for by the model.

Based on observed and model-predicted bycatch (for unobserved hauls), we estimated a total of 23,992 Black-browed Albatross deaths between 2015 and 2022, with a median of approximately 4,000 deaths per year during the pre-regulation period (2015–2019; Table 3). This figure dropped to about 500 deaths per year during the post-regulation period (2020–2022; Table 3), following the implementation of mitigation measures. These measures were applied in an average of 67% of fishing hauls over that period (64% in 2020, 71% in 2021, and 76% in 2022), primarily consisting of Bird Scaring Lines, which were used in approximately 97% of mitigated sets. This pattern was corroborated by the “mitigation model” (Figure 5f, GAMLSS), which revealed a strong and statistically significant negative effect of mitigation use (i.e., the proportion of fishing hauls employing mitigation) on bycatch rates ( $\beta = -1.62$ , 95% CI:  $-1.95$  to  $-1.30$ ,  $t = -9.83$ ,  $P < 0.001$ ). Specifically, bycatch decreased by approximately 15% for every 10% increase in mitigation use ( $\exp(-1.62 \times 0.1) \approx 0.85$ ). All other effects included in the mitigation model were consistent with those identified in the bycatch model.

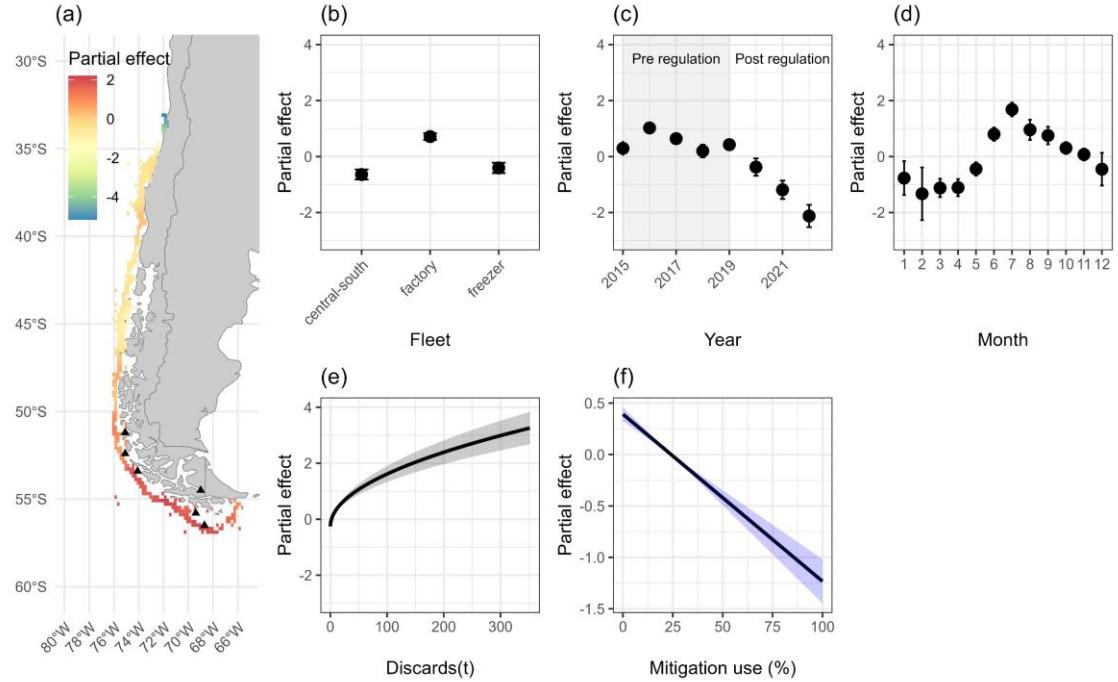
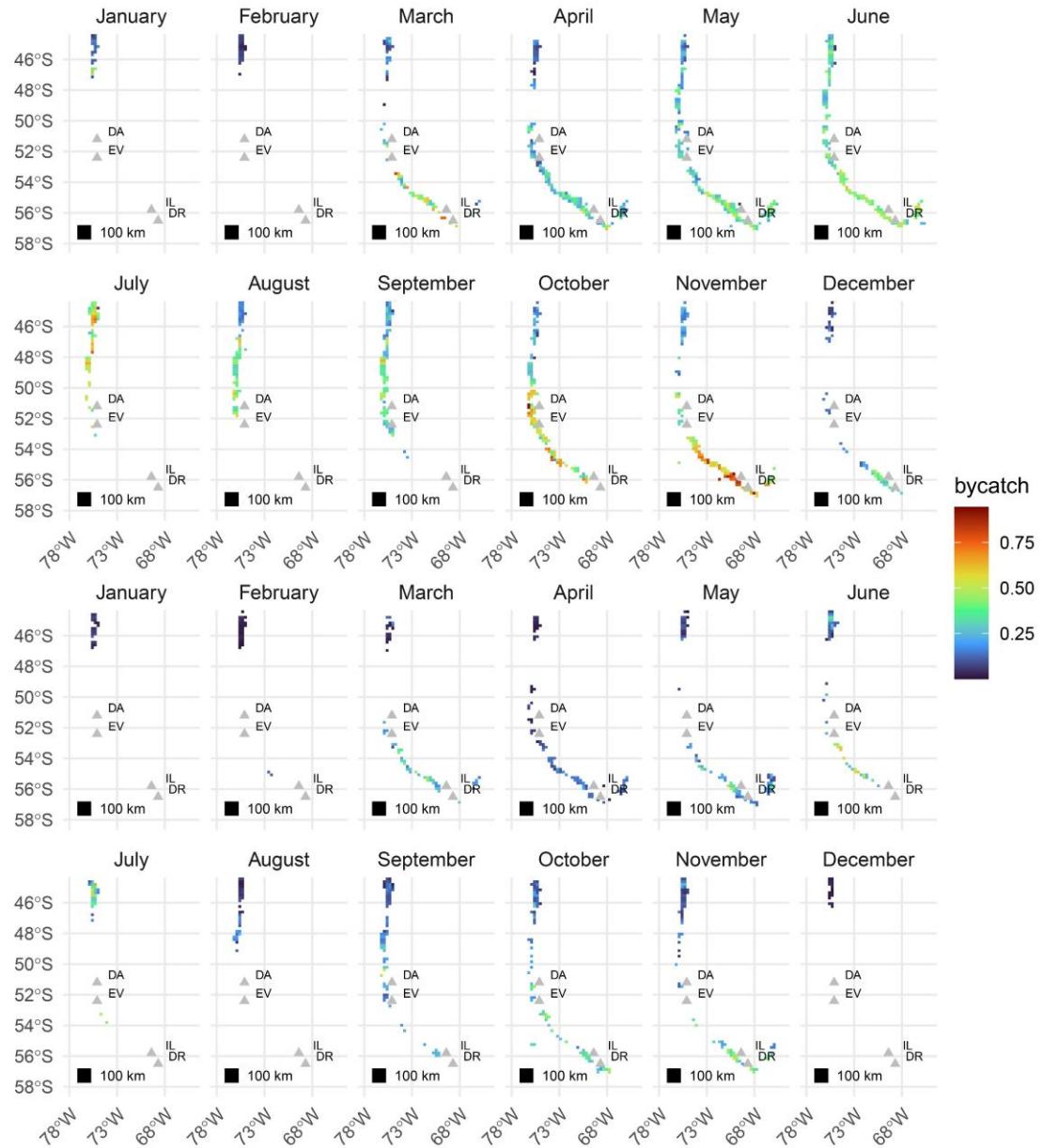


Figure 5. (a–f) Partial effects of each predictor on the estimated bycatch of Black-browed albatrosses in demersal trawl fisheries, based on the “bycatch model” fitted using GAMLSS. Panel (f) shows the effect of mitigation measures (i.e., the percentage of fishing hauls using mitigation) on bycatch, as estimated by the separate “mitigation model” (also fitted using GAMLSS). The y-axis displays the contribution of each predictor to the expected value of the response variable (on the log scale), holding all other predictors constant. The triangles in panel (a) show the locations of the six colonies in Chile.

