Review

A review of niche segregation across sympatric breeding seabird assemblages

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Breeding seabirds challenge the concept of niche segregation among competing species because similar competitors with comparable life histories can coexist in large multi-species colonies. This makes them an ideal model organism for studying the Hutchisonian niche model, which proposes interspecific niche segregation, across *n*-dimensions. Recent advances in assessment of ecological niches have improved our understanding of the mechanisms leading to at-sea segregation. We examine 152 published studies investigating one or more of three niche spaces in breeding seabirds: dietary items, stable isotopes (isotopic niche) and spatial distribution (horizontal and vertical). Most studies focused on one rather then multiple niche spaces in combination. When multiple niche spaces were combined, higher segregation than overlap was reported, compared with when niche spaces were assessed individually, as is predicted by the *n*-dimensional hypervolume concept. Studies investigating vertical (diving) foraging dimensions in addition to the more traditional horizontal (spatial) assessment reported more spatial segregation than overlap, compared with studies focusing only on horizontal or vertical dimensions. Segregation increased with colony size, suggesting an effect of competition. Segregation also increased during chick-rearing, when taxa were more phylogenetically distant, and when foraging ecology was more similar. To gain a comprehensive understanding of sympatric competitors' interactions and their ecological niche space, it is important to combine approaches and standardize methodologies. Embracing multidimensional approaches to assess niche segregation in seabird species can inform effective conservation and management practices in marine ecosystems.

Keywords: central-place foraging, coexistence, hypervolume, interspecific competition, niche overlap.

Competitive interactions can shape entire natural assemblages by driving evolution and diversity (Schoener 1974, Abrams 1990). The competitive exclusion principle predicts that when sympatric species share ecological preferences and generate competitive environments, one species may exclude the other (Volterra 1928, Gause 1934, Hardin 1960). A niche is the

conceptual space in which a species thrives and interacts. The Grinellian niche is defined by a species' abiotic requirements to survive (its habitat; Grinnell 1924); the Eltonian niche expands this idea to include community biotic interactions, such as prey and predators (Elton 1927). Hutchinson (1957) defined the *fundamental niche* as the space a species occupies in the absence of competitors assessed by a series of variables, or dimensions (also called *n*-dimensional), whereas in the presence of competitors, species are confined to their *realized niche*.

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Researchers' conceptualization of a niche varies greatly across studies (Sales *et al.* 2021). In this review, we use the term niche to refer to the *n*-dimensional realized ecological niche that considers the functional role of an organism in its community (Alley 1982; see Box 1). The theory of niche segregation suggests that competitors with shared limited resources can coexist in a community by adjusting one or more dimensions within their niche (Hutchinson 1957, 1959). Niche theory is a key concept in ecology (Chase & Leibold 2004) and provides a framework for studying community structures across taxa, including sympatric plants (Sorensen *et al.* 2020), lizards (Bergeron & Blouin-Demers 2020) and ungulates (Cromsigt & Olff 2006). However, because *n*-dimensional niches are challenging to quantify in wild animals, especially wide-ranging marine animals, most niche studies use proxies for diet and habitat axes, such as stable isotopes or movement behaviour. Despite the prominence of niche theory studies, there is currently no comprehensive niche framework available to standardize research practices with these various proxies, highlighting a research gap in the field.

Sympatric marine species, particularly seabirds, often share resources and congregate at sea in time and space where prey is predictably aggregated (Belkin *et al.* 2009, Bost *et al.* 2009, Humphries *et al.* 2010). This can lead to competition due to potential overlap in diet and foraging areas. Seabirds frequently breed synchronously, share life-history traits and have a limited distribution of suitable breeding colonies, which results in multi-species aggregations (Gochfeld 1980). Although

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Box 1 Niche definitions.

The definition and interpretation of the 'niche' vary widely in ecological literature across studies (Sales *et al.* 2021).

We investigate published literature focusing on the ecological niche space occupied by *competition-centred sympatric species*. Our review will follow the *Hutchinsonian niche concept*, where a species' *n*-dimensional niche space considers both abiotic and biotic dimensions (Hutchinson 1959).

Thus, we define a niche space as an approximation to study a species' ecological *n*-dimensional hypervolume, consisting of an *n*-number of dimensions that collectively contribute to its respective space.
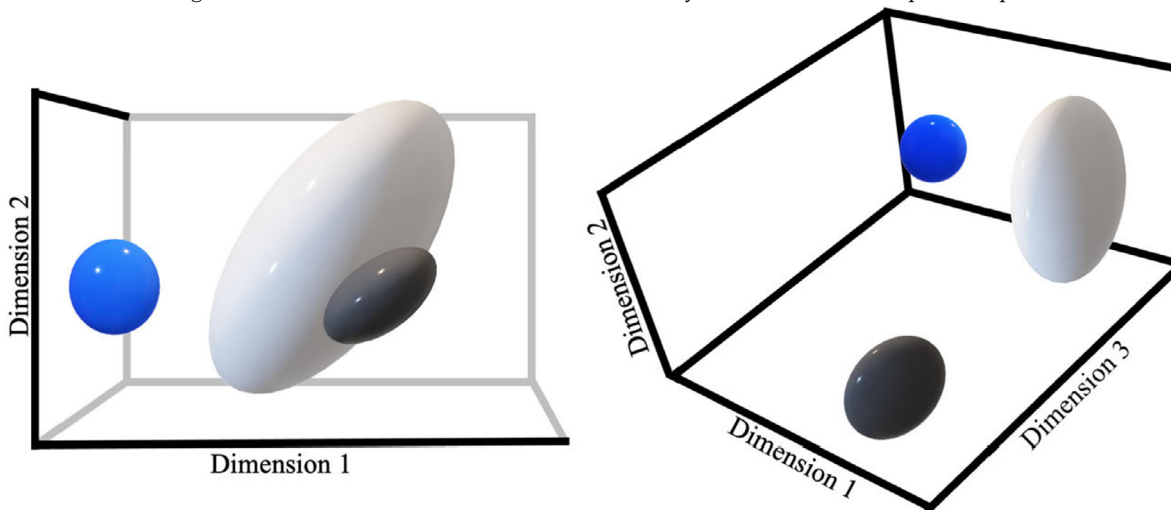
Theoretical depiction of overlapping niche spaces in a study using two dimensions of a niche space, and the potential difference when another dimension is considered to compute the niche space segregation where each species is represented as an ellipse.

these colonies can provide benefits such as information exchange on prey patches, they can also intensify potential competition for limited prey during foraging (Danchin & Wagner 1997, Brown & Brown 2001). Due to these factors, seabirds are used as a model system to study interspecific niche segregation (Hinke *et al.* 2015, Gulka *et al.* 2019).

