



Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review

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Abstract

This paper is part of a comprehensive review of the oceanography of the eastern tropical Pacific, the oceanic region centered on the eastern Pacific warm pool, but also including the equatorial cold tongue and equatorial current system, and summarizes what is known about oceanographic influences on seabirds and cetaceans there. The eastern tropical Pacific supports on the order of 50 species of seabirds and 30 species of cetaceans as regular residents; these include four endemic species, the world's largest populations for several others, three endemic sub-species, and a multi-species community that is relatively unique to this ecosystem. Three of the meso-scale physical features of the region are particularly significant to seabirds and cetaceans: the Costa Rica Dome for blue whales and short-beaked common dolphins, the Equatorial Front for planktivorous seabirds, and the countercurrent thermocline ridge for flocking seabirds that associate with mixed-species schools of spotted and spinner dolphins and yellowfin tuna. A few qualitative studies of meso- to macro-scale distribution patterns have indicated that some seabirds and cetaceans have species-specific preferences for surface currents. More common are associations with distinct water masses; these relationships have been quantified for a number of species using several different analytical methods. The mechanisms underlying tropical species–habitat relationships are not well understood, in contrast to a number of higher-latitude systems. This may be due to the fact that physical variables have been used as proxies for prey abundance and distribution in species–habitat research in the eastern tropical Pacific.

Though seasonal and interannual patterns tend to be complex, species–habitat relationships appear to remain relatively stable over time, and distribution patterns co-vary with patterns of preferred habitat for a number of species. The interactions between seasonal and interannual variation in oceanographic conditions with seasonal patterns in the biology of seabirds and cetaceans may account for some of the complexity in species–habitat relationship patterns.

Little work has been done to investigate effects of El Niño–Southern Oscillation cycles on cetaceans, and results of the few studies focusing on oceanic seabirds are complex and not easy to interpret. Although much has been made of the detrimental effects of El Niño events on apex predators, more research is needed to understand the magnitude, and even direction, of these effects on seabirds and cetaceans in space and time.

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1. Introduction

Ocean processes greatly influence marine organisms, and seabirds and cetaceans are no exception. Oceanography is the study of their habitat: the medium in which they, their prey, and their predators live. A comprehensive understanding of the ecology of any marine organism will therefore be incomplete without incorporating oceanography.

Among ecologists, the significance of species–habitat relationships has long been appreciated. The concepts of the ecological niche (that each species has a unique relationship to all aspects of its environment) and competitive exclusion (that two similar species cannot coexist on a single limiting resource), and the mechanistic linkages between community diversity and habitat diversity, have all become central tenets of ecological theory. These concepts developed from research focusing on species–habitat relationships, research that has been conducted almost entirely in terrestrial systems. In comparison, little is known about species–habitat relationships in the marine environment, particularly in oceanic ecosystems, but there is little doubt that these relationships are significant.

This paper reviews what is known about oceanographic influences on seabirds and cetaceans in the eastern tropical Pacific, the oceanic region centered on the eastern Pacific warm pool, but also including the equatorial cold tongue and equatorial current system. We will refer to other papers of this volume for reviews of physical oceanography and forcing–atmospheric processes (Amador et al., 2006), hydrography (Fiedler and Talley, 2006), circulation (Kessler, 2006), and eddies and mesoscale processes (Willett et al., 2006); oceanographic influences on primary production (Pennington et al., 2006), zooplankton (Fernández-Álamo and Färber-Lorda, 2006), and regional variability at interannual or El Niño/Southern Oscillation (Wang and Fiedler, 2006) and interdecadal scales (Mestas-Nuñez and Miller, 2006).

1.1. A brief overview of seabirds and cetaceans

Seabirds and cetaceans share a number of characteristics that influence the nature of their relationships with oceanographic features and water masses. Seabirds and cetaceans are predators that feed at a range of trophic levels, but many are apex predators. They feed closer to the top of the food chain than the bottom. For these species, relationships to physical features can be (but are not always) indirect, likely mediated by the responses of their prey (and the prey of those prey, in turn) to these physical features. Because of this, statistical correlations between seabirds and cetaceans and any given set of oceanographic parameters may be weak relative to values for organisms feeding lower on the food chain.

Seabirds and cetaceans are termed “K-selected” species. This means that they are relatively long-lived, have delayed reproductive maturity, and low reproductive output. This suite of life history traits generally buffers species from environmental perturbation compared to those with shorter lives and higher reproductive output (“r-selected species”). Therefore, oceanographic variation on seasonal and interannual scales, the latter including variation associated with the El Niño–Southern Oscillation (ENSO; Wang and Fiedler, 2006), is expected to be reflected more by changes in distribution or reproductive output, than by changes in survival.

Cetaceans and especially tropical seabirds are highly mobile. They can travel from 10s to 100s of km on a daily basis. Therefore, the spatial scale at which they experience oceanic habitat can be large, and investigations of species–habitat relationships will be more complete if they incorporate similarly large spatial scales. At the same time, high mobility can confound interpretation of species–habitat relationships, particularly in the case of seabirds, which can spend much of their time flying over unsuitable habitat in transit to foraging areas. If detected when commuting, links between species and oceanographic measures will not reflect significant habitat preferences, and may contribute to the low variance in species density that can be explained by habitat variables.

Finally, seabirds and cetaceans of the eastern tropical Pacific include residents, seasonal residents, and migrants. Residents remain within the region for the duration of their lives, seasonal residents inhabit the region for only part of the year, generally breeding or feeding elsewhere, and migrants simply move through the region, transiting between breeding and/or feeding areas. The distinction is important because seasonal residents or migrants may be using habitat in different ways than those that are resident throughout the year.

For example, migrants may not be feeding, and so may cue into current strength and direction or atmospheric dynamics rather than prey abundance and availability. In such cases, oceanography as it pertains to the foraging ecology of these species may reveal little. Of note then, investigations of apex predators and their relationships to ocean processes will provide better insight within the general context of how and why these predators are using their habitat.

1.2. The eastern tropical Pacific as a unique system for seabirds and cetaceans

Some 50 species of seabirds and 30 species of cetaceans regularly occur in the eastern tropical Pacific (Appendices A and B; we will use common species names in the text; Latin names are in those appendices). Recent and comprehensive overviews of the biology, ecology, and taxonomy of these groups can be found in Brooke (2002) and Berta and Sumich (1999). An important feature of the eastern tropical Pacific is the “tuna-dolphin-seabird assemblage”, a multi-species feeding association between yellowfin tuna (*Thunnus albacares*), spotted and spinner dolphins, and a relatively large number of seabird species (Perrin, 1969; Au and Perryman, 1985; Au and Pitman, 1986; Au, 1991). The tuna and dolphins in this assemblage occur in mixed-species schools, and are accompanied by flocks of seabirds which feed on prey made available at the surface by the subsurface predators. The tunas in these schools are much larger than yellowfin found in other types of aggregations (IATTC, 2002), and occur near the surface. Their large size, near-surface occurrence, and visibility through their association with air-breathing cetaceans and seabirds form the basis for one of the world’s largest yellowfin tuna fisheries (Perrin, 1969; Gosliner, 1999). Although the tuna, dolphins, and many of the seabirds are found throughout tropical oceans of the world, compared to the eastern tropical Pacific, the association is rare in the central and western Pacific (Miyazaki and Wada, 1978), the eastern tropical Atlantic (Levenez et al., 1980), and the western tropical Indian Ocean (Ballance and Pitman, 1998). Many have speculated about the mechanisms underlying the association. Most hypotheses focus on enhanced abilities to detect predators or prey, and the shallow thermocline (Fiedler and Talley, 2006) has been identified as a possible cause for the geographic uniqueness of the association (Green, 1967; Perrin, 1968, 1969; Au and Perryman, 1985; Au and Pitman, 1986, 1988; Au, 1991; Edwards, 1992; Norris et al., 1994; Scott and Cattanach, 1998). To date, however, there is no consensus on this issue.

