# SEABIRD DISTRIBUTION IN THE GULF OF PAPAGAYO, COSTA RICA, DURING NON-UPWELLING CONDITIONS

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## SUMMARY

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The Gulf of Papagayo off the northwestern coast of Costa Rica is one of a series of upwelling localities along the coast of Central America. We surveyed its marine avifauna during the non-upwelling season in 1988, using transects at sea and inspection of islands for nesting birds. The most common species at sea was Black Tern *Chlidonias nigra*, although these were only seen on one transect. We found a density of 3.76 (SD 6.8) birds/km<sup>2</sup> or 2.1 birds/km<sup>2</sup>, if the Black Terns are removed. Despite differences in transect methods and timing, these values are generally comparable to estimates from the Bay of Panama upwelling but much lower than from upwellings off Peru and California. Sea surface temperature did not appear to affect bird numbers. Breeding numbers on the islands were small, either because of human disturbance or because it was the non-upwelling period. These small upwellings may be important to North American seabirds as migratory stopovers or wintering grounds.

# INTRODUCTION

Although the populations and ecologies of seabirds of the world's larger upwelling ecosystems are relatively well studied (e.g. Murphy 1936, Duffy *et al.* 1987, Spear & Ainley 2008, Ainley & Hyrenbach 2009), comparatively little is known of the seabirds of many smaller upwelling ecosystems. This paper reports on inshore seabird distributions and numbers around the Santa Elena Peninsula in the Gulf of Papagayo, off northwestern Costa Rica, in relation to surface water temperature. We also present general observations on island breeding and roosting sites, as well as initial data on foraging.

The Gulf of Papagayo is the central of three local upwelling ecosystems off the Pacific coast of Central America, the others being the Bay of Tehuantepec and the Bay of Panama. These seasonal upwellings are generated by wind jets from high pressure cells in the Gulf of Mexico and Caribbean passing westward through mountain gaps on the respective isthmuses (Hurd 1929, Coen 1983, McCleary et al. 1989). Sustained winds of up to 180 km/h in the Bay of Tehuatepec (Strumpf 1975) generate upwelling of cooler waters to the surface, reducing sea surface temperatures (SST) by as much as 10°C (Roden 1961); SST in the Gulf of Papagayo may drop as low as 16 °C, from temperatures of 28-31 °C found during non-upwelling (US Hydrographic Office 1947, Hubbs & Roden 1964). The resulting cold water masses, or eddies, may be displaced more than 2500 km offshore (Hansen 1987, Palacios & Bograd 2005). The biological effects of Central American upwelling are poorly understood, most information being from the Bay of Panama (e.g. Bayliff 1963, Forsberg 1963).

The inshore seabirds of the Papagayo region also are poorly studied. Jehl (1974) summarized previous work along the Central American coast and reported on three days of observations made 5–20 miles

(8–32 km) offshore between Nicaragua and the Gulf of Nicoya, south of the Gulf of Papagayo. Stiles & Smith (1977) reported on 16 transects made during 1974–1975 in the southern Gulf of Papagayo, within 10 km of land, and Stiles (1984) summarized data on seabird distributions and breeding for Costa Rica, including the Papagayo region. Apparently, the only published study of breeding seabirds in a Central American upwelling concerns the Brown Pelican *Pelecanus occidentalis* in the Bay of Panama (Montgomery & Martínez 1984).

## METHODS

## Transects

We conducted transects in the Gulf of Papagayo region (Fig. 1) during 6–10 September 1988. We counted seabirds observed within an estimated 300 m of a vertical line extending perpendicularly abeam of one side of the vessel, a 10 m traditional, longline wooden fishing boat with a 3 m observation height while standing on deck. The methodology is similar to that used by Duffy & Schneider (1984), Duffy & Merlen (1986) and Duffy *et al.* (1988). As the transects were conducted in 1988, GPS and other positioning devices were not available, so bearings were taken by compass on conspicuous land features.