Breeding seabirds are central-place foragers, returning to their nests after each foraging trip (Orians & Pearson 1979). Foraging performance is usually evaluated in terms of transit time (time commuting to and from the central colony) combined with foraging time (time searching and handling; Elliott *et al.* 2009). Optimal foraging theory predicts that breeding individuals constrained around a colony should maximize their foraging efficiency by foraging nearby, travelling along the most direct path, and minimizing both transit and foraging time (Baird 1991). Sympatric seabirds within competitive assemblages exhibit differences in feeding areas and prey preferences driven by optimal foraging strategies, which serve as a means of reducing competition (Oppel *et al.* 2015, Weber *et al.* 2021).

There has been research on at-sea niche segregation among seabirds since the 1970s, primarily relying on observations from research vessels or the coast (Cody 1973, Croxall & Prince 1980). Recent methods have been developed to study ecological niche spaces over multiple dimensions (Quillfeldt *et al.* 2015, Jessopp *et al.* 2020). Indeed, as a result of parallel advancements in dietary collection techniques, the emergence of stable isotope analysis, and the development of smaller and more precise biologging devices (Newsome *et al.* 2007, Yoda 2019, Hoenig *et al.* 2022), our understanding of seabird niche spaces has significantly improved in recent decades (Lescroël *et al.* 2009, Byrne *et al.* 2019). However, despite this progress, studies on niche segregation often focus on a limited number of dimensions that are often correlated with each other and are contained within a single niche space (Box 1). Such focus will produce a particular approach to a niche, which we refer to as a 'niche space' (e.g. isotopes for the isotopic niche space). This restrictive approach limits our ability to understand the multidimensional nature of Hutchinson's niche space concept (Hutchinson 1959).

Maintaining dietary segregation can be crucial for ecologically similar species coexisting in the same area (Kartzinel *et al.* 2015). Differences in seabird diets have been suggested as a primary driver allowing coexistence (Duffy & Jackson 1986). However, collecting dietary information can be challenging due to the varying invasiveness and biases of techniques (Table 1). This raises ethical questions where researchers should weigh the trade-off between invasiveness and information when choosing a collection technique and the diet dimensions they want to consider (Table 1).

Stable isotope analysis is a commonly used method to investigate seabird segregation within competitive assemblages (Newsome *et al.* 2007, Boecklen *et al.* 2011). Researchers compare stable isotope values between species, where each isotope represents a particular dimension of a species' *n*-dimensional hypervolume (Shipley & Matich 2020). These values are calculated based on animal tissues metabolizing heavy and light isotopes of atoms at predictable rates depending on their habitat and position in the food chain (e.g. type of consumed prey; Newsome *et al.* 2007). The stable isotope dimensions used most often are carbon (ratio of $^{13}C/^{12}C$; as represented in a relative measurement as $\delta^{13}C$) and nitrogen (ratio of $^{15}N/^{14}N$; $\delta^{15}N$), which can reveal information about the base of the food chain and the trophic position of species, respectively (Peterson & Fry 1987, Hobson & Welch 1992). Stable isotope analysis has assumptions and limitations, and most isotope studies only use two variables to quantify a complex multidimensional niche space (Bond & Jones 2009). Moreover, commonly used isotopes ($\delta^{15}N$ and $\delta^{13}C$) vary both with habitat and diet and so isotopic niche space includes both diet and spatial niche components, often in ways that are difficult to disentangle (but see recent amino acid-specific analyses: McMahon *et al.* 2013, Gagné *et al.* 2018, Elliott *et al.* 2021).

Isotopes can be a proxy for prey assimilated over a broad range of time periods, unlike most dietary collection techniques that represent the last meal or require exhaustive monitoring to acquire sufficient results (Table 1; Ramos *et al.* 2009). Stable isotope analysis can provide a broader view of the diet of animal diet and the environment in which they forage (trophic position, inshore/offshore and pelagic/benthic), while generally requiring a single sampling and a small amount of tissue (Table 1; Fernández *et al.* 2011). Therefore, exploring dimensions within the stable isotope niche space can complement some of the limitations encountered when studying the dietary niche space.

Table 1. A description of methods and their characteristics commonly used when measuring niche spaces.

Niche space	General purpose	Method examples	Representative timeframe	Spatial accuracy	Recapture	Weight of logger (g)	Dimensions	Invasiveness (CCAC)	Percentage % (n)
Dietary	Diet choice	Feeding observations	Sampling period				Chick prey species, length	B	20 (15)
		Prey collection	Last meal				Prey species, length, mass, age, sex	C[c]	5 (4)
		Scat collection	Last meal				Prey species	C[c]	5 (4)
		Pellets	Last few meals				Prey species, length, mass	C	22 (16)
		Regurgitations	Last meal				Prey species, length, mass, age, sex	D[c]	43 (32)
		Stomach contents (water off-loading)	Last meal				Prey species, length, mass, age, sex	D	27 (20)
		Stomach extractions	Last meal – several months				Prey species, length, mass, age, sex	Lethal	8 (6)
Isotopic	Chemical signature of tissues	Isotopic analyses	Weeks (blood) or months (feathers) before sampling				Isotopic signatures, prey habitat	C–D	100 (70)
		Fatty acid analyses[a]	Weeks (blood) or months (feathers) before sampling				Fatty acid signatures	D	1 (1)
Spatial	Behaviour at sea	GPS-TDR	Weeks (for larger birds that can be equipped with a backpack for up to years)	< 5 m	Variable[b]	< 22	Location, depth	D	53 (37)
		PTT	Days–years	< 150 m	No	~70	Location	D	28 (20)
		VHF	Weeks (in most cases VHF tracking can only occur in breeding)	~2 km	No	< 0.3	Location	D	7 (5)
		GLS	Days–years	~200 km	Yes	< 0.5	Location	D	8 (6)

The percentage of occurrence and the number of studies gives the frequency of use in the niche space found within the literature for a different group of methods all investigating niche segregation in breeding seabirds. Invasiveness of methods is based on the Canadian Council of Animal Care (CCAC): B, experiments causing little or no stress of discomfort; C, minor stress or pain for a short duration; D, moderate to severe distress or discomfort. Note that a single study often incorporated multiple methods of collection. All classifications were done based on the papers within this literature review. [a]Although fatty acids are not isotopes, they are considered complementary to isotope analysis. [b]Depending on whether the GPS-logger type downloads remotely or not. [c]Invasiveness level can vary depending on whether sampling was taken while capturing a bird (D level) or passive collections from the ground/rocks (C level).

