



Sympatric seabirds: exploring multidimensional niche partitioning among four cormorant species

Annick Morgenthaler^{1,2,*}, Ana Millones¹, Patricia Gandini^{1,2}, Diego Procopio¹, Esteban Frere^{1,2}

¹Centro de Investigaciones de Puerto Deseado, Universidad Nacional de la Patagonia Austral, 9050 Puerto Deseado, Santa Cruz, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), 9050 Puerto Deseado, Santa Cruz, Argentina

ABSTRACT: The competitive exclusion theory suggests that closely related and ecologically similar species living in sympatry should differ along some axes of their n-dimensional ecological niches to reduce interspecific competition. Cormorants (Phalacrocoracidae) are foot-propelled pursuit-diving aquatic birds that constitute an interesting model to study resource partitioning at a local level, due to their colonial breeding habits and limited foraging ranges. The aim of this study was to investigate the partitioning of the multidimensional niche among 4 cormorant species that coexist within a marine inlet along the Argentine Patagonian coast: red-legged, rock, neotropic, and imperial cormorants. For this, we estimated their diet composition, isotopic niches, foraging areas, and reproductive schedules, while assessing pairwise multidimensional overlap. While our analysis showed some degree of pairwise overlap in certain dimensions — mainly spatial and temporal, and more pronounced between rock and neotropic cormorants — the 4 cormorant species overall exhibited resource partitioning. This study highlights that, despite residing and foraging in close proximity in a spatially delimited coastal inlet situated at a latitude marked by strong seasonality, the studied seabirds, belonging to the same guild, clearly partitioned the use of their trophic resources by occupying different volumes, or combinations of dimensions, within the ecological niche. The cumulative effect of the pairwise segregations found in trophic, spatial, and temporal dimensions was the key to determining the overall niche partitioning between these sympatric seabird species.

KEY WORDS: Phalacrocoracidae · Ecological niche · Niche dimensions · Resource use · Partitioning · Overlap · Interspecific competition · Trophic ecology · Seabirds

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1. INTRODUCTION

Interspecific competition for trophic resources is considered the major force in organizing and structuring animal communities of higher trophic levels and could affect the way in which species co-exist (Hutchinson 1959, MacArthur & Levins 1967, Schoener 1974, 1983, Connell 1980). The theory of competitive exclusion predicts that when resources are limited, species with similar trophic requirements can only co-exist if there are differences in some dimen-

sions of their ecological niche (Gause 1934, Hutchinson 1959, Schoener 1974). In other words, this theory predicts that closely related and ecologically similar species living in sympatry should differ along some of the axes of the n-dimensional hypervolume ecological niche (MacArthur 1958, Hutchinson 1959, Pianka 1969).

Seabirds are frequently used as models to study interspecific trophic partitioning (Sabarros et al. 2012, Rosciano et al. 2016, Will & Kitaysky 2018), since several aspects of their life history, like central-

*Corresponding author: annick.morgenthaler@gmail.com

place foraging and colonialism, can enhance interspecific competition, especially during the breeding season when resource demand is higher (Ballance et al. 2009, Elliott et al. 2009, Barger et al. 2016, Fromant et al. 2022). In sympatric breeding seabirds, resource utilization can be partitioned across various dimensions: spatially — by foraging in distinct areas (Navarro et al. 2013, Rayner et al. 2016) or at different depths (Wilson 2010, Kokubun et al. 2016, Fromant et al. 2022); temporally — by varying diurnal/nocturnal activities (Barger et al. 2016) or breeding periods (Croxall & Prince 1980, Clewlow et al. 2019); and trophically — by consuming different prey types/sizes (Quillfeldt et al. 2013, Mancini & Bugoni 2014, Moreno et al. 2016, Rayner et al. 2016) or using different habitats (Will & Kitaysky 2018, Petalas et al. 2021). The large number of possible dimensions of the ecological niche of seabirds implies great potential for niche partitioning between potentially competing species (Privitera et al. 2008). Due to practical constraints, most studies examining seabird trophic niches tend to focus on only one or a few dimensions, often failing to detect any partition. However, the limited studies that have explored 3 or more dimensions have revealed that even minor segregation across several dimensions can lead to significant overall segregation among species. For example, Wilson (2010) studied the spatial and temporal foraging patterns (3-dimensional spatial axis and 1-dimensional temporal axis) of 3 sympatric penguin species; a mathematical model analysis involving the multiplication of the overlap found at each dimension/axis found that minor differences in each of them can result in a major global difference. Therefore, multidimensional studies can provide more reliable and precise estimates, and an enhanced ecological understanding of niche breadth and the structure of the community under study, which can inform effective conservation and management practices in marine ecosystems (Navarro et al. 2013, Petalas et al. 2024).

Coastal cormorants and shags (Phalacrocoracidae, herein cormorants s.l.) form a guild of foot-propelled pursuit-diving seabirds that constitutes an interesting model to study sympatric resource partitioning at a local level, due to their colonial habits and limited foraging ranges (Humphries et al. 1992, Gremillet et al. 1998, Sapoznikow & Quintana 2003, Frere et al. 2008). The coast of Atlantic Patagonia is one of the few areas in the world where more than 3 species of cormorants overlap their distribution ranges (Nelson 2005), and within this broad region, the Ría Deseado inlet is one of the rare places where 4 species co-exist in sympatry (Frere et al. 2005): red-legged *Poikilocarbo gaimardi*,

rock *Leucocarbo magellanicus*, neotropic *Nannopterum brasilianus*, and imperial *L. atriceps* cormorants. All 4 species primarily feed on fish and/or invertebrates, mostly in shallow waters. Imperial and rock cormorants are endemic to Patagonia and the Malvinas/Falkland Islands and are the most studied among the 4 species (Frere et al. 2005, Quintana et al. 2022). The imperial cormorant is also the largest and most abundant of these 4 species, and is found not only along the coastline but also in a few lakes (Frere et al. 2005). This species dives the deepest and has the greatest foraging range (Quintana et al. 2022), in contrast to the rock cormorant, which is restricted to shallow coastal areas near its small colonies (Quintana et al. 2002a, Frere et al. 2008). The neotropic cormorant displays more opportunistic habits, as reflected by its wide distribution and habitat range, inhabiting rivers, lakes, and coastal areas from the tropics to the southern cone (Telfair & Morrison 1995, Quintana et al. 2002b). The red-legged cormorant has a small population confined to a limited stretch of the southwestern Atlantic coast, apart from its primary population on the Pacific coast. It is classified on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List as Near Threatened due to a moderately rapid population decline (Millones et al. 2015, BirdLife International 2023). This small-sized cormorant forages in close proximity to its colonies, which are situated on cliffs often shared with the rock cormorant (Frere et al. 2008). Seasons are very marked in southern Patagonia, and these species breed during the austral spring and summer.

While previous research has identified resource partitioning between red-legged and rock cormorants (Frere et al. 2008), there has been limited exploration into trophic partitioning among the other coexisting cormorant species (Punta et al. 2003, Sapoznikow & Quintana 2003, Bulgarella et al. 2008). This study delves into the trophic, spatial, and temporal dimensions of the ecological niche of 4 coexisting cormorant species within a marine inlet along the Argentine Patagonian coast. Using a multidimensional approach, the aim was to characterize their trophic niches, foraging areas, and reproductive schedules to unravel the extent of niche segregation or overlap among these species. Building upon prior data and the competitive exclusion theory, it is expected that the 4 sympatric species should differ in certain dimensions of their niches to coexist. However, the constraints of limited geographic range, pronounced seasonality, and restricted movement patterns seem to offer limited opportunities for such niche segregation to occur.

While previous studies on sympatric seabirds have employed similar methodologies, our study introduces a novel multi-disciplinary approach by integrating pellet analysis, stable isotope analysis, observation-based determination of foraging areas, and breeding phenology assessment.

2. MATERIALS AND METHODS

2.1. Study site and species

The narrow (2.5 km maximum width) and lengthy (>40 km) inlet of the Ría Deseado is situated in southern Patagonia, near the town of Puerto Deseado, Argentina (47° 45' S, 65° 53' W, Fig. 1). It is formed by the partial submergence of a river valley, featuring strong tidal currents (Iantanos et al. 2002), and is part of a protected area, the Reserva Provincial Ría Deseado.

