COMPARATIVE DIET ANALYSIS OF THREE LARID SPECIES NESTING AT ISLA RASA, GULF OF CALIFORNIA, MEXICO

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ABSTRACT

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Isla Rasa, situated in highly productive waters of the Gulf of California, has the largest nesting colony of Royal Terns *Thalasseus maximus* (as many as 17,000 individuals) in the Mexican Pacific, sharing this site with 300,000 Elegant Terns *T. elegans* and 260,000 Heermann's Gulls *Larus heermanni*. During eight breeding seasons between 1996 and 2011, we found that the Royal Tern diet contained over twice the number of prey species as the other two seabirds' diets: the Royal Tern's diet included 36 species of fishes, in 20 families, and pelagic squat lobster *Grimothea planipes*, whereas the Elegant Tern and Heermann's Gull preyed upon 17 taxa (15 fishes and two pelagic crustaceans), in nine families. Most fishes taken by Elegant Terns and Heermann's Gulls (93.8%) represented only three pelagic species (Pacific Sardine *Sardinops sagax*, Northern Anchovy *Engraulis mordax*, and Pacific Chub Mackerel *Scomber japonicus*), whereas these three species made up only 73.3% of the Royal Tern diet—a high proportion, nonetheless. The Royal Tern diet also reflected more diverse prey habitats. Only ~50% of Royal Tern prey species were pelagic, far fewer than for the other two seabirds (99%). The dietary differences among these three species appear to be key to their sharing of a crowded nesting site. The continuing regional growth of the commercial fishery for pelagic forage fish represents a threat to these seabirds and other components of the Gulf of California food web.

Key words: comparative seabird diets, fishery impacts, Gulf of California, Isla Rasa, *Larus heermanni*, *Thalasseus elegans*, *Thalasseus maximus*

INTRODUCTION

Seabirds generally breed at predator-free locations, although additional factors also affect where they nest (Furness & Monaghan, 1987). The fact that the size of the nesting colony is affected by prey availability and colony distribution suggests the importance of competition for food supplies during the breeding season (Ashmole, 1963; Furness & Birkhead, 1984). Seabirds are generally consumers of marine prey, either fishes or invertebrates (Ashmole, 1971). Diets may be specialized or generalized, but many seabirds seek and consume prey relative to their availability. Thus it has long been recognized that studies of seabirds' diets are key to understanding the way breeding patterns are affected by ocean conditions (Boersma, 1978; Harris, 1969; Velarde & Ezcurra, 2002; Vieyra et al., 2009), as well as how seabird species interact with each other with respect to their food habits (Cherel et al., 2005; Dorward, 1962). Breeding success depends on seasonal availability of prey (Ainley & Boekelheide, 1990; Anderson et al., 1982; Hunt, 1972; Vieyra et al., 2009; and others), and nesting colonies are generally located in areas of high marine productivity or, in the case of tropical and relatively less productive waters, in zones where parents can readily find the food necessary to nourish their young (Ashmole, 1963). Ecological segregation between regionally coexisting (and often phylogenetically closely related) seabird species has been a matter of study for several decades, in which attempts have been made to explain how two or more species nesting in the same place can avoid competition for food resources (Ainley & Boekelheide, 1990; Croxall & Prince, 1980; Petalas et al., 2021). Given their consumption of marine prey, seabirds can also act as indicators of the effects on the food web of commercial fisheries that target the same prey (Anderson & Gress, 1984; Anderson et al., 1982; Velarde et al., 1994, 2004).

Isla Rasa Seabirds' Trophic Guilds

On Isla Rasa, in the Gulf of California, four larid seabird species nest—Royal Tern *Thalasseus maximus*, Elegant Tern *T. elegans*, Heermann's Gull *Larus heermanni*, and Yellow-footed Gull *L. livens*—and how they coexist is of interest.

Isla Rasa supports the largest nesting colony of Royal Terns in the Mexican Pacific. On this island, the Royal Tern, with nesting colonies approaching 17,000 individuals, shares nesting habitat with the Elegant Tern and Heermann's Gull, with colonies of *ca*. 300,000 and 260,000 individuals, respectively, and Isla Rasa is the main nesting site for these two species, supporting approximately 95% of the total nesting population of each (Velarde, 1999; Velarde & Anderson, 1994; Velarde & Ezcurra, 2002; Velarde et al., 2005).

The Royal Tern is distributed along subtropical and tropical coasts of both sides of the Americas and in western Africa (American Ornithologists' Union [AOU], 1998; BirdLife International, 2018). Royal Tern nesting colonies are scarce along the Mexican Pacific and have been relatively little studied. Nesting colony information summarized by Mellink et al. (2007) indicates there are eight extant plus three presently unoccupied nesting sites in the Mexican Pacific. Of the sites currently in use, two are mostly occupied during El Niño years (i.e., during the El Niño phase of the El Niño

Southern Oscillation, ENSO), when small colonies experience large fluctuations in numbers. Mellink et al. estimated some 13,000 breeding pairs for this species, with the colony on Isla Rasa being the largest, with some 8,500 pairs, or 65% of the nesting population for the Mexican Pacific; the colony on Isla El Rancho, off northern Sinaloa, was reported to be the next largest, with some 1,000 to 1,800 nests (Angulo-Gastelum et al., 2011; Mellink et al., 2007). Although not considered to be threatened or of special concern, the Royal Tern is abundant only locally within its distribution (Barbour, 1978; Portnoy, 1978; Schaffner, 1985; Van Velzen & Benedict, 1972). Although this species has not been studied extensively at Isla Rasa, it is known that many tern species generally nest in mixed colonies with other species of terns and often also with gulls (Laridae) and other seabirds (Ashmole & Tovar, 1968; Bent, 1921; Clapp & Buckley, 1984; Clapp et al., 1982; Erwin, 1977; Escalante, 1968; Grant, 1981; Kale et al., 1965; Kilham, 1981; Toland & Gilbert, 1987).