There are a number of additional unique characteristics of the eastern tropical Pacific with respect to the seabirds and cetaceans that occur here. The region supports a diverse and abundant community of seabirds and cetaceans relative to other tropical oceans. For example, it is the only tropical ocean where four subspecies of spinner dolphin occur, two of which are endemic (Appendix A; Perrin, 1990). The eastern tropical Pacific supports an endemic subspecies of spotted dolphin (Appendix A; Perrin and Hohn, 1994) and an endemic beaked whale (Pitman et al., 1987; Pitman and Lynn, 2001). The eastern tropical Pacific is the only ocean that supports four species of seabirds in the booby genus (Appendix B); one is endemic, and the world’s largest colonies for the other three are found there (Pitman, unpublished data). Finally, the eastern tropical Pacific is used heavily as a feeding area for seasonally resident seabirds that breed elsewhere. For example, of the 13 species of *Pterodroma* petrels that are commonly recorded in the eastern tropical Pacific, only two breed on islands there (Appendix B). The remaining species breed in tropical, subtropical, or temperate waters of the southern hemisphere, well outside of the eastern tropical Pacific, and then disperse to the eastern tropical Pacific, some in huge numbers (Ballance, unpublished data), to feed during the non-breeding season.

Why the eastern tropical Pacific Ocean should support such a diverse and abundant community of seabirds and cetaceans with a number of endemic species and sub-species remains unknown, but most speculation centers around its unique oceanographic characteristics, particularly the thermal structure of the water column (see Fiedler and Talley, 2006). For example, a strong and shallow thermocline has been correlated with the success of the yellowfin fishery based on the association with dolphins (Green, 1967). Au and Perryman (1985) hypothesized that the shallow thermocline was a key feature that may constrain yellowfin tuna to the surface layer, thereby allowing for the association with dolphins. The strong, shallow thermocline characteristic of this region does not limit primary productivity: macronutrients are never depleted in the surface layer and production is limited by iron availability and/or zooplankton grazing (Pennington et al., 2006). Thus, the eastern tropical Pacific is moderately productive, not only in coastal waters, where wind-driven

upwelling supplies nutrients, but also in oceanic regions, particularly along the equator and countercurrent thermocline ridge.

2. Historical review of research on oceanographic influences on seabirds and cetaceans

The history of research on oceanographic influences on seabirds and cetaceans revolves around four key developments: (1) species identification guides, (2) quantitative survey methods, (3) sophisticated statistical and modeling techniques, and (4) recognition of scale-dependence in species–habitat relationships.

Before seabirds and cetaceans can be studied, they must be identified and a critical catalyst in this effort has been species identification guides. There are now some 200–300 described species of seabirds (Brooke, 2002) and some 80 species of cetaceans (Rice, 1998). Even today, the diagnostic field identification features of some groups (e.g. *Mesoplodon* whales and *Pterodroma* petrels, both common in the eastern tropical Pacific) remain little known. Field guides have long been in existence, but only recently have single guides included individual treatment of all species and subspecies, color plates and photographs, range maps, and descriptions of behavior. The significance of these field guides cannot be overstated. They have made identification of seabirds and cetaceans to the species level easier and, in many cases, possible. Furthermore, by synthesizing extensive data into simplified range maps establishing basic distribution, these field guides have served as catalysts in the ever more refined documentation of these patterns (e.g. Harrison, 1985; Reeves et al., 2002).

A second key development in the study of oceanographic influences on seabirds and cetaceans has been the use and refinement of quantitative survey methods. The first data on species distributions were collected opportunistically from catch records, stranding reports, sightings and collections from early museum expeditions, informally aboard ships during routine passages, whaling and fishing expeditions, or as piggyback projects on oceanographic research vessels (e.g. Beebe, 1926; Murphy, 1936; Townsend, 1935). At sea, data were recorded in the form of simple lists of species sighted on a daily basis regardless of their distance from a ship. At times, approximate numbers of individuals or, less commonly, numbers sighted per unit time, were recorded, but these methods were semi-quantitative at best. Since that time, survey methods have been standardized, and strip- and line-transect methods developed to allow for quantitative collection, analysis, and comparison of data in a systematic way (Brown, 1980; Tasker et al., 1984; Haney, 1985; Tasker et al., 1985; Briggs et al., 1987; Gaston et al., 1987; Gould and Forsell, 1989; Hibby and Hammond, 1989; Van Franeker, 1990; Spear et al., 1992; Wade and Gerrodette, 1993; Barlow, 1995; Forney et al., 1995; Aragonés et al., 1997; Spear and Ainley, 1997; Garner et al., 1999; Buckland et al., 2001; Clarke et al., 2003). These methods have made it possible to document distribution patterns at precise temporal and spatial scales, and to link seabird and cetacean data with other data sets corresponding in space and time.

The third key development in the study of oceanographic influences on seabirds and cetaceans has been the introduction, evolution, and widespread use of sophisticated analytical methods. Early investigations of species–habitat relationships focused on simple correlations between distribution and one or two directly-measured oceanographic variables (e.g. Pocklington, 1979; Brown, 1980). Today, investigators explore empirical associations between density and a number of physical or biological variables, predict density based on known species–habitat relationships, or test specific hypotheses about the ecological mechanisms determining distribution and density patterns (Redfern et al., 2006 and references therein). The purpose of the investigation determines the appropriate analytical tool, but all methods integrate two quite different types of data: species and oceanographic. Species data are often autocorrelated (Lennon, 2000) and habitat variables often exhibit multicollinearity (Neter et al., 1996), further complicating analyses. Together, these factors require sophisticated statistical and modeling techniques and, consequently, access to high-powered computers for computationally intensive analyses. Analytical tools fall into two basic categories (reviewed by Redfern et al., 2006): descriptive techniques (e.g. overlays of species data on maps of oceanographic measures, correlation analysis, goodness of fit metrics, analysis of variance, and ordination) and modeling techniques (e.g. environmental envelope models, regression models, and classification and regression trees). The use of modeling techniques requires parameter estimation (most commonly with least squares, maximum likelihood, and Bayesian methods), model selection (most commonly with deviance tests, or Akaike's or Bayesian Information Criterion), uncertainty estimation (most commonly with confidence intervals, bootstrap, jackknife, or model averaging methods), and model evaluation. The development of many of these analytical methods is still in the

early stages, but they represent potentially powerful tools for predicting species distribution and density and for understanding the mechanisms underlying species–habitat patterns.