The vessel's mean speed during transects, estimated from elapsed time between mapped transect endpoints, was 9.6 km/h (SD = 3.03 km/h, n = 15). When traveling less than 0.5 km from the coast, we oriented our transects to the seaward side of the boat; otherwise, we chose the side with the best light conditions for observation. We did not undertake transects when less than 0.25 km from islands or headlands, areas that are often used for nesting or roosting. Sea surface temperatures were measured every 15–30 min using bucket sampling while underway and at the beginning and end of each

transect. During this study, our boat did not fish and attracted no following seabirds, and no other vessels were observed crossing or approaching any of our transects.

### Islands

Nine major islands and six obvious headlands were included in the study area (Fig. 1). As these present potential breeding and roosting sites, we approached or circled nearly all of them by boat. Where possible, we landed and examined five islands for nesting. We used the island nomenclature of the Instituto Geográfico de Costa Rica (Chart 3048 IV, 1965), although this nomenclature appears to differ slightly from that used by local fishermen.

## Weather conditions

During the five-day study, winds were variable from the east southeast and west southwest and light to moderate, with sea surface conditions ranging from flat calm to 3–4 m swells, and seas of 0.5 m or less. Visibility was generally at least 1 km, based on observations of the coastline and islands.

Mean values are presented  $\pm$  standard deviation. We used the coefficient of variation (CV) to examine relative variability across species (Zar 1974).

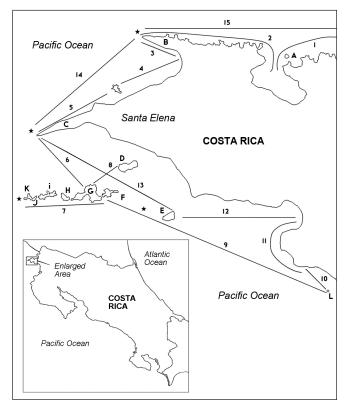


Fig. 1. Transects and sea surface temperatures in the survey area of the Gulf of Papagayo. Observations for each numbered transect shown in Table 1. Stars indicate sites where temperatures fell below 28 °C. Locations include A. Isla Los Cabras and Isla Leoncillo; B. Punta Blanca; C. Islas Negritos; D. Punta Santa Elena; E. Isla Pelado; F. Isla Colorado; G.–L. Islas Murciélagos (G. Isla Cocinero; H. Isla San José; I. Isla Catalina; J. Isla Golondrina; K. Isla San Pedrito; L. San Pedrillo Farallones [not named on maps but called this by local fishermen]); M. Peña Bruja.

#### RESULTS

## Transects

During 6–10 September 1988, we ran 15 transects of 20–144 min duration (mean = 51.7 min; total duration of all observations = 775 min) for an estimated total length of transects of 133 km; mean = 8.9 km) (Table 1). Most of the transects were located within 2 km of the coast, the farthest being approximately 5 km offshore while crossing from Punta Santa Elena to Islas Murciélagos (Fig. 1).

Sea surface temperatures (SST) ranged from 27.2 °C to 32.8 °C, mean 28.9 °C, indicative of non-upwelling conditions (US Hydrographic Office 1947). Temperatures <28.0 °C were recorded off two coastal headlands (Punta Blanca and Punta Santa Elena); at a shallow passage where a northward-moving current passed between the two outermost Murciélagos Islands; and in the channel between Isla Colorado and Islas Murciélagos (Fig. 1).

We saw 239 seabirds of eight species (Table 1; mean transect encounter rate 1.1 birds/km; mean density  $3.76 \pm 6.8$  birds/km<sup>2</sup>. Transect 15 was an outlier (167 birds, 27.2 birds/km<sup>2</sup>; Table 1). If it is removed, the remaining 14 transects gave a weighted mean density of  $2.1 \pm 2.0$  birds/km<sup>2</sup>. The most common species were Black Tern *Chlidonias nigra* (152), Brown Noddy *Anous stolidus* (38), Magnificent Frigatebird *Fregata magnificens* (18) and Brown Pelican *Pelecanus occidentalis* (14). Two-thirds of the records were of species not known to breed in the area, and are thus assumed to have been migrants, the Black Tern and Osprey being breeders from farther north, whereas the Wedge-tailed Shearwater is a migrant from the south or from Hawai'i.

