



Year-round niche segregation of three sympatric *Hydrobates* storm-petrels from Baja California Peninsula, Mexico, Eastern Pacific

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ABSTRACT: Ecologically similar species partition their use of resources and habitats and thus coexist due to ecological segregation in space, time, or diet. In seabirds, this segregation may differ over the annual cycle or vary inter-annually. We evaluated niche segregation in 3 sympatric storm-petrel species (*Hydrobates melania*, *H. leucorhous*, and *H. microsoma*) from the San Benito Islands, Mexico, during 2012 and 2013. We used diet samples and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values obtained from egg membranes, blood, feathers, and prey. We used krill samples to delineate marine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes for the Baja California Peninsula. During the breeding season, storm-petrels segregated regarding diet composition, stable isotope values, and isotopic niches. *H. melania* consumed higher trophic-position prey from neritic waters, while *H. leucorhous* and *H. microsoma* foraged on lower-trophic position prey from oceanic waters. Isotopic niches among species did not overlap in 2013, whereas those of *H. microsoma* and *H. leucorhous* overlapped in 2012. The feeding strategies of *H. melania* varied among breeding phases, and adults consumed different prey items from different areas compared to those of their offspring. *H. microsoma* adults and their chicks consumed the same prey items but from different habitats. During the non-breeding period, niche segregation between species persisted, except for *H. microsoma* and *H. leucorhous* during the molt of primary (P1) and undertail cover feathers. These 3 sympatric species coexist through niche segregation based on prey items and foraging areas that vary seasonally and year-round, probably due to changes in oceanographic conditions and the distribution and availability of prey.

KEY WORDS: Ecological segregation · Seabird · Diet · Stable isotopes · Breeding phase · Marine isoscape · *Oceanodroma*

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1. INTRODUCTION

Niche theory postulates that species that compete for similar and limited resources may coexist due to different segregation mechanisms to reduce niche

overlap and thus occupy different ecological niches (Hutchinson 1957, Grant 1972, Pianka 2000). Closely related species avoid competition through resource partitioning and show differential prey selection and spatio-temporal foraging patterns (MacArthur &

Levins 1964, Roughgarden 1976). Generalist species, which may exploit a wide range of diet items and habitat types, may segregate in prey type (van de Pol et al. 2010). In contrast, specialist species that rely on a restricted range of resources and habitat might segregate in space (Patrick et al. 2014).

Sympatric seabirds reduce interspecific competition by segregating among foraging areas (Quillfeldt et al. 2013, Rayner et al. 2016) and depths (Navarro et al. 2013), selection of different prey items (Masello et al. 2010), selecting different sizes of the same prey (Croxall et al. 1997), and/or foraging at different times (Masello et al. 2010, Navarro et al. 2013). Ecological segregation is expected to be more evident during the breeding season when adults forage in restricted geographic zones near their nests (Navarro et al. 2013, 2015) and may be particularly apparent in morphologically and closely related species (Robertson et al. 2014). During the breeding season, segregation might vary intra- and inter-specifically along different breeding life phases. Pre-laying females, which can disperse widely, usually show broader niches than those of chick-rearing adults that are constrained to their nests (Ausems et al. 2020). In some species, adults feed their chicks and themselves with similar prey items from similar areas, which saves energy, because preying on predictable patches of prey decreases foraging time and secures food supply (Hedd & Montevecchi 2006, Adams et al. 2010, Hipfner et al. 2014, Ausems et al. 2020). In contrast, adults of other species forage for prey items of higher quality for their chicks compared to those that they themselves feed upon, which improves chick development (Cherel et al. 2014, Leal et al. 2017, Ausems et al. 2020). Niche segregation mechanisms also occur during the non-breeding period when individuals disperse over wide ranges and forage in different areas and at different trophic levels (Quillfeldt et al. 2013, 2015a, Navarro et al. 2015, Delord et al. 2016). During this period, segregation might still persist when resources are limited or patchily distributed (Navarro et al. 2015, Quillfeldt et al. 2015a). Resource partitioning along the annual cycle may present inter-annual variation in response to environmental variability or changes in food availability (Barger et al. 2016, Calado et al. 2018).

Conventional diet research that is complemented with stable isotope analysis and quantitative stable isotope metrics represents a solid methodological approach to quantify resource partitioning in seabirds. Stable carbon isotope ratios ($\delta^{13}\text{C}$) are used to infer the origin of diet resources (e.g. neritic vs. oceanic sources) or to track latitudinal movements between

breeding and non-breeding periods in regions with pronounced marine isoscape gradients (Cherel & Hobson 2007, Quillfeldt et al. 2010). Stable nitrogen isotope ratios ($\delta^{15}\text{N}$) can be used to identify relative trophic levels (Vanderklift & Ponsard 2003). Ellipse areas constructed from stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope data (Jackson et al. 2011, 2012) have been widely used to investigate niche segregation among seabird species because they can quantify the width and degree of overlap of isotopic niches (Quillfeldt et al. 2015a, Carvalho & Davoren 2020). Also, the contributions of the main prey items to the overall diet can be inferred from stable isotope mixing models (e.g. MixSIAR Stock) (Semmens 2016, Stock et al. 2018).

Blood and feathers are commonly sampled tissues in seabird studies because they integrate information from different periods during the annual cycle. Whole blood can provide information regarding recent (i.e. 10–16 d) feeding activity (Bearhop et al. 2002, Evans Ogden et al. 2004). For birds sampled during the breeding period, whole-blood analysis can reveal the composition of seabird diets during this period (Hobson & Clark 1992). On the other hand, feathers, which are metabolically inert, can be used as reliable indicators of the composition of seabird diets during the non-breeding season (Ainley et al. 1976). Typically, seabirds start molting their feathers after the breeding period ends, and thus isotopic values of feathers sampled in the breeding period contain information from the previous non-breeding period (Jaeger et al. 2010).

Storm-petrels are pelagic seabirds that occupy diverse and extensive areas in the Pacific and Atlantic Oceans during their annual breeding cycle (Brooke 2004, Spear & Ainley 2007). They can breed sympatrically in various locations (Brooke 2004) and migrate to temperate, tropical, and subtropical areas during the wintering period (Brooke 2004, Spear & Ainley 2007). Storm-petrels are excellent models to study niche segregation because this family comprises closely related and morphologically similar species that may compete for space and resources during breeding and non-breeding periods. Although tracking storm-petrels can be challenging for some of the smallest species, indirect methods, such as interspecific comparisons of temporal visitation patterns at colonies (e.g. Ainley et al. 1974, Adams 2016), as well as stable isotope analyses, may offer additional means of investigating niche segregation.

Leach's storm-petrel *Hydrobates leucorhous*, black storm-petrel *H. melania*, and least storm-petrel *H. microsoma*, commonly included in the genus *Oceano-*

droma, breed sympatrically on Mexican islands in the Eastern Pacific and seasonally migrate to subtropical and tropical waters (Brooke 2004, Spear & Ainley 2007). These storm-petrels consume a wide variety of prey items, including crustaceans, cephalopods, and fish larvae (Bedolla-Guzmán et al. 2017, Everett et al. 2020, Pollet et al. 2020). However, no quantitative estimation of the main prey items exists in this region for these species that could indicate if trophic segregation is present, although some information is available for *H. microsoma* (Bedolla-Guzmán et al. 2017). At-sea distribution studies have shown that these storm-petrels present an apparent segregation in foraging areas. Specifically, *H. melania* is mostly distributed over the continental slope and shelf waters (less than 360 km from the coast, Spear & Ainley 2007), while *H. leucorhous* is found further offshore (200–1600 km from the coast), and *H. microsoma* prefers the warm (~28°C) shelf waters (less than 320 km from the coast, Spear & Ainley 2007). Analysis of global location sensor (GLS) data has shown that *H. leucorhous* may travel greater distances over foraging ranges than previously thought (350–550 km, maximum 1600 km) during the breeding period (Pollet et al. 2014, Halpin et al. 2018, Hedd et al. 2018). In addition, GLS analysis has detected several ecologically critical non-breeding foraging grounds off central Mexico, Peru, and Ecuador (Halpin et al. 2018). Stable isotope analysis of *H. leucorhous* primary feathers has shown annual differences in carbon values, which suggests variation in the timing of migration and/or molt locations among years (Hedd & Montevecchi 2006), high $\delta^{15}\text{N}$ variability between molting periods, and a wide range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to a broad diet and/or latitudinal movements (Hedd & Montevecchi 2006, Halpin et al. 2018). However, year-round segregation among species, breeding stages, and age classes (adults vs. chicks), and how this may vary inter-annually, has not yet been evaluated.

The aim of the present study was to evaluate niche segregation in 3 small (20–60 g) storm-petrel species (*H. melania*, *H. leucorhous*, and *H. microsoma*) breeding in sympatry in the Eastern Pacific during 2 consecutive breeding seasons (2012 and 2013) using diet samples and isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). In particular, we investigated how this segregation varies over the entire annual cycle as well as inter-annually in relation to both age and breeding phase. We expected that: (1) isotopic niche segregation would be present among the species during the breeding season, (2) an overlap between *H. melania* and *H. microsoma* would occur during the non-breeding period

based on at-sea distributions, (3) inter-annual differences in isotopic niches would be present because environmental conditions in the region showed variation between 2012 (high coastal upwelling and productivity) and 2013 (normal upwelling-favorable conditions; Bjorkstedt et al. 2012, Wells et al. 2013, Leising et al. 2014), and (4) segregation would be evident between chicks and adults, and between different phases of storm-petrels during the breeding period.