Species–habitat relationships are scale-dependent and recognition of this is the fourth key development in the study of oceanographic influences on seabirds and cetaceans. The concept of scale-dependence, a change in some measure of pattern with change in the resolution or range of measurement in both space and time (Schneider, 1994), is far from new, but the increased attention it has received from ecologists is a relatively recent phenomenon (Wiens, 1989). In the context of this review, scale-dependence means that the outcome of species–habitat investigations will depend upon the spatial and temporal scale at which data are collected and analyzed (Wiens, 1989). Many physical and biological processes are best measured at characteristic spatial and temporal scales, and temporal variability tends to be high at small spatial scales and low at large spatial scales (Haury et al., 1978; Steele, 1978; Hunt and Schneider, 1987; Wiens, 1989; Schneider, 1994). It is, therefore, of primary importance that the scale of data collection and the units used in analyses match the temporal and spatial scales of the specific research question (Redfern et al., 2006). Recognition of this has facilitated the development of hypotheses proposed to explain distribution and abundance (e.g. Briggs et al., 1987; Hunt and Schneider, 1987; Cairns and Schneider, 1990; Schneider et al., 1990). There is general consensus that large scale distribution patterns may be constrained by large water masses or surface currents, while local oceanographic features, often due to their effects on prey distribution, may play a stronger role in determining small scale distribution patterns. However, matching the research question with the appropriate analytical scale is not always straightforward. Although there is an increased likelihood of detecting significant relationships at larger scales, in many instances, the explanatory power of habitat variables will vary significantly with the scale of the unit of analysis (Wu et al., 1997; and references therein; Ballance et al., 2001; Dungan et al., 2002). For this reason, many studies focus exclusively on identifying the appropriate scale of analysis (e.g. Schneider and Piatt, 1986; Heinemann et al., 1989; Erikstad et al., 1990; Piatt, 1990; Hunt et al., 1992; Jaquet et al., 1996; Logerwell and Hargreaves, 1996; Fauchald et al., 2000) and there is much yet to be learned from these types of investigations. In the review that follows, we will use spatial scale terms as defined in Hunt and Schneider (1987), and based on Haury et al. (1978): mega-scale (larger than 3000 km), macro-scale (1000–3000 km), meso-scale (100–1000 km), and coarse scale (1–100 km). However, in many cases, researchers have not specifically identified the spatial scale of investigation and we will, therefore, be necessarily vague with respect to the scale to which these studies pertain.

3. Oceanographic features of significance to seabirds and cetaceans

The first step in identifying habitat relationships is to document distribution and abundance patterns. Much work has progressed only this far, with correlations between spatial distribution patterns and major surface currents in the region being noted in some cases. For example, distribution patterns plotted from data collected during an 11-year time period clearly indicate that the Tahiti Petrel associates with the North Equatorial Countercurrent, and that the Herald Petrel, White-throated Storm Petrel, Sooty and White tern associate with the South Equatorial Current (Pitman, 1986). Bottlenose, Risso's, and, to a lesser extent, common dolphins and short-finned pilot whales are the prevalent species in nearshore waters, particularly in the Gulf of Panama (Polacheck, 1987). Newell's Shearwater and Hawaiian Petrel occur mostly in the North Equatorial Current and North Equatorial Countercurrent, Townsend's Shearwater in the Costa Rica Coastal Current and the Galapagos Petrel in the northern boundary of the Peru Current, the southern end of the Costa Rica Coastal Current, and the eastern edges of the South Equatorial Current and North Equatorial Countercurrent (Spear et al., 1995). In the above cases, when variables defining the currents are not measured, such labels are descriptors of location rather than indicators of true ecological relationships. However, broad generalizations based on qualitative correspondence between distribution and abundance, and oceanographic features provide the basis for further quantitative investigations. For example, when viewed in 5° square latitude–longitude grids, there are clear patterns in distribution and density for 33 cetaceans, patterns that differ for virtually every species, suggesting that our understanding of these patterns could be greatly improved by modeling distributions as functions of oceanographic and geographic variables (Ferguson and Barlow, 2001; see also Wade and Gerrodette, 1993).

Indeed, the eastern tropical Pacific has many distinct, macro- and meso-scale features that, although somewhat variable in space and time, are relatively permanent and predictable. These include the major surface currents, the boundaries between them, larger gyres and eddies and surface waters downstream of islands (Kessler, 2006; Fiedler and Talley, 2006). Three physical features are particularly significant to seabirds and/or cetaceans: the Equatorial Front, the Costa Rica Dome, and the countercurrent thermocline ridge (along 10°N latitude). All are sites of enhanced productivity relative to surrounding waters, and all attract marine predators. One general rule holds for all three: significance is species-specific. That is, a feature is only important to a particular species or species groups, not to seabirds and cetaceans as a whole. This may not be surprising to an ecologist; after all, different species have different habitat requirements. Nevertheless, the general idea persists that “fronts” are significant to all marine organisms (e.g. Olson et al., 1994; Schreiber, 2002).

3.1. The Equatorial Front

The Equatorial Front is the boundary lying just north of the equator, between the Equatorial Surface Water of the equatorial cold tongue and the warm Tropical Surface Water to the north (Fiedler and Talley, 2006). It is a permanent feature, but its intensity varies in space and time (see Fig. 2 in Willett et al., 2006). It is markedly unstable and distorted by long waves west of the Galapagos, due to high shear between the westward South Equatorial Current along the equator and the eastward North Equatorial Countercurrent to the north (Kessler, 2006; Willett et al., 2006). One of the first to recognize it as a significant feature to marine organisms in general was Beebe (1926), who documented increased biological activity along the front east of the Galapagos. This description of a proliferation of birds, mammals, fish, and plankton within “ten yards” (9 m) of a “Current Rip” followed for a hundred miles became classic for the significance of fronts to marine organisms in general; in fact, the Equatorial Front is the most prominent oceanic, low latitude front in the world.

The Equatorial Front can be a significant feature for planktivorous seabirds (species that consume planktonic organisms), particularly for Leach’s and Galapagos storm petrels. They aggregate at the front, being found there in significantly higher densities than in waters on either side (Spear et al., 2001). This association was particularly strong in October of 1998 (a La Niña year, see below), when the front was well developed. On 11 October of that year, when moving across the front from the North Equatorial Countercurrent to the South Equatorial Current, there was an immediate and dramatic change in oceanographic conditions: a 2.1 °C decrease in sea surface temperature, a 0.2 pss increase in sea surface salinity, and a 54 m decrease in thermocline depth (Table 1, Spear et al., 2001). At the same time, the density of five species of planktivorous seabirds along the front was one to two orders of magnitude higher than on either side (Table 1, Spear et al., 2001). The mechanisms responsible for this association remain unknown. These authors speculated that physical forces structuring the front serve to transport zooplankton, concentrating them at this boundary and thereby attracting planktivorous species. This is the consensus in general regarding the mechanism responsible for the association between planktivorous seabirds and fronts (Schneider, 1990). In addition, Ainley and Boekelheide (1983) found consistent peaks in species turnover when crossing the Equatorial Front,

Table 1

Changes in oceanographic conditions and seabird density (birds per km²) when passing across the Equatorial Front on 11 October 1998 at 3° 34’N, 117° 37’ W, from the South Equatorial Current (SEC) to the North Equatorial Countercurrent (NECC)

	SEC	Equatorial front	NECC
Sea surface temperature (°C)	23.7	–	25.8
Sea surface salinity (pss)	34.20	–	34.00
Thermocline depth (m)	11	–	65
Seabird density	0.18 ± 0.04	8.18 ± 3.40	0.38 ± 0.13
Planktivorous seabird density	0.06 ± 0.04	7.27 ± 1.58	0.12 ± 0.03
Piscivorous seabird density	0.12 ± 0.05	0.90 ± 0.67	0.26 ± 0.05

Sea surface temperature, salinity, and thermocline depth values were measured at a single location on either side of the approximately 10 m-wide front. Modified from Spear et al. (2001).

and speculated that the large changes in sea surface temperature and salinity there serve as an avifaunal boundary, with surface temperature and salinity characteristics representing significant indicators of species–habitat relationships.

Of note, seabirds that consume fish and squid show no association with the Equatorial Front (Spear et al., 2001). Nor, to our knowledge, have there been any documented records of an association between any cetacean species and this feature.