Foraging group size ranged from solitary for Magnificent Frigatebird (n = 2) and Brown Booby (n = 3) to  $10.25 \pm 19.3$  for Brown Noddy (CV = 188.5%; n = 20) and 37.5 for Black Terns ( $\pm$  29.1, CV = 77.6%; n = 4).

Bird distributions had no apparent relation to SST. Transects with Brown Noddies, the most abundant species, had a mean SST of 29.0 (SD =  $0.88 \,^{\circ}$ C, CV = 3.0%; n =5) compared with transects without noddies, with a mean SST of 28.8 (±  $6.7 \,^{\circ}$ C, CV = 2.3%; n = 8). SST sampling may have been too infrequent to detect small local patches of cold water that might have attracted small aggregations of birds.

We observed nine surface schools of what the fishermen on our boat told us was "bonito" *Sarda chiliensis/orientalis*. Six schools did not attract any seabirds, whereas the three others were attended by 84% of all the Black Terns sighted during transects. In addition, 29% of all Brown Noddies were associated with bonito schools, but only those where Black Terns were also present. These two seabird species formed dense aggregations, the noddies hovering higher in the groups and appearing less agile than the Black Terns.

#### Breeding and roosting on islands

Proceeding from north to south (Fig. 1), we found no evidence of seabird nesting on either Isla Los Cabros or Isla Leoncillo at the mouth of Bahía de Santa Elena. Both islands were heavily wooded in parts, with steep, exposed rock in other parts. We circled the largest of the Islas Negritos. The main island was grassy on its inshore, eastern section and rocky on the west, with scrub in between. The northwest islet, "Mogatillo" to the fishermen but unnamed on the chart, was bare, except for two leafless *Portulaca* sp. or *Sesuvium* sp. and another unidentified forb. We estimated 120 Brown Noddies and 3 Bridled Terns *Onychoprion [Sterna] anaethetus* circling the island when the boat approached close enough to flush birds. A single immature Brown Booby appeared to be roosting on the island. One of us (JGF) landed and found a single Bridled Tern young with its pin feathers just erupting. Komar & Rodríguez (1996) reported Bridled Tern chicks at a colony in the Gulf of Fonseca, off Nicaragua in August, but Hamel (*in* Thurber *et al.* 1987) and Monroe (1968) reported no breeding activity at Central American sites in July or October, indicating that breeding seasons of this species in the eastern tropical Pacific are either irregular or differ between Central American upwellings. We did not see Bridled Terns on any of the transects, nor did we see this species foraging at any other time during the study period. While circling the Islas Murciélagos, we observed several Bridled Terns returning from the west, suggesting that this species feeds farther offshore. No Brown Noddy young were observed on any of the Murciélagos, but several birds were very reticent to fly and there were more than a dozen nest remains on one of the smaller islands. We also found at least 20 burrows 5 cm wide, none of which had the oily smell characteristic of procellarid nesting sites. A smaller islet to the west of the main Murciélagos chain had approximately 20 roosting frigatebirds, including one male with its gular patch inflated.

In the Islas Murciélagos (composed of seven main islands), only Cocinero and San José islands were circled and landed upon.