2. MATERIALS AND METHODS

2.1. Study area and species

This study was carried out from August to November during 2012 and 2013 on San Benito Oeste Island (28° 18' 12" N, 115° 35' 24" W; 3889 km²). This island is part of an archipelago consisting of 3 small islands located 72 km off the Baja California Peninsula, Mexico, in the Eastern Pacific. The temperate and semi-arid archipelago is habitat for about 885 000 breeding pairs of storm-petrels (510 000 pairs of *Hydrobates leucorhous*; 240 000 pairs of *H. melania*; 135 000 pairs of *H. microsoma*; Wolf et al. 2006). San Benito Oeste Island is part of the large Baja California Pacific Islands Biosphere Reserve (DOF 2016). This reserve is located in an oceanographic transition zone that is highly productive year-round (Espinosa-Carreón et al. 2004). *H. leucorhous* is listed as Vulnerable, while *H. melania* and *H. microsoma* are listed as species of Least Concern by the International Union for Conservation of Nature (IUCN; www.iucnredlist.org).

H. melania (60 g) breeds in natural crevices or in burrows built by other species; *H. leucorhous* (50 g) excavates its own burrows or uses crevices among rocks; and *H. microsoma* (20 g), the smallest species of the family Hydrobatidae, commonly breeds in clefts and cavities found among or under rocks (Ainley 1984). All 3 species lay a single egg, have intense and extended biparental care, and return to feed the chick only at night (Brooke 2004). On San Benito Oeste Island, these 3 species present similar phenologies (Table S1 in the Supplement at www.int-res.com/articles/suppl/m664p207_supp.pdf). The laying period occurs approximately from mid-June to early August, while the hatching period takes place from mid-August to late September, and fledging ranges between mid-October and late November (Bedolla-Guzmán et al. 2017, Everett et al. 2020; Y. Bedolla-Guzmán unpubl. data; Table S1). Storm-

petrels leave San Benito Oeste Island during late October and late November (Bedolla-Guzmán et al. 2017; Y. Bedolla-Guzmán unpubl., see Table S1).

The 3 species are surface feeders that take individual organisms while hovering or resting briefly on the sea surface (Brooke 2004). *H. melania* has a diverse diet that consists of euphausiids, squid, caridean shrimp, gammarid amphipods, and lantern fish (Everett et al. 2020). *H. leucorhous* primarily consumes fish, euphausiids, and amphipods, although with considerable geographic and seasonal variability (Hedd & Montevecchi 2006, Pollet et al. 2020). *H. microsoma* preys mostly on fish larvae but also consumes euphausiids and squid (Bedolla-Guzmán et al. 2017).

2.2. Sample collection

Breeding adults of each species were captured with mist nets at night during the breeding period of each year. Breeding *H. melania* individuals were also captured in artificial nest boxes (Bedolla-Guzmán et al. 2016). Adults were banded with individually labeled steel rings at first capture, and no bird was sampled more than once. A total of 69 regurgitated food samples were collected from adults and chicks during 2012 (*H. melania* = 4 adults, 12 chicks; *H. leucorhous* = 19 adults, 1 chick; and *H. microsoma* = 2 adults) and 2013 (*H. melania* = 3 adults, 6 chicks; *H. leucorhous* = 14 adults; and *H. microsoma* = 5 adults, 3 chicks). All adult samples were collected at the mist net (47 samples), while chick samples were collected from the nests (22 samples). As pre-breeders may develop a brood patch (Ainley et al. 1990), we considered birds captured at the mist net after mid-August (peak of the hatching period) with bare, bare and vascularized, or re-feathering brood patches as probable breeders (Adams 2016). We collected regurgitates in 25 ml screw cap vials during bird handling and fixed the samples with 70% ethanol. The diet data for *H. microsoma* were obtained from Bedolla-Guzmán et al. (2017).

Blood samples (0.1–0.5 ml) were collected from adults during the chick-rearing phase by puncturing their brachial veins with needles and using heparinized capillary tubes to collect the samples, which were immediately transferred to labeled 0.5 ml vials and dried in a portable oven at 40°C. We also collected a small section from the inner vanes of the primary feathers P1 and P6 and 2 undertail covert feathers by gentle pulling. The primary feather molt of the 3 storm-petrel species takes place during the non-breeding period upon departing from the breeding

colony after the chick has fledged (Ainley et al. 1976, Pyle 2008; Table S1). These species molt primary feathers sequentially, from P1 to P10 (proximal to distal), beginning when the birds leave the breeding colonies, continuing during migration and in the wintering grounds, and completing this process before the start of the next breeding period (Ainley et al. 1976, Pyle 2008). The molt period of undertail coverts is unknown in these species.

To evaluate niche segregation between chicks and breeding adults, whole blood was also collected from *H. melania* chicks that were 6–7 wk old during 2012 and 2013, and from *H. microsoma* chicks that were 9–12 wk old in 2013. This analysis was not performed for *H. leucorhous* because we did not find any accessible nests. To assess resource partitioning during 3 phases of the breeding cycle of *H. melania* (i.e. pre-laying, incubation, and chick-rearing), egg membranes were also collected during both years to evaluate the pre-laying phase (Quillfeldt et al. 2009), and whole blood was collected from incubating adults in 2012.

2.3. Conventional diet analysis

Diet samples were examined in the laboratory using a Meiji Emz-5 stereomicroscope (Meiji Techno) at 40× magnification. Prey taxa were identified to the most precise taxonomic level possible using published identification keys and guides (Iverson & Pinkas 1971, Wolff 1984, Brinton 1996, Moser 1996). Several well-preserved euphausiids and fish larvae specimens from regurgitated samples were analyzed to measure the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of storm-petrel prey and to create Bayesian mixing models (see Section 2.6.3).

2.4. Marine isoscape

Adult euphausiid specimens that are representative of the Pacific zooplankton communities off the Baja California Peninsula and that were collected by IME-COCAL cruises (Mexican Research Program of the California Current) during 1997–2001 (summer and fall), 2005 (spring), 2010 (summer), and 2013–2014 (winter) were obtained from the Collection of Planktonic Invertebrates of the Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California (CICESE), Mexico. Samples were preserved with 4% formalin and sodium borate (Lavaniegos et al. 2015). Adult euphausiid specimens from the Gulf of California that were collected by the

CAPEGOLCA-UNAM (Small Pelagic Fish Schools in the Gulf of California) and GOLCA (Gulf of California) cruises during 2010 (summer), 2013 (summer and winter), and 2014 (winter), and stored in the Zooplankton Laboratory of the Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), Baja California Sur, Mexico, were also included. These specimens were also preserved in formalin. The isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of these specimens were measured to create geographical maps of the marine isoscape.

2.5. Stable isotope analysis

Dry whole blood, egg membranes, and feathers from adults and chicks as well as well-preserved euphausiids and fish larvae specimens taken from regurgitated samples, and euphausiids from zooplankton samples described in Section 2.4 were used for stable carbon and nitrogen isotope analysis. Only feather samples free of any obvious contamination were selected for isotopic analysis. Surface contaminants were not cleaned because cleaning agents may change feather isotope values (Paritte & Kelly 2009). Euphausiid samples from collections preserved in formalin and fish larvae and euphausiids from diet samples preserved in 70% ethanol were first oven-dried at 40°C until completely dry. Lipids were extracted from euphausiids and fish larvae using Soxhlet extraction with a methanol:chloroform (2:1) solvent following standard methods (Weiss et al. 2009, Masello et al. 2010). After extraction, the samples were dried under a fume hood for 12 h and ground to a homogeneous fine powder with a mortar and pestle (Weiss et al. 2009). Euphausiid sub-samples of 1 mg were acid-washed with HCl (3.8% w/w) to remove inorganic carbonates, and the remaining tissue was cleaned with deionized water. All euphausiid specimens were subsequently dried at 60°C for at least 24 h. The sub-samples were used to measure euphausiid isotopic values.

Stable isotope analyses of all samples (diet regurgitates, zooplankton specimens, egg membranes, blood, and feathers) were carried out at the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin, Germany, as previously described by Quillfeldt et al. (2010). Stable carbon and nitrogen analyses were carried out on 0.35 mg aliquots in tin cups. Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry using a Flash Elemental Analyzer (Thermo Finnigan) linked to a Delta V Advantage Isotope Ratio Mass Spectrometer (Thermo Finnigan).

Two laboratory standards were analyzed for every 10 unknown samples, allowing any instrument drift to be corrected over a typical 14 h run. Stable isotope ratios were expressed in δ notation as parts per thousand deviation (‰) from the international standards Vienna Pee Dee belemnite (carbon) and air (atmospheric nitrogen), according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where X is ^{15}N or ^{13}C and R is the corresponding $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratio. Based on internal standards ($N = 165$, tyrosin; Roth), the analytical precision (± 1 SD) was equal to $\pm 0.16\%$ for $\delta^{15}\text{N}$ and $\pm 0.29\%$ for $\delta^{13}\text{C}$ values.

2.6. Data analyses

Statistical analyses were carried out using Statistica 12 (Statsoft) and R 4.0.2 (R Core Team 2020) considering $\alpha = 0.05$ as the significance level. We tested normality using the Kolmogorov-Smirnov test and homoscedasticity using Levene's test.