Three cormorant species nest within Ría Deseado. The red-legged cormorant is distributed across 6 colonies located on rocky cliffs (totaling 228–322 breeding pairs between 1993 and 2013; Frere et al. 2005, Morgenthaler 2019). This species is classified by the IUCN as Near Threatened due to its overall relatively small population, which is showing a moderately rapid decline (Millones et al. 2015, BirdLife International 2023). The rock cormorant has a single colony in the inlet (80–124 breeding pairs between 1993 and 2013; Frere et al. 2005, Morgenthaler 2019) on the

rocky cliffs of Isla Elena, sharing its habitat with the red-legged cormorant. The neotropic cormorant nests on bushes at Isla de los Pájaros (196–376 breeding pairs between 1993 and 2013; Frere et al. 2005, Morgenthaler 2019) forming a mixed colony with kelp gulls *Larus dominicanus* and Magellanic penguins *Spheniscus magellanicus*.

In addition to the 3 nesting cormorant species, the imperial cormorant uses the ria as a feeding ground. A permanent roosting site of approximately 300 non-breeding individuals is located at the entrance of the ria on Península Foca. The nearest breeding ground for the imperial cormorant is 20 km south of the ria, at Isla Chata (47° 54' S, 65° 44' W), comprising a significant colony with 4604–8750 breeding pairs between 1993 and 2013 (Frere et al. 2005, Morgenthaler 2019) situated within the protected area of the Parque Interjurisdiccional Marino Isla Pingüino. Fieldwork was conducted between 2009 and 2013, with the number of breeding seasons sampled varying depending on the niche dimension and species studied (details specified in the respective subsections of Section 2). Reference to a particular season always corresponds to the year of the beginning of the austral breeding season (for example, the season running from October 2009 to March 2010 is referred to as 2009).

The manipulation of cormorants in the field was consistent with local legislation and ethical practice guidelines. Special care was taken to limit the time handling chicks, which were carefully returned to

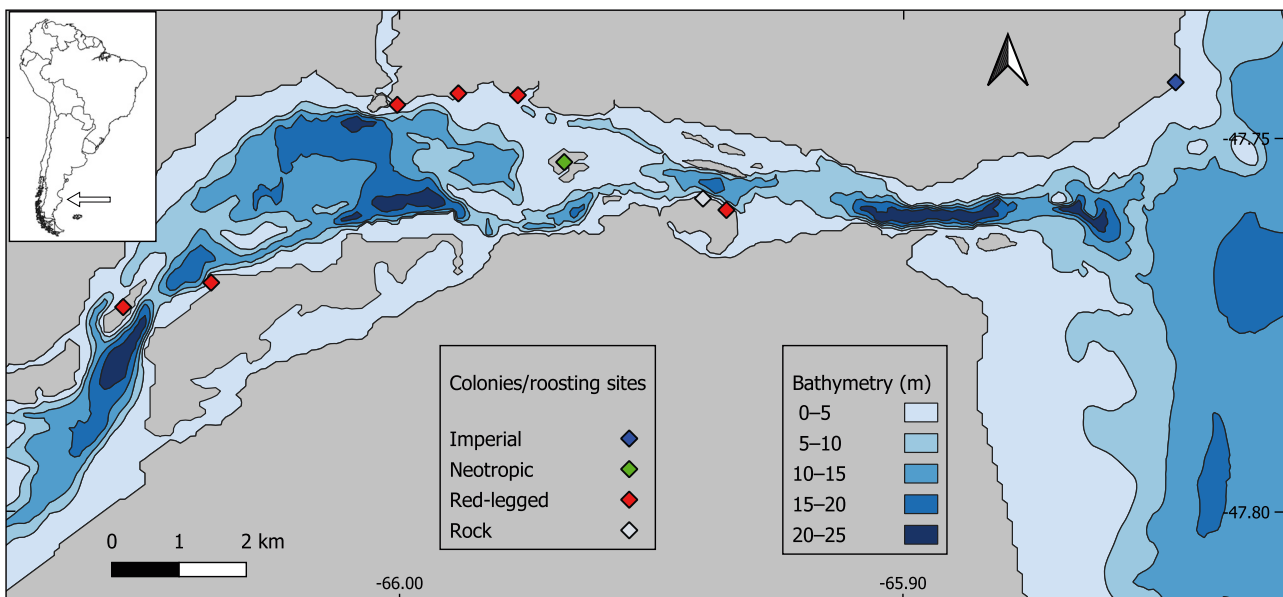


Fig. 1. Bathymetry of the Ría Deseado inlet and surrounding sea. The diamonds indicate cormorant colonies/roosting sites, colour coded by species in the key. The approximate location of the study site in southern Argentina is indicated by an arrow in the inset (top left)

their nests. The appropriate permit was obtained from the competent authority (Consejo Agrario Provincial, Santa Cruz, Argentina, permit No. 491756/09).

2.2. Conceptual and methodological framework

To assess potential niche overlap, metrics corresponding to different dimensions within the trophic niche were defined: (1) dietary composition, (2) isotopic niche, (3) spatial distribution, and (4) temporal factors. Although these dimensions are interrelated, each provides unique insights into resource use. (1) The dietary composition examines the proportions of specific prey types, offering detailed data on prey taxonomy, abundance, and diversity. (2) The isotopic niche dimension reflects the integrated diet over time, revealing habitat preferences, trophic levels, and a measure of overall breadth of resource use. (3) The spatial dimension assesses the primary foraging areas and associated bathymetry for each species. (4) The temporal dimension compares the breeding phenology and identifies the peak chick-rearing period, a time of high resource demand and the period of major use of the estuary based on the foraging records.

2.3. Dietary composition analysis

Pellets and/or regurgitates of the 3 cormorant species breeding at Ría Deseado were collected during 4 breeding seasons (2009, 2011–2013) at Ría Deseado: red-legged and rock cormorants at Isla Elena ($N_{\text{pellets}} = 209$ and 70 , respectively), and neotropic cormorant at Isla de los Pájaros ($N_{\text{pellets}} = 55$). The pellets of imperial cormorants were collected in the breeding colony of Isla Chata during 2 seasons (2012 and 2013; $N_{\text{pellets}} = 40$). Detailed methodology and original dietary results for each species are described by Morgenthaler et al. (2016, 2020, 2021, 2022). For the current study, the biomass estimates (wet weight) of the main prey were calculated for each cormorant species, considering all years together.

Multivariate analyses of similarity (ANOSIM) using the R package 'vegan', run in R v. 3.6.3, were used to test for pairwise interspecific dissimilarities (R index) and to calculate the overlap of dietary composition ($1 - R$) (Clarke & Warwick 2001, R Core Team 2020, Oksanen et al. 2024). Using the same package, similarity percentages (SIMPER) analyses were performed to determine which prey contributed the most to the dietary differences between cormorant pairs (percent contribution to the difference $> 10\%$).

Finally, prey richness (S) and Shannon-Weaver diversity indices (Tramer 1969), based on numerical estimates (H'_N) and wet weight estimates (H'_W), were calculated for each cormorant species (all years together).

2.4. Isotopic niche analysis

Blood samples were collected from 3 to 5 wk old chicks of red-legged ($N = 29$), rock ($N = 29$), and neotropic cormorants ($N = 44$) during 3 seasons (2011–2013), and imperial cormorants ($N = 18$) during 2 seasons (2012 and 2013). These samples were obtained from the same colonies where the pellets/regurgitates were collected. Blood samples were dried and analyzed to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (refer to Morgenthaler et al. 2016, 2020, 2021, 2022 for detailed methodology and original published values for each species). Bayesian standard ellipse areas (SEA_B) were calculated using the 'Stable Isotope Bayesian Ellipses in R' ('SIBER') package 2.1.9 to estimate the breadth of isotopic niches (median of the SEA_B areas and 95% credible interval) for each species and each year (Jackson et al. 2011). This analysis generated ellipses based on approximately 40% of the bivariate isotopic data (core isotopic niche). The pairwise overlap of SEA_B ellipses (median and 95% credibility interval of the draw) was then calculated with the function 'bayesianOverlap', with null values of p. interval and n, and with number of draws = 100 (Jackson et al. 2011). For visual representation, the standard ellipse area (SEA) was used in the figures. Finally, isotopic niche positions were analyzed using Layman's metrics, with niche centroid locations determined via nested linear models and residual permutation procedures (Layman et al. 2007, Turner et al. 2010). The Euclidean distances (EDs) between the centroid locations of each species were calculated annually to assess species separation (Turner et al. 2010). When pairwise isotopic niches did not overlap, nonparametric Wilcoxon tests were performed to identify which axis of the isotopic niche ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) contributed to the observed differences (Hammerschlag-Peyer et al. 2011).