Transect information	Length, km	SST °C	No. birds	Density, birds/ km <sup>2</sup>	Species, no. birds							
					Storm- petrel <sup>a</sup>	WT	Brown Pelican	MF	Brown Booby	Osprey	Brown Noddy	Black Tern
<ol> <li>Cuajiniquil–Bahía de Santa Elena</li> </ol>	9.9	ND	6	2.02			2	4				
<ol> <li>Bahía de Santa Elena– Playa Blanca</li> </ol>	9.45	ND	7	2.47		1	3	1			2	
3. Playa Blanca	3.3	28.0	2	2.02			2					
<ol> <li>Playa Blanca– Islas Negritos</li> </ol>	4.4	29.6	5	3.79				5				
<ol> <li>Islas Negritos– Punta Santa Elena</li> </ol>	6.7	29.0	14	6.96							14	
<ol> <li>Punta Santa Elena– Isla Cocinero</li> </ol>	5.7	30.5	3	1.75							3	
7. Islas Murciélagos	6.6	28.3	0	0								
<ol> <li>Isla Cocinero– Isla Pelado</li> </ol>	2.2	28.8	0	0								
<ol> <li>Isla San José– Nancite</li> </ol>	22	28.2	9	1.36			3	2	4			
10. Nancite–south of Punta Velas	8.6	29.8	0	0								
<ol> <li>South of Punta Velas–Portrero</li> </ol>	5.5	29.2	1	0.61					1			
12. Portrero– Isla Colorado	7.2		1	0.46						1		
13. Isla Colorado– Punta Santa Elena	11	28.5	10	3.03			4	6				
14. Punta Santa Elena to Punta Blanca	9.9	28.3	14	4.7	1			2	2		9	
15. Punta Blanca to Cuajiniquil	20.5	28.8	167	27.2				4	1		10	152
Total	132.95		239		1	1	14	24	8	1	38	152
Mean	8.86	29.0	15.9	3.8								

TABLE 1Results of transects in the Gulf of Papagayo

<sup>a</sup> Species of storm-petrel not identified.

MF = Magnificent Frigatebird, SST = sea surface temperature, WT = Wedge-tailed Shearwater.

No seabird colonies were noted, although noddies may nest on isolated cliffs around these islands. We inspected Isla Catalina, Isla Golondrinas and Isla Pedrito from the sea and saw no evidence of nesting. On the southwestern cliff of Isla San Pedrito we saw 120 Magnificent Frigatebirds, seven Bridled Terns and one adult Brown Booby roosting. The islets west of San Pedrito are unnamed on the maps, but we were told they are called the San Pedrillo Farallones. The two outermost islets had the largest seabird colonies that we encountered during the survey. Although accurate counts were impossible, as the birds mixed once flushed, we estimated 1000 Magnificent Frigatebirds, 300 Brown Boobies, 200 Bridled Terns and 100 Brown Noddies. Brown Boobies nested on both islets. We estimated at least 30 booby nest sites visible from the water. We attempted to climb the outermost island but were stopped by a loose rock and guano slope at the cliff edge. We observed several almostfledged Bridled Terns and several juvenile Brown Boobies. Another major concentration of roosting frigatebirds (approximately 600 individuals) occurred on the north side of Isla San José.

Closer inshore, we landed on Isla Pelado and found no evidence of seabird nesting. We passed Isla Colorado without landing and did not see any evidence of seabirds. Finally, we circled Peña Bruja, off Playa Naranjo. Stiles (1984) reported this as a possible nesting site for Bridled Tern, but we observed only roosting birds of other species: a single Brown Booby, three Brown Pelicans and 16 Magnificent Frigatebirds.

## DISCUSSION

#### Oceanography

The Gulf of Papagayo was not in its upwelling phase when we visited it. Winds were light and variable, with a southerly component, instead of northerly, as associated with upwelling in this area (McCreary et al. 1989). Nevertheless, we found several small areas of reduced SST, below 28°C, indicating that local upwelling persists even during the non-upwelling season. Two of these cold water patches were off headlands, and a third was in a shallow passage between two islands. The fourth was in open water with unknown bathymetry. The first three are consistent with local upwelling of water forced to the surface as a northward-moving current deflects upward off a shallow bottom. Currents off the Pacific coast of Central America are generally northerly throughout the year (US Hydrographic Office 1947), indicating that such patches of cold water may be persistent even outside the upwelling season and may serve as refugia for fish or other prey, providing local foraging opportunities for seabirds.

