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Authors: Goodenough, Katharine S., Patton, Robert T., and Lorda, Julio

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Dietary Plasticity Mitigates Impacts to Reproduction for the Gull-billed Tern *Gelochelidon nilotica* During Abnormally Warm Sea Surface Temperature Events in California, U.S.A.

Katharine S. Goodenough*[1,2], Robert T. Patton[3] and Julio Lorda[4,5]

[1]Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK, U.S.A. 73019

[2]Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK, U.S.A 73019

[3]Patton Biological LLC, 4444 La Cuenta Drive, San Diego, CA 92124

[4] Facultad de Ciencias, Universidad Autónoma de Baja California, Carretera Transpeninsular Ensenada - Tijuana No. 3917, Colonia Playitas, Ensenada, Baja California, Mexico, CP 22860

[5]Tijuana River National Estuarine Research Reserve, 301 Caspian Way, Imperial Beach CA, U.S.A. 91932

*Corresponding author, Email: kate.goodenough@gmail.com

Abstract.—Large scale oceanic processes can have profound consequences for marine and coastal food webs. Mortality and reproductive related impacts to seabirds have been documented for decades, and current research suggests that dietary flexibility may be a key component by which birds can mitigate environmental variation. Our motivation for this research was to better understand how a dietary generalist in the coastal environment responds to changes in prey food availability. The Gull-billed Tern *Gelochelidon nilotica* is a coastal nesting species that has an opportunistic generalist diet. We monitored both tern diet and density of a main prey resource to examine how responsive these terns are to annual variation in prey resources. Our results documented that the loss of a ubiquitous prey resource did not appear to influence tern annual reproductive success even though, in some years, *Emerita analoga* comprised greater than 70% of Gull-billed Tern diet. During breeding seasons with warmer than average sea surface temperatures, the Gull-billed Tern switched to a more terrestrial diet and focused aquatic foraging activities upon crustacean species that are more tolerant of warmer water temperatures. Dietary plasticity can be beneficial to mitigate variation in prey resource availability and impacts on reproductive success, and the ability to respond rapidly to changes in resources may play an important role in how coastal species can acclimate or adapt to annual changes in the prey base. *Received 17 Aug 2022, accepted 19 Feb 2023.*

Key words.—diet-switching, dietary plasticity, *Emerita analoga,* foraging ecology, El Niño Southern Oscillation, Blob, Pacific sand crab, reproduction, tern

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Dietary plasticity has long been an important focus of avian research in an attempt to understand how species may alter their foraging strategies to address seasonal change. This research focus has become increasingly important with heightened awareness of global climate change impacts upon both avian reproductive activities and shifting prey resource dynamics (Piatt *et al.* 2007). Seabirds are considered good sentinels to note changing prey resources because their diet choices typically reflect the occurrence of prey within foraging ranges making them sensitive to environmental change. Foraging parameters (e.g., foraging effort, success, and efficiency) have been documented to co-vary with environmental aspects, and links between seabird population pathology and global climate change have been documented (Harding *et al.* 2006, Parsons *et al.* 2008, reviewed by Piatt *et al.* 2007, Gremillet and Charmantier 2010).

Generalist predator foraging strategies can be difficult to understand given that these generalists feed on a variety of prey species at differing trophic levels. For some species, dietary flexibility may extend to prey within a particular taxon such as fish (Hamer *et al.* 2007), while, for other species, dietary flexibility may extend to a range of prey taxa (Schwemmer and Garthe 2007). Prey or diet switching has been observed in many groups including gulls (Annett and Pierotti 1989; Schwemmer and Garthe 2007) and penguins (Booth *et al.* 2018 and references within). This diet switching allows for a flexible foraging strategy which provides organisms with a way in which to mitigate seasonal variation in prey resources through alteration of foraging behavior.

From 2013–2016, the eastern Pacific Ocean experienced the largest marine heat wave on record with above normal sea surface temperatures (SST) due to a combination of the 'Blob', a persistent high-pressure system in the northeastern part of the Pacific Ocean (Bond *et al.* 2015, Di Lorenzo and Mantua 2016; Thompson *et al.* 2019), and a strong El Niño Southern Oscillation (ENSO). The 'Blob' extended as far south as northern Baja California by late 2013, and it was responsible for fisheries collapses and massive seabird die-offs (Bond *et al.* 2015; Piatt *et al.* 2020). In late 2014, conditions in Southern California waters were further compromised by the start of a strong ENSO that produced anomalous warm SST through 2016 (Cavole *et al.* 2016). These combined events had many impacts to marine ecosystems of the Northeast Pacific affecting higher trophic levels (Arafeh-Dalmeo *et al.* 2019; Cavanaugh *et al.* 2019; Lonhart *et al.* 2019; Rogers-Bennett and Catton 2019; Piatt *et al.* 2020). Seabird declines in reproductive success (Ainley *et al.* 1995), range-wide shifts in seabird distribution (Velarde *et al.* 2015), and high mortality (Cavole *et al.* 2016; Piatt *et al.* 2020) are documented regularly with strong ENSO events.

These above-normal SST events provided a unique opportunity to study the foraging ecology of a dietary generalist, the Gull-billed Tern *Gelochelidon nilotica*. Pacific sand crabs *Emerita analoga*, hereafter referred as *Emerita*, sand crab, or Pacific sand crab, are an important prey resource for the Gull-billed Tern in southern California. These crabs are ubiquitous in the sandy beach environment and have been documented in Western Snowy Plover *Charadrius nivosis* diet (Page *et al.* 2020) and migrating shorebird diet along the Pacific coast of North America (Dugan et al. 1991, 1994, 2003). Sand crab populations along the California coastline have been greatly impacted by both anthropogenic activities of beach nourishment and ENSO large-scale oceanic effects (Wooldridge *et al.* 2016, Cavole *et al.* 2016).