Technological advances and the miniaturization of biologgers have allowed ecologists to estimate quantitative spatial niche dimensions (both in horizontal and vertical movements) in coexisting seabirds (Pickett *et al.* 2018, Bernard *et al.* 2021). Very high frequency (VHF) telemetry was the first tracking system used without necessary recapture but it is limited by its small triangulated range of manual detection (Table 1; Wilson *et al.* 2002). Platform terminal transmitters (PTTs) relay satellite information in real time but are only suitable for large spatial scales, as their location accuracy relies on satellite visibility and weather conditions (Hays *et al.* 2001, Northrup *et al.* 2018). Global positioning system (GPS) loggers provide accurate positions (5–30 m), making them appropriate for studies on finer scales. However, heavier devices are needed for extended battery life, which limits the range of species that can be studied (Bridge *et al.* 2011). Global location sensors (GLS) have low location accuracy (two positions recorded a day from ambient light levels and an error of *c.* 186 km; Rakhimberdiev *et al.* 2016) and require individuals to be recaptured. Thus, GLS devices are unsuitable for small-scale movements over discrete periods, such as when a seabird performs short foraging trips during the breeding season.

When multiple species forage in the same horizontal dimensions (including foraging areas and/or several foraging parameters such as foraging distance from the colony), the preferential use of different depths by diving species can reduce competition and explain how similar species coexist (Wilson 2010). Devices that simultaneously register location and dive depth provide the potential to reconstruct the precise foraging movements of diving or plunging seabirds (Masello *et al.* 2010). Time depth recorders (TDRs) are ideal for comparing the spatial niche vertical dimensions, as they often record depth, dive duration, temperature and time of day (Elliott & Gaston 2009).

Anthropogenic activities, particularly commercial fisheries, can impact the foraging strategies of breeding seabirds. Fishing vessels and seabirds tend to aggregate in areas of high productivity, increasing competition and making it easier for seabirds to detect prey and scavenge on fishery discards (Copello *et al.* 2008, Bertrand *et al.* 2012). The impact of commercial fishing on seabird populations has been a growing concern, with a significant decline globally linked to fisheries-induced mortality (Montevecchi 2001, Good *et al.* 2020). Changes in these activities (e.g. ban on fishing discards) around breeding colonies where commercial fishing occurs can produce competitive interactions, influencing the partitioning of niche spaces.

Although the niche spaces often studied include a few of the potentially infinite dimensions within the suggested *n*-dimensional hypervolume, investigating parameters within and across spaces enables us to assess quantifiable patterns of niche segregation. Here, we review the literature on niche segregation among sympatrically breeding seabirds subject to interspecific competition. We focus on three widely investigated niche spaces: dietary items, stable isotopes (also known as an isotopic niche, which represents a combination of diet and foraging space) and spatial (foraging space). We aim to understand how researchers test segregation by investigating (1) which niche spaces and combinations of dimensions are being used in the published literature to answer questions on niche segregation, (2) whether studies report segregation or overlap, (2a) which niche spaces and dimensions segregation is occurring in, and (2b) the external factors influencing the detection of segregation patterns. We also aim to determine whether (3) niche segregation is most evident among closely related species, as a result of interspecific competition. Finally, we propose (4) a comprehensive framework by recommending standardized research practices and addressing gaps in current approaches that will be valuable to future research.

METHODS

Literature search

We performed a literature search in March 2022, using the electronic databases *Web of Science* (https://www.webofknowledge.com) and *Scopus* (https://www.scopus.com) to identify publications that studied niche segregation within sympatric breeding seabirds (SOM Fig. S1). We used keywords and combinations of the following search terms to find English peer-reviewed literature: 'seabird', 'segregation', 'partitioning', 'niche', 'coexistence', 'sympatric', 'competition', 'foraging', 'trophic', 'tracking', 'diet', 'interspecific', 'overlap', 'chick-rearing', 'incubating', 'breeding'. The review protocol was applied following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page *et al.* 2021).

The search from both databases returned 3469 records (Fig. S1). We screened all records by reading the title and abstract. To meet the criteria, an article needed to compare at least two different seabird species that breed sympatrically within the same island/archipelago during overlapping breeding periods. We disregarded articles that investigated niche segregation between species that have allochrony because breeding time offset is known to be an evolutionary factor that can eliminate interspecific competition at mixed species colonies (Granroth-Wilding & Phillips 2019, Quillfeldt *et al.* 2020). Articles were retained only if they were investigating differences in dietary, isotopic and/or spatial niche spaces. Therefore, we disregarded articles that did not test segregation patterns between species. We excluded articles that tracked seabirds spatially using land, boat or aerial surveys, and instead only included biologging spatial niche studies, allowing adequate comparisons between spatial niche articles. We then screened all remaining articles ($n = 2545$) by reading the methods and discussion sections. We disregarded articles that considered only intraspecific interactions, the non-breeding season and/or inter-island segregation. After this, 119 articles fulfilled the criteria and were fully retained and read. We screened reference lists of the latter articles to identify any other relevant publications by backward referencing, adding another seven articles. A total of 126 articles were included in the final synthesis. To be able to assess adequately segregation patterns between an article that included multiple isolated studies that investigated more than one island colony site and/or multiple breeding stages, we produced multiple respective data points for each. This resulted in 152 isolated data points of segregation patterns from the 126 articles (SOM Fig. S1, Table S1). Therefore, a studied *instance* in this review is a single site within a study that includes two or more species and is separated by breeding stage. Finally, when examining taxonomic differences, segregation patterns for each separate species pair were also recorded, generating multiple data points for an initial single instance ($n = 410$).

Data extraction

For the 152 studied niche segregation instances included in our review, we extracted the variables outlined in Table 2.

RESULTS

Diet segregation

We identified 74 studied instances, from 1968 onwards, that compared breeding seabird species' dietary niche spaces (49%, Fig. 1). Of these, 30 instances considered only prey species as a dietary prey dimension (40%). When additional prey dimensions are incorporated, we found increased segregation compared with overlap in reports. This ranges from 8% more overlap than segregation when studying one dimension, to 125% more segregation than overlap when studying three prey dimensions (Fig. 2a).

Of all dietary investigations, 28% used various overlap indexes to quantify the degree of niche segregation (Czechanowski $n = 3$, Morisita's $n = 9$, Pianka's $n = 1$, Schoener's $n = 2$, Petraitis' $n = 1$, Levin's $n = 1$, or an original overlap index $n = 4$). The remaining dietary instances did not quantify the degree of dietary niche overlap, but instead visually assessed segregation based on the frequency of occurrence and/or proportion of prey items (46%), and/or used parametric/non-parametric statistical tests for prey metrics (18%; model metrics included prey species, numbers and/or lengths). The remaining 8% reached conclusions about dietary segregation patterns but made no formal assessment.

Isotopic segregation

Isotopic niche spaces were investigated in 46% of cases beginning in 1994 (Fig. 1). All stable isotopic niche segregation instances within our review focused on nitrogen and carbon. Other isotopes (e.g. $\delta^{34}S$; $n = 3$) or chemical tracers (fatty acids; $n = 1$) were rarely used. The analysis of isotopic niche segregation was predominantly performed by comparing mean isotopic signature ratios between species (39%), using Bayesian models (23%), or a combination of both (38%).