2.6.1. Diet analysis

We grouped prey items in 4 groups to make the conventional analysis and Bayesian mixing models comparable: krill group I (*Euphausia eximia* and *Euphausia gibboides*), krill group II (*Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Thysanoessa spinifera*), fish larvae (*Vinciguerria lucetia*), and others (amphipods, copepods, squid, unidentified items). We calculated the volume percentage of each prey group in relation to the total volume of the diet samples and the frequency of occurrence (FO) as the percentage of samples with a certain prey group, for each storm-petrel species in each year. Samples from both years for each storm-petrel species were pooled as no significant differences were present between years ($p > 0.30$). We used Kruskal-Wallis and post hoc Steel-Dwass tests to compare prey between species. We used chi-squared tests to compare the FO of the different prey groups between storm-petrel species.

2.6.2. Stable isotope analysis

To compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from different tissues between species and from different phases of the breeding cycle of *H. melania* within the same year, we used ANOVA and post hoc Tukey's HSD

test or Kruskal-Wallis *H*-test and post hoc Steel-Dwass test. To compare *H. melania* and *H. microsoma* adults and chicks, we used a *t*-test or Mann-Whitney *U*-test. We only compared similar tissues in the inter-specific analysis, i.e. blood and feathers were not compared. When comparing different tissues, tissue-dependent metabolic routing has to be taken into account. Blood is generally less enriched with the heavier isotopes of both carbon and nitrogen compared to that of feathers, while the discrimination factors for feathers and egg membranes are in the same range (Quillfeldt et al. 2008 and references therein). To compare blood and egg membranes, we corrected the stable isotope data of egg membranes by subtracting the correction factors of 2‰ from the $\delta^{13}\text{C}$ values and 1‰ from the $\delta^{15}\text{N}$ values to account for different diet–tissue fractionation. This was based on the difference between the discrimination rates for blood (Bearhop et al. 2002: $\Delta^{13}\text{C}_{\text{diet}} - \text{red blood cells} = 1\text{‰}$, $\Delta^{15}\text{N}_{\text{diet}} - \text{red blood cells} = 3\text{‰}$) and egg membranes (Hobson 1995: $\Delta^{13}\text{C}_{\text{diet}} - \text{egg membrane} = 3\text{‰}$ and $\Delta^{15}\text{N}_{\text{diet}} - \text{egg membrane} = 4\text{‰}$).

2.6.3. Bayesian mixing models

The proportions of the main prey sources in the diet of each storm-petrel species and their chicks as well as in different phases of the breeding cycle of *H. melania* were estimated using the Bayesian stable isotope mixing model MixSIAR (Stock & Semmens 2016, Stock et al. 2018) that allowed the inclusion of fixed factors (i.e. species, year, and age class). We grouped prey together for MixSIAR analyses because the number of potential prey species was high. We included 3 ecologically different prey groups as sources in the mixing model: krill group I (*Euphausia* spp.; $\delta^{15}\text{N}$: 10.4 ± 1.5 , $\delta^{13}\text{C}$: -20.4 ± 0.6 , $n = 25$), krill group II (*N. simplex*, *N. difficilis* and *T. spinifera*; $\delta^{15}\text{N}$: 13.6 ± 0.7 , $\delta^{13}\text{C}$: -19.1 ± 1.3 , $n = 36$), and fish larvae ($\delta^{15}\text{N}$: 13.9 ± 1.0 , $\delta^{13}\text{C}$: -21.0 ± 0.4 , $n = 6$; Fig. S1).

Although stable isotope mixing models account for variability and inherent uncertainty (Phillips et al. 2014), they require accurate discrimination factors specific for species and tissues given that the models are highly sensitive to the input values, which may result in significantly different prey proportions depending on the values used (Bond & Diamond 2011). To date, no diet–blood discrimination factors are available for any storm-petrel species or any procellariiform species. We used values of $\delta^{13}\text{C} = 1.2\text{‰}$ and $\delta^{15}\text{N} = 3.0\text{‰}$ based on the means of the discrimination factors that have been reported for rhinoceros

auklets *Cerorhinca monocerata* ($\delta^{15}\text{N} = 3.49\text{‰}$; Sears et al. 2009) and common murre *Uria aalge* ($\delta^{13}\text{C} = 1.09\text{‰}$, 1.2‰ ; $\delta^{15}\text{N} = 2.91\text{‰}$, 2.6‰ ; Sorensen et al. 2009, Jenkins et al. 2020) raised in captivity. Common murre feed mostly on fish during summer, but prey on small cephalopods and euphausiids during winter and early spring (Ainley et al. 2020). Similarly, rhinoceros auklets also feed on cephalopods, and euphausiids are a major component in the northwestern Pacific (Gaston & Dechesne 2020). Moreover, these species occupy trophic positions similar to those of storm-petrels (Hobson et al. 1994, Sydeman et al. 1997). The standard deviation was fixed at 1.0 to account for differences among species.

Prior to the mixing model analysis, we evaluated the appropriateness of the prey sources and discrimination factors using a simulated mixing polygon (Smith et al. 2013). The results of this analysis showed that all storm-petrel isotopic values fell within a polygon formed by the isotopic values of the prey, except for 3 to 5 values. These values were deleted, as recommended by Smith et al. (2013; Figs. S2 & S3). In the mixing models, we used uninformative priors, and the Markov chain Monte Carlo parameters were set as follows: chain length = 1 000 000, burn-in = 500 000, thin = 500, and number of chains = 3. For the breeding phases of *H. melania*, the parameters were set as follows: chain length = 3 000 000, burn-in = 1 500 000, thin = 500, and number of chains = 3. Model convergence was evaluated using the Gelman-Rubin and Geweke diagnostic tests (Stock & Semmens 2016). We first ran a model considering both species and year as fixed factors. As the proportion of prey items in each species did not vary between breeding seasons (Table S2), we pooled data and ran a second model including species as the only fixed factor. The same was done to compare *H. melania* chicks and adults and the different phases of the *H. melania* breeding cycle because the proportion of prey items did not differ between years (Table S3).

2.6.4. Isotopic niches

We compared the niche overlap and niche width among storm-petrel species during the entire annual cycle, between adults and chicks, and among different breeding phases using the 'Stable Isotope Bayesian Ellipses (SIBER)' package in R (Jackson et al. 2011, 2012). We used the 95 % ellipse area, which includes nearly all values (95 %) and more accurately represents the total isotopic niche compared to that

of the standard ellipse, which only reflects 40% of the values (Jackson et al. 2011). Niche overlap, which indicates the overlap in foraging areas, diet, or both, was calculated as the overlap percentage among 95% ellipse areas. An overlap $\geq 50\%$ was considered to be high (Carvalho & Davoren 2020). We calculated the Bayesian estimate of the 95% standard ellipse area (SEA_B) as a measure of isotopic niche width (Jackson et al. 2011). Ellipse areas were compared by calculating the probability that one ellipse area was smaller or larger than another.

2.6.5. Marine isoscape

We analyzed $\delta^{13}C$ and $\delta^{15}N$ spatial patterns of euphausiid species obtained from the California Current and Gulf of California (IMECOCAL, CAPEGOLCA, and GOLCA oceanographic cruises) only during the summer season because $\delta^{13}C$ values may vary tempo-

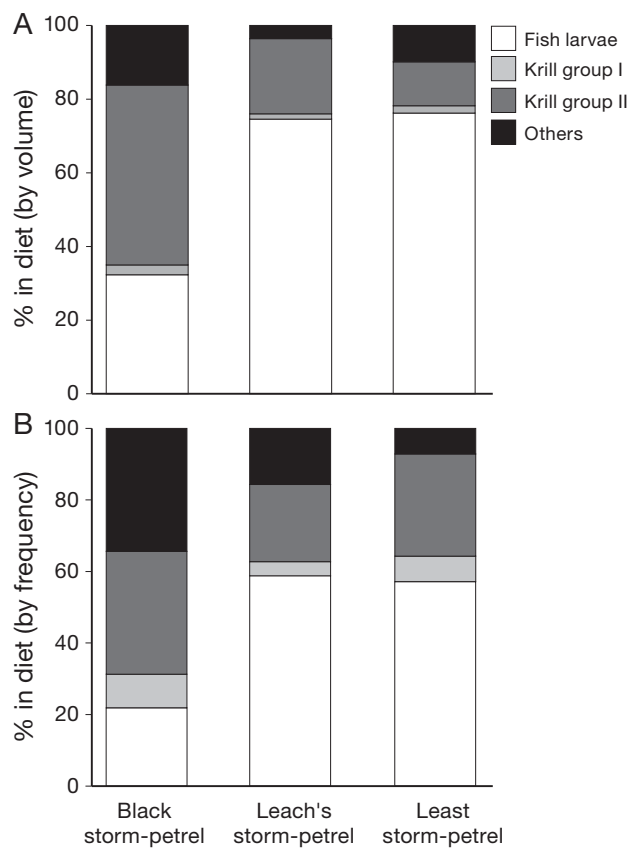


Fig. 1. Diet composition of black storm-petrels *Hydrobates melania*, Leach's storm-petrels *H. leucorhous*, and least storm-petrels *H. microsoma* on San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons. Percentage of diet by (A) volume and (B) frequency of occurrence. 'Others' includes copepods, amphipods, squid, and unidentified items