The Gull-billed Tern ranges along both the Atlantic and Pacific Coasts of North America and is well known for its generalist diet foraging on a range of ephemerally abundant aquatic and terrestrial prey items across trophic levels in estuarine ecosystems of Europe, Africa, North America, and Australia (Cramp *et al.* 1985; Bogliani *et al.* 1990; Sánchez *et al.* 1993; Sánchez *et al.* 2004; Dies *et al.* 2005; Molina and Marschalek 2003; Goodenough 2014; Molina *et al.* 2020;). It is not well understood how changes in prey resources might influence Gull-billed Tern reproduction as this particular species can alternate to other food resources when primary prey are not available (Bogliani *et al.* 1990; Dies *et al.* 2005). The Gull-billed Tern may be able to mitigate seasonal variation in prey availability by using flexible foraging strategies, e.g., diet and habitat switching such that there is not a detectable influence of diet variation upon reproductive activities. The alternative outcome of prey resource variation is that major changes in the prey base, e.g., loss of a ubiquitous food resource could negatively influence tern reproductive activities such as altering clutch size and the number of offspring produced.

To better understand the relationship between seasonal variation in food resources and potential impacts to reproductive activities for this estuarine generalist, we focused research upon three goals: monitoring variation in Gull-billed Tern diet during the breeding season using analyses of regurgitated pellets, monitoring *Emerita* density at six beaches within the tern's foraging range and evaluating the relationship between annual variation of food resources and Gull-billed Tern reproductive success based upon annual clutch size and the number of offspring produced. We hypothesize that: (1) annual variation in *Emerita* density will be reflected in the tern diet and (2) *Emerita* availability will drive Gull-billed Tern annual reproductive success. These comparisons contribute to the knowledge base of foraging ecology and will increase our understanding of the impacts of annual diet variation on reproductive success for coastal foraging and nesting species like the Gull-billed Tern.

METHODS

Study area

Research was conducted in the coastal estuarine ecosystems of South San Diego Bay and the Tijuana River Estuary in southern California (Fig. 1). The site is highly fragmented and comprised of multiple habitats including intertidal areas, sandy beaches, coastal strand, dune and transition habitats, invasive *Carpobrotus* sp.-dominated dunes, coastal marsh, and coastal sage scrub uplands interspersed among highly urbanized areas. The Gull-billed Tern nests in only one location in coastal southern California—at the South San Diego Bay National Wildlife Refuge, (32° 35′ 56.81″ N, 117° 6′ 11.32″ W, Fig. 1), herein referred to as the Refuge. The majority of tern foraging occurs within the Refuge, to the west and northwest along the Silver Strand peninsula, and south along the coast from the Refuge to the US-Mexico border that includes the Tijuana River National Estuarine Research Reserve and Border Field State Park (Goodenough 2014).

Diet sample collection

We chose regurgitated pellet analyses to monitor tern diet as it is an inexpensive and non-invasive method to quantify diet composition. For certain avian species, (i.e., owls, raptors, seabirds, and some waterbirds), non-digestible parts of prey are regurgitated in the form of pellets. This type of diet analysis has been previously employed as a method to monitor diet for terns and their allies (Duffy and Jackson 1986; Rosenberg and Cooper 1990; Bugoni and Vooren 2004; Mariano-Jelicich and Favero 2006; Favero and Becker 2007). Regurgitant pellets can be biased towards prey species that are less easily digested; but in a previous study, the Gull-billed Tern diet was compared across two years using both bulk carbon and nitrogen stable isotopes and focused observation of

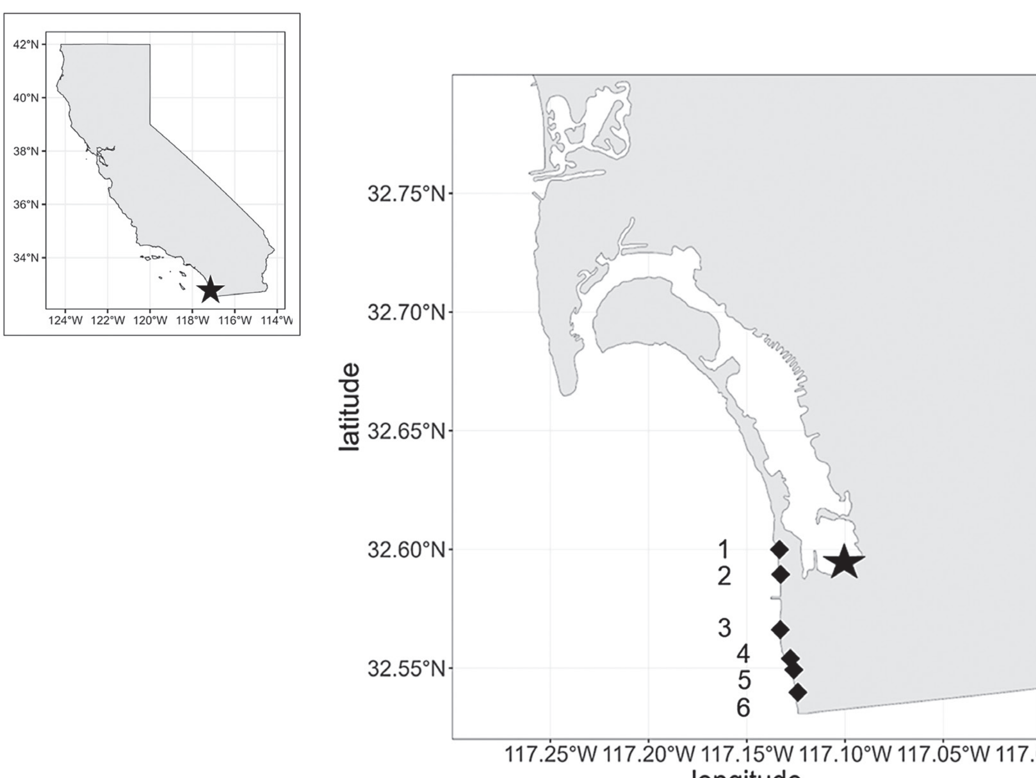

Figure 1. A map of the study area that encompasses the San Diego Bay National Wildlife Refuge, US Naval Base Coronado Silver Strand Training Complex, Imperial Beach, and Tijuana River National Estuarine Research Reserve, and Border Field State Park in southern San Diego County, California, USA. (star) indicates the location of the Gull-billed Tern nesting colony at the South Bay Unit of the San Diego Bay NWR. Beach sampling locations are highlighted by diamonds (black) and are listed from north to south: 1-US Naval Base Coronado Silver Strand Training Complex North (SSTC-N), 2-Naval Base Coronado Silver Strand Training Complex South (SSTC-S), 3-Seacoast Drive- Imperial Beach, 4-North of the Tijuana River Mouth, 5-South of Tijuana River Mouth, 6-Border Field State Park, California, USA.

prey delivery to Gull-billed Tern chicks. Both analyses documented a low percentage of fish and soft-bodied organisms and a higher percentage of crabs within the San Diego colony diet (Goodenough 2014). Hence, we felt regurgitant pellets would be an adequate methodology to assess Gull-billed Tern diet variation over time.