2.5. Foraging area analysis

To determine the feeding areas of the 4 species in the Ría Deseado, feeding cormorants were directly observed from a semi-rigid boat during the period from November to February over 3 seasons (2010–2012). The surveyed area spanned 30.7 km^2 and ex-

tended from the entrance of the ria to approximately 18 km into it. The western (inner) limit was delineated by the change in turbidity and depth, encompassing the region with the highest cormorant presence within the ria (Nasca et al. 2004, Frere et al. 2008, Millones 2009). The boat transects were executed perpendicular to the coast, separated by approximately 300 m, following a similar approach to Millones et al. (2010). Observations were made on days with low winds to facilitate locating the cormorants on the water surface. Binoculars were occasionally used for species identification. Data were recorded for each diving event, including GPS coordinates, time, species, and the number of individuals, distinguishing between solo and group feeding. In total, 14 comprehensive surveys were conducted throughout the 3 seasons, which added up to a cumulative effort of 73.4 h. While this method lacks information on the breeding status of monitored individuals (in contrast to traditional methods involving captures and bio-logger fitting), it offers the advantage of providing highly comparable data by simultaneously and evenly studying all 4 species over several months, without the need for captures.

Spatial analyses were performed using the complete data set (solo and flocks), and solo feeding localizations ($N = 1240$) were also analyzed separately. Flock feeding events may indicate pulses of pelagic resource abundance (Nasca et al. 2004), potentially influencing interspecific competition.

Kernel analyses of sampling localizations were conducted using the 'animal movement' extension in ArcView 3.2 software (Worton 1989, Hooge & Eichenlaub 1997). For each species, core feeding areas, indicative of regions containing 50% of the volume of a density probability distribution, were determined through kernel analyses of 50% (Wood et al. 2000). The h bandwidths (smoothing factor) for the kernel analyses were calculated with the 'adehabitat' package (Calenge 2006) in R 3.4.1 (R Core Team 2020). Spatial overlap percentages of core areas between different species were computed for the 2 data sets (solo and flock, and only solo). Figures were created using QGIS 2.18 software (QGIS Development Team 2017).

For each species, the distances between the feeding locations and their nearest colony/roosting site were calculated. The spatial distribution of feeding locations was further analyzed by calculating the nearest-neighbor index (NNI), representing the average distance between closest locations, with NNI values ranging from 0 (grouped pattern) to 1 (random dispersed pattern) (Clark & Evans 1954). These analyses

were performed with QGIS 2.18 software (QGIS Development Team 2017).

A bathymetric map of the study area, presenting 5 depth categories (0–5, 5–10, 10–15, 15–20, and 20–25 m) was created (Fig. 1) with QGIS 3.36.2 software (QGIS Development Team 2024). The information was obtained from the Nautical Chart Number H361 (Servicio de Hidrografía Naval de la República Argentina, Buenos Aires), and the depth measurements correspond to low tide marks. Finally, the depth categories associated with each surface feeding record from the 4 species were determined by overlaying 2 layers in QGIS: bathymetric categories (polygons) and the distribution of cormorant feeding records (points). The frequency of depth categories was then calculated for 2 data sets: (1) solo and flock feeding records, and (2) solo feeding records only.

2.6. Temporal overlap

Two separate comparisons were made for temporal overlap analysis, one based on breeding phenology of the 3 species nesting in the ria and the other based on frequency of foraging observations of all 4 species.

To assess the temporal overlap during what was considered the period of most intensive use by the species nesting in the ria (red-legged, rock, and neotropical), the phenology of breeding stages was identified, including incubation, early chick rearing (chicks <20 d old), late chick rearing (>20 d, still with down on the body and neck), and fledglings still at the nest (without down). For red-legged and rock cormorants from Isla Elena, 27 nests of each species were monitored during 3 breeding seasons (2010–2012). Colony visits occurred approximately every 10 d to determine the stage of each nest. For neotropical cormorants nesting on Isla de los Pájaros, individual nest monitoring was impractical due to nesting ground characteristics and species sensitivity. Instead, observations of a sector with approximately 70 breeding pairs were conducted at a distance (50–100 m) using binoculars during 5 breeding seasons (2009–2013). At each visit, the proportion of nests in each stage was estimated.

For each of the 3 species, the average annual percentage of nests in each reproductive stage was calculated at the beginning (Days 1–10), middle (11–20), and end of each month (21–30/31) between October and April. The core period for each stage was defined when more than 25% of the nests were found in this stage. The core period of the early chick-rearing stage was selected to calculate the temporal overlap between species, considering that this period

reflects high overall resource demand when most pairs have chicks (later, the individual chick demand can be higher, but overall, there might be fewer pairs with chicks).

Since imperial cormorants do not nest in the ria, their temporal overlap with other species was estimated using an analysis of the core period of their presence in the ria based on feeding location dates. For each species, the core period of presence in the ria was calculated as the temporal interquartile range (50% of the data) of the dates of solo feeding locations.

2.7. Multidimensional synthesis

The values of pairwise overlaps (0–100%) at each dimension were categorized into 4 levels (segregated, low, moderate, and high overlap) to provide a synthesized overview of the 4-dimension overlaps among the 4 cormorant species. These criteria were chosen based on established benchmarks in dietary studies, where an overlap greater than 60% is often considered biologically significant (Schoener 1974, Clarke et al. 1993, Rodríguez-Graña et al. 2018). The overlap categories for the dietary and temporal dimensions were defined as follows: 0–30%: segregated; 31–60%: low; 61–80%: moderate; and >80%: high overlap. Since isotopic and spatial overlap were derived from the core data (isotopic niches: 40% of the data, and foraging areas: kernel 50%), the overlap categories for these dimensions were defined as follows: 0–10%: segregated; 11–30%: low; 31–60%: moderate; and >60%: high overlap, consistent with the spatial overlap categories defined by Rodríguez-Graña et al. (2018). The overlap categories aim to capture the biological relevance of interactions among cormorant species across these dimensions.

3. RESULTS

3.1. Dietary composition analysis

The average pairwise dietary overlap, considering the prey biomass estimates (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m752p169_supp.pdf), was 48.1% (range: 40.8–

63.0%), and significant differences in dietary composition between each pair of cormorants were found (ANOSIM, $R = 0.519$, all $p < 0.0001$, Table 1). The only pair with a dietary overlap greater than 60% was the rock/neotropic pair (63.0%). Those with the lowest overlap were red-legged/rock (40.8%) and red-legged/neotropic (41.2%; Table 1). According to SIMPER analyses, the prey that contributed the most to the differences between cormorant species were the squid *Dorytheutis gahi* for the red-legged cormorant; the benthic fishes *Paranotothenia magellanica* and *Patagonotothen* spp. for the neotropic cormorant; the benthic fishes *Patagonotothen* spp. and Zoarcidae for the rock cormorant; and the benthic fishes *Cottoperca gobio* and *Patagonotothen* spp. for the imperial cormorant (Table 1).

The prey richness (S) and diversity H'_N indices varied among species (Table S1); rock ($S = 26$; $H'_N = 1.59$) and imperial ($S = 21$; $H'_N = 2.02$) cormorants had the highest values, while neotropic ($S = 8$; $H' = 0.97$) and red-legged ($S = 16$; $H'_N = 0.59$) had the lowest. When considering H'_W , the differences between species were smaller (Table S1); rock cormorants had the highest value (1.43), followed by neotropic (1.23), imperial (1.19), and red-legged cormorants (0.83).