3.2. The Costa Rica Dome

The Costa Rica Dome is a 300–500 km² quasi-permanent shoaling of the thermocline with a mean position at 9°N, 90°W, about 300 km off the Gulf of Papagayo, between Nicaragua and Costa Rica. It is associated with a cyclonic circulation of surface currents and is seasonally affected by large- and coastal-scale wind patterns (Kessler, 2006; Fiedler and Talley, 2006). Upwelling associated with the cyclonic circulation, combined with the presence of a strong and shallow thermocline, make the Costa Rica Dome a distinct biological habitat (Fiedler, 2002a). Surface waters are lower in temperature and higher in nitrate and chlorophyll than surrounding areas. Zooplankton biomass is increased here and, perhaps consequently, abundance of at least two cetacean species is markedly higher in the vicinity than in the surrounding tropical waters (Fig. 1; Au and Perryman, 1985; Reilly and Thayer, 1990; Fiedler, 2002a).

One of these, the blue whale, feeds on euphausiids worldwide, in areas with cold currents and upwelling (Sears, 2002). Like most baleen whales, blue whales typically migrate seasonally between tropical breeding grounds in the winter and temperate/polar feeding grounds in the summer. However, they are present year-round in Costa Rica Dome waters (Reilly and Thayer, 1990), and these authors speculate that this may represent (1) a resident population, (2) animals from both northern and southern hemispheres migrating into the area during their respective winters, or (3) juveniles not taking part in the full migration. A single blue whale fitted with a satellite tag off the coast of southern California in September migrated south along the coast of Mexico to a location within 450 km of the Costa Rica Dome, thus supporting the hypothesis

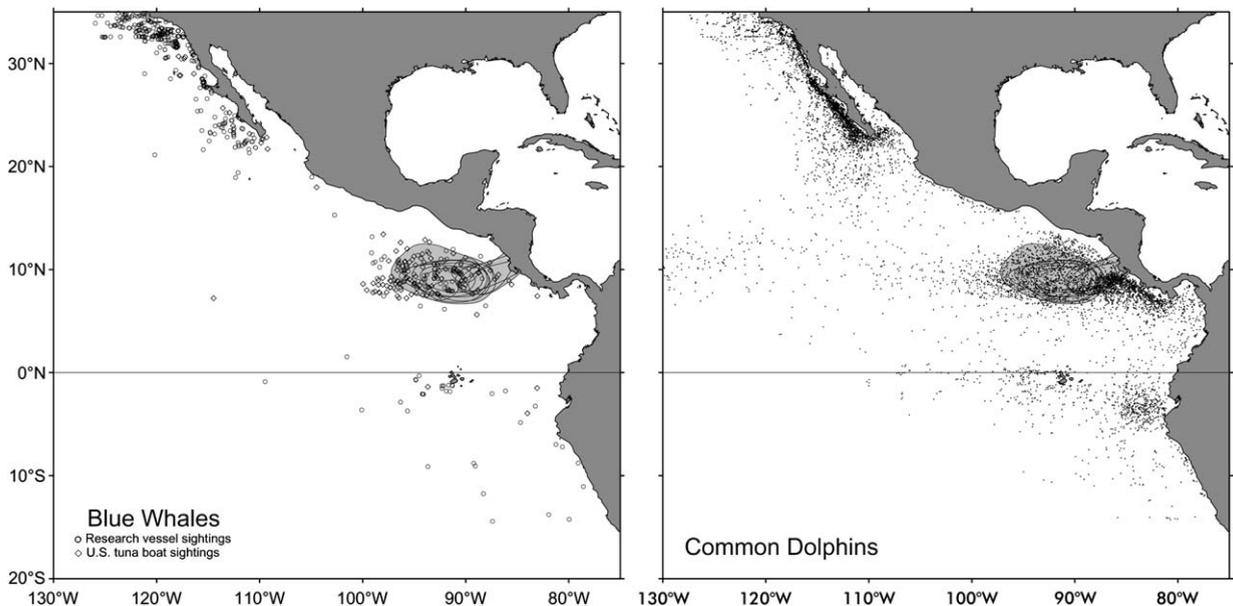


Fig. 1. (Left) Sighting locations of blue whales (*Balaenoptera musculus*) from research vessels (1976–2003, $n = 516$) and US tuna boats (1971–1990, $n = 142$). (Right) Sighting locations of short-beaked (between the equator and 20°N latitude) and long-beaked (north of approximately 20°N and south of the equator) common dolphins (*Delphinus delphis* and *D. capensis*) from research and tuna vessels (1971–2003, $n = 9467$). Monthly positions of the Costa Rica Dome are also shown. Updated from Fiedler (2002a), with permission from Elsevier.

that northern populations migrate here to calve (Mate et al., 1999; see also Tagging of Pacific Pelagics tracks at <http://www.topp census.org/>). Clearly, their year-round presence indicates that the Costa Rica Dome is important habitat for this species, and physical and biological characteristics of these waters indicate that these whales may very well feed here (Reilly and Thayer, 1990; Fiedler, 2002a). Blue whale distribution has been closely tied to productive areas throughout the eastern tropical Pacific (and in other tropical oceans), where upwelling-enriched surface waters have been associated with high planktonic biomass and, possibly, feeding opportunities (Reilly and Thayer, 1990; Ballance and Pitman, 1998; Palacios, 1999).

A second cetacean species, the short-beaked common dolphin, is also found in greater abundance here than in surrounding waters outside of the Costa Rica Dome (Fig. 1). This species feeds at a higher trophic level than blue whales on a variety of prey, including small mesopelagic fishes and squids that occur in the deep scattering layer, and epipelagic schooling species such as small scombrids, clupeoids, and market squids (Perrin, 2002), none of which are known to be particularly abundant in Costa Rica Dome waters relative to surrounding areas (but see Owen, 1981). Short-beaked common dolphins appear to prefer “upwelling-modified” water in general (Au and Perryman, 1985; Reilly and Fiedler, 1994), and Au and Perryman speculated that water mass-specific differences in the distribution and availability of their prey were the reason. This idea remains largely untested.

Finally, it is of note that the Costa Rica Dome does not appear to be a significant feature for any of the seabirds of the eastern tropical Pacific (Ballance and Pitman, unpublished data). Why this is so remains unknown.

3.3. *The thermocline and the countercurrent thermocline ridge*

The thermocline, a subsurface vertical gradient in temperature, and thus water density, beneath the surface mixed layer is an effective physical and biological barrier in the ocean. In the eastern tropical Pacific, thermocline depth and strength (magnitude of the vertical temperature gradient) are important oceanographic predictors of abundance and distribution for a great many species of seabirds and cetaceans (Au and Perryman, 1985; Reilly, 1990; Reilly and Fiedler, 1994; Ballance et al., 1997; Ribic and Ainley, 1997; Spear et al., 2001; Vilchis et al., 2006; see “Significant Water Mass Types” below). The thermocline is uniquely shallow and strong here, and is reinforced by a coincident halocline (salinity gradient) beneath low-salinity Tropical Surface Water (Fiedler and Talley, 2006). As noted above, this sharp, shallow thermocline has been suggested as a primary factor explaining the prevalence of the tuna-dolphin-seabird assemblage in the eastern tropical Pacific (Green, 1967; Au and Perryman, 1985).

In general, the thermocline is shallow in the eastern regions of the eastern tropical Pacific and deepens to the west. In addition, the thermocline shoals significantly along the equator and along the countercurrent ridge, located at approximately 10° N latitude (Fiedler and Talley, 2006). Of these two shoaling regions, the countercurrent ridge is clearly a significant feature for a number of apex predators, including yellowfin tuna, spotted and spinner dolphins, and flocking seabirds (Figs. 2–5; Au and Perryman, 1985; Pitman, 1986; Reilly, 1990; Ballance et al., 1997; IATTC, 2002), all part of the tuna-dolphin-seabird assemblage characteristic of the eastern tropical Pacific. The unusual thermocline structure here may induce vertically migrating prey to aggregate, thereby becoming more readily available to predators here than elsewhere (Fiedler et al., 1998). But this idea remains untested; the mechanisms which make the countercurrent thermocline ridge significant for these animals remain unknown.