Spatial segregation

Since 1988, 46% of instances investigated segregation in the spatial niche space (Fig. 1). When instances of plunging or diving seabirds investigated only the horizontal or vertical dimension in isolation, there were 18% more reports of spatial segregation relative to overlap compared with 50% when combined (Fig. 2b).

Table 2. Variables and their corresponding descriptions extracted from publications investigating niche partitioning in sympatric breeding seabird species.

Variable extracted	Description
Number of species studied	All breeding seabird species considered
Year of the study	Year(s) data collection was conducted
Duration of the study	Short (1–2 years) or long ($\geq$ 3 years)
Breeding stage studied	Chick-rearing, incubation, entirety of breeding season, or not specified
Highest common taxon of the studied species	Were seabird species within the same genus, family, order, or from different orders?
Colony size	When the instance reported the number of studied breeding individuals on islands/colonies during data collection
Foraging guild of the studied species	Diver/plunger, surface forager, or a combination, following Ashmole (1971) and Shealer (2002)
Whether the study considered impacts of anthropogenic fishing activities	Yes or no
Niche space(s) studied	Diet (prey dimensions considered: prey species, age, length, mass, and/or sex)
	Isotopic (isotopic signatures considered)
	Spatial (foraging parameters considered (horizontal and/or vertical))
Whether the study reported niche segregation or overlap between all compared species within the study	We used a categorical classification system as in Bolton *et al.* (2019) to classify pairs of species based on Results and Discussion sections. Segregation was classified as a tiered approach rather than a continuum, based on their interaction within a particular niche space.
	1 Segregation: when all investigated niche dimensions showed segregation between species pairs (thus species are occupying non-overlapping niches across all studied dimensions)
	2 Variable Segregation: both segregation and overlap observed in one or more dimensions in the niche space(s) (species are both non-overlapping and overlapping in various studied dimensions)
	3 Overlap: when all investigated niche dimensions showed overlap between species pairs (species share identical or highly overlapping niches across all studied dimensions)
Evidence of segregation in respective niche space(s)	Qualitative (visual assessment) or quantitative analysis (linear mixed model, Bayesian ellipse, density distribution overlap)

Among the instances investigating the spatial niche space, 61% used kernel density estimations (KDEs) to estimate overlap extent. Of these, 55% combined KDEs with statistical tests to compare differences in foraging metrics between species (e.g. trip length and duration). Thirty-six per cent used statistical tests to compare differences in foraging metrics and 3% created unique overlap models for their reports (Lynnes *et al.* 2002, Wilson 2010). Instances also used a wide range of KDE contours (ranging from 10% to 95% utilization distributions) but most often assessed 95% contours, representing the home-range of a species (the area of broad active use) and/or the 50% utilization distribution contours, representing the core foraging range (Ford & Krumme 1979).

Interspecific overlap in the estimated foraging range among species using KDEs was assessed either by visually observing the contours and determining segregation (21%), calculating the percentage of overlap between species' contour polygons (45%) or using statistical measures to assess the extent to which two species overlap (33%; Bhattacharyya's Affinity (BA) index ($n = 8$) and/or utilization distribution overlap index ($n = 8$; Utilization Distribution Overlap Index (UDOI); Fieberg & Kochanny 2005)).

Niche space combinations

Our review found that only 5% of instances investigated all three spaces, beginning in the mid-
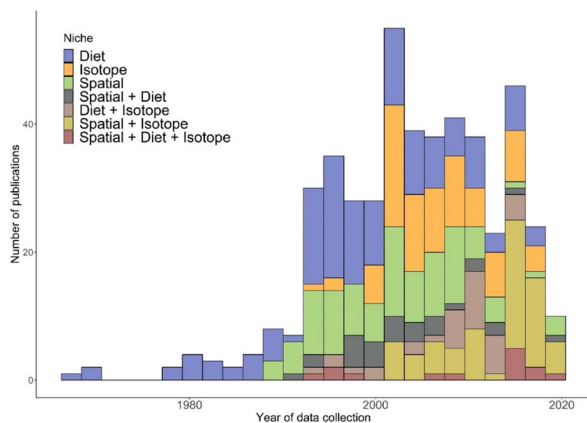
Figure 1. Number of seabird niche segregation instances during the breeding season across 1976–2022. Instances with datasets spanning multiple years are represented in all corresponding columns. Each bar represents data points (publications) for a period of 2 years.

Figure 2. (a) Dietary segregation findings of instances that investigated the dietary niche space considering one ($n = 30$), two ($n = 24$) or three ($n = 19$) dietary prey dimensions (prey species, age, length, mass and/or sex). Only one study considered four prey dimensions and is not depicted here. Five, two and six variable segregation instances were reported in each respective prey dimension(s) studied. (b) Studies investigating spatial niche space segregation by examining a single spatial dimension (horizontal or vertical, $n = 43$) or a combination of two spatial dimensions ($n = 27$; both horizontal and vertical) during the breeding season for diving and/or plunging seabirds. Three and six variable segregation instances were reported in each respective spatial dimension(s) studied.

1990s, and most assessed a single niche space (63%). Instances that considered two niche spaces reported 33% more segregation instances than overlap, whereas studies considering only one niche space reported 11% more. The most frequently studied niche space was dietary, followed by isotopic and finally spatial (SOM Fig. S2). The most studied niche space combinations investigated both spatial and isotopic spaces (43%), beginning in the 2000s. This was followed by the combination of dietary and isotopic spaces, which began in the mid-1990s (33%), and spatial and dietary, beginning in the early 1990s (24%).

Factors influencing breeding seabird segregation patterns

Study period
The length of the study period varied between 1 and 25 years (Shoji *et al.* 2015, Dakwa *et al.* 2021). Most instances were conducted over 1 or 2 years (70%). The short-term (1–2 years) instances reported 47% more segregation than overlap, whereas long-term (> 3 years) instances reported 24% more overlap than segregation ($n = 107$ vs. $n = 45$, respectively; Fig. 3a).

Breeding stage
Most instances investigated seabird niche segregation during the chick-rearing stage (62%, $n = 94$) with only 20% ($n = 30$) at the incubation stage (Fig. 3b). Eighteen per cent of instances did not
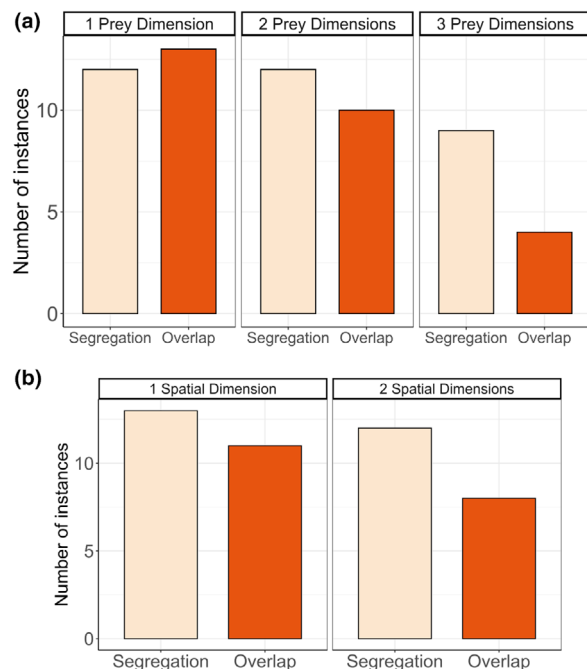
consider reproductive stages individually, but either examined segregation over the entire breeding season or did not specify the breeding stage ($n = 28$). Instances that investigated segregation during the incubation stage reported segregation and overlap equally, whereas instances during chick-rearing reported 23% more segregation than overlap.