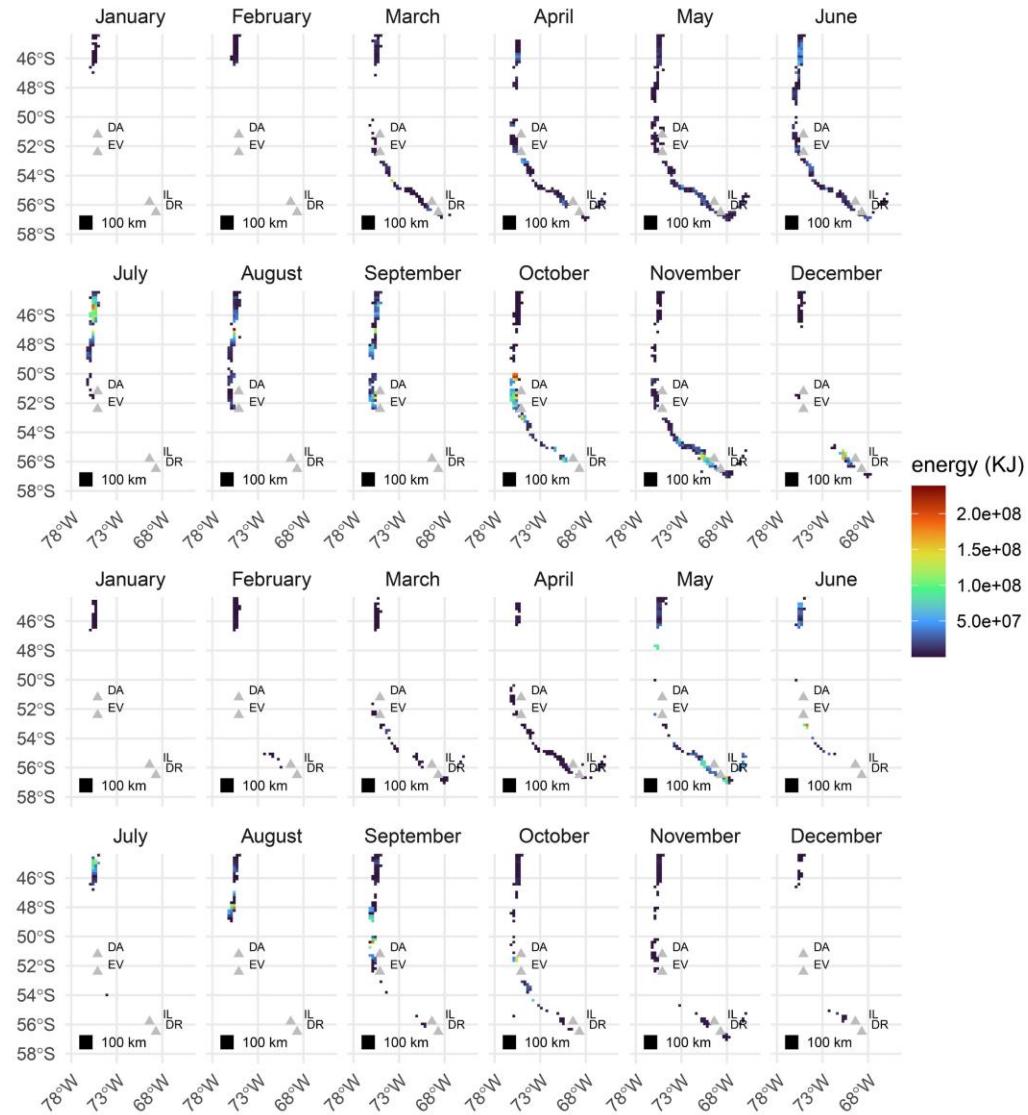
Total discards from demersal trawl fisheries showed a substantial reduction between the pre-regulation period (2015–2019) and the post-regulation period (2020–2022). The average annual volume of discards decreased nearly fourfold following the implementation of fishery regulations, dropping from approximately 11,000 t to 3,000 t (Table 3). The associated energy (Kilojoules) available to the environment exhibited a spatiotemporal pattern similar to that of bycatch during the pre-regulation period (Figure 7). During the winter months, it was concentrated at lower latitudes (north of 50°S), then shifted southward in spring, reaching areas closer to the Black-browed Albatross colonies. In autumn, the distribution broadened across the region. While the

spatial pattern during the post-regulation period remained broadly similar to that of the pre-regulation period, it was characterized by a substantially lower magnitude—nearly fourfold. Additionally, there was a marked contraction in spatial extent, particularly in the southernmost areas (Figure 7).



**Figure 6.** Spatiotemporal variation in the probability of Black-browed Albatross bycatch in Chilean demersal trawl fisheries, before (top panel, 2016–2019) and after (bottom panel, 2020–2022) the implementation of regulations. The figure shows the monthly

average bycatch probability estimated by the “bycatch model” (fitted using GAMLS) for both study periods, based on total fishing effort (see Table 3). Only the area south of 45°S is shown to highlight the regions of closest interaction with the colonies (DA, Diego de Almagro; EV, Evangelista; IL, Ildefonso; DR, Diego Ramirez).



**Figure 7.** Spatiotemporal variation in the discard-related energy (Kilojoules, KJ) provided to the environment by demersal trawl fisheries, before (top panel, 2016–2019) and after (bottom panel, 2020–2022) the implementation of regulations. The figure shows the monthly average energy provided for both study periods (see Table 3), based on total fishing effort. Only the area south of 45°S is shown to highlight the regions of closest interaction with the colonies (DA, Diego de Almagro; EV, Evangelista; IL, Ildefonso; DR, Diego Ramirez)

### **4.3. Population Responses of Black-browed Albatrosses Under Trap and No-Trap**

#### **Scenarios**

**No-trap:** Overall, the model revealed distinct patterns of habitat use and population dynamics among colonies. Southern colonies (Diego Ramírez and Ildefonso) exhibited a broader southerly foraging range, extending toward the Antarctic Peninsula, while northern colonies (Diego de Almagro and Evangelistas) remained at lower latitudes.

Within the southern group, Ildefonso reached stability in the number of breeding pairs within three years, limited by breeding habitat, whereas Diego Ramírez began to stabilize after approximately 75 years, constrained by food availability (Figure 8, Figure 9). Among the northern colonies, Diego de Almagro stabilized after 50 years due to habitat limitations, while Evangelistas exhibited low recruitment of both breeders (i.e., the proportion of potential breeders that actually reproduce) and fledglings (Figure 10), leading to a long-term decline in breeding pair numbers (Figure 8, Figure 9).

**Pre-regulation trap:** Within the southern colonies, Diego Ramírez accounted, on average, for 24% of total bycatch mortality but followed a population trajectory broadly similar to the no-trap scenario, ultimately reaching its maximum size by the end of the simulation, albeit with greater interannual variability. Ildefonso accounted, on average, for 47% of total bycatch mortality. Although it initially resisted population decline, it subsequently showed a slight decrease, stabilizing at levels lower than those currently observed (Figure 9). Among the northern colonies, Diego de Almagro experienced, on average, 24% of total bycatch mortality and was able to maintain a population size

similar to present-day levels in the short term, before declining to lower levels after 100 years. Evangelistas, which accounted on average for 5% of total bycatch mortality, maintained a population size similar to the no-trap scenario in the short and long term, but showed a higher population size in the midterm (50 years into the trap scenario) (Figure 9).

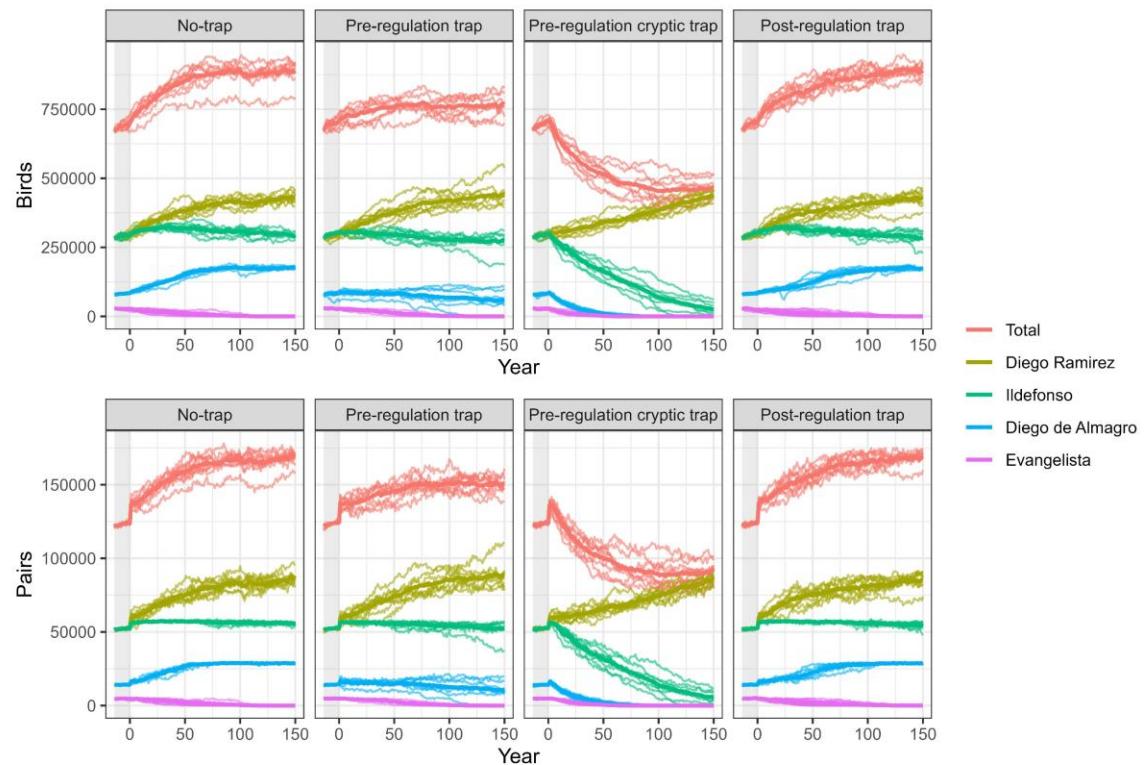


Figure 8. Population responses (total population and number of breeding pairs) of Black-browed Albatrosses under a fishery-free environment and three scenarios involving compensatory ecological traps associated with demersal trawl fisheries ( $n = 36$  simulations; 9 replicates per scenario). The shaded gray area indicates the 15-year initialization phase during which individuals became familiar with their environment and the population reached a stable age distribution. During this period, carrying capacity was set equal to the initial population size. At year 16 (denoted as year zero in the plots), carrying capacities were adjusted to the maximum values estimated from habitat availability. In trap scenarios, the ecological trap was introduced at that point. Thin lines represent individual simulation replicates; the thick line shows the average across replicates.