As for the Elegant Tern and Heermann's Gull, their distributions are restricted to the Pacific coastal waters of North and South America, with Heermann's Gull dispersing seasonally in waters between southern Canada and Guatemala (Islam & Velarde, 2020), while the Elegant Tern ranges between British Columbia and Chile (Veit et al., 2021). The nesting populations of both species in Isla Rasa are affected by ocean climate (ENSO) and fishing pressure, with small temporal reductions or even a total lack of nesting during El Niño years (Velarde & Ezcurra, 2018; Velarde, Ezcurra, et al., 2015; Vieyra et al., 2009). While both species have a very similar diet, feeding mostly on small pelagic schooling ("forage") fishes (Velarde & Anderson, 1994; Velarde et al., 2004, 2013; Velarde, Ezcurra, & Anderson, 2015), a stable isotope analysis has shown that they exhibit disjunct feeding trophic niches, the tern being a more coastal forager than the gull (Elias-Valdez et al., 2023). In contrast, the Royal Tern elsewhere has been reported to exhibit a wider diet spectrum and also to feed on more coastal-occurring (shallower-water) species (Aygen & Emslie, 2006; Gochfeld & Burger, 1996; Liechty et al., 2016; McGinnis & Emslie, 2001; Tomkins, 1963; Wambach & Emslie, 2003). Intrigued by such reports, we compared the diet composition of the two tern species and Heermann's Gull at Isla Rasa.

We report here the diet composition of Royal Terns at Isla Rasa during eight years between 1996 and 2011, comparing it to the diets of Elegant Terns and Heermann's Gulls. We have no observations to report on the diet of the Yellow-footed Gull, which has only a small population, at most 10 nests, on Isla Rasa. Its diet has been poorly studied, but the few existing reports indicate a diverse diet, including small seabirds, fishing bats, small fish, crustaceans, mollusks, land invertebrates, some prey of the phyla Cnidaria and Porifera, and marine plants (Flores-Martínez et al., 2015), as well as seabird eggs and chicks (Anderson & Keith, 1980; Velarde, 1992).

METHODS

Study Area

Isla Rasa (0.6 km²) is located in Mexico's north-central Gulf of California (28°49′24″N, 112°59′03″W), one of the most species-rich and productive seas in the world (Alvarez-Borrego, 1983; Brusca et al., 2017; Santamaría-del-Ángel et al., 1994). The island is a federally protected area declared as a natural reserve and bird refuge (Decreto que declara Zona de Reserva Natural y Refugio de Aves, 1964) on the basis that populations of seabirds nesting at Isla Rasa are now globally important and had been severely affected by egg poaching. Both Heermann's Gull and the Elegant Tern are listed in the Mexican Endangered Species List for species at risk, under the category of Threatened (Norma Oficial Mexicana, NOM-059-SEMARNAT-2010, 2010).

Sample Collection

One of us (EV) and her students collected food samples from the three seabird species during eight nesting seasons between 1996 and 2011. During each nesting season, fresh regurgitations were collected between early April and late June. For terns, prey carried in the bill were also collected and were either identified in the field (see below) or preserved as labeled specimens for subsequent identifications in LTF's lab in Guaymas. Regurgitations and/or prey carried in the bill were obtained from adult birds returning to the colony, following foraging forays, during the first three hours after sunset. To prevent unnecessary disturbance, birds were captured in mist nets placed at least 300 m from their nesting colony. To obtain a substantial number of samples per sampling effort, nets were placed in what were observed to be flight corridors for birds returning with food items for their chicks. Most birds spontaneously regurgitated their crop's contents when entrapped in the net or did so during manipulation when they were being liberated. If a tern was carrying a fish in its bill, it simply dropped the fish. Birds were set free after being liberated from the net. Each Heermann's Gull regurgitation was considered a diet sample. For terns, a sample was the whole fish dropped by an individual when trapped in the net and/or the regurgitated crop content, if the individual regurgitated.

Sample Analysis

Each sample was assigned a letter and number code. Whenever possible, whole fishes or fish fragments were identified to species level in the field through diagnostic parts of specimens. Such determinations were carried out early on by reference to identification guides and keys (Eschmeyer & Herald, 1983; Froese & Pauley, 2025; Miller & Lea, 1972; Roedel, 1948; Thomson & McKibbin, 1976) or—especially for Heermann's Gull regurgitations, which were generally more advanced in digestion than those of terns—by subsequent comparative examination of fish otoliths (inner ear bones). When field determination was not possible or confirmation was desired, the first author preserved the sample in a solution of 10% formalin or 70% ethyl alcohol and forwarded it to the second author for identification using detailed taxonomic treatises (not listed here) and comparisons with curated (archived) material. Such voucher specimens will be deposited in the National Fish Collection at Instituto de Biología of the Universidad Nacional Autónoma de México in Mexico City. Because most regurgitations contained only a single species of fish, diet composition was determined via the frequency method, in which the number of regurgitations with a certain type of prey was divided by the total number of regurgitations and expressed as a percentage (Velarde et al., 1994).

