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COMPARATIVE ECOLOGY OF SYMPATRIC STORM-PETRELS:

Breeding biology, niche segregation, and response to environmental changes

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Comparative ecology of sympatric storm-petrels: Breeding biology, niche segregation, and response to environmental changes

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CONTENTS

ABSTRACT

Seabirds, including storm-petrels, are integral to marine ecosystems, yet significant gaps persist in understanding their ecology. This PhD thesis examines the niche segregation, breeding biology, and responses to environmental variability of three sympatric storm-petrel species: Leach's storm-petrel (*Hydrobates leucorhous*), which is widely distributed across the Atlantic and Pacific Oceans, and the black storm-petrel (*Hydrobates melania*) and least storm-petrel (*Hydrobates microsoma*), both restricted to the Eastern Tropical Pacific. These species breed in sympatry on the San Benito Archipelago, Mexico, which supports a population of approximately two million individuals. The thesis aims to advance knowledge of their resource use, reproductive strategies, and adaptive responses to environmental changes, addressing critical gaps in their ecological understanding. The research is structured into three chapters, each exploring distinct ecological aspects. Chapter 1 evaluates niche segregation among the three storm-petrel species using stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from tissues such as blood, feathers, and egg membranes, along with diet samples collected in 2012–2013. A marine isoscape was constructed using krill samples from the Pacific waters off Baja California. The findings demonstrated significant dietary and isotopic niche segregation during the breeding season, with black storm-petrels consuming high-trophic-level krill from neritic waters, while Leach's and least storm-petrels fed on lower-trophic fish larvae in oceanic regions. Additionally, black storm-petrels exhibited shifts in foraging strategies across breeding phases, reflecting dietary flexibility. Chapter 2 focuses on the breeding biology of the least storm-petrel, investigating breeding phenology, reproductive success, chick growth, and diet over three breeding seasons (2013–2015). Eggs, chicks, and adults were monitored, and diet samples were collected to evaluate feeding ecology. Morphometric differences between sexes were analyzed using mist-net captures and molecular sexing in 2012. Results revealed consistently high breeding success, with inter-annual variations in timing of breeding and chick growth linked to anomalous climate conditions. Females exhibited longer wings and tails than males, while dietary analyses identified larval fish, euphausiids, and squid as key prey items. Chapter 3 investigates inter-annual variability in the breeding biology, chick growth, and provisioning behavior of the black storm-petrel over six consecutive breeding seasons (2012–2017). Parameters such as peak mass, fledging mass, feeding rate, and meal size showed significant inter-annual variation, although these trends were not explained by regional or local environmental indices. This suggests that other factors such fine-scale habitat or pre-breeding ocean conditions may play a more influential role in shaping these reproductive traits. In conclusion, this thesis provides valuable insights into the resource partitioning, breeding biology, and adaptive strategies of storm-petrels, highlighting the importance of niche segregation in facilitating coexistence and reducing interspecific competition. The results emphasize the need to account for environmental variability and anthropogenic pressures in conservation strategies. By contributing to a broader understanding of storm-petrel ecology, this work establishes a

foundation for enhancing conservation and management efforts for these and other seabird species in dynamic and rapidly changing marine ecosystems.

ZUSAMMENFASSUNG

Seevögel, darunter auch Sturmschwalben, sind ein wesentlicher Bestandteil der marinen Ökosysteme, doch gibt es noch immer erhebliche Lücken im Verständnis ihrer Ökologie. In dieser Dissertation werden die Nischentrennung, die Brutbiologie und die Reaktionen auf Umweltschwankungen von drei sympatrischen Sturmschwalbenarten untersucht: Wellenläufer (*Hydrobates leucorhous*), die im Atlantik und Pazifik weit verbreitet ist, sowie die Schwarzwellenläufer (*H. melania*) und die Zwerg-Sturmschwalbe (*H. microsoma*), die beide auf den östlichen tropischen Pazifik beschränkt sind. Diese Arten brüten in Sympathie auf dem San-Benito-Archipel in Mexiko, das eine Population von etwa zwei Millionen Tieren beherbergt. Ziel dieser Arbeit ist es, das Wissen über ihre Ressourcennutzung, ihre Fortpflanzungsstrategien und ihre Anpassungsfähigkeit an Umweltveränderungen zu erweitern und kritische Lücken zum Verständnis ihrer Ökologie zu schließen. Die Arbeit ist in drei Kapitel gegliedert, die jeweils unterschiedliche ökologische Aspekte beleuchten. In Kapitel 1 wird die Nischentrennung zwischen den drei Sturmschwalbenarten anhand der Analyse stabiler Isotope von Kohlenstoff ($\delta^{13}C$) und Stickstoff ($\delta^{15}N$) aus Geweben wie Blut, Federn und Eimembranen sowie aus 2012-2013 gesammelten Nahrungsproben bewertet. Anhand von Krillproben aus den pazifischen Gewässern vor Baja California wurde eine marine Isolandschaft erstellt. Die Ergebnisse zeigten eine signifikante Trennung der Nahrungs- und Isotopennischen während der Brutzeit, wobei Schwarzwellenläufer Krill mit hohem Trophiegrad aus neritischen Gewässern verzehrten, während Wellenläufer und Zwerg-Sturmschwalbe sich von Fischlarven mit niedrigerem Trophiegrad in ozeanischen Regionen ernährten. Darüber hinaus zeigten die Sturmschwalben in den verschiedenen Brutzeiträumen Veränderungen in ihren Nahrungsstrategien, was ihre Flexibilität bei der Ernährung widerspiegelt. Kapitel 2 konzentriert sich auf die Brutbiologie der Zwergsturmschwalbe und untersucht die Brutphänologie, den Fortpflanzungserfolg, das Wachstum der Küken und die Ernährung über drei Brutsaisons (2013-2015). Eier, Küken und ausgewachsene Tiere wurden beobachtet, und es wurden Nahrungsproben entnommen, um die Nahrungsökologie zu bewerten. Morphometrische Unterschiede zwischen den Geschlechtern wurden mit Hilfe von Netzfängen und molekularer Geschlechtsbestimmung im Jahr 2012 analysiert. Die Ergebnisse zeigten einen gleichbleibend hohen Bruterfolg, wobei die jahreszeitlichen Schwankungen in Bezug auf den Zeitpunkt des Brütens und das Wachstum der Küken mit anomalen Klimabedingungen zusammenhängen. Die Weibchen wiesen längere Flügel und Schwänze auf als die Männchen, während Nahrungsanalysen Fischlarven, Euphausiiden und Tintenfische als Hauptbeutetiere identifizierten. Kapitel 3 untersucht die interannuelle Variabilität der Brutbiologie, des Kükenwachstums und des Ernährungsverhaltens der Schwarzwellenläufer über sechs aufeinanderfolgende Brutsaisons (2012-2017). Parameter wie die Peakmasse, die Masse der flüggen Küken, die Fütterungsrate und die Größe der Mahlzeiten wiesen signifikante interannuelle Schwankungen auf, obwohl diese Trends nicht

durch regionale oder lokale Umweltindizes erklärt werden konnten. Dies deutet darauf hin, dass andere Faktoren, wie z. B. der Lebensraum oder die Meeresbedingungen vor der Brut, eine einflussreichere Rolle bei der Ausprägung dieser Fortpflanzungsmerkmale spielen könnten. Zusammenfassend lässt sich sagen, dass diese Arbeit wertvolle Einblicke in die Ressourcenaufteilung, die Brutbiologie und die Anpassungsstrategien der Sturmschwalben liefert und die Bedeutung der Nischensegregation für die Koexistenz und die Verringerung des interspezifischen Wettbewerbs hervorhebt. Die Ergebnisse unterstreichen die Notwendigkeit, Umweltvariabilität und anthropogene Einflüsse bei der Planung von Artenschutzmaßnahmen zu berücksichtigen. Diese Arbeit trägt zu einem umfassenderen Verständnis der Ökologie der Sturmschwalben bei und schafft damit eine Grundlage für die Verbesserung von Schutz und Management für diese und andere Seevogelarten in dynamischen und sich schnell verändernden marinen Ökosystemen.

SYNTHESIS

1 | General introduction

1.1 Seabirds

Seabirds represent a highly diverse and specialized group of marine avifauna, uniquely adapted to the oceanic environment where they forage and spend most of their lives, returning to land primarily for breeding and resting (Furness and Monaghan 1987; Hamer et al. 2001). Comprising more than 368 species distributed across nine taxonomic orders (Schreiber and Burger 2001; Young and Ballance 2023), seabirds exhibit life-history traits shaped by their reliance on marine resources, including remarkable longevity (>20 years), delayed sexual maturity (2–5 years), and low reproductive output, often limited to a single or few eggs per breeding season (Schreiber and Burger 2001). Morphological adaptations such as elongated wings and streamlined bodies enable efficient, long-distance travel and foraging (Warham 1990; Shealer 2001), while salt glands specialized for osmoregulation facilitate the excretion of excess salt, a critical adaptation for life in saline environments. Their waterproof plumage provides insulation in cold oceanic waters, allowing them to exploit marine habitats across a wide range of latitudes (Schreiber and Burger 2001). Many species exhibit strong site fidelity, returning annually to the same breeding colonies, often on remote islands, and frequently reuniting with the same mate (Coulson 2001).

Seabirds play critical roles within marine ecosystems, functioning as apex or meso-predators that regulate prey populations, thereby contributing to ecosystem balance and stability (Cury et al. 2011). Additionally, seabirds act as nutrient vectors, connecting marine and terrestrial ecosystems by transporting marine-derived nutrients via guano deposition, which enhances productivity in breeding colonies and nearby coastal habitats (Mulder et al. 2011; Otero et al. 2018). Their sensitivity to environmental variability, such as changes in prey availability, oceanographic conditions, and anthropogenic disturbances, makes seabirds valuable bioindicators of ocean health (Piatt and Sydeman 2007). This characteristic, coupled with their accessibility at breeding colonies and at sea, positions seabirds as effective models for studying ecological processes and evaluating environmental changes across spatial and temporal scales (Furness and Camphuysen 1997).

Despite their ecological importance, seabirds are among the most threatened avian groups, with 43% of species currently listed as Critically Endangered, Endangered, Vulnerable, or Near Threatened by the International Union for Conservation of Nature (IUCN 2025). Major threats include invasive predators, incidental bycatch in commercial fisheries, and the accelerating impacts of climate change, such as increased frequency of extreme weather events and alterations in prey availability and distribution (Croxall et al. 2012; Dias et al. 2019). These cumulative pressures underscore the urgent need for comprehensive ecological studies to fill existing knowledge gaps and inform evidence-based conservation and management strategies to ensure the resilience and long-term survival of seabird populations.

1.2 The order Procellariiformes

Within the diverse group of seabirds, the Procellariiformes, often referred to as the truly oceanic birds, comprise albatrosses, petrels, shearwaters, and storm-petrels. This group is characterized by several morphological and behavioral adaptations that enable their survival in the open ocean. Procellariiform seabirds exhibit low reproductive rates, typically producing a single egg per breeding season, coupled with strong site fidelity and prolonged biparental care. These traits ensure a high degree of reproductive investment, with individuals often returning to the same breeding colonies, nest sites, and partners each year (Coulson 2001). Their exceptional migratory capabilities are facilitated by long, narrow wings adapted for dynamic soaring, enabling them to cover vast distances between breeding and foraging grounds with remarkable efficiency (Brooke 2004). Other physiological adaptations, such as tubular nostrils, allow for the excretion of excess salt, a critical mechanism for osmoregulation in marine environments (Ashmole 1971; Warham 1990).

The feeding strategies of Procellariiform seabirds are also diverse, encompassing surface seizing, shallow diving, and deep plunging, which enable them to exploit a broad range of prey, including fish, squid, and crustaceans (Brooke 2004; Rodríguez et al. 2019). Breeding strategies vary among taxa: petrels, shearwaters, and storm-petrels typically nest in burrows or rocky crevices, providing protection against predators and harsh environmental conditions, while albatrosses nest on open ground in relatively predator-free environments (Warham 1990; Brooke 2004).

Despite their widespread distribution and ecological significance, Procellariiformes are among the most threatened avian groups, facing numerous challenges across both marine habitats and terrestrial breeding sites. Key threats include habitat loss, invasive predators, fisheries bycatch, and the impacts of climate change (Phillips et al. 2023). Of the 149 recognized species within this order, 11% are classified as Critically Endangered, 13% as Endangered, and 19% as Vulnerable by the International Union for Conservation of Nature (IUCN 2025). Significant knowledge gaps persist for many species, particularly regarding their breeding biology, trophic ecology, and resilience to changing in ocean conditions. Addressing these gaps is essential for the development of conservation strategies aimed at protecting this ecologically important group of seabirds.

1.3 Storm-petrels

Among the Procellariiformes, storm-petrels are represented by two families: Hydrobatidae (northern storm-petrels) and Oceanitidae (southern storm-petrels), and are recognized as the smallest seabirds globally (Brooke 2004). These species are characterized by their distinctive fluttering flight, surface-foraging behavior, and cryptic, nocturnal habits, often breeding in remote and inaccessible locations, such as burrows or rocky crevices (Brooke 2004). The Hydrobatidae family alone comprises 28 species widely distributed across the Pacific and Atlantic Oceans, where they occupy temperate, tropical, and subtropical regions throughout their annual cycle (Brooke 2004; Spear and Ainley 2007). Similar to other Procellariiformes, storm-petrels face a range of conservation challenges, including habitat destruction, introduced predators, and the impacts of climate change. Consequently, 12 species are currently listed as Critically Endangered, Endangered, or Vulnerable by the IUCN (IUCN 2025).

Storm-petrels are ideal models for investigating mechanisms of species coexistence and responses to environmental variability. As primary consumers that predominantly feed on zooplankton, they occupy a lower trophic level compared to larger Procellariiformes, making them highly sensitive to fluctuations in oceanographic conditions (Brooke 2004). This positions storm-petrels as valuable indicators of environmental changes and shifts in marine dynamics. Furthermore, the Hydrobatidae family includes closely related and morphologically similar species that often breed sympatrically, potentially competing for space and food resources during breeding and non-breeding periods. These ecological traits provide an ideal framework for exploring niche segregation in marine ecosystems.

The remote Mexican islands along the Pacific coast of the Baja California Peninsula and within the Gulf of California host breeding colonies of seven storm-petrel species (Spear and Ainley 2007). These islands offer essential predator-free habitats that are critical for storm-petrel populations (Aguirre-Muñoz et al. 2018), including the black storm-petrel (*Hydrobates melania*), Leach's storm-petrel (*Hydrobates leucorhous;* synonyms *Hydrobates leucorhoa, Oceanodroma leucorhoa*), and least storm-petrel (*Hydrobates microsoma*). All three species are listed as threatened under Mexican legislation (DOF 2010). In this thesis, I focus on addressing significant knowledge gaps for these sympatric storm-petrel species on the San Benito Archipelago. Specifically, I investigated their trophic interactions, breeding biology, and adaptations to environmental variability, providing critical insights for the conservation and management of these vulnerable seabirds.

1.3.1 Black storm-petrel

The black storm-petrel, one of the largest storm-petrel (~60 g), is widely distributed across the Eastern Tropical Pacific. Breeding colonies are primarily located on islands off the Baja California Peninsula and within the Gulf of California, Mexico, with smaller colonies reported off the coast of California, USA (Everett et al. 2021). The species is characterized by its uniformly dark plumage and distinct flight pattern, features that facilitate its identification at sea. Black storm-petrels nest predominantly in rocky crevices and burrows, which offer shelter and protection during the breeding season, reducing the risk of predation and environmental stress (Everett et al. 2021).

During the non-breeding season, black storm-petrels exhibit a seasonal migratory behavior, traveling northward to California or southward to Peru (Spear and Ainley 2007). Globally, the species is classified as Least Concern by the IUCN, with an estimated population of approximately 600,000 mature individuals (BirdLife International 2020). However, within Mexico, it is officially designated as Threatened under national legislation (DOF 2010), reflecting concerns about its localized breeding distribution and potential vulnerability to regional threats. Despite its relatively broad geographic range, the ecology of the black storm-petrel remains poorly understood. Existing research has largely focused on small colonies, such as those on the Coronado Islands, resulting in significant knowledge gaps regarding its breeding biology, population dynamics, and responses to environmental variability (Everett et al. 2021).

1.3.2. Leach's storm-petrel

Leach’s storm-petrel, one of the most widely distributed storm-petrel species, occurs across both the Atlantic and Pacific Oceans (Pollet et al. 2021). Weighing approximately 40 g, this small, dark storm-petrel breeds on remote offshore islands, where it builds its nests in burrows, often in dense colonies (Everett and Anderson 1991). The species is recognized for its extensive foraging trips, frequently traveling distances exceeding 100 km from its breeding sites to forage on fish larvae, euphausiids, and amphipods, which form the bulk of its diet (Pollet et al. 2021). Notably, Leach’s storm-petrel exhibits considerable adaptability, adjusting its foraging strategies and breeding timing in response to environmental variability, a trait that has likely contributed to its broad distribution (Hedd and Montevecchi 2006).

In Mexico, the subspecies *Hydrobates leucorhous chapmani* is endemic to the Coronado and San Benito Archipelagos. It is morphologically distinct from other populations, displaying a darker rump and a more pronounced tail notch (Power and Ainley 1986). Despite its global population estimate of 6.7–8.3 million individuals, significant declines have been documented in recent decades, primarily driven by threats such as habitat loss, predation by introduced mammals, and environmental changes. These declines have resulted in its classification as Vulnerable on the IUCN Red List (BirdLife International 2018a) and as Threatened under Mexican legislation (DOF 2010). While Leach’s storm-petrel has been extensively studied in the Atlantic (Pollet et al. 2021), information on its populations in the Eastern Pacific remains limited.

1.3.3 Least storm-petrel

The least storm-petrel, the smallest member of the Hydrobatidae family and the smallest seabird species, weighs approximately 20 g. Its breeding range is highly restricted, confined to islands in the Eastern Pacific, including the San Benito Archipelago and various islands within the Gulf of California (Brooke 2004; Howell 2012). Unlike its sympatric counterparts, which typically nest in burrows, the least storm-petrel predominantly nests in rocky crevices, utilizing natural cavities as protective shelters during the breeding season (Ainley 1984).

During the non-breeding season, this species occupies both coastal and pelagic waters, with its range extending from southern California to northern Peru (Spear & Ainley, 2007; Fig. 1). Globally, the least storm-petrel is categorized as Least Concern due to its broad distribution, but it is listed as Threatened in Mexico, reflecting the vulnerability associated with its limited breeding range and potential exposure to localized threats (DOF 2010; BirdLife International 2018b). However, knowledge of its breeding biology remains sparse. Existing data are largely restricted to historical accounts describing its general breeding phenology (Anthony 1896), with critical information on chick development, provisioning rates, and population dynamics still lacking.

The three storm-petrel species investigated in this dissertation present an ideal comparative framework for addressing fundamental ecological and conservation questions. Their sympatric breeding on the San Benito Archipelago, coupled with their overlapping distributions, provides a unique opportunity to examine species interactions, mechanisms of resource partitioning, and adaptive responses to environmental variability. The outcomes of this research will contribute to broader conservation strategies, offering insights necessary to protect storm-petrel populations within the Eastern Tropical Pacific.