Overall, breeder recruitment increased across all colonies compared to the no-trap scenario (Figure 10). Fledgling recruitment increased in Diego Ramírez and Evangelistas relative to the no-trap scenario, remained stable in Ildefonso, and declined over the long term in Diego de Almagro (Figure 10). Overall, the model predicts the highest mortality rates in juveniles (1–3 years: 47%), followed by immatures (4–5 years: 12%) and adults (>5 years: 13%).

**Pre-regulation cryptic trap:** This scenario produced a mortality distribution among colonies similar to the high bycatch–subsidy scenario but led to consistent population declines across all colonies except Diego Ramírez, which continued to grow throughout the simulation period without evidence of stabilization by its end (Figure 8, Figure 9). Ildefonso exhibited a sharp and continuous decline with no signs of stabilization, while the northern colonies declined rapidly and became extinct approximately 50 to 75 years after the start of the simulation (Figure 8, Figure 9). During the first 100 years of the simulation, breeder and fledgling recruitment in Diego Ramírez and Ildefonso reached their highest levels relative to the other scenarios. Breeder and fledgling recruitment in Diego de Almagro and Evangelistas declined progressively over the long term until both colonies became extinct.

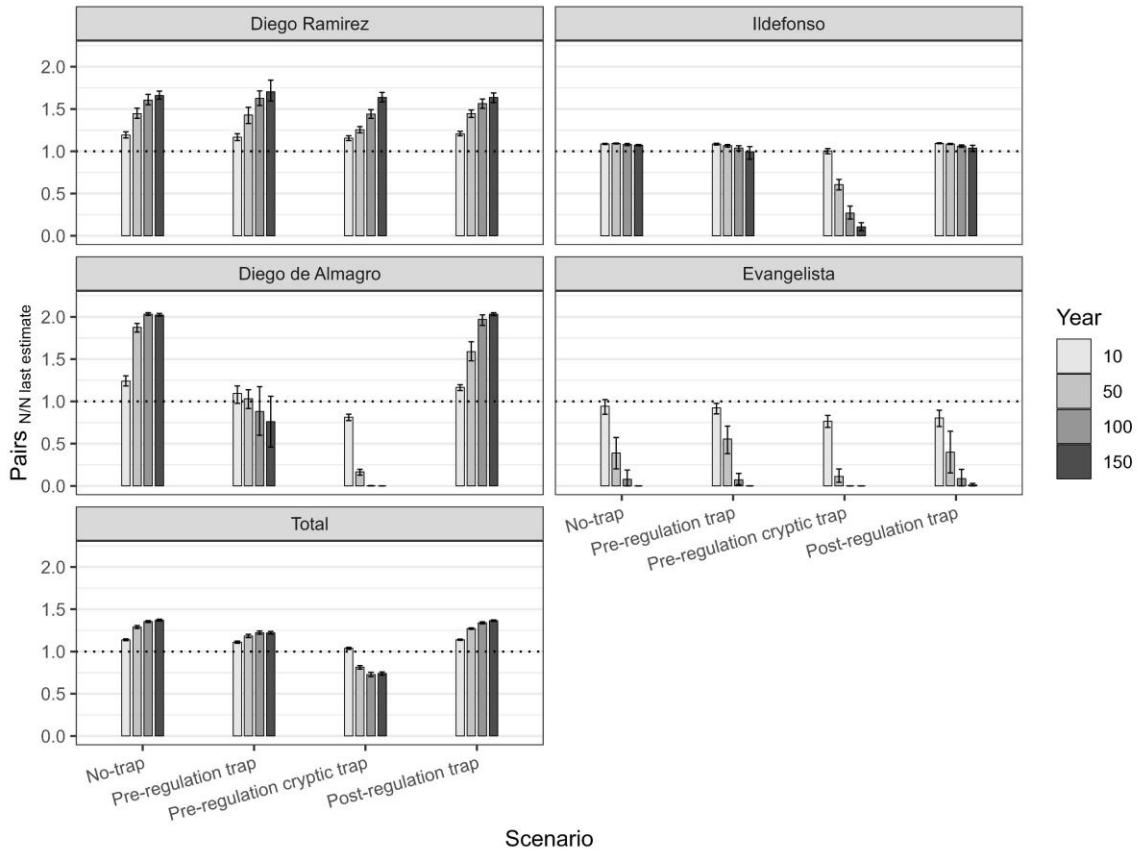


Figure 9. Breeding pairs relative to the most recent population size estimate of Black-browed Albatrosses (dotted line), in a fishery-free environment and under three scenarios involving compensatory ecological traps associated with demersal trawl fisheries ( $n = 36$  simulations; 9 replicates per scenario). The figure shows the mean and bootstrap-based confidence intervals calculated over four 20-year time windows centered around simulation years 10, 50, 100, and 150 (i.e., 10 years before and after each focal year).

**Post-regulation trap:** The southern colonies and Diego de Almagro exhibited population dynamics closely resembling those of the no-trap scenario, with only minor declines attributable to bycatch (Figure 8, 9). However, these impacts led to slightly slower population growth and a longer time to reach a stable equilibrium (Figure 8). Evangelistas, decreased in the short term but, over the medium term, followed a trend similar to the no-trap scenario—eventually reaching slightly larger population sizes over the long term (Figure 9). Ildefonso experienced a mortality level comparable to the other

scenarios (45% on average), while mortality increased to 35% in Diego Ramírez and decreased to 19% in Diego de Almagro. Evangelistas showed the lowest mortality, at just 1%. Breeder and fledgling recruitment in Diego Ramírez remained comparable to the no-trap scenario (Figure 10). In Ildefonso, breeder recruitment increased over the long term, while fledgling declined over the long term. In Diego de Almagro, breeder recruitment and fledgling increased over the long term. In contrast, breeder and fledgling recruitment initially declined but later increased over the long term in Evangelistas (Figure 10).

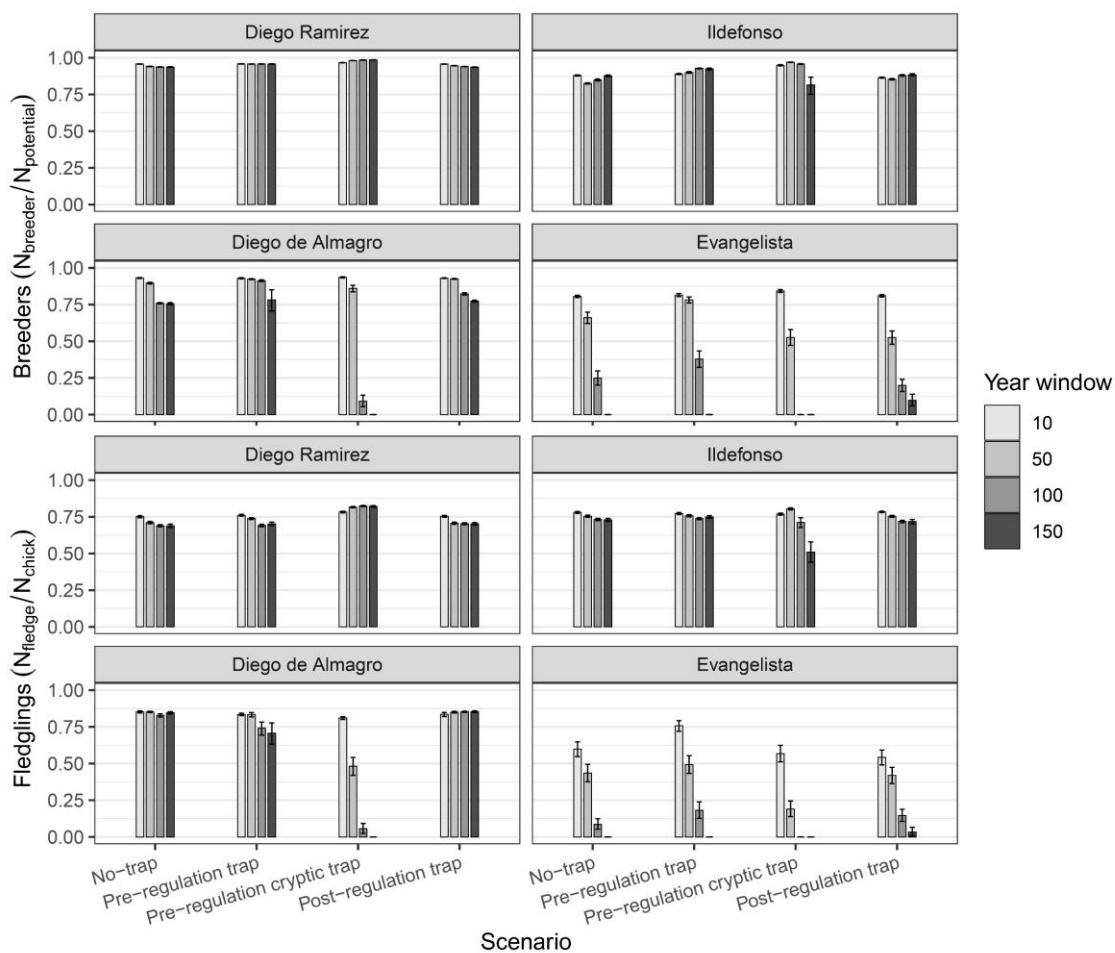


Figure 10. Breeder and fledgling recruitment of Black-browed Albatrosses in a fishery-free environment and under the three scenarios involving compensatory ecological traps

with demersal trawl fisheries ( $n = 36$  simulations; 9 replicates per scenario). The figure shows the mean and bootstrap-based confidence intervals calculated over four 20-year time windows centered around simulation years 10, 50, 100, and 150 (i.e., 10 years before and after each focal year).

