en aves marinas polares. La importancia de la asociación entre aves marinas y depredadores de tope de piscina en el sistema tropical se enfatizó por su ausencia en el sistema polar, afectando el comportamiento, morfología y dieta de aves marinas ETP. Mayor información de dicha asociación es importante para el manejo exitoso de ecosistemas tropicales del Océano Pacífico.

Understanding the factors that affect community organization among seabirds requires detailed information on inter- and intra-specific differences in diet and foraging behavior to define trophic niches and their overlap (Ashmole 1971, Duffy and Jackson 1986). Several studies have examined the diets of entire marine avifaunas during the breeding season at colonies located on a specific group of islands: three tropical (Ashmole and Ashmole 1967, Diamond 1983, Harrison et al. 1983), two temperate (Pearson 1968, Ainley and Boekelheide 1990), and three polar (Belopol'skii 1957, Croxall and Prince 1980, Schneider and Hunt 1984). These studies have provided considerable information on choice of prey fed to nestlings. However, they provided little information on: (1) diet during the remainder of the annual cycle, (2) diet of the non-breeding component of the community, (3) factors that affect prey availability and how these affect diet, or (4) the methods and diel patterns by which seabirds catch prey. Given the logistical difficulties involved in at-sea studies in order to obtain such information, it is not surprising that few of these broader studies have been conducted (Baltz and Morejohn 1977, Ainley et al. 1984, Ainley et al. 1992); those that have have been completed in temperate or polar waters.

Only three studies, as noted above, have been concerned with diet partitioning among seabird communities in the tropics (between 20° N and 20° S), despite the fact that tropical waters cover about 40% of the Earth's surface. Furthermore, none of these studies have considered the highly pelagic component of seabird communities that is not constrained to remain within foraging range of breeding colonies. The results presented herein are the first to examine diets in a tropical, open-ocean avifauna, in this case occupying the 25,000,000 km² expanse of the eastern tropical Pacific (ETP) and defined here as pelagic waters within 20° of the Equator and from the Americas to 170° W.

Two factors that characterize pelagic waters, as opposed to coastal, neritic waters, have a major effect on the structure of seabird avifaunas and the strategies used by component species to exploit them (Ballance et al. 1997). The first is the relatively greater patchiness of potential prey over the immense expanses of these oceans (Ainley and Boekelheide 1983, Hunt 1990). These conditions require that

tropical seabirds, especially, possess energy-efficient flight to allow them to search for and find food (Ainley 1977, Flint and Nagy 1984, Ballance 1993, Ballance et al. 1997, Spear and Ainley 1997a, Weimirskirch et al. 2004). Another important factor is the minimal structural complexity of the open ocean compared to coastal, neritic areas (McGowan and Walker 1993) and polar waters (Ainley et al. 1992). In regard to the tropics, the intense vertical and horizontal gradients, e.g., water-mass and water-type boundaries and other frontal features that serve to concentrate prey in somewhat predictable locations (Hunt 1988, 1990, Spear et al. 2001) are widely dispersed. For one thing, no tidal fronts or currents occur in the open ocean, which often provide a micro- to meso-scale complexity to coastal waters. The primary frontal feature in the ETP is the Equatorial Front, a boundary on the order of 200 km wide between the South Equatorial Current and the North Equatorial Countercurrent (Murphy and Shomura 1972, Spear et al. 2001; Fig. 1). A second important physical gradient, the thermocline, exists on a vertical scale. This feature has an important effect on the distribution of tuna (*Thunnus*, *Euthynnus* spp.; Murphy and Shomura 1972, Brill et al. 1999), which in turn are important in chasing seabird prey to near the surface (Au and Pitman 1986, Ballance and Pitman 1999).

In fact, the tropical ocean, especially that of the ETP, has the most intense gradients of any ocean area due to the fact that surface waters are very warm but waters as cold as those of subpolar areas lie beneath at less distance than the height of the tallest of trees on continents (Longhurst and Pauly 1987). This water upwells along the equatorial front, bringing a high degree of spatial complexity to mid-ocean surface waters. This complexity and the increased productivity affect the occurrence of seabirds and the prey available to them at multiple spatial scales (Ballance et al. 1997, Spear and Ainley 2007).

