



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

Alexei Elias-Valdez<sup>1</sup>, Enriqueta Velarde<sup>2</sup>, Alejandro Medina-Quej<sup>1</sup>, José Manuel Castro-Perez<sup>1</sup>, Joan Navarro<sup>3</sup>, Rigoberto Rosas-Luis<sup>1,4,\*</sup>

<sup>1</sup>Tecnológico Nacional de México/IT de Chetumal, Av. Insurgentes 330, Col. David Gustavo Gtz., 77013 Chetumal, Quintana Roo, Mexico

<sup>2</sup>Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Av. Hidalgo 617, Col. Río Jamapa, 94290 Boca del Río, Veracruz, Mexico

<sup>3</sup>Institut de Ciències del Mar (ICM), CSIC, Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

<sup>4</sup>IxM CONACyT-Tecnológico Nacional de México/IT de Chetumal, Av. Insurgentes 330, Col. David Gustavo Gtz., 77013 Chetumal, Quintana Roo, Mexico

**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 ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis in 3 consecutive breeding seasons (2017, 2018, and 2019). Results of the stable isotope analysis revealed that although some segregation in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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

Resale or republication not permitted without written consent of the publisher

## 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 func-

tioning (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 occidentalis 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 ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) 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-

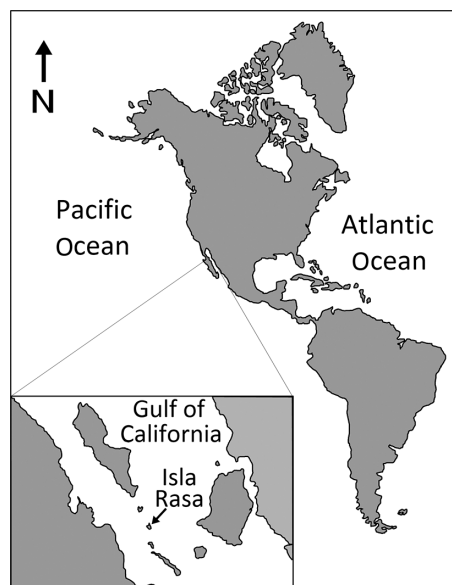


Fig. 1. Isla Rasa in the Gulf of California, a vital breeding area for Heermann's gulls *Larus heermanni* and elegant terns *Thalasseus elegans*

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 Heermann'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<sup>2</sup>, with 898 islands, including Isla Rasa (Sans-Aguilar 2018). Isla Rasa is a volcanic island that has a surface area of 0.68 km<sup>2</sup> 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  $\delta$  (‰) relative to Vienna Pee Dee belemnite carbon ( $\delta^{13}\text{C}$ ) and atmospheric nitrogen  $\text{N}_2$  ( $\delta^{15}\text{N}$ ). Based on laboratory standards, the measurement error was approximately  $\pm 0.1$  and  $\pm 0.2$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , 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 ( $\pm 2$  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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $4.15 \pm 1.63$  for  $\delta^{15}\text{N}$  and  $1.90 \pm 2.40$  for  $\delta^{13}\text{C}$  were used, corresponding to the average of the transfer factors of feathers of the ring-billed gull *Larus delawarensis* ( $\delta^{13}\text{C}$  TEF =  $0.20 \pm 1.30$  and  $\delta^{15}\text{N}$  TEF =  $3.00 \pm 0.20$ ) (Hobson & Clark 1992) and feathers of the black-tailed gull *L. crassirostris* ( $\delta^{13}\text{C}$  TEF =  $3.60 \pm 0.50$  and  $\delta^{15}\text{N}$  TEF =  $5.30 \pm 0.80$ ) (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  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  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 et 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  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  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  $\text{TP} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{prey}}/\text{TEF}) + \text{TP}_{\text{prey}}$  (Post 2002). The  $\text{TP}_{\text{prey}}$  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  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  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