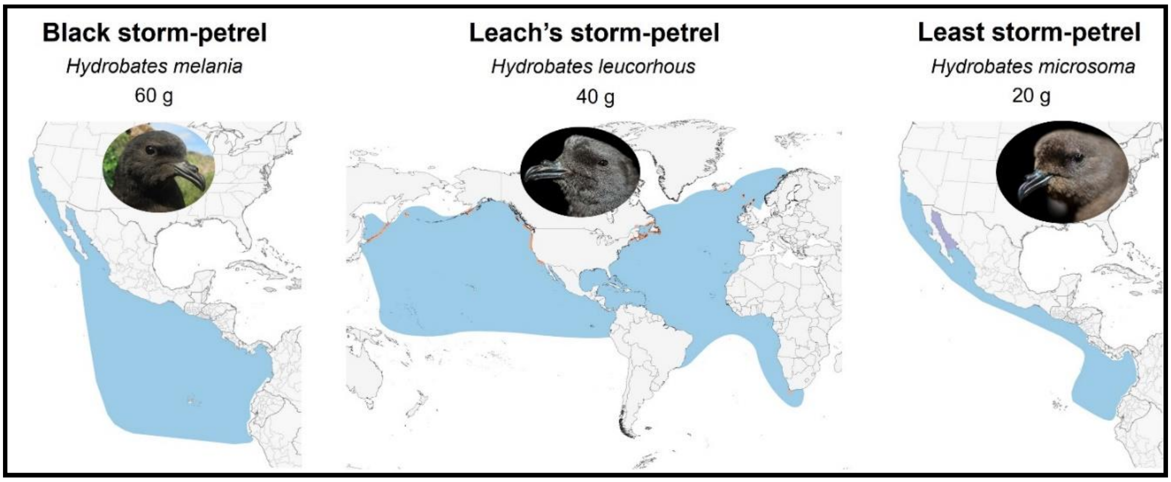

Figure 1. Maps of distribution during the annual cycle of black storm-petrel, Leach's storm-petrel, and least storm-petrel. Maps adapted from Birds of the World (2024).

1.4 The importance of ecological studies for species conservation

Despite their wide global distribution and critical ecological roles, storm-petrels remain among the least studied seabird groups (Rodríguez et al. 2019). Significant knowledge gaps persist regarding their trophic interactions, breeding biology, and responses to environmental variability. Bridging these gaps is essential to develop evidence-based conservation and management strategies, particularly for species breeding in biodiversity hotspots such as the Eastern Tropical Pacific Ocean. The California Current System, renowned for its exceptional biodiversity and productivity, represents a key area for the conservation and ecological study of storm-petrels, underscoring its importance in addressing these knowledge deficits (Spear and Ainley 2007).

Understanding the resource partitioning, breeding biology, and environmental responses of storm-petrels is pivotal for identifying the factors that influence their reproductive success, habitat utilization, and survival. Resource partitioning plays a crucial role in minimizing interspecific competition among sympatric species. Procellariiform seabirds, including storm-petrels, achieve coexistence through spatial, time, and dietary niche segregation, thereby reducing resource overlap and competition (Phillips et al. 2011; Quillfeldt et al. 2013). Understanding these mechanisms is essential for informing conservation strategies aimed at mitigating anthropogenic impacts, such as habitat degradation and changes in prey availability, which could disrupt these ecological dynamics (Dias et al. 2019).

Studying the breeding biology of storm-petrels provides valuable insights into their reproductive success and feeding performance and the factors influencing it, such as food availability, environmental variability, nest-site conditions, or human stressors (Büßer et al. 2004; Michielsen et al. 2019). These data are critical for identifying potential bottlenecks to reproduction and determining how breeding performance varies across different environmental conditions (Quillfeldt 2001; Pollet 2017). Furthermore, monitoring chick growth and provisioning can provide indirect evidence of prey availability and parental foraging efficiency (Hedd et al. 2002; Baduini 2002), key determinants of seabird population stability.

Investigating how seabirds respond to environmental variability is essential for understanding their adaptability to changing oceanographic conditions. Studies in other procellariform species have demonstrated that reproductive parameters are tightly linked to environmental conditions and prey availability (Quillfeldt et al. 2007; Hernández et al. 2017). Environmental drivers, such as sea surface temperature anomalies, have been shown to influence breeding success and foraging behavior in Procellariiform species (Quillfeldt et al. 2007; Eizenberg et al. 2021). This knowledge enhances our ability to predict species’ responses under future climate change scenarios and to incorporate climate resilience into conservation planning (Lewison et al. 2012; Sydeman et al. 2012).

Although all three storm-petrel species targeted in this dissertation are nationally classified as threatened, and the least storm-petrel is endemic to Mexico, critical knowledge gaps persist regarding their ecological characteristics. For example, little is known about their responses to environmental variability or the ecological mechanisms driving resource partitioning among these species. In addition, available information on the breeding biology and dietary habits of the least storm-petrel and black storm-petrel remains sparse and primarily descriptive, often based on brief observations at breeding colonies (Anthony 1896; Everett 1991). While Leach's storm-petrel has been extensively studied in other regions (Pollet et al. 2021), its ecological role and conservation needs in Mexico remain poorly understood despite its threatened status in the country.

To address these critical gaps, this dissertation provides a comparative analysis of two ecological aspects of these sympatric storm-petrel species: trophic ecology and climate ecology. The results advance our understanding of the ecological dynamics of these vulnerable seabirds while providing a foundation for future research and evidence-based conservation initiatives.

1.4.1 Trophic ecology - Niche segregation and sympatric species coexistence

Understanding trophic ecology is essential to exploring how coexisting species partition resources within shared habitats, particularly in marine ecosystems where competition can be intense. Niche segregation refers to the mechanisms by which species minimize direct competition by specializing in resource use, such as through dietary preferences or spatial separation during foraging (Grant 1972; Pianka 2000). This segregation facilitates the coexistence of closely related seabird species in sympatric breeding colonies by reducing overlap in resource utilization (Navarro et al. 2013; Quillfeldt et al. 2013). Storm-petrels primarily feed on a variety of prey, including euphausiids, amphipods, and small fish (Brooke 2004), yet the extent of dietary overlap and niche partitioning among sympatric species remains poorly documented (Ausems et al. 2020).

Traditional methods for investigating seabird diets, such as stomach content and pellet analysis, offer direct evidence of prey consumption but are limited in scope. These techniques are biased, as they reflect only recent meals and depend on the recovery of intact prey remains, potentially excluding soft-bodied organisms like gelatinous zooplankton or other highly digestible prey (Ainley et al. 1974; Votier et al. 2003). As a result, items that are rapidly degraded during digestion may be underrepresented (González-Solís et al. 1997; Abraham and Sydeman 2006). To address these limitations, stable isotope analysis has been applied as a complementary approach, providing an integrated perspective on dietary patterns (Cherel and Hobson 2007).

Stable isotope analysis measures the ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in tissues such as feathers, blood, and egg membranes, offering insights into dietary composition and habitat use. Carbon isotopes provide information on foraging location, as coastal and oceanic food webs exhibit distinct $\delta^{13}C$ values (Cherel & Hobson, 2007). Nitrogen isotopes, on the other hand, reflect trophic level, with $\delta^{15}N$ values increasing progressively with each step in the food chain (Vanderklift and Ponsard 2003). Statistical tools, including Bayesian mixing models like MIXSIAR in R, have been developed to estimate the proportional contribution of different prey items to seabird diets based on isotopic data (Stock et al. 2018). Additionally, SIBER analysis (Stable Isotope Bayesian Ellipses in R) quantifies isotopic niche width, representing the dietary and habitat space occupied by a species (Jackson et al. 2011; Fig. 2).

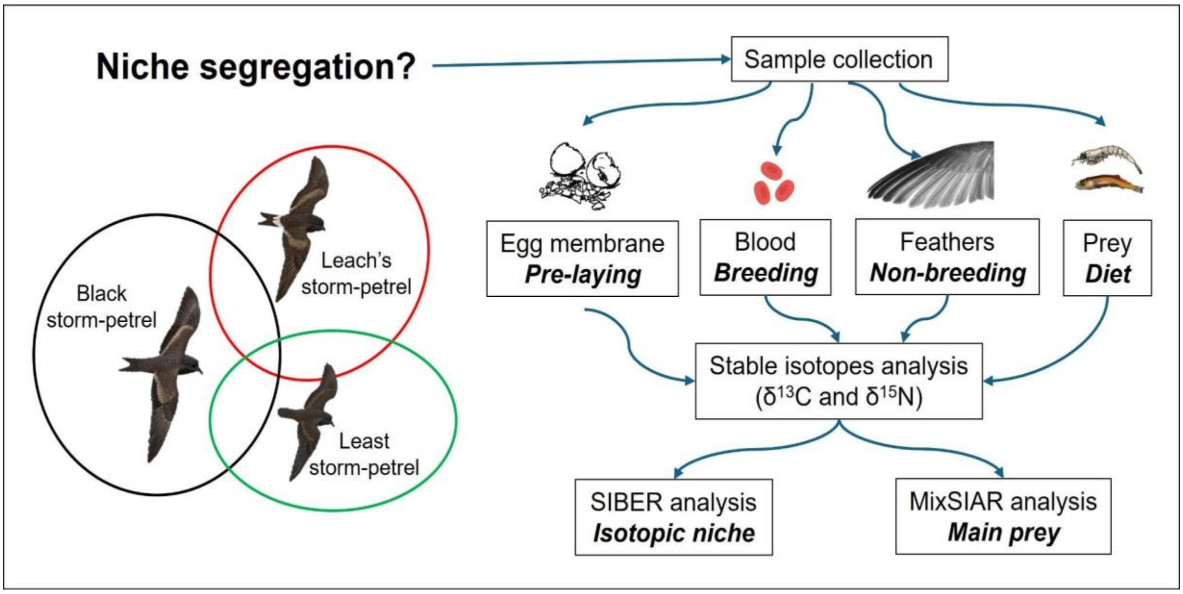

Figure 2. Flowchart diagram illustrating the key steps of stable isotope analysis for examining year-round niche partitioning in sympatric storm-petrels, based on different sample types. Illustrations of storm-petrels are from Birds of the World (https://birdsoftheworld.org).

Niche segregation among the storm-petrel species studied in this thesis remains unexamined. Current knowledge is limited to sparse data on diet and foraging distributions. The black storm-petrel feeds predominantly on euphausiids, squid, caridean shrimp, gammarid amphipods, and lanternfish (Everett et al. 2021). By contrast, the diet of the Leach's storm-petrel in the Atlantic consists of fish larvae, euphausiids, and amphipods (Hedd and Montevecchi 2006; Pollet et al. 2021) while the least storm-petrel primarily consumes crustaceans and small fish (Ainley 1984). However, detailed and quantitative dietary studies are lacking for both the black and least storm-petrels, and no such studies exist for the Leach's storm-petrel subspecies inhabiting the Eastern Tropical Pacific. At-sea observations provide evidence of niche differentiation among these species. The black storm-petrel and least storm-petrel typically forage in coastal waters within 20 km of the shoreline, whereas Leach's storm-petrel forage into more oceanic habitats, often traveling over 100 km offshore (Spear and Ainley 2007). These differences in foraging range suggest that the three species occupy distinct ecological niches, likely reducing competition for resources.

1.4.2 Climate ecology - Environmental variability and seabird life-history responses

Local-scale oceanographic variables, such as sea surface temperature (SST) and chlorophyll-a concentration, play a critical role shaping seabirds foraging ecology and reproductive dynamics. SST acts as a proxy for prey availability and can significantly influence foraging efficiency and chick provisioning rates (Frederiksen et al. 2004; Sydeman et al. 2012). Elevated SSTs, typically associated with reduced upwelling and prey abundance, have been linked to decreased provisioning rates and breeding failures in other Procellariiform species (Smithers et al. 2003; Peck et al. 2004; Quillfeldt et al. 2007). Similarly, chlorophyll-a concentration serves as indicator of primary productivity and correlate with the abundance of key prey species, such as euphausiids and amphipods (Espinosa-Carreon et al. 2004; Hipfner 2009). These environmental factors likely influence not only the reproductive performance of storm-petrels but also the spatial distribution of their foraging areas (Paiva et al. 2010; De Pascalis et al. 2021).

Extreme environmental events, including tropical storms, hurricanes, and marine heatwaves, exacerbate the challenges faced by seabirds. These events often cause habitat destruction, such as the flooding of burrows and erosion of nesting sites, which directly impacts breeding success (Catry et al. 2013; Zuberogoitia et al. 2016). For example, storm surges associated with hurricanes can inundate breeding habitats on islands and coastal areas, leading to the loss of eggs and chicks, as observed in various Procellariiform species (White et al. 1976; Frederiksen et al. 2008). Marine heatwaves, such as the 2013–2015 Pacific warm anomaly, disrupt marine food webs by reducing prey availability and altering their distribution, further limiting foraging success (Amaya et al. 2016; Cavole et al. 2016). Such events have caused widespread reproductive failures and population declines, as documented for Cassin’s Auklets (*Ptychoramphus aleuticus*) during 2014–2015 in the California Current system (Wolf et al. 2009).

Investigating the influence of environmental variability in reproductive parameters of cryptic and burrow-nesting seabirds like storm-petrels is challenging due to the inaccessibility and fragility of their nesting sites. Methods employed to minimize disturbance include selecting accessible nests at the periphery of colonies and using tools such as hand lamps and borescopes to observe nests located deep within rocky crevices or burrows (Carey 2009). Artificial nest boxes have also proven to be valuable research and conservation tools, offering controlled environments for examining breeding parameters while reducing disturbance to natural nests (Bolton et al. 2004). These boxes, often made of wood, plastic, or wood-concrete, provide durable and insulated alternatives for monitoring nesting behavior and chick development (Priddel and Carlile 1995; Bedolla-Guzmán et al. 2016).

Chick provisioning in burrow-nesting seabirds has been studied using both direct and indirect methods, each offering unique insights into feeding behaviors. Direct methods include the use of infrared cameras placed in artificial boxes, which allow for continuous monitoring of chick feeding without disturbing the nesting adults (Gladbach et al. 2009). Additionally, VHF tags can be deployed in adult birds to track their nest visits, offering precise data on the frequency and timing of provisioning events (Rishworth et al. 2014). Although these direct methodologies yield accurate results, they often come with high costs and logistical challenges. On the other hand, indirect methods, such as daily weight measurements of chicks corrected for metabolic loss, offer a more cost-effective approach to studying provisioning (Quillfeldt and Peter 2000). This approach has proven reliable and capable of yielding comparable results to direct observations (Gladbach et al. 2009).

Despite the ecological importance of these storm-petrels, detailed data on how these variables affect them at both local and large scales in the Eastern Pacific are scarce. Existing studies on the Leach's storm-petrel in Atlantic colonies suggest flexibility in foraging strategies and breeding phenology during periods of environmental fluctuation (Hedd and Montevecchi 2006). However, comparable information for black and least storm-petrels is entirely lacking. Additionally, knowledge of the breeding biology of the black and least storm-petrels remains sparse. For the black storm-petrel, available data are confined to a small colony on the Coronado Islands in the Pacific Ocean, Baja California, Mexico. The incubation period occurs from early May to late August, and the chick-rearing period extends from late June to mid-November (Anthony 1896; Everett 1991). Nestlings remain in the burrow for approximately 11 to 12 weeks, with chick development described only in terms of body mass during a single breeding season (Everett 1991). For the least storm-petrel, the limited data consists of general descriptions of breeding phenology and egg morphology, gathered from brief visits to breeding colonies. On San Benito Oeste Island, hatching occurs from mid-August to early September, with fledging observed from September to October (Anthony 1896; Howell 2012). In contrast, colonies in the Gulf of California may begin laying as early as mid-March or May (Carmona et al. 1994; Howell 2012). No studies have documented chick development or provisioning for this species. Although Leach's storm-petrel has been extensively studied elsewhere (Pollet et al. 2021), research specific to its Eastern Pacific populations is also lacking. Addressing these knowledge gaps is essential to advancing our understanding of their ecological responses and informing conservation strategies tailored to their specific needs.

1.5 Study site

The San Benito Archipelago, characterized by a temperate and semi-arid climate, comprises three small islands: San Benito Oeste, San Benito Medio, and San Benito Este. Situated approximately 72 km off the coast of the Baja California Peninsula, Mexico, the archipelago forms part of the extensive Baja California Pacific Islands Biosphere Reserve (Fig. 3). It hosts one of the largest storm-petrel colonies in Mexico, supporting over two million individuals during the breeding season annually (Wolf et al. 2006).

The San Benito Islands are also notable for their seabird diversity, hosting breeding populations of 13 species, the highest diversity recorded along the Pacific coast of the Baja California peninsula (Méndez Sánchez et al. 2022). Located in a highly productive oceanographic transition zone, the islands benefit from year-round elevated primary productivity, driven by persistent upwelling (Espinosa-Carreon et al. 2004). The research for this dissertation was conducted over six breeding seasons (August to November) from 2012 to 2017, focusing on Isla San Benito Oeste (3.64 km²; 28°18′N, 115°35′W, Fig. 1), the westernmost island of the archipelago (Fig. 4).

Historically, seabird populations, particularly burrow-nesting species, faced significant threats on Isla San Benito Oeste due to the presence of invasive mammals, including European rabbits, donkeys, goats, and cactus mice. These invasive species caused extensive habitat degradation, compromising the viability of seabird colonies. However, eradication programs successfully removed these mammals between 1998 and 2013, leading to the recovery of native seabird populations and their habitats (Aguirre-Muñoz et al. 2018). The exceptional abundance of storm-petrels and favorable conservation status make San Benito Oeste Island a critical site for investigating storm-petrel breeding biology and ecological interactions.

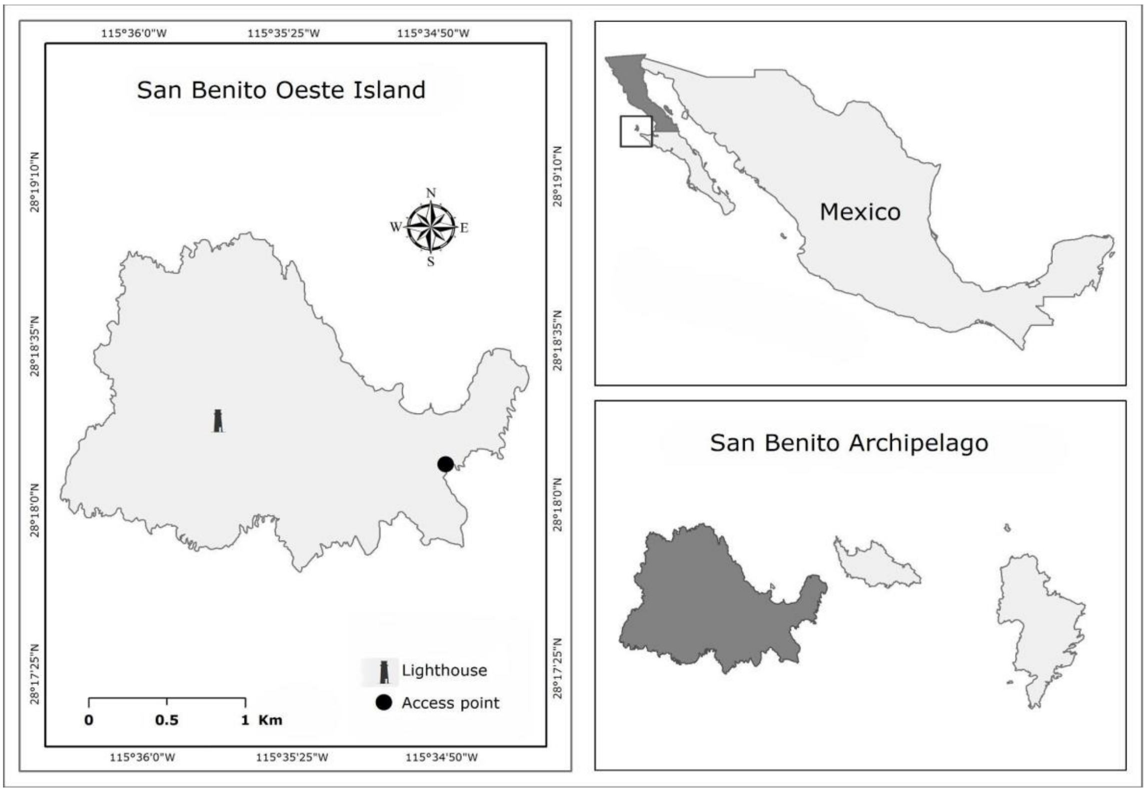

Figure 3. Geographic location of San Benito Oeste Island, off the Pacific coast of the Baja California peninsula, Mexico.


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Figure 4. Landscape of San Benito Island, off the Pacific coast of the Baja California peninsula, Mexico.

2 | Aims and structure of the thesis

The main objective of this thesis was to provide a comprehensive understanding of the niche segregation, breeding biology, and environmental responses of three sympatric storm-petrel species—black storm-petrel, Leach's storm-petrel, and least storm-petrel—breeding on the San Benito Archipelago, Mexico.

