Feeding ecology of coexisting Heermann's gull (*Larus heermanni*) and elegant tern (*Thalasseus elegans*) chicks, based on stable isotope measurements

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ABSTRACT: The Heermann's gull and the elegant tern are considered Near Threatened by the IUCN Red List of Threatened Species and under special protection under Mexican environmental law. Close to 95% of the world populations of both species breed on Isla Rasa (Gulf of California). As both species breed on the same island, competition for trophic resources can be expected to be high. Here, the feeding ecology of chicks of both species, as well as the contribution by prey species provided by adults, was studied using stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis in 3 consecutive breeding seasons (2017, 2018, and 2019). Results of the stable isotope analysis revealed that although some segregation in the δ^{13}C and δ^{15}N values exists between both species, isotopic mixing model outputs indicated that fishes were the most important prey group for both. However, at the prey species level, the most important prey consumed by Heermann's gulls were northern anchovy, Pacific sardine, and Pacific mackerel, followed by pelagic crab, whereas elegant terns consumed mainly northern anchovy. The trophic width estimated with the stable isotope values during 2017 and 2019 was higher for the Heermann's gull than for the elegant tern. In contrast, for 2018, the trophic width of the elegant tern was higher than that of the Heermann's gull. In addition, both species showed a high degree of trophic width overlap during 2017 and 2019 (overlap probability 0.67 and 0.79, respectively). These results highlight the ability of the Heermann's gull to redirect its food intake to what might be the most accessible prey groups, a feeding strategy that allows the coexistence.

KEY WORDS: Vulnerable seabird species · Feeding ecology · Stable isotopes · Isla Rasa · Gulf of California

1. INTRODUCTION

Seabirds are important organisms in marine ecosystems because they occupy different trophic levels, from primary consumers to top predators, and constitute a key group to understanding ecosystem functioning (Williams & Buck 2010, Mancini & Bugoni 2014). The Heermann's gull *Larus heermanni* and the elegant tern *Thalasseus elegans* are 2 seabirds categorized as Near Threatened by the IUCN (BirdLife International 2020a,b) and subject to special protection by the Government of Mexico

(SEMARNAT 2010); thus, it is necessary to promote research to improve knowledge about these species for better management and conservation strategies. Over 90% of the nesting populations of both species coexist during the breeding season on Isla Rasa (Gulf of California, Mexico) (Velarde et al. 1994, Velarde 1999, Perez et al. 2020). This island hosts the most important breeding colonies for both species on a global scale, estimated at more than 200 000 individuals of each species during peak years (Velarde 1999, Velarde et al. 2015b). The high abundance of pelagic fishes in the Gulf of California (Páez-Osuna et al. 2016) explains the importance of this marine region for these and other species of seabirds such as the California brown pelican *Pelecanus occidenetalis californicus*, yellow-footed gull *L. livens*, royal tern *T. maximus*, and others (Velarde et al. 2005); in this context, if fishes are the main prey resources, what feeding strategies do seabirds use to coexist?

Regarding feeding ecology, both Heermann's gulls and elegant terns feed mainly on the Pacific sardine *Sardinops sagax*, northern anchovy *Engraulis mordax*, and Pacific mackerel *Scomber japonicus* during the breeding season (Velarde et al. 1994, 2013, 2015a), leading to a possible overlap of their trophic niches and increasing the interspecific competition for food (Baker et al. 2007, Mancini & Bugoni 2014, Marinao et al. 2019). The study of the feeding ecology of seabirds has traditionally relied on sampling regurgitates from crop content, which produces short-term diet information (Polito et al. 2011). Previous reports of the diet of Heermann's gulls and elegant terns were based on the identification of prey sources (Velarde et al. 1994, 2013, 2015a), without understanding the trophic interaction by competition or the feeding strategy of each species. More recently, stable isotope analysis (SIA) has been used as a complementary tool to investigate the feeding ecology, trophic position, and niche width of marine predators including seabirds (Hobson et al. 1994, Navarro et al. 2010). SIA is based on the concept that the concentrations of the stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C) in an animal's tissues are a direct reflection of its diet (Cherel et al. 2005). Depending on the type of tissue analyzed, a different insight into the ecological niche and diet of seabirds can be obtained, allowing the study of different windows of time in the development of seabird tissues: for short periods, blood and liver and muscle tissues are used, while for longer periods (weeks to months), feathers, bones, or claws are used (Hobson 1993). In addition, the use of stable isotope values for consumers and for their potential prey results in the esti-
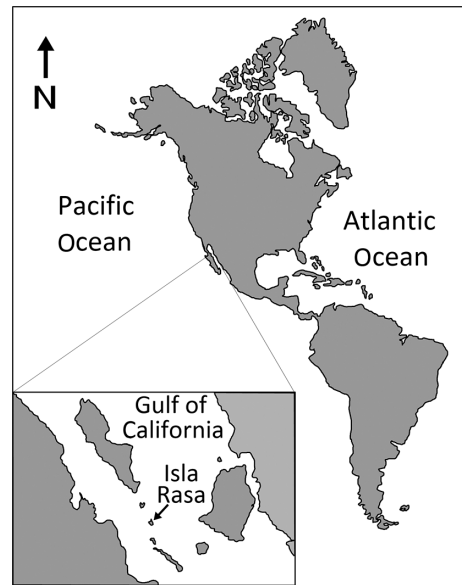