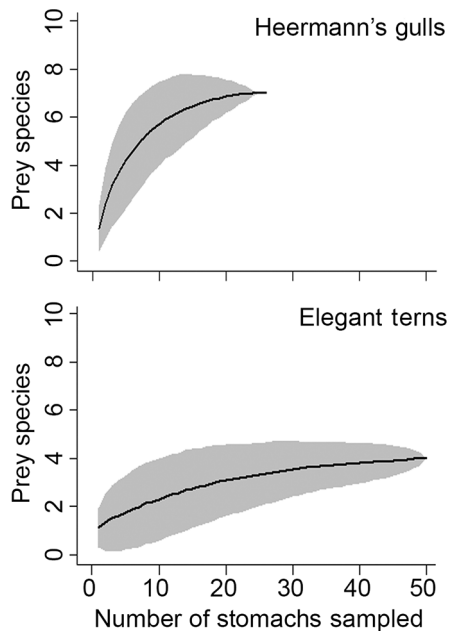


Fig. 2. Cumulative prey curves of Heermann's gulls (top panel) and elegant terns (bottom panel) based on prey identified in regurgitations

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

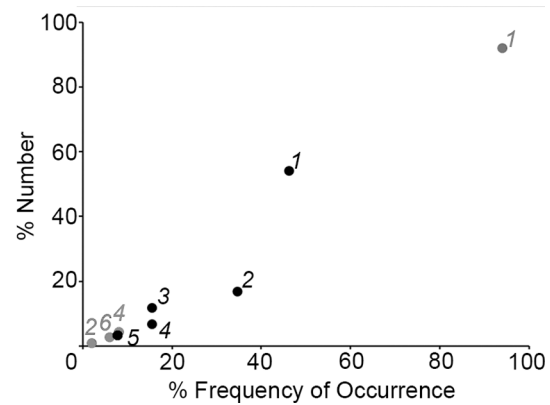


Fig. 3. Graphical representation of the predatory feeding strategy of Heermann's gulls (black dots) and elegant terns (gray dots) and prey importance to the diet based on occurrence (% frequency of occurrence) and abundance (% number). 1: *Engraulis mordax*; 2: *Sardinops sagax*; 3: *Cetengraulis mysticetus*;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

tively. The median value of elegant terns in 2017 was  $-15.37\text{‰}$ , and the mean was  $-15.44 \pm 0.40\text{‰}$ . However, in 2018, the median value increased to  $-14.83\text{‰}$ , and the mean was  $-15.05 \pm 0.70\text{‰}$ . In 2019, the median value dropped to  $-14.88\text{‰}$ , and the mean was  $-14.94 \pm 0.39\text{‰}$ . According to the Kruskal-Wallis test, the median  $\delta^{13}\text{C}$  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  $\delta^{15}\text{N}$  value of Heermann's gulls in 2017 was  $19.35\text{‰}$ , and the mean was  $19.10 \pm 1.05\text{‰}$ ; in 2018, the median value was  $19.87\text{‰}$ , and the mean was  $19.81 \pm 0.38\text{‰}$ ; in 2019, the median value was  $20.31\text{‰}$ , and the mean was  $20.24 \pm 0.45\text{‰}$ . The median  $\delta^{15}\text{N}$  value of elegant terns in 2017 was  $19.07\text{‰}$ , and the mean was  $19.15 \pm 0.45\text{‰}$ ; in 2018, the median value increased to  $19.87\text{‰}$  and the mean to  $19.70 \pm 0.70\text{‰}$ ; in 2019, the median value was  $20.47\text{‰}$ , and the mean was  $20.41 \pm 0.28\text{‰}$ . Regarding the Kruskal-Wallis results, the median values of  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values of Heermann's gulls were different between 2017 and 2019. For elegant