Because morphology of tropical seabirds is adapted for efficient flight in order to search large areas for food, nearly all tropical seabirds are able to obtain prey only within a few meters of the ocean surface. This is a result of their large wings, which are not well suited for diving more than a few meters subsurface. In fact, tropical seabirds use four foraging strategies, in part affected by their flight capabilities (Ainley 1977, Imber et al. 1992, Ballance et al.
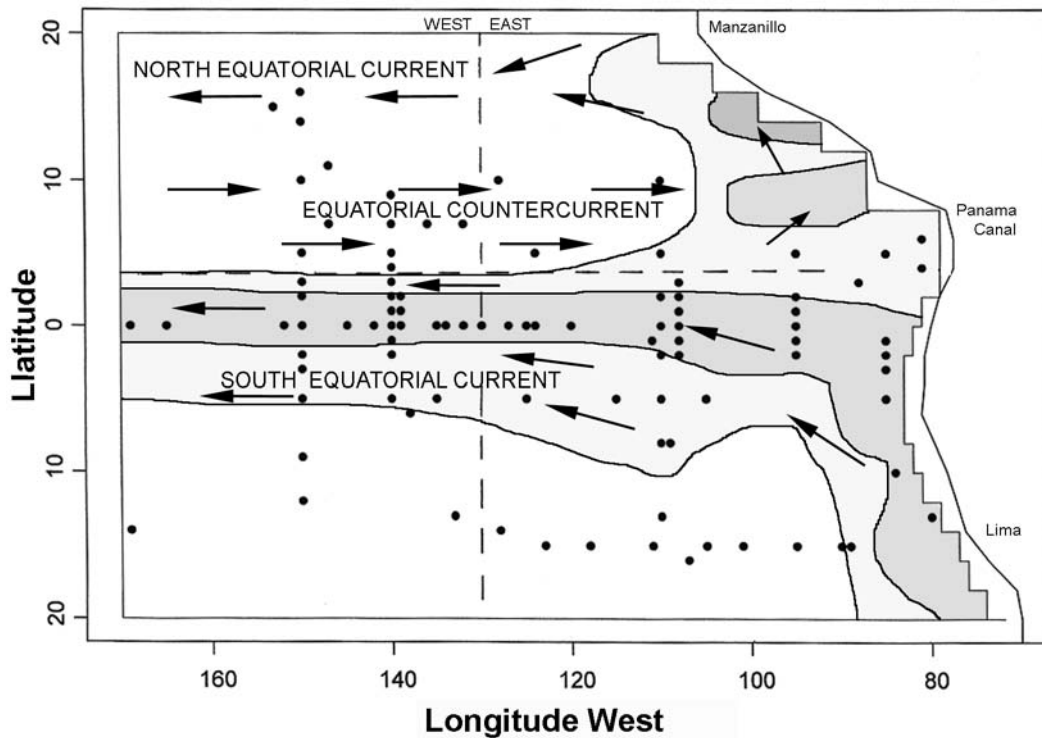
FIGURE 1. The study area in the eastern tropical Pacific Ocean, including locations (shown with dots) where birds were collected. The horizontal dashed line separates the Equatorial Countercurrent from the South Equatorial Current (Tropical Front); and the vertical line separates east from west as referred to in the text. The staircase line effect along the coast on the east side of the study area denotes the boundary separating pelagic waters to the west and coastal waters to the east. Shading indicates large-scale patterns of ocean productivity: the three gradations shown are, darker meaning higher values: <200, 201–300, and >300 mgC m^{-2} d^{-1} (from Longhurst and Pauly 1987, p. 122).

1997, Spear and Ainley 1998, this paper): (1) associating with aquatic predators (especially tuna) that chase prey to the ocean surface during the day, (2) taking advantage of the vertical movement of prey to feed at the ocean surface at night, (3) scavenging of dead prey, particularly cephalopods that die and float on the surface after spawning (Croxall and Prince 1994), and (4) diurnal feeding on non-cephalopod invertebrates (and teleost eggs) that live on or near the ocean surface. The first strategy requires rapid flight to maintain pace with tuna, the fastest and most mobile fish in the ocean (Longhurst and Pauly 1987), but the others require flight that is efficient enough to allow long search patterns.