Pellets were collected within the Gull-billed Tern breeding colony in the San Diego Bay National Wildlife Refuge, California, USA from May through August over seven years (2012–2019) during weekly monitoring surveys. The only exception was in 2013 as colony dynamics were disrupted by an acanthocephalan-related mass mortality event (Patton *et al.* 2017). The pellets were dried at room temperature, dissected, and sorted under a dissecting scope to the lowest possible taxa depending on the extent of diagnostic features of the food items that were available for identification. We quantified prey items within the pellets as frequency of occurrence (percentage of sample/all samples) as suggested by Duffy and Jackson (1986). Frequency of occurrence data were categorized by taxa and further grouped into aquatic versus terrestrial prey sources.

Tern reproductive success

Reproductive data from the Inventory and Monitoring Program at San Diego Bay National Wildlife Refuge were used to calculate annual mean clutch size and the number of chicks produced, represented as fledgling-breeding pair ratios from 2012 through 2019 (Table 2). We used both fledgling-breeding pair ratio and mean annual clutch size as proxy metrics for annual reproductive success. Fledgling-breeding pair ratios were calculated by summing the number of fledglings produced for the season and dividing by the total number of breeding pairs for the season. We then used a linear regression to assess the relationship between *Emerita* in the Gull-billed Tern diet with annual fledgling-breeding pair data. We analyzed mean clutch size across years using a 2-tailed t-test ($\alpha = 0.05$).

Crab density sampling

We used previous telemetry research on the Gull-billed Tern home range in San Diego, California to select *Emerita* crab sampling locations, as the majority tern foraging occurs within 10 km of the nesting colony (Goodenough 2014). Six Pacific sand crab sampling locations were selected: four locations along the barrier beach of the Tijuana River estuary (Border Field State Park, North and South of the Tijuana River mouth, and Seacoast), and two along the coastal beaches of South San Diego Bay at the U.S. Naval Base Coronado Silver Strand Training Complex North (SSTC-N) and South (SSTC-S) located 1.5 km west of the Gull-billed Tern breeding colony (see Fig. 1, Table 1). All sampling locations were within 7 km of the breeding colony to ensure that the terns would use the resource if available during the breeding season.

Emerita sampling was conducted annually in June at lowest tide to coincide with peak energetic demands of nesting terns. At each sample location, we laid out an 800 m transect in the intertidal zone of the beach parallel to the surf line. We collected nine sand core samples every 20 m along the transect with a 20 cm diameter core sampler. The samples were sieved and the quantity and size of crabs within each core was documented.

We used a Chi-squared test for comparing differences in diet over time (species composition) and terrestrial vs marine among years. We first arcsine square root transformed the proportion of pellets of each prey per year to achieve normality and homoscedasticity. We then used year as the independent continuous variable and the transformed pellet composition data as the response variable. Linear regressions were used to assess individual prey variation through time. We did not use data from 2013 due to Gull-billed Tern colony die-off (Patton et al. 2017). Packages 'car' and 'stat' in R were used for linear regressions, chi-squared analyses, and two-tailed *t*-test (R Core Team 2021).

RESULTS

We collected 1,276 pellets during the 2012, and 2014–2019 breeding seasons from May through August at the San Diego Bay National Wildlife Refuge, California, USA (Fig. 1). Crab species included Pacific sand crab (*Emerita analoga*), Mexican fiddler crab (*Leptuca crenulata*), striped shore-crab (*Pachygrapsus crassipes*), and tuna crab (*Pleuroncodes planipes*). Lizard taxa included western fence lizard (*Sceloporus occidentalis*) and side-blotched lizard (*Uta stansburiana*).

Table 1. Location of beaches sampled for Pacific sand crab (*Emerita analoga*) density and distance to the Gull-billed Tern (*Gelochelidon nilotica*) breeding colony at the South San Diego Bay National Wildlife Refuge, San Diego, California, U.S.A., 2013–2017.

ID	Location Sampled	Latitude	Longitude	Distance from breeding colony (km)
1 - SSTC-N	west of Refuge	32.599933	−117.133348	2.25
2 - SSTC-S	north of jetty, Imperial Beach	32.589477	−117.132766	2.75
3 - Seacoast	Seacoast Drive, Imperial Beach	32.566203	−117.132959	4.0
4 - North River	north of Tijuana River Mouth	32.554045	−117.127805	5.0
5 - South River	south of Tijuana River Mouth	32.549328	−117.126059	5.5
6 - Border Field	Border Field State Park	32.535982	−117.124007	6.2

Insects included sphinx moth (*Hiles lineata*), tiger beetle (*Cincindela* sp.), and brine fly (Ephydridae). Avian prey items were present in the form of unfledged chicks including California Least Tern (*Sternula antillarum browni*), Western Snowy Plover (*Charadrius nivosus nivosus*), Horned Lark (*Eremophila alpestris*), Killdeer (*Charadrius vociferis*), and Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*). Fish were present for only one year and in small quantities and consisted of California killifish (*Fundulus parvipinnis*), and long-jawed mudsuckers (*Gillichthys mirabilis*).

Diet variation

To understand if the prey base changed significantly among breeding seasons, we binned the pellet frequency of abundance data into aquatic versus terrestrial sources. Prey sources were predominantly aquatic but varied significantly across years (from 53%–78%, n = 1276, χ^2_6 = 53.34, P < 0.0001; Fig. 2). Significant differences were also observed in the prey base among years (n = 1276, χ^2_{48} = 591.71, P < 0.0001), but aquatic resources were more prevalent (58–87%) than terrestrial resources (15–47%, Fig. 2).