Table 1. Percentage of overlap (similarity) of diet composition, based on biomass estimates between pairs of cormorants, and prey contributing to the differences, with respective percentage of contribution to the difference (>10%). Prey are benthic fishes (*Patagonotothen* spp., *Paranotothenia magellanica*, Zoarcidae, and *Cottoperca gobio*), squid (*Dorytheutis gahi*), and octopus (*Enteroctopus megalocyathus*). The cormorant species whose prey contributes to the difference are shown in parentheses (R: rock, I: imperial, RL: red-legged, N: neotropic). The star (*) indicates a significant pairwise difference in diet composition (ANOSIM, $p < 0.001$)

Pairwise dietary overlap	%	Prey contributing to differences	% of contribution
Rock/neotropic:	63.0*	<i>Patagonotothen</i> spp. (R)	33.9
		<i>Paranotothenia magellanica</i> (N)	24.7
		Zoarcidae (R)	12.9
Red-legged/imperial:	51.3*	<i>Cottoperca gobio</i> (I)	54.0
		<i>Patagonotothen</i> spp. (I)	17.3
Imperial/neotropic:	46.6*	<i>Cottoperca gobio</i> (I)	51.0
		<i>Patagonotothen</i> spp. (N)	15.5
Rock/imperial:	45.4*	<i>Cottoperca gobio</i> (I)	55.2
		<i>Patagonotothen</i> spp. (R)	13.5
Red-legged/neotropic:	41.2*	<i>Patagonotothen</i> spp. (N)	39.2
		<i>Paranotothenia magellanica</i> (N)	34.3
Red-legged/rock:	40.8*	<i>Patagonotothen</i> spp. (R)	35.4
		Zoarcidae (R)	17.9
		Octopus (R)	12.1
		Squid (RL)	10.4

3.2. Isotopic niche analysis

The width of the core isotopic niches (SEA_B) differed among species and years (Fig. 2). Red-legged (SEA_B range: $0.08\text{--}0.26\text{‰}^2$) and imperial ($0.13\text{--}0.34\text{‰}^2$) cormorants had the smallest SEA_B , followed by rock ($0.21\text{--}0.84\text{‰}^2$) and neotropic cormorants ($0.85\text{--}0.92\text{‰}^2$), which had the largest. Annual and specific SEA_B median values with their respective confidence intervals are reported in Fig. 2.

Rock and neotropic cormorants overlapped their core isotopic niches (SEA_B) in 2012 and 2013 (Fig. 2). In 2012, the overlapped area represented 36.8% (CI: 27.4–41.4%) of the rock cormorant core isotopic niche and 33.4% (CI: 27.7–44.7%) of the neotropic core isotopic niche. In 2013, it represented 15.8% (CI:

4.8–34.4%) of the rock cormorant niche and 7.7% (CI: 4.7–11.3%) of the neotropic niche; the lower overlap that year resulted from the smaller isotopic niche area of rock cormorants ($SEA_B\text{-CI}$: $0.19\text{--}0.23\text{‰}^2$). In 2011, no overlap was observed, and their niche positions differed significantly ($ED = 0.88$, $p < 0.001$, Fig. 2); the difference was the result of higher $\delta^{15}\text{N}$ values in rock than in neotropic cormorants (Wilcoxon, $p < 0.001$).

Besides the rock/neotropic pair, no other pair of species overlapped their core isotopic niches, and the niche positions of each cormorant species differed from the others in all study years (Fig. 2; all $ED > 0$, $p < 0.001$). The species whose niche position was situated furthest from the others (overall greatest ED) was the red-legged cormorant (Fig. 2). This species presented lower mean $\delta^{15}\text{N}$ values during all years (Wilcoxon,

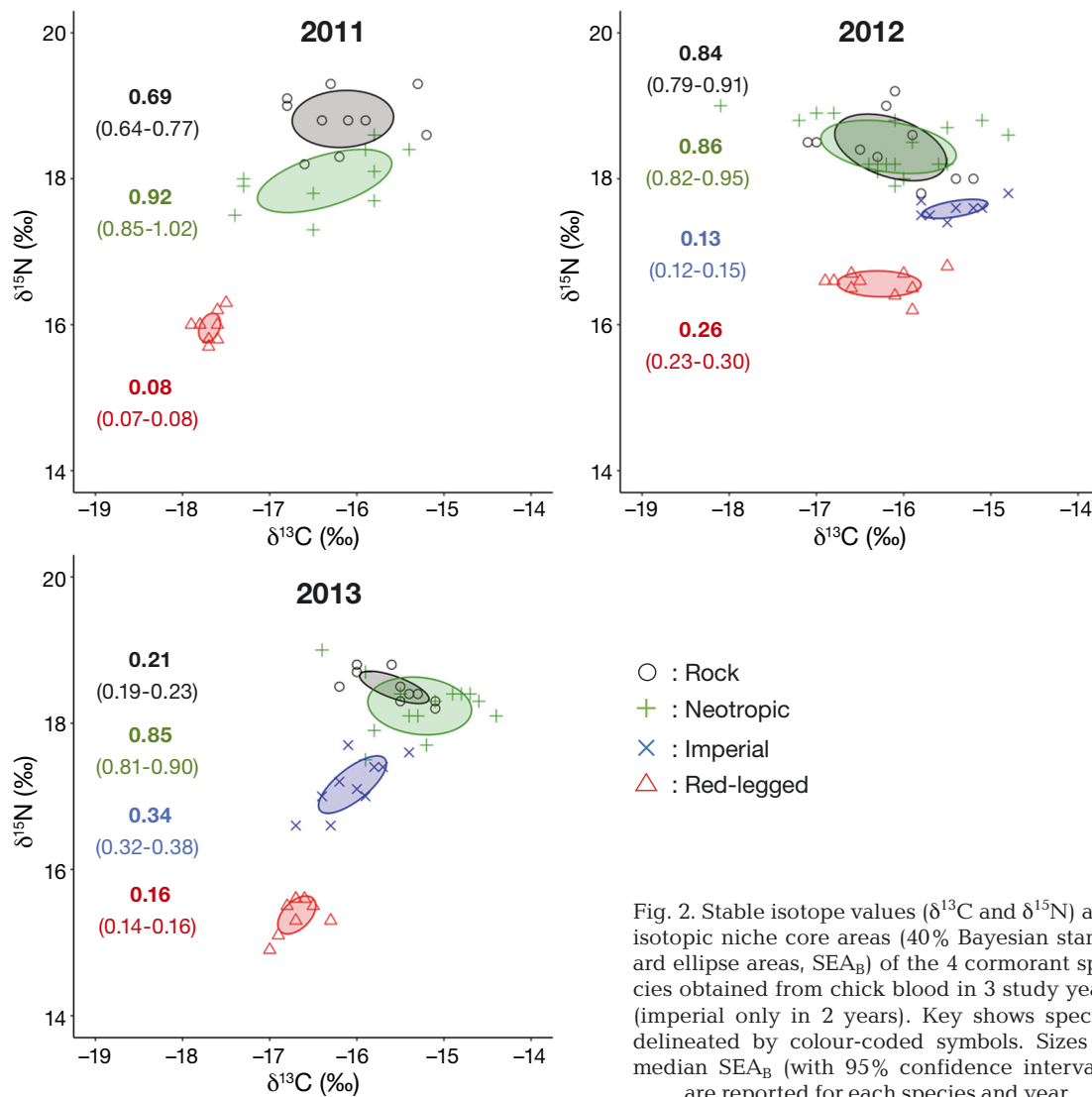


Fig. 2. Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and isotopic niche core areas (40% Bayesian standard ellipse areas, SEA_B) of the 4 cormorant species obtained from chick blood in 3 study years (imperial only in 2 years). Key shows species delineated by colour-coded symbols. Sizes of median SEA_B (with 95% confidence intervals) are reported for each species and year

all $p < 0.001$) and also lower mean $\delta^{13}\text{C}$ values in 2011 and 2013 (Wilcoxon, all $p < 0.001$). The niche position of the imperial cormorant differed from the other species in the 2 study years, mainly due to its $\delta^{15}\text{N}$ values, which were higher than those of red-legged but lower than those of rock and neotropic cormorants (Fig. 2). Imperial $\delta^{13}\text{C}$ values differed between the 2 study years (Wilcoxon, all $p < 0.001$).