It is of note that the shoaling of the thermocline along the equator, often accompanied by extensive upwelling, does not appear as a significant feature in the basin-wide distribution for any seabird (Pitman, 1986). Meso- to macro-scale distribution patterns indicate that there may be a higher density of Bryde’s, sei, and Cuvier’s beaked whales in some longitudinal sections along the equator (Ferguson and Barlow, 2001), and charts of 19th-century sperm whale catches in the Pacific clearly show a concentration along the equator (Fig. 8 in Jaquet et al., 1996). Feeding success of sperm whales is increased in colder water associated with upwelling at the Galapagos (Whitehead et al., 1989) and along the coast of northern Chile (Rendell et al., 2004) relative to surrounding regions, presumably due to increased availability in deep waters of squid prey supported by the high primary productivity of upwelled surface waters.

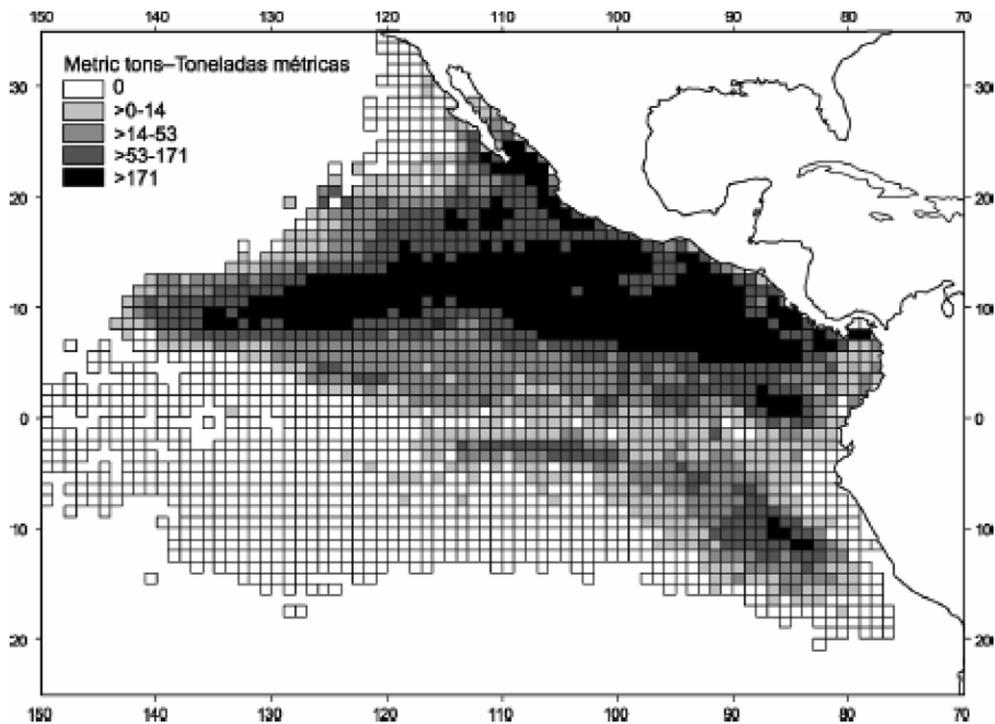


Fig. 2. Average annual catches of yellowfin tuna (*Thunnus albacares*) in the eastern tropical Pacific during 1985–1999 for sets on fish associated with dolphins on all purse-seine trips for which usable logbook data were obtained. The average catches and effort represent only those 1-degree blocks for which three or more years of data were available. From IATTC (2002).

4. Associations with surface currents and water masses

In addition to distinct hydrographic features being of significance to seabirds and cetaceans, there are obvious species-specific habitat preferences that are defined by combinations of physical, chemical, and biological variables. Some of these associations correspond to hydrographic or functional water masses, or to major surface currents; others are more subtle. Because the nature and extent of investigations focusing on these associations differ extensively between seabirds and cetaceans, we treat each in turn below.

4.1. Cetaceans

At the macro-scale, cetacean habitat associations seem to be based on preferences for specific water masses, rather than preferences for surface currents, though these relationships have been quantified for a few species only. Most of what is known about cetacean habitat associations in the eastern tropical Pacific is focused around a suite of four dolphin species, three from the genus *Stenella*, and the fourth from the genus *Delphinus*. Their distribution patterns are shown in Fig. 3. Spotted and spinner dolphins occur predominately in regions corresponding to Tropical Surface Water. Common dolphins are found along the coast of Baja California, near the Costa Rica Dome, and in the eastern equatorial Pacific. Striped dolphins are more cosmopolitan, but are rare in both the warmest Tropical Surface Water off southern Mexico and in eastern boundary current coastal upwelling regions.

The first to describe habitat preferences in the eastern tropical Pacific for these species (and any cetacean) were Au and Perryman (1985). They recognized two major cetacean communities, centered broadly around two separate water masses (Fig. 6). The first was an assemblage of spotted and spinner dolphins found in greatest frequency in waters underlain by a sharp thermocline, generally $>2\text{ }^{\circ}\text{C } 10\text{ m}^{-1}$, at depths usually much less than 50 m, with surface temperatures above $25\text{ }^{\circ}\text{C}$ and surface salinities below 34 pss. These oceanographic