Crustaceans were a major component of the Gull-billed Tern diet in all years (range 53–78%). The increase or maintenance of aquatic resources in the years after the Gull-billed Tern die-off in 2013 appears to be due to increases in the consumption of other crab species (i.e., increased proportions of *Leptuca* and *Pleuroncodes*; Fig. 2). Lizard contributions to diet ranged from a low of 9% (2017) to a high of 44% (2018–2019). Insect taxa were also variable ranging from a low of 4% (2015) to a high of 24% (2016). Avian contributions were low in all years with 0–5% abundance within the tern pellets. Fish species were only documented in 2017 and 2019 (1–3%; Fig. 2).

When comparing among crab taxa, we found only two prey items that statically varied across years. *Emerita* was at high frequency of abundance of 76% in 2012 that declined to just 5% in 2019 (R^2 = 0.78, F = 17.82, P = 0.008; Fig. 2). In contrast *Leptuca* increased in frequency from 2% in 2012 to a high of 40–42% in 2018 and 2019 (R^2 = 0.90, F = 46.91, P = 0.001; Fig. 2). *Pachygrapsis* remained in low abundance in all years (1–3%). Another change in diet was the inclusion of a novel prey item, tuna crab *Pleuroncodes planipes,* in the tern diet for the 2015–2016 breeding seasons (Fig. 3). Southern range species such as *Plueroncodes* are documented to shift distributions northward in ENSO influenced years (Stewart *et al.* 1984).

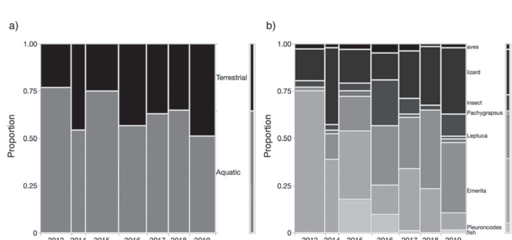

Figure 2. Proportion of prey items found in Gull-billed Tern (*Gelochelidon nilotica*) pellets per year by prey base (a) and by species (b). Aquatic prey are indicated by gray color while terrestrial prey are indicated in black. The width of the bar indicates represents the number of pellets examined per year. The bars on the left with terrestrial and aquatic prey base is mean across years. No pellet collection occurred in 2013 due to a mass mortality event (Patton et al. 2017). Prey base sources were predominantly aquatic but varied significantly across years from 53% to 78% (n =1276, X2,48 = 591.71, P < 0.0001.

Tern reproductive success

The Gull-billed Tern had a mean fledgling-to-breeding pair ratio of 0.68 for the duration of the study (Table 2). Fledgling-breeding pair ratios were lower during the Blob-ENSO period but started to recover in 2017 after SST began to return to normal temperatures (Table 2). We regressed *Emerita* frequency in pellets with tern productivity and found no significant relationship between frequency of abundance of *Emerita* in the tern diet with fledgling to breeding pair ratios (Pearson Correlation = –0.002). Annual mean clutch size was used as a secondary metric of reproductive activity. Gull-billed Tern mean clutch size varied from a low of 1.50 eggs per clutch (2014) to a high of 2.39 eggs per clutch (2017) and differences were detected for the study period (t_6 = 2187.7 P < 0.01).

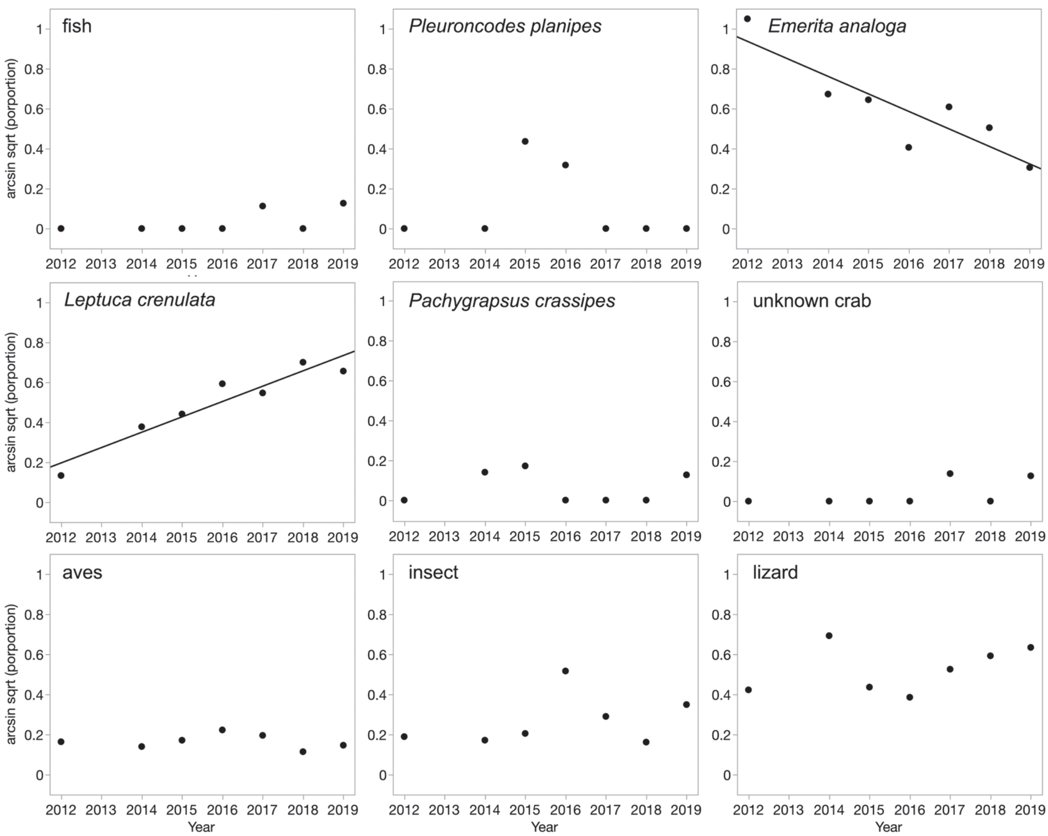

Figure 3. Relationship between the proportion of prey item found in Gull-billed Tern *Gelochelidon nilotica* pellets and years. Red lines show significant linear relationships for Pacific sand crab (*Emerita analoga*) and Mexican fiddler crab (*Leptuca crenulata*). *Emerita analoga* [R^2 = 0.78, F = 17.82, P = 0.008; = 177.33–0.09*Year]. *Leptuca crenulata R^2 = 0.90, F = 46.91, P = 0.001.* There was an overall decline in Pacific sand crab *Emerita analoga* abundance in tern diet (78–5%) overlayed by an increase in Mexican fiddler crabs *Leptuca crenulata* (2–40%). Of note is the inclusion of *Pleuroncodes planipes.*, a southern ranging crustacean species in the Gull-billed Tern diet during the ENSO-influenced seasons of 2015–2016.