Due to the varying locations of Elegant and Royal Tern nesting colonies and because we wanted to avoid disturbing nesting birds, the number of samples obtained varied among years. To detect potential relationships between the number of species observed in the diet each year and the total number of samples, we performed a regression analysis for these parameters and an analysis of variance (ANOVA) test for goodness of fit. Additionally, we compared the diet of the Royal Tern to the diets of the Elegant Tern and Heermann's Gull (which have been sampled almost yearly since 1983) at Isla Rasa. To determine the similarity of the diets of the three species, we performed two chi-square tests: one comparing the diets of the Elegant Tern and Heermann's Gull and the other comparing those of the Elegant Tern and Royal Tern.

RESULTS

Royal Tern Diet Composition

The diet of Royal Terns at Isla Rasa consisted predominantly of fishes, rarely supplemented by pelagic squat lobster, or langostilla in Spanish, *Grimothea planipes*, when it was locally available (year 2011). Fish species composition varied between years, but some species were present in all or most years (Table 1; Figs. 1, 2). Thirty-six fish species, representing 20 families of fishes, were found in the samples (plus pelagic squat lobster in 2011). General habitats occupied by these species are classified as benthic, demersal, epipelagic, and mesopelagic (Table 1). The number of prey species in the Royal Tern diet fluctuated between five and 11 species among years.

The prey families represented in the samples, in descending order of frequency throughout the eight years, were as follows: Engraulidae (anchovies, n = 67, 27.6%); Alosidae (shads, n = 58, 23.9%); Scombridae (mackerels, n = 37, 15.2%); Dussumieriidae (herrings, n = 15, 6.2%); Carangidae (jacks, n = 13, 5.3%); Munididae (pelagic squat lobster, n = 10, 4.1%); Atherinopsidae and Haemulidae (New World silversides and grunts, respectively, with n = 8 and 3.3% each); Gerreidae (mojarras, n = 6, 2.5%); Ophidiidae, Exocoetidae, and Hemiramphidae (cusk-eels, flyingfishes, and halfbeaks, respectively, with n = 3 and 1.2% each); Serranidae, Paralichthyidae, and Dorosomatidae (sea basses, sand flounders, and thread herrings, respectively, with n = 2 and 0.8% each); and Ophichthidae, Myctophidae, Batrachoididae, Syngnathidae, Pomacentridae, and Pleuronectidae (snake eels, lanternfishes, toadfishes, seahorses, damselfishes, and righteye flounders, respectively, with n = 1 and 0.4% each) (Table 1). Regarding the general habitats occupied by these prey fishes, 51.6% can be classified as epipelagic, 22.9% as benthic, 22.9% as demersal, and 2.7% as mesopelagic.

Elegant Tern and Heermann's Gull Diet Composition

In contrast to the diet of the Royal Tern, only 15 species of fishes and two pelagic crustaceans, representing nine families of fishes and two families of invertebrates, were found in the sampled diets of Elegant Terns and Heermann's Gulls. Here, 81.8% of prey fishes were epipelagic, and only 9.1% were benthic (the paralichthyid) and epipelagic/mesopelagic (the myctophid), respectively (Table 2). A total of 93.8% of the diets of each of these two seabird species consisted of the triad of Northern Anchovy *Engraulis mordax*, Pacific Sardine *Sardinops sagax*, and Pacific Chub Mackerel *Scomber japonicus*, with only 6.2% representing other species. In contrast, for Royal Terns, these values are 73.7% (the same triad) and 26.3% (others), respectively. The largest number of samples recorded for the diets of both the Elegant Tern and Heermann's Gull, taken together, was from Engraulidae (64.6%), followed by Alosidae (27.5%) and, in much smaller proportions, Scombridae (2.4%), Atherinopsidae and Myctophidae (with 2.3% each), Dorosomatidae (2.0%), Carangidae (1.7%), Dussumieriidae (0.9%), epipelagic shrimps (0.39%), and Paralichthyidae (0.03%), in that order (Table 2).

Comparison of Seabird Species' Diets

The highest yearly number of prey species per sample in the Royal Tern diet was for 1996, followed by 2010 (Table 1). For Heermann's Gull, the highest number of prey species per sample was for year 2011, followed by 2006. The Elegant Tern showed the highest number of prey species per sample for 2006, followed by 2010 (Table 2). For Royal Terns, the regression calculated between sample size and number of prey species recorded in the samples showed a nonsignificant positive logarithmic relationship ($y = 1.9085\ln(x) + 2.0673$, $R^2 = 0.4074$). However, the regression value is higher and significant if we remove two outlier points corresponding to 1997 and 2008, the two years preceding strong El Niño oceanographic events ($y = 1.902\ln(x) + 2.0406$, $R^2 = 0.7074$, $F(1,4) = 9.669$, $P = .0359$). Chi-square tests revealed no significant difference between the diets of Elegant Terns and Heermann's Gulls, whereas the test comparing Royal Tern and Elegant Tern diets indicated a significant difference ($df = 21$, $P < .05$).