rally (Quillfeldt et al. 2015b). We applied a correction factor of 2‰ to $\delta^{13}C$ values prior to analysis because formalin may affect isotope values in marine zooplankton (Sarakinis et al. 2002, Bicknell et al. 2011) and lowered the $\delta^{13}C$ values by about 1–3‰ (Mullin et al. 1984, Bicknell et al. 2011). We corrected $\delta^{13}C$ values using the Kline (1999) equation because $\delta^{13}C$ values are enriched by trophic level (Rau et al. 1983):

$$\delta^{13}C_{TL} = \delta^{13}C - \epsilon_C / \epsilon_N (\delta^{15}N_{sample} - \delta^{15}N_{reference}) \quad (2)$$

where $\delta^{13}C_{TL}$ is the $\delta^{13}C$ value normalized by trophic level based on the $\delta^{15}N$ value of the sample relative to a reference $\delta^{15}N$ value, ϵ_C is the carbon fractionation (1.0), and ϵ_N is the nitrogen fractionation (3.4). The average $\delta^{15}N$ value of *E. gibboides* (10.3‰) was used to represent Baja California Pacific, while the average $\delta^{15}N$ value of *E. eximia* (14.7‰) was used to represent Gulf of California values because these species had the lowest $\delta^{15}N$ isotopic values in each respective region. Color-shaded contour maps were produced to display isotope values in Ocean Data View v. 5.0.0 (Schlitzer 2018; <https://odv.awi.de>) using Data Interpolation Variational Analysis (DIVA) gridding software (Barth et al. 2010). In stations where different zooplankton taxa were collected, $\delta^{13}C$ and $\delta^{15}N$ mean values were calculated.

3. RESULTS

3.1. Diet analysis and Bayesian mixing models

The range of prey items found in the regurgitated food samples of the 3 storm-petrel species included 10 crustacean species, 2 fish species, and 1 squid species (Table S4). The FO of the different prey groups (krill group I, krill group II, and fish larvae) varied among species ($\chi^2 = 29.3$, $df = 4$, $p < 0.001$, Fig. 1). *Hydrobates leucorhous* consumed significantly more fish larvae than *H. melania* ($H_{2,70} = 23.8$, $p < 0.001$; Fig. 1).

Bayesian mixing models showed that during the breeding period, the 3 storm-petrel species preyed on fish larvae in similar proportions (about 0.5) but differed in the proportion of krill consumed (Fig. 2). *H. melania* consumed a higher proportion of krill group II (0.44), whereas *H. leucorhous* mainly preyed upon krill group I (0.40), and *H. microsoma* consumed krill groups I and II in the same proportion (around 0.20; Fig. 2). Blood samples from adults and chicks indicated that while *H. melania* adults utilized fish larvae and krill in similar proportions to feed themselves, their chicks were raised primarily with

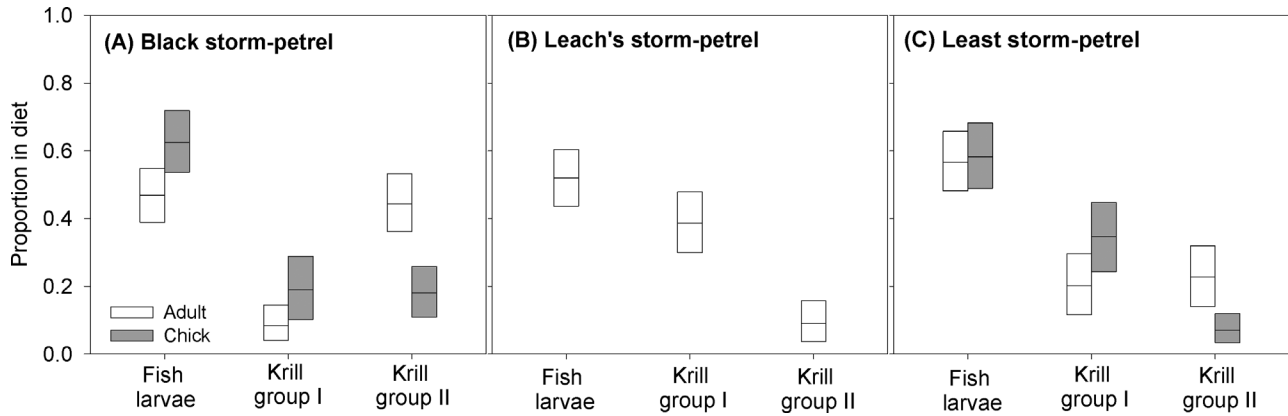


Fig. 2. Proportions of the main prey items in the diet of (A) black storm-petrel *Hydrobates melania*, (B) Leach's storm-petrel *H. leucorhous*, and (C) least storm-petrel *H. microsoma* adults and chicks according to the MixSIAR stable isotope mixing model (median values and 5th to 95th percentiles) with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the blood samples collected at San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons

fish larvae. In contrast, *H. microsoma* adults consumed similar proportions of fish larvae and krill to feed both themselves and their chicks (Fig. 2). The diet of *H. melania* differed among breeding phases. During egg formation, egg membrane values indicated that females mainly consumed krill, while a high proportion of fish larvae was consumed by incubating birds. During chick-rearing, adults preyed on fish larvae and krill group II in similar proportions (Fig. 3).

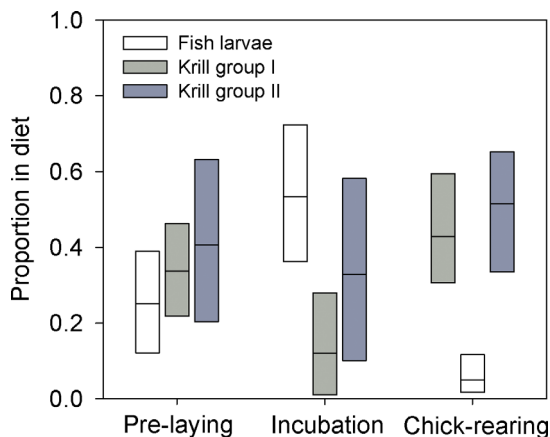


Fig. 3. Proportions of the main prey items in the diets of black storm-petrels *Hydrobates melania* during 3 breeding phases (pre-laying, incubation, chick-rearing) according to the MixSIAR stable isotope mixing model (median values and 5th to 95th percentiles) with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from egg membranes and blood collected at San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons. Egg membrane samples values were corrected by subtracting 2‰ from the $\delta^{13}\text{C}$ values and 1‰ from the $\delta^{15}\text{N}$ values, to ensure the data were comparable with the blood values

3.2. Stable isotope values and isotopic niche

3.2.1. Breeding season

Stable isotope analyses showed differences among the 3 storm-petrel species during the breeding season. Blood isotope values revealed that *H. melania* had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the other 2 storm-petrel species in both years (Table 1). *H. leucorhous* and *H. microsoma* $\delta^{13}\text{C}$ values did not vary between years, although the $\delta^{15}\text{N}$ values were higher in both years for *H. microsoma* (Table 1). The SIBER analysis showed that the isotopic niche overlap between *H. melania* and the other 2 species was low, whereas *H. microsoma* and *H. leucorhous* largely overlapped in 2012 but not in 2013 (Fig. 4; Table S5). The isotopic niche width did not differ among species in 2012, although *H. leucorhous* had the smallest niche breadth in 2013 (Fig. 4; Table S6).

For both years, *H. melania* adults had higher blood $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values than their chicks (Table 2, Fig. 5). The adult and chick isotopic ellipses overlapped in 2012 but not in 2013, and the isotopic niche width was similar between both years (Fig. 5; Tables S7 & S8). *H. microsoma* adults had higher $\delta^{13}\text{C}$ values compared to chicks, while no differences were present among $\delta^{15}\text{N}$ values (Table 2). Similarly, ellipse overlap represented only 30% of the adult niche area but 90% of the chick niche area. Adults and chicks had similar isotopic niche width (Fig. 5; Tables S7 & S8).

H. melania $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from blood and egg membrane samples varied among the pre-laying, incubation, and chick-rearing phases measured during the 2012 breeding cycle (Table 3, Fig. 6). Egg

Table 1. Statistical analyses comparing mean \pm SD $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) isotopic values of whole blood and feathers (primary feathers; P1 and P6, undertail covert feathers; UT) of black storm-petrels *Hydrobates melania* (BLSP), Leach's storm-petrels *H. leucorhous* (LESP), and least storm-petrels *H. microsoma* (LSTP) sampled on San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons (n values are given as BLSP/LESP/LSTP). Adult P1 feathers reflect dietary inputs from the previous year of sampling. Significant values are shown in **bold**; results of Kruskal-Wallis H -tests or ANOVA F -tests are given in parentheses. For each isotope, different superscript letters between columns indicate significant differences between species