## 5. Discussion

### 5.1. Predicted Foraging Habitat of the Black-browed Albatross During the Breeding Season

The ensemble SDM identified distance to breeding colonies and to the Falkland Islands super colonies as the strongest predictors of Black-browed albatross foraging distribution during the breeding season. This aligns with previous findings on spatial segregation among Southern Hemisphere colonies (Wakefield et al. 2011) and supports central-place foraging theory, which predicts reduced space use with increasing distance from the colony due to parental constraints (Olsson et al. 2008). Wakefield et al., (2011) also showed that foraging areas are spatially segregated between colonies, likely to reduce inter-colony competition. Consistent with this, our results suggest that Chilean colonies might avoid the Atlantic to minimize overlap with the Falklands, home to ~70% of the global population (Wakefield et al. 2014). However, the high overlap among Chilean colonies (Diego de Almagro, Diego Ramírez, and Ildefonso) suggests that competition may be mitigated by lower travel costs or access to productive waters. Our model also predicted a higher probability of occurrence in areas with elevated primary production, in line with prior studies showing that albatrosses concentrate in neritic and shelf-break waters with high productivity (Weimerskirch et al. 1996, Gremillet et al. 2000, Phillips et al. 2004, Wakefield et al. 2011). Lastly, we found peak albatross

occurrence at wind speeds around 8 m/s. While albatrosses are adapted to strong winds, excessively high speeds (>10 m/s) can reduce foraging success by impairing gliding efficiency and prey detection (Darby et al. 2024).

## 5.2. Bycatch and Discard Rates of Trawl Fisheries Affecting Black-browed Albatrosses

Consistent with previous studies, our results shows that temporal and spatial patterns in bycatch align closely with the breeding phenology of Black-browed albatrosses—peaking in spring (September–November) during incubation and early chick-rearing, in autumn during post/guard and fledgling period and again in winter (June–August) as birds migrate north along the Pacific coast (Robertson et al. 2014, Adasme et al. 2019). In spring, high discard rates south of 50°S match with long foraging trips across the continental shelf, likely increasing vulnerability to bycatch. In autumn-winter, elevated discards at lower latitudes provide a predictable food source for post-breeding and non-breeding birds, again raising bycatch risk. Our model also shows that bycatch rates increase in response to discards, strongly suggesting that discards drive this ecological trap by attracting birds to fishing vessels (Chapter 1, 2). This finding aligns with prior studies linking discarding to increased seabird mortality (Sullivan et al. 2006, González-Zevallos and Yorio 2006, Watkins et al. 2008, Favero et al. 2011). However, it contrasts with Adasme et al. (2019), who found no effect of discards at the haul level in the same fisheries. This discrepancy highlights the importance of scale: discard effects may extend beyond individual hauls through vessel attraction or spatial autocorrelation. Overlooking these dynamics may obscure key mechanisms and hinder effective bycatch mitigation.

Finally, our results showed that mitigation measures are highly effective: bycatch rates decreased by approximately 15% for every 10% increase in mitigation use, primarily due to widespread adoption of Bird Scaring Lines (used in ~97% of mitigated sets). This supports previous findings on their effectiveness in preventing collisions (Melvin et al. 2011, Koopman et al. 2018, Jiménez et al. 2022, ACAP 2024). Although other devices—such as visual curtains and snatch blocks—were used infrequently during the study period, their broader implementation could further reduce bycatch, particularly from third-wire collisions, which are a frequent cause of bycatch in factory trawlers (Adasme et al. 2019).

Beyond efforts to mitigate direct seabird mortality, Chilean fisheries have also advanced in reducing discards. In addition to regulatory measures—such as eliminating size limits for common hake—the implementation of Electronic Monitoring Systems (EMS), including Image Recording Devices (DRI), has played a key role (Cocas et al. 2024). Originally designed for compliance, EMS has indirectly improved fishing behavior by discouraging undesirable practices and encouraging the retention of lower-quality fish that would previously have been discarded (C. Bernal, IFOP, personal communication). These changes have been supported by strict enforcement, continuous feedback between agencies and fishers, and greater transparency across the fleet (Cocas et al. 2024). Future studies could formally evaluate the relative influence of regulatory changes, monitoring technologies, and catch levels on discard reduction.

### **5.3. Population Responses of Black-browed Albatrosses Under Trap and No-Trap**

#### **Scenarios**

The model predicts that under the pre-regulation scenario the breeding population at Diego Ramírez withstands bycatch impacts and reaches a larger size than under the no-trap scenario. In contrast, the Ildefonso and Diego de Almagro populations persist in the short term but exhibit slight and sharp long-term declines, respectively. With the introduction of cryptic mortality (three times higher than observed), these differences become more pronounced: Diego Ramírez continues growing without stabilization, whereas Ildefonso and Diego de Almagro experience sharp declines after 10 years of exposure to the trap. Meanwhile, the smallest colony, Evangelista, trends toward extinction under both scenarios.

Interestingly, increases in fledgling and breeder recruitment were observed under the pre-regulation scenario, particularly in declining colonies. However, these increases were not driven by the energetic benefits of discards. Rather, they appear to reflect a density-dependent compensatory mechanism, whereby elevated mortality reduced population size and competition for food, thus facilitating recruitment of individuals previously excluded by habitat saturation (Beverton and Holt 1975). The resulting energetic surplus also allowed breeders to provision chicks more effectively, temporarily boosting reproductive success (Figures 10 and 11). This mechanism was most evident in Ildefonso and Diego de Almagro, where initial recruitment gains delayed the onset of decline. It was also present in Diego Ramírez, where recruitment increased despite population growth—suggesting that declines in nearby colonies indirectly benefited this population through competitive release.

Previous studies have shown that increased fishery discards can enhance chick and breeder recruitment in albatrosses, with the potential to partially compensate for bycatch (Rolland et al. 2008, 2009b, 2010, Pardo et al. 2017). In our case, however, the reduction in exploitation competition resulting from the high bycatch rates had a greater demographic effect than the energetic contribution of discards. Moreover, the limited compensatory response likely reflects the modest energetic input from discards relative to the population's total energy demands—equivalent to only 5% of annual requirements and spatially restricted to 4.7% of the predicted habitat identified by the species distribution model. These findings suggest that, while discards may help buffer bycatch impacts, their compensatory potential is constrained and can be confounded by density-dependent processes and spatial trade-offs among colonies. Moreover, in species with slow life histories such as albatrosses, the scope for demographic compensation is inherently limited (see Chapter 2), as their population dynamics are more sensitive to changes in survival than to changes in reproduction (Saether and Bakke 2000).

Model predictions raise two key questions: At what levels of bycatch did the pre-regulation trap operate, and for how long? Aerial surveys at Diego Ramírez and Ildefonso reported population increases of 52% and 18%, respectively, between 2002 and 2011 (Robertson et al. 2014) with a further 29% increase in Diego Ramírez by 2014 (8.8% annually; Robertson et al. 2017). These trends suggest that bycatch mortality prior to the 2019–2020 mitigation measures most likely resembled the pre-regulation scenario. If mortality had reached the levels assumed in the cryptic scenario (i.e., three times

higher), the Ildefonso population would likely have shown a decline in the most recent census—something not observed. An even higher estimate, proposed by (Richard and Adasme 2019) of eight times the baseline ( $\approx$ 63,500 albatrosses annually), appears implausible, as it would likely have led to rapid extinction across most colonies.

Although official bycatch records prior to 2013 are unavailable (Adasme et al. 2019), trawl fleets associated with the highest mortality—factory and freezer vessels—have maintained relatively stable fishing effort (5,000–10,000 trawling hours annually) since 2002 (Robertson et al. 2017). High bycatch rates in longline fisheries before mitigation measures were introduced in 2005–2006 (Robertson et al. 2014) suggest that seabird interactions were more intense during the 1990s and early 2000s. Similar shifts in seabird-fishery interactions have been observed elsewhere following regulatory changes. Taken together, these trends strongly suggest that an ecological trap with trawl fisheries resembling the pre-regulation scenario has likely been operating since at least 2006, coinciding with the implementation of mitigation measures in longline fisheries.

Following the implementation of mitigation and regulatory measures targeting bycatch and discards, model predictions indicate that population dynamics across colonies increasingly resemble those observed under the no-trap scenario. These results suggest that current levels of bycatch and discards exert limited demographic pressure on Black-browed Albatross populations and may be compatible with their long-term persistence. Evangelistas exhibited slightly higher breeder and fledgling recruitment than under no-trap conditions, resulting in marginally greater long-term persistence compared to the other scenarios. This represents the most evident, albeit modest, case

of discard-driven compensation observed in our simulations. The energetic benefits of discards—concentrated near Evangelistas during the spring and autumn months—appear to enhance reproductive performance and delay extinction. However, these gains were ultimately insufficient to prevent a high probability of long-term extinction, underscoring the colony's inherent vulnerability. These findings suggest that Chilean colonies may exhibit a source–sink dynamic (Pulliam 1988), with Evangelistas likely functioning as a demographic sink reliant on sustained immigration from nearby colonies due to the low quality of its surrounding habitat. This dynamic may be further reinforced by competition with Diego de Almagro—its neighboring colony, which has a substantially higher carrying capacity and may limit the demographic contribution of Evangelistas through spatial exclusion.