Fig. 1. Isla Rasa in the Gulf of California, a vital breeding area for Heerman's gulls *Larus heermanni* and elegant terns *Thalasseus elegans*

mation of the relative contribution of each prey to the diet of the consumer (Parnell et al. 2010).

Considering that Heermann's gulls and elegant terns are species of ecological importance in the Gulf of California, the main objective of this work is to describe the feeding ecology of chicks of both species nesting on Isla Rasa. This study provides new information about the ecology of the Hermann's gull and the elegant tern in their most important breeding area, offering new data on how these 2 sympatric marine predators exploit available resources.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted on Isla Rasa (Midriff Islands region of the Gulf of California; Fig. 1). The Gulf of California is in the northwestern part of the Mexican Republic, occupying a marine surface area of 283 000 km^2, with 898 islands, including Isla Rasa (Sans-Aguilar 2018). Isla Rasa is a volcanic island that has a surface area of 0.68 km^2 with a maximum elevation of 35 m, flat areas covering 22% of the island's surface, and rocky ridges that are covered by rocky mounds and volcanic structures (Velarde et al. 2014, 2015b). This island, located in the northwestern section of the gulf, has high primary productivity levels resulting from the nutrient transport of

waters from under a shallow pycnocline into the euphotic zone (Valdez-Holguín & Lara-Lara 1987), driven by 2 mechanisms: (1) a permanent vertical mixing system promoted by strong tidal currents around the region of the larger islands in the central area and (2) coastal wind-driven upwelling (Roden & Groves 1959). The high primary productivity favors the reproduction of massive populations of small pelagic fishes (Lluch-Cota 2000, Murphy et al. 2002).

2.2. Collection of prey samples

Fresh regurgitations of adult birds of the 2 species were collected during the breeding season in 2017, as the diet for both species included the same species through time (Velarde et al. 1994, 2004, 2013, 2015a); no samples of regurgitation were collected in 2018 and 2019. Regurgitations were collected from adults returning to the colony within a period of approximately 3 h after sunset. Adults were captured with a 9 m long by 2 m high mist net with a 70 mm mesh. The net was placed directly above the ground and about 200 to 300 m from the target colony. According to Velarde et al. (1994), this distance does not cause disturbances or alteration to the nesting birds. Only adults with prey in the stomach were included in the diet analysis. Each regurgitation was stored in a plastic bag and transported to the field camp for identification on the same day of collection. Complete individuals of prey species were identified in the field according to the field guides and reports of Quinlivan (1974), Miller & Lea (1976), Thompson & McKibbin (1981), Tordesillas-Barnard (1992), and Roedel (1948). Lastly, approximately 5 g of muscle tissue of each prey species was collected. Prey samples were dried, stored, and transported to the Instituto Tecnológico de Chetumal in sterilized glass vials to avoid contamination.

2.3. SIA

Samples of down feathers (3–5 feathers) of 32 Heermann's gull chicks and a dorsal feather (1 feather) of 39 elegant tern chicks were used for the isotopic analysis in 2017. For 2018 and 2019, 30 dorsal feathers from each species were used. Feathers were used because no damage is caused to the individuals and because the feathers integrate the chick-rearing period of both species (Hobson & Clark 1992). Those from 2017 were pectoral down feathers from chicks between 3 and 7 d old; those from 2018

were dorsal feathers of chicks averaging 11 d old; and those from 2019 were dorsal feathers of chicks averaging 19 d old. Muscle and feather samples were dried, powdered, and lipid extracted (following Bligh & Dyer 1959), and 0.28 to 0.33 mg of each sample was packed into tin capsules. Isotopic analyses of prey samples and feather samples from 2017 were performed at the stable isotope laboratory of the Estación Biológica de Doñana (LIE-EBD, Sevilla, Spain), whereas feather samples from 2018 and 2019 were analyzed at the stable isotope laboratory of the Universidad Nacional Autónoma de México (LAIE, UNAM, Mérida, Mexico). Encapsulated samples were combusted at 1020°C using a continuous-flow isotope ratio mass spectrometry system by means of a Flash HT Plus elemental analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific). The isotopic composition is expressed in the standard notation of δ (‰) relative to Vienna Pee Dee belemnite carbon ($\delta^{13}C$) and atmospheric nitrogen N_2 ($\delta^{15}N$). Based on laboratory standards, the measurement error was approximately ± 0.1 and ± 0.2 for $\delta^{13}C$ and $\delta^{15}N$, respectively.