DISCUSSION

While sympatric species of nesting seabirds usually differ in some aspects of feeding ecology, dietary segregation of closely related species has remained an important part of seabird feeding ecology, evolution, and more recently, conservation biology (Ainley, 2019; Ashmole & Ashmole, 1967; Bearhop et al., 2006; Cherel et al., 2005; Diamond, 1975, 1983; Martin & Prince, 2001). Here we provide the results of monitoring the Royal Tern diet at Isla Rasa for only a few years, so we have information limited in time and by number of samples. These limitations have been considered in the interpretation of our data.

Comparative Diet and Trophic Breadth

The most common species of fishes observed in the Royal Tern diet during this long-term and continuing study are those also most frequent in the diets of the Elegant Tern and Heermann's Gull. However, the total number of species (and families) in the Royal Tern diet was about twice that in the diets of the other two seabirds and covered a much wider taxonomic spectrum. This coincides with reported diet observations performed in different locations, such as the western North Atlantic (Aygen & Emslie, 2006; Liechty et al., 2016; McGinnis & Emslie, 2001; Wambach & Emslie, 2003), as well as Patagonia (Favero et al., 2000; Gatto & Yorio, 2009), where a wide spectrum of prey has been observed. The regression statistic for number of prey species and sample size (Fig. 3) reveals that a yet larger sample might well increase the number of prey species documented for Royal Terns in the Isla Rasa region.

Additionally, many of the species recorded in the diet of the Royal Tern are represented by a single individual during the whole sampling period. Nineteen species (over half of the 36 species identified) and five families are represented by single-occurrence observations. These single observations may be opportunistic catches. Interestingly, the two years when more of these catches of single individuals of a previously unreported species occurred were 1997 and 2010, which were the two commercial fishing seasons within the sampling period when sardine catches were severely reduced. In those years, catch reductions were 73% and 47%, respectively, of the previous fishing season (Fig. 4). If preferred forage species had much lower availability at those times, Royal Terns may have had to capture alternative prey, regardless of species.

TABLE 1
Diet composition of Royal Terns *Thalasseus maximus* nesting at Isla Rasa, Gulf of California, during eight years between 1996 and 2011*

Family	Species	Year							
		1996	1997	2000	2001	2006	2008	2010	2011
FISHES									
Ophichthidae[b] (snake eels)	*Myrophis vafer*[F]	–	–	1	–	–	–	–	–
Dussumieriidae[e] (herrings)	*Etrumeus acuminatus*[F,V]	–	–	–	–	8	2	–	5
Dorosomatidae[e] (thread herrings)	*Opisthonema libertate*[F]	1	1	–	–	–	–	–	–
Alosidae[e] (shads)	*Sardinops sagax*[F,V]	3	4	7	12	10	18	4	–
Engraulidae[e] (anchovies)	*Anchoa ischana*[F]	–	–	–	–	–	–	1	–
	Cetengraulis mysticetus[F]	–	–	1	–	–	–	–	–
	Engraulis mordax[F,V]	1	4	5	12	10	3	2	28
Myctophidae[e/m] (lanternfishes)	*Benthosema panamense*[K]	–	–	–	1	–	–	–	–
Batrachoididae[b] (toadfishes)	*Porichthys* sp.[F]	–	–	–	–	1	–	–	–
Ophidiidae[b] (cusk-eels)	*Ophidion galeoides*[L]	–	–	–	–	–	1	–	–
	Ophidion iris[L]	–	–	–	–	1	–	–	1
Exocoetidae[e] (flyingfishes)	*Fodiator rostratus*[F]	–	–	1	–	–	–	–	–
	Unident. exocoetid[F (tail only)]	–	–	–	1	1	–	–	–
Hemiramphidae[e] (halfbeaks)	*Hyporhamphus naos*[F]	–	–	–	–	–	–	2	–
	Hyporhamphus rosae[F]	–	1	–	–	–	–	–	–
Atherinopsidae[e] (New World silversides)	*Colpichthys regis*[F]	–	1	–	–	–	–	–	–
	Leuresthes sardina[F]	–	2	–	–	–	–	–	–
	Unident. atherinopsid[V]	–	–	–	5	–	–	–	–
Syngnathidae[d] (seahorses)	*Hippocampus ingens*[F]	–	–	–	–	–	–	1	–
Serranidae[d] (sea basses)	*Diplectrum* sp.[F (missing head)]	–	–	–	–	–	1	–	–
	Paralabrax maculatofasciatus[F]	–	–	–	–	–	–	1	–
Carangidae[e] (jacks)	*Oligoplites refulgens*[F]	–	–	–	–	2	–	–	–
	Oligoplites saurus[F]	1	–	–	–	–	–	–	1
	Oligoplites spp.[F (photos only)]	–	–	–	–	–	–	–	2
	Trachurus symmetricus[F,V]	–	2	–	1	2	2	–	–
Gerreidae[d] (mojarras)	*Eucinostomus dowii*[F]	–	–	–	–	–	–	–	1
	Eucinostomus spp.[V]	–	1	2	–	2	–	–	–
Haemulidae[d] (grunts)	*Brachygenys californiensis*[V]	–	1	–	1	–	–	–	–
	Haemulon flaviguttatum[F (juv.)]	–	–	–	–	–	–	1	–
	Microlepidotus inornatus[F]	–	–	–	–	–	–	4	1
Pomacentridae[d] (damselfishes)	*Abudefduf troschelii*[F]	–	–	–	–	–	–	1	–
Scombridae[e] (mackerels)	*Scomber japonicus*[F,V]	–	7	2	2	9	–	–	17
Paralichthyidae[b] (sand flounders)	*Paralichthys aestuarius*[F]	1	–	–	–	–	–	–	–
	Xystreurys liolepis[F]	–	1	–	–	–	–	–	–
Pleuronectidae[b] (righteye flounders)	*Pleuronichthys ritteri*[F]	–	–	–	1	–	–	–	–
CRUSTACEA									
Munididae[e] (pelagic squat lobster)	*Grimothea planipes*[V]	–	–	–	–	–	–	–	10
	Total species	5	12	7	9	10	6	9	9
	Total samples	7	26	19	36	46	27	17	66
	Species per sample	0.71	0.41	0.37	0.25	0.22	0.22	0.53	0.14