terns, the median  $\delta^{15}\text{N}$  values were different between 2017 and 2018 and between 2017 and 2019. According to the Mann-Whitney  $U$ -test results, the comparison of the  $\delta^{15}\text{N}$  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‰<sup>2</sup> for 2017, 2018, and 2019, respectively (Fig. 4). For elegant terns, the SEAc values were 0.58, 0.89, and 0.32‰<sup>2</sup> 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  $\delta^{15}\text{N}$  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  $18.56 \pm 0.43$ ‰ for  $\delta^{15}\text{N}$ , and  $-15.57$  and  $-15.67 \pm 0.37$ ‰ for  $\delta^{13}\text{C}$ ; for *E. mordax*, they were 17.12 and  $16.80 \pm 0.86$ ‰ for  $\delta^{15}\text{N}$  and were  $-17.00$  and  $-17.07 \pm 0.93$ ‰ for  $\delta^{13}\text{C}$ ; for *S. sagax*, they were 16.99 and  $16.95 \pm 0.83$ ‰ for  $\delta^{15}\text{N}$  and were  $-17.19$  and  $-17.76 \pm 1.13$ ‰ for  $\delta^{13}\text{C}$ ; for *S. japonicus*, they were 16.00 and  $16.10 \pm 0.72$ ‰ for  $\delta^{15}\text{N}$  and were  $-18.91$  and  $-18.95 \pm 0.71$ ‰ for  $\delta^{13}\text{C}$ ; for *Pleuroncodes planipes*, they were 16.14 and  $16.14 \pm 0.64$ ‰ for  $\delta^{15}\text{N}$  and were  $-17.91$  and  $-17.91 \pm 0.01$ ‰ for  $\delta^{13}\text{C}$ ; lastly, for *D. gigas*, the mean values were 19.69‰ for  $\delta^{15}\text{N}$  and  $-16.53$ ‰ for  $\delta^{13}\text{C}$ .

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-

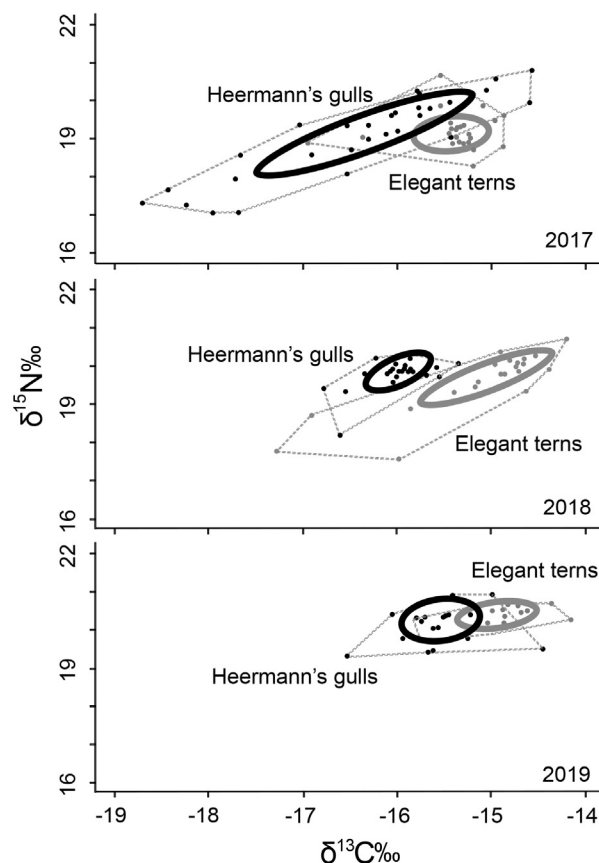


Fig. 4. Isotopic standard ellipses of Heermann's gulls (black dots) and elegant terns (gray dots) during 2017 (top panel), 2018 (middle panel), and 2019 (bottom panel).  $\delta^{15}\text{N}$ : stable nitrogen isotope;  $\delta^{13}\text{C}$ : stable carbon isotope