Tissue	Year (n)	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)			p	
		BLSP	LESP	LSTP	BLSP	LESP	LSTP		
Blood	2012 (17/21/19)	-18.85 ^a \pm 0.5	-19.70 ^b \pm 0.4	-19.48 ^b \pm 0.4	<0.001 (H_2 = 21.9)	17.80 ^a \pm 0.4	16.57 ^b \pm 0.4	16.85 ^c \pm 0.3	<0.001 (F_2 = 59.0)
	2013 (20/18/17)	-18.60 ^a \pm 0.3	-19.51 ^b \pm 0.2	-19.28 ^b \pm 0.4	<0.001 (H_2 = 36.9)	17.80 ^a \pm 0.5	16.17 ^b \pm 0.4	16.87 ^c \pm 0.3	<0.001 (F_2 = 72.8)
P1	2012 (20/20/19)	-16.94 ^a \pm 0.7	-17.68 ^b \pm 0.5	-17.60 ^b \pm 0.7	0.001 (H_2 = 13.6)	16.14 ^a \pm 1.4	14.10 ^b \pm 1.8	14.26 ^b \pm 1.3	<0.001 (H_2 = 19.8)
	2013 (20/17/15)	-17.00 ^a \pm 0.6	-18.12 ^b \pm 0.7	-17.94 ^b \pm 0.7	<0.001 (H_2 = 22.3)	15.98 ^a \pm 1.7	15.95 ^a \pm 0.9	15.16 ^b \pm 1.5	0.004 (H_2 = 11.3)
P6	2012 (20/20/19)	-16.31 ^a \pm 0.5	-17.35 ^b \pm 0.4	-17.22 ^b \pm 0.7	<0.001 (H_2 = 27.0)	15.74 ^a \pm 1.0	13.67 ^b \pm 1.1	14.49 ^{a,b} \pm 1.7	<0.001 (H_2 = 19.1)
	2013 (20/16/16)	-16.52 ^a \pm 0.5	-17.55 ^b \pm 0.7	-17.54 ^b \pm 0.8	<0.001 (F_2 = 16.3)	15.43 \pm 0.8	15.23 \pm 0.4	15.49 \pm 1.8	0.42 (H_2 = 1.7)
UT	2012 (20/20/19)	-16.90 ^a \pm 0.5	-17.58 ^b \pm 0.3	-18.04 ^b \pm 0.7	<0.001 (H_2 = 27.9)	15.60 ^a \pm 1.2	13.86 ^b \pm 1.1	14.53 ^{a,b} \pm 2.5	0.009 (H_2 = 9.5)
	2013 (20/16/17)	-16.78 ^a \pm 0.6	-18.04 ^b \pm 0.6	-18.06 ^b \pm 0.5	<0.001 (F_2 = 28.4)	16.25 \pm 0.9	15.63 \pm 1.1	15.68 \pm 1.7	0.11 (H_2 = 4.5)

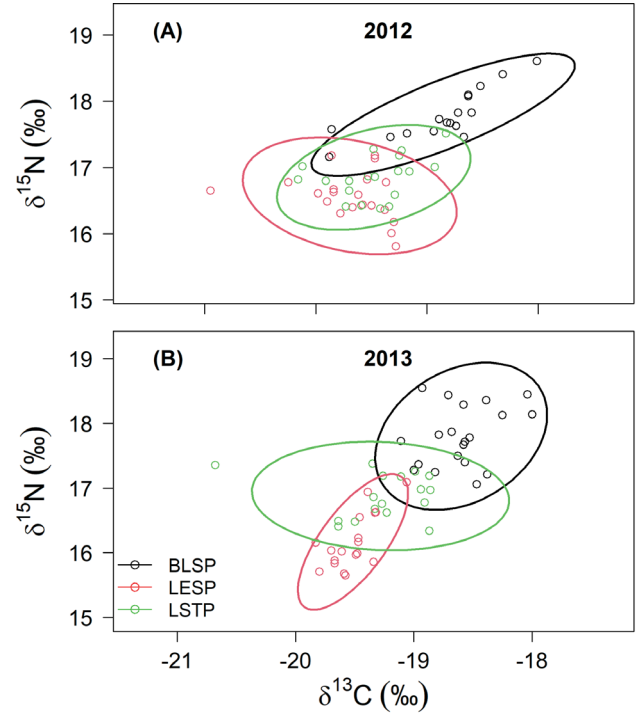


Fig. 4. Sample 95% ellipses calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the blood samples taken from black storm-petrels *Hydrobates melania* (BLSP), Leach's storm-petrels *H. leucorhous* (LESP), and least storm-petrels *H. microsoma* (LSTP) sampled at San Benito Oeste Island, Mexico, during the breeding seasons of (A) 2012 and (B) 2013

membrane samples (pre-laying phase) and blood samples from the chick-rearing phase had the highest $\delta^{13}\text{C}$ values. In addition, $\delta^{15}\text{N}$ values were lower during the pre-laying phase than during the incubation and chick-rearing phases (no differences were present between the latter 2 phases) (Table 3). Furthermore, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were higher during the 2013 chick-rearing phase than during the pre-laying phase (Table 3). The SIBER analysis showed that the isotopic niche of females during the pre-laying phase did not overlap with that of either incubating or chick-rearing adults. In contrast, incubating and chick-rearing adults overlapped between 40 and 60% (Fig. 6, Table S7). Adults showed the broadest isotopic niche width during the pre-laying phase of 2013 (Fig. 6, Table S8).

3.2.2. Non-breeding season

The adults of all 3 species also had different feather isotope values, with higher $\delta^{13}\text{C}$ values in *H. melania* compared to those of the other 2 storm-petrel species for all feathers (P1, P6, undertail covers; Table 1). In

Table 2. Statistical analyses comparing mean \pm SD $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) isotopic values of whole blood samples from black storm-petrel *Hydrobates melania* (BLSP) and least storm-petrel *H. microsoma* (LSTP) adults and chicks sampled on San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons (n values are given as adults/chicks). Significant values are shown in **bold**; results of *t*-tests and Mann-Whitney *U*-tests are given in parentheses

Species	Year (n)	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		Adults	Chicks	p	Adults	Chicks	p
BLSP	2012 (17/20)	-18.85 ± 0.5	-19.59 ± 0.4	<0.001 ($t_{35} = 4.9$)	17.80 ± 0.4	17.35 ± 0.4	0.002 ($t_{35} = 3.3$)
	2013 (20/20)	-18.60 ± 0.3	-19.34 ± 0.2	<0.001 ($t_{38} = 8.8$)	17.80 ± 0.5	17.04 ± 0.5	<0.001 ($t_{38} = 5.3$)
LSTP	2013 (17/20)	-19.28 ± 0.4	-19.84 ± 0.2	<0.001 ($U = 22.0$)	16.87 ± 0.3	16.75 ± 0.3	0.244 ($t_{35} = 1.2$)

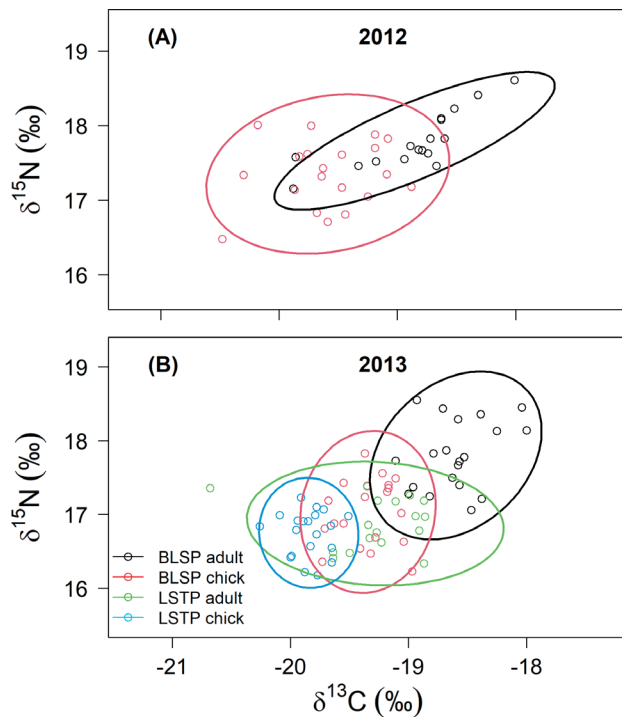


Fig. 5. Sample 95% ellipses calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blood samples collected from black storm-petrel *Hydrobates melania* (BLSP) and least storm-petrel *H. microsoma* (LSTP) adults and chicks sampled at San Benito Oeste Island, Mexico, during the breeding seasons of (A) 2012 and (B) 2013

contrast, $\delta^{15}\text{N}$ values greatly varied between species, feathers, and years. *H. melania* showed the highest $\delta^{15}\text{N}$ values in P1 feathers during 2012, while *H. leucorhous* presented lower values than *H. melania* for P6 feathers and undertail covers in 2012. In 2013, $\delta^{15}\text{N}$ values of all 3 species did not differ among P6 feathers and undertail covers. *H. microsoma* and *H. leucorhous* largely overlapped with regard to their P1 feathers ellipses in both years and undertail covers ellipses during 2013. In both years, the niche overlap between *H. melania* and *H. microsoma* based on P6 feathers and undertail covers repre-

sented >80% of the *H. melania* niche area. During 2013, *H. melania* and *H. microsoma* did not overlap with regard to their undertail covers (Fig. 7; Table S5). *H. microsoma* had a significantly larger isotopic niche width based on its P6 feather ellipses in both years compared to those of the other 2 storm-petrel species. During 2012, *H. microsoma* also had a broader isotopic niche width based on its undertail covers ellipses compared to those of the other 2 storm-petrel species (Fig. 7; Table S6).