An interesting suggestion emerging from both pre-regulation scenarios is the potential influence of ecological traps on the metapopulation dynamics of seabirds. Under the pre-regulation trap, the Diego Ramírez population—limited by energy availability—expands due to the decline of the Ildefonso and Diego de Almagro populations, which reduces inter-colony competition. Under the cryptic mortality trap, Diego Ramírez continues to grow without stabilizing within the 150-year simulation period. Similarly, the pre-regulation trap increases the population of Evangelista colony in the midterm by reducing the population size at Diego de Almagro, its nearest neighboring colony, thereby increasing food availability and recruitment at Evangelista. These results demonstrate that ecological traps associated with fisheries can alter metapopulation dynamics not only by modifying migration between populations

(Inchausti and Weimerskirch 2002), but also by redistributing mortality and competition for food among colonies.

#### **5.4. Model Assumptions, Caveats, and Future Improvements**

First, we assume that population size on Diego de Almagro, the Evangelista Islets, and the Ildefonso Archipelago are primarily limited by breeding habitat availability. While this limitation is well documented for Evangelista and Ildefonso (Robertson et al. 2014, 2017), further data are needed to assess whether the Diego de Almagro population could expand beyond current habitat-based estimates (Lawton et al. 2003). In contrast, population size at Diego Ramírez is assumed to be limited by food availability during the breeding season, a mechanism supported for other Black-browed albatross colonies worldwide (Wakefield et al. 2014). This form of density-dependent regulation—driven by prey depletion around breeding colonies—is increasingly recognized in central-place foragers, including seabirds (Ashmole 1963, Gaston et al. 2007, Oppel et al. 2015, Weber et al. 2021). However, the maximum population size Diego Ramírez can support remains uncertain. Although it may exceed our estimate (~83,000 pairs), it is likely much smaller than the populations in the Falkland Islands (~273,000 at Steeple Jason and ~103,000 at Beauchêne Island), where foraging habitat is considerably more extensive (Wakefield et al. 2011, 2014).

Understanding the carrying capacity of Black-browed albatrosses is key to assessing the effects of fishery-associated ecological traps. As epipelagic consumers, they feed on non-commercial prey such as crustaceans, fish, and squid (Mills et al. 2020),

making prey availability difficult to estimate. This is further complicated by competition with other marine predators, including fish, whales, seabirds, and pinnipeds (Croxall and Prince 1980, Brooke 2004). Future research should reduce these uncertainties, especially given that the benefits of fishery subsidies depend on the baseline availability of natural resources.

Second, we assume no emigration or immigration occurs among the modeled populations. However, immigration rates of 4.4% have been reported for Black-browed Albatrosses at Kerguelen (Rolland et al. 2009b), and up to 10% for Indian Yellow-nosed Albatrosses (*Thalassarche carteri*) on Amsterdam Island (Rolland et al. 2009a). Future research should investigate the degree of connectivity among Black-browed Albatross colonies in Chile, particularly as the Ildefonso Archipelago approaches its carrying capacity and may already be contributing individuals to other established colonies (e.g., Diego Ramírez; Robertson et al. 2017) or facilitating the formation of new ones. For instance, the most recently established colony in Chile—Albatross Islet (not included in our model)—comprises an even mix of individuals from southern Chilean colonies (52%) and the Falklands/Malvinas (48%) (Burg et al. 2025). Understanding colony connectivity may be especially important for assessing the dynamics of the Evangelistas colony, which appears to function as a demographic sink reliant on immigration from other colonies (Pulliam 1988).

Third, the model also assumes negative density-dependent reproduction (Sibly et al. 2005, Brook and Bradshaw 2006), whereby winter foraging success declines as populations approach carrying capacity due to competition. While compensatory effects—

such as social facilitation in foraging (Stephens and Sutherland 1999, Grünbaum and Veit 2003)—have been suggested in small colonies (Pardo et al., 2017), these are unlikely to dominate in our study populations, which are considerably larger. Clarifying the form and strength of density dependence is crucial, as it can alter model predictions and lead to either over- or underestimation of population vulnerability (Horswill et al. 2017, Merrall et al. 2024).

Fourth, we assume that habitat quality exhibits positive temporal autocorrelation with an approximate three-year periodicity, reflecting environmental variability in the Southern Ocean driven by El Niño–Southern Oscillation and the Southern Annular Mode. However, there is no direct evidence regarding the direction or magnitude of such autocorrelation in prey availability for albatrosses. While slow-lived species like albatrosses generally show low demographic sensitivity to environmental variability (Paniw et al. 2018, Le Coeur et al. 2022), future studies should assess how habitat autocorrelation influence their responses to ecological traps.

Regarding the caveats, we did not differentiate among reproductive stages (incubation, guard, post-guard) in the model, and the SDM combined tracking data from all three. This resulted in a generalized pattern of breeding habitat use that, while centered near the colonies, extended to the Antarctic Peninsula for Diego Ramírez and Ildefonso. However, stage-specific data from Diego Ramírez show clear spatial shifts: birds forage off Arauco Gulf during incubation, remain near the colony during the guard phase, and move farther south post-guard (Robertson et al. 2014). Despite these shifts, most habitat use occurred south of 50°S, which our model broadly captured. The model

also predicts that the Ildefonso population—and to a lesser extent, those of Diego de Almagro and Evangelistas—utilize habitat around the Antarctic Peninsula. While this is plausible given Ildefonso’s proximity to Diego Ramírez, the absence of stage-specific tracking data for Ildefonso prevents confirmation.

Beyond these caveats, the model could be improved by refining behavioral mechanisms and integrating additional ecological processes. Our model is grounded in optimal foraging theory, which posits that individuals make movement and feeding decisions to maximize fitness, guided by hunger and previous foraging success. However, the foraging mechanism could be improved by incorporating trade-offs—such as those between hunger and risk—mediated by individual experience. For example, Weimerskirch et al. (2023) found that the wandering albatross attraction to fishing vessels increases during immaturity, peaks in adulthood, and declines in old age, suggesting a life-stage shift in risk-taking behavior. Juveniles may avoid risky but energy-rich discards due to high future reproductive value, while adults take greater risks, and senescent individuals become more cautious as physical condition and reproductive value decline (Weimerskirch et al. 2023). Modeling these dynamics could help clarify how behavioral trade-offs shape population responses to ecological traps.

Further refinements could include foraging algorithms that integrate sensory mechanisms—such as vision, or faction (e.g., in burrow-nesting procellarids; Nevitt 2008), and audition (Gillies et al. 2023). Lastly, while the model (including the SDM) was developed under current environmental conditions, the same approach could be extended to climate change scenarios, where poleward shifts in both fisheries and

seabird distributions may increase the risk of emergent ecological traps (Krüger et al. 2018).

## **5.5. Incorporating Ecological Traps into Management and Conservation Initiatives of seabirds**

The ecological trap framework has been largely overlooked in seabird–fishery studies, except for cases involving low-quality subsidies (Grémillet et al. 2008). Applying this framework to scenarios where fisheries subsidies simultaneously increase habitat attractiveness and bycatch risk can strengthen conservation and management efforts in several ways. First, it provides a conceptual foundation for ecosystem-based fisheries management by highlighting how behavioral responses to human-induced changes—such as trophic subsidies from discards—can drive maladaptive outcomes and reduced fitness, clarifying the mechanisms underpinning seabird–fishery interactions (Chapter 1) and informing both stakeholder engagement and regulatory strategies. Second, it can improve the estimation of sustainability thresholds and guide management actions by accounting for how fisheries subsidies dynamically amplify or compensate bycatch impacts (Chapter 2), enabling the identification of critical thresholds where discards shift population dynamics toward unsustainability and informing discard management and long-term mitigation planning. Third, it integrates behavioral mechanisms by linking individual decisions to population persistence, thereby identifying opportunities for mitigation measures to deactivate ecological traps and enhance population resilience. Finally, as demonstrated in this study, it can help identify key knowledge gaps that are critical to understanding and managing seabird–fisheries interactions; by explicitly

parameterizing mechanistic models, uncertainties in habitat quality and selection, demographic parameters, and metapopulation dynamics can be revealed.

## 6. Conclusions

This study provides a mechanistic evaluation of the population-level consequences of seabird–fishery interactions through the lens of compensatory ecological traps. By integrating empirical data on bycatch and discards into a spatially explicit, individual-based model, we assessed whether interactions between Black-browed Albatrosses and demersal trawl fisheries in southern Chile give rise to ecological traps under contrasting management scenarios, and whether fishery-derived trophic subsidies can offset the demographic costs of bycatch. Our results show that discard availability increases bycatch risk, supporting the hypothesis that discards attract birds and drive trap formation. While one colony (Diego Ramírez) withstood bycatch pressure, others (Ildefonso and Diego de Almagro) declined, particularly under cryptic mortality scenarios that led to extinction. Although initial gains in breeder and fledgling recruitment were observed, these were driven by reduced competition following elevated mortality, rather than by energetic subsidies from discards, which accounted for only a small fraction of the population’s energy needs and habitat use. These findings indicate that trophic subsidies offer limited compensation for bycatch and that the net effect of ecological traps—prior to regulatory measures—was largely negative. Our results also show that ecological traps can restructure metapopulation dynamics by redistributing mortality risk and food competition among colonies, underscoring the importance of incorporating spatial processes into population models. Finally, our findings highlight the

critical role of bycatch mitigation and discard reduction in supporting the long-term viability of Black-browed Albatross populations. Regulatory measures implemented in Chile since 2019 have markedly reduced bycatch and discards, leading to population trajectories that closely resemble the no-trap scenario. Sustaining and strengthening these measures will be essential for long-term conservation success. More broadly, ecological trap theory offers a valuable framework for understanding maladaptive habitat selection and informing ecosystem-based fisheries management.