2.4. Diet analysis

The analysis of prey identified in the regurgitations was performed using the numerical percentage (%N) and frequency of occurrence (%FO) following Liao et al. (2001). The %FO of each prey was calculated as the percentage of birds in which the prey occurs in any given sample. The %N was calculated as the number of a certain prey type relative to the total number of prey. To identify the feeding strategy of both seabirds, a graphical representation of the %FO and %N of prey items was created following Costello (1990): points positioned close to 100% occurrence and 100% abundance are the dominant prey item, points positioned close to 100% occurrence and 1% abundance indicate that the predator has a generalized diet, and points close to 1% occurrence and 100% abundance indicate a specialized diet by some predators. According to Costello (1990), if the points are spread along and below the diagonal originating at the origin to the 100% occurrence and abundance, this suggests that the feeding was homogeneous among the predators.

The number of prey species found in the regurgitations of both species was used to build randomized cumulative prey curves using the vegan package (Oksanen et al. 2010) in R (R Development Core

Team 2017). This routine generates a graphic representing a species accumulation curve (±2 SD) by plotting 500 random permutations of the data, and the significance between the last 3 points was tested to identify the asymptote; the diet is well described when the last 3 points approach the asymptote (Hurtubia 1973, Bizzarro et al. 2007).

To estimate the diet composition of both seabird species based on their isotopic values, stable isotope analysis in R (SIAR) was applied (R Development Core Team 2017). The SIAR routine is based in a Bayesian isotopic mixing model (Parnell et al. 2010). The model was based on the concentrations of $\delta^{13}C$ and $\delta^{15}N$ in both chicks and prey, with the inclusion of the stable isotope ratios and variability of the predators and prey (Parnell et al. 2010). Six prey species were used in the model: 3 individuals of *Cetengraulis mysticetus*, 5 *Engraulis mordax*, 5 *Sardinops sagax*, 5 *Scomber japonicus*, 1 *Dosidicus gigas*, and 2 *Pleuroncodes planipes*. The use of fresh prey collected from the adult regurgitates guarantees that it corresponds to the actual prey that is being consumed by chicks (Hobson & Clark 1992). Additionally, trophic enrichment factors (TEFs) of 4.15 ± 1.63 for $\delta^{15}N$ and 1.90 ± 2.40 for $\delta^{13}C$ were used, corresponding to the average of the transfer factors of feathers of the ring-billed gull *Larus delawarensism* ($\delta^{13}C$ TEF = 0.20 ± 1.30 and $\delta^{15}N$ TEF = 3.00 ± 0.20) (Hobson & Clark 1992) and feathers of the black-tailed gull *L. crassirostris* ($\delta^{13}C$ TEF = 3.60 ± 0.50 and $\delta^{15}N$ TEF = 5.30 ± 0.80) (Mizutani et al. 1992), since there are no TEF reports for Heermann's gulls and elegant terns.

Estimation of the diet composition through the 3 years was based on the following assumptions: (1) Down feathers were produced inside the egg; thus, the $\delta^{15}N$ and $\delta^{13}C$ values corresponded to the prey consumed by the mother. It is known that adult Heermann's gulls arrived at Isla Rasa 45 d before the breeding season (Velarde 1999), so the prey consumed by females in the area is reflected in the eggs. Also, the dorsal feathers reflect the prey consumed by chicks, because feathers represent a temporal sequence of tissue synthesis over days to weeks and provide a short-term record of diet (Wiley at al. 2010). (2) No bias was introduced by using different feather tracts on different species and in different years. We are comparing the isotope values of feathers before chicks left the island without moulting. There is no information related to the isotope values of different feathers for the 2 seabirds, but Deme et al. (2021) found no differences in the isotope values when comparing primary, secondary, back, rump, or throat feathers of *Setophaga citrina*. (3) Different

ages of chicks in each year would not affect the $\delta^{15}N$ or $\delta^{13}C$ isotope ratios or sources, because the prey provided by parents did not vary between years. (4) There are no age-specific changes in physiology that would affect the isotope ratios at these early chick states. Since all seabirds excrete uric acid, this is not an issue to be considered for the isotope analysis in seabirds (Becker et al. 2007).