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-

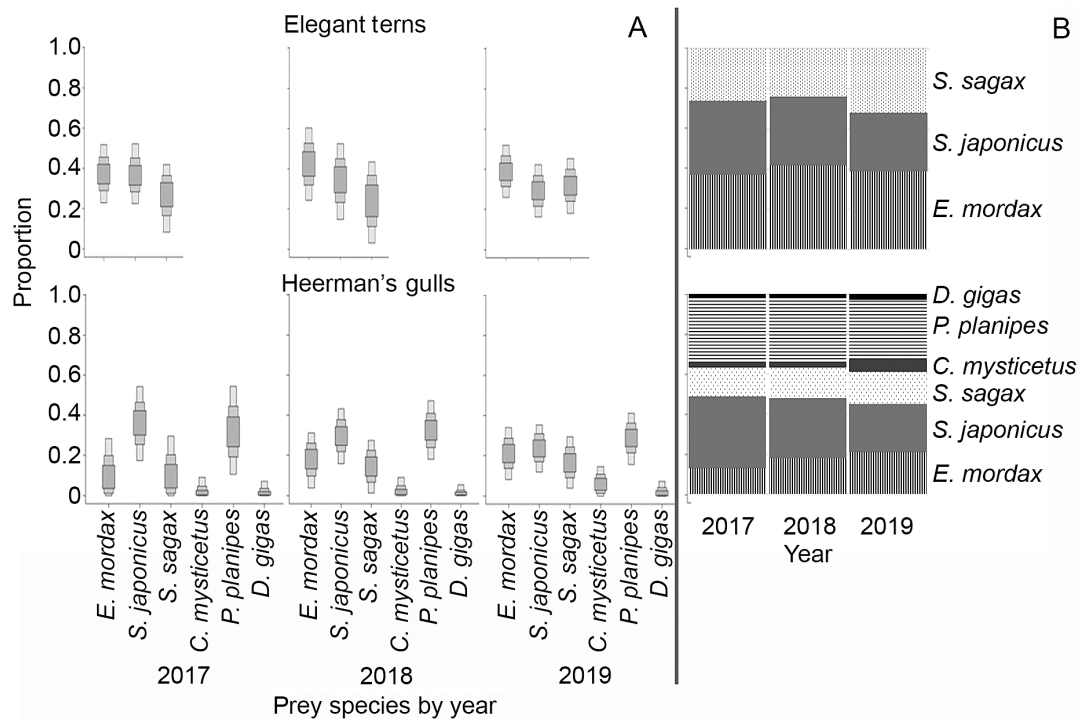


Fig. 5. (A) Modeled proportion of prey groups in the diet of Heermann's gulls and elegant terns. (B) Cumulative proportion of prey species by year

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-Farías 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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 Heermann'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 Heermann'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  $\delta^{13}\text{C}$  values than those of Heermann's gulls. These higher positive  $\delta^{13}\text{C}$  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  $\delta^{15}\text{N}$  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, Auriolles-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 Heermann'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.

**Acknowledgements.** Permits for fieldwork and sample collection were provided by the Dirección General de Vida Silvestre of the Secretaría de Medio Ambiente y Recursos Naturales. Financial support for the fieldwork, supplies, and transportation to Isla Rasa was provided by Fondo Mexicano para la Conservación de la Naturaleza, Lindblad Expeditions/National Geographic, and Packard Foundation under the project Isla Rasa como modelo de manejo de recursos naturales y pesqueros. Logistic support for marine transportation was provided by Comisión Nacional de Áreas Naturales Protegidas Baja California. Pronatura Noroeste AC provided support for local housing. Local fisherman José 'El Güero' Arce Smith provided local transportation and together with several students helped during the fieldwork and data collection. The authors thank Ricardo A. Álvarez and Susana Carrasco of the LIE Doñana for their support in the isotope analysis. This work acknowledges the Severo Ochoa Centre of Excellence accreditation (CEX2019-000928-S).