This cumulative thesis is organized into three chapters, each presented as an individual publication, addressing specific ecological aspects of these species. Chapter 1 integrates all three species, providing a community-level perspective. Chapters 2 and 3 focus on single-species analyses, with Chapter 2 examining the least storm-petrel and Chapter 3 evaluating the black storm-petrel (Fig. 5). The specific aims of each chapter are as follows:

CHAPTER 1 | Year-round niche segregation of three sympatric *Hydrobates* storm-petrels from Baja California Peninsula, Mexico, Eastern Pacific.

- Assess niche among the three storm-petrel species *(H. melania*, *H. leucorhous*, and *H. microsoma)* breeding sympatrically during two consecutive breeding seasons (2012 and 2013).

- Examine how niche segregation varies throughout the annual cycle, across years, and among age groups and breeding phases.

CHAPTER 2 | Breeding biology, chick growth, and diet of the Least Storm-Petrel *Oceanodroma microsoma* on Islas San Benito, Mexico

- Investigate the breeding biology of the least storm-petrel, including the timing of breeding, breeding success, egg measurements, chick growth, adult morphometry, and diet over three breeding seasons (2013-2015).

CHAPTER 3 | Inter-annual variations in the breeding biology, chick growth and feeding parameters of the black storm-petrel (*Hydrobates melania*) in relation to environmental conditions.

- Analyze inter-annual variations in reproductive performance, chick growth, and adult provisioning in the black storm-petrel over six breeding seasons (2012–2017).

- Investigate the relationship between these parameters and local oceanographic conditions as well as large-scale climate indices.

3 | Chapter outline

CHAPTER 1 | Year-round niche segregation of three sympatric *Hydrobates* storm-petrels from Baja California Peninsula, Mexico, Eastern Pacific [PUBLISHED]

Outline – This study investigated niche differentiation among three sympatric storm-petrel species, the black storm-petrel, Leach's storm-petrel, and least storm-petrel, breeding on Isla San Benito Oeste, Mexico. Diet sampling and stable isotope analysis were used to assess niche segregation throughout the annual cycle, inter-annually (2012 and 2013), and across age groups (adults and chicks) and breeding phases (pre-laying, incubation, and chick-rearing). Prey taxa were identified from regurgitated diet samples, and the proportional contributions of main prey groups were estimated using Bayesian mixing models applied to carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values derived from prey, adult, and chick blood samples. Isotopic niche segregation was evaluated using Stable Isotope Bayesian Ellipses in R (SIBER), incorporating isotopic signatures from egg membranes, blood, and feathers. The results revealed clear segregation in diet and isotopic niches among the species during the breeding season. Black storm-petrels consumed higher trophic-level prey from neritic waters, while Leach's and least storm-petrels relied on lower trophic-level prey from oceanic waters. In 2013, complete isotopic niche segregation was observed among all three species, whereas in 2012, isotopic niche overlap occurred between Leach's and least storm-petrels. Temporal differences in isotopic niches were evident across breeding phases. For example, black storm-petrel females consumed lower trophic-level prey during pre-laying but switched to higher trophic-level prey during incubation and chick-rearing. Niche segregation persisted during the non-breeding season, except during the molting period of primary feathers in Leach's and least storm-petrels. The study also found no clear latitudinal patterns in marine isoscapes. These findings demonstrated that niche segregation through dietary and habitat differentiation reduce interspecific competition during both breeding and non-breeding periods. However, temporal variations in the niche overlap likely reflected responses to oceanographic changes.

Contributions – Lead author including manuscript writing and editing, corresponding author, field data collection, diet samples analysis, preparation of stable isotopes samples, statistical analyses of stable isotopes data.

CHAPTER 2 | Breeding biology, chick growth, and diet of the Least Storm-Petrel *Oceanodroma microsoma* on Islas San Benito, Mexico [PUBLISHED]

Outline – This publication represents the first detailed account of the breeding biology, chick growth, diet composition, and morphological sex differences of the least storm-petrel, an endemic breeder to Mexico and one of the least studied seabirds. Research was conducted over three consecutive breeding seasons (2013–2015) on Isla San Benito Oeste, Mexico. Natural nests were monitored to record breeding parameters, including hatching and fledging success, while chick growth was assessed through repeated measurements of wing, bill, and tarsus length. Adults were captured using mist nets to collect morphometric measurements and blood samples for molecular sex determination. Regurgitated food samples from adults and chicks were analyzed to characterize diet composition. The findings demonstrated consistently high reproductive success across the study period, with hatching success averaging 80% and fledging success ranging between 87% and 90%. Breeding phenology varied across years, with earlier hatching in 2013, delayed hatching in 2014, and later fledging in 2014 compared to 2013. Inter-annual differences were also observed in chick growth, with nestlings fledging in 2015 exhibiting longer wings, bills, and tarsi compared to previous years. Dietary analysis revealed a diet dominated by larval fish, alongside euphausiids and squid. Molecular analysis showed an equal sex ratio (1:1), with females having longer wings and tails, and males characterized by longer bills. These variations in breeding phenology and chick growth are linked to fluctuations in prey availability, likely driven by anomalous warm oceanographic conditions in 2014 and 2015.

Contributions – Lead author including manuscript writing and editing, corresponding author, field data collection, data analysis.

CHAPTER 3 | Inter-annual variations in the breeding biology, chick growth and feeding parameters of the black storm-petrel (*Hydrobates melania*) in relation to environmental conditions [SUBMITTED]

Outline – This study assessed inter-annual variations in the reproductive performance, chick provisioning, and chick growth of the black storm-petrel over six breeding seasons (2012–2017) on Isla San Benito Oeste, Mexico. Artificial nests were used to monitor breeding success (hatching and fledging rates), breeding phenology (hatching and fledging dates), feeding performance (meal size and feeding frequency), and chick growth (peak mass, age at peak mass, and fledging mass). To investigate potential drivers of these variations, large-scale oceanographic indices, including the El Niño Oscillation Index, the Pacific Decadal Oscillation Index, and the North Pacific Gyre Oscillation Index, were analyzed alongside local variables such as chlorophyll-a concentrations, sea surface temperature anomalies, and coastal upwelling index anomalies. The findings revealed significant inter-annual differences in breeding success, feeding performance, and chick growth. Hatching and fledging success exceeded 70% in most years, except in 2013, when a tropical storm caused extensive nest flooding, resulting in a mortality rate of approximately 50%. Breeding phenology remained relatively stable across years, but variations in feeding performance were evident. During 2013, chicks received less food per night, and smaller meal sizes were observed between 2013 and 2015. Consequently, chicks in 2013 and 2014 achieved lower peak masses, with chicks in 2013 reaching peak mass earlier than in other years and fledging with lower body mass. Large-scale oceanographic indices reflected anomalously warm conditions in 2014 and 2015; however, local oceanographic variables near the island did not show significant inter-annual differences. The observed variations in breeding parameters were not directly correlated with these large-scale indices, suggesting that broader oceanographic patterns may not fully capture the environmental influences affecting black storm-petrel. The species exhibited resilience to changing ocean conditions through flexible provisioning strategies, prioritizing reproductive success despite reduced chick quality. Nevertheless, vulnerability to extreme weather events, such as the tropical storm in 2013, remains a significant concern for the species' long-term viability. The complex relationship between environmental variables and life-history traits suggests that other local conditions may buffer the species from broader oceanographic changes.

Contributions – Lead author including manuscript writing and editing, corresponding author, field data collection, data analysis.

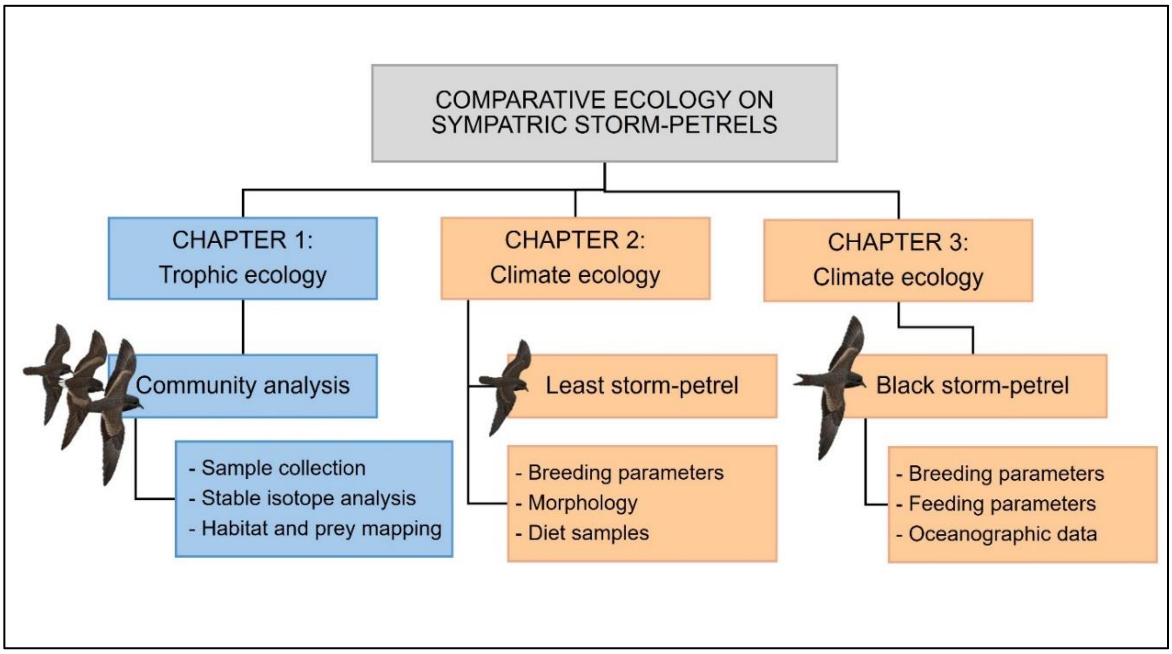

Figure 5. Thesis outline presenting the two main research topics, the species investigated, and an overview of the methods employed for each chapter.

4 | General conclusions and future outlook

4.1 General conclusions

This cumulative thesis contributes to a better understanding of the ecology of three sympatric storm-petrel species, all of which are classified as threatened in Mexico, by focusing on their trophic ecology and climate ecology (Figure 5). The research centers on the black storm-petrel (*Hydrobates melania*), the least storm-petrel (*Hydrobates microsoma*), and a subspecies of the Leach's storm-petrel (*Hydrobates leucorhous chapmani*), for which detailed ecological information was previously unavailable. Chapter 1 adopts a community-based perspective, while Chapters 2 and 3 provide single-species analyses.

Chapter 1 investigated the mechanisms enabling the coexistence of the three storm-petrel species throughout their annual cycles and across years. The findings demonstrated that isotopic niche segregation, driven by dietary and spatial differences in foraging, is a key mechanism reducing interspecific competition. Black storm-petrels primarily consumed higher trophic-level krill from neritic waters, while Leach's and least storm-petrels relied on lower-trophic fish larvae from oceanic waters. This resource partitioning was stable consistent both breeding and non-breeding periods and between but varied among 2012 and 2013 seasons. Disruptions to prey distribution and abundance caused by climate change could destabilize these niche dynamics, increasing interspecific competition and affecting survival and diversity (Leising et al. 2014; Barger et al. 2016). The study also revealed interspecific differences in age-related niche segregation. Black storm-petrels provisioned their chicks with prey distinct from their own diet, while least storm-petrels fed their chicks the same prey items but from different locations. These distinct strategies may enhance chick growth and survival, highlighting the ecological adaptations that support reproductive success (Hedd and Montevecchi 2006; Ausems et al. 2020). Seasonal variations in isotopic niche width further indicate the flexibility and resilience of these species to environmental variability. However, their reliance on specific prey groups underscores potential vulnerabilities to shifts in prey availability driven by climate change.

Chapters 2 and 3 revealed that both the least storm-petrel and the black storm-petrel exhibit high resilience to fluctuating oceanic conditions, albeit with species-specific differences in their responses. Both species maintained consistently high hatching and fledging success over several breeding seasons, even during years marked by warm ocean anomalies that resulted in widespread reproductive failures and massive mortality in other seabird species in the region (Cavole et al. 2016; Mcclatchie et al. 2016). However, the least storm-petrel demonstrated higher sensitivity to oceanographic variability, particularly in breeding phenology and chick growth. The timing of breeding shifted during anomalously warm conditions, indicating an adaptive response to changes in food supply. Despite this flexibility, reduced chick growth during these periods suggests constraints in provisioning rates or access to high-energy prey resources (Peck et al. 2004; Quillfeldt et al. 2007).

The black storm-petrel exhibited inter-annual variations in chick growth and provisioning strategies but maintained stable breeding phenology. These variations were not correlated with local or large-scale oceanographic indices during the breeding season, suggesting that factors such as pre-breeding oceanic conditions, prey distribution, or fine-scale habitat features may influence breeding and feeding parameters (De Pascalis et al. 2021). While the species showed resilience to fluctuating environmental conditions, it proved vulnerable to extreme weather events, such as the tropical storm in 2013, which caused significant chick mortality. Both species prioritized reproductive success over chick quality, a strategy that may compromise post-fledging survival and long-term population stability. These findings emphasize the complexity of seabird responses to environmental variability, as even closely related species can exhibit different behaviors, and highlight the importance of long-term monitoring programs to assess the impacts of climate change. Such efforts are essential for developing effective conservation strategies to mitigate the effects of changing oceanographic conditions and extreme weather on storm-petrel populations.

4.2 Future outlook

4.2.1 Niche segregation

The results presented in Chapter 1 emphasize the importance of studying dietary segregation among sympatric storm-petrel species in greater detail. Employing genetic tools, such as DNA barcoding from fecal samples, could refine our understanding of dietary overlap by identifying prey items at the species level. This approach would offer a finer-scale perspective on trophic interactions and provide valuable insights into dietary changes across breeding and non-breeding periods. Extending research to migration areas and incorporating stable isotope analyses from years with contrasting oceanographic conditions could elucidate how niche segregation is affected under variable environmental scenarios.

Year-round tracking of storm-petrels using GPS during the breeding season and geolocators (GLS) during the non-breeding season could further clarify the mechanisms of niche segregation. Such studies would help identify critical foraging areas and migratory routes, key data for effective conservation planning. Integrating tracking data with environmental variables will offer a comprehensive understanding of habitat preferences and storm-petrels’ responses to oceanographic changes.

The unique assemblage of six storm-petrel species breeding along the Pacific coast of the Baja California Peninsula presents a unique opportunity for comparative studies. Exploring how these species partition resources and coexist at a regional scale could reveal broader ecological mechanisms underlying niche segregation and community dynamics in Procellariiformes.

4.2.2 Response to environmental changes

Inter-annual variations in timing of breeding and chick growth, observed in the least storm-petrel (Chapter 2), emphasize further investigation into the influence of local and large-scale environmental variables. The relationship between environmental factors and the reproductive performance of the black storm-petrel (Chapter 3) remains complex, highlighting the need for multi-scale analyses, including temporal lags, to better understand these dynamics. Given the increasing frequency and intensity of tropical storms due to climate change, assessing their long-term impacts on storm-petrel populations is a critical research priority. The black storm-petrel's resilience to environmental variability, as demonstrated through flexible provisioning strategies, may come at the expense of chick quality. Future research should investigate how this trade-off influences population dynamics and long-term adaptability to changing oceanographic conditions. Studies addressing the interactions between environmental drivers and reproductive success will be crucial for informing conservation strategies aimed at mitigating the impacts of climate change on storm-petrels.

This thesis provided critical baseline data on the breeding biology of the black and least storm-petrels, yet additional research is needed to further understand their reproductive strategies. Long-term monitoring of all three target species, particularly Leach's storm-petrel, is essential to evaluate breeding parameters such as chick growth and feeding performance at Isla San Benito Oeste. Locating natural nests of Leach's storm-petrel during fieldwork was challenging, and the low occupancy rates of artificial nests limited the study's scope. Enhancing artificial nest design and placement to increase occupancy, particularly for Leach's storm-petrel, should be prioritized. The use of advanced methodologies, such as infrared cameras within artificial burrows or Radio Frequency Identification (RFID) systems equipped with Passive Integrated Transponders (PIT tags) on individual birds, could provide more detailed data on chick provisioning and parental behaviors.

The observed morphological differences between males and females in the least storm-petrel highlight the need for further investigation into sex-specific roles in breeding biology. Future studies should address variations in parental investment and foraging behaviors, considering the potential implications for reproductive success. Expanding research efforts to include other breeding colonies will help identify local adaptations and variations in reproductive strategies, further enriching our understanding of these species.

4.2.3 Emerging threats

Emerging threats such as plastic pollution and disease show additional challenges to storm-petrel populations. Assessing the ingestion of microplastics and the accumulation of persistent organic pollutants (POPs) in storm-petrel tissues is necessary to evaluate their potential effects on individual health and reproductive success. Monitoring the prevalence of diseases, such as avian influenza and parasitic infections, will provide insights into their impacts on breeding performance and chick survival. Research into the role of endoparasites and ectoparasites in influencing chick growth and overall survival could offer a more comprehensive understanding of the health status of storm-petrel populations.

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CHAPTERS

Chapter 1

YEAR-ROUND NICHE SEGREGATION OF THREE SYMPATRIC *HYDROBATES* STORM-PETRELS FROM BAJA CALIFORNIA PENINSULA, MEXICO, EASTERN PACIFIC

Bedolla-Guzmán, Y., Masello, J. F., Aguirre-Muñoz, A., Lavaniegos, B. E., Voigt, C. C., Gómez-Gutiérrez, J., Sánchez-Velasco, L., Robinson, C. J., & Quillfeldt, P.

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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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values obtained from egg membranes, blood, feathers, and prey. We used krill samples to delineate marine $\delta^{13}C$ and $\delta^{15}N$ 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*

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 &

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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 ($\delta^{13}C$) 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 ($\delta^{15}N$) can be used to identify relative trophic levels (Vanderklift & Ponsard 2003). Ellipse areas constructed from stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) 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 δ^{15}N variability between molting periods, and a wide range of δ^{13}C and δ^{15}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 (δ^{13}C and δ^{15}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 km^2). 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-

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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 $\delta^{15}N$ variability between molting periods, and a wide range of $\delta^{13}C$ and $\delta^{15}N$ 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 ($\delta^{13}C$ and $\delta^{15}N$). 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 km^2). 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 $\delta^{13}C$ and $\delta^{15}N$ 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 IMECOCAL 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 ($\delta^{13}C$ and $\delta^{15}N$) 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:

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

where X is ^{15}N or ^{13}C and R is the corresponding $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio. Based on internal standards (N = 165, tyrosin; Roth), the analytical precision (±1 SD) was equal to ±0.16‰ for $\delta^{15}N$ and ±0.29‰ for $\delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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 δ^{13}C values and 1‰ from the δ^{15}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: Δ^{13}Cdiet – red blood cells = 1‰, Δ^{15}Ndiet – red blood cells = 3‰) and egg membranes (Hobson 1995: Δ^{13}Cdiet – egg membrane = 3‰ and Δ^{15}Ndiet – egg membrane = 4‰).

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.; δ^{15}N: 10.4 ± 1.5, δ^{13}C: −20.4 ± 0.6, n = 25), krill group II (*N. simplex*, *N. difficilis* and *T. spinifera*; δ^{15}N: 13.6 ± 0.7, δ^{13}C: −19.1 ± 1.3, n = 36), and fish larvae (δ^{15}N: 13.9 ± 1.0, δ^{13}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 δ^{13}C = 1.2‰ and δ^{15}N = 3.0‰ based on the means of the discrimination factors that have been reported for rhinoceros auklets *Cerorhinca monocerata* (δ^{15}N = 3.49‰; Sears et al. 2009) and common murres *Uria aalge* (δ^{13}C = 1.09‰, 1.2‰; δ^{15}N = 2.91‰, 2.6‰; Sorensen et al. 2009, Jenkins et al. 2020) raised in captivity. Common murres 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 ≥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 temporally (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 (Sarakinos 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):

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

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, $^{\varepsilon}C$ is the carbon fractionation (1.0), and $^{\varepsilon}N$ 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.