* Superscript letters by species name indicate principal identification in lab by LTF(F), by C. Klepadlo(K), or by R. N. Lea(L) and in field by EV(V); superscript letters by family name indicate its normal habitat: benthic(b), demersal(d), epipelagic(e), or epi/mesopelagic(e/m). Samples of some fishes were either represented by juveniles (juv.) of large-size species as adults or represented by identifiable body parts. A database maintained by EV records such details as well as lengths and weights of samples taken in the field.

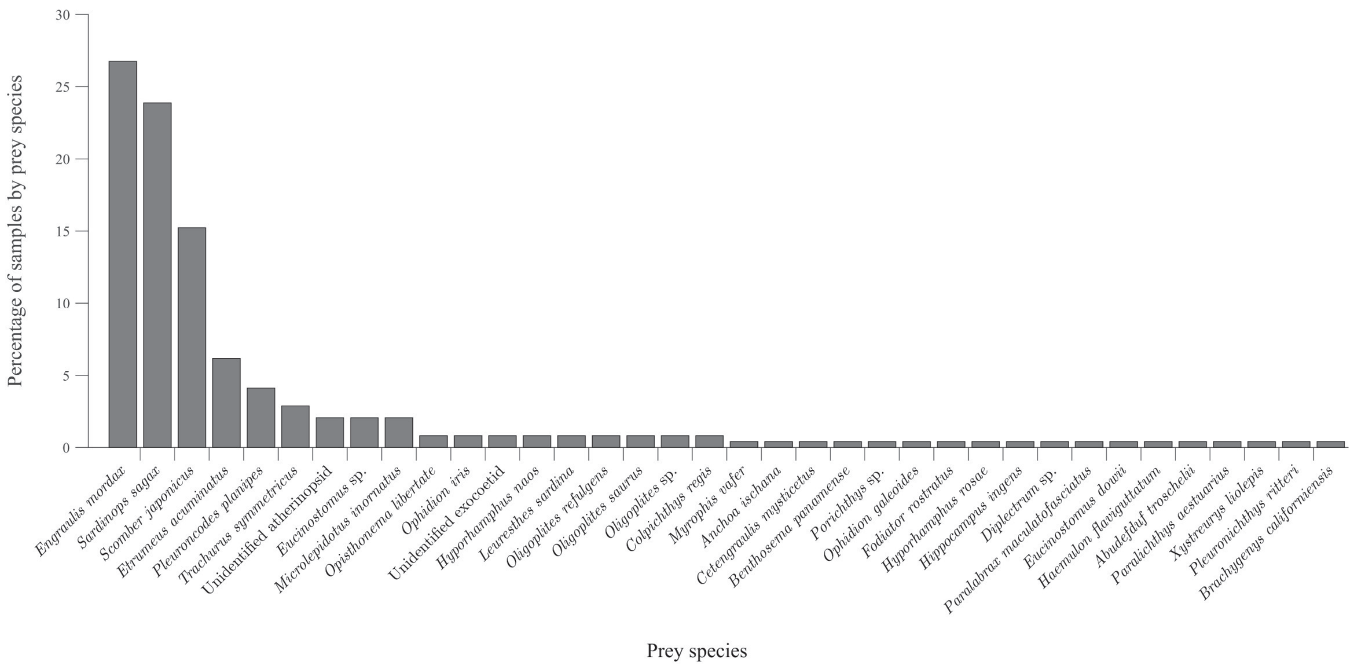

Fig. 1. Percentage diet composition, by prey species, for Royal Tern *Thalasseus maximus* nesting at Isla Rasa, Gulf of California, Mexico, during eight sampling years.