3.3. Marine isoscape

Isotope $\delta^{13}\text{C}$ values of all euphausiid species combined and normalized by trophic level from the Pacific coast of the Baja California Peninsula (31.5° – 24.4° N, $n = 34$) ranged from -18.50 ‰ near the coast of the middle portion of the peninsula (28° N) to -22.5 ‰ north of Guadalupe Island (30° N, Fig. 8A; Table S9). Euphausiid $\delta^{15}\text{N}$ values varied, although no pattern was observed. The highest $\delta^{15}\text{N}$ euphausiid value (14.8 ‰) was recorded in the southernmost sampling location near the coast, and the lowest $\delta^{15}\text{N}$ value (7.3 ‰) was associated with the middle portion of the peninsula in an offshore location (Fig. 8C; Table S9).

In the Gulf of California (29.6° – 23.8° N, $n = 44$), the highest $\delta^{13}\text{C}$ values (-17.1 ‰) were recorded in the northernmost area near the coast, while the lowest values (-20.1 ‰) were present at the mouth of the gulf (Fig. 8A; Table S9). The $\delta^{15}\text{N}$ values varied around 18.1 ‰, and the lowest values (13 – 14 ‰) were recorded at the mouth of the Gulf of California (Fig. 8C; Table S9). The $\delta^{15}\text{N}$ values in the Gulf of California were considerably higher than those along the west coast of the Baja California Peninsula.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of storm-petrels corrected by trophic level suggested an apparent difference in foraging areas between species. Isotopic ranges of *H. melania* ($\delta^{13}\text{C}$: -20.3 to -22.0 ‰; $\delta^{15}\text{N}$: 15.2 to 13.7 ‰) showed this species probably used waters in the Pa-

Table 3. Statistical analyses comparing mean \pm SD $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) isotopic values of egg membranes and whole blood representing 3 breeding stages (pre-laying, incubation, and chick-rearing; n values are given in this order) of black storm-petrels *Hydrobates melania* sampled on San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons. Significant values are shown in **bold**; results of Kruskal-Wallis H -tests, ANOVA F -tests, and Mann-Whitney U -tests are given in parentheses. For each isotope, different superscript letters between columns indicate significant differences between species. (-): not sampled that year

Year (n)	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Pre-laying	Incubation	Chick-rearing	p	Pre-laying	Incubation	Chick-rearing	p
2012 (21/15/17)	-18.82 ^a \pm 0.4	-19.26 ^b \pm 0.4	-18.85 ^a \pm 0.5	0.009 ($F_2 = 5.2$)	16.17 ^a \pm 0.5	17.59 ^b \pm 0.2	17.80 ^b \pm 0.4	<0.001 ($H_2 = 37.6$)
2013 (18/20)	-19.18 \pm 0.8	-	-18.60 \pm 0.3	0.010 ($U = 95.0$)	16.52 \pm 1.1	-	17.80 \pm 0.5	<0.001 ($U = 65.0$)

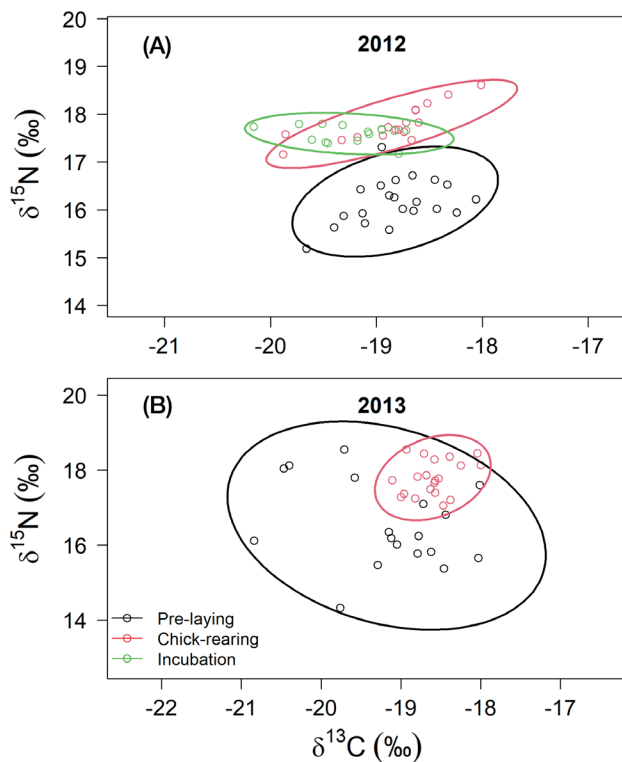


Fig. 6. Sample 95% ellipses calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from blood and egg membrane samples collected from black storm-petrels *Hydrobates melania* during the different phases of the breeding period (egg membrane: pre-laying; whole blood: incubation and chick-rearing) sampled at San Benito Oeste Island, Mexico, during the breeding seasons of (A) 2012 and (B) 2013. Egg membranes samples values were corrected by subtracting 2‰ from the $\delta^{13}\text{C}$ and 1‰ from the $\delta^{15}\text{N}$ values, to ensure the data were comparable with blood values

cific coast from the middle to the southern part of the Baja California Peninsula (Fig. 8). On the other hand, $\delta^{13}\text{C}$ ranges of *H. leucorhous* (-20.9 to -22.8‰) and *H. microsoma* (-20.6 to -22.8‰) suggested that these 2 species foraged in areas to the north and south of

San Benito Islands, while their $\delta^{15}\text{N}$ ranges (*H. leucorhous*: 13.8 to 12.3‰; *H. microsoma*: 14.1 to 12.9‰) showed that these species could exploit areas all along the peninsula (Fig. 8).

4. DISCUSSION

4.1. Niche segregation during the breeding season

Ecologically similar species are expected to partition their use of resources and habitats to coexist sympatrically as a result of ecological segregation in space, time, or diet (Hutchinson 1957, Grant 1972, Pianka 2000). In seabirds, this resource partitioning may be more intense during the chick-rearing period given the high energy demands of nestlings (Barger et al. 2016) and the range limitations imposed by central-place foraging. In agreement with this, we found that the 3 storm-petrel species in this study (*Hydrobates melania*, *H. leucorhous*, and *H. microsoma*) differed in diet composition, isotope values, and isotopic niches during the chick-rearing period. However, isotopic niche overlap and niche width varied between years. Niche segregation among these 3 sympatric species was reflected in a higher $\delta^{13}\text{C}$ values and a higher trophic position (similar consumption of fish larvae and krill group II) by *H. melania* compared to that of both *H. leucorhous* and *H. microsoma*, which indicates that *H. melania* probably foraged in neritic waters associated with higher productivity as shown by Ballance et al. (1997). Despite both *H. leucorhous* and *H. microsoma* foraging in oceanic waters (lower $\delta^{13}\text{C}$ values) and preying primarily on fish larvae, *H. leucorhous* consumed lower trophic-position prey (krill group I). These results partially coincide with ship-based surveys and tracking studies in the Pacific that have revealed a higher density of *H. melania* over the continental