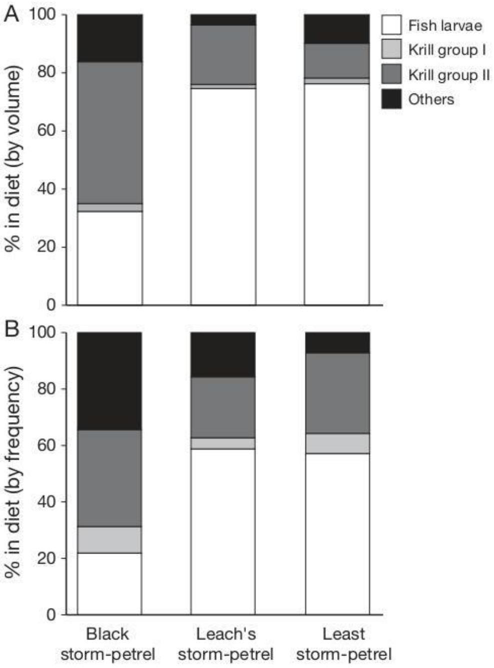

Fig. 1. Diet composition of black storm-petrels *Hydrobates melania*, Leach's storm-petrels *H. leucorhous*, and least storm-petrels *H. microsoma* on San Benito Oeste Island, Mexico, during the 2012 and 2013 breeding seasons. Percentage of diet by (A) volume and (B) frequency of occurrence). 'Others'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

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

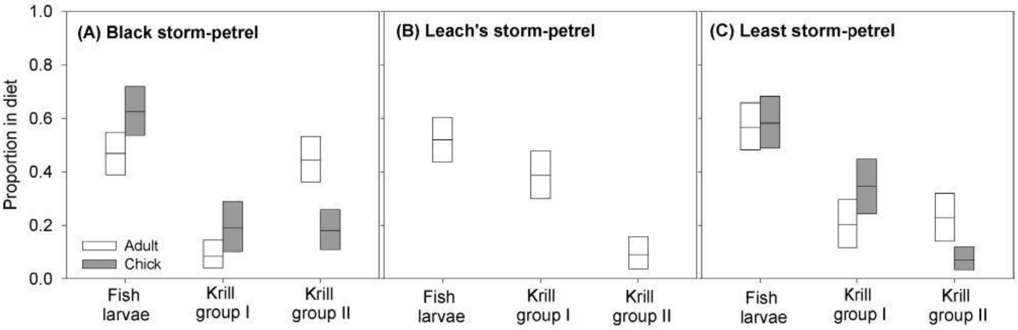

Fig. 2. Proportions of the main prey items in the diet of (A) black storm-petrel *Hydrobates melania*, (B) Leach's storm-petrel *H. leucorhous*, and (C) least storm-petrel *H. microsoma* adults and chicks according to the MixSIAR stable isotope mixing model (median values and 5th to 95th percentiles) with $\delta^{13}C$ and $\delta^{15}N$ 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).

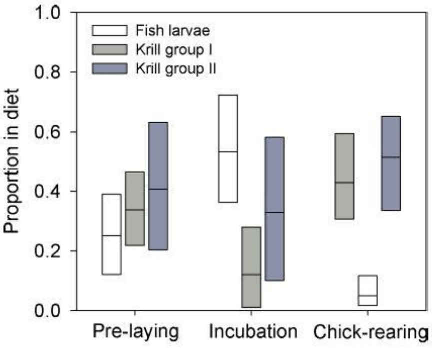

Fig. 3. Proportions of the main prey items in the diets of black storm-petrels *Hydrobates melania* during 3 breeding phases (pre-laying, incubation, chick-rearing) according to the MixSIAR stable isotope mixing model (median values and 5th to 95th percentiles) with $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ values and 1‰ from the $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ values than the other 2 storm-petrel species in both years (Table 1). *H. leucorhous* and *H. microsoma* $\delta^{13}C$ values did not vary between years, although the $\delta^{15}N$ 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 breath in 2013 (Fig. 4; Table S6).

For both years, *H. melania* adults had higher blood $\delta^{13}C$ values and $\delta^{15}N$ 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 $\delta^{13}C$ values compared to chicks, while no differences were present among $\delta^{15}N$ 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 $\delta^{15}N$ and $\delta^{13}C$ 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 ± SD $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) 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)	$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)			
		BLSP	LESP	LSTP	p	BLSP	LESP	LSTP	p
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 ± 0.8	15.23 ± 0.4	15.49 ± 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 ± 0.9	15.63 ± 1.1	15.68 ± 1.7	0.11 ($H_2 = 4.5$)

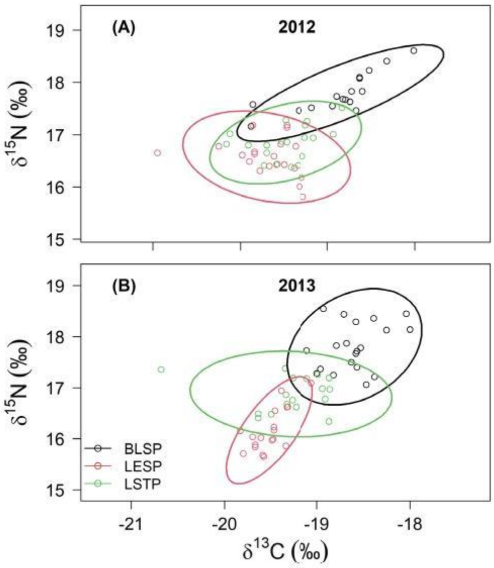

Fig. 4. Sample 95% ellipses calculated from the $\delta^{13}C$ and $\delta^{15}N$ values from the blood samples taken from black storm-petrels *Hydrobates melania* (BLSP), Leach's storm-petrels *H. leucorhous* (LESP), and least storm-petrels *H. microsoma* (LSTP) sampled at San Benito Oeste Island, Mexico, 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 $\delta^{13}C$ values. In addition, $\delta^{15}N$ 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, $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ 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 ± SD $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) 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)	$\delta^{13}C$			$\delta^{15}N$		
		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 ($t_{35} = 1.2$)

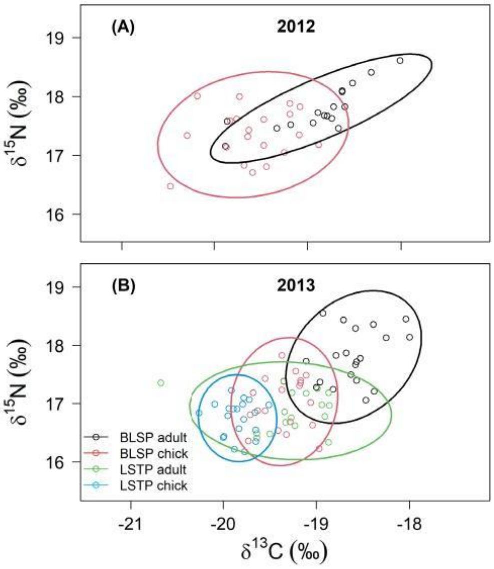

Fig. 5. Sample 95% ellipses calculated from the $\delta^{13}C$ and $\delta^{15}N$ values of blood samples collected from black storm-petrel *Hydrobates melania* (BLSP) and least storm-petrel *H. microsoma* (LSTP) adults and chicks sampled at San Benito Oeste Island, Mexico, during the breeding seasons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

contrast, $\delta^{15}N$ values greatly varied between species, feathers, and years. *H. melania* showed the highest $\delta^{15}N$ 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, $\delta^{15}N$ 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 represented >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 $\delta^{13}C$ 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 $\delta^{15}N$ values varied, although no pattern was observed. The highest $\delta^{15}N$ euphausiid value (14.8‰) was recorded in the southernmost sampling location near the coast, and the lowest $\delta^{15}N$ 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 $\delta^{13}C$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ values in the Gulf of California were considerably higher than those along the west coast of the Baja California Peninsula.

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

Table 3. Statistical analyses comparing mean ± SD $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) 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)	$\delta^{13}C$				$\delta^{15}N$			
	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 ± 0.8	–	−18.60 ± 0.3	**0.010** (*U* = 95.0)	16.52 ± 1.1	–	17.80 ± 0.5	**<0.001** (*U* = 65.0)

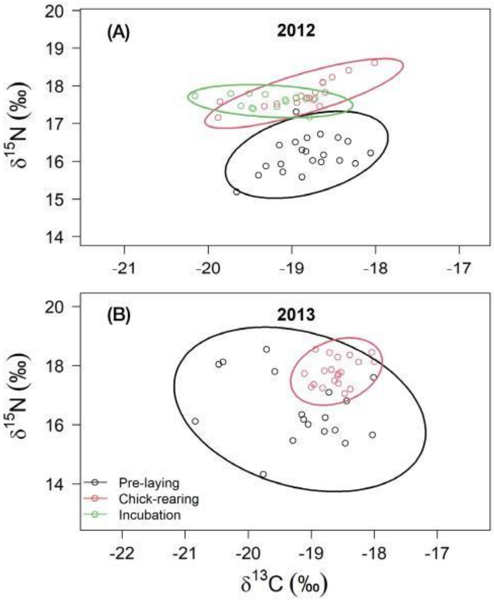

Fig. 6. Sample 95% ellipses calculated from the $\delta^{13}C$ and $\delta^{15}N$ values from blood and egg membrane samples collected from black storm-petrels *Hydrobates melania* during the different phases of the breeding period (egg membrane: pre-laying; whole blood: incubation and chick-rearing) 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 $\delta^{13}C$ and 1‰ from the $\delta^{15}N$ 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, $\delta^{13}C$ 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 $\delta^{15}N$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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

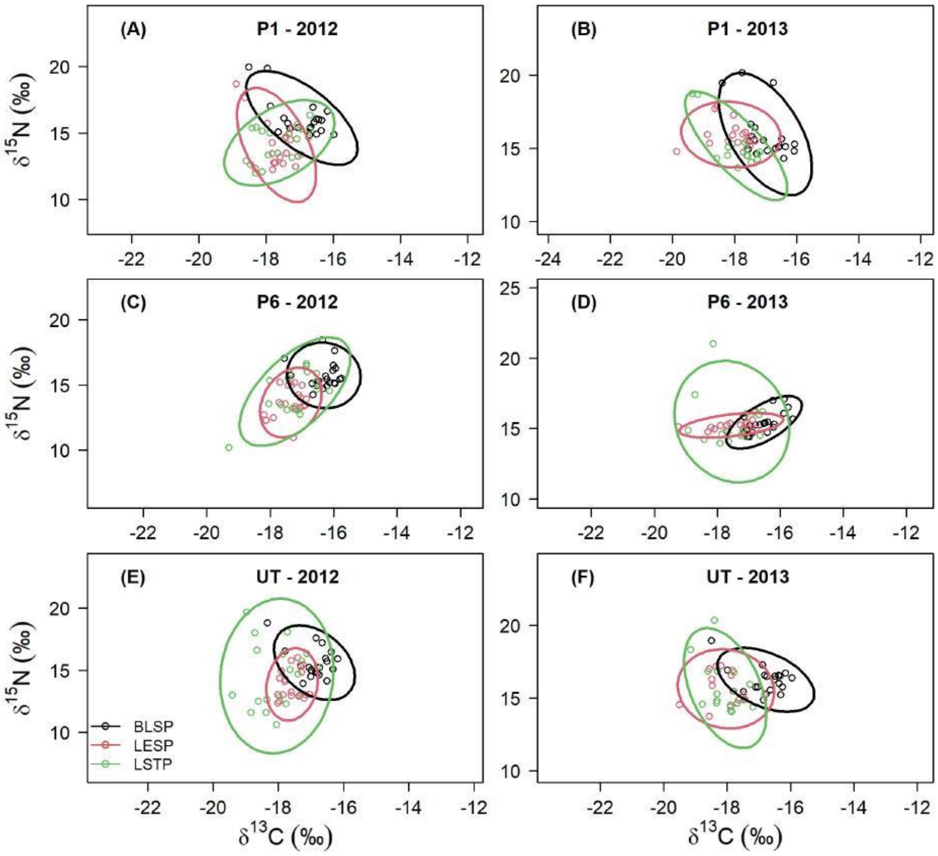

Fig. 7. Sample 95% ellipses calculated from the δ^{13}C and δ^{15}N values from feather samples taken from black storm-petrels *Hydrobates melania* (BLSP), Leach's storm-petrels *H. leucorhous* (LESP), and least storm-petrels *H. microsoma* (LSTP) sampled at San Benito Oeste Island, Mexico, during the breeding seasons of 2012 and 2013. (A) and (B): P1 primary feathers; (B) and (C): 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 δ^{13}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‰ ± 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

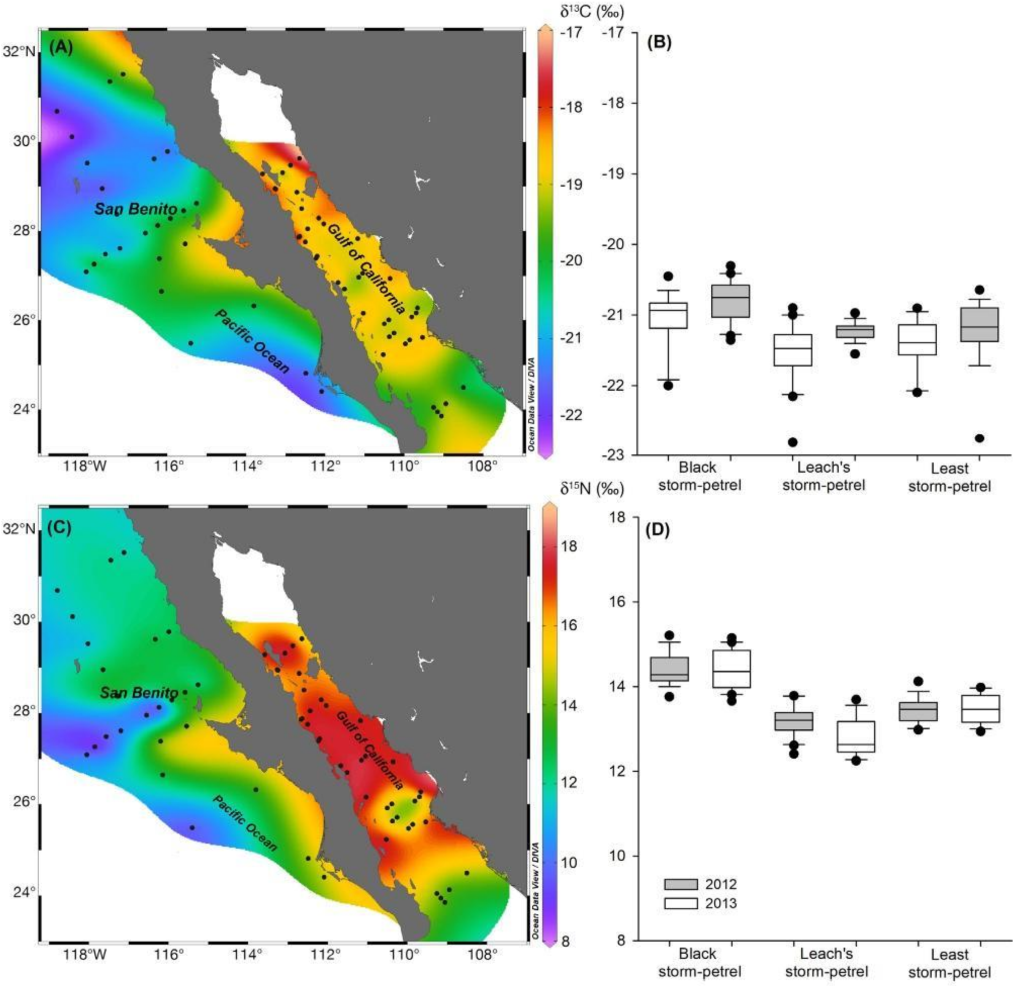

Fig. 8. Marine isoscapes of (A) δ^{13}C values and (C) δ^{15}N values of all euphausiid species combined from the Pacific coast of the Baja California Peninsula and the Gulf of California. Sampling stations are shown as black dots. Data were collected by IMECOCAL (Mexican Research Program of the California Current), CAPEGOLCA-UNAM (Small Pelagic Fish Schools in the Gulf of California), and GOLCA (Gulf of California) cruises from summer 1997–2013. (B) δ^{13}C range values and (D) δ^{15}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 δ^{13}C and δ^{15}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 (smaller) value no further than 1.5 × 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, Ausems et al. 2020).

H. melania adults showed higher $\delta^{13}C$ and $\delta^{15}N$ 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, Ausems 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 $\delta^{13}C$ but similar $\delta^{15}N$ 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* (Ausems 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 $\delta^{13}C$ values (from neritic waters) and lower $\delta^{15}N$ 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 (Ausems 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 δ^{13}C values showed high variability during the non-breeding period. Such δ^{13}C ranges were similar to the δ^{13}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 δ^{13}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 δ^{13}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 δ^{15}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 δ^{15}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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Chapter 2

BREEDING BIOLOGY, CHICK GROWTH, AND DIET OF THE LEAST STORM-PETREL OCEANODROMA MICROSOMA ON ISLAS SAN BENITO, MEXICO

Bedolla-Guzmán, Y., Masello, J. F., Aguirre-Muñoz, A., Lavaniegos, B. E., & Quillfeldt, P.

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BREEDING BIOLOGY, CHICK GROWTH, AND DIET OF THE LEAST STORM-PETREL *OCEANODROMA MICROSOMA* ON ISLAS SAN BENITO, MEXICO

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ABSTRACT

BEDOLLA-GUZMÁN Y., MASELLO J.F., AGUIRRE-MUÑOZ, A., LAVANIEGOS, B.E. & QUILLFELDT, P. 2017. Breeding biology, chick growth, and diet of the Least Storm-Petrel *Oceanodroma microsoma* on Islas San Benito, Mexico. *Marine Ornithology* 45: 129–138

The Least Storm-Petrel *Oceanodroma microsoma* is endemic to islands on both coasts of Baja California, in Mexico. It is the smallest seabird species and one of the least studied of the order Procellariiformes. We present a detailed account of its breeding success, chick growth, and diet at Islas San Benito, Baja California, during three consecutive breeding seasons (2013 to 2015) and of sex differences in adult morphology, a study conducted in 2012. Eggs hatched between late July and mid-September, and the fledging period started in mid-October. The timing of breeding varied from year to year: the hatching period began earlier in 2013 than in 2015 and was longer in 2014, while the fledging period started later in 2014 than in 2013. Hatching success (around 80%) and fledging success (about 90%) were consistently high in all three years. Nevertheless, nestlings fledged with longer wings, tails, and bills in 2015. Four species of euphausiids, two species of larval fish, and one species of squid were identified in food samples. Differences in the timing of breeding and chick growth during the period of this study may reflect a variation in food supply associated with anomalous climate conditions recorded in 2014 and 2015.

Key words: Baja California, breeding success, chick growth, diet composition, Least Storm-Petrel, Islas San Benito, timing of breeding

INTRODUCTION

Storm-petrels are among the most abundant seabirds. However, due to their nocturnal arrival at the colonies and their hidden and often inaccessible nests, they remain relatively poorly studied. Most species nest exclusively on islands, where threats such as introduced predators, human disturbance, and contamination have led to the decline of many populations (Croxall *et al*. 2012). Of the 24 storm-petrel species, 38% are listed under a category of protection, and four species are considered Data Deficient by the International Union for Conservation of Nature (IUCN; http://www.iucnredlist.org). The breeding biology information for these species is relevant to understand ecological and evolutionary processes, to evaluate the impact of threats at breeding and on sea grounds as well as their vulnerability to changing climate conditions, and to design conservation management guidelines.

The Least Storm-Petrel *Oceanodroma microsoma* is the smallest species of the Hydrobatidae family (weighting approximately 20 g; Brooke 2004) and one of the least studied species of the order Procellariiformes. Its breeding is narrowly distributed among colonies confined to Islas San Benito, off the Pacific coast of the Baja California peninsula, and islands in the Gulf of California, Mexico (Brooke 2004, Howell 2012). Its geographic distribution during non-breeding periods includes coastal and pelagic waters from southern California to Peru (Veit *et al*. 1996, Spear & Ainley 2007, Howell 2012). Consistent with other Procellariiformes, Least Storm-Petrels lay a single egg, and have a slow reproductive rate, an intense and extended biparental care, and a slow chick development (Brooke 2004). This species commonly breeds in clefts and cavities among and under rocks (Ainley 1984). The diet of Least Storm-Petrels includes planktonic crustaceans and small fish (Ainley 1984). In the last century, introduced mammals negatively affected the main colony sites, but important restoration efforts have recently eliminated this threat (Aguirre-Muñoz *et al*. 2016). The Least Storm-Petrel is listed as Threatened under the Mexican law (Diario Oficial de la Federación 2010), but as Least Concern by the IUCN (BirdLife International 2016).