Colony size
Most instances investigated either a small colony (0–10 000, $n = 40$) or a medium-sized colony (10 000–1 000 000, $n = 39$); fewer studies investigated larger colonies with >1 000 000 individuals ($n = 14$). Larger colony studies reported more segregation than overlap. This ranges from 7% more overlap than segregation in small colonies to 23% more segregation than overlap in large colonies
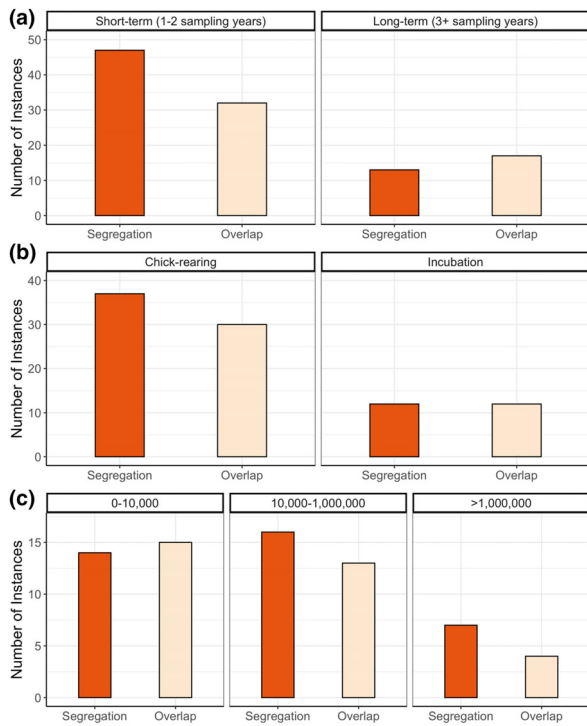
Figure 3. Sympatric seabird niche segregation patterns based on (a) short- (1–2 years, $n = 107$) and long-term (≥ 3 years, $n = 45$) instances, with 47 and 13 variable segregation instances reported, respectively, and (b) the chick-rearing ($n = 94$) or incubation ($n = 30$) stage. Twenty-seven and six variable segregation instances were reported in respective chick-rearing and incubation studies. Studies that generalized over the entire breeding cycle ($n = 21$) or did not specify breeding stage ($n = 7$) were excluded. (c) Distribution of findings of instances investigating sympatric seabird niche segregation relative to their colony size (number of investigated breeding individuals reported) in colonies ranging from 0 to 10 000 ($n = 40$), 10 000 to 1 000 000 ($n = 39$) and > 1 000 000 ($n = 14$) individuals. Eleven, 10 and three variable segregation instances were reported in respective different colony sizes.

and 75% more segregation than overlap in mid-sized colonies (Fig. 3c).

Niche segregation in relation to phylogeny
The reviewed instances investigated two to eight coexisting species (Bodey *et al.* 2014). Most compared two sympatric breeding seabirds (69%, $n = 105$).

Thirty-nine per cent of pair-wise comparisons investigated seabirds within the same genus ($n = 159$), 31% within the same family ($n = 126$), 17% within the same order ($n = 70$) and 13% within the same class ($n = 55$). Pair-wise species
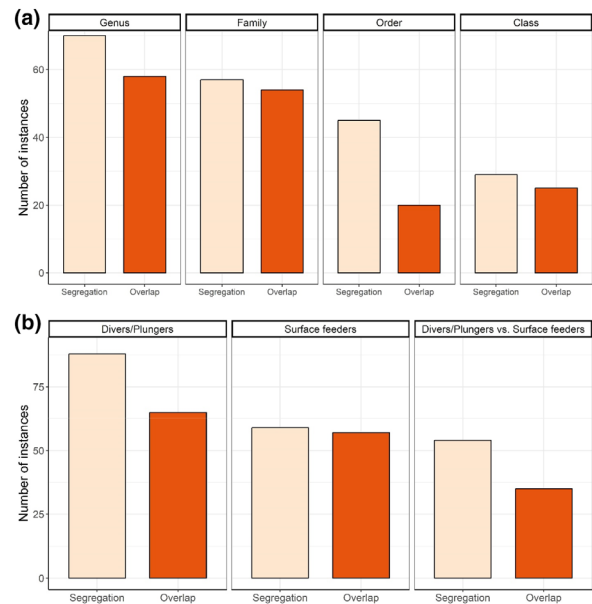

Figure 4. (a) Findings of niche segregation studies comparing species within the same genus, family, order or class (i.e. from different orders within the seabird class). (b) Findings of niche segregation studies comparing species within the same foraging guild (surface feeders or pursuit diving/plunging) and comparing species from two different guilds.

comparisons within the same genus or family had, respectively, 21% and 5% more instances of segregation than overlap, whereas comparisons within the same order reported 125% more instances of segregation than overlap (Fig. 4b). Seventy-seven per cent of pair-wise comparisons investigated species within the same foraging guild (surface feeders $n = 133$, or pursuit divers/plungers $n = 183$). Comparisons within the same plunging or diving foraging guild reported 35% more instances of segregation than overlap, whereas species within the same surface feeding guild had only 3% more instances of segregation (Fig. 4b). When comparing species from different foraging guilds, there were 54% more instances reporting segregation than overlap.

DISCUSSION

How competing species segregate their ecological niche space is central to evolutionary theories (Schoener 1983). This review has shown that breeding seabird studies typically involve segregation investigation along dimensions within a single niche space, whether dietary, isotopic or spatial. Despite the relative lack of multi-niche space

studies, those that study multiple niches demonstrated that competing seabirds could segregate along multiple dimensions within and across niche spaces. External abiotic and biotic factors, frequently overlooked, can ultimately determine observed niche segregation patterns by modifying the prey available to competing predators (Vlietstra 2005, Ceia & Ramos 2015), consequently affecting the degree of segregation (Fig. 5).