3.3. Foraging area analysis

From the 2526 locations of cormorants feeding in the ria, obtained over the 3 seasons, 44% belonged to imperial, 26% to red-legged, 21% to neotropic, and 9% to rock cormorants. The relative proportions of the locations of red-legged, neotropic, and rock cor-

morants were consistent with the relative proportions of individuals of the 3 species that nest at Ría Deseado (χ^2 : 1.94, $p = 0.38$). Among all of the feeding locations of the 4 species, 49% were attributed to cormorants feeding solo (or in loose groups) and 51% to cormorants feeding in flocks (mono- or multispecific) that contained an average of 44 ± 55 individuals ($N_{\text{flocks}} = 27$). The proportion of solo feeding records varied among species: 99.5% in rock, 56.3% in red-legged, 48.6% in neotropic, and 35% in imperial cormorants.

Considering the entire data set (solo and flock feeding records together; Fig. 3A), there were almost no pairwise overlaps of core feeding areas (mean: 1.0%; range: 0–7.1%). When considering only the solo feeding records (Fig. 3B), the mean pairwise overlap of the core areas was 15.2%, and it greatly varied among the species pairs (range: 0–82.3%). The spe-

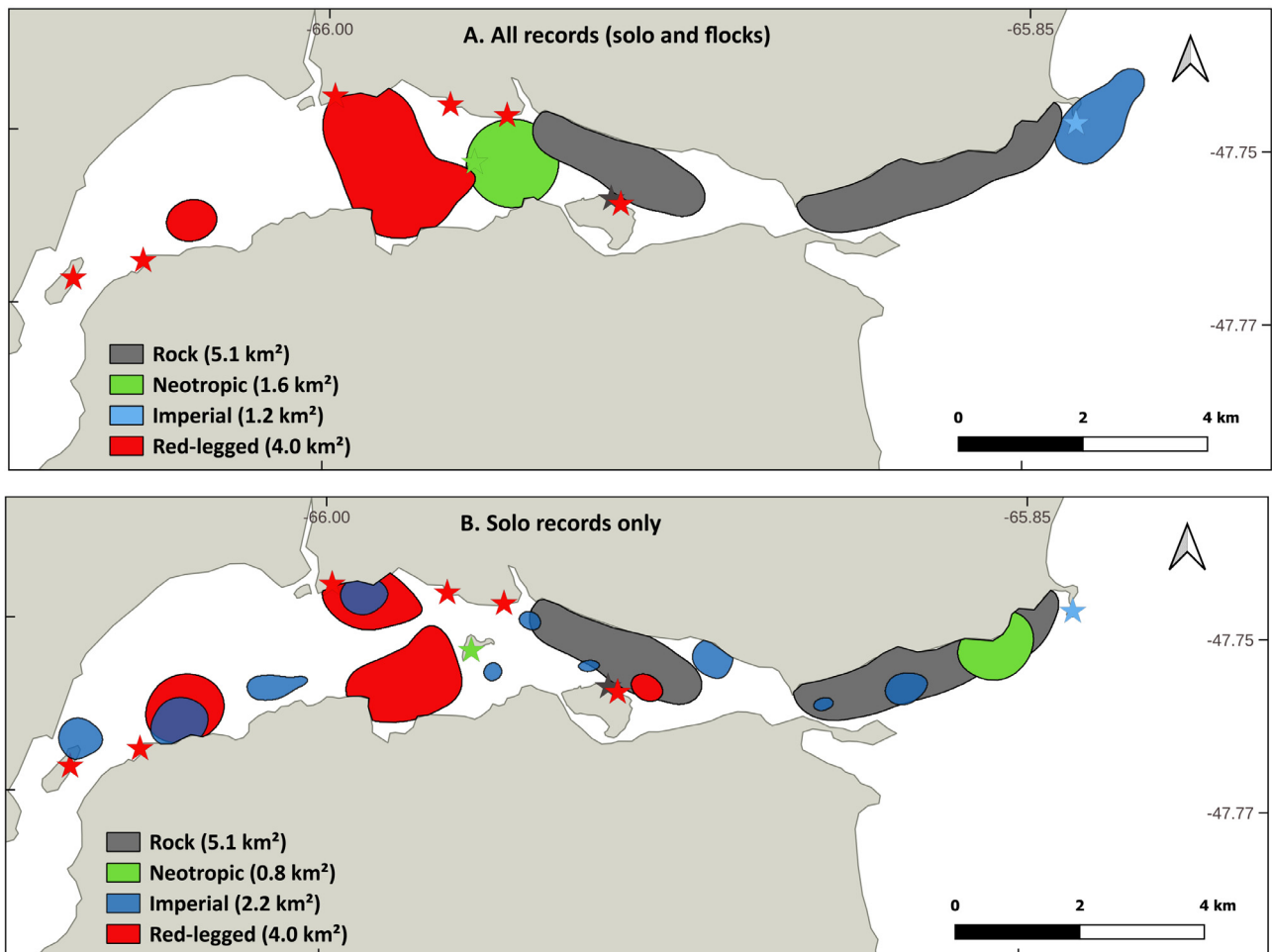


Fig. 3. Feeding areas (50% kernel) of the 4 cormorant species within the Ría Deseado, taking into account: (A) all records (birds foraging solo and in flocks) (N_{total} : 2526; red-legged [RL]: 668, rock [R]: 219, neotropic [N]: 523, imperial [I]: 1116) and (B) only solo feeding records (N_{total} : 1240; RL: 376, R: 218, N: 253, I: 387). See key for colour coding by species. The stars indicate the respective colonies/roosting sites

cies that most overlapped its core area with that of other species was the neotropic cormorant (82.3% overlap with rock), followed by the imperial cormorant (36.5% with red-legged and 16.4% with rock). Red-legged and rock cormorants showed the least overlap of their core areas with the other species (Fig. 3B).

The spatial analysis of the feeding locations (considering only solo records; Fig. 3B, Table S2B) showed that red-legged cormorants fed at a mean distance to the nearest colony/roosting site of 1.1 km, rock cormorants at 3.5 km, neotropic cormorants at 5.2 km, and finally imperial cormorants at 9.4 km. When considering the full data set (solo + flocks; Fig. 3A), neotropic and imperial cormorants fed closer to their colony/roosting sites (3.0 and 4.1 km, respectively) and their distributions were more clustered than when considering only solo feeding records (Fig. 3B; Table S2). No differences were observed for red-legged cormorants; this species always foraged closest to one of its colonies (Table S2). The red-legged cormorant is also the only species with more than 1 colony (6) inside the ria (Fig. 3).

After analyzing the bathymetry of the feeding areas, neotropic and rock cormorants predominantly foraged in locations associated with the shallowest depths, with over 80% of records in the first depth category (up to 5 m; Fig. 4). In contrast, red-legged and imperial cormorants primarily foraged in areas associated with the first 3 depth categories (up to 15 m) and were only occasionally associated with deeper waters (Fig. 4). For these latter 2 species, when considering only solo records (Fig. 4B), the proportions of shallower areas (0–5 m) were higher than when considering all records (solo and flocks; Fig. 4A).