The breeding biology information for this species is limited to anecdotal observations from brief visits to the colonies or isolated observations. Current knowledge is restricted to partial information on breeding phenology, measurements of eggs, diet, and adult morphometry (Anthony 1896, Murphy 1936, Carmona *et al*. 1994, Pyle 2008, Howell 2012). This article presents an account of the breeding biology of the Least Storm-Petrel, including timing of breeding and breeding success, egg measurements, chick growth, adult morphometry, and diet of individuals nesting on Islas San Benito from 2013 to 2015.

METHODS

Ethics statement

The fieldwork and sample collection were approved by the Secretaría de Medio Ambiente y Recursos Naturales, and Secretaría de Gobernación (Mexico). Extreme care was taken to minimize stress of captured adults and to protect eggs from potential predators. Handling time was kept to a minimum, mostly less than 15 min and always less than 20 min, and the heads of the birds were covered. During this procedure, the birds remained relatively calm and no significant signs of stress were detected. Blood sampling showed no detectable adverse effects; during release, birds flew almost immediately; and sampled individuals recaptured showed good body condition.

Study species and area

This study was carried out from August 2012 to November 2015 at Isla San Benito Oeste (3.64 km^2; 28°18′N, 115°35′W, Fig. 1), the westernmost island of the archipelago consisting of three small islands off the Pacific coast of Baja California. These islands have a continental origin and an arid climate, and the dominant vegetation is maritime desert scrub (Junak & Philbrick 2000). The three Islas San Benito support a population estimated at 270 000 breeding Least Storm-Petrels (Wolf *et al.* 2006), which breed in sympatry with Black Storm-Petrels *O. melania* and Leach's Storm-Petrels *O. leucorhoa*, forming a community of approximately two million breeding individuals (Wolf *et al.* 2006). Based on brief visits by early naturalists, it appears that Least Storm-Petrels start laying in June, and records indicate that eggs reach an advanced stage of incubation in late July. The hatching period spans from August to September (Anthony 1896, Murphy 1936) and fledging from September to October (Howell 2012).

These islands are in an oceanographic transition zone where the surrounding waters are divided into two regions (González-Rodríguez *et al.* 2012): 1) the northern marine zone, which is characterized by subarctic waters and upwelling events that persist throughout the year, and 2) a southern regime of upwelling peaks, which occurs during spring and summer, changing from a temperate to a tropical-subtropical domain during summer and autumn (Durazo & Baumgartner 2002, Durazo 2009, 2015).

Nest monitoring and mist netting

We monitored eggs, chicks, and adults from natural nests every four days from 2013 to 2015. We searched for nests among rock crevices using a flashlight in the main nesting area, located on the northern coast of the island in an area called "Cerro Colorado" (Fig. 1). We selected nests in which chicks were more accessible to handling. Nests were individually marked. In 2013, we monitored 39 nests from 9 October to 28 November, when all chicks fledged. During this time, the chick-rearing period was very advanced; therefore, all nests contained hatched chicks. In 2014, we followed 88 nests from 20 August to 26 November. In 2015, we monitored 66 nests from 2 September to 20 November. We did not monitor nests in 2012.

We recorded breeding success using the following metrics: hatching success relative to eggs laid (percentage that hatched), fledging success relative to chicks hatched (percentage that fledged), and overall success (percentage of eggs that resulted in a fledgling).

An egg was considered deserted when the breeding pair did not return to incubate it even though it was in good condition; as broken when we observed signs of damage and abandonment; and as probably predated when the egg went missing. Nest failure also was considered when chicks died at the nest site or when obvious evidence of predation was observed, such as presence of feather remains. In 2014 and 2015, we left the island before the last chick fledged. Therefore, we considered successful nests those with chicks older than 70 d, and that apparently were in healthy condition. This assumption is based on feathering and body condition; after that age, chicks showed fully developed feathers and had already reached peak mass. Similar to Fork-tailed Storm-Petrels *O. furcata*, Least Storm-Petrels show the highest mortality rates in chicks younger than 20 d (Boersma *et al.* 1980, Drummond & Leonard 2009, Y. Bedolla-Guzmán pers. obs.).

During our first visit to the nests, if an egg was present, we measured its length and width (SE 0.1 mm, with calipers) and checked its weight (SE 0.1 g, with a digital balance). As several species of storm-petrels neglect their eggs for around 1 to 6 d (Pefaur 1974, Campos & Granadeiro 1999), we considered an egg deserted when no adult was found after our third visit (i.e., after at least 12 d). If an adult was present during nest controls, we captured it, ringed it with stainless steel rings for individual identification, measured tarsus length (SE 0.1 mm, with calipers), wing length (SD 1 mm, using a wing rule, not flattened), inner tail feather length (± 1 mm, using a stopped tail rule), bill length (SE 0.1 mm, with calipers), and checked the weight (SE 0.1 g).

In addition to birds captured during nest monitoring, we also captured adults returning to feed chicks at night using mist nets. Mist nets were deployed from 20h00 to 02h00 during a) 36 nights from September to November 2012; b) 21 nights from September to November 2013; c) 14 nights from August to October 2014; and d) eight nights from September to October 2015. This method was applied to a total of 216 adults, who were captured, ringed with stainless steel rings, and measured as described above. Blood and feather samples were taken from all measured adults for molecular sexing. Molecular sex determination of the 113 adults captured in mist nets in 2012 was carried out following standard methods (Griffiths *et al.* 1996).

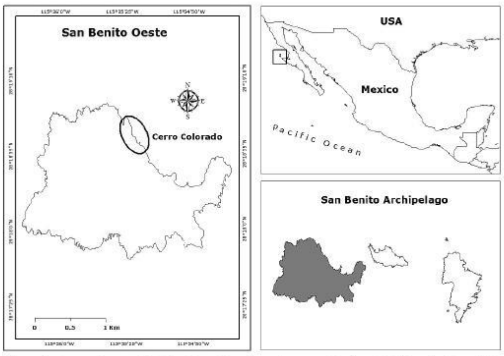

Fig. 1. Location of Isla San Benito Oeste, Baja California Pacific coast, Mexico.

Chick growth

We followed growth patterns by measuring tarsus, wing, bill, and outer as well as inner tail feather lengths every four days. We were able to follow the complete development of the chicks in 2014 and 2015. In 2013, we obtained only partial data on growth; consequently, only some parameters were calculated. The last time pre-fledging measurements were taken was before nestlings left the nest (i.e., 1–4 d before fledging). To estimate the age of chicks of unknown age, in 2014 we followed 11 chicks with known hatch dates from hatching to fledging and obtained a logistic regression from a growth curve for wing length: chick age (d) = $[66.99 \times (\text{wing chord} - 12.21 / 168.59 - \text{wing chord})]^{0.25}$ ($R^2 = 0.94$, $F_{3,198} = 966.90$, $P < 0.001$; Fig. 2). In 2013 and 2015, the ages and approximate hatching dates of chicks already hatched upon our arrival at the island were estimated using the same equation.

Diet composition

We collected regurgitated food samples from adults and chicks opportunistically. Each individual was sampled only once. Adults were sampled while returning to feed the chicks at night, using mist nets (in 2012) or during nest control (2013–2014), and chicks were sampled from natural nests, while being removed from the nests during standard controls. We collected two food samples in 2012, eight samples in 2013, and 19 samples in 2014. We collected regurgitates in 25 mL screw-cap vials during bird handling and fixed them with 70% ethanol. We examined the samples in a laboratory using a stereomicroscope at 40× magnification. Prey taxa were determined with the help of experts and of published keys and guides (Iverson & Pinkas 1971, Wolff 1984, Brinton 1996, Moser 1996, Brinton *et al*. 2000).

Statistical analysis

Statistical analyses were carried out using Statistica 12 (Statsoft Inc. 2014), using $P < 0.05$ to indicate significance; data were plotted using SigmaPlot 11.0 (Systat Software, Inc. 2008). Means are given with standard errors. We tested normality using Kolmogorov-Smirnov tests and homoscedasticity using Levene's tests. All analyses were carried out on chick means calculated for the field season. Breeding parameters were compared among years using chi-square tests, and hatching dates and fledging dates (Julian calendar) were compared using one-way analysis of variance (ANOVA) or the Kruskal-Wallis test.

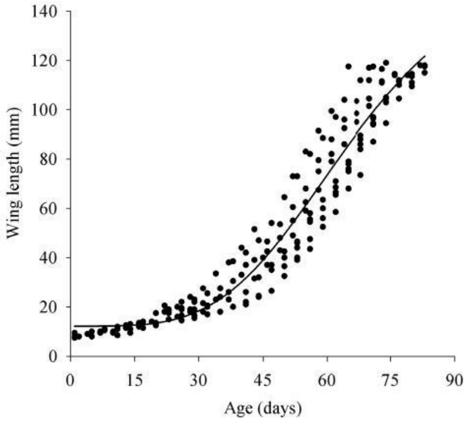

Fig. 2. Wing growth curve of 11 nestling Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2014 breeding season.

RESULTS

Timing of breeding

In 2013, hatching began in late July and, with a few exceptions, continued until early August; in 2014 and 2015, it started around the same time but continued until mid-August (Fig. 3a). The hatching period spanned from 39 to 51 d, and the median hatching date differed between years (Kruskal-Wallis $H_{2,150} = 9.63$, $P = 0.008$); in 2013, chicks hatched 8 d earlier than in 2015 (Table 1). The fledging period started in mid-October and continued through late November in all three years, lasting ~40 d (Table 1, Fig. 3b). The median fledging date also varied among seasons ($H_{2,149} = 12.01$, $P = 0.002$); in 2014, nestlings left the nest 9 d later than in 2013 (Table 1). In 2013, nestlings fledged at a mean age of 81.4 (standard error [SE] 0.4 d; range 77–86 d), whereas in 2014, nestlings left the nest at a mean age of 82.6 (SE 0.7 d; range 72–100 d), and in 2015

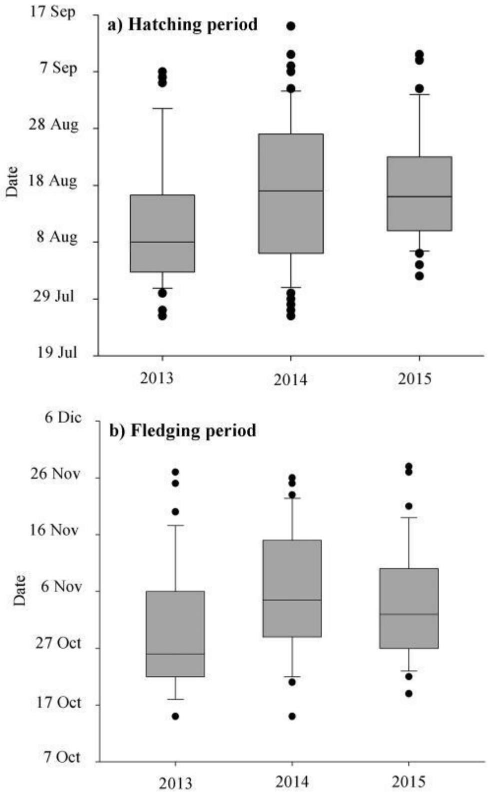

Fig. 3. Hatching and fledging periods of Least Storm-Petrel on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons.

at a mean age of 78.4 (SE 0.6 d; range 70–85 d). Age at fledging differed among years ($H_{2,116} = 23.08$, $P < 0.001$). In 2015, chicks left the nest younger than in the two previous seasons. In 2013, 30% of the chicks that fledged were older than 82 d, whereas in 2014, this percentage increased to 50%, and in 2015, only 17% were older than 82 d.

Breeding success

We calculated hatching success and overall success only in 2014 and 2015, as in 2013, all chicks had already hatched when monitoring started. In 2014 and 2015, hatching success was high (Table 1). The main source of egg failure was desertion (11%), followed by eggs broken (6%), and probable predation (3%; Table 1). In all three years, fledging success remained consistently high (87%–90%) and did not differ among years ($\chi^2 = 0.01$, $df = 2$, $P = 0.993$; Table 1). The causes of chick mortality were starvation (one in 2013, four in 2014, and four in 2015), death after hatching (one chick in 2014), probable predation (three chicks each year), and flooding (one chick in 2014 was found buried after a tropical storm; Table 1).

Measurements of eggs and adults

In 2014 and 2015, the total of 36 eggs averaged 25.8 mm (SE 0.2 mm; range 24.2–28.7 mm) in length and 18.8 mm (SE 0.1 mm; range 17.2–20.0 mm) in width. The mean egg weight was 4.0 g (SE 0.1 g; range 1.9–5.2 g).

TABLE 1
Variation in breeding timing and breeding success of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons

	2013	2014	2015
No. eggs	[a]	88	66
No. eggs deserted		9	8
No. eggs broken		4	5
No. eggs probably predated		4	
No. eggs hatched	39	71	53
No. chicks dead after hatching		1	
No. chicks killed by flooding		1	
No. chicks starved	1	4	4
No. chicks probably predated	3	3	3
Hatching success (% of eggs)	[a]	81%	80%
Hatching period (days)	43 (26 Jul–7 Sep)	51 (26 Jul–15 Sep)	39 (2 Aug– 10 Sep)
Median day of hatching	8 Aug ($n = 38$)	17 Aug ($n = 64$)	16 Aug ($n = 43$)
No. chicks fledged	35	62	46
Fledging success (% of eggs hatched)	90%	87%	87%
Fledging period (days)	43 (15 Oct–27 Nov)	42 (15 Oct–26 Nov)	40 (19 Oct–28 Nov)
Median day of fledging	26 Oct ($n = 35$)	4 Nov ($n = 62$)	2 Nov ($n = 39$)
Overall success (fledglings as a % of eggs)	[a]	70%	70%

[a] Not calculated, as the breeding season was very advanced at the beginning of the monitoring period and only chicks were found.

TABLE 2
Sex differences of adult Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2012 breeding season

	Females				Males				
Measurement	**Mean SE**	**Min.**	**Max.**	***n***	**Mean SE**	**Min.**	**Max.**	***n***	**Test**
Body mass (g)	19.4 SE 0.2	16.6	23.5	57	19.5 SE 0.2	20.2	22.7	56	$t = -0.13$, $df = 111$, $P = 0.898$
Wing length (mm)	123.4 SE 0.4	118	129	57	122.0 SE 0.3	117	128	56	$t = 2.8$, $df = 111$, $P = 0.006$
Tarsus length (mm)	21.6 SE 0.08	19.6	23.0	57	21.6 SE 0.08	20.2	22.7	56	$t = 0.147$, $df = 111$, $P = 0.884$
Inner tail length (mm)	55.1 SE 0.4	46.0	61.0	57	53.5 SE 0.3	47.0	59.0	56	Mann–Whitney $U = 1014.5$, $P < 0.001$
Outer tail length (mm)	46.5 SE 0.4	38.0	53.0	57	44.9 SE 0.4	39.0	53.0	53	$t = 2.6$, $df = 111$, $P = 0.010$
Bill length (mm)	11.0 SE 0.06	11.9	10.1	56	11.2 SE 0.06	10.3	12.2	56	$t = -2.2$, $df = 110$, $P = 0.030$

Females had significantly longer wings and tails than males, whereas males had longer bills than females (Table 2). All other morphological parameters did not differ significantly between sexes (Table 2). We found a sex ratio of 1 male: 1 female in the 113 individuals sexed using molecular methods.

Chick growth

We described chick growth during 2014 and 2015, when it was possible to follow the whole developmental period. In 2013, we were able to calculate partial results only. In 2014, the body mass

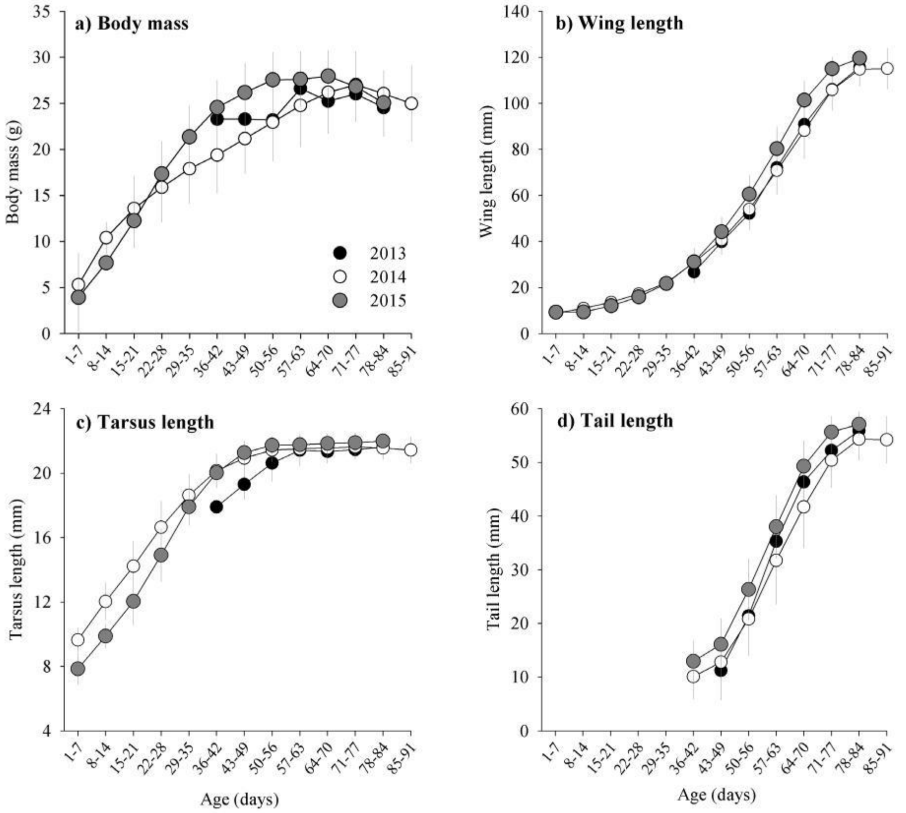

Fig. 4. Chick growth curves of Least Storm-Petrel on Isla San Benito Oeste, Mexico, during the breeding seasons of 2013 (*n* = 27), 2014 (*n* = 53), and 2015 (*n* = 36). The mean and standard error of the mean are given.

TABLE 3
Variation in chick growth parameters of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons

	2013				**2014**				**2015**			
Measurement	**Mean SE**	**Min.**	**Max.**	***n***	**Mean SE**	**Min.**	**Max.**	***n***	**Mean SE**	**Min.**	**Max.**	***n***
Peak mass (g)					26.0 SE 0.5	16.9	32.3	57	27.4 SE 0.3	23.1	31.8	39
Pre-fledging mass (g)	22.5 SE 0.4	18.4	27.0	27	24.6 SE 0.3	18.7	29.5	53	23.7 SE 0.4	19.3	29.5	35
Pre-fledging wing length (mm)	115.9 SE 0.7	110	122	27	118.2 SE 0.4	111	126	53	119.0 SE 0.7	108	126	36
Tarsus length asymptote (mm)	21.7 SE 0.1	19.9	22.6	27	21.9 SE 0.08	20.5	23.5	53	22.2 SE 0.09	21.2	23.2	36
Pre-fledging inner tail length (mm)	56.1 SE 0.5	50.0	63.0	26	55.8 SE 0.3	51	63.5	53	56.9 SE 0.4	50.0	60.0	36
Pre-fledging outer tail length (mm)	48.5 SE 0.4	44.0	54.0	27	47.1 SE 0.3	42	52	53	47.9 SE 0.4	42.0	54.0	36
Pre-fledging bill length (mm)	11.0 SE 0.07	10.2	11.7	27	11.3 SE 0.05	10.4	12.2	53	11.5 SE 0.07	10.7	12.4	36

curve (Fig. 4a) showed a long period of rapid growth (from day 9 to 57). This was followed by a short interval of decelerated growth until day 77, and then a quick mass loss until fledging. In contrast, in 2015 the rapid weight increase was shorter from day 8 to day 43, and peak mass occurred from day 44 to day 74 (Fig. 4a). Peak mass differed among years (Mann–Whitney $U_{102} = 841$, $P = 0.04$) and was higher in 2015 (Table 3). Body mass was described by quadratic regressions (Table 4), while the growth of wings (Fig 4b), tarsi (Fig. 4c), and inner tail lengths (Fig. 4d) were well described by logistic regressions (Table 4).