Crab density sampling

To assess *Emerita* density at beaches within the Gull-billed Tern home range, six beaches in south San Diego County, California were sampled for five breeding seasons (Fig. 4). We documented the overall highest density of *Emerita* across all six beaches in 2013, while the lowest density occurred in 2017. *Emerita* had the highest density at the South Tijuana River (S River), North Tijuana River (N River), and Border Field State Park (Border Field) sampling locations (Table 1, Fig. 4). Between the 2013 and 2014, we documented a 57–96% decline in *Emerita* densities at five of the six beaches. Silver Strand Training Complex-South (SSTC-S) was the only beach to show an increase in *Emerita* abundance in 2013–14 (191%), although a strong decline was observed the following season at SSTC-S in 2014–15 (79%) with a continued decline through 2017 and an overall decline in sand crab density at all beaches across the five breeding seasons sampled (Fig. 4). Beaches sampled in 2017 had the lowest density of sand crabs. As *Emerita* density declined on the sampled beaches, abundance within the Gull-billed Tern diet also declined (Figs. 2, 4).

DISCUSSION

The effects of ENSO upon terrestrial and coastal species are complex and not straightforward with secondary and tertiary primary productivity and predator-prey interactions (Holmgren *et al.* 2001, Goldenberg

Table 2. Annual fledgling to breeding pair ratios and mean clutch size (SD) for the Gull-billed Tern colony in San Diego, California, U.S.A., 2012 through 2019.

Year	No. Breeding Pairs	FL:PR ratio*	Clutch Size Mean (SD)
2012	62	0.62	2.28 (0.71)
2013	65[a]	0.02[a]	[a]
2014	10	0.70	1.50 (0.59)
2015	23	0.57	1.76 (0.49)
2016	35	0.37	1.95 (0.48)
2017	35	1.15	2.39 (0.53)
2018	38	0.61	1.78 (0.63)
2019	32	0.41	2.38 (0.61)

*FL PR is the calculated fledgling to breeding pair ratio that is considered a metric of annual reproductive success. aIndicates an acanthocephaliasis outbreak in the Gull-billed Tern breeding colony. 2013 values were not used in the analysis because mortality occurred mid-nesting in early May (Patton et al. 2017).

et al. 2017). The intent of our research was to better understand how a dietary generalist dependent upon coastal resources could weather significant variation in prey resource abundance during extended anomalous warm water periods. We hypothesized that annual variation in *Emerita analoga* density would be reflected in the Gull-billed Tern diet and that *Emerita* availability would drive tern annual reproductive success. Our results suggest that dietary plasticity allows the Gull-billed Tern to be able to adapt itself successfully to local changes in food availability to mitigate potential impacts to reproduction.

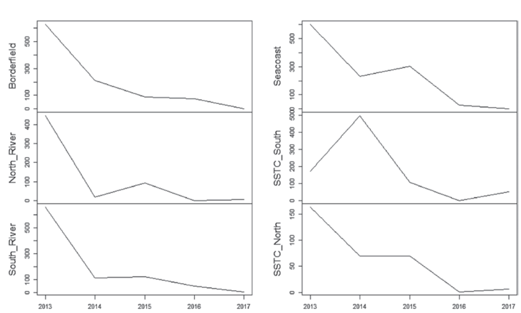

Figure 4. Observed decline in Pacific sand crab (*Emerita analoga*) densities at six beaches in South San Diego County, 2013–2017. Sample collection of sand crabs began in 2013 after Gull-billed Tern colony mortality. Six beach sampling locations included US Naval Base Coronado Silver Strand Training Complex North (SSTC-N), US Naval Base Coronado Silver Strand Training Complex South (SSTC-S), Seacoast Drive- Imperial Beach, North of the Tijuana River Mouth, South of Tijuana River Mouth, and Border Field State Park. Our study documented a strong decline in Pacific sand crab density at all six beaches over the five-year period monitored (–95.7%). The 2013–2016 seasons were influenced by above average sea surface temperatures influenced by the El Nino Southern Oscillation (ENSO) and the 'Blob' high pressure event of 2013.

In California, prior to 2013, Gull-billed Tern diet was dominated by *Emerita analoga* [60–76% of diet, (Goodenough 2014; this study)]. After 2013, tern diet was more varied consisting of both terrestrial and aquatic species with important declines noted in *Emerita* occurrence (Fig. 2). During the warmer than average years of 2014–2016, aquatic prey in the Gull-billed Tern diet declined while terrestrial prey increased (e.g., lizards, flying insects, and avian species). We also documented a switch from *Emerita* to temporarily more abundant crustaceans (e.g., *Pleuroncodes planipes*) and a switch to crustaceans more resistant to warm water temperature effects (e.g., increased proportions of *Leptuca crenulata*) which highlights the high degree of dietary plasticity evident in the Gull-billed Tern diet.

Emerita can be very abundant, reaching thousands per square meter and comprise over 80–90% of intertidal invertebrate biomass on beaches in southern California. It is an important prey resource for coastal nesting birds (Page *et al.* 2020) and migrating shorebirds (Dugan *et al.* 1991, 1994, 2000, 2003). Warmer "Blob"-related SST at the end of 2013 may have precipitated a collapse of *Emerita* that resulted in lower densities in 2014. The combined influences of the 'Blob' and the ENSO from late 2013 through 2016 had strong negative impacts on *Emerita* population density and recruitment resulting in declines of *Emerita* along southern San Diego beaches that were also observed in other studies occurring during the same time period as our research (Wooldridge *et al.* 2016).