2.5. Trophic position and width

Based on the stable isotope values, the trophic position of each species was calculated as TP = $(\delta^{15}N_{consumer} − \delta^{15}N_{prey}/TEF) + TP_{prey}$ (Post 2002). The TP_{prey} was 3.12, which corresponds to the species *E. anchoita* (Sanger 1987, Tudela & Palomera 1997, Forero et al. 2004), and the TEF was 4.15.

The trophic width for both species and years was estimated using the standard corrected ellipse area (SEAc) (Jackson et al. 2011). SEAc was calculated using stable isotope Bayesian ellipses in R (SIBER) (Jackson et al. 2011, R Development Core Team 2017). Trophic width is related to the extent of the isotopic niche exploited by a particular predator; the routine includes Bayesian inference techniques that allow the comparison between data sets with different sample sizes (Jackson et al. 2011). The overlap probability between SEAc was calculated using the nicheRover package, which calculates the probability that an individual of group 1 is found in the ellipse of group 2 (Swanson et al. 2015).

2.6. Statistical analysis

Kruskal-Wallis tests with *a posteriori* contrast by pairs between years adjusted with Bonferroni corrections were applied to compare the stable isotopic values of $\delta^{15}N$ and $\delta^{13}C$ between species and years. Differences of isotope values between species were tested using a Mann-Whitney *U*-test. All analyses were performed using the IBM SPSS v. 19 statistics program.

3. RESULTS

3.1. Diet information based on regurgitation analysis

Fig. 2 shows the 2 cumulative prey curves of seabirds; the cumulative prey curves were adequate to
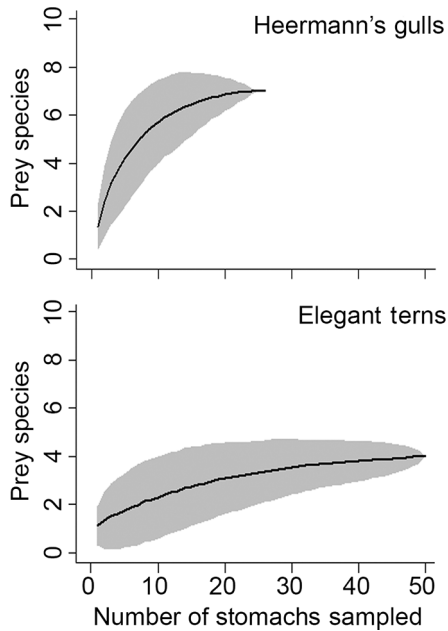
Fig. 2. Cumulative prey curves of Heermann's gulls (top panel) and elegant terns (bottom panel) based on prey identified in regurgitations
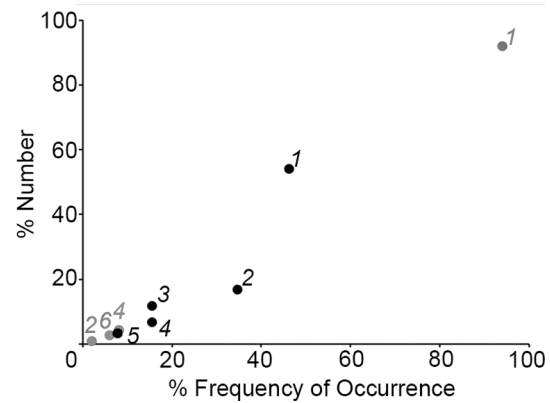

Fig. 3. Graphical representation of the predatory feeding strategy of Heermann's gulls (black dots) and elegant terns (gray dots) and prey importance to the diet based on occurrence (% frequency of occurrence) and abundance (% number). 1: *Engraulis mordax*; 2: *Sardinops sagax*; 3: *Ctengraulis mysticetus*; 4: *Scomber japonicus*; 5: *Pleuroncodes planipes* and *Dosidicus gigas* (coincident); 6: other fishes

describe the diet (p > 0.05). The analysis of regurgitations from 25 adult Heermann's gulls allowed the identification of 6 prey species: 4 fishes, 1 crustacean, and 1 cephalopod. According to the %N and the %FO, the most important prey for the studied year were *Engraulis mordax* (%N = 55, %FO = 46), followed by *Sardinops sagax* (%N = 18, %FO = 35), *Cetengraulis mysticetus* (%N = 12, %FO = 15), *Scomber japonicus* (%N = 7, %FO = 15), *Pleuroncodes planipes* (%N = 4, %FO = 8), and *Dosidicus gigas* (%N = 4, %FO = 8). For 50 adult elegant terns, the analysis of regurgitations showed 3 fishes as prey. According to the %N and %FO, the most important prey was *E. mordax* (%N = 94, %FO = 94), the second was *S. japonicus* (%N = 5, %FO = 8), and the last was *S. sagax* (%N = 1, %FO = 2). The feeding strategy for both seabirds suggested that the feeding was homogeneous among the predators (Fig. 3), but *E. mordax* resulted as the most dominant prey species for both predators.