Pre-fledglings from 2015 developed longer wings ($F_{2,121} = 9.12$, $P < 0.001$), tarsi (Kruskal-Wallis test, $H_{2,121} = 12.33$, $P = 0.002$), and bills ($F_{2,121} = 11.40$, $P < 0.001$) than nestlings from the previous two seasons (Table 3). Nestlings from 2015 left the nest with an inner tail longer than nestlings from 2014 ($H_{2,121} = 7.72$, $P = 0.021$; Table 2). In 2014, pre-fledglings had higher body mass than in 2013 ($F_{2,121} = 7.17$, $P < 0.001$; Table 3).

Diet composition

We found a range of prey items in regurgitated food samples, including crustaceans, squid, and larval fish. Only two species of larval fish were found in 2012: *Vinciguerria lucetia* and *Synodus lucioceps*. In 2013, we identified three species of euphausiids (*Euphausia gibboides*, *Nyctiphanex simplex*, and *Thysanoessa*

TABLE 4
Chick growth curves of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2014 and 2015 breeding seasons

Parameter	Curve shape	Equation
Body mass	Quadratic	2014: mass (g) = $4.45 + 0.51 \times \text{age} - 0.003 \times \text{age}^2$, $R^2 = 0.64$, $F_{3,3037} = 2\,714.0$, $P < 0.001$ 2015: mass (g) $-2.81 + 1.02 \times \text{age} - 0.008 \times \text{age}^2$, $R^2 = 0.70$, $F_{3,1846} = 2\,138.7$, $P < 0.001$
Wing length	Logistic	2014: wing (mm) = $12.99 + 155.82/1 + (\text{age}/68.14)^{-3.9}$, $R^2 = 0.96$, $F_{3,963} = 7\,121.12$, $P < 0.001$ 2015: wing (mm) = $12.83 + 149.30/1 + (\text{age}/62.3)^{-4.4}$, $R^2 = 0.98$, $F_{3,691} = 1\,0318.4$, $P < 0.001$
Tarsus length	Logistic	2014: tarsus (mm) = $9.88 + 12.21/1 + (\text{age}/22.69)^{-2.9}$, $R^2 = 0.88$, $F_{3,969} = 2\,417.24$, $P < 0.001$ 2015: tarsus (mm) = $9.46 + 12.76/1 + (\text{age}/2\,698)^{-4.3}$, $R^2 = 0.94$, $F_{3,696} = 3\,472.8$, $P < 0.001$
Inner tail length	Logistic	2014: inner tail (mm) = $8.07 + 51.34/\ (1 + (\text{age}/61.37)^{-8.0})$, $R^2 = 0.88$, $F_{3,677} = 1\,576.9$, $P < 0.001$ 2015: inner tail (mm) = $9.54 + 52.11/(1 + (\text{age}/58.40)^{-8.0})$, $R^2 = 0.93$, $F_{3,437} = 2\,004.5$, $P < 0.001$

TABLE 5
Diet composition of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2012–2014 breeding seasons

	2012 *n* = 2			2013 *n* = 8			2014 *n* = 19		
	F[a]		*V*[b]	*F*		*V*	*F*		*V*
	n	%	%	*n*	%	%	*n*	%	%
Euphausiacea				5	63	25	8	42	19
Euphausia gibboides				1	13				
Nematoscelis difficilis							3	16	
Nyctiphanes simplex				2	25		3	16	
Thysanoessa spinifera				2	25				
Unidentified							2	11	
Amphipoda							1	5	1
Unidentified							1	5	1
Cephalopoda				1	13	18			
Doryteuthis opalescens				1	13				
Unidentified									
Fish larvae	2	100	100	6	75	57	11	58	67
Vinciguerria lucetia	2	100		2	25		2	11	
Synodus lucioceps	1	50							
Unidentified	1	50		4	50		9	47	

[a] *F* (frequency of occurrence) is the percentage of samples in which prey items of each type were found, and

[b] *V* is the estimated volume in percentage for each main prey group.

spinifera), one species of squid *Doryteuthis opalescens,* and one species of larval fish (*V. lucetia*). In 2014, although most of the samples were too digested for prey identification, we were able to identify the euphausiids *Nematoscelis difficilis* and *N. simplex* as well as larval fish *V. lucetia*. In 2013 and 2014, Least Storm-Petrels consumed a larger volume of larval fish than euphausiids (Table 5).

DISCUSSION

This study provides the first detailed account of breeding phenology, breeding performance, chick growth, and diet during the breeding of Least Storm-Petrels. We determined that the hatching period started in late July, and fledging extended until late November. These results contrast with previous observations that indicated that the hatching period spanned from mid-August to early-September at Isla San Benito Oeste (Anthony 1896, Murphy 1936) and the fledging period from September to October (Howell 2012). This discrepancy might result from the fact that our study was more detailed, facilitated by a longer stay on the island compared to the studies conducted previously, which lasted a shorter period of time.

The timing of breeding differed among years: the hatching period started earlier in 2013 than in 2015 and was longer in 2014, while the fledging period started later in 2014 than in 2013. Differences in the timing of breeding in other storm-petrel species have been related to food supply (Boersma *et al.* 1980) and weather conditions (Drummond & Leonard 2009). On Isla San Benito Oeste, differences in breeding phenology among years might be in response to two anomalous climatic conditions observed in the region during the time span of this study. The first difference is related to the anomalously warm sea-surface temperature that prevailed along the Baja California Pacific coast from the winter of 2013–2014 until April 2015. This phenomenon, identified as the Pacific Warm Anomaly—also known as the "blob"—affected the northeast Pacific, causing low productivity and subsequent decrease in prey availability (Bond *et al.* 2015, Kintisch 2015). The second difference was related to a strong El Niño, which lasted from September to December 2015 (Robinson 2016). The differences in the duration of the hatching period observed in 2014 could be related to lower food availability, consequence of the anomalous conditions. Some birds could have been forced to forage for longer periods in search of less abundant prey, extending the time needed for incubation and, consequently, prolonging the hatching period.

During our study, the anomalous oceanic conditions severely affected other seabird species in the region. For instance, on some Baja California Pacific islands, breeding individuals of Brown Pelican *Pelecanus occidentalis* and Brandt's Cormorant *Phalacrocorax penicillatus* massively deserted their nests in 2015 (Bedolla-Guzmán *et al.* 2016). Similarly, marine mammals, such as California sea lions *Zalophus californianus* and Guadalupe fur seals *Arctocephalus philippii townsendi* breeding on Islas San Benito, decreased in abundance, with pup production reduced to 52%–55% in 2015 compared with 2014 (California sea lion pup production: 2014 = 8792 pups, 2015 = 4585; Guadalupe fur seal pup production: 2014 = 71 pups, 2015 = 39) (Elorriaga-Verplancken *et al.* 2016).

Studies in the Gulf of California indicate that the Least Storm-Petrel breeding seasons are asynchronous among colonies, starting earlier than on Islas San Benito. In the northern Gulf islands (e.g., Isla Partida Norte, 28°53′N, 113°02′W), laying extends from May to June and the fledging period from August to September (Howell 2012, Grupo de Ecología y Conservación de Islas, A.C., unpubl. data). On the other hand, in the southern Gulf colonies (La Lobera, Isla Espíritu Santo, 24°35′N, 110°24′W), laying starts around mid-March and fledging around the beginning of June (Carmona *et al.* 1994). The differences could be related to the marked seasonal-productivity peak, which occurs during winter and spring in that region (Álvarez-Borrego 2010). However, this information should be considered cautiously, as there are no detailed studies for any area in the Gulf of California.

Breeding parameters did not differ among the years studied, as the overall success was consistently high (up to 70%; Table 1). Similarly, Black Storm-Petrels that breed on Islas San Benito also had high hatching and fledging success rates during our study (72%–87%) (Y. Bedolla-Guzmán, unpubl. data). A comparison with storm-petrels investigated elsewhere may offer clues as to why Islas San Benito had such a high success rate. Other members of the genus *Oceanodroma* have also exhibited high breeding success (*O. furcatus* — Boersma *et al.* 1980; *O. homochroa* — Ainley 1995; *O. leucorhoa* — Huntington *et al*. 1996). In contrast, the success rate of species breeding on islands with invasive predators such as the house mouse *Mus musculus* was only 54% (*Pelagodroma marina* — Campos & Granadeiro 1999). Buffer mechanisms that may keep breeding success high and constant in procellariiform species include changes in diet composition (García-Godos *et al.* 2002, Hedd *et al.* 2009, Quillfeldt *et al.* 2010), a flexible foraging strategy (Baduini & Hyrenbach 2003), and regulation of chick provisioning parameters (Weimerskirch *et al.* 2001, Büsser *et al.* 2004, Quillfeldt *et al.* 2007).

Breeding success of other burrow-nesting seabirds, such as alcids breeding on islands off the Pacific Baja California coast, may provide evidence of the impacts of anomalous ocean conditions, such as the "blob" or El Niño, on species with similar foraging strategies as storm-petrels. The Guadalupe Murrelet *Synthliboramphus hypoleucus,* on Isla Guadalupe, had a breeding success rate of 80.9% in 2014 and 2015 (Hernández-Montoya *et al.* 2015, 2016); similarly, the Scripps's Murrelet *S. scrippsi,* on Islas Todos Santos, had an overall success rate of 90% in 2015 (Bedolla-Guzmán *et al.* 2016). In contrast, the Scripps's Murrelet had a very low success rate (28%) on Islas San Benito in 2014 (Ramos-Rendón *et al.* 2014), and the Cassin's Auklet *Ptychoramphus aleuticus* breeding on Isla San Roque and Isla Asunción had a low breeding success rate in 2015 (40%, Bedolla-Guzmán *et al.* 2016).

In 2015, chick growth was higher than during the two previous seasons, and this was reflected in nestlings of higher quality, as chicks showed longer wings, tarsi, and bills. This variable growth pattern observed among the years is in accordance with other species such as Black Storm-Petrel breeding on Isla San Benito (Y. Bedolla-Guzmán, unpubl. data) and Fork-tailed Storm-Petrel in Alaska (Boersma *et al.* 1980, Boersma & Parrish 1998). In contrast to Least Storm-Petrel, Leach's Storm-Petrel on the east coast of North America appears to exhibit uniform growth rates among years (Ricklefs *et al.* 1985). It has been suggested that high chick growth is reached when provisioning rates and food quality are high (Boersma & Parrish 1998). On Isla San Benito, food availability was probably more favorable in 2015. Similar to Least Storm-Petrels, other procellariiform species such as Thin-billed Prions *Pachyptila belcheri* (Quillfeldt *et al.* 2007), Yellow-nosed Albatross *Thalassarche chlororhynchos* (Weimerskirch *et al.* 2001), and Fairy Prions *P. turtur* (Manno *et al.* 2014) can maintain a high fledging success rate despite unfavorable conditions. However, in those species the quality of the offspring was negatively correlated with fledging success.

Least Storm-Petrels preyed mainly on larval fish during all three years. One of the prey, *V. lucetia*, is a tropical-subtropical midwater fish that occurs from Chile to central California and is more abundant during warm events compared with cold events (Funes-Rodríguez *et al.* 2010, Jiménez-Rosenberg *et al.* 2010). In fact, in 2015, according to records, *V. lucetia* larvae were very abundant off the coast of Baja California, perhaps the result of the combination of the "blob" with El Niño 2015–2016 (McClatchie *et al.* 2016). This could explain why in 2014 adults fed their chicks mainly with larval fish, but further study is necessary to evaluate diet composition in cold years. Three euphausiids identified in food samples, *E. gibboides, N. simplex,* and *N. difficilis*, are abundant off the coast of Baja California, with *N. simplex* being more abundant in coastal waters and *N. difficilis* more abundant in oceanic waters (Lavaniegos & Ambriz-Arreola 2011).

In conclusion, we suggest that differences in the timing of breeding and chick growth among years may reflect a variation in food supply associated with the anomalous climate conditions recorded in 2014 and 2015. Long-term data would be necessary to better evaluate the effect of local oceanographic conditions on diet and breeding biology of Least-Storm Petrels in the Baja California region.

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Chapter 3

INTER-ANNUAL VARIATIONS IN THE BREEDING BIOLOGY, CHICK GROWTH AND FEEDING PARAMETERS OF THE BLACK STORM-PETREL (*HYDROBATES MELANIA*) IN RELATION TO ENVIRONMENTAL CONDITIONS AND EXTREME EVENTS

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Inter-annual variations in the breeding biology, chick growth and feeding parameters of the black storm-petrel (*Hydrobates melania*) in relation to environmental conditions and extreme events

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Abstract

Changing environmental conditions may affect the breeding biology and feeding parameters of seabirds. Understanding how species respond to variations in ocean climate conditions is crucial for evaluating their vulnerability to changing oceans. This study examined the influence of inter-annual variations in ocean climate on the breeding biology, chick growth, and provisioning rates of black storm-petrels (*Hydrobates melania*) at San Benito Oeste Island, Mexico (28°18'12" N, 115°35'24" W) over six consecutive breeding seasons (2012-2017). Large-scale climate indices, including the Oceanic Niño Index, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation, as well as local oceanographic conditions (sea-surface temperature, coastal upwelling, chlorophyll-a concentration), were analyzed to assess their relationship with breeding success, breeding phenology, chick growth, and adult provisioning. Oceanographic conditions varied across breeding seasons, with anomalous warming occurring in 2014 and 2015 in the region. Despite these changes, the species maintained high hatching and fledging success (71-90%), except in 2013, when a tropical storm caused high chick mortality (48%). The timing of hatching and fledging remained consistent across seasons. However, feeding parameters varied significantly across years, with smaller meal sizes and reduced feeding rates observed in 2013 and 2014, leading to chicks with lower body masses at fledging. No significant relationships were found between large-scale climate indices or local oceanographic conditions and chick provisioning and chick growth. These results suggest that the black storm-petrel is a resilient species to environmental variability, but vulnerable to extreme weather conditions, and food availability. Further research is needed to understand the influence of other fine-scale processes or preceding ocean conditions on chick provisioning.

Keywords: *Oceanodroma*, provisioning, chick growth, climate change, California Current System, seabird, Procellariiformes.

Introduction

Seabirds are a diverse group adapted to life at sea, highly dependent on marine ecosystems for food and returning to land only to nest or rest (Schreiber and Burger 2001). As apex predators in marine food webs, they are sensitive indicators of ecological changes, reflecting the overall health of marine environments (Piatt and Sydeman 2007; Lescroël et al. 2016). Changes in ocean conditions, such as those driven by climate variability, can impact primary productivity at spatial and temporal scale, subsequently altering the availability and distribution of prey species for seabirds (Sydeman et al. 2001). These variations can influence seabird foraging behavior, trophic ecology, and ultimately their reproductive outcomes, particularly during the breeding season when seabirds are central-place foragers, reflecting the environmental conditions near their breeding colonies (Ramos et al. 2018; Mark Hipfner et al. 2020).

Large-scale climate phenomena such as the El Niño Southern Oscillation (ENSO), characterized by warmer ocean temperatures, disrupt normal upwelling patterns, reducing nutrient availability and productivity in the food web (Barber and Chavez 1983; Chavez et al. 1999; McPhaden et al. 2020). Such disruptions can have cascading effects on seabird populations, decreasing reproductive success and causing higher chick mortality (Jaksic 2004; Jaksic and Fariña 2010; Tompkins and Anderson 2021). Local environmental factors, such as sea surface temperature (SST) and chlorophyll a (Chl a) concentration, play also a critical role in shaping seabird breeding outcomes. SST, a proxy for ocean productivity, is often linked to higher prey abundance and availability (Durant et al. 2007; Hipfner 2009). Cold productive waters are associated with a high frequency of short foraging trips and increase in provisioning rates, leading to greater breeding success and a higher-quality offspring (Weimerskirch et al. 2001; Peck et al. 2004; Quillfeldt et al. 2007; Einoder et al. 2013). In contrast, elevated SSTs and, therefore, low productive waters may increase foraging trip lengths, changes in foraging behavior, and shifts in diet composition (Xavier et al. 2003; Quillfeldt et al. 2010), ultimately resulting in lower breeding success, delay in timing of breeding, lower chick growth rates (Smithers et al. 2003; Quillfeldt et al. 2007), and lower chick body mass at fledging (Weimerskirch et al. 2001).

Additionally, extreme weather events, such as tropical storms, can have devastating effects on seabird colonies by flooding nests and increasing egg and chick mortality, and reducing breeding success (Chambers et al. 2011; Fagundes et al. 2016; Zuberogoitia et al. 2016; Ritenour et al. 2022). These events can also alter prey availability, resulting in lower provisioning rates and poor chick growth (Clairbaux et al.

2021). Over time, these cumulative effects may lead to population declines and increased vulnerability to climate change (Frederiksen et al. 2008; Guéry et al. 2019).

Given the wide range of behavioral and physiological traits in seabirds, understanding how environmental changes impact their breeding biology and feeding behaviors is essential for assessing species resilience for the ongoing and future climate change. Rising sea temperatures, shifting ocean currents, and changes in prey availability have been linked to global declines in seabird populations (Grémillet and Boulinier 2009; Sydeman et al. 2012; Bestley et al. 2020). The extent of these impacts can be species, population or geographically dependent (Waugh et al. 2000; Sandvik et al. 2008; Paiva et al. 2010), according to their foraging strategies, habitat preferences, and physiological adaptations (Hamer et al. 2001). Species with generalist diets and broader habitat ranges may exhibit high behavioral plasticity under variable ocean conditions, enabling them to sustain a constant reproductive effort and moderate the effects of extreme perturbations in the environment (Weimerskirch et al. 2001; Quillfeldt et al. 2007; Einoder et al. 2013; Manno et al. 2014). In contrast, specialist species with more restricted diets and habitats may be more vulnerable to adverse climate changes and may not have the ability to adjust their behavior and therefore experience significant declines in breeding success, and strong changes in ocean climate conditions could be detrimental to them (Thompson and Ollason 2001; Drummond and Leonard 2009; Riou et al. 2011).

Among seabirds, the order Procellariiformes (albatrosses, shearwaters, petrels, diving petrels, and storm-petrels) are pelagic species with long-life traits such as low fecundity, single-egg clutches, and slow growth rates (Brooke 2004). These traits allow them to buffer some environmental variability, employing mechanisms such as shifts in diet composition (García-Godos et al. 2002; Hedd et al. 2009; Quillfeldt et al. 2010), a flexible foraging strategy (Baduini and Hyrenbach 2003), and changes in provisioning behaviour (Weimerskirch et al. 2001; Büsser et al. 2004; Quillfeldt et al. 2007). Storm-petrels *Hydrobates* spp, the smallest seabirds, primarily feeds on zooplankton (Brooke 2004), and as lower trophic level predators in comparison with other larger Procellariiformes, they are expected to quickly respond to changes in oceanic conditions, making it an ideal model for studying climate-ecosystem interactions. Additionally, studies examining how environmental conditions affect reproductive outcomes of storm-petrels are scarce (Oliveira et al. 2023).

The black storm-petrel (*Hydrobates melania*) is a small burrow-nesting pelagic seabird (~60 g) that primarily feeds on Euphausiidae (Bedolla-Guzmán et al. 2021). Its breeding range is restricted to islands off southern California, the Pacific coast of Baja California, and in the Gulf of California, in Mexico (Everett et al. 2021). During the breeding season, black storm-petrel forages within the California Current System, a highly productive but increasingly variable ecosystem influenced by human-induced climate change (Sydeman et al. 2009). This variability has significantly affected foraging success and reproductive outcomes in many seabirds breeding in the region (Wolf et al. 2009; Schmidt et al. 2014). In the Pacific coast of Baja California, other Procellariiformes have exhibited different responses to ocean conditions. For instance, the black-vented shearwater (*Puffinus opisthomelas*) responded to warm events reducing burrow occupancy and delaying nest initiation (Keitt et al. 2003), while the least storm-petrel (*Hydrobates microsoma*) showed a variable breeding phenology and chick growth, but a high breeding success rate (Bedolla-Guzmán et al. 2017).