The dietary breadth of the Gull-billed Tern is striking compared to other tern species. Research in Europe has revealed considerable variation in prey and diet composition (Fasola *et al.* 1989, Bogliani *et al.* 1990, Quinn and Wiggins 1990, Goutner 1991, Erwin *et al.* 1998, Dies *et al.* 2005, Stienen *et al.* 2005, Goodenough 2014) and significant variation in Gull-billed Tern chick growth rates associated with differences in diet (Albano *et al.* 2011). Although variation in Gull-billed Tern prey and diet have been widely reported, we are unaware of any previous studies examining year-to-year variation of diet or monitoring of both prey availability in the environment and prey consumption. Nor are we aware of research which attempts to understand the influence of such diet variation upon Gull-billed Tern reproductive success. Populations monitored in Italy reported varied diet with predominantly lizards (Fasola *et al.* 1989 and Bogliani *et al.* 1990). In Spain, tern diet was predominantly crayfish (Dies et al. 2005), while in West Africa, fiddler crabs were the predominant prey species (Stienen *et al.* 2005). In North American populations, prey species provisioned to Gull-billed Tern chicks in Texas were predominantly terrestrial invertebrates (Quinn and Wiggins 1990) while tern diet mostly consisted of marine invertebrates in Virginia (Erwin *et al.* 1998).

Dietary flexibility is beneficial in terms of mitigating variation in prey availability as what we observed with the Gull-billed Tern population in California, U.S.A., but it is a double-edged sword. The ability to diet- and habitat-switch has been suggested as an important factor in the stability of gull populations in the German Black Sea (Schwemmer and Garthe 2007). Upland, coastal estuarine, and ocean beach systems of San Diego may provide numerous opportunities for the tern to forage for aquatic and terrestrial prey. Having access to variable foraging habitats may allow the Gull-billed Tern a higher level of dietary plasticity in San Diego that influences the tern's ability to compensate for variation in prey resources. Greater foraging success can then result in higher rates of reproductive success. Hence, a highly malleable foraging ecology could translate to a strong capability to withstand variation in prey resources associated with widescale oceanic events such as the 'Blob' and ENSO.

In contrast, there is evidence that being an opportunistic generalist can positively influence disease infection rates thereby impacting populations negatively through potential disease outbreaks (Hoodless *et al.* 2002, Morgan *et al.* 2007, Hoch *et al.* 2010, Byers *et al.* 2015, Patton *et al.* 2017, Daversa *et al.* 2018, Byers 2021). Frequent visits to parasite-infected areas over time can lead to exacerbated disease and parasite infections (Smith 2007). Sand crabs such as *Emerita analoga* are a known intermediate host of *Profilicollis altmanti* (Order Ancanthocephala), and both *P. altmani* and *P. kenti* have been responsible for mass mortalities of seaducks and sea otters that consume large quantities of crabs (Kreuder et al. 2003). The 2013 Gull-billed Tern colony mortality was a result of such parasite infection resulting in the loss of greater than 85% of the breeding population in San Diego, California (Patton *et al.* 2017). Increased SST in San Diego during the 'Blob' event in early 2013 may have resulted in a stress-induced decline in immunity for *Emerita* that resulted in increased parasite infection rates for the Gull-billed Tern later in May during the breeding season.

Annual Gull-billed Tern fledgling-breeding pair ratios were lower but not significantly different during our study than in non-ENSO years. There was also significant variation in clutch size means across years. The variation we observed in clutch size and fledgling-breeding pair ratios may have been due more to nesting inexperience of returning first time breeders rather than food resource influences (Klomp 1970, Pianka and Parker 1975, Crawford 1977) as productivity rates in later breeding seasons were similar to those observed prior to the ENSO-Blob event. Greater than 72% of the Gull-billed Tern breeding population returning to breed during 2014–2016 were young birds returning to nest for the first time (Patton unpubl. data). We also note that *Emerita* densities have still not recovered to pre-ENSO years suggesting there may be additional influences upon *Emerita analoga* recruitment to southern California beaches that have not as yet been identified.

Continued shifts in prey resource quality associated with climate change may influence tern energetics long term, i.e., prey species range shifts and changes in trophic dynamics, even though generalists like the Gull-billed Tern may be able to mitigate short term, annual variation. The diet study by Albano *et al.* (2011) revealed that chicks fed an invertebrate diet grew slower and fledged later than chicks fed a vertebrate diet. Hence, a diet shift towards prey that is not as energetically beneficial for offspring could affect body condition and immune responses and thus population dynamics depending upon the time scale of variation (Navarro-Lopez *et al.* 2014). Our study was not designed to obtain data on chick growth rates nor assess prey energetics, hence we have no data to be able to compare nutritional values of prey in the Gull-billed Tern diet.

Both environmental and anthropogenic stressors in concert with climate change are leading to changes in foraging strategies of marine and coastal species highlighting a critical need to continue diet research focused upon the relationships between foraging plasticity, chosen behavioral tradeoffs, and the synergistic influences of global climate change upon important stages of the avian annual lifecycle. We encourage more diet research focused upon prey energetics to better understand the underlying nutritional influences of dietary plasticity and the behavioral mechanisms that generalists use to mitigate annual variation in diet.

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LITERATURE CITED

Ainley, D. G., W. J. Sydeman and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series 9: 69–79.

Albano, N., J. A. Masero, J. M. Sánchez-Guzmán, A. Villegas and F. Santiago-Quesada. 2011. Effects of diet on growth-related patterns of energy and macronutrient assimilation efficiency in a semi-precocial bird, the Gull-Billed Tern *Gelochelidon nilotica*. Ardea 99: 93–10.

Annett, C. and R. Pierotti. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. Colonial Waterbirds 12: 4–11.

Arafeh-Dalmau, N., G. Montaño-Moctezuma, J. A. Martinez, R. Beas-Luna, D. S. Schoeman and G. Torres-Moye. 2019. Extreme marine heatwaves alter kelp forest community near its equatorward distribution limit. Frontiers in Marine Science 6: 499.