#### Seabird distributions and numbers

Our observations of 3.8 (or 2.1 if Black Terns are removed) seabirds/ km<sup>2</sup> are comparable to the 3.7 birds/km<sup>2</sup> over the continental shelf of the Bay of Panama reported by Spear & Ainley (1999). These densities are low compared with larger upwellings: Duffy & Schneider (1984) reported 123.4 birds/km<sup>2</sup> in a portion of the Benguela upwelling off South Africa; Briggs *et al.* (1987) found 110 birds/km<sup>2</sup> over the shelf in the California upwelling system; and Spear & Ainley (2008) reported 7–23 birds/km<sup>2</sup> during summer (upwelling) and 15–26 birds/km<sup>2</sup> in winter for coastal waters of the central and northern sections of the Peru Current. In contrast, in the non-upwelling offshore areas of the South Pacific Ocean, Ainley & Boekelheide (1983) reported 3.4–9.5 birds/km<sup>2</sup>. Farther offshore from Panama, Spear & Ainley (1999) reported 1.63 birds/km<sup>2</sup> for continental slope waters and 1.2 birds/km<sup>2</sup> for pelagic waters.

Densities, as well as diversity, of seabirds in the Gulf of Papagayo may differ between upwelling and non-upwelling periods, but the existing data are equivocal. Uncertainties related to differences in transect methodology between studies over the last 40 years, interannual variation in seabird distributions and numbers, and anthropogenic and other changes in marine and terrestrial environments, such as increasing SST and overfishing (e.g. Spear & Ainley 2008), confound seasonal differences in bird distributions and numbers among various areas. In the Gulf of Papagayo, Stiles & Smith (1977), using inshore transects of unstated length within approximately 5 km of the coast south of the present survey area, reported 132.5 birds/transect (range 75–90 birds/transect, n = 2) during the upwelling period (November to March) and 154.25 birds/ transect ( $\pm$  24.1, n = 4) during the non-upwelling period from April to October (n = 8). Transects conducted in a broader area out to approximately 10 km offshore averaged 810.0 birds/ transect during upwelling (range 288-1332, n = 2) and 738.25  $(\pm 183.6, n = 8)$  during the rest of the year. In the Gulf of Panama to the south, Loftin (1991), using different transect methods, reported 32.8-65.5 birds/h during the upwelling season and 32.4-65.0 during non-upwelling.

## Nesting on islands

The numbers of seabirds recorded breeding in the survey area were small. The restriction of nesting to small offshore islets indicates that human exploitation through egg gathering has selected against seabirds nesting on accessible islands. We observed bivalve middens in the supralittoral of the Santa Elena Peninsula, showing that human exploitation of marine resources is ancient. Brown Pelicans and Magnificent Frigatebirds may nest on the larger accessible islands in the Gulf of Papagayo, as they do to both the north and the south (Montgomery & Martínez 1984, Stiles 1984), but, if so, we did not visit during their breeding seasons.

## CONCLUSION

The Papagayo upwelling is seasonal and relatively small, but these characteristics offer opportunities to examine ideas that are difficult to test in larger upwellings, without a multi-disciplinary effort (e.g. Ainley *et al.* 2009). For example, fronts and upwelled plumes of cooler water often produce concentrated prey and seabird feeding (Brown 1980, Hunt & Schneider 1987, Hoefer 2000). Both of these oceanographic characteristics are likely to occur and to be relatively smaller and closer inshore in the Gulf of Papagayo than in larger upwelling ecosystems, thereby facilitating fieldwork.

Group, as opposed to solitary, feeding appears to be the dominant foraging behavior in upwelling ecosystems, and group size also appears to be larger in upwelling areas than elsewhere (Duffy 1983, 1989). Whether the percentage of seabirds involved in group feeding changes between upwelling and non-upwelling conditions in the Gulf of Papagayo could be tested by comparing foraging groups during the upwelling and non-upwelling seasons and inside and outside the upwelling of the Gulf.