#### LITERATURE CITED

- approach using stable isotope analysis. *J Anim Ecol* 73: 1007–1012
- ✦ Becker BH, Newman SH, Inglis S, Beissinger SR (2007) Diet–feather stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) fractionation in common murre and other seabirds. *Condor* 109: 451–456
- ✦ BirdLife International (2020a) *Larus heermanni*. The IUCN Red List of Threatened Species 2020: e.T22694296 A132539371. <https://www.iucnredlist.org/es/species/22694296/178958787> (accessed 7 Nov 2022)
- ✦ BirdLife International (2020b) *Thalasseus elegans*. The IUCN Red List of Threatened Species 2020: e.T22694552 A132559886. <https://www.iucnredlist.org/es/species/22694552/178970750> (accessed 7 Nov 2022)
- ✦ Bizzarro JJ, Robinson HJ, Rinewalt CS, Ebert DA (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. *Environ Biol Fish* 80:197–220
- ✦ Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37: 911–917
- ✦ Case TJ, Cody ML, Ezcurra E (eds) (2002) A new island biogeography of the Sea of Cortés. Oxford University Press, New York, NY
- ✦ Cherel Y, Hobson KA, Bailleul F, Groscolas R (2005) Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. *Ecology* 86: 2881–2888
- ✦ Costello MJ (1990) Predator feeding strategy and prey importance: a new graphical analysis. *J Fish Biol* 36: 261–263
- ✦ Coulson R, Coulson G (1993) Diets of the Pacific gull *Larus pacificus* and the kelp gull *Larus dominicanus* in Tasmania. *Emu–Austral Ornithol* 93:50–53
- ✦ Dahdul WM, Horn MH (2003) Energy allocation and postnatal growth in captive elegant tern (*Sterna elegans*) chicks: responses to high- versus low-energy diets. *Auk* 120:1069–1081
- de la Rosa J, González-Farías F (1995) Temas de oceanografía biológica en México, Vol 2. Universidad Autónoma de Baja California, Baja California
- ✦ Deme S, Yeung LY, Sun T, Lee CTA (2021) Study of a comprehensive set of feathers from two *Setophaga citrina*. *PLOS ONE* 16:e0236536
- ✦ Forero MG, Bortolotti GR, Hobson KA, Donazar JA, Bertelotti M, Blanco G (2004) High trophic overlap within the seabird community of Argentinean Patagonia: a multi-scale approach. *J Anim Ecol* 73:789–801
- ✦ Gagné TO, Hyrenbach KD, Hagemann ME, Bass OL and others (2018) Seabird trophic position across three ocean regions tracks ecosystem differences. *Front Mar Sci* 5: 1–5
- Hammann MG, Cisnerosmata MA (1989) Range extension and commercial capture of the northern anchovy, *Engraulis mordax* Girard, in the Gulf of California, Mexico. *Calif Fish Game* 75:49–53
- ✦ Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar Ecol Prog Ser* 95:7–18
- ✦ Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes II: factors influencing diet–tissue fractionation. *Condor* 94:189–197
- ✦ Hobson K, Piatt J, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- ✦ Albo-Puigserver M, Muñoz A, Navarro J, Coll M, Pethybridge H, Sánchez S, Palomera I (2017) Ecological energetics of forage fish from the Mediterranean Sea: seasonal dynamics and interspecific differences. *Deep Sea Res II* 140:74–82
- ✦ Aurióles-Gamboa D, Rodríguez-Pérez MY, Sánchez-Velasco L, Lavín MF (2013) Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis. *Mar Ecol Prog Ser* 488:275–290
- ✦ Baker AJ, Pereira SL, Paton TA (2007) Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biol Lett* 3:205–209
- ✦ Barger C, Young R, Will A, Ito M, Kitaysky A (2016) Resource partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere* 7:1–15
- ✦ Bearhop S, Adams CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel

- Hurtubia J (1973) Trophic diversity measurement in sympatric predatory species. *Ecology* 54:885–890
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602
- Liao H, Pierce CL, Larscheid JG (2001) Empirical assessment of indices of prey importance in the diets of predatory fish. *Trans Am Fish Soc* 130:583–591
- Liechty JS, Fontenot QC, Pierce AR (2016) Diet composition of royal tern (*Thalasseus maximus*) and Sandwich tern (*Thalasseus sandvicensis*) at Isles Dernieres Barrier Island Refuge, Louisiana, USA. *Waterbirds* 39:58–68
- Lluch-Cota SE (2000) Coastal upwelling in the eastern Gulf of California. *Oceanol Acta* 23:731–740
- Mancini PL, Bugoni L (2014) Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago. *ICES J Mar Sci* 71: 2599–2607
- Marinao C, Suárez N, Yorio P (2019) Trophic interactions between the kelp gull (*Larus dominicanus*) and royal and cayenne terns (*Thalasseus maximus maximus* and *T. sandvicensis eurygnathus*) in a human-modified environment. *Can J Zool* 97:904–913
- Miller DJ, Lea RN (1976) Guide to the coastal marine fishes of California. *Fish Bull Calif Dep Fish Game* 157
- Mizutani H, Fukuda M, Kabaya Y (1992) C<sup>13</sup> and N<sup>15</sup> enrichment factors of feathers of 11 species of adult birds. *Ecology* 73:1391–1395
- Murphy RW, Sanchez-Piñero F, Polis GA, Aalbu RL (2002) New measurements of area and distance for islands in the Sea of Cortés. In: Case T, Cody M, Ezcurra E (eds) *A new island biogeography of the Sea of Cortés*. Oxford University Press, New York, NY, p 447–464
- Navarro J, Oro D, Bertolero A, Genovart M, Delgado A, Forero MG (2010) Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. *Mar Biol* 157:2453–2459
- Oksanen J, Simpson GL, Blanchet FG, Kindt R and others (2010) vegan: community ecology package. R package version 1.17-5. <https://CRAN.R-project.org/package=vegan>
- Páez-Osuna F, Sanchez-Cabeza JA, Ruiz-Fernández AC, Alonso-Rodríguez R and others (2016) Environmental status of the Gulf of California: a review of responses to climate change and climate variability. *Earth Sci Rev* 162:253–268
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLOS ONE* 5:e9672
- Parra-Torres Y, Ramírez F, Afán I, Aguzzi J, Bouten W, Forero MG, Navarro J (2020) Behavioral rhythms of an opportunistic predator living in anthropogenic landscapes. *Mov Ecol* 8:17
- Perez GS, Goodenough KS, Horn MH, Patton RT, Ruiz EA, Velarde E, Aguilar A (2020) High connectivity among breeding populations of the elegant tern (*Thalasseus elegans*) in Mexico and southern California revealed through population genomic analysis. *Waterbirds* 43:17–27
- Polito MJ, Trivelpiece WZ, Karnovsky NJ, Ng E, Patterson WP, Emslie SD (2011) Integrating stomach content and stable isotope analyses to quantify the diets of pygoscelid penguins. *PLOS ONE* 6:e26642
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 83: 703–718
- Quinlivan KR (1974) Some insights into the feeding habits of Heermann's gulls along the coast of California. BSc thesis. University of California, Santa Cruz, CA
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ramírez F, Afán I, Bouten W, Carrasco JL, Forero MG, Navarro J (2020) Humans shape the year-round distribution and habitat use of an opportunistic scavenger. *Ecol Evol* 10:4716–4725
- Reside AE, VanDerWal J, Garnett ST, Kutt AS (2016) Vulnerability of Australian tropical savanna birds to climate change. *Austral Ecol* 41:106–116
- Roden GI, Groves GW (1959) Recent oceanographic investigations in the Gulf of California. *J Mar Res* 18:10–35
- Roedel PM (1948) Common marine fishes of California. Nabu Press, Sacramento, CA
- Sanger GA (1987) Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. In: Croxall JP (ed) *Seabirds: feeding biology and role in marine ecosystems*. Cambridge University Press, Cambridge, p 229–257
- Sans-Aguilar CA (2018) El Golfo de California en su totalidad como aguas interiores o territoriales mexicanas. *Revista del Centro de Estudios Superiores Navales* 1: 95–126
- SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales) (2010) Norma oficial Mexicana NOM-059-SEMARNAT-2010. Diario oficial de la Federación. [https://dof.gob.mx/nota\\_detalle\\_popup.php?codigo=5173091#:~:text=Esta%20Norma%20Oficial%20Mexicana%20tiene,riesgo%20para%20las%20especies%20o](https://dof.gob.mx/nota_detalle_popup.php?codigo=5173091#:~:text=Esta%20Norma%20Oficial%20Mexicana%20tiene,riesgo%20para%20las%20especies%20o)
- Shlepr KR, Ronconi RA, Hayden B, Allard KA, Diamond AW (2021) Estimating the relative use of anthropogenic resources by herring gull (*Larus argentatus*) in the Bay of Fundy, Canada. *Avian Conserv Ecol* 16:1–18
- Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying *n*-dimensional ecological niches and niche overlap. *Ecology* 96:318–324
- Thompson DA, McKibbin N (1981) Gulf of California fish-watcher's guide. Golden Puffer Press, Tucson, AZ
- Tordesillas-Barnard MS (1992) Dieta del gallito de mar elegante (*Sterna elegans*) durante la temporada de reproducción de 1985 y 1986 en Isla Rosa BC (Aves: Laridae). BSc thesis, Universidad Nacional Autónoma de México, Mexico City
- Tudela S, Palomera I (1997) Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). *Mar Ecol Prog Ser* 160: 121–134
- Valdez-Holguín JE, Lara-Lara R (1987) Primary productivity in the Gulf of California effects of El Niño 1982–1983 event. *Cienc Mar* 13:34–50
- Veen J, Dallmeijer H, Van Damme CJG, Leopold MF, Veen T (2018) Analyzing pellets and feces of African royal terns (*Thalasseus maximus albidorsalis*) results in different estimates of diet composition. *Waterbirds* 41: 295–304
- Veit RR, Velarde E, Horn MH, Manne LL (2021) Population growth and long-distance vagrancy leads to colonization of Europe by elegant terns *Thalasseus elegans*. *Front Ecol Evol* 9:725614
- Velarde E (1999) Breeding biology of Heermann's gulls on Isla Rasa, Gulf of California, Mexico. *Auk* 116: 513–519