3.4. Temporal overlap

Among the 3 cormorant species breeding in the ria, a high temporal overlap of the overall breeding calendar was found between red-legged and rock cormorants, and a moderate overlap of neotropic with red-legged and rock cormorants (Fig. 5). The start of egg laying varied between years, but within the same sea-

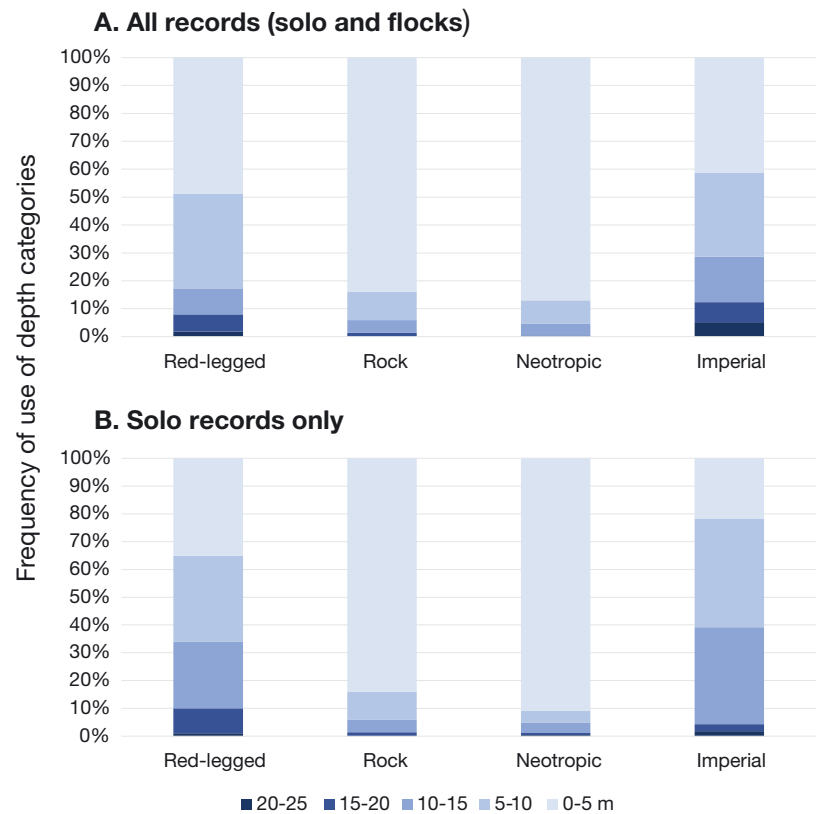


Fig. 4. Frequency of depth categories associated with surface feeding records of the 4 cormorant species within the Ria Deseado, taking into account (A) all records (birds foraging solo and in flocks) (N_{total} : 2526; RL: 668, R: 219, N: 523, I: 1116; abbreviations as in Fig. 3) and (B) only solo feeding records (N_{total} : 1240; RL: 376, R: 218, N: 253, I: 387)

son and species, the breeding schedules of red-legged and rock cormorants were very synchronous, with a start of laying of no more than 3 wk apart among breeding pairs in both species. In general, incubation in these 2 species occurred between October and December (Fig. 5). In return, the dates of laying of neotropic cormorants were very asynchronous, even within one season; laying was observed from October to February (Fig. 5).

The peak of the early chick-rearing stage (median 10 d period) was early December for red-legged, mid-December for rock, and early February for neotropic cormorants (Fig. 5). The temporal overlap of the early chick-rearing stage (core data) of red-legged and rock cormorants was 80%, that of rock and neotropic cormorants was 20%, and that of neotropic and rock cormorants was 17%. Red-legged and neotropic cormorants did not overlap each other temporally.

By comparing the temporal distribution of solo feeding records of the 4 species throughout the spring and summer seasons, including imperial cormorants that do not nest inside the ria, we found that

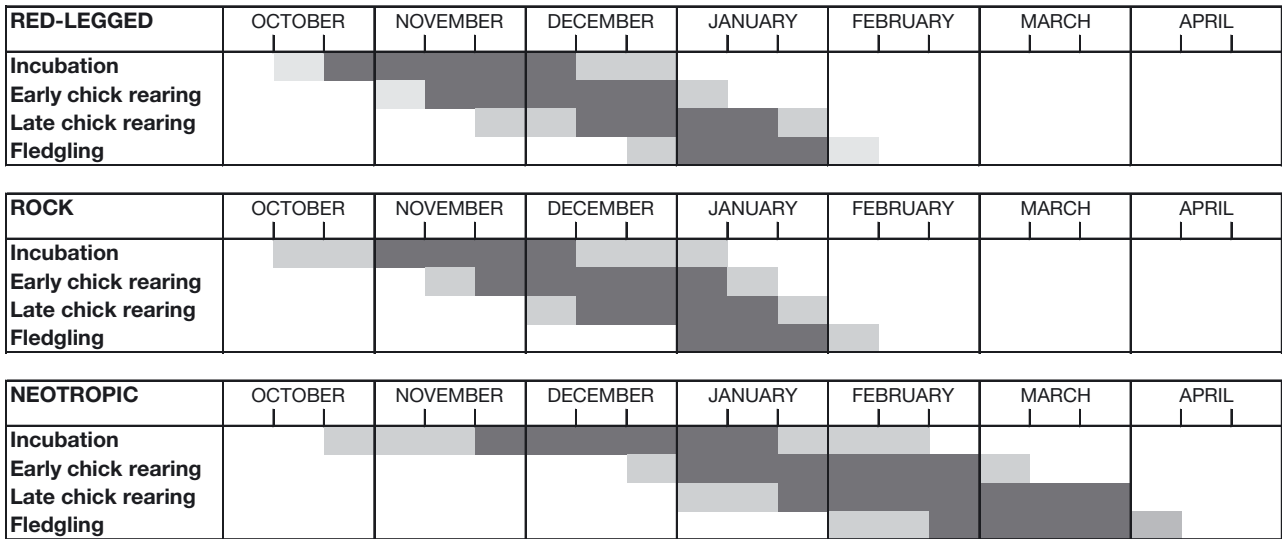


Fig. 5. Breeding calendar of the 3 species of cormorants that nest in the Ría Deseado. For each breeding stage, dark gray corresponds to the period during which >25% of the nests were found at this stage, and light gray corresponds to the period during which 5–25% of the nests were found at this stage. Data were collected at Isla Elena for red-legged and rock cormorants and at Isla de los Pájaros for neotropic cormorants

imperial cormorants appeared in higher numbers late in the season (core dates of presence: 18 January to 26 February), compared with the other species (red-legged: 13 November to 10 January; neotropic: 7 December to 7 February; rock: 30 November to 27 February). Therefore, the temporal overlaps of the core dates of presence based on foraging observations with imperial cormorants were: 0% for red-legged, 32.3% for neotropic, and 44.1% for rock cormorants. The core dates of presence of imperial cormorants overlapped 51.3 and 100% with those of neotropic and rock cormorants, respectively.

3.5. Multidimensional synthesis

By integrating and categorizing the pairwise overlap values of the 4 different dimensions of the niche, we found that no species overlapped all in 4 dimensions (when considering the overlap categories 'moderate' or 'high') with another species (Table 2). Neotropic cormorants overlapped in more dimensions with any other species; they significantly overlapped 3 of the 4 dimensions (high spatial, moderate dietary, and isotopic) with rock cormo-

rants (Table 2). Rock cormorants overlapped 2 dimensions with neotropic cormorants (moderate dietary and isotopic) and 1 dimension with red-legged cormorants (high temporal) (Table 2). Imperial cormorants overlapped the temporal dimension with rock

Table 2. Pairwise overlap (%) in each of the 4 dimensions of the ecological niche. The overlap categories for the dietary and temporal dimensions are as follows: segregated (0–30%, green), low (31–60%, yellow), moderate (61–80%, orange), and high (>80%, red). For isotopic and spatial dimensions, the overlap was based on core data only and the categories are as follows: segregated (0–10%, green), low (11–30%, yellow), moderate (31–60%, orange), and high (>60%, red)

Dimension		Red-legged	Neotropic	Rock	Imperial
Red-legged	Dietary		41.2	40.8	51.3
	Isotopic		0	0	0
	Spatial		0	3.8	20.3
	Temporal		0	80	0 ^a
Neotropic	Dietary	41.2		63.0	46.6
	Isotopic	0		13.7	0
	Spatial	0		82.3	0
	Temporal	0		17	32.3 ^a
Rock	Dietary	40.8	63.0		45.4
	Isotopic	0	17.5		0
	Spatial	3.1	12.8		7.3
	Temporal	80	0		44.1 ^a
Imperial	Dietary	51.3	46.6	45.4	
	Isotopic	0	0	0	
	Spatial	36.5	0	16.4	
	Temporal	0 ^a	51.3 ^a	100 ^a	

^aTime window for the imperial cormorant is based on its presence in the ria (feeding locations), not the breeding calendar

cormorants (high) and the spatial dimension with red-legged cormorants (moderate). Finally, red-legged cormorants overlapped the temporal dimension only with rock cormorants (high) (Table 2).