This study aims to examine how inter-annual variations in both local (SST, chlorophyll-*a*, coastal upwelling intensity) and large-scale (Oceanic Niño Index, Pacific Decadal Oscillation, North Pacific Gyre Oscillation) ocean conditions affect the breeding biology, chick growth, and feeding parameters of black storm-petrels at San Benito Oeste Island, Mexico, over six breeding seasons (2012–2017). We hypothesize that: 1) cooler ocean conditions enhance primary productivity, favoring adult provisioning and consequently chick growth and breeding parameters, 2) warmer and low productivity conditions will lead to decreased provisioning rates and lower chick growth and survival, and 3) extreme weather events will negatively impact reproductive success.

Methods

Study species

The black storm-petrel is widely distributed along the Eastern Pacific, from northern California (39°N) to southern Peru (15°S) (Everett et al. 2021). As a typical Procellariiformes, it lays a single egg, has a slow reproductive rate, intense and extended biparental care, and slow chick development (Brooke 2004). This species nests in natural crevices or in burrows built by other species such as auklets (Ainley 1984). The incubation period ranges from early May to late August and the chick-rearing period spans from late June to mid-November. Parents return to feed their chicks only at night, and nestlings remain in the nest for about 11 to 12 weeks (Everett et al. 2021). Adults and fledglings leave breeding colonies every fall and disperse north to Baja California and central California, and south to Central America and South America (Everett et al. 2021).

Study site

We studied black storm-petrels from 2012 to 2017 on San Benito Oeste Island (28°18'12" N, 115°35'24" W; 3.64 km^2), the westernmost island of the archipelago consisting of three small islands, off the Pacific coast of the Baja California Peninsula, Mexico (Figure 1). These islands hold a population of 580,000 breeding black storm-petrels that breed in sympatry with the Leach’s storm-petrel (*Hydrobates leucorhous*) and the least storm-petrel (*Hydrobates microsoma*) (Wolf et al. 2006). The San Benito archipelago is a natural protected area (Diario Oficial de la Federación 2016) located in the southern limit of the California Current System in an oceanographic transition zone that is highly productive year-round (Espinosa-Carreon et al. 2004). We monitored eggs, chicks, and adults from August to November using artificial wooden nest boxes distributed on the western side of the island near active natural burrows. These nest boxes were installed in 1999 as part of a study of the breeding biology of Cassin’s auklet *Ptychoramphus aleuticus* (Shaye Wolf pers. comm.). Cassin’s auklets breed in winter; therefore, nests become available for black storm-petrels during late spring. The high environmental variability of this region produces fluctuations in plankton at different times and spatial scales (Lavaniegos 2009; Gaxiola-Castro 2010; Lavaniegos and Ambriz-Arreola 2012) which may affect prey availability for seabirds.

Breeding parameters

We checked nests with eggs every three days for hatched chicks, and then at intervals of 1 7 days until fledging. We recorded breeding success using the following metrics: hatching success relative to eggs laid (the percentage that hatched) and fledging success relative to chicks hatched (the percentage that fledged). Nest failure was considered when the egg was broken or abandoned after more than 10 days, when the chick died at the nest site, or when obvious evidence of predation was observed, such as the presence of feathers remains. In 2012, 2016, and 2017, we left the island before the last chicks fledged, thus, we considered successful nests those with chicks older than 70 days, and that apparently were in healthy condition, considering that higher mortality occurs in the early growth stage similar than the least storm-petrels (Bedolla-Guzmán et al. 2017). Breeding phenology was investigated using hatching and fledging dates. The hatching date was considered as the first day we recorded the hatched chick in regular checks, otherwise hatching dates were estimated using body measurements-age relationships (see Supplement). The fledging date was the first day we recorded a healthy fully- feathered chick leaving the nest.

To evaluate chick growth patterns, we measured body mass (± 0.1 g, with a digital balance) almost daily to estimate peak mass (g) and pre-fledging mass (g), and wing length (mm, with a caliper). A similar regular chick handling in Leach's storm-petrels had no influence on growth rates and acute stress response (Fiske et al. 2013). The last time pre-fledging measurements were taken was before nestlings left the nest (i.e., 1–4 d before fledging).

We estimated chick-feeding rates (g per night) and meal sizes (g) based on daily chick mass and metabolic mass loss correction (Quillfeldt and Peter 2000), a method that has been shown to be reliable (Gladbach et al. 2009). Chicks were weighed in the same order, starting at 1600 hours local time approximately. We recorded the exact weighing time for each chick almost daily. In 2013, chicks were weighed for three nights and days at an interval of 3-4 hours to determine weight loss after and before a feeding event. For this, we monitored chicks weighing 30 g to 96 g and aged 17 to 77 days. The metabolic mass loss after a feeding event was higher than before a feeding event ($P < 0.05$). The mass loss (dm; in g/h) after a feeding event was described as follows: $dm\ (g/h) = -0.013\ g/h + 0.005\ g/h \times m$, where m is the mass of the chicks at the start of the interval. The metabolic mass loss before a feeding event was described as: $dm\ (g/h) = 0.069\ g/h + 0.003\ g/h \times m$. Meal sizes were calculated as the sum of estimated metabolic mass loss and the mass change overnight.

Environmental data

To evaluate the influence of environmental conditions on the breeding parameters of the black storm-petrel we chose the chick-rearing period (July to November). During this time, parental conditions and investment may be influenced by environmental variations, potentially affecting the chicks' body condition and survival (Fay et al. 2015). To describe regional environmental conditions in the eastern Pacific Ocean, we used three climatic indices: 1) the Oceanic Niño Index (ONI) 3.4, 2) the Pacific Decadal Oscillation (PDO) index, and 3) the North Pacific Gyre Oscillation (NPGO) index. These climatic indices were selected because they affect zooplankton abundance in the region (Lavaniegos et al. 2015), the main prey for black storm-petrel (Bedolla-Guzmán et al. 2021).

ONI index values were obtained from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center at: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). El Niño events are ≥ +0.5, and for La Niña ≤ -0.5 in 5 consecutive 3-months running means.

Monthly PDO values were obtained from NOAA at: https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat (Mantua 1999). The PDO index is based on the leading principal component of monthly SST variability in the North Pacific Ocean, north to 20°N (Mantua et al. 1997). The PDO values consist of persistent positive or negative temperature anomalies, classified as warm (positive value) or cool (negative value), which have been shown to impact marine ecosystems through changes in the species composition, distribution and abundance (Mantua and Hare 2002; Becker et al. 2007).

The NPGO is derived from the second principal component of sea surface height anomalies, positive values indicate the strengthening of the North Pacific Current and in consequence the California Current (Di Lorenzo et al. 2008). NPGO values were obtained at: https://www.o3d.org/npgo/data/NPGO.txt.

To characterize local oceanographic conditions close to the San Benito Islands we chose three fine-scale indices: 1) sea-surface temperature anomaly (SSTa), 2) coastal upwelling index anomaly (CUIa), and 3) chlorophyll-a surface concentration anomaly (Chl-a), within 450 km around San Benito Islands. The daily composites of SST values at 0.1° resolution and 8-days composites of Chl-a values at 0.04° resolution were downloaded from http://coastwatch.pfeg.noaa.gov/erddap from POES AVHRR and Aqua MODIS satellite images, respectively. The daily and monthly CUI situated within this range (24°N, 113°W; 27°N, 116°W; 30°N, 119°W) was obtained from NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Data Services website (https://oceanview.pfeg.noaa.gov/products/upwelling/dnld) (Schwing et al. 1996).

Data analysis

Statistical analyses were carried out using R 4.4.1 (R Core Team 2023) considering $\alpha = 0.05$ as the significance level. We used generalized linear mixed-effects models (GLMMs) to test interannual differences on breeding success (binomial family), phenology (Gaussian family), chick provisioning (Gaussian family), and chick growth parameters (Gaussian family) using the "nlme" and "lme4" packages (Bates et al. 2014). Nest identification number was fitted as a random effect to account for pseudo-replication, as several same nests were followed during most of six years of study. Models were ranked based on their Akaike's Information Criterion (AIC) and were checked to ensure normality and homoscedasticity of residuals before further statistical analysis. For significant differences among years, we used estimated marginal means *post hoc* test with multiple comparison adjustments (Tukey's HSD) using the "emmeans" package (Lenth 2022).

Inter-annual variations in regional and local environmental variables were assessed using One-way ANOVA or Kruskal-Wallis tests and Tukey tests as post-doc test. Data normality was tested with Shapiro-Wilk test and homogeneity of variances with Brown-Forsythe test.

We evaluated the influence of large-scale climate indices and local ocean conditions on breeding parameters with significant interannual differences (fledging success, peak body mass, mass at fledging, feeding rate, and meal size) using GLMMs and following the same considerations described above.

Results

Hatching success and fledging success of black storm-petrels were relatively high (71 to 90%) over time, except in 2013 when fledging success was 36% (Table 1). We did not find significant differences among seasons in hatching success, but we did in fledging success ($P < 0.001$). In 2013, a tropical storm reached the island at the end of August and caused the mortality of 48% of chicks hatched because many of the wooden nest boxes were flooded. During the six years of the study, the mean hatching period spanned from 9 to 17 August, and the mean fledging period occurred from 23 to 31 October (Table 1). Mean hatching and fledging dates did not vary significantly between years ($P > 0.05$).

Feeding parameters, including both feeding rate and meal size, varied significantly across the years. Chicks in 2013 received less food per night compared to those in other seasons ($P < 0.001$; Fig. 2). Additionally, chicks were provided with smaller meals during the 2013, 2014, and 2015 breeding seasons than in 2012, 2016, and 2017 ($P < 0.001$; Fig. 3). Consequently, we observed significant differences in chick growth across the years (Table 2). Chicks from 2013 and 2014 reached a lower peak mass compared to other years, except for 2016 ($P < 0.001$; Fig. 4). The peak mass was attained at a younger age in 2013 and 2017 (around 55 days) compared to 2012 and 2015 (around 62 days; $P < 0.01$). In 2013, chicks left the nest with a lower body mass than in the other five years ($P < 0.001$), and chicks from 2014 fledged lighter than those from 2016 and 2017 ($P < 0.001$; Fig. 5).

Large-scale climate indices during the breeding period of storm-petrels (July to November) varied significantly between years (Table 3). The Oceanic Niño index ($H_{5,30} = 23.912$, $P < 0.001$) was significantly different in 2015 (positive value) than in years with negative values (2013, 2016, and 2017). Similarly, the Pacific Decadal Oscillation index ($F_{5,30} = 26.65$, $P < 0.001$) was significantly different in years with positive trends 2014, 2015, and 2016 than in the rest of the years that showed a negative trend. The North Pacific Gyre Oscillation index ($F_{5,30} = 20.40$, $P < 0.001$) presented significantly higher values in 2012 than the other breeding seasons. In contrast, local oceanographic conditions within 450 km of San Benito Islands did not significantly vary among years (Table 3). Sea-surface temperature anomaly ($H_{5,30} = 6.285$, $P = 0.279$), coastal upwelling anomaly ($F_{5,30} = 1.565$, $P = 0.222$), and chlorophyll-a concentration ($H = 3.034$, $P = 0.695$) showed similar patterns among the years. Even though large-scale climate indices were highly variable during the study period, they did not explain inter-annual differences in fledging success, mass at fledging, and chick provisioning parameters ($P > 0.05$).

Discussion

In this study, we evaluated the influence of inter-annual variations in oceanographic conditions at local- and large-scale on the breeding biology, chick provisioning, and chick growth of the black storm-petrel during six consecutive years (2012–2016). We found that black storm-petrels sustained high breeding success during the six years, except when an extreme event caused high chick mortality in 2013. In contrast, chick provisioning and chick growth differed among seasons. However, our hypotheses that cooler ocean conditions would explain favorable feeding parameters and, as a result, high breeding parameters and chick growth, while warmer conditions and extreme weather events would depress these variables, were only partially supported.

Our results indicated that neither large-scale climate indices or local ocean processes explained differences in the breeding and feeding parameters of the black storm-petrel. In contrast to our findings, several studies have shown that seabirds provisioning is affected negatively by warm SST events that may modify prey availability and accessibility in foraging areas (Peck et al. 2004; Erwin and Congdon 2007; Quillfeldt et al. 2007; Devney et al. 2010). Likewise, long-term studies have shown seabirds in the California Current System modify timing of breeding and diet composition in relation to upwelling intensity (Abraham and Sydeman 2004, 2006; Wolf et al. 2009). But, our results are aligned with other studies that did not find a relationship with environmental variables (Manno et al. 2014). Additionally, the local oceanographic conditions were relatively stable between the years or our study. This lack of correlation suggests that other regional or local processes may be modifying adult provisioning that were not considered in this study. For instance, prey patchiness or fine-scale oceanic features such as eddies and fronts might be important factors that could influence foraging behavior and therefore seabird breeding parameters (De Pascalis et al. 2021). San Benito Islands are in a transitional zone where eddies and fronts are developed due to the peninsula topography, enhancing ocean productivity in the area (Espinosa-Carreon et al. 2004).

The consistently high hatching success and fledging success (>70%) of black storm-petrels exhibited during most of the years are in line with findings from other studies. This result is similar to Everett et al. (2021) which in a two-year study on Coronado Islands, located in northern Baja California, reported a hatching success of around 50% and a fledging success that ranged from 81% to 100%. The least storm-petrel *Hydrobates microsoma*, a sub-tropical species that breeds on San Benito Islands sympatrically with the black storm-petrel, also exhibited high hatching success and fledging success (80-90%) in 2013 and 2014 (Bedolla-Guzmán et al. 2017), despite variable ocean conditions at regional scale. This suggests that this species exhibits resilient behavior under changing conditions, adjusting chick provisioning, and probably foraging locations or diet composition as observed in other species (Baduini and Hyrenbach 2003; Quillfeldt et al. 2010). In fact, black storm-petrels mainly consumed krill during 2012 and 2013 (Bedolla-Guzmán et al. 2021), while shifted to larval fish in 2014 (YBG unpublished data). However, this flexibility resulted in fledglings leaving the nest with lower body mass and this trade-off could reduce post-fledging survival and future recruitment (Reid et al. 2000). The body mass and the size of flight feathers at fledging are two crucial factors that influence fledgling survival as high body reserves increase the probability to overcome unfavorable prey availability conditions after leaving the nest and larger wings allow to expand foraging range (Ricklefs et al. 1985; Sagar and Horning 1998). This high breeding success might be related to the relatively stable local environment around San Benito (e.g., SST, upwelling, chlorophyll-a), but probably small daily or weekly changes not detected in this study, could have influenced chick provisioning and probably diet composition. Similar studies have found that shifts at short-time scale in local environmental conditions can significantly affect seabird foraging success and chick growth (Frederiksen et al. 2004; Durant et al. 2007).

The severe impact of the tropical storm in 2013 revealed the high vulnerability of the black storm-petrel to extreme weather events. This finding is consistent with studies on other seabird species, where extreme weather has led to catastrophic breeding failures (Catry et al. 2013; Ramos et al. 2018). The flooding of nest boxes caused high chick mortality (48%) and also destroyed natural sandy burrows used by the black storm-petrels (YBG personal observations). As climate change is expected to increase the frequency and intensity of such extreme events (Walsh et al. 2016), the long-term viability of black storm-petrels breeding on sandy burrows on San Benito Islands could be at risk. Natural nests located in rocky areas could be the least affected during these events, but this habitat is limited in this archipelago.

We found significant variation in chick provisioning, but no differences in chick survival, with lower provisioning parameters (feeding rates and meal size) in 2013, 2014, and 2015. Similarly, other species of Procellariiformes have shown the same pattern (Weimerskirch et al. 2001; Quillfeldt et al. 2007; Einoder et al. 2013) which pointed out the higher sensibility of provisioning measurements over breeding parameters to identify changing environmental conditions in species with high behavioural plasticity (Quillfeldt et al. 2007). The significant reduction of these parameters, which may reflect suboptimal foraging conditions, might be linked to changes in prey availability in response to varying oceanographic conditions. Other studies have found a link between poor ocean conditions and reduced prey availability to a decrease in chick provisioning and consequently in chick growth (Peck et al. 2004; Quillfeldt et al. 2007). From 2014 to the beginning of 2016, anomalous warming conditions prevailed in the California Current System due to the conjunction of two phenomena, The Blob and El Niño Southern Oscillation (Leising et al. 2015). The Blob was an anomalous warming extratropic event that appeared in the winter 2013 2014 and by 2015 extended from the Gulf of Alaska to Baja California (Di Lorenzo and Mantua 2016), with the highest temperatures off Baja California recorded in winter-spring 2015 (Amaya et al. 2016). These events together suppressed coastal upwelling and ocean productivity, and severely affected seabird populations in the whole region (Cavole et al. 2016). For instance, other burrowing seabirds such as the Cassin's Auklet experienced high chick and adult mortality (Jones et al. 2024). However, the lesser chick quality in 2013 contrasts with favorable La Niña cooler conditions. A possible explanation may be that prey availability and abundance in the region during summer and autumn were driven by the conditions during the most productive period in the previous spring. In 2013, in waters off Baja California, there were upwelling-favorable average yearly values but anomalies in spring were not greater than normal (Leising et al. 2014). In contrast, in spring 2012 temperatures remained cooler than long-term average and positive upwelling index anomalies and a high and positive anomaly for chlorophyll-a concentration were registered (Bjorkstedt et al. 2012; Wells et al. 2013). Chlorophyll-a surface concentration during 2013 was approximately half compared to 2012. A time-lag in seabird response to oceanographic conditions is plausible because zooplankton does not increment its abundance simultaneously with upwelling events and may lag productivity by weeks to months, depending on the reproductive rate of the species and the hydrographic conditions (Lavaniegos et al. 2010). However, information about the effect of previous local oceanographic conditions on zooplankton abundance is not available for the breeding period of black storm-petrels (summer-autumn) for 2013, only during July-August 2014 a negative anomaly in Euphausiidae abundance was recorded (Leising et al. 2015).

In conclusion, our results suggest that the black storm-petrel is resilient to fluctuating oceanographic conditions, maintaining high breeding success despite inter-annual environmental variability. However, the species is vulnerable to extreme weather conditions such as tropical storms, and variations in food availability. The lack of a clear relationship between large- and local-scale oceanographic variables and chick provisioning or chick growth indicates that fine-scale processes, such as eddies, prey patchiness, or preceding ocean conditions, may play a more critical role. Future research should focus on high-resolution oceanographic monitoring and detailed prey availability assessments during the pre-breeding and breeding seasons to better understand factors influencing chick provisioning. Additionally, long-term studies on post-fledging survival and recruitment are needed to assess the potential long-term impacts of reduced chick quality during years of suboptimal food supply.

Supplementary Information The online version contains supplementary material available at:

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Author contributions Study conception and design: PQ, JMF, AAM. Data acquisition: YBG, JFM, PQ. Data analysis: YBG, ERM, BRM, GOG, MVB. Drafting the manuscript: YBG. All authors revised the manuscript. All co-authors agreed to be listed and approved the submitted version of the manuscript.

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Data and code availability The datasets and code used during this study are available from the corresponding author on reasonable request.

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval Fieldwork was conducted with ethical international standards for the care and use of wild animals and approved by the Mexican environmental authority Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) thought the Dirección General de Vida Silvestre (DGVS); research permits SGPA/DGVS/01411/12, SGPA/DGVS/00232/13, SGPA/DGVS/01190/14, SGPA/DGVS/02918/15, SGPA/DGVS/02292/16, and SGPA/DGVS/03625/17. Extreme care was taken to minimize stress of chicks and to protect eggs from potential predators. Handling time was kept to a minimum, mostly less than 15 min.

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Figure 1 Location of San Benito Oeste Island, Baja California Pacific coast, Mexico.