3.2. SIA results

The median $\delta^{13}C$ value of Heermann's gulls in 2017 was −16.09‰, and the mean (±SD) was −16.33 ± 1.11‰; in 2018, the median was −15.92‰, and the mean was −15.96 ± 0.31‰. In 2019, the median and mean values were 15.54 and −15.52 ± 0.39‰, respec-

tively. The median value of elegant terns in 2017 was −15.37‰, and the mean was −15.44 ± 0.40‰. However, in 2018, the median value increased to −14.83‰, and the mean was −15.05 ± 0.70‰. In 2019, the median value dropped to −14.88‰, and the mean was −14.94 ± 0.39‰. According to the Kruskal-Wallis test, the median $\delta^{13}C$ values for Heermann's gulls differed significantly among the 3 years ($H_{(2)}$ = 20.24, p < 0.05); differences were found in the comparisons of values between years 2019 and 2018 and between years 2019 and 2017. For elegant terns, the median values of 2017 were significantly different to those of 2018 and 2019 ($H_{(2)}$ = 27.05, p < 0.05). According to the Mann-Whitney U-test results, differences were observed in the comparisons of isotope values between species for each year (U-2017 = 1001, U-2018 = 805, U-2019 = 772, p < 0.05).

The median $\delta^{15}N$ value of Heermann's gulls in 2017 was 19.35‰, and the mean was 19.10 ± 1.05‰; in 2018, the median value was 19.87‰, and the mean was 19.81 ± 0.38‰; in 2019, the median value was 20.31‰, and the mean was 20.24 ± 0.45‰. The median $\delta^{15}N$ value of elegant terns in 2017 was 19.07‰, and the mean was 19.15 ± 0.45‰; in 2018, the median value increased to 19.87‰ and the mean to 19.70 ± 0.70‰; in 2019, the median value was 20.47‰, and the mean was 20.41 ± 0.28‰. Regarding the Kruskal-Wallis results, the median values of $\delta^{15}N$ for both species showed differences among the 3 years (Heermann's gull $H_{(2)}$ = 20.24, elegant tern $H_{(2)}$ = 27.05, p < 0.05); the post hoc Tukey tests showed that the $\delta^{15}N$ values of Heermann's gulls were different between 2017 and 2019. For elegant

terns, the median δ^{15}N values were different between 2017 and 2018 and between 2017 and 2019. According to the Mann-Whitney *U*-test results, the comparison of the δ^{15}N values between species showed no significant differences (*U*-2017 = 574, *U*-2018 = 442, *U*-2019 = 358.50, p > 0.05).

3.3. Isotopic niche and trophic level

The isotopic niche breadths measured by the SEAc for Heermann's gulls were 1.57, 0.32, and 0.54‰^{2} for 2017, 2018, and 2019, respectively (Fig. 4). For elegant terns, the SEAc values were 0.58, 0.89, and 0.32‰^{2} for 2017, 2018, and 2019, respectively (Fig. 4). The overlap probability values to find Heermann's gulls within the SEAc of elegant terns were 0.67, 0.12, and 0.79 for 2017, 2018, and 2019, respectively. The overlap probability values to find elegant terns within the SEAc of Heermann's gulls were 0.34, 0.38, and 0.58 for 2017, 2018, and 2019, respectively.

According to the δ^{15}N values, the trophic levels for Heermann's gulls were 3.63 in 2017, 3.80 in 2018, and 3.90 in 2019, while for elegant terns, the trophic levels were 3.64 in 2017, 3.77 in 2018, and 3.94 in 2019.

3.4. Isotopic contribution of prey

The median and mean values, respectively, for *C. mysticetus* were 18.75 and 18.56 ± 0.43‰ for δ^{15}N, and −15.57 and −15.67 ± 0.37‰ for δ^{13}C; for *E. mordax*, they were 17.12 and 16.80 ± 0.86‰ for δ^{15}N and were −17.00 and −17.07 ± 0.93‰ for δ^{13}C; for *S. sagax*, they were 16.99 and 16.95 ± 0.83‰ for δ^{15}N and were −17.19 and −17.76 ± 1.13‰ for δ^{13}C; for *S. japonicus*, they were 16.00 and 16.10 ± 0.72‰ for δ^{15}N and were −18.91 and −18.95 ± 0.71‰ for δ^{13}C; for *Pleuroncodes planipes*, they were 16.14 and 16.14 ± 0.64‰ for δ^{15}N and were −17.91 and −17.91 ± 0.01‰ for δ^{13}C; lastly, for *D. gigas*, the mean values were 19.69‰ for δ^{15}N and −16.53‰ for δ^{13}C.