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## 8. Supplementary material

### S1. Tracking data from Black-browed albatross used in the study.

Table S1. Number of individual Black-browed Albatrosses tracked at each colony and breeding stage used to model foraging habitat.

Colony	Breed stage	Individuals tracked (n)	years
Diego de Almagro	incubation	12	2001
Diego Ramirez	incubation	69	1997, 1999, 2000, 2001
Diego Ramirez	brood-guard	33	1999, 2000, 2001
Diego Ramirez	post-guard	23	2001, 2002
Ildefonso	incubation	26	2001

### S2. Fishery-specific calorific estimates based on main discarded species.

For each fleet, we estimated the average energy density and its standard deviation (Table S2.1) using available data for the main discarded species (Bernal et al., 2019) whenever possible. When such data were unavailable, we used information from closely related species as proxies (Table S2.2). For the south-central fleet, we used values from the Merluccidae and Ommastrephidae families, as no specific data were available for *Merluccius gayi gayi* and *Dosidicus gigas*. For the factory trawl fleet, we used values for *Micromesistius australis*, *Macruronus magellanicus*, and *Merluccius australis*, while for the freezer fleet we considered *Macruronus magellanicus* and *Merluccius australis* (Table S2.2).

Table S2.1. Fishery-specific calorific estimates.

Fishery	mean KJ g <sup>-1</sup>	Std. dev. KJ g <sup>-1</sup>
South-central	4.6	1.2
Factory	5.5	1.0
Freezer	6.0	0.7

Table S2.2. Energy density of the main discarded species by trawl fisheries or closely related species, based on available information.

Family	Species	KJ g <sup>-1</sup>	Reference
Merlucciidae	<i>Micromesistius australis</i>	4.54	(Ciancio et al. 2007)
Merlucciidae	<i>Macruronus magellanicus</i>	6.51	(Eder & Lewis, 2005)
Merlucciidae	<i>Merluccius australis</i>	5.48	(Eder & Lewis, 2005)
Merlucciidae	<i>Merluccius hubbsi</i>	4.91	(Eder & Lewis, 2005)
Merlucciidae	<i>Merluccius hubbsi</i>	4.08	Ciancio et al., (2007)
Ommastrephidae	<i>Ommastrephes bartrami</i>	3.13	(Croxall & Prince, 1982)
Ommastrephidae	<i>Todarodes pacificus</i>	3.26	(Croxall & Prince, 1982)
Ommastrephidae	<i>Todarodes pacificus</i>	4.19	(Croxall & Prince, 1982)
Ommastrephidae	<i>Todarodes pacificus</i>	3.53	(Croxall & Prince, 1982)
Ommastrephidae	<i>Todaropsis eblanae</i>	4.46	(Croxall & Prince, 1982)
Ommastrephidae	<i>Illex argentinus</i>	6.42	(Eder & Lewis, 2005)

### S3. Energy distribution

We simulate the spatial and temporal distribution of energy using a Poisson distribution, where the rate parameter  $\lambda_t$  is based on habitat suitability predicted by the species distribution model (SDM) and adjusted to account for temporal dependence. The goal was to generate realistic energy values in each spatial cell over time with the possibility of incorporating correlation between successive years. The energy available in each spatial cell in any given year follows a Poisson distribution:

$$E_t \sim \text{Poisson}(\lambda_t)$$

where  $E_t$  is the energy value at year  $t$  and  $\lambda_t$  is the rate parameter of the Poisson distribution. The rate parameter is defined as the product of habitat suitability from the SDM, a scaling parameter  $\beta_{\text{lambda\_habitat}}$  that controls the patchiness of the distribution (Table 2), and a temporally correlated term  $Z_t$  that introduces temporal dependence:

$$\lambda_t = \beta_{\text{lambda\_habitat}} \cdot \text{habitat suitability} \cdot \exp(Z_t)$$

Specifically,  $Z$  is a matrix of simulated values correlated over time, with dimensions equal to the number of cells (rows) and the number of years (columns). This matrix is generated from a multivariate normal distribution:

$$Z \sim N(0, C)$$

where,  $0$  is the mean vector (all means are zero), and  $C$  is a correlation matrix that controls the temporal dependence structure.

The correlation structure of  $C$  is defined by an AR(1) correlation matrix, which follows an exponential decay function that represents the correlation between years:

$$C_{ij} = \beta \text{rho}^{|i-j|}$$

where  $C_{ij}$  is the correlation between energy values at times  $i$  and  $j$ ,  $\beta \text{rho}$  (Table 2) is the temporal autocorrelation parameter (between 0 and 1), and  $|i-j|$  is the time difference between the two time points. The matrix  $C$  defines the temporal dependence structure, where higher values of  $\beta \text{rho}$  result in stronger correlations between neighboring years.

#### S4. Initial populations

Table S4. Initial number of individuals per colony at the start of the simulation. The most recent census data on breeding pairs were used to estimate the initial population size for each colony. Total population size was calculated using a breeder-to-population ratio of 0.375, which represents the average proportion of breeders derived from the simulation model based on the vital rates of the Black-browed Albatross.

colony	pairs	year	breeding birds	total	super individuals	super breeders	Reference
Diego de Almagro Island	15,594	2001	31188	83,168	416	156	(Lawton et al. 2003)
Evangelista Islet	4,818	2014	9636	25,696	128	48	(Robertson et al. 2017)
Ildefonso archipelago	54,284	2014	108568	289,515	1448	543	(Robertson et al. 2017)

Diego Ramirez archipelago	55,000	2002	110000	293,333	1467	550	(Robertson et al. 2007)
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### S5. Assimilation efficiency estimated for the Black-browed Albatross

Due to the lack of species-specific data on assimilation efficiency for the Black-browed Albatross, we estimated an average value derived from 46 observations across 23 seabird species consuming various fish and invertebrate diets (Table S5.1). We fitted a beta regression to these observations using the gamlss package in R (Figure S5.1) and used the resulting parameters (mean and dispersion Table S5.2) as a proxy estimates for the Black-browed Albatross.

Table S5.1. Observations used to estimate a proxy for assimilation efficiency in the Black-browed Albatross. References in bold indicate new observations not included in Sherley et al., (2019). Only these references are included in the main reference list; for all others, see Sherley et al. (2019).

Specie	Assimilation efficiency	Reference
Adélie penguin (chick)	0.8	Kooyman et al. 1982
African penguin (chick)	0.75	Cooper 1977
Atlantic puffin	0.79	Hilton et al. 2000
Atlantic puffin	0.78	Hilton et al. 2000
Black-legged kittiwake	0.74	Hilton et al. 2000
Black-legged kittiwake	0.77	Hilton et al. 2000

Black-legged kittiwake	0.72	Brekke & Gabrielsen 1994
Black-legged kittiwake	0.81	Brekke & Gabrielsen 1994
Blue petrel	0.77	Jackson 1990
Brunnich's guillemot	0.75	Brekke & Gabrielsen 1994
Brunnich's guillemot	0.71	Brekke & Gabrielsen 1994
Cape gannet	0.79	Batchelor & Ross 1984
Cape gannet	0.76	Jackson 1990
Cape gannet	0.74	Cooper 1978
Cape gannet (juvenile)	0.76	Cooper 1978
Common guillemot	0.78	Hilton et al. 2000
Common guillemot	0.79	Hilton et al. 2000
Double-crested cormorant	0.75	Brugger 1993
Double-crested cormorant	0.79	Brugger 1993
Double-crested cormorant	0.78	Brugger 1993
Double-crested cormorant (chick)	0.85	Dunn 1975
Emperor penguin	0.82	Robertson & Newgrain 1992
Eurasian shag	0.8	Hilton et al. 2000
Eurasian shag	0.81	Hilton et al. 2000
Gentoo penguin	0.78	Jackson 1990
Great skua	0.83	Hilton et al. 2000
Great skua	0.8	Hilton et al. 2000

Great white pelican	0.73	Cooper 1980
Herring gull	0.79	Hilton et al. 2000
Herring gull	0.8	Hilton et al. 2000
King penguin	0.71	Jackson 1990
King penguin	0.81	Adams 1984
Northern fulmar	0.83	Hilton et al. 2000
Northern fulmar	0.84	Hilton et al. 2000
Razorbill	0.78	Hilton et al. 2000
Razorbill	0.79	Hilton et al. 2000
<b>Rockhopper penguin</b>	<b>0.75</b>	<b>Jackson 1990</b>
Short-tailed shearwater (fledglings)	0.8	Oka 2011
Short-tailed shearwater (fledglings)	0.85	Oka 2011
Short-tailed shearwater (fledglings)	0.78	Oka 2011
<b>Sooty albatross</b>	<b>0.76</b>	<b>Jackson 1990</b>
<b>wandering albatrosses</b>	<b>0.82</b>	<b>Battam et al. 2010</b>
White-chinned petrel	0.76	Jackson 1990
White-chinned petrel (fledgling)	0.78	Jackson 1986
White-chinned petrel (fledgling)	0.74	Jackson 1986
White-chinned petrel (fledgling)	0.76	Jackson 1986

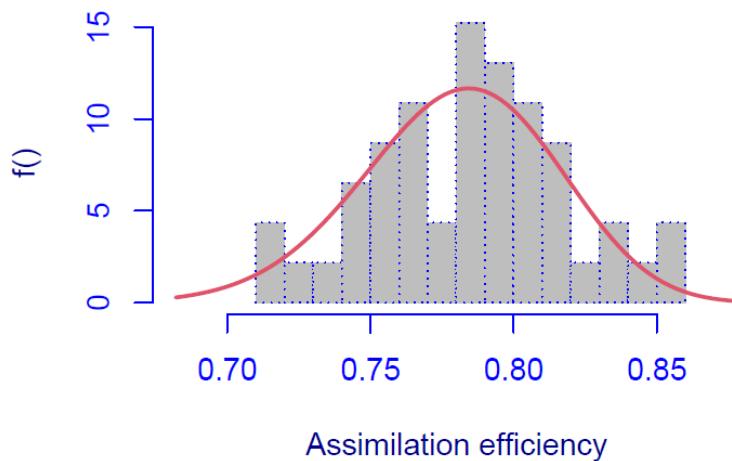


Figure S5.1. Empirical distribution of assimilation efficiency of 23 seabird's species (histogram) and fitted distribution (in red).