- Velarde E, Tordesillas MS, Vieyra L, Esquivel R (1994) Seabirds as indicators of important fish populations in the Gulf of California. *Calif Coop Ocean Fish Invest Rep* 35:137–143
- ✦ Velarde E, Ezcurra E, Cisneros-Mata MA, Lavín MF (2004) Seabird ecology, El Niño anomalies, and prediction of sardine fisheries in the Gulf of California. *Ecol Appl* 14: 607–615
- Velarde E, Cartron JLE, Drummond H, Anderson DW, Rebón-Gallardo F, Palacios E, Rodríguez C (2005) Nesting seabirds of the Gulf of California's offshore islands: diversity, ecology and conservation. In: Cartron JLE, Ceballos G, Felger RS (eds) *Biodiversity, ecosystems, and conservation in northern Mexico*. Oxford University Press, New York, NY, p 452–470
- ✦ Velarde E, Ezcurra E, Anderson DW (2013) Seabird diets provide early warning of sardine fishery declines in the Gulf of California. *Sci Rep* 3:1332
- ✦ Velarde E, Wilde BT, Felger RS, Ezcurra E (2014) Floristic diversity and dynamics of Isla Rasa, Gulf of California — a globally important seabird island. *Bot Sci* 92:89–101
- ✦ Velarde E, Ezcurra E, Anderson DW (2015a) Seabird diet predicts following-season commercial catch of Gulf of California Pacific sardine and northern anchovy. *J Mar Syst* 146:82–88
- ✦ Velarde E, Ezcurra E, Horn M, Patton R (2015b) Warm oceanographic anomalies and fishing pressure drive seabird nesting north. *Sci Adv* 1:e1400210
- Whitcombe CD (2014) Dietary and stable isotope analyses reveal the role of kelp pipefish (*Syngnathus californiensis*), a presumed cryptic prey, in the diet of the elegant tern (*Thalasseus elegans*) in southern California waters. MSc thesis, California State University, Fullerton, CA
- ✦ Wiley AE, Ostrom PH, Stricker CA, James HF, Gandhi H (2010) Isotopic characterization of flight feathers in two pelagic seabirds: sampling strategies for ecological studies. *Condor* 112:337–346
- ✦ Williams CT, Buck LL (2010) Using fatty acids as dietary tracers in seabird trophic ecology: theory, application, and limitations. *J Ornithol* 151:531–543

*Editorial responsibility: Stephen Wing,  
Dunedin, New Zealand*  
*Reviewed by: D. Ainley, B. Becker and 1 anonymous referee*

*Submitted: January 12, 2023;  
Accepted: May 12, 2023  
Proofs received from author(s): June 5, 2023*