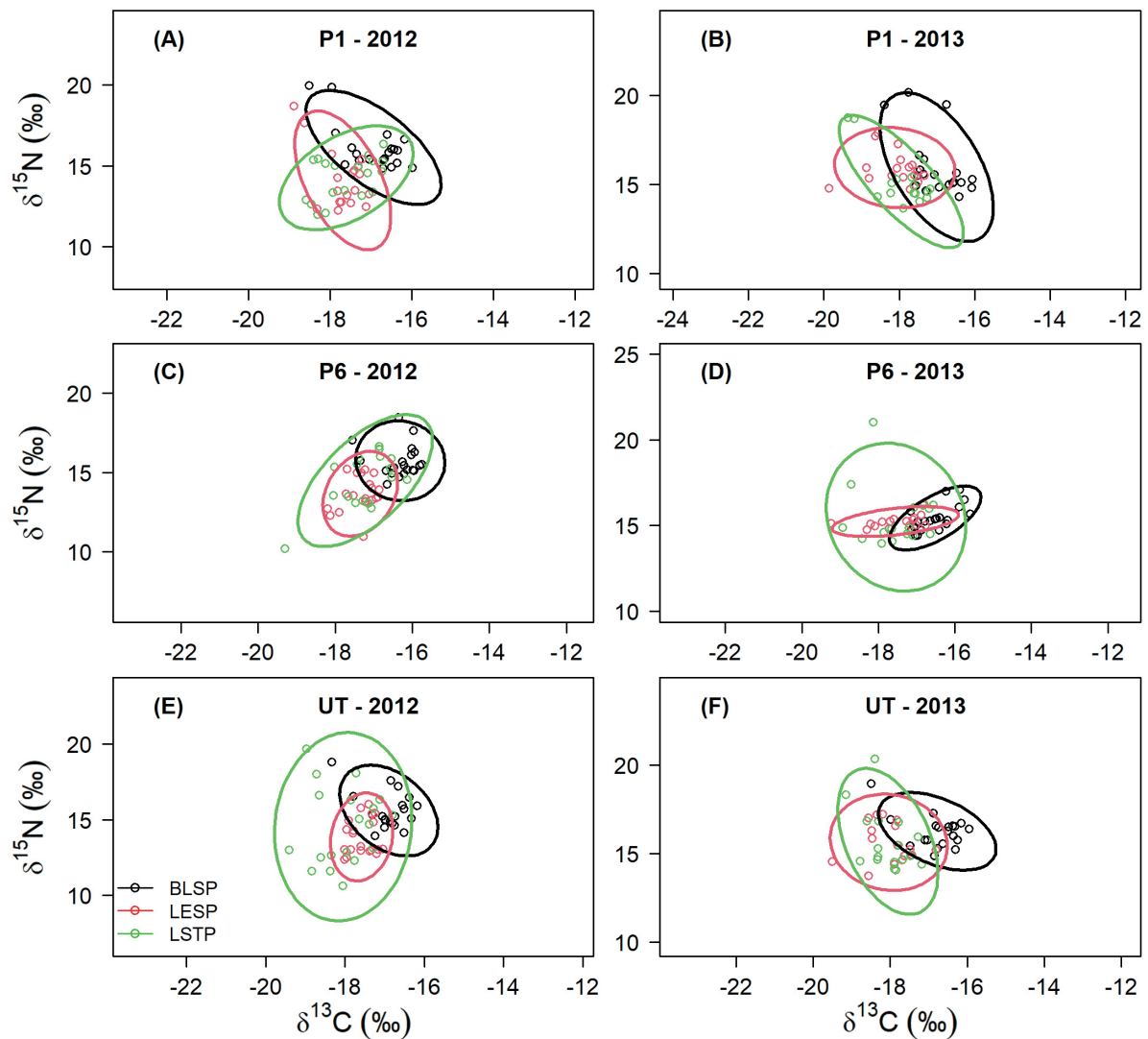


Fig. 7. Sample 95% ellipses calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from feather samples taken from black storm-petrels *Hydrobates melania* (BLSP), Leach's storm-petrels *H. leucorhous* (LESP), and least storm-petrels *H. microsoma* (LSTP) sampled at San Benito Oeste Island, Mexico, during the breeding seasons of 2012 and 2013. (A) and (B): P1 primary feathers; (C) and (D): P6 primary feathers; (E) and (F): undertail covert feathers (UT). P1 feathers reflect dietary inputs from the previous year of sampling

slope within 360 km from the coast (Spear & Ainley 2007) and a high density of *H. leucorhous* over the continental slope but further offshore (200–1600 km from the coast; Spear & Ainley 2007, Halpin et al. 2018). Conversely, at-sea surveys have indicated that *H. microsoma* prefers nearshore continental shelf waters (less than 330 km from the coast; Spear & Ainley 2007). The blood $\delta^{13}\text{C}$ values of the storm-petrels in this study (-18.0 to -21.0 ‰) presented a similar range to those of the Cassin's auklet *Ptychoramphus aleuticus* (mean = -19.9 ‰ \pm 0.4, range = -18.6 to -21.0 ‰) blood samples collected in 2016–2017 from San Benito Oeste Island (Y. Bedolla-Guzmán unpubl. data). *P. aleuticus* foraged close to the limit of the

continental shelf according to GPS data (Y. Bedolla-Guzmán unpubl. data).

Other quantitative diet studies in the Pacific have also shown that fish larvae are the most important prey group for both *H. leucorhous* (Watanuki 1985, Vermeer & Devito 1988) and *H. microsoma* (Bedolla-Guzmán et al. 2017). No previous quantitative studies exist for *H. melania*. Conventional diet analysis agreed with the results of the Bayesian mixing models for *H. microsoma*, which estimated that chicks were raised mainly with fish larvae. However, the *H. melania* diet samples showed that a higher proportion of krill group II was delivered to the chicks compared to the proportion predicted by the mixing

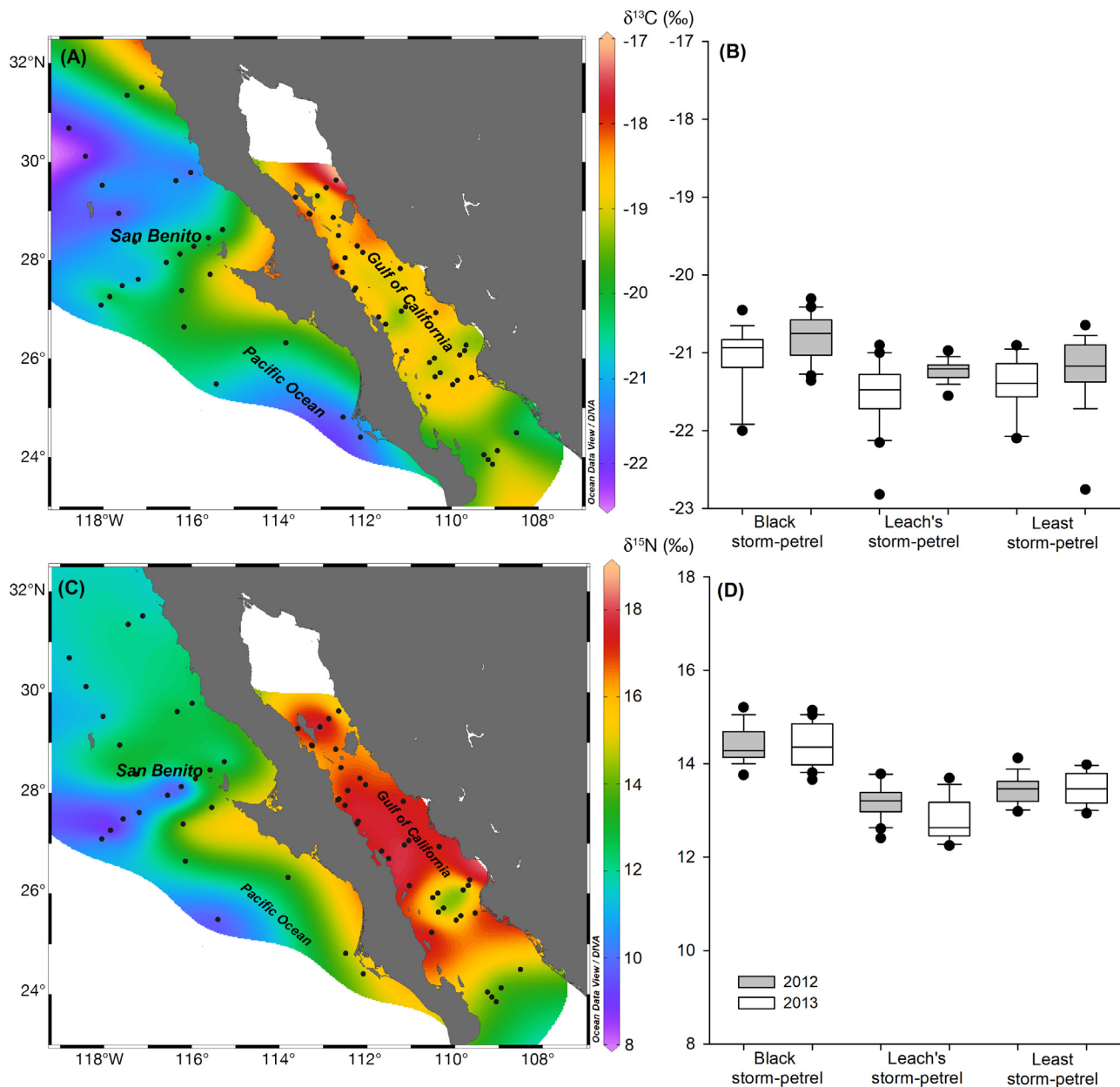


Fig. 8. Marine isoscapes of (A) $\delta^{13}\text{C}$ values and (C) $\delta^{15}\text{N}$ values of all euphausiid species combined from the Pacific coast of the Baja California Peninsula and the Gulf of California. Sampling stations are shown as black dots. Data were collected by IME-COCAL (Mexican Research Program of the California Current), CAPEGOLCA-UNAM (Small Pelagic Fish Schools in the Gulf of California), and GOLCA (Gulf of California) cruises from summer 1997–2013. (B) $\delta^{13}\text{C}$ range values and (D) $\delta^{15}\text{N}$ range values of the storm-petrels (*Hydrobates melania*, *H. leucorhous*, *H. microsoma*) sampled at Islas San Benito, Mexico, during the 2012 and 2013 breeding seasons. Values were estimated using the DIVA gridding function (Barth et al. 2010) of Ocean Data View v. 5.0 (Schlitzer 2018). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of storm-petrels were corrected by trophic level. For each boxplot, lower hinge corresponds to the first quartile (25th percentile) and the upper hinge represents the third quartile (75th percentile), and the horizontal line within the boxplot indicates the median. The upper (lower) whisker extends to the largest (smallest) value no further than $1.5 \times$ interquartile range (IQR = the distance between the first and third quartiles). Black dots represent outliers

models, which predicted that the chicks were fed mostly with fish larvae. This discrepancy highlights the importance of combining both methods to ensure an accurate and integrated view of the ecological niches of these 3 storm-petrel species.

The results of the conventional diet analysis also indicated that differences in habitat preferences were present among these 3 species. *H. melania* more frequently consumed *Thysanoessa spinifera* compared to the other 2 storm-petrel species, indicating that *H.*

melania prefers nearshore waters, given that *T. spinifera* are distributed in areas of coastal upwelling (Lavaniegos et al. 2010, Lavaniegos & Ambriz-Arreola 2012). In contrast, a higher FO of *Nematoscelis difficilis*, the most abundant euphausiid species in oceanic regions off the Baja California Peninsula (Lavaniegos & Ambriz-Arreola 2012), was present in the diet of *H. leucorhous* compared to the other 2 species, which reflects the preference of *H. leucorhous* for oceanic waters. Coastal euphausiid species were also more frequently found in *H. microsoma* samples, which disagrees with the results of the stable isotopes, probably due to our low sample size. During 2012 and 2013, when high upwelling activity occurred (Wells et al. 2013, Leising et al. 2014), the availability of these cold-water euphausiid species might have increased. All species consumed similar proportions of fish larvae, possibly dominated by *Vinciguerria lucetia*, which is highly abundant and widely distributed along the Baja California Peninsula, and is principally found in oceanic waters during summer and autumn, i.e. the breeding season of storm-petrels (Funes-Rodríguez et al. 2011).