Bogliani, G., M. Fasola, L. Canova and L. Saino. 1990. Food and foraging rhythm of a specialized Gull-billed Tern population *Gelochelidon nilotica*. Ethology, Ecology and Evolution 2: 175–182.

Bond, N. A., M. F. Cronin, H. Freeland and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophysical Research Letters 42:3414–3420.

Booth, J. M., A. Steinfurth, M. Fusi, R. J. Cuthbert and C. D. McQuaid. 2018. Foraging plasticity of breeding Northern Rockhopper Penguins, *Eudyptes moseleyi*, in response to changing energy requirements. Polar Biology 41: 1815–1826.

Bugoni, L. and C. M. Vooren. 2004. Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil. IBIS 146: 438–453.

Byers, J. E., A. J. Malek, L. E. Quevillon, I. Altman and C. L. Keogh. 2015. Opposing selective pressures decouple pattern and process of parasitic infection over small spatial scale. Oikos 124: 1511–1519.

Byers, J. E. 2021. Marine parasites and disease in the era of global climate change. *Annual Review of Marine Science* 13: 397–420.

Cavanaugh, K. C., D. C. Reed, T. W. Bell, M. C. Castorani and R. Beas-Luna. 2019. Spatial variability in the resistance and resilience of giant kelp in southern and Baja California to a multiyear heatwave. Frontiers in Marine Science 6: 413.

Cavole, L. A., A. M. Demko, R. E. Diner, A. Giddings, I. Koester, C. M. L. S. Pagniello, M. L. Paulsen, A.

Ramirez-Valdez, S. M. Schwenck, N. K. Yen, M. E. Zill and P. J. S. Franks. 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: Winners, losers, and the future. Oceanography 29: 273–285.

Cramp, S., D. J. Brooks, E. Dunn, R. Gillmor, P. A. D. Hollum, R. Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, C. S. Roselaar, K. E. L. Simmons, K. H. Voous, D. I. M. Wallace, J. Wattel, M. G. Wilson (Eds.). 1985. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume IV terns to woodpeckers. Oxford University Press. Oxford, U.K.

Crawford, R. D. 1977. Breeding biology of one-year old and older female Red-winged and Yellow-headed Blackbirds. Wilson Bulletin 89: 73–80.

Daversa, D. R., A. Manica, J. Bosch, J. W. Jolles and T. W. Garner. 2018. Routine habitat switching alters the likelihood and persistence of infection with a pathogenic parasite. Functional Ecology 32: 1262–1270.

Dies J. I., J. Marín and C. Perez. 2005. Diet of nesting Gull-billed Terns in eastern Spain. Waterbirds 28: 106–109.

Di Lorenzo, E. and N. Mantua. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change 6: 1042–1047.

Duffy, D.C. and S. Jackson. 1986. Diet studies of seabirds: a review of methods. Colonial Waterbirds 9: 1–17.

Dugan, J. E., A. M. Wenner and D. M. Hubbard. 1991. Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. Journal of Experimental Marine Biology and Ecology 150: 63–81.

Dugan, J. E., D. M. Hubbard and A. M. Wenner. 1994. Geographic variation in life history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: Relationships to environmental variables. Journal of Experimental Marine Biology and Ecology 181: 255–278.

Dugan, J. E., D. M. Hubbard and M. Lastra. 2000. Burrowing abilities and swash behavior of three crabs, *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall, *and Lepidopa californica* (Anomura, Hippoidea), of exposed sandy beaches. Journal of Experimental Marine Biology and Ecology 255: 229–245.

Dugan, J. E., D. M. Hubbard, M. D. McCrary and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58: 25–40.

Erwin, R. M., T. B. Eyler, J. S. Hatfield and S. McGary. 1998. Diets of nestling Gull-billed Terns in coastal Virginia. Colonial Waterbirds 21: 323–327.

Fair, J., E. Paul and J. Jones (Eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., U.S.A.

Fasola, M., G. Bogliani, N. Saino and L. Canova. 1989. Foraging, feeding and time-activity niches of eight species of breeding seabirds in the coastal wetlands of the Adriatic Sea. Bolletino di Zoologia 56: 61–72.

Favero, M. and P. H. Becker. 2007. Effect of NAO and ENSO on return rates, body mass and timing of migration of common terns breeding in Germany. Pages 258–262 *in* Waterbirds of the World (Boere G. C. C. A. Galbraith, D. Scott, D. A. Stroud and L. G. Underhill, Eds.). The Stationery Office, U.K.

Goldenberg, S. U., I. Nagelkerken, C. M. Ferreira, H. Ullah and S. D. Connell. 2017. Boosted food web productivity through ocean acidification collapses under warming. Global change biology 23: 4177–4184.

Goodenough, K. S. 2014. Gull-billed Tern, *Gelochelidon nilotica*, inter-and intra-annual variation in movements and diet in San Diego, California M.S. thesis, San Diego State University, San Diego, CA, U.S.A.

Goutner, V. 1991. Food and feeding ecology of Gull-billed Terns (*Gelochelidon nilotica*) in Greece. Revue d'Ecologie, Terre et Vie, 46: 373–384.

Grémillet, D. and A. Charmantier. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. Ecological Applications, 20: 1498–1503.

Hamer, K. C., E. M. Humphreys, S. Garthe, J. Hennicke, G. Peters, D. Grémillet, D., . . . and S. Wanless. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Marine Ecology Progress Series 338: 295–305.

Harding, A. M., J. F. Piatt and W. J. Sydeman. 2006. Bibliography of literature on seabirds as indicators of the marine environment. Science 231: 373–376.

Hoch, T., Y. Monnet and A. Agoulon. 2010. Influence of host migration between woodland and pasture on the population dynamics of the tick *Ixodes ricinus*: A modelling approach. Ecological Modelling 221: 1798–1806.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutiérrez and G. M. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology & Evolution 16: 89–94.

Hoodless, A. N., K. Kurtenbach, P. A. Nuttall and S. E. Randolph. 2002. The impact of ticks on pheasant territoriality. Oikos 96: 245–250.

Klomp, H. 1970. The determination of clutch-size in birds: a review. Ardea 58: 1–124.

Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998–2001. Journal of Wildlife Diseases, 39: 495–509.