Individual niche spaces: diet, isotopes and space

Diet has been the only seabird niche space consistently studied since the 1970s (Fig. 1), aligning with the emergence of many niche segregation theories (Pianka 1973). Considering additional dimensions of the diet, such as prey species, size, weight, age and/or sex, leads to increased reporting of dietary segregation (Fig. 2a). Previous studies have demonstrated the importance of subtle dietary choices among species, such as for prey size, in promoting coexistence (e.g. Atiénzar
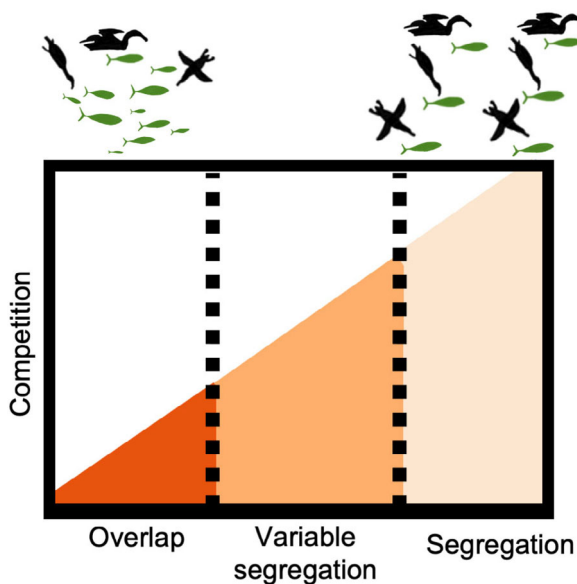

Figure 5. Theoretical diagram of how competition intensity increases the segregation percentage within sympatric seabird species. When shared prey resources are abundant, coexisting seabirds with differing feeding strategies can occupy overlapping niche spaces with no detriment to one another. However, when prey is limited due to various external factors (colony size, breeding stage, morphological/feeding strategy similarities) and increasing competition, species must segregate within their specialized feeding niche spaces to meet energy requirements.

et al. 2013). Complementing traditional diet techniques with more recent technologies such as animal-borne cameras and faecal DNA barcoding could allow for further insight into dietary segregation across many dimensions (Handley et al. 2018, Young et al. 2020). Considering multiple dimensions of diet specialization beyond prey species can therefore provide a comprehensive approach to identifying complex dietary segregation mechanisms.

Isotopic studies have increased in recent decades, aiming to improve niche estimates (Fig. 1). Although the incorporation of additional isotope dimensions or molecular markers (e.g. fatty acids, amino acids) holds the potential to improve understanding of isotopic segregation, only a few studies have used more than two dimensions in seabirds (Newsome et al. 2012). Recent research emphasizes the importance of a multidimensional isotopic approach in breeding seabird assemblages to uncover previously undetectable behaviours (Connan et al. 2019), suggesting that two-dimensional approaches oversimplify trophic ecology (Elliott et al. 2021, Potapov et al. 2021). Morera-Pujol et al. (2018) showed that incorporating a third isotope (i.e. δ^{34}S, amino or lipid amino acids) enabled a more precise assessment of isotopic niche spaces that would otherwise go unnoticed with two dimensions (carbon and nitrogen). We therefore recommend that future researchers should incorporate additional isotopic dimensions to increase the discriminatory power required to reveal segregation.

Emerging methods such as compound-specific stable isotope analyses on amino acids (CSIA-AA) can provide additional dimensions. Nitrogen is mostly used to represent trophic position, but spatial variations in baseline δ^{15}N values can obscure accurate assessment (Quillfeldt & Masello 2020). By using trophic amino acid isotopic ratios, one can overcome spatial and temporal biases of δ^{15}N values in different habitats or temporal shifts (Seminoff et al. 2012). For instance, by using isotopic ratios of well-described source amino acids, differences in the isotopic signature of carbon sometimes caused by the Suess effect may be better explained (McMahon et al. 2013, Gagné et al. 2018, Elliott et al. 2021).

Biologging is an excellent tool to reveal spatial niche segregation depending on the context of the study (seabird species, breeding location and foraging behaviour; Table 1). We found that the

overlap of foraging areas of breeding seabirds has been frequently assessed using biologging, and may be high (Rey *et al.* 2013) or low (Weimerskirch *et al.* 2009). By incorporating both horizontal and vertical dimensions, studies on plunging or diving seabirds showed clearer spatial segregation patterns than when looking at one of these dimensions in isolation (Fig. 2b). Our review found several cases where horizontal foraging areas overlapped but diving depth ranges were segregated (Blanchet *et al.* 2013, Peck-Richardson *et al.* 2018). Thus, investigations of predators, such as diving or plunging seabirds, should examine all spatial dimensions of potential competition. Further, foraging time of day (a dimension within the spatial niche space) may be another important factor determining spatial segregation patterns. Thirty spatial studies within this review considered differences in spatiotemporal foraging patterns on a diel scale (43%). This temporal dimension may play a role in determining the degree of spatial segregation (Gatto *et al.* 2019). Although a size bias towards larger species has existed in biologging to date, ongoing miniaturization has allowed tag deployment on smaller species that exploit both horizontal and vertical dimensions. Nevertheless, limitations persist for smaller species (Chung *et al.* 2021).

Niche space combinations

When studies investigated two niche spaces (spatial, diet or isotope), there were > 50% more reports of segregation than overlap. This suggests that when studies take a multi-niche space approach, as Hutchinson (1959) suggested, fewer instances of overlap are observed, providing a more complete representation of niche segregation (Pianka 1973).

Isotopic analyses, in combination with other dietary techniques, can reveal niche segregation patterns by overcoming biases and inaccuracies of traditional diet collection techniques (Table 1; Ramos *et al.* 2009). Low-invasiveness techniques such as feeding observations may inaccurately reflect the dimensions of a seabird's diet (prey species and size) if there is a discrepancy between the prey given to chicks and the prey ingested by parents (Davoren & Burger 1999). Stable isotope analysis, although unable to identify the species level, eliminates biases related to prey digestibility by considering only assimilated food. This

approach, when used alongside other methods, provides a powerful tool to provide a clearer understanding of niche segregation patterns during overlapping timeframes (Hobson 2011, Karnovsky *et al.* 2012, Mancini & Bugoni 2014). Steenweg *et al.* (2011) and Polito *et al.* (2015) combined dietary prey collections and stable isotope analysis, and showed consistent segregation across both niche spaces. Those studies concluded that combining techniques from both approaches produces a reliable method to monitor segregation patterns in terms of diet and trophic ecology. Future research should therefore use a complementary framework for more precise estimates of niche segregation along more dimensions.

By combining spatial and isotopic niche spaces, a more comprehensive understanding of the breadth of the ecological niche space can be achieved (Masello *et al.* 2010, Hinke *et al.* 2015). For example, $\delta^{13}C$ values of source amino acids in seabirds can indicate the source at the base of the food web and offer insights into specific foraging habitats (Vander Zanden *et al.* 2015).