The stable isotope values and the SIBER analyses results also support habitat and trophic niche segregation among these 3 storm-petrel species but showed temporal variation. Isotopic niches (95% ellipses) of the 3 species did not overlap in 2013, while the ellipses of *H. leucorhous* and *H. microsoma* largely overlapped in 2012. Inter-annual variation in niche overlap could principally be due to the proportion of krill group I consumed by these 2 species in addition to their niche width. In 2012, *H. leucorhous* and *H. microsoma* showed a similar niche width, whereas in 2013, *H. leucorhous* presented the narrowest niche width of all 3 species. This implies that *H. leucorhous* specialized in a narrow range of prey items and foraging habitats during 2013. Temporal variability in seabird foraging areas and trophic positions has been associated with changes in both the distribution and availability of prey in response to different oceanographic conditions (Sydeman et al. 2001, Abraham & Sydeman 2006). Although 2012 and 2013 were cold years, more favorable conditions were present in 2012 due to higher upwelling intensity and primary production along the west coast of Baja California Peninsula compared to 2013 (Bjorkstedt et al. 2012, Wells et al. 2013). Owing to the limitations imposed by being central-place foragers, the storm-petrels were constrained to obtain what was available within their foraging range. In 2012, they were probably able to find a similar variety of prey items.

Other studies in closely related and sympatric petrel and storm-petrel species have shown that either complete niche segregation or high niche overlap may occur among species during the breeding season. Niche divergence might be the result of differences in diving behavior (Navarro et al. 2013), morphology (Navarro et al. 2013), foraging areas (Quillfeldt et al. 2013), or trophic position (Bond et al. 2010). On the other hand, niche overlapping has been observed in species with generalist diets (Dehnhard et al. 2020) or in habitats with low diversity of highly abundant prey (Hodum & Hobson 2000, Aulsems et al. 2020).

H. melania adults showed higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared to their chicks, and their isotopic niches did not overlap in either year. Parents preyed on krill and fish larvae in neritic waters for themselves but captured mostly fish larvae in oceanic waters for their chicks. This has also been observed in other seabird species, like petrels, in which adults select prey items with high energy values to satisfy the nutritional requirements of their chicks (Cherel et al. 2014, Leal et al. 2017, Aulsems et al. 2020). On the other hand, according to optimal foraging theory, adults should maximize food delivery to their chicks by minimizing travel distances between foraging sites and the breeding colony (MacArthur & Pianka 1966, Schoener 1971). As a result of these 2 contrasting demands, *H. microsoma* adults had different $\delta^{13}\text{C}$ but similar $\delta^{15}\text{N}$ values compared to their offspring, indicating that adults and their chicks consumed the same prey items (mainly fish larvae) but from different habitats. This feeding strategy has also been reported for *H. leucorhous* in other colonies (Hedd & Montevecchi 2006) and for Wilson's storm-petrels *Oceanites oceanicus* (Aulsems et al. 2020).

H. melania consumed prey from different habitats and trophic levels during the different phases of its breeding cycle. Adults of *H. melania* showed higher $\delta^{13}\text{C}$ values (from neritic waters) and lower $\delta^{15}\text{N}$ values (mainly due to krill) during the pre-laying phase and foraged primarily on fish larvae from oceanic waters during incubation. Females exhibited a very broad isotopic niche width in 2013, suggesting they exploited an extensive area and consumed a highly diverse diet, or both. This has also been reported in other storm-petrel species (Aulsems et al. 2020) and probably indicates that adults have different energy requirements depending on the breeding phase (Elliott et al. 2010), or it could reflect seasonal variability in prey abundance and species composition in the region (Lavaniegos et al. 2010, 2015).

4.2. Niche segregation during the non-breeding season

Niche segregation in these 3 storm-petrel species persisted during the non-breeding period but varied among feathers and between 2012 and 2013. The isotopic niche area overlap, considering shared niche space between species, was low during the P6 feather and undertail cover molt, except in 2013, in which the isotopic niche area of *H. leucorhous* and *H. microsoma* largely overlapped. Also, an extensive overlap occurred during the P1 feather molt between *H. leucorhous* and *H. microsoma* in both years. However, *H. microsoma* had a broader isotopic niche width during the P6 feather molt of both years and during the undertail cover feather molt of 2012. These results suggest that *H. leucorhous* and *H. microsoma* forage in areas with similar conditions but that *H. microsoma* exploits a wider range of habitats and food resources, as has been suggested for other seabird species that show a positive relationship between isotopic niche width and at-sea spatial distributions (Ceia et al. 2014). Our results are consistent with previous studies in sympatric petrel species showing that prey partitioning and habitat segregation during the non-breeding period are driven by environmental variables (Quillfeldt et al. 2013, Navarro et al. 2015, Rayner et al. 2016).

Feather $\delta^{13}\text{C}$ values showed high variability during the non-breeding period. Such $\delta^{13}\text{C}$ ranges were similar to the $\delta^{13}\text{C}$ values from the P10 feathers of *H. leucorhous* individuals that breed in western Canada, which may be reflective of large-scale latitudinal movements (Halpin et al. 2018). The 3 storm-petrel species in this study are highly migratory outside of their breeding grounds. *H. melania* is a regular visitor to the waters of the continental shelf and slope of the northern Peru Current System during winter (Spear & Ainley 2007), while *H. leucorhous* may spend the non-breeding season in the highly productive areas of the Eastern Tropical Pacific (Gulf of Tehuantepec in Mexico, and coasts of Ecuador and Peru; Spear & Ainley 2007, Halpin et al. 2018, Pollet et al. 2020). Furthermore, *H. microsoma* is distributed in the Costa Rica Current and Equatorial Eastern Pacific (Brooke 2004, Spear & Ainley 2007). These distributions change during the non-breeding period. At the end of the breeding period when the P1 feather molt begins in autumn, *H. leucorhous*, *H. microsoma*, and *H. melania* present their highest densities from southern Baja California to Ecuador, from southern Baja California to Costa Rica, and from the sub-tropical Mexican Pacific to southern

Peru, respectively (Spear & Ainley 2007). When P6 feather molt occurs in spring, *H. melania* and *H. leucorhous* have their highest densities off California and the Baja California Peninsula, whereas *H. microsoma* are more abundant from Costa Rica to the northern Panama Bight (Spear & Ainley 2007).

Storm-petrel carbon isotope values did not correspond to the values measured in copepods in the Tropical Eastern Pacific (26–6°N; Olson et al. 2010). Nevertheless, storm-petrel $\delta^{13}\text{C}$ values agreed with those measured in *Dosidicus gigas* and *Sthenoteuthis oualaniensis* from the Eastern Pacific region (10°N to 20°S; Ruiz-Cooley & Gerrodette 2012, Argüelles et al. 2012) and from the zooplankton of the northern Humboldt Current System (Espinoza et al. 2017). Moreover, recent models of phytoplankton $\delta^{13}\text{C}$ suggest that peak values (–18 to –16‰) occur in equatorial upwelling regions (Magozzi et al. 2017). As such, storm-petrels may grow their feathers in this region. The differences in feather $\delta^{15}\text{N}$ values (between 6 and 11‰) and in isotopic niche width between the species in this study were pronounced, as previously observed for *H. leucorhous* during the breeding periods on both Canadian coasts (Hedd & Montevecchi 2006, Halpin et al. 2018). Thus, storm-petrels may have exploited a broad variety of feeding resources or used very different foraging habitats, as effects of diet differences may be confounded with effects of geographic differences because $\delta^{15}\text{N}$ values vary at the base of the food web in the distinct ocean basins (Somes et al. 2010).

4.3. Conclusions

Our results show clear niche segregation among 3 sympatric and closely related storm-petrels during the breeding and non-breeding seasons, which agrees with the predictions of niche theory. These 3 species reduce competition through dietary and habitat segregation. However, our study demonstrated that temporal variation in niche segregation occurs and is probably associated with changes in ocean conditions that lead to differences in the distribution and availability of prey. The feeding strategies detected were age-dependent and varied among the phases of the storm-petrel breeding cycle. Although carbon stable isotopes are a useful indicator of foraging areas in other geographical areas in terms of latitude, a clear gradient was not evident in the study area probably due to the oceanographic complexity present in the region. Future bio-logging studies of these elusive pelagic seabirds are needed to identify

their foraging areas throughout the year and to understand the main threats that their populations are exposed to both at-sea and near their nesting areas.

We only were able to analyze 3 groups of prey (fish larvae, krill group I, and krill group II) using stable isotope analysis, as most diet samples were too digested to analyze other groups such as squid. Additional diet samples will be required to evaluate the contribution of other potential prey. We found inconsistencies between conventional diet sampling and stable isotope analysis. For instance, *H. microsoma* showed a high frequency of krill on diet samples but a low proportion on SIAR analysis. This could be the result of our small sample size of diet samples in this species.

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