4. DISCUSSION

This novel study of 4 sympatric coastal seabirds revealed the advantages of simultaneously integrating results of overlap from dietary, isotopic, spatial, and temporal axes of the niche hypervolume. Technically, the combination of the different methods offered a robust framework to address multidimensional trophic partitioning in the context of the coexistence of 4 closely related cormorant species. Three of these 4 coastal species live in a geographically restricted spatial area during a period when they are limited to exploit resources close to their colonies, and the fourth species, although not breeding within this inlet, also uses it intensively for foraging. Therefore, the potential for competition between these sympatric species is high, and the overlap in the use of resources, which originally appeared difficult to avoid, was likely minimized to avoid competition. This approach allowed us to find that the degree of interspecific segregation varied according to the pair of species and also according to the dimension examined, a central theme for the concept of the *n*-dimensional hypervolume of the ecological niche (Hutchinson 1957, Navarro et al. 2013), and that the incorporation of multiple dimensions enhanced the potential for overall segregation.

For logistical reasons mainly, most studies on sympatric seabirds usually consider only a few axes of the niche. By doing so, results considering trophic segregation are often not conclusive, probably not because there is no ecological segregation overall, but because of focusing on only one or few dimensions/axes. Also, when segregation is found in a one-dimensional study, the limited information given by this single dimension is often insufficient to interpret the ecological processes behind that segregation. For example, when the segregation of rock and red-legged cormorant foraging areas was observed by studying this spatial dimension only at Ría Deseado in 1999 (Frere et al. 2008), a mechanism of competitive exclusion was suspected, but lack of competition could not be ruled out considering that the prey could easily move between these nearby areas due to their mobility, and even more so in a context of strong tidal currents. The incorporation of dietary and isotopic dimensions (Millones et al. 2005, Morgenthaler et al.

2016, 2020, this study) helped confirm that the spatial segregation between these 2 species effectively reflects an overall different diet and the exploitation of different prey types, therefore allowing for a much more detailed ecological interpretation on the origin of the observed spatial segregation. In both cases, whether segregation in the studied dimension is found or not, it reinforces the importance of incorporating additional dimensions of the niche, enabling a more in-depth ecological comprehension of its structure.

Wilson (2010) found that the multiplication of minor differences in each dimension can result in a major global difference leading towards apparent overall separation of the niches. In the case of our study, if we consider it hypothetically correct to multiply the overlap found at each dimension, we found that even the species that overlap the most with another species (neotropic with rock) would result in high overall segregation (final overlap of only 1.2%). However, given that the studied dimensions are inter-related, it would not be appropriate to multiply each of the 4 dimensions in this study, even though there is a certain degree of overlap enhancement between them.

4.1. Resource use by each cormorant species and how each species segregated from the others

Overall segregation was found among the 4 species studied when considering all dimensions together. However, we observed that some species were segregated in more dimensions than others. Here, we present and discuss aspects of the trophic ecology of each species and the dimensions in which they overlapped and/or segregated from the others (Table 3).

4.1.1. Rock

Rock and neotropic cormorants were the 2 species that overlapped the most dimensions of their niches (Table 3). The rock cormorant had a benthic diet and fed exclusively solitary. Its diet was rich and diverse, including various invertebrate taxa in addition to fish, consistent with the use of predictable and stable benthic food sources, low in abundance and low in energy value (Sapoznikow et al. 2009, Morgenthaler et al. 2020). The fact that both rock and neotropic cormorants have an overall generalist and broad diet (moderate to high diversity index and broad isotopic niches) could help explain their coexistence despite

Table 3. Evidence obtained in this study on segregation/overlap for each dimension of the ecological niche. Asterisk (*): overlap or similarity <60%

Species	Niche dimension			
	Dietary dimension: - Diet type - Overlap of diet composition	Isotopic dimension: - Trophic level - Overlap of isotopic niches	Spatial dimension: - Size of feeding areas - Overlap of core feeding areas	Temporal dimension: - Breeding period - Overlap of early chick-rearing period
Red-legged	- Pelagic, low diversity - Overall low overlap*	- Low trophic level - Segregated*	- Medium-sized area - Low overlap with imperial	- Synchronous and early - High overlap with rock
Rock	- Benthic, high diversity - Moderate overlap with neotropic	- High trophic level - Moderate overlap with neotropic	- Medium-sized area - Moderate overlap with neotropic	- Synchronous and early - High overlap with red-legged
Neotropic	- Benthic and pelagic, low diversity - Moderate overlap with rock	- High trophic level - Moderate overlap with neotropic	- Very small area - High overlap with rock	- Asynchronous and late - Segregated*
Imperial	- Benthic and pelagic, high diversity - Overall low overlap	- Intermediate trophic level - Segregated*	- Small area - Low overlap with red-legged & rock	- Late presence in the ría - Overall low overlap ^a

^aThe temporal overlap of the imperial cormorant is based on its presence in the ría (feeding localizations), not on the breeding calendar

significant spatial and dietary overlap. Exploiting a wider range of resources provides versatility, potentially reducing competition with other species that specialize in specific niches, thereby promoting coexistence (Mittelbach & McGill 2019).

4.1.2. Neotropic

The neotropic core feeding area (considering solo data only) had a high degree of overlap with that of the rock cormorant. The isotopic niches of these 2 species overlapped partially in some years, with their positions reflecting the consumption of prey from high trophic levels, mostly benthic. Despite significant dietary overlap with the rock cormorant, the diet of the neotropic cormorant consisted entirely of fish, encompassing both benthic and coastal pelagic species, with some prey being unique to its diet. Its apparent versatile and opportunistic feeding behavior, as observed in this study and noted in various previous studies (Telfair & Morrison 1995, Barquete et al. 2008, Petracci et al. 2009, Muñoz-Gil et al. 2013), was also reflected in the widest mean isotopic niche among the 4 species.

The interannual differences in the isotopic niche position and sizes led to interannual variations in the rock–neotropic isotopic niche overlap. Although these interannual differences could be due to slight

interannual variation of the dietary composition (Morgenthaler et al. 2021), they are more likely attributable to possible interannual variation in isotopic values of some of the prey (Satterfield & Finney 2002, Morgenthaler et al. 2016, 2020, 2021, Ciancio et al. 2021).

Furthermore, the dimension of the niche that allowed for greater segregation between neotropic and rock cormorants was allochrony of the breeding season. Although environmental seasonality is very marked at these latitudes, neotropic cormorants presented a very asynchronous reproductive schedule (wide date interval of egg laying between pairs) with a late peak of the chick-rearing stage (not described for any other site along the Patagonian coast), the period of greatest demand, temporarily segregated from the other 2 species nesting in the ría (rock and red-legged). The breeding chronogram of neotropic cormorants in the Ría Deseado appears to be 2 to 4 wk delayed compared to the chronogram from colonies found in colonies situated 300 km north (Quintana et al. 2002b), where the composition of the guild is somewhat different (allopatry or less sympatric species). This provides evidence pointing towards an allochronic adaptive mechanism allowing for reduced interspecific competition, distributing the peak of maximum food requirements in a more uniform way during a longer period and separated from congeners. This shift could have been possible thanks to the nest-

ing plasticity of the neotropic cormorant, an important feature in the life history of this species, which successfully colonized a very wide latitudinal range and adapted to highly varied aquatic environments, which are made up of highly diverse communities (Orta 1992).

4.1.3. Red-legged

The red-legged cormorant segregated the most from the other species (Table 3). It presented the least pairwise overlap of the dietary composition and the main feeding areas. It fed at the lowest trophic level, almost exclusively on pelagic or demersal-pelagic prey (sprat and squid), unlike any of the other cormorant species. Surprisingly, this highly energetic prey (Sánchez et al. 1995) was not found in the diet of any of the other 3 cormorant species, despite being abundant and despite the fact that this type of prey (sprat or other ecologically similar species) is used by imperial and rock cormorants at other colonies along the Patagonian coast (Punta et al. 2003, Ferrari et al. 2004, Yorio et al. 2010, 2017, Ibarra et al. 2018, 2022). The red-legged is the only cormorant species in the ria that depends almost exclusively on the pulse of this 'external' abundant but less predictable resource.