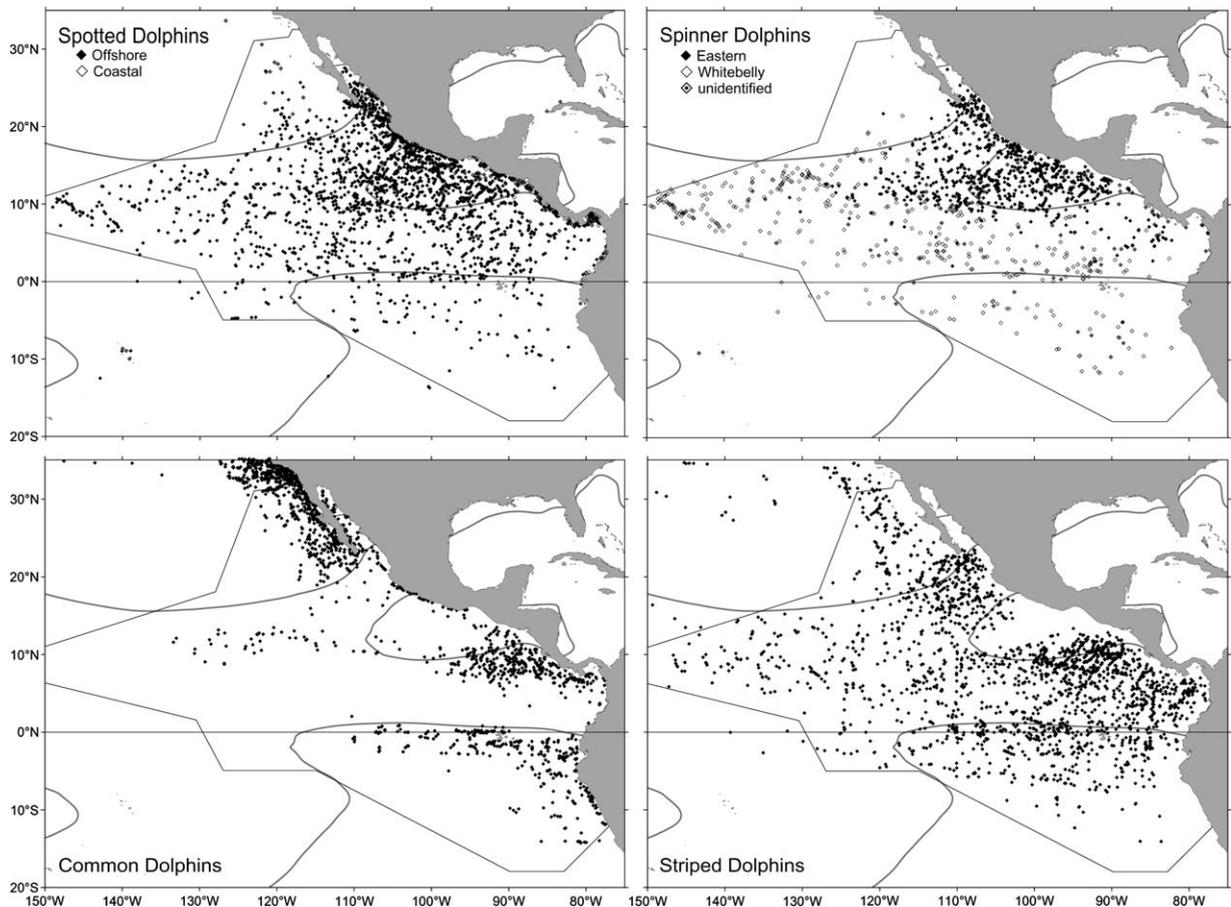


Fig. 3. Sighting locations of spotted dolphins (2 stocks), spinner dolphins (2 stocks), common dolphins, and striped dolphins from research vessels (1976–2003), mostly during August–November. Thick gray lines are the annual mean 28 °C isotherm, marking the Eastern Pacific Warm Pool off Central America, and the 25 °C isotherm marking the equatorial cold tongue (Shea et al., 1992). Thin black line marks the current NMFS survey area (Kinzey et al., 2001).

graphic characteristics are typical of Tropical Surface Water (Wyrtki, 1966, 1967; Fiedler and Talley, 2006). The second was an assemblage of striped and common dolphins whose distribution was broadly centered around equatorial waters and extending to include Tropical Water near Central America and Subtropical Water south of the Galapagos off Peru. This preferred habitat of striped and common dolphins corresponds with regions of highly variable oceanographic features that Au and Perryman (1985) termed “upwelling-modified,” characterized by year-round or seasonal upwelling, weak thermoclines, surface temperatures below 25 °C and surface salinities above 34.5 pss. Au & Perryman further noted that these general habitat preferences extend to other species, with rough-toothed dolphins apparently sharing habitat preferences of spotted and spinner dolphins, and pilot whales sharing those of common and striped dolphins. They hypothesized that the mechanisms for these habitat preferences were based on water mass-specific differences in the nature of epipelagic prey, as evidenced by differences in surface distribution of nutrients and primary production, ultimately affecting which top predators would be able to successfully forage there. In particular, they proposed that food chains were not only different, but shorter, in upwelling-modified waters, and that this could form the basis for the differences in communities of cetaceans.

The habitat preferences described by Au and Perryman (1985) were based on qualitative assessments. Reilly (1990) expanded upon this study by directly quantifying dolphin distributions with simple indices of physical habitat. He documented significant differences in surface water density and thermocline depth for three species or species groups (spotted and spinner dolphins as a group, common dolphins, and striped

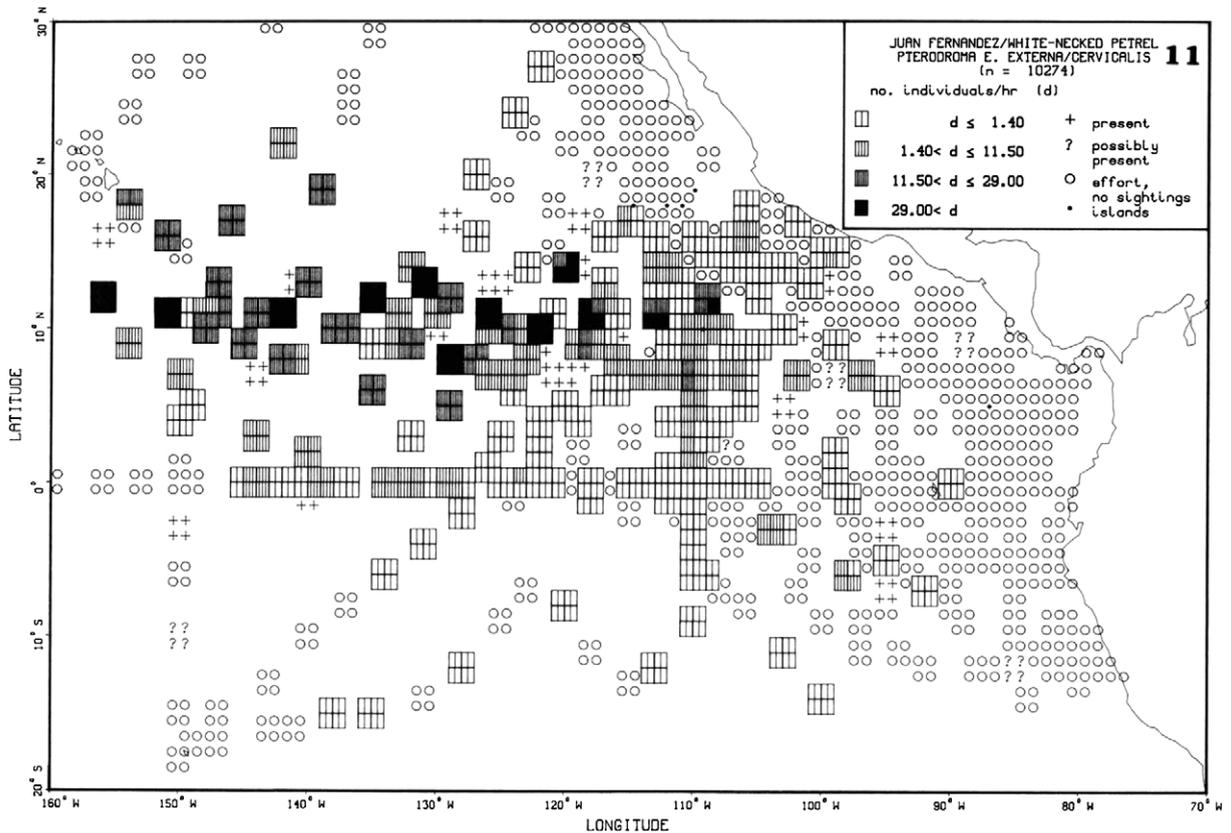


Fig. 4. Distribution and relative abundance of Juan Fernandez and White-necked petrels, 1974–1984, showing a clear association with the thermocline ridge at 10°N latitude. From Pitman (1986).

dolphins; Fig. 7), and used multivariate methods to document that spotted and spinner dolphins had significantly different habitat preferences from common dolphins. Further work using Canonical Correspondence Analysis (Reilly and Fiedler, 1994) confirmed previously documented habitat differences between spotted and spinner dolphins on the one hand, and common dolphins on the other, but also identified habitat preferences for sub-species. Eastern spinner dolphins, found predominately in the Eastern Pacific Warm Pool, associated with waters characterized by high surface temperature and chlorophyll, low surface density, and shallow thermoclines, whereas whitebelly spinner dolphins, found to the west and south of the Eastern Pacific Warm Pool, associated with waters characterized by cooler surface temperature and chlorophyll, higher surface density, and deeper thermoclines (Fig. 8). The significance of this quantification is that distribution patterns could now be understood not merely in terms of geographic location with respect to latitude/longitude coordinates or general location of water mass types, but in terms of significant physical variables, providing the opportunity to test hypotheses about mechanisms underlying these habitat associations, to understand temporal variation in distribution patterns within the eastern tropical Pacific (see below), and spatial variation in distribution patterns for these same species in other ocean basins. Despite the significant relationship between certain habitat variables and species density, only 14.7% of the variance in dolphin abundance for the community as a whole (considering seven school types) could be explained with six oceanographic variables: sea surface temperature, salinity, chlorophyll, density, and thermocline depth and strength, with between 5.1% (for whitebelly spinner dolphins) and 35.5% (for short-beaked common dolphins) of the variance in abundance for individual species explained (Reilly and Fiedler, 1994). These variance values are low, due in part to the fact that the dolphin data undoubtedly contain sightings of animals that may be merely commuting through habitat, rather than utilizing it in some way. Because these commuting animals may not have selected the habitat in which they were recorded, this likely