Table S5.2. Parameters estimated (logit scale) from the beta regression fitted to 46 observations across 23 seabird species consuming various fish and invertebrate diets (see Table S5.1).

Parameter	Estimate	Std. Error	t value	Pr(> t )
mu	1.26805	0.02945	43.06	<2e-16
sigma	-2.4064	0.1126	-21.37	<2e-16

## S6. Intra-annual variation in the abundance of Black-browed Albatrosses in central Chile.

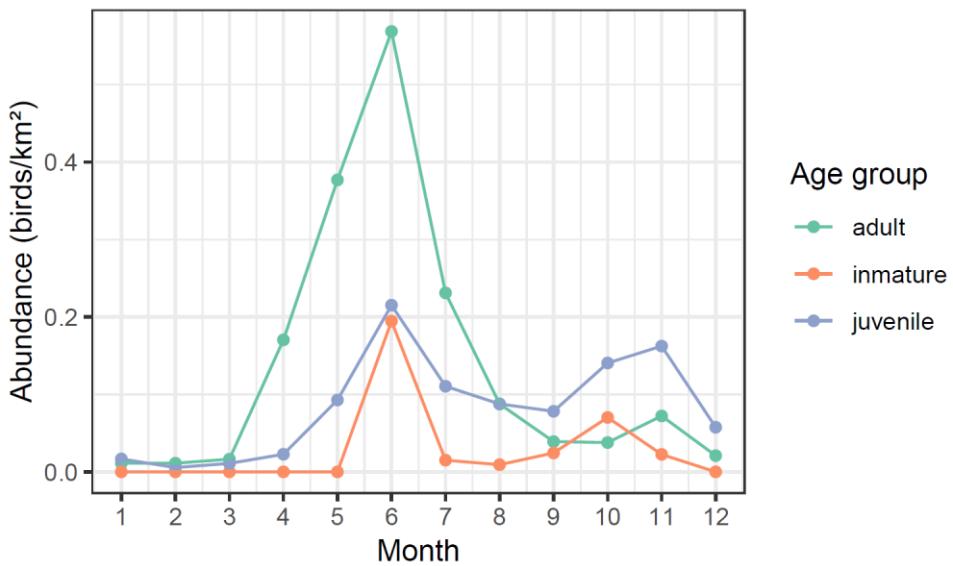


Figure S6. Mean density of Black-browed Albatrosses observed in Valparaíso Bay, central Chile (~33°S), based on a systematic monthly monitoring program conducted between 2006 and 2018 (see, Simeone et al., 2014).

### S7. Observed and simulated foraging distances traveled per individual

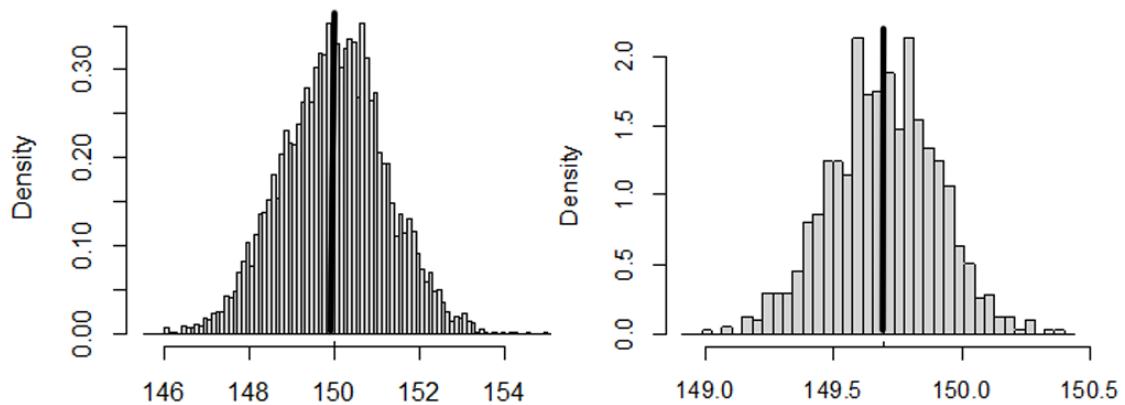


Figure S7. Left panel: observed average distance traveled per individual (km per 6 hours) during foraging trips of Black-browed Albatrosses breeding in Chile (including individuals

from Diego Ramírez, Ildefonso, and Diego de Almagro; see Table S1). Right panel: average movement distance of simulated individuals (km per 6-hour time step).

#### **S8. Estimated number of provisioning events for Black-browed albatross**

Table S8. Estimated number of provisioning events (incubation + chick feeding) performed by Black-browed Albatrosses during the breeding season. The second column reports the mean foraging trip duration derived from the average values reported across the selected studies for each breeding phase. The third column presents the estimated duration of each breeding phase for Chilean colonies. Based on these two columns, the total number of provisioning events was estimated and used as a reference to calibrate the fledging function in the model.

Phase	Trip duration (days)	Phase duration (days)	“Provisioning events”	“Provisioning events” (2 parents)	Reference
Incubation	6.6	60	9	18	(Huyn 2002, Phillips et al. 2004, Granadeiro et al. 2018, Gillies et al. 2021)
brood-guard	2.03	45	22	44	(Huyn 2002, Phillips et al. 2004, Catry et al. 2010, Granadeiro et al. 2018, Gillies et al. 2021)
post-guard	2.42	135	56	111	(Huyn 2002, Phillips et al. 2004)
				<b>175</b>	

### S9. Age-related mortality

Table S9. Age-specific mortality rates used in the simulation, following Nevoux et al. (2010) and Pardo et al. (2013).

Age (years)	Probability of mortality
0	0.224
1	0.219
2	0.214
3	0.208
4	0.203
5	0.198
6	0.154
7	0.110
8 - 30	0.066
31	0.123
32	0.180
33	0.237
34	0.294
35	0.351
36	0.408
37	0.465
38	0.522

39	0.579
40	0.636

#### S10. Carrying capacity of each colony based on the availability of breeding habitat.

We estimated the total number of breeding pairs that could be supported in each archipelago or island based on the availability of nesting habitat, using different methodological approaches depending on the information available. These estimates were produced using the *terra* (Hijmans 2023) and *dplyr* (Wickham et al. 2023) packages in R (R Core Team 2023). Colony carrying capacities are shown in Table S10.

Table S10. Estimated carrying capacity of each colony based on the availability of breeding habitat.

	Pairs	Breeding birds	Super breeder
Diego de Almagro Island	30000	60000	300
Evangelista Islet	5000	10000	50
Ildefonso Archipelago	61000	122000	610
Diego Ramirez Archipelago	180000	360000	1800

Below, we describe the procedures used for each colony. Currently, no information is available on the number of pairs that Diego de Almagro Island could potentially support.

On this island, colonies are located along the western edge, on slopes covered with tussock grass (*Poa flabellata*) (Lawton et al. 2003). To assess habitat availability, we used

the land cover map of Chile (Zhao et al. 2016), which provides detailed classification categories, including grassland cover, at a resolution of 30 m. From this raster, we generated a contour extending 200 meters inland from the island's edge. We then selected only the area within a 5 km buffer around the existing colonies, as we considered it more likely that albatrosses would expand into areas closer to their current nesting sites. Finally, we estimated the number of breeding pairs by multiplying the total area classified as "grassland" by the breeding pair density recorded on Ildefonso Island for this habitat type (0.1 pairs/m<sup>2</sup>) (Robertson et al. 2008), assuming that 50% of the total area would be suitable for nesting.

The Diego Ramírez Archipelago still appears to be far from reaching its carrying capacity (personal observation, Graham Robertson, Robertson et al., 2014). The islands with the greatest potential for population growth are those in the southern group, which contain 97% of the archipelago's population. To assess habitat availability in these islands, we generated a digital elevation model (10 × 10 m) using the terra package in R (Hijmans 2023), including the islands of Gonzalo, Bartolomé, Ester, and Santander. For Gonzalo Island, we used GPS data collected by us in the summer of 2022, consisting of 6,234 points distributed across the island. For the remaining islands in the southern group, we digitized Nautical Chart No. 20 (2021), "*Diego Ramírez Islands: Geographic Position of Normal Base Points*", produced by the Hydrographic and Oceanographic Service of the Chilean Navy. From this model, we derived a slope raster (in degrees) using the terrain function of the terra package (Hijmans 2023) and then estimated the density of breeding pairs for each cell using an exponential function of the island's slope, as follows:

$$\text{Density} = \beta_{\min} + \beta_{\max} \cdot e^{-k(\text{slope})}$$

We assumed a decay rate ( $k$ ) of 0.2, a maximum density of 0.8 pairs/m<sup>2</sup> ( $\beta_{\max}$ ), and a minimum density of 0.1 pairs/m<sup>2</sup> ( $\beta_{\min}$ ), based on average values recorded on Isla Grande in the Ildefonso Archipelago for low-slope and high-slope areas covered with tussock grass, respectively (Robertson et al., 2008). Additionally, we calculated a probability of nest presence for each cell using a logistic function based on the elevation of the islands, as follows:

$$\text{Probability of presence} = 1 + e^{k(\text{elevation} - \beta_{\text{elevation}})}$$

Where  $\beta_{\text{elevation}}$  represents the midpoint of the function and  $k$  controls the steepness of the curve ( $k = 0.2$ ). We set  $\beta_{\text{elevation}}$  to 40 m, as albatrosses tend to nest above this elevation, while lower elevations are primarily occupied by other species, mostly penguins (Schlatter & Riveros, 1987). We then calculated the estimated number of breeding pairs by multiplying the area of each cell by the density of pairs, the probability of presence, and the proportion of habitat available for Black-browed albatrosses relative to grey-headed albatrosses (*Thalassarche chrysostoma*) (Robertson et al. 2014). We assumed that 60% of the total area was suitable for Black-browed albatrosses on Gonzalo Island, while for the remaining islands in the southern group, we used 80% (Robertson et al. 2014).