4.1.4. Imperial

Finally, the imperial cormorant is the only one of the 4 species that does not nest in the ria. The number of individuals using the ria for feeding is probably only a small fraction of its nearby breeding population, and many of them are likely non-breeders or post-breeders (Morgenthaler et al. 2022). This species seemed to use resources within the ria without significantly overlapping its different trophic dimensions with the other cormorant species. It segregated spatially and predominantly frequented the ria late in the season, foraging among the deepest areas. The imperial fed at a trophic level situated in between the red-legged (low), and the neotropic/rock group (high).

Furthermore, the imperial is the largest of the 4 species and the one that is better adapted to sustained flight as well as deep diving, allowing it to exploit a much wider feeding range than the others (Frere et al. 2005, Quintana et al. 2022). This combination of morphological and behavioral differences has probably been key in the development of resource exploita-

tion strategies in a context of coexistence with the other species of the guild, eventually leading to its structuration.

4.2. Use of the water column: the most explanatory potential dimension?

In other cormorant species, the efficient use of the feeding space has resulted from selective/specialized behavior leading to the use of restricted feeding areas, high fidelity to certain sites, and opportunistic behavior, evidenced by flexibility in feeding areas, diving patterns, and/or the type of prey consumed (Grémillet et al. 1998, Kotzerka et al. 2011, Camprasse et al. 2017). In a multidimensional study of 2 sympatric cormorants from the estuary of the Columbia River, USA, Peck-Richardson et al. (2018) found that feeding depth segregation was important in areas where the core foraging areas of the 2 species otherwise overlapped. While studying the foraging area and behavioral pattern of the neotropic cormorant in an area of coastal Patagonia where it lives in sympatry with imperial and rock cormorants, Quintana et al. (2004) suggested that the diving depths, feeding techniques, and diet could explain the apparent different behavioral patterns of the neotropic compared with the other species.

In our work, although we did not study the use of the water column directly, the prey type, carbon isotopes, foraging mode (flocks vs. solo), and the bathymetry of the main foraging areas provided useful information to help understand aspects of the use of the water column and the foraging habitat of each studied species. We inferred that rock cormorants foraged most likely near the benthos at shallow sites (<5 m), often in or near kelp forests. Neotropic cormorants fed on an array of prey of very variable mobility and ecology: benthos, kelp forest including its canopy, midwater, and surface, seemingly making a wide use of the whole water column with a strong preference for shallow areas (<5 m). The red-legged cormorant foraged near its colonies, most likely in midwater and near surface-pelagic or demersal-pelagic prey, mainly in waters of up to 15 m deep (see Frere et al. 2002). The imperial cormorant, known to be a very proficient diver (Quintana et al. 2007, 2011), used mainly areas of up to 15 m depth, and occasionally deeper, possibly using both the benthos and midwater column. Therefore, it is suggested that the differences in the use of the water column by these 4 species are likely among the most important dimensions explaining the observed trophic partitioning.

4.3. Pulses of pelagic resources: effect on guild structure?

In addition to the low energetic benthic and demersal-benthic resources found in the ria, offering a diverse and predictable pool of prey, the tidal currents allow for an abundant, although less predictable, higher energetic food source to enter the ria. This superabundance of resources (mainly small forage fish, squid, and lobster krill) can temporarily relax competition, and as a consequence, several of the cormorant species can be found foraging in mixed-species flocks (Nasca et al. 2004, this study). This phenomenon has been observed in other coastal areas of the world where several sympatric species of cormorants overlap their foraging areas while relying on superabundant pelagic resources (Humphries et al. 1992, Peck-Richardson et al. 2018). Due to the possible relaxation of competition while feeding in flocks on schools of abundant pelagic prey, the feeding areas of our 4 studied species were expected to overlap more when considering the entire data set (flocks + solo), compared with solo feeders only. Surprisingly, however, we found that the spatial overlap was lower when considering the whole data set, apparently because the flocks formed near each of the specific colonies/roosting sites. The consequence of this super-abundance was that the cormorants in feeding flocks (all species except rock cormorants) took advantage of the schools as they were passing alongside their colony/roosting site with the tidal current and consequently would have to travel a shorter distance to find food. This is further evidenced by the greater use of deeper areas by flocks, indicating more extensive use of the water column regardless of depth. Conversely, when feeding alone, imperial and red-legged cormorants used a higher proportion of shallower areas, suggesting a greater reliance on benthic resources. Also, interestingly, the spatial analysis of red-legged cormorants revealed foraging areas and mean distances to colonies that were similar considering either the whole data set or solo records, indicating that they always fed in close proximity to their colonies (Gandini et al. 2005, Frere et al. 2008). This is in accordance with their diet and with the fact that the red-legged cormorant was the only species to rely almost exclusively on pelagic or demersal-pelagic prey (sprat and squid). However, unlike what happens in some areas of the world with large cormorant populations, the presence of these 4 species in this inlet does not appear to result from the superabundance of a particular resource, despite occasional temporary pulses of abundant food.

4.4. Competitive exclusion as the structuring force?

The observed interspecific partition within our studied guild could be the result of an ecological segregation mechanism—a process that these species would have presumably developed to reduce the intensity of current or past interspecific competition, facilitating co-existence (Hutchinson 1957, Schoener 1974). The theory of competitive exclusion states that the niche of a species should be wider in the absence of potential competitors (fundamental niche) than it is when they are present (effective niche) (Hutchinson 1957). Therefore, when species are found in sympatry, the utilization of the resources by each species to maintain viable populations may be restricted to a more limited spectrum than in allopatry, when competition is relaxed. Niches are expected to be broader in allopatry. If the niche width is not greater in allopatry, this could indicate that interspecific competition is not the process that shapes the observed partitioning, and it could be the result of other past processes, such as preferences for microhabitats that species have developed allopatrically (speciation in allopatry; see, for example, Arlettaz et al. 1997, González-Solís et al. 2000).

A study of the feeding behavior of rock cormorants in sympatry with red-legged cormorants at Ría Deseado and in allopatry in another locality along the Patagonian coast found that rock cormorants in allopatry foraged closer and made shorter foraging trips than when in sympatry with red-legged cormorants (Frere et al. 2008). Furthermore, the diet of rock cormorants at this allopatric site included small pelagic fish (Punta et al. 2003), which were absent from their diet at Ría Deseado in sympatry (Morgenthaler et al. 2021, this study). This suggests that this species could adapt its feeding behavior and restrict its diet to certain prey in the presence of this potential competitor, most likely by avoiding interference competition. Moreover, the differences observed in the breeding schedule at neotropical sites with different specific assemblages within the guild (see Section 4.1.2) support the idea of an interspecific competition mechanism leading to temporal partitioning of the peak hatching period. In both cases, however, the effect of habitat differences between the different sites is impossible to disentangle from the hypothetical process, but these examples support the hypothesis of a mitigation of interspecific competition (competitive exclusion) as the structuring process leading to niche partitioning within the cormorant guild.

It is important to highlight that niche segregation is stage-dependent, and the chick-rearing stage is often the stage of maximum segregation due to higher resource demand (see Fromant et al. 2022 and review by Petalas et al. 2024). Therefore, the pattern of segregation observed in this study during the breeding season may not be applicable during the rest of the year, when competition might relax.

5. CONCLUSIONS

This study offers evidence pointing towards a driving force leading to resource segregation within a seabird guild. Despite living and foraging in close proximity within a spatially delimited coastal inlet characterized by marked seasonality and temporarily superabundant food pulses, these 4 closely related coastal seabird species distinctly partitioned resource utilization, which they achieved by occupying different volumes within the multidimensional ecological niche. The specific differentiation or restriction to a combination of prey type and habitat, likely through differential use of the water column, along with breeding allochrony, probably sufficiently alleviates interspecific competition—the most likely driver structuring this cormorant guild within this restricted geographical area. Our multidimensional approach, combining diet, stable isotope, foraging area, and breeding calendar overlap analyses, provided a robust study framework to address trophic segregation, and would certainly have been less conclusive if fewer dimensions of the niche were considered. Although a certain degree of pairwise overlap was observed in some dimensions of the trophic niche, and between one pair of species more than the others, in general the 4 cormorant species exhibited an overall partition in the use of resources when considering the cumulative combination of the pairwise segregation found in each dimension.

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