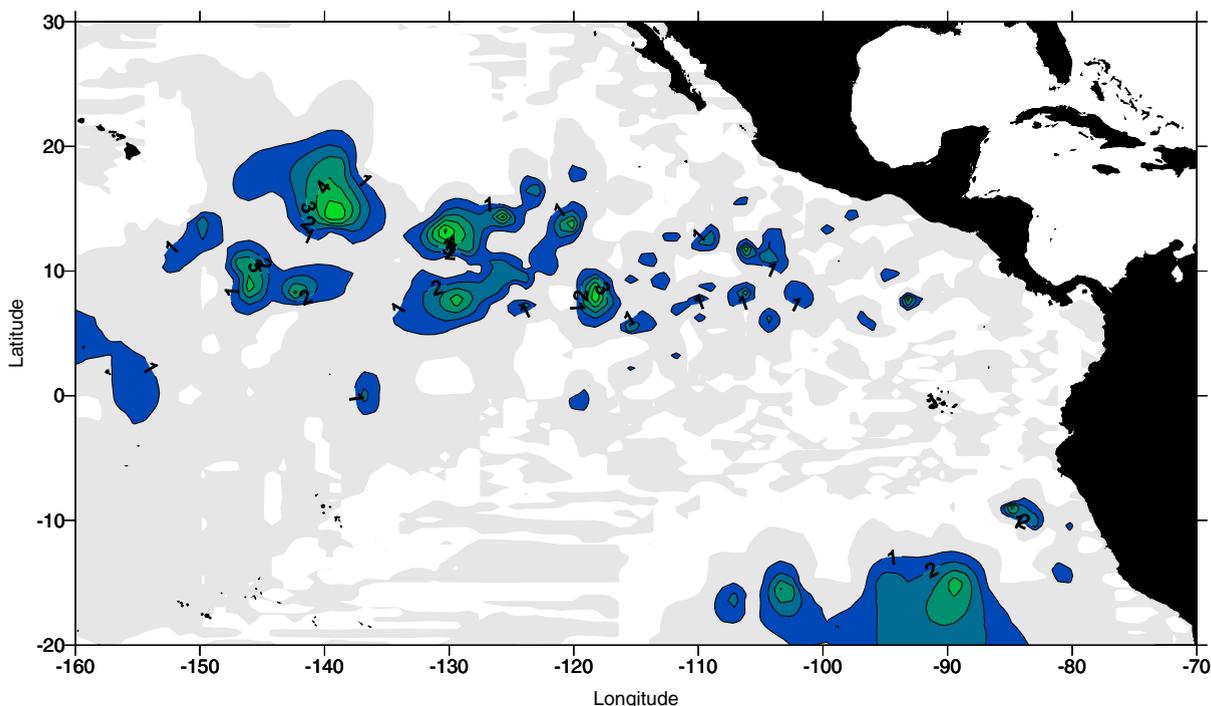


Fig. 5. Distribution of seabird feeding flocks numerically dominated by Juan Fernandez Petrels and Wedge-tailed Shearwaters feeding in association with yellowfin tuna, 1979–1988. Density of these flocks is enhanced along the thermocline ridge at 10°N latitude. Contours represent number of flocks recorded per day. Flock data were collected from research vessels using mounted 20 × 120 or 25 × 150 binoculars to scan the ocean area in front of the research vessel from beam to beam and out to the horizon. Search effort ranged from 2 to 10 h/d. Binocular height ranged from 10 to 15 m above the water and distance to the horizon from 13 to 16.5 km. Modified from Ballance et al. (1997); reprinted by permission of the Ecological Society of America.

introduces a fair bit of noise into the species–habitat correlations. This is a problem in general for species–habitat investigations of highly mobile marine organisms, as noted above.

Using identical analytical methods and data collected during the late 1990s, Reilly et al. (2002) confirmed these habitat preferences for the same species and species groups. By incorporating geographic variables into the suite of environmental parameters included in the model, and by separating common dolphins into three stocks, the proportion of variance in species abundance accounted for by these habitat preferences for the dolphin community as a whole increased to 30%, ranging from merely 8% of the variance for eastern spinner dolphins to 62% for southern common dolphins (Reilly et al., 2002).

The habitat preferences described above have been confirmed in a localized (coarse-scale) study of cetaceans off the Galápagos Islands. Specifically, spotted and spinner dolphins preferred areas of strong water-column stratification, whereas common dolphins (along with bottlenose and Risso's dolphins, and Bryde's and short-finned pilot whales) preferred upwelling (and, in this study, nearshore) areas (Palacios, 2003). The dominant environmental gradient was from cold, upwelling, near-island waters high in phytoplankton to warm, stratified waters far from islands that were low in phytoplankton. This suite of habitat characteristics explained 27–35% of the variance in cetacean community structure in a small area dominated by a single habitat gradient.

Finally, Ferguson et al. (2006) used an analytical scale of 9 km applied to a macro-scale study area in the eastern tropical Pacific to quantify beaked whale habitat preferences using generalized additive models. These models predicted highest densities in equatorial waters, in the Gulf of California, and off the west coast of the Baja Peninsula, all regions of relatively high productivity. Densities of whales from the genus *Mesoplodon* peaked in waters approximately 2000 m deep, with a second peak around 6000 m. High densities were also found in regions where thermoclines were strong, particularly around 10°N near the coast, and where sea surface salinity was high. Cuvier's beaked whales were encountered most often in offshore waters, approximately 2000 m deep, with smaller groups at higher latitudes and in waters with stronger thermoclines.