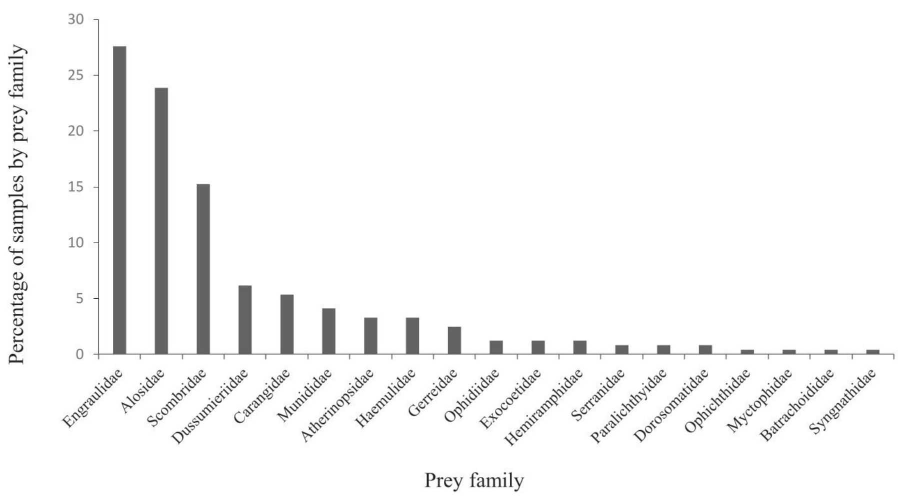

Fig. 2. Percentage diet composition, by prey family, for Royal Tern *Thalasseus maximus* nesting at Isla Rasa, Gulf of California, Mexico, during eight sampling years.

Comparison of diet compositions of Royal Terns and Elegant Terns nesting at Isla Rasa showed less overlap than the diets of Elegant Terns and Heermann's Gulls. The Elegant Tern is phylogenetically closely related to the Royal Tern, yet at Isla Rasa they share nesting area. Although alternative explanations are possible, the differences in diet composition (i.e., the wider spectrum of prey species and foraging habitats for Royal Terns) may result in less foraging competition between these two tern species during periods of scarce food availability, while Elegant Terns and Heermann's Gulls have a more similar diet. This result can also be reinforced by diet analysis previously performed on these two species plus the California Brown Pelican *Pelecanus occidentalis californicus*, which show these three seabird species to be excellent indicators of forage fish availability, such as for Pacific Sardines and Northern Anchovies (Velarde et al., 2013; Velarde, Ezcurra, & Anderson, 2015).

Foraging Areas and Depths

Heermann's Gull is closer in body size to the Royal Tern but has different feeding preferences and methods than the Royal Tern. Heermann's Gulls feed only at the sea's surface, while floating/paddling, whereas both species of terns are shallow "plunge divers." Heermann's Gull usually targets prey items at or very near the surface, probably no more than *ca*. 25 cm deep, whereas the terns can target prey as deep as 45 to 60 cm. Although the feeding methods of the terns studied here are almost identical, our results indicate that these two species are exploiting different habitats, with the Royal Tern apparently foraging more inshore than the Elegant Tern. However, when a comparative isotopic analysis of the diet of Elegant Terns and Heermann's Gulls was performed, the results showed that Heermann's Gull is an even more pelagic forager than

TABLE 2
Diet composition of Elegant Terns *Thalasseus elegans (T.e.)* and Heermann's Gulls *Larus heermanni (L.h.)* at Isla Rasa, Gulf of California, during 1996–2011*

	Year, bird species															
	1996		1997		2000		2001		2006		2008		2010		2011	
Prey	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***	***T.e.***	***L.h.***
FISHES																
Dussumieriidae (herrings)[e]																
Etrumeus acuminatus[F,V]	–	–	1	–	3	–	–	–	2	1	–	–	–	–	4	–
Dorosomatidae (thread herrings)[e]																
Opisthonema libertate[F,V]	2	3	–	–	–	13	–	6	–	–	1	–	–	–	–	–
Alosidae (shads)[e]																
Sardinops sagax[F,V]	61	29	50	57	32	34	18	10	1	4	48	4	–	3	–	–
Unidentified clupeoid[F] (tail)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Engraulidae (anchovies)[e]																
Anchoa ischana[F]	–	–	–	–	–	–	–	–	–	–	–	–	1	2	1	–
Cetengraulis mysticetus[F]	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Engraulis mordax[F]	32	13	45	6	120	71	182	38	24	8	78	8	43	9	137	2
Unident. engraulid(s)[F]	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–
Myctophidae (lanternfishes)[e/m]																
Benthosema panamense[K]	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1
Atherinopsidae (New World silversides)[e]																
Colpichthys regis[F]	–	–	–	1	–	1	–	–	–	–	1	–	–	–	–	–
Carangidae (jacks)[e]																
Oligoplites saurus[F]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Seriola dorsalis[F] (j)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Trachurus symmetricus[F,V]	–	–	1	–	1	–	4	1	1	2	7	1	2	–	–	–
Scombridae (mackerels)[e]																
Scomber japonicus[F,V]	–	–	10	9	1	4	–	1	1	1	–	–	–	–	1	2
Paralichthyidae (sand flounders)[b]																
Paralichthys aestuarius[F] (j)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
CRUSTACEA																
Euphausiidae[Vi,e] (krill)																
Nyctiphanes simplex[V]	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	1
Mysida[Vi,e] (opossum shrimps)																
Unidentified Mysida	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Total species	3	3	6	4	6	7	3	5	6	5	6	3	5	4	5	5
Total samples	95	45	108	73	158	127	204	56	30	16	136	13	48	16	144	7
Species per sample	0.03	0.07	0.06	0.05	0.04	0.06	0.01	0.09	0.20	0.31	0.04	0.23	0.10	0.25	0.03	0.71

* Superscript letters by species name indicate principal identification in lab by L. T. Findley(F), in field by E. Velarde(V), and in lab by J. L. Villalobos(Vi) (Crustacea) or C. Klepadlo(K) (the 1997 myctophid specimen = tentative ID, only head and anterior thorax present); superscript letters by family name indicate its normal habitat (see text): benthic(b), epipelagic(e), or epi/mesopelagic(e/m). Samples of several fishes represented juvenile (j) stages of large-size species as adults, and several were represented by identifiable body parts. Most unidentified species were very partial specimens.

the Elegant Tern (Elias-Valdez et al., 2023).