Finally, the presence of North American breeding species indicates that the relatively small Central American Pacific

upwellings, active from approximately November to April, may be important migration or wintering areas for seabirds such as Black Terns (cf. Loftin 1991, Nisbet 1997), as are other Pacific upwellings for Arctic Terns *S. paradisaea* (McKnight *et al.* 2013). Given changes in fisheries and potential effects of anthropogenic climate change, more attention should be paid to the biology of seabirds in the Central American upwellings between Mexico and Panama.

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#### REFERENCES

- AINLEY, D.G. & BOEKELHEIDE, R.J. 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *Studies in Avian Biology* 8: 2–23.
- AINLEY, D.G., DUGGER, K.D., FORD, R.G., PIERCE, S.D., REESE, D.C., BRODEUR, R.D., TYNAN C.T. & BARTH, J.A. 2009. The spatial association of predators and prey at frontal features in the northern California Current: Competition, facilitation, or merely co-occurrence? *Marine Ecology Progress Series* 389: 271–294.
- AINLEY, D.G. & HYRENBACH, K.D. 2009. Top-down and bottomup factors affecting seabird population trends in the California current system (1985–2006). *Progress in Oceanography* 84: 242–254.
- BAYLIFF, W.H. 1963. The food and feeding habits of the anchovy, *Centengraulis mysticetus*, in the Gulf of Panama. *Bulletin of the Inter-American Tropical Tuna Commission* 7: 398–432.
- BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & CARLSON, D.R. 1987. Bird communities at sea off California: 1975–1983. *Studies in Avian Biology* 11: 1–74.
- BROWN, R.G.B. 1980. Seabirds as marine animals. In: Burger, J., Olla, B.L. & Winn, H.E. (Eds.). Behavior of marine animals. New York: Plenum, pp. 1–39.
- COEN, E. 1983. Climate. In: Janzen, D.H. (Ed.). Costa Rican natural history. Chicago: University of Chicago, pp. 35–46.
- D'CROZ, L. & O'DEA, A. 2007. Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal, and Shelf Science* 73: 325–340.
- DUFFY, D.C. 1983. The foraging ecology of Peruvian seabirds. Auk 100: 800–810.
- DUFFY, D.C. 1989. Seabird foraging aggregations: a comparison of two southern upwellings. *Colonial Waterbirds* 12: 164–175.
- DUFFY, D.C. & SCHNEIDER, D.C. 1984. A comparison of two transect methods of counting birds at sea. *Cormorant* 12: 95–98.
- DUFFY, D.C. & MERLEN, G. 1986. Seabird densities and aggregations during the1983 El Niño in the Galapagos Islands. *Wilson Bulletin* 98: 588–591.
- DUFFY, D.C., SIEGFRIED, W.R. & JACKSON, S. 1987. Seabirds as consumers in the southern Benguela region. *South African Journal of Marine Science* 5: 771–790.
- DUFFY, D.C., RYAN, P., WILSON, R.P. & WILSON, M.P. 1988. Spring seabird distribution in the Straits of Magellan. *Cormorant* 16: 98–102.