Regarding the isotope contribution, fishes were the most important prey contributors for both species (Fig. 5). For Heermann's gulls in 2017, the contribution of prey showed that the most important prey was *S. japonicus* (36%), followed by *P. planipes* (32%), *S. sagax* (14%), *E. mordax* (13%), *C. mysticetus* (3%), and *D. gigas* (2%). In 2018, the most important prey was *P. planipes* (32%), followed by *S. japonicus* (30%), *E. mordax* (18%), *S. sagax* (15%), *C. mysticetus* (3%), and *D. gigas* (2%). In 2019, the most impor-
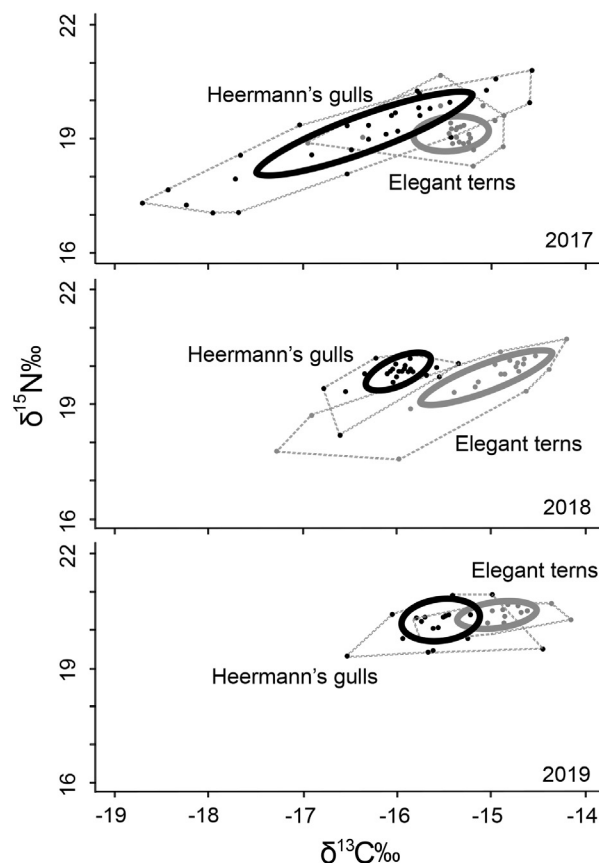

Fig. 4. Isotopic standard ellipses of Heermann's gulls (black dots) and elegant terns (gray dots) during 2017 (top panel), 2018 (middle panel), and 2019 (bottom panel). δ^{15}N: stable nitrogen isotope; δ^{13}C: stable carbon isotope

tant prey was *P. planipes* (29%), followed by *S. japonicus* (24%), *E. mordax* (21%), *S. sagax* (16%), *C. mysticetus* (7%), and *D. gigas* (3%) (Fig. 5). For elegant terns in 2017, the most important prey was *E. mordax* (37%), followed by *S. japonicus* (37%) and *S. sagax* (26%). In 2018, the most important prey was *E. mordax* (42%), followed by *S. japonicus* (34%) and *S. sagax* (24%). In 2019, the most important prey was *E. mordax* (39%), followed by *S. sagax* (32%) and *S. japonicus* (29%) (Fig. 5).