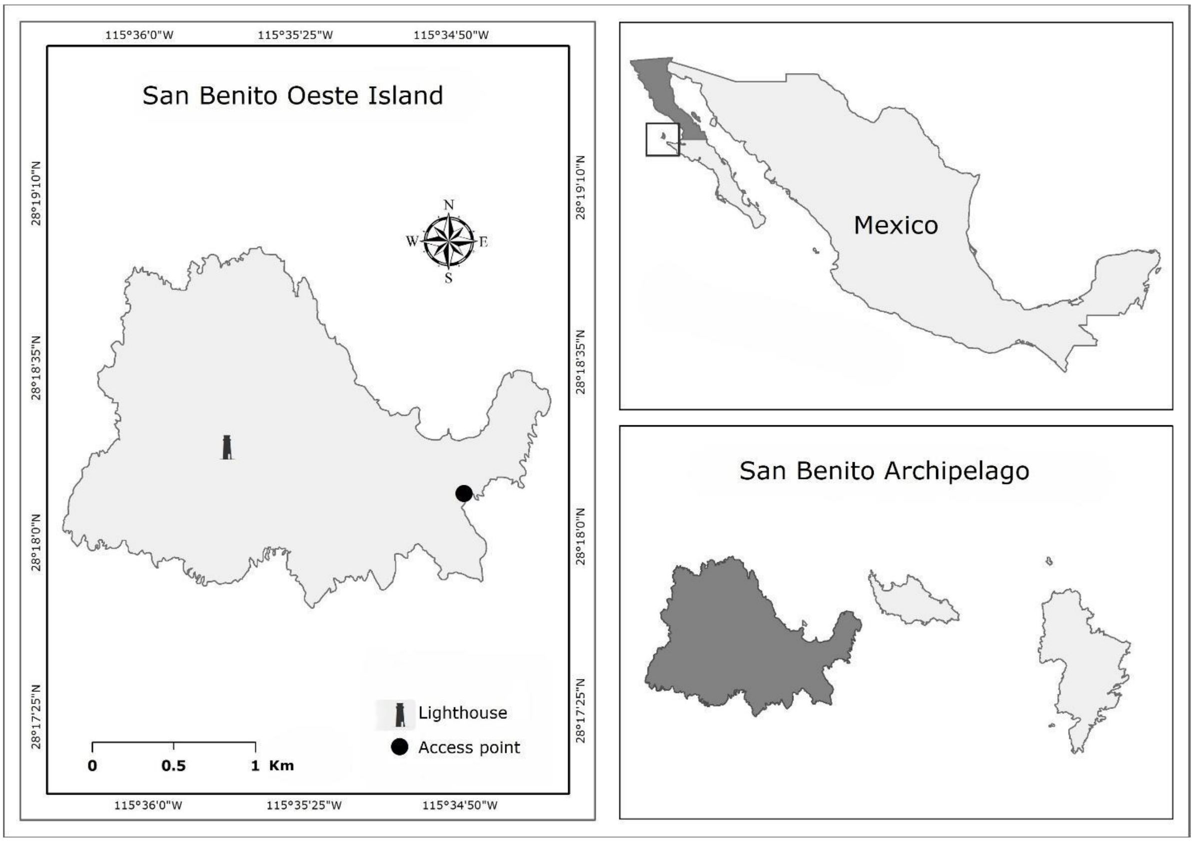

Figure 2 Mean feeding rate (g/night) of the black storm-petrel *Hydrobates melania* at San Benito Oeste Island, Mexico during breeding seasons 2012–2017.

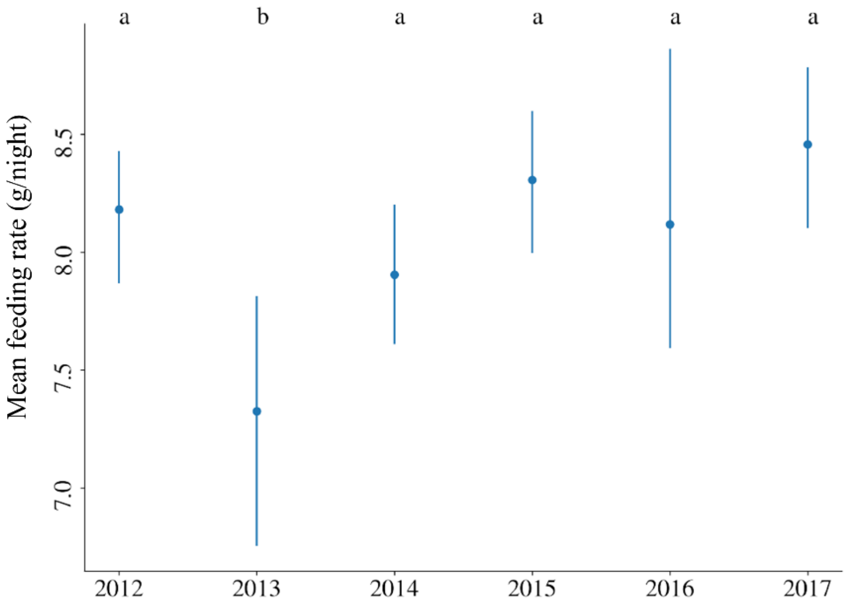

Figure 3 Mean meal size (g) of the black storm-petrel *Hydrobates melania* at San Benito Oeste Island, Mexico during breeding seasons 2012–2017.

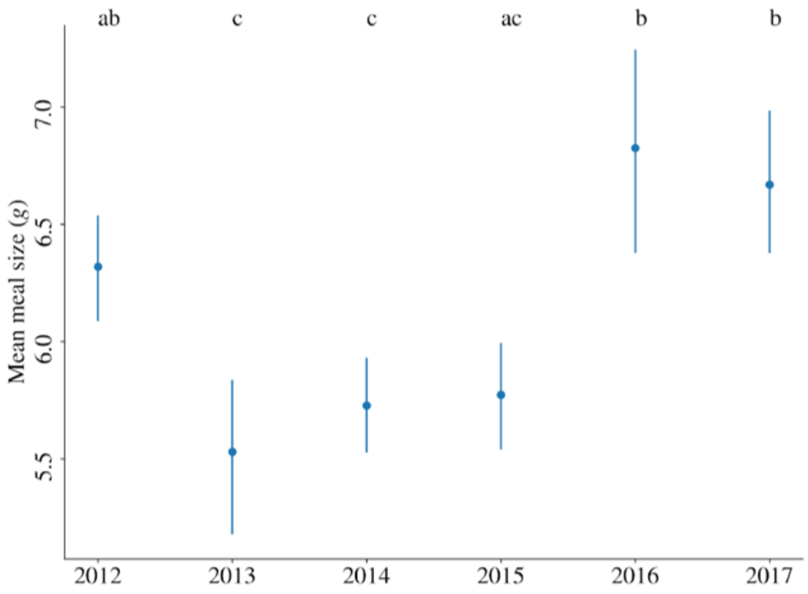

Figure 4 Mean peak mass (g) of the black storm-petrel *Hydrobates melania* at San Benito Oeste Island, Mexico during breeding seasons 2012–2017.

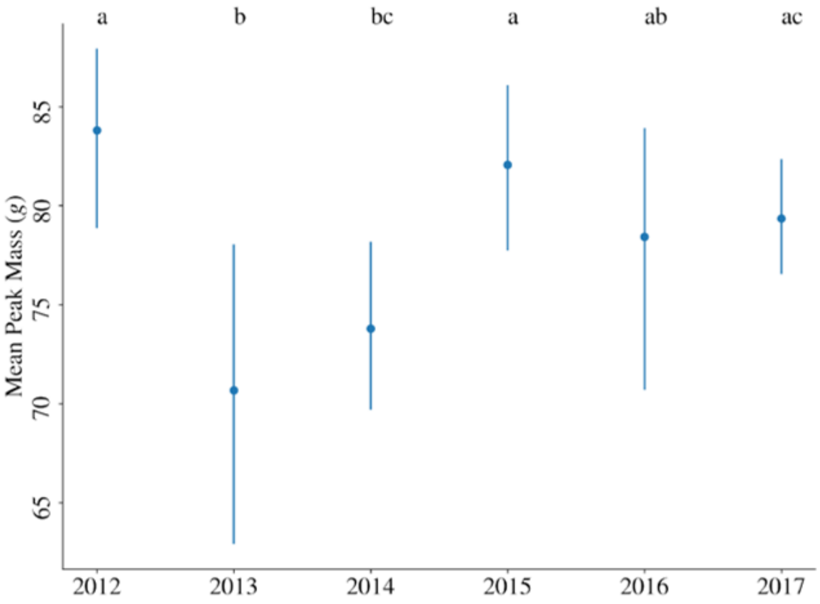

Figure 5 Mean pre-fledging mass (g) of the black storm-petrel *Hydrobates melania* at San Benito Oeste Island, Mexico during breeding seasons 2012–2017.

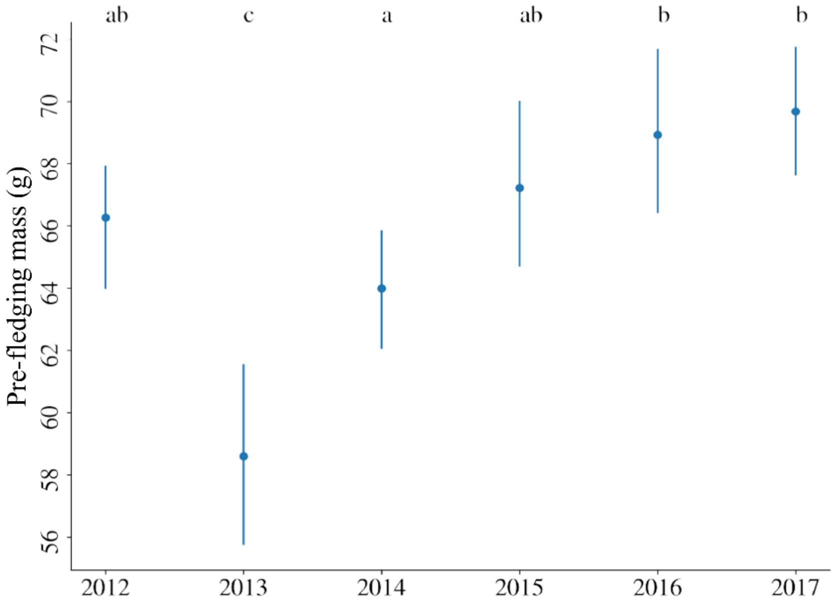

Table 1. Inter-annual comparison of breeding success (hatching success relative to eggs and fledging success relative to chicks) and breeding phenology (hatching dates and fledging dates) of black storm-petrels *Hydrobates melania* on San Benito Oeste Island, Mexico, during breeding seasons 2012–2017. Medians and confidence intervals of 95% are given. Sample sizes are shown in parentheses.

Breeding season	**Breeding success**				**Breeding phenology**			
	Hatching success (%)	**95% C.I.**	**Fledging success (%)**	**95% C.I.**	**Hatching date**	**95% C.I.**	**Fledging date**	**95% C.I.**
2012	72.4	59.6 - 83.7	87.8[a]	76.5 - 96.9	12 Aug (35)	9 - 15 Aug	28 Oct (34)	22 Oct - 1 Nov
2013	73.3	64.1 - 83.0	36.4[b]	23.7 - 49.1	11 Aug (28)	7 - 15 Aug	25 Oct (20)	22 Oct - 1 Nov
2014	81.8	71.6 - 90.6	81.8[a]	69.8 - 92.0	9 Aug (49)	6 - 12 Aug	26 Oct (40)	23 - 31 Oct
2015	89.6	79.5 - 97.7	90.7[a]	80.0 - 97.8	17 Aug (38)	13 - 22 Aug	31 Oct (36)	29 Oct - 5 Nov
2016	88.9	77.8 - 97.4	87.2[a]	74.2 - 97.1	17 Aug (37)	11 - 20 Aug	29 Oct (31)	24 Oct - 1 Nov
2017	85.3	72.7 - 95.0	88.6[a]	76.3 - 97.2	13 Aug (34)	9 - 17 Aug	23 Oct (30)	21 - 27 Oct

Table 2. Inter-annual comparison of chick growth (peak mass, age at peak mass and pre-fledging mass) and chick provisioning (meal size and feeding rate) of black storm-petrels *Hydrobates melania* on San Benito Oeste Island, Mexico, during breeding seasons 2012−2017. Medians and confidence intervals of 95% (C.I.) are given. Sample sizes are shown in parentheses.

Breeding season	**Chick growth**						**Chick provisioning**			
	Peak mass (g)	**95% C.I.**	**Age at peak mass (days)**	**95% C.I.**	**Pre-fledging mass (g)**	**95% C.I.**	**Meal size (g)**	**95% C.I.**	**Feeding rate (g d^{-1})**	**95% C.I.**
2012	83.8 (34)^{b}	78.9 - 87.9	62.7 (34)^{b}	60.2 - 65.5	66.3 (30)^{b,c}	64.0 - 68.0	6.3 (35)^{b}	6.1 - 6.5	8.2 (35)^{b}	7.9 - 8.4
2013	70.7 (19)^{a}	62.9 - 78.0	54.9 (19)^{a}	49.1 - 60.7	58.6 (20)^{a}	55.7 - 61.6	5.5 (25)^{a}	5.2 - 5.8	7.3 (25)^{a}	6.8 - 7.8
2014	73.8 (39)^{a}	69.7 - 78.2	59.7 (39)^{b}	56.3 - 63.0	64.0 (38)^{c}	62.0 - 65.9	5.7 (47)^{a}	5.5 - 5.9	7.9 (47)^{b}	7.6 - 8.2
2015	82.0 (32)^{b}	77.7 - 86.1	61.7 (32)^{b}	59.2 - 64.3	67.2 (35)^{b,c}	64.7 - 70.0	5.8 (38)^{a}	5.5 - 6.0	8.3 (38)^{b}	8.0 - 8.6
2016	78.4 (37)^{a}	70.7 - 83.9	58.8 (37)^{b}	55.1 - 62.6	68.9 (23)^{b}	66.4 - 71.7	6.8 (37)^{b}	6.4 - 7.2	8.1 (37)^{b}	7.6 - 8.9
2017	79.4 (31)^{b}	76.5 - 82.3	56.0 (31)^{a}	53.2 - 58.5	69.7 (25)^{b}	67.6 - 71.8	6.7 (32)^{b}	6.4 - 7.0	8.5 (32)^{b}	8.1 - 8.8

Table 3. Comparison of regional and local environmental predictors among breeding seasons 2012 2017 (July to November) of the black storm-petrel *Hydrobates melania*. Local environmental predictors were extracted within 450 km of San Benito Oeste Island, Mexico. Mean and standard deviation (SD) are given.

Environmental predictor	**2012**		**2013**		**2014**		**2015**		**2016**		**2017**	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Large scale predictor												
El Niño Oceanic index 3.4	0.2^{a}	0.14	-0.28^{a}	0.09	0.3^{a}	0.26	2.2^{b}	0.32	-0.68^{a}	0.05	-0.53^{a}	0.35
PDO index	-1.4^{a}	0.81	-0.75^{a}	0.42	1.13^{b}	0.46	1.53^{b}	0.45	0.93^{b}	0.62	0.14^{a}	0.11
NPGO index	1.64^{a}	0.25	0.09^{b}	0.57	-0.14^{b}	0.52	-1.81^{b}	0.41	-0.06^{b}	0.80	-0.99^{b}	0.71
Local scale predictor												
Chlorophyll *a* concentration (mg m^{-3})	0.14	0.03	0.12	0.02	0.12	0.03	0.13	0.02	0.12	0.03	0.13	0.03
SST anomaly	0.08	0.48	0.01	0.27	-0.01	0.14	0.35	0.41	-0.33	0.67	0.27	0.31
Coastal upwelling index anomaly	-0.07	37.7	9.8	29.0	-27.6	13.2	-18.3	31.4	1.67	19.9	12.5	22.4

APPENDIX

Curriculum vitae

Education

2012 to present	Doctoral candidate – Dissertation at the Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Germany, Supervisor: Prof. Dr. Petra Quillfeldt
2007-2009	MSc. Coastal Oceanography. Marine Sciences Faculty. Autonomous University of Baja California, Mexico.
2002-2006	BSc. Marine Biology. Autonomous University of Baja California Sur, Mexico.

Work experience

2015–present	Grupo de Ecología y Conservación de Islas, A.C. Project Director. Marine Birds Project.
2010–2012.	Grupo de Ecología y Conservación de Islas, A.C. Project Coordinator. Wildlife Fauna Project.
2009	Grupo de Ecología y Conservación de Islas, A.C. 2009. Field biologist. Wildlife Fauna Project
2006	Teacher Assistant, Autonomous University of Baja California Sur.

Teaching experience

2016- 2019	Co-supervisor for MSc degree students: ● Filogenia y diferenciación genética de las poblaciones de *Oceanodroma cheimomnestes* y *O. socorroensis* en Isla Guadalupe, Baja California, México. ● Diagnóstico de la población reproductiva de Pardela de Islas Revillagigedo (*Puffinus auricularis*) en Isla Socorro.

Field experience

2012–2014	Field work in Mexico capturing, sampling, and measuring black, Leach's and least storm-petrels.
2015–present	Field work in several islands in Mexico monitoring, capturing, sampling, tracking with GPS and GLS, and implementing social attraction techniques with 15 seabird species including storm-petrels.
2017	Training in seabird monitoring in Maine, USA.

Memberships

2015 to present	Pacific Seabird Group

List of publications

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Bolam, F. C., Mair, L., Angelico, M., Brooks, T. M., Burgman, M., Hermes, C., **Bedolla-Guzmán, Y.** ... & Butchart, S. H. (2021). How many bird and mammal extinctions has recent conservation action prevented?.Conservation Letters, 14(1), e12762.

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Conference contributions

52nd Annual Meeting of Pacific Seabird Group / 48th Annual Meeting of the Waterbird Society. Community-led biosecurity and seabird conservation on the Baja California Pacific Islands, Mexico. 6-9 January, 2025. Heredia, Costa Rica. [*Talk*]

7th International Albatross and Petrel Conference. Inter-annual variation in the reproductive performance, provisioning and growth of the Black Storm-Petrel in relation to environmental conditions. 20-26 May 2024. Ensenada, Mexico. [*Talk*]

Pacific Seabird Group 49th Annual Meeting. Breeding success, breeding phenology, chick growth, and provisioning of the Black Storm-Petrel under variable ocean conditions. 22-25 February 2022. Virtual Meeting. [*Talk*]

3rd World Seabird Conference. Restoring breeding seabird colonies using social attraction on the Baja California Pacific Islands, Mexico. 4-8 October 2021. Virtual Conference. [*Talk*]

Pacific Seabird Group 48th Annual Meeting. Year-round niche segregation of three sympatric *Hydrobates* storm-petrels from Northwest Mexico, Eastern Pacific. 22-26 February 2021. Virtual Meeting. [*Talk*]

27th International Ornithological Congress. Two decades of achievements in the restoration of seabirds on Mexico’s islands. 19-26 August 2018. Vancouver, Canada. [*Talk*]

Pacific Seabird Group 45th Annual Meeting. Seabird restoration on the Baja California Pacific Islands, Mexico: A five-year binational and multinstitutional experience. La Paz, Baja California, Mexico. 21-24 February 2018. [*Talk*]

9th California Islands Symposium. Seabird restoration program on Mexican islands: a decade of sistematic activities, outcomes and lessons learned. 3-7 October 2016. Ventura, California, USA. [*Talk*]

6th International Albatross and Petrel Conference. Breeding successfully under variable ocean conditions: provisioning, diet, and chick growth of the black storm-petrel *Oceanodroma melania*. 19-23 September 2016. Barcelona, Spain. [*Talk*]

Pacific Seabird Group 43rd Annual Meeting. Monitoring and restoration of burrow nesting seabirds on the Baja California Pacific Islands, Mexico. 10-13 February 2016. O’ahu, Hawaii, USA. [*Talk*]

Pacific Seabird Group 43rd Annual Meeting. Spatial and dietary segregation among three sympatric stormpetrels *Oceanodroma* spp. breeding on islands off Baja California, Mexico. 10-13 February 2016. O’ahu, Hawaii, USA. [*Talk*]

2nd World Seabird Conference. Breeding biology of the least storm-petrel *Oceanodroma microsoma*. 26-30 October 2015. Cape Town, South Africa. [*Poster*]

Waterbird Society 38th Annual Meeting. Breeding success, chick provisioning and diet of the black storm-petrel *Oceanodroma melania*. 4-7 November 2014. La Paz, Baja California. Mexico. [*Talk*].

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