Factors influencing segregation patterns

The duration of the study was an important factor in detecting segregation. Long-term studies reported more overlap than segregation when compared with short-term studies (Fig. 3a). This difference may be attributed to the stability of the environmental variables over a single annual cycle within a system, as opposed to interannual variations over several years. These abiotic and biotic fluctuations will determine the intensity of competition from year to year, leading to inconsistent patterns of segregation. It is thus crucial to recognize that environmental variation over time may make segregation more apparent in some years than others. Specifically, competition intensity will be influenced by prey availability or oceanographic conditions that are known to change annually in a dynamic marine environment (Dehnhard *et al.* 2016, Bourgeois *et al.* 2022). For example, Barger and Kitaysky (2012) investigated sympatric Thick-billed *Uria lomvia* and Common *Uria aalge* Murres in the Bering Sea over 6 years and found that the degree of niche segregation varied annually. In years when prey availability was high for both species, isotopic niche spaces overlapped considerably more than in years when resource

conditions deteriorated. Similarly, Lynnes et al. ([2002](#)) found that sympatric Adélie *Pygoscelis adeliae* and Chinstrap *Pygoscelis antarctica* Penguins segregated significantly in spatial niche spaces when prey availability was low, and overlapped in a year when availability was high. Ausems et al. ([2020](#)) controlled for interannual variability of Black-bellied Storm Petrels *Fregetta tropica* and Wilson's Storm Petrels *Oceanites oceanicus* by comparing multiple fluctuating environmental conditions between years (chlorophyll-a and sea surface temperatures). Thus, although long-term studies can provide a general understanding of life histories and the plasticity of foraging strategies by averaging findings over several years, they are susceptible to greater variability in environmental conditions, necessitating the consideration of interannual variations.

Breeding stage is recognized as a key factor influencing competition levels and, consequently, the foraging strategies of central-place foraging seabirds (Barger et al. [2016](#)). We found that seabird studies reported more segregation than overlap at the chick-rearing than the incubation stage (Fig. [3b](#)). According to optimal foraging theories, chick-rearing leads to constrained foraging trips and, as a result, competition levels are anticipated to peak during chick-rearing (Pyke [1984](#), Birt et al. [1987](#)). Therefore, it is expected that seabirds would exhibit more distinct niche segregation at the chick-rearing stage (Navarro et al. [2014](#)). Barger et al. ([2016](#)) reported variable segregation between Thick-billed and Common Murres in the Bering Sea due to differences in breeding stages. Specifically, the sympatric murres partitioned their dietary niches during chick-rearing but overlapped considerably during incubation. These findings highlight the issues of generalizing patterns over the entirety of the breeding season, as niche segregation is stage-dependent.

Colony size has been found to influence competition intensity among sympatric species (Bolton et al. [2019](#)). We found an increase in segregation with colony size, which corroborates this hypothesis. Ashmole's theoretical halo reflects the depletion of prey around the colony, increasing with colony size (Gaston et al. [2007](#)). Therefore, a larger halo is associated with longer foraging trips and decreased provisioning of broods, resulting in reduced reproductive outputs (Elliott et al. [2009](#), Farner & King [1972](#)). A recently proposed density-dependent hinterland model (Wakefield et al.

[2013](#)) suggests that within-species niche foraging segregation is more likely to occur in larger colonies. Conversely, smaller-sized colonies should experience lower levels of competition and thus have a higher availability of limiting resources (smaller halo), which allows for more overlapping foraging niche spaces (Young et al. [2010a](#)). Differences in colony sizes should be considered as a driving force for differences in segregation patterns when birds are foraging at sea.

Fisheries worldwide have been linked to changes in seabird foraging behaviour (Montevecchi [2001](#)). Our review found 24 instances that considered the impacts of fishing vessels around colonies (16%). Calado et al. ([2018](#)) found that the population increase of sympatric Audouin's *Larus audouinii* and Yellow-Legged *Larus michahellis* Gulls in Portugal could be attributed to the increase in fishing activities around the colony, leading to complete overlap in diet and isotopic niche spaces by permitting fishery-assisted foraging tactics. Similarly, González-Solís et al. ([2000](#)) found extensive overlap in spatial niche volumes between sympatric Northern *Macronectes halli* and Southern *Macronectes giganteus* Giant Petrels and commercial fishing distributions in the Southern Ocean. Although many seabird species may prey on fish that are not commercially important or fish that are not exploited by large fishing fleets, a significant effect of fisheries on several other species is evident (Bartumeus et al. [2010](#)). In addition, there may be indirect effects of fisheries on non-commercial fish species. Thus, care should be taken when studying species that depend on fishery discards or forage in areas with substantial fishing activity. Simultaneously, monitoring behavioural changes in foraging strategies due to fisheries is important for effective management strategies that can accurately assess how seabirds adapt to environmental changes (Matos et al. [2018](#)).

Niche segregation among closely related species

Investigating niche segregation mechanisms within assemblages of closely related sympatric seabird species is particularly interesting because they are more likely to experience competition and therefore are expected to have evolved mechanisms for niche segregation (Young et al. [2010b](#), Navarro et al. [2013](#)). Species in the same genus or family

had fewer reported instances of segregation relative to overlap compared with species within the same order (Fig. 4a). These findings reinforce the idea that taxonomically similar species, probably exploiting similar resources, may overlap more obviously under certain circumstances than species that are dissimilar. Therefore, overlap reports decrease with taxonomic dissimilarity.

The morphologies of the competing seabirds play a major role in defining capabilities and metabolic costs, ultimately controlling their foraging behaviours. Bodey *et al.* (2014) investigated eight breeding species and found segregation more at the functional group level than at the species level, where there were substantial changes in segregation patterns depending on the species compared. They suggest that evaluating only pairs of species can provide a distorted representation of the reality of the assemblage, highlighting that competition rarely occurs solely between only two species. More instances of overlap for species within the same genus or family may be expected from species that are morphologically or physiologically similar (or both) and within the same foraging guild. We found that species exploiting the water column or belonging to different guilds, which might have a lower potential for interaction, reported more instances of segregation. This was particularly evident when studies compared plungers/divers with surface foragers (Fig. 4b). Therefore, depending on the taxonomic similarity between seabirds there may be a more appropriate evaluation of niche segregation depending largely on foraging guild strategy (Jessopp *et al.* 2020). These findings accord with other segregation studies that suggest that the extent of foraging overlap will be determined by the ability to exploit the environment (Thaxter *et al.* 2010). Studies comparing species within the same foraging guild and with taxonomic similarity may be required to incorporate more niche spaces into their investigation than when working with species in different foraging guilds.

Recommendations for future studies

The inclusion of a multi-approach niche space framework can change our understanding of coexisting seabird dynamics. A potential way to do this could be by combining multiple techniques, including those within three niche spaces where segregation is already often studied, namely dietary collections, stable isotope analysis and spatial tracking. Considering one niche space showed lower segregation than when combining them. We recommend that seabird studies aiming to investigate niche segregation within a community of sympatric species should assess all three niche spaces when feasible. This would ideally involve equipping individuals with high-accuracy GPS loggers (and TDR devices if exploiting the water column), conducting dietary prey item collections (preferably assessing a combination of dietary dimensions to finely assess the extent of partitioning closely) and collecting biological tissues (e.g. blood) after being tracked, for isotope analysis (Table 1). This will allow spatial, dietary and isotopic data to be matched to the same discrete period and allow for adequate comparisons between spaces and a comprehensive understanding of niche segregation mechanisms.