Our primary objective in this study was to understand better the factors that structure tropical avifaunas, to compare them to the factors underlying community organization among polar avifaunas (Ainley et al. 1984, 1992, 1993, 1994; Spear and Ainley 1998), and to resolve several information gaps in our understanding

of tropical seabird ecology. Previous diet studies have consistently shown that diets of seabirds in temperate or polar latitudes are less diverse than those of tropical latitudes and that in both areas there is considerable overlap in diet composition (cf. Harrison et al. 1983, Ainley and Boekelheide 1990). In the absence of data from foraging areas, these patterns have led to questions of whether trophic-niche partitioning exists in tropical waters (Ashmole and Ashmole 1967, Diamond 1983, Harrison and Seki 1987). Such partitioning has been well documented in colder waters, although not necessarily expressed strongly by prey species differences (Ainley and Boekelheide 1990, Ainley et al. 1992). Finally, controversy exists regarding the relative importance of different foraging strategies of tropical seabirds, especially in regard to nocturnal vs. diurnal feeding and solitary vs. flock feeding (Imber 1973, 1976; Imber et al. 1992, Brown 1980, Harrison and Seki 1987, Ballance and Pitman 1999).

None of these questions can be addressed without studies of seabirds at sea. Therefore, we examined niche partitioning by collecting and analyzing data on the species and size of prey taken, and preference for use of the four feeding strategies, including timing of feeding. To do this we examined (1) the effects on diet and its diversity in relation to season, current system, interannual environmental variability (El Niño Southern Oscillation [ENSO] phase), sex, body condition, and predator mass (2) the propensity of the migratory, temperate component of the ETP avifauna to feed in tropical waters rather than merely passing through, and (3) effects on diet due to preferential use of different species of tuna. We were also interested in comparing diets and feeding strategies of seabird species that specialize by foraging in flocks over large aquatic predators vs. birds that feed solitarily, and we were interested in making comparisons to the analogous study we completed in the Southern Ocean (Ainley et al. 1992, 1993, 1994), realizing that we would learn much about the structuring of both communities based on how they differed.

METHODS

DATA COLLECTION

Specimens

Beginning in the autumn 1983, seabirds were collected during spring and autumn of each year through 1991. To do this, we participated in 17 cruises designed to study spatial and temporal marine climate variability of the ETP by deploying, retrieving and maintaining weather and ocean buoys as well as obtaining comparative, real-time ocean data (Table 1). Each cruise, sponsored by the U.S. National Oceanographic and Atmospheric Administration (NOAA) lasted 2–3 mo. At locations where an inflatable

boat (5-m long with 20–35 hp motor) could be deployed, bird sampling was conducted using a shotgun. These locations included recovery/ deployment sites of NOAA buoys and deep CTD (conductivity-temperature-depth) stations (Fig. 1), operations that required most of a day. Sampling in which at least one bird was collected occurred at 96 different locations on 264 d. Thirty-four of the sites were sampled on multiple days (2–29 d/site), but no site was sampled more than once/season/year. Between ocean stations, we conducted surveys to collect data on species composition, at-sea densities, and foraging behavior (Ribic and Ainley 1997, Ribic et al. 1997, Spear et al. 2001).

During each of the 264 sample days, an attempt was made to collect five or six birds of each avian species present in the area. Bird collecting was conducted using two methods. The first was to drive the inflatable boat 2–3 km from the ship where the motor was stopped and a slick was created by pouring fish oil on the water. The slick was freshened periodically by the addition of oil, about every 1–2 hr depending on wind speed (and our drift), which was the primary factor causing the oil slick to break up and disperse. The scent of the oil attracted mainly storm-petrels and gadfly petrels, but generally not shearwaters, larids, or pelecaniforms. Secondly, we also watched for feeding flocks while positioned at slicks. When one was sighted, the boat was moved to the flock where an attempt was made to collect a sample of birds. This allowed us to collect species not attracted to the oil slicks and also to determine the diet of seabirds that foraged over tuna. When at the flocks, we also attempted to determine the species of tuna that were forcing to the surface the prey on which the birds were feeding. We collected 85 birds (Table 2) from 11 flocks foraging over yellowfin (*Thunnus albacares*) and 46 birds from five flocks foraging over skipjack tuna (*Euthynnus pelamis*).

TABLE 1. SAMPLE SIZES, BY SEASON AND YEAR, OF SEABIRDS COLLECTED IN THE ETP AND THAT CONTAINED PREY [a].

Year	Spring–summer	Autumn–winter	Total
1983	0	74	74
1984	81	57	138
1985	39	91	130
1986	31	144	175
1987	128	211	339
1988	126	229	355
1989	75	115	190
1990	58	207	265
1991	100	55	155
Total	638	1,183	1,821

[a] Shown with respect to season (spring–summer [March–August] and autumn–winter [September–February]) and year; 30 species represented (See Table 3).