- FORSBERG, E.D. 1963. Some relationships of meteorological, hydrographic, and biological variables in the Gulf of Panama. *Bulletin of the Inter-American Tropical Tuna Commission* 7: 1–109.
- HANSEN, D.V. 1987. History and status of the NOAA EPOC5 program. In: Katz, E.J. & Witte, J.M. (Eds.). Further progress in equatorial oceanography. Fort Lauderdale, Florida: Nova University Press.
- HOEFER, C.J. 2000. Marine bird attraction to thermal fronts in the California Current system. *Condor* 102: 423–427.
- HUBBS, C.L. & RODEN, G.I. 1964. Oceanography and marine life along the Pacific coast of Middle America. In: West, R.C. (Ed.). Handbook of Middle American Indians, vol. 1. Austin: University of Texas Press, pp. 143–534.
- HUNT, G.L. & SCHNEIDER, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J.P. (Ed.). The feeding ecology of seabirds and their role in marine ecosystems. Cambridge: Cambridge University Press, pp. 7–41.
- HURD, W.E. 1929. Northers in the Gulf of Tehuantepec. *Monthly Weather Review* 57: 192–194.
- INSTITUTO GEOGRÁPHICO DE COSTA RICA. 1965. Chart 3048 IV. San José, Costa Rica.
- JEHL, J. R. 1974. The near-shore avifauna of the Middle American west coast. Auk 91: 681–699.
- KOMAR, O. & RODRÍGUEZ, W. 1996. A major Bridled Tern (Sterna anaethetus) colony in the Gulf of Fonseca, Nicaragua. Colonial Waterbirds 19: 264–267.
- LOFTIN, H. 1991. An annual cycle of pelagic birds in the Gulf of Panama. *Ornitologia Neotropical* 2: 85–94.
- MCCREARY, J.P., LEE, H.S. & ENFIELD, D.B. 1989. The response of the coastal ocean to strong offshore winds: with application to circulations in the gulfs of Tehuantepec and Papagayo. *Journal of Marine Research* 47: 81–109.
- MCKNIGHT, A., ALLYN, A.J., DUFFY, D.C. & IRONS, D.B. 2013. "Stepping stone" patterns in migrating Arctic Terns reveals the importance of upwelling areas. *Marine Ecology Progress Series* 491: 253–264.
- MONROE, B.L. 1968. A distributional survey of the birds of Honduras. *Ornithological Monographs* 8: 1–458.
- MONTGOMERY, G.C. & MARTÍNEZ, M.L. 1984. Timing of Brown Pelican nesting on Taboga Island in relation to upwelling in the Bay of Panama. *Colonial Waterbirds* 7: 10-21.
- MURPHY, R.C. 1936. Oceanic birds of South America. New York: American Museum of Natural History.
- NISBET, I.C.T. 1997. Status, biology and management of the Black Tern: symposium summary and overview. *Colonial Waterbirds* 20: 622–625.
- PALACIOS, D.M. & BOGRAD, S.J. 2005. A census of Tehuantepec and Papagayo eddies in the northeastern tropical Pacific. *Geophysical Research Letters* 32: L23606. doi:10.1029/2005GL024324
- RODEN, G.I. 1961. On the wind-driven circulation in the Gulf of Tehuantepec and its effect upon surface temperatures. *Geofisica International* 1: 55–72.
- SPEAR, L.B. & AINLEY, D.G. 1999. Seabirds of the Panama Bight. Waterbirds 22: 175–198.
- SPEAR, L.B. & AINLEY, D.G. 2008. The seabird community of the Peru Current, 1980–1995, with comparisons to other eastern boundary currents. *Marine Ornithology* 36: 125–144.

- STILES, F.G. 1984. Status and conservation of seabirds in Costa Rican waters. In: Croxall, J.P., Evans P.G.H. & Schreiber, R.W. (Eds). Status and conservation of the world's seabirds. Technical Publication 2. Cambridge: International Council for Bird Preservation, pp. 223–230.
- STILES, F.G. & SMITH, S.M. 1977. New data on Costa Rican waterbirds. *Condor* 79: 90–97.
- STRUMPF, H.G. 1975. Satellite detection of upwelling in the Gulf of Tehuantepec, Mexico. *Journal of Physical Oceanography* 5: 383–388.
- THURBER, W.A., SERRANO, J.F., SERMEÑO, A. & BENITEZ, M. 1987. Status of uncommon and previously unreported birds of El Salvador. *Proceedings of the Western Foundation of Vertebrate Zoology* 3:109–293.
- US HYDROGRAPHIC OFFICE. 1947. Atlas of surface currents: northeastern Pacific. Publication 570. Washington, DC: US Hydrographic Office.
- ZAR, J.H. 1974. Multiple comparisons. *Biostatistical analysis* 1: 185–205.