4. DISCUSSION

In this study, we present new information on the feeding ecology of the Heermann's gull and the elegant tern during the breeding period on Isla Rasa, Gulf of California, by combining the use of stable isotope and regurgitation analyses. As previous reports demonstrated, fishes were the main prey sources for both species; nevertheless, the use of other prey spe-
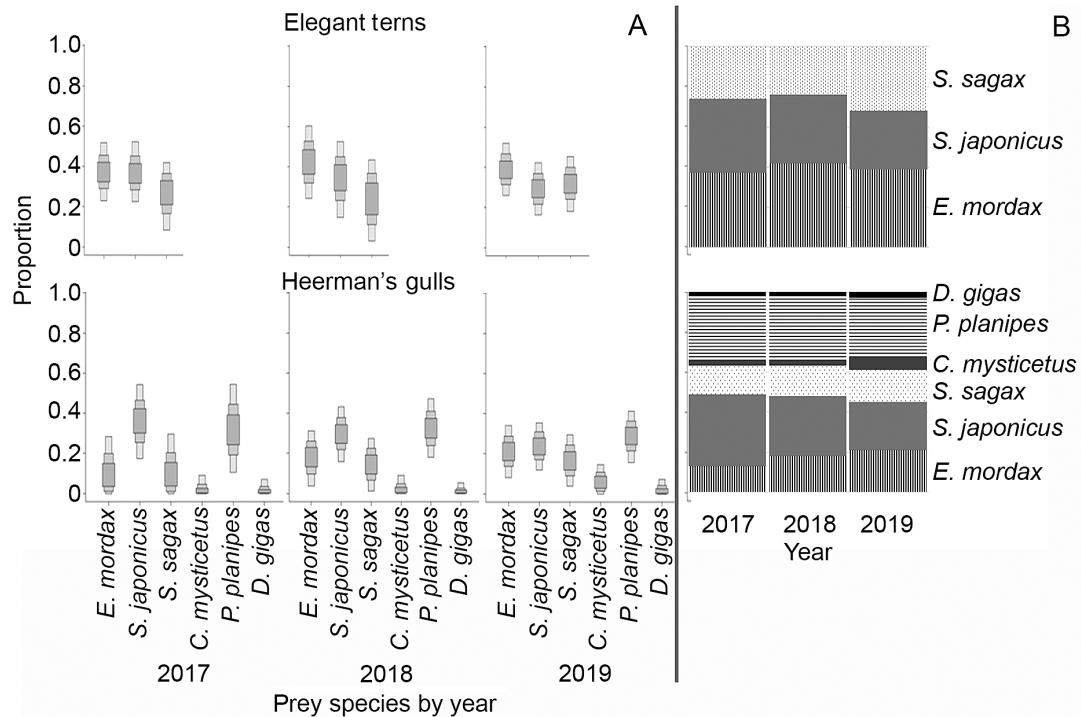
Fig. 5. (A) Modeled proportion of prey groups in the diet of Heermann's gulls and elegant terns. (B) Cumulative proportion of prey species by year

cies by Heermann's gulls resulted in a more varied diet and trophic segregation avoiding competition. Our results highlighted the importance of small pelagic fishes in the diet of both seabird species during the chick-rearing period, and the discussion was focused on the description of the feeding strategy and mechanisms that these seabirds used during the breeding season.

Based on the analysis of the regurgitations, the fishes *Engraulis mordax*, *Sardinops sagax*, and *Scomber japonicus* were identified as important prey for elegant terns and Heermann's gulls; however, *Cetengraulis mysticetus* was only identified in the diet of Heermann's gulls. Similarly, the isotopic mixing models also indicated that fishes were the main contributors to chick feathers. The graphical representation of the feeding strategy highlighted the dominance of *E. mordax* in the feeding of both seabirds; these results are in line with previous studies that also indicated that some fish species of the genera *Engraulis*, *Sardinops*, and *Scomber* are the main feeding sources exploited by these 2 seabirds and the entire community of seabirds inhabiting the Gulf of California (Velarde et al. 1994, 2015b, de la Rosa & González-Farias 1995). Consumption of fishes by both seabird species has been attributed to the high energy content of small pelagic fishes (Albo-

Puigserver et al. 2017). For example, *E. mordax* provides a great amount of energy for the development of seabird hatchlings (Dahdul & Horn 2003). Another factor related to the consumption of fishes is their prey availability around Isla Rasa; the high concentration of upwelling events in the Gulf of California results in high primary productivity, allowing a high abundance of small pelagic species (Case et al. 2002, Murphy et al. 2002), making them available for predators. On the other hand, the inclusion of these prey in the diet is enforced by the overlap between the migratory movements of some small fish species in the area and the breeding season of both seabirds (Hammann & Cisneros-Mata 1989, Velarde et al. 2015b), which results in an increase in the availability of high-energy prey, securing the breeding success.

Regarding the elegant tern, fishes were the only prey group found in the regurgitations and used for the isotopic mixing models. For species of the genus *Thalasseus*, the consumption of fishes has been reported as a general pattern (Liechty et al. 2016, Veen et al. 2018, Marinao et al. 2019). In the eastern Pacific, these species also perform long trips, allowing them to exploit feeding grounds far from their breeding colony (Whitcombe 2014, Veit et al. 2021). In the Gulf of California, they can find fishes around

Isla Rasa or fly to other areas where these species are abundant and available. For the Heermann's gull, the crustacean *Pleuroncodes planipes* and the squid *Dosidicus gigas* were found in its diet during all 3 study years. The consumption of these prey by birds of the genus *Larus* is not rare; it has been reported that *Larus pacificus* and *L. dominicanus* feed on large quantities of invertebrates such as cephalopods, gastropods, and crustaceans and even plants (Coulson & Coulson 1993, Navarro et al. 2010). The use of diverse food resources in gulls is associated with their high plasticity in the use of different habitats (both marine and terrestrial; Ramírez et al. 2020) and trophic opportunities, in comparison with open water foragers such as the elegant tern (Whitcombe 2014, Shlepr et al. 2021, Veit et al. 2021). Based on these results, it can be suggested that Heermann's gulls may exploit available prey resources around Isla Rasa, including crustaceans and cephalopods, which were found to be integrated in the diet of adults and chicks.