Lonhart, S. I., R. Jeppesen, R. Beas-Luna, J. A. Crooks and J. Lorda. 2019. Shifts in the distribution and abundance of coastal marine species along the eastern Pacific Ocean during marine heatwaves from 2013 to 2018. Marine Biodiversity Records 12:13.

Mariano-Jelicich, R. and M. Favero. 2006. Assessing the diet of the Black Skimmer through different methodologies: Is the analysis of pellets reliable? Waterbirds 29: 81–87.

Molina, K. C., and D. A. Marschalek. 2003. Foraging behavior and diet of breeding Western Gull-billed

Terns (*Sterna nilotica vanrossemi*) in San Diego Bay, California. Species Conservation and Recovery Program Report, 2003-01. Unpublished report, State of California, Department of Fish and Game, San Diego, CA, U.S.A.

Molina, K. C., J. F. Parnell, R. M. Erwin, J. del Hoyo, N. Collar, G. M. Kirwan and E. F. J. Garcia. 2020. Gull-billed Tern (*Gelochelidon nilotica*), version 1.0. *in* Birds of the World (S. M. Billerman, Ed.). Cornell Lab of Ornithology, Ithaca, NY, U.S.A.

Morgan, E. R., G. F. Medley, P. R. Torgerson, B. S. Shaikenov and E. J. MilnerGulland. 2007. Parasite transmission in a migratory multiple host system. Ecological Modelling 200: 511–520.

Navarro-López, J., P. Vergara and J. A. Fargallo. 2014. Trophic niche width, offspring condition and immunity in a raptor species. Oecologia 174: 1215–1224.

Page, G. W., L. E. Stenzel, J. S. Warriner, J. C. Warriner and P. W. Paton.2020. Snowy Plover (*Charadrius nivosus*), version 1.0. *in* Birds of the World (A. F. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, NY, U.S.A.

Parsons, M., I. Mitchell, A. Butler, N. Ratcliffe, M. Frederiksen, S. Foster and J. B. Reid. 2008. Seabirds as indicators of the marine environment. ICES Journal of Marine Science, 65: 1520–1526.

Patton, R. T., K. S. Goodenough, S. E. De La Cruz, H. Nevins, R. Cole, B. Bodenstein, V. Shearn-Bochsler, B. Collins, J. Beck, M. Sadowski and J. Y. Takekawa 2017. Mass mortality attributed to acanthocephaliasis at a Gull-billed Tern (*Gelochelidon nilotica*) colony in coastal California, USA. Journal of Wildlife Diseases 53: 885–90.

Pianka, E. R. and W. S. Parker. 1975. Age-specific reproductive tactics. American Naturalist 109: 453–464.

Piatt, J. F., W. J. Sydeman, and F. Wiese. 2007. Introduction: a modern role for seabirds as indicators of marine ecosystems. Marine Ecology Progress Series 352: 199–204.

Piatt, J. F., J. K. Parrish, H. M. Renner, S. K. Schoen, T. T. Jones, M. L. Arimitsu, . . . and W. J. Sydeman. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014-2016. PloS one 15: e0226087.

Quinn, J. S. and D. A. Wiggins. 1990. Differences in prey delivered to chicks by individual Gull-billed Terns. Colonial Waterbirds 13: 67–69.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed 16 January 2021.

Rogers-Bennett, L. and C. A. Catton. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific reports 9: 1–9.

Rosenberg, K. V. and R. J. Cooper. 1990. Approaches to avian diet analysis. Studies in Avian Biology 13: 80–90.

Sánchez, J. M., M. Blasco, A. Muñoz del Viejo and J. M. Cabo. 1993. Evolución de la dieta de *Sterna nilotica* durante la estación reproductora. Pages 377-382 *in* Status and Conservation of Seabirds: Ecogeography and Mediterranean Action Plan (J. S. Aguilar, X. Mombailliu, A. M. Paterson, Eds). Proceedings II Mediterranean Seabird Symposium. MEDMARAVIS, SEO/BirdLife, Madrid, Spain.

Sánchez, J. M., A. Muñoz del Viejo, C. Corbacho, E. Costillo and C. Fuentes. 2004. Status and trends of Gull-billed Tern *Gelochelidon nilotica* in Europe and Africa. Bird Conservation International 14: 335–351.

Schwemmer, P. and S. Garthe. 2007. Regular habitat switch as an important strategy of an opportunistic seabird species at the interface between land and sea. Estuarine, Coastal and Shelf Science 77: 12–22.

Smith, N. F. 2007. Associations between shorebird abundance and parasites in the sand crab, *Emerita analoga*, along the California coast. Journal of Parasitology 93: 265–273.

Speybroeck, J., D. Bonte,W. Courtens, T. Gheskiere, P. Grootaert, J. P. Maelfait, M. Mathys, S. Provoost, K. Sabbe, E. W. Stienen and V. V. Lancker. 2006. Beach nourishment: an ecologically sound coastal defense alternative? A review. Aquatic conservation: Marine and Freshwater ecosystems 16: 419–435.

Stewart, B. S., P. K. Yochem and R. W. Schreiber. 1984. Pelagic red crabs as food for gulls: a possible benefit of El Niňo. The Condor 86: 341–342.

Stienen, E. W. M., A. Brenninkmeijer and M. Klaassen. 2008. Why do Gull-billed Terns *Gelochelidon nilotica* feed on fiddler crabs *Uca tangeri* in Guinea-Bissau? Ardea 96: 243–250.

Thompson, A. R., C. J. Harvey, W. J. Sydeman, C. Barceló, S. J. Bograd, R. D. Brodeur and E. L. Hazen. 2019. Indicators of pelagic forage community shifts in the California Current large marine ecosystem. 1998–2016. Ecological Indicators 105: 215–228.

Velarde, E., E. Ezcurra, M. H. Horn and R. T. Patton. 2015. Warm oceanographic anomalies and fishing pressure drive seabird nesting north Science Advances 1: e1400210.

Wooldridge, T., H. J. Henter and J. R. Kohn. 2016. Effects of beach replenishment on intertidal invertebrates: A 15-month, eight beach study. Estuarine, Coastal and Shelf Science 175: 24–33.