The way niche segregation has been and continues to be investigated varies immensely across studies, with no standard measurement used within a particular niche space. The lack of any common quantifiable measurements of dietary overlap presents a clear need for a standardized method to report dietary differences (see issues with varying overlap indexes and recommendations highlighted by Duffy & Jackson (1986) and Barrett *et al.* (2007)). More complex approaches should also be included to describe qualitative differences in multivariate diet niche spaces, for example by using principal component analysis (PCA), which can provide meaningful diet dimensions across different species. Alternatively, non-metric multidimensional scaling (NMDS; Hoenig *et al.* 2022) can be performed based on the relative abundance of each prey species to show dissimilarities in dietary composition (such as prey numbers, weight and lengths) between seabird species.

Bayesian ellipses (e.g. the SIBER package in R; Jackson *et al.* 2011, Parnell *et al.* 2012) allow researchers to analyse and standardize the size (standard ellipse area; SEA) and quantify overlap of two-dimensional isotopic niche spaces between or among species (see best practices for models and data collection: Bond & Diamond 2011, Phillips *et al.* 2014, Hoenig *et al.* 2022). Bayesian models incorporate more robust and comprehensive analyses into investigations of isotopic niche space by integrating multiple stable isotopes into a single model and approximating a niche area for

each species. This allows standardized quantification of isotopic niche overlap across studies. If research projects are restricted to a single niche space approach (e.g. due to budget restrictions) then increasing the number of dimensions studied within that space may help to eliminate biases and produce more accurate results. For instance, the incorporation of more than two isotopes (such as sulphur or compound-specific isotopic analysis of amino acid) would increase the detail of information provided in the Bayesian estimation of the niche (e.g. NicheROVER package in R; Swanson *et al.* 2015), overcome baseline issues and probably better delineate niche segregation among species (Bowes *et al.* 2017).

KDEs are widely used for analysing spatial distributions of seabirds. When setting the smoothing factor h, issues associated with arbitrarily setting parameters should be considered because these can change depending on data characteristics (Worton 1989, Wand & Jones 1994). It is also imperative to report the chosen smoothing factors and grid resolution (Laver & Kelly 2008). KDEs can be valuable in describing the probability of occurrence of individuals based on their locations and can identify key foraging areas at fine spatial scales (O'Brien *et al.* 2012). We recommend that KDE analysis should be standardized to assess both the 50% and 95% contours and include a statistical measure of overlap on these contours (such as UDOI), to assess the extent of overlap between foraging areas. Importantly, as we have highlighted, horizontal foraging overlap must be complemented by vertical foraging movements in species that forage within the water column. Ignoring potential vertical segregation could lead to misleading conclusions (Fig. 2b).

Given the complexity of the *n*-dimensional ecological niche concept proposed by Hutchinson (1959), we must also consider other aspects of a niche space not considered by this review. For example, habitat differences such as foraging bathymetric depths or sea surface temperature may allow species to segregate in environmental space (Dehnhard *et al.* 2020) independently of other factors (e.g. prey abundance). Moreover, as shown in our review, variations in interannual prey abundance can facilitate the coexistence and success of competing species (Calado *et al.* 2018). Surprisingly, a gap in research exists regarding resource availability around studied colonies, with only 8% of instances in this review assessing prey abundance. Among these, Weimerskirch *et al.* (2012) investigated the segregation mechanisms of Peruvian Boobies *Sula variegata* and Guanay Cormorants *Phalacrocorax bougainvillii* by combining analyses of their foraging movements with estimations of anchovy distributions around the colony. They found that overlapping horizontal movements between the two species were dependent on the abundance and accessibility of anchovies during the breeding season. Further, interspecific competition is not the only type of competition pressure that can modulate mechanisms of coexistence and determine niche segregation patterns of natural assemblages. Within a single species, intraspecific competition can occur between sexes, where dimorphism affects behaviour and capacities (Reyes-González *et al.* 2021), between individuals, where specializations in foraging can lead to different diet compositions (Jakubas *et al.* 2018), and between age classes, where experience may influence foraging habitat selection (Zango *et al.* 2020). Therefore, we must consider these intrinsic factors, as they have the potential to modify foraging strategy patterns, particularly during the breeding season, before reaching any conclusions about niche segregation processes.

Research indicates that methods previously considered non-impactful on birds can cause significant detriment to individuals (Table 1). For instance, Lopez *et al.* (2023) found that the use of harness-mounted GPS devices, a routinely used attachment method without prior device-effect investigations, was a lead driver of nest failure in Great Black-backed Gulls *Larus marinus*. This underscores the complexity of ethical considerations, emphasizing the need to prioritize species-specific effects (Vandenabeele *et al.* 2012). Researchers should continually reassess their methods in alignment with evolving ethical standards.

CONCLUSIONS

Published literature on ecological segregation among breeding seabirds has primarily focused on investigating a single niche space. As a result, numerous studies have found instances of ecological overlap between species. However, by incorporating additional dimensions (variables) or exploring other niche spaces (e.g. diet and isotopes), researchers have been able to identify more pronounced segregation. While there are

increasing numbers of dimensions that could be addressed when studying segregation of seabirds, the limited resources for ecological research necessitate the careful selection of the appropriate combination of variables specific to the system of interest. Researchers should consider factors that may influence segregation, including colony size, fish stocks and environmental variability. Embracing multidimensional approaches in marine ecosystems offers insights into the significance of delineated areas within marine protected zones for the well-being of the entire ecosystem, transcending the constraints of conservation practices focused on single species. This shifts towards a more holistic approach, highlighting the role of investigating community dynamics to inform and guide comprehensive ecosystem conservation strategies.

AUTHOR CONTRIBUTIONS

Christina Petalas: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation; funding acquisition. **Francis van Oordt:** Formal analysis; methodology; conceptualization; writing – review and editing. **Raphaël A. Lavoie:** Writing – review and editing; methodology; investigation; supervision. **Kyle H. Elliott:** Supervision; resources; project administration; conceptualization; investigation; writing – review and editing; funding acquisition.

ETHICAL NOTE

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Flowchart following PRISMA guidelines (Page *et al.* 2021) for interspecific breeding seabird niche segregation. Note that some articles generated multiple isolated instances when evaluating multiple study locations.

Figure S2. Breeding seabird niche segregation is found in studies investigating either one, two or three niche space(s).

Table S1. Published peer-reviewed instances of niche segregation in sympatric breeding seabird species. Species considers the highest grouping taxon classification between studied species.