The Ildefonso archipelago is currently near its carrying capacity (personal observation, Graham Robertson). Isla Grande hosts 62% of the total population and consists predominantly of bare rock, with little apparent available space for further population

expansion (Robertson et al. 2008). Therefore, we assumed the maximum potential breeding population size to be only 5% greater than the highest number of breeding pairs recorded in 2011 (Robertson et al. 2017).

The Evangelistas Islets are four small rock stacks (Arata et al. 2003) that appear to have reached their carrying capacity (Robertson et al., 2017). We assumed the maximum potential breeding population size to be 5% greater than the highest recorded number of breeding pairs in 2014 (Robertson et al. 2017).

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## GENERAL CONCLUSION

This thesis offers a mechanistic and integrative perspective on how ecological traps emerge from the interaction between trophic subsidies, incidental bycatch, and the slow–fast continuum of life history in seabirds. By integrating a systematic literature review, formal theoretical simulations, and a case study grounded in empirical data on Black-browed Albatrosses and demersal trawl fisheries in southern Chile, this thesis offers both novel and methodologically robust insights into the fitness trade-offs underlying maladaptive responses and their consequences for conservation and fisheries management.

The central hypothesis proposed that the population dynamics of seabirds interacting with fisheries are shaped by a trade-off between bycatch-induced mortality and recruitment gains associated with trophic subsidies, and that the outcome of this trade-off is modulated by species' life-history strategies and fishery management regimes. Overall, the findings of this thesis support this hypothesis, while also highlighting the system-specific nature of ecological trap outcomes in seabird populations

Chapter 1 provides a conceptual foundation for interpreting seabird–fishery interactions as potential ecological traps. To this end, global data from 341 seabird species were compiled and analyzed using a phylogenetically controlled Bayesian multilevel model to assess the relationship between scavenging behavior and bycatch, as well as the influence of the slow–fast life-history continuum on the occurrence and

severity of ecological traps. Specifically, three hypotheses were tested regarding how life-history strategy influences both the likelihood of selecting trap-like habitats and the demographic consequences of such behavior at the population level.

Consistent with theoretical and empirical evidence suggesting that species at the “slow” end of the slow–fast continuum—those that prioritize survival over reproduction and therefore have a greater time budget—tend to explore their environment more thoroughly and exhibit superior learning performance than fast-lived counterparts, our results supported the first of the two behavioral hypotheses: slow-lived species (e.g., albatrosses and petrels) displayed a higher propensity to scavenge. Likewise, in line with the population-level hypothesis, these same species showed a higher probability of being threatened by bycatch according to IUCN assessments.

Together, the findings from Chapter 1 support a central element of the thesis’s main hypothesis by showing that slow-lived species are both more likely to scavenge and more vulnerable to the demographic costs of bycatch. This highlights their susceptibility to compensatory ecological traps, where fishery-derived trophic subsidies fail to offset increased juvenile and adult mortality. These results provide comparative evidence that the demographic consequences of seabird–fishery interactions are shaped by species’ position along the slow–fast life-history continuum. We argue that incorporating ecological trap theory into fisheries management could strengthen ecosystem-based approaches by clarifying the causal mechanisms underlying this global conservation issue, enhancing the design of conservation strategies, and supporting the implementation of effective mitigation measures. In an era of accelerating

environmental change, recognizing and managing ecological traps may be critical for conserving long-lived species and promoting sustainability in marine ecosystems.

Chapter 2 explicitly tested the central hypothesis of the thesis using a spatially explicit simulation model. By comparing species with contrasting life-history strategies under varying levels of bycatch and trophic subsidies, we examined whether demographic trade-off could result in divergent population outcomes depending on species' position along the slow–fast continuum. The model revealed a critical interaction between trap-related subsidies and mortality, with species-specific thresholds determined by their life-history position. These thresholds defined the transition from positive effects of subsidies to negative, synergistic effects with mortality, driven by higher effective mortality linked to stronger habitat preference.

As predicted by life-history theory, our results showed that, under similar exposure conditions, slow-lived species were more vulnerable to extinction in compensatory trap scenarios than fast-lived species, which exhibited greater demographic resilience and growth potential. This supports the thesis' central hypothesis by demonstrating that demographic compensation is shaped by the interaction between life-history strategy and fisheries management. Moreover, consistent with evidence from albatrosses and gulls, our findings suggest that fisheries may act as selective filters on life-history strategies—disproportionately impacting slow-lived species while favoring fast-lived ones. By extending ecological trap theory to incorporate multiple fitness trade-offs, our results highlight the need for a broader

framework to anticipate and mitigate the unintended consequences of human-derived trophic subsidies.

Chapter 3 applied the simulation framework developed in Chapter 2 to an empirical case study of Black-browed Albatrosses interacting with demersal trawl fisheries in southern Chile. The aim was to assess whether such interactions give rise to ecological traps under contrasting management regimes and to evaluate the potential for demographic compensation. The results showed that under pre-regulation conditions, high bycatch and discard levels could lead to population declines or extinction, especially when cryptic mortality was considered. In contrast, the post-regulation scenario produced population trajectories resembling the no-trap scenario, supporting long-term persistence in most colonies. These results demonstrate the effectiveness of regulatory measures implemented between 2019 and 2020 and highlight the importance of maintaining strict bycatch mitigation and discard reduction to prevent the formation of ecological traps.

This chapter also revealed novel findings that emphasize the importance of considering the spatial structure of populations. First, the Evangelistas colony showed a consistent trajectory toward extinction under all scenarios, suggesting it may function as a demographic sink within a source–sink metapopulation dynamic. Second, the results suggest that compensatory ecological traps can reshape metapopulation dynamics by redistributing mortality risk and food competition among colonies. These findings suggest that while discards may partially buffer the effects of bycatch, their

compensatory potential may be limited and confounded by density-dependent processes and spatial trade-offs among colonies.

Overall, the findings from Chapter 3 support the central hypothesis by showing that the net effect of the interaction between trophic subsidies and bycatch is critically shaped by fishery management regimes and species-specific demographic buffering capacity. In the case of the Black-browed Albatross—a slow-lived species characterized by low fecundity and high longevity—this compensatory capacity is limited. Our findings confirm that, for slow-lived species like the Black-browed Albatross, the demographic trade-off between subsidies and mortality resolves negatively when management conditions are unfavorable, as predicted by life history theory. In this context, the results further underscore the need to maintain and strengthen bycatch mitigation measures in trawl fisheries, as only under strict management regimes can populations achieve sustainable trajectories and avoid falling into ecological traps with severe demographic consequences.

Finally, as discussed throughout Chapters 2 and 3 of this thesis, a promising avenue for future research lies in the development of models in which individual decisions reflect trade-offs between competing components of fitness (e.g., through Bayesian updating). Such models could identify optimal behavioral trajectories from among multiple alternatives aimed at maximizing a given fitness metric—such as expected future survival or reproductive output—while explicitly accounting for the combined effects of food acquisition and mortality risks, including bycatch. Incorporating these trade-offs, together with the influence of individual experience—such as memory

of past foraging success or exposure to threats—could yield more realistic behavioral and demographic patterns. For instance, individuals previously exposed to bycatch risk may develop avoidance behaviors or modify their foraging site fidelity, particularly if they associate specific locations or cues with danger. Over time, such experience-based plasticity could lead to improvements in foraging efficiency and risk management, thereby contributing to age- or experience-related increases in reproductive success, as observed in several albatross species. These mechanisms would enhance both the explanatory and predictive power of the model and strengthen its applicability to other species and fisheries contexts.

The results from Chapter 3 that suggest that the colonies may function as a source–sink system for the Black-browed Albatross, point to the necessity to further explore the model’s predictions to determine under what scenarios the Evangelistas colony may have originated, and what levels of migration—from which source colonies—are required to sustain its persistence. Furthermore, the recent reduction in bycatch pressure on Black-browed Albatrosses may facilitate future range expansion into new colonies as the Diego Ramírez population approaches its carrying capacity. Under this scenario, reducing uncertainty surrounding the system’s carrying capacity becomes especially important.

Finally, an important question that remains to be formally addressed is the historical impact of demersal trawl fisheries on Black-browed Albatrosses. Southern fleets have been operating since the 1970s, and generating postdictions of past bycatch

and discard effects could provide valuable insights into the historical and current population dynamics of the species.

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## APENDIX

The code for the models from Chapters Two and Three can be found at:

<https://github.com/cristobalanguita/Compensatory-ecological-trap>