Based on diet composition, the trophic width estimated with stable isotope values was higher for Heermann's gulls than for elegant terns. The trophic niche dimensions and isotopic composition represent the integration of the diet over time, and their variation can be a consequence of primary production shifts or modifications of nutrient inputs, as well as dietary shifts of prey (Bearhop et al. 2004). The trophic width of the Heermann's gull is the result of a variation of the isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ in its tissue because predator species that exhibit the consumption of a wide range of prey species tend to show a broader isotopic niche (Bearhop et al. 2004). It can be speculated that Heermann's gulls are relatively opportunistic predators capable of changing their prey consumption in relation to prey species availability. For example, the yellow-legged gull *L. michahellis* changes its schedule of foraging behavior and also feeding sources in relation to its habitats and fluctuations of resource abundances: during the week, that species consumes fishes discarded by fishery activities, but when those activities cease during the weekend, it moves to open waters for fishing (Parra-Torres et al. 2020). A similarly flexible feeding strategy is an advantage for the Hermann's gull because it can be more resilient in cases of variations in prey abundance or composition in its distribution area (Reside et al. 2016).

The trophic niche of Heermann's gulls and elegant terns showed evidence of overlap in the 3 sampling years, with Hermann's gulls the most likely to overlap the niche of elegant terns. Since gulls and terns are phylogenetically related (Baker et al. 2007), it is common to find them in mixed nesting colonies (Marinao et al. 2019). In this context, it can be inferred that mixed colonies are formed as a result of the sharing of feeding resources in the surroundings of the nesting areas. This may result in resource partitioning, because adults need to obtain food for themselves and their chicks (Barger et al. 2016). Results also showed a displacement of the foraging area for elegant terns evident in more positive $\delta^{13}C$ values than those of Heermann's gulls. These higher positive $\delta^{13}C$ values could be related to elegant terns moving to high-productivity areas for foraging. For the Heermann's gull, the decrease of the trophic width during 2018 could be related to a low diversity of prey species in the diet, as a result of a greater abundance of certain preferred prey species close to Isla Rasa. Unfortunately, no samples of regurgitations were available for 2018 and 2019, which limited the comparison with the isotopic results for these years. Thus, for both species, continuous sampling is necessary to obtain a better description of feeding habits and its changes and to identify key foraging areas with the use of data loggers. This information would be crucial for establishing no-fishing periods for small pelagic fishes around Isla Rasa during the seabirds' nesting season to guarantee the reproductive success of Heermann's gulls and elegant terns.

In addition to the trophic width, the trophic level of both species based on $\delta^{15}N$ values indicated that these 2 seabirds have similar trophic positions in the food web, with a trophic level between 3.6 and 3.9. This is within the overall values of 3 and 5, which have been reported for the trophic position of seabirds (Hobson et al. 1994, Aurioles-Gamboa et al. 2013, Gagné et al. 2018). Since diet has a direct relationship with the exhibited trophic level (Hobson 1993), it is evident that the consumption of small pelagic fishes resulted in high values of trophic level for these seabirds.

5. CONCLUSIONS

The present study highlights the importance of *Engraulis mordax*, *Sardinops sagax*, and *Scomber japonicus*, small pelagic prey fishes contributing to the development of chick feathers in Heerman's gulls and elegant terns during their breeding season on Isla Rasa. For the elegant tern, fishes were the only prey found in the samples during the studied years. The inclusion of other prey sources (crustaceans and cephalopods) in the diet of the Heermann's gull

resulted in a wider trophic niche compared to that of the elegant tern. It can be suggested that this trophic strategy allows the coexistence of these sympatric species during the breeding season on Isla Rasa. It is important to mention that trophic niche separation is more complex than just what the species eat; it also includes when, where, and how they eat. As predators that occupy a high trophic level, these seabirds are indicators of the ecosystem's health; thus, ensuring the availability of these prey sources is pivotal for the stability of their populations. In this context, fishery management of small pelagic fishes in the Gulf of California must be revised with the integration of ecosystem management and conservancy of endangered species related to small pelagic fish consumption in the ecosystem, ensuring the reproductive success of marine birds as indicators of ecosystem wellness.

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