Unexpectedly, all three species of seabirds were found, albeit sporadically, to include at least one normally mesopelagic lanternfish (Myctophidae) in their diets. A midshipman toadfish (Batrachoididae) and a sand flounder (Paralichthyidae) were found

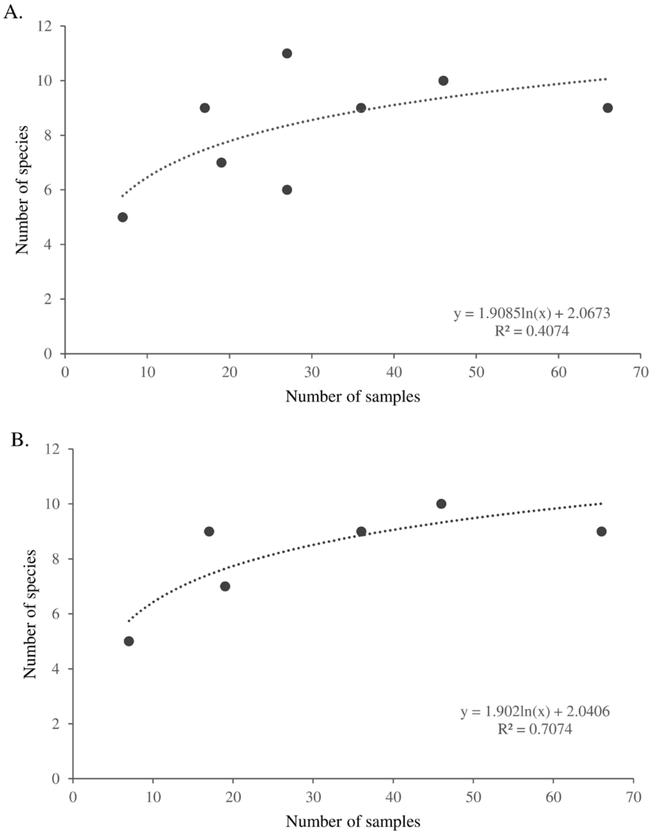

Fig. 3. Regressions between sample size and number of fish species identified in the diet of Royal Terns *Thalasseus maximus* nesting at Isla Rasa, Gulf of California, Mexico, for (A) eight years and (B) six years. Best fit to the regression curve is obtained if the two extreme points shown in panel A for the case when 27 samples were obtained are eliminated from the analysis, as shown in panel B; these two points represent the values for the years just previous to an El Niño (1997 and 2008, respectively).

in the diet of the Royal Terns. Prey of these families have been reported previously in the diet of Royal Terns (Liechty et al., 2016), and although mesopelagic and benthic, respectively, these fishes are known to exhibit vertical diel movements/migrations. In the case of myctophids, migrations have been found to start in the early afternoon and reach peak speed at sunset (Barham, 1971). It is interesting to note that all myctophid specimens, the toadfish, and the flounder were captured during moonless hours of the night when these fishes must have been close to the surface. Adult Panama Lanternfish *Benthosema panamense*—epipelagic to mesopelagic near the coast—form dense aggregations at night (Moser & Ahlstrom, 1996) and are fed on by jumbo squid *Dosidicus gigas*, a "nyctoepipelagic" species, sporadically common in the Guaymas Basin and nearby areas (Markaida & Sosa-Nishizaki, 2003; Robison, 1972). Panama Lanternfish constituted 2.8% of total catch recorded in this study for the Royal Tern.

Potential Effect of Kleptoparasitism

Terns generally nest in mixed colonies with other seabirds, deriving several benefits from this habit, but also exposing themselves to kleptoparasitism (robbing of prey items among spatially closely occurring species) and predation of eggs and chicks from colony mates (Loftin & Sutton, 1979; García et al., 2010; Velarde, 1992). In the present case, nesting Royal Terns appear to provide some protection for Elegant Terns due to their more aggressive behavior toward egg and chick predators, such as the quasi-endemic and sympatric Yellow-footed Gull and Heermann's Gull (Velarde, 2012). Conversely, the much higher number of Elegant Terns nesting on Isla Rasa may convey an advantage to the Royal Terns by reducing the probability of their eggs and chicks being preyed upon by the Yellow-footed and Heermann's Gulls.

Additionally, while Heermann's Gulls may sometimes kleptoparasitize both California Brown Pelicans, while they feed, and terns, when they deliver fish to their chicks, this is a practice that involves only a small proportion of Heermann's Gulls in this

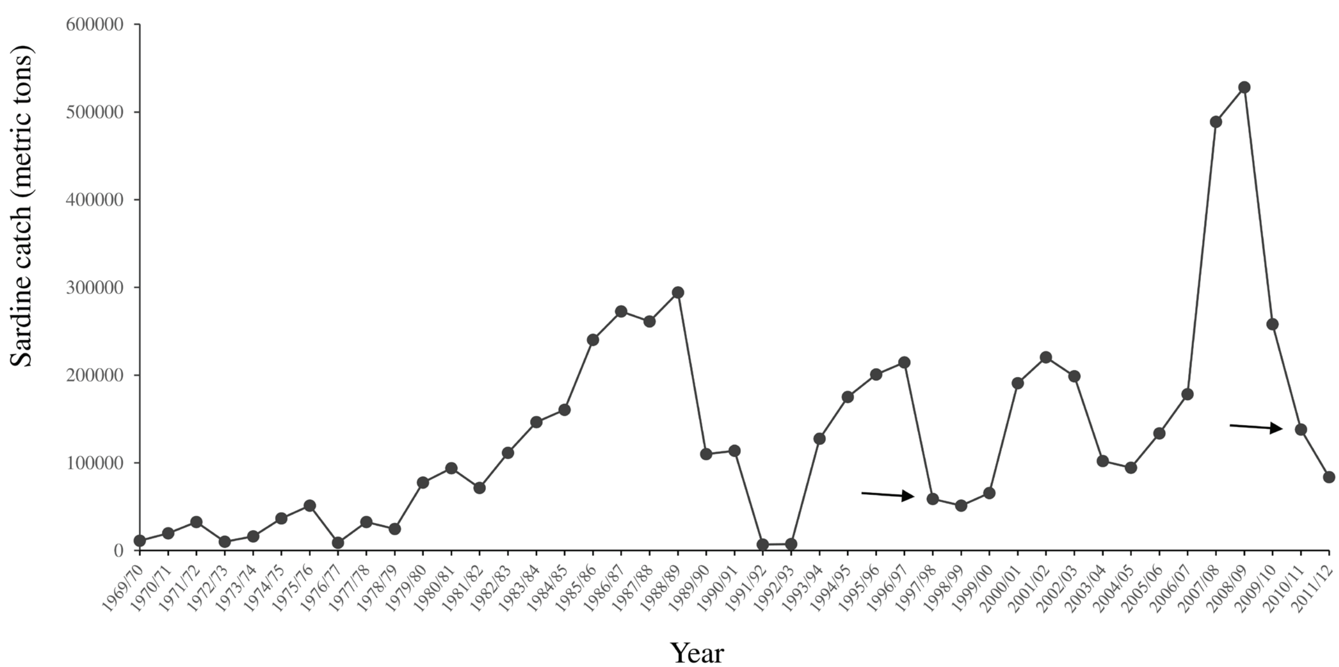

Fig. 4. Pacific Sardine catch by the industrial fleet, with arrows indicating years of collapse of the catch, coinciding with the highest number of single-specimen records of prey species.

area. For example, Tershy et al. (1990) found that when pelicans and gulls were foraging together, only about 13% of pelican foraging dives elicited a kleptoparasitic attempt by a Heermann's Gull. However, not all attempts were successful, due to unsuccessful fishing by pelicans as well as evasive behaviors of successful pelicans, which hindered gulls from actually stealing the fish.

In the case of kleptoparasitism of terns, only a few gulls have been observed feeding in this fashion in the vicinity of the terns' nesting area at Isla Rasa, and territorial behavior of gulls prevents a large number of them from congregating to kleptoparasitize terns at their nesting sites (Velarde, 1980). The trophic level differences between Heermann's Gulls and Elegant Terns reported by Elias-Valdez et al. (2023) show a trophic niche separation.

Probable Interactions With Human Activities

The productive waters of the Gulf of California allow the establishment and subsistence of large colonies of the three seabird species studied (in addition to several other seabird species, e.g., Velarde et al., 2005), all nesting synchronously. However, although the islands and portions of the adjacent marine habitat are nominally protected, not all the waters surrounding these important seabird breeding islands are under federal protection. Recent and increasing growth of the commercial industrial fishery for small pelagic (forage) fishes—especially Pacific Sardines but also other forage fish species—looms as an imminent resource-depletion threat to these seabirds. However, the fishery also potentially affects other components of the ecosystem, such as marine mammals (García-Rodríguez & Aurioles-Gamboa, 2004), the endemic fishing bat *Myotis vivesi* (Drinkwater et al., 2021), and several species of predatory fishes. Also, other fisheries—such as artisanal and sport fisheries that take large predatory fishes and macroinvertebrates (including groupers, sea basses, snappers, Dolphinfish or dorado *Coryphaena hippurus*, California Yellowtail *Seriola dorsalis* and other jacks, sharks, jumbo squid, etc.)—are negatively affected by forage-fish fishery. The commercial forage fish fishery in the area operates for about 10 or 11 months each year (stopping only during September and occasionally August of each year), and fishing boat catch storage capacity has been in constant growth.

Velarde, Ezcurra, et al. (2015) demonstrated that the size of the Elegant Tern nesting colony is affected not only by oceanographic factors but also by the level of Pacific Sardine commercial catch (Fig. 4 in cited work) and fishing effort. In short, this fishery directly affects Elegant Tern colony size and movements of Elegant Terns outside of their traditional nesting areas in the Gulf of California. The effect of this fishery on Royal Tern breeding population size and breeding success is still to be determined. We hope that studies of the type we report here, where the principal food of seabird species has been found to coincide with one or more important commercial fisheries, provide useful information for management of the fisheries in question and appropriate regulation of their fishing efforts.

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AUTHOR CONTRIBUTIONS

EV: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, review & editing. LTF: Specimen curation, data curation, investigation, resources, validation, writing—original draft, review & editing.

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