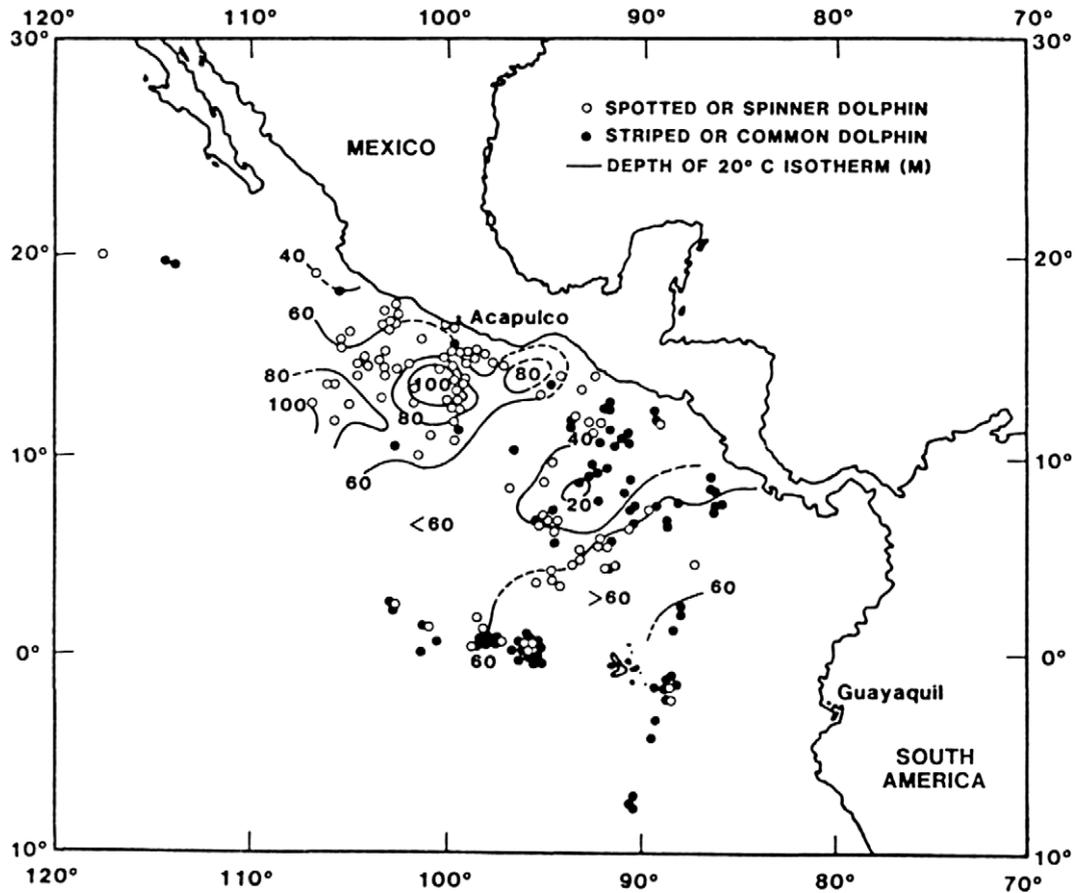


Fig. 6. Distribution of dolphin schools by species type in the Central American Bight, with reference to the depth of the 20 °C isotherm. Data from January to March, 1979. This represents the first documentation in the eastern tropical Pacific of an association between species distributions and oceanographic habitat. From Au and Perryman (1985).

4.2. Seabirds

Work on seabirds has covered many more species and investigations at a number of different spatial scales than is the case for cetaceans. At the macro-scale, it appears that at least some species regularly associate with habitats corresponding to current systems. This conclusion is reached by qualitatively comparing distribution patterns with those of surface currents (see “Oceanographic Features of Significance” above), as well as through more direct, quantitative analyses. For example, significant associations have been documented between Wedge-rumped Storm Petrel, White-winged and Black-winged petrels (when considered individually and together as an assemblage), and Sooty Tern with the South Equatorial Current, and between Juan Fernandez Petrel and the North Equatorial Countercurrent; these habitat associations persisted over a number of years and seasons (Ribic and Ainley, 1997; Ribic et al., 1997a).

Taxon-specific associations between seabirds and water masses have also been documented. Abundant genera in Equatorial Surface Water include *Oceanodroma* storm petrels, *Pterodroma* petrels, *Puffinus* shearwaters, and, to a lesser extent, *Sterna* terns (Ribic et al., 1992; Ribic and Ainley, 1997). Abundant taxa in Subtropical Surface Water include fewer genera and species, primarily consisting of *Oceanodroma* storm petrels and *Puffinus* shearwaters (Ribic et al., 1992; Ribic and Ainley, 1997).

At coarse to meso-scales, relationships between seabirds and habitat with distinct physical and biological characteristics have been quantified in at least five separate studies, detailed below. Many of these do not explicitly characterize spatial distribution of the seabirds studied, or oceanographic properties. This is in part

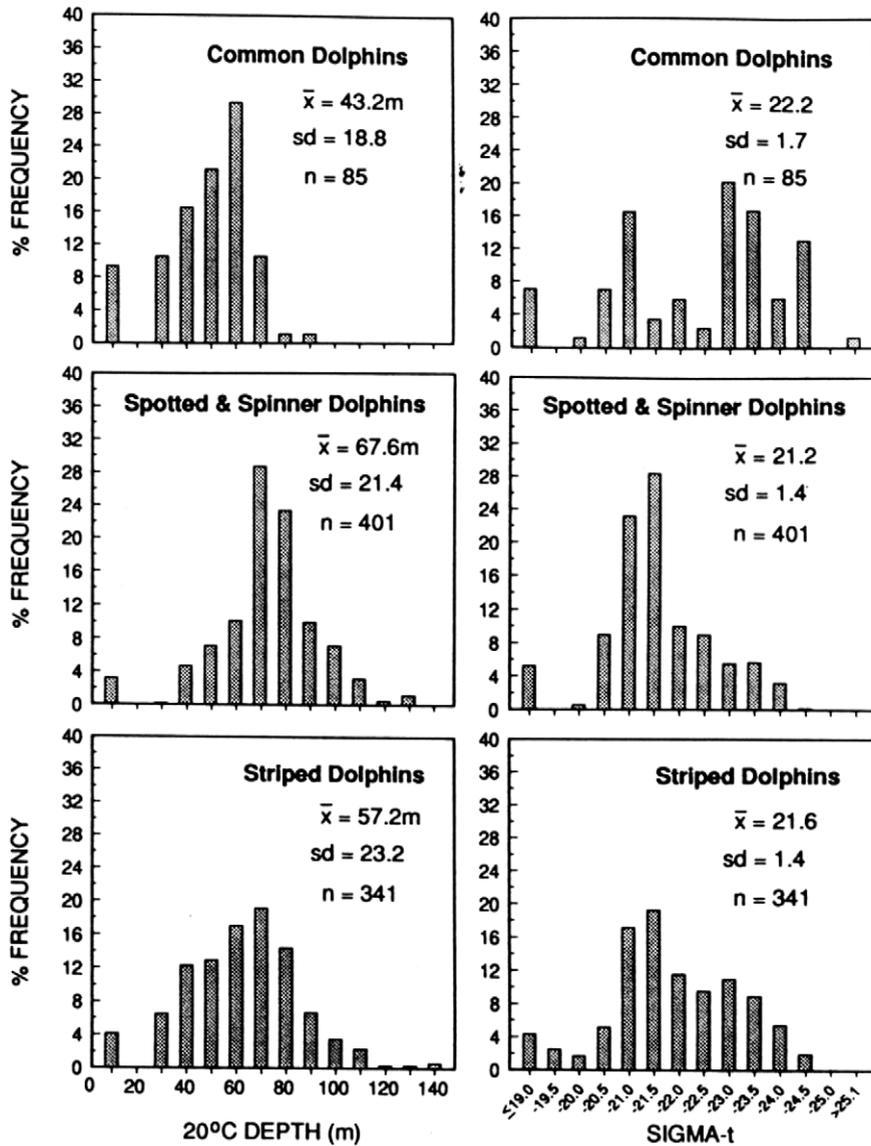


Fig. 7. Frequency histograms, transformed to percentages, of surface water density (sigma-t) and 20 °C isotherm depths (Z20, m) in areas where dolphins were sighted, by dolphin school type. From Reilly (1990).

because it is widely recognized that species distribution patterns are not static over time, presumably because the same is true of oceanographic habitat. By directly relating seabird density to physical and biological variables, changes in species distribution can be understood in terms of species selection of preferred habitat as it moves spatially over time.

Ribic and Ainley (1988/1989) found five species associations in the eastern Pacific that persisted over space and time, two of which were characteristic of tropical waters (warmer than 22 °C): (1) Sooty Tern, Wedge-tailed Shearwater, Tahiti Petrel, (2) Masked Booby, Wedge-rumped Storm Petrel, Leach’s Storm Petrel. The tropical data were collected along only four N–S transect lines spread longitudinally from the Central American coast to 180° W longitude, and the authors did not explicitly document spatial distribution patterns, in species or hydrography, but they did quantify associations between species groups and environmental variables, finding that the main variability in species density was explained by sea surface temperature, sea surface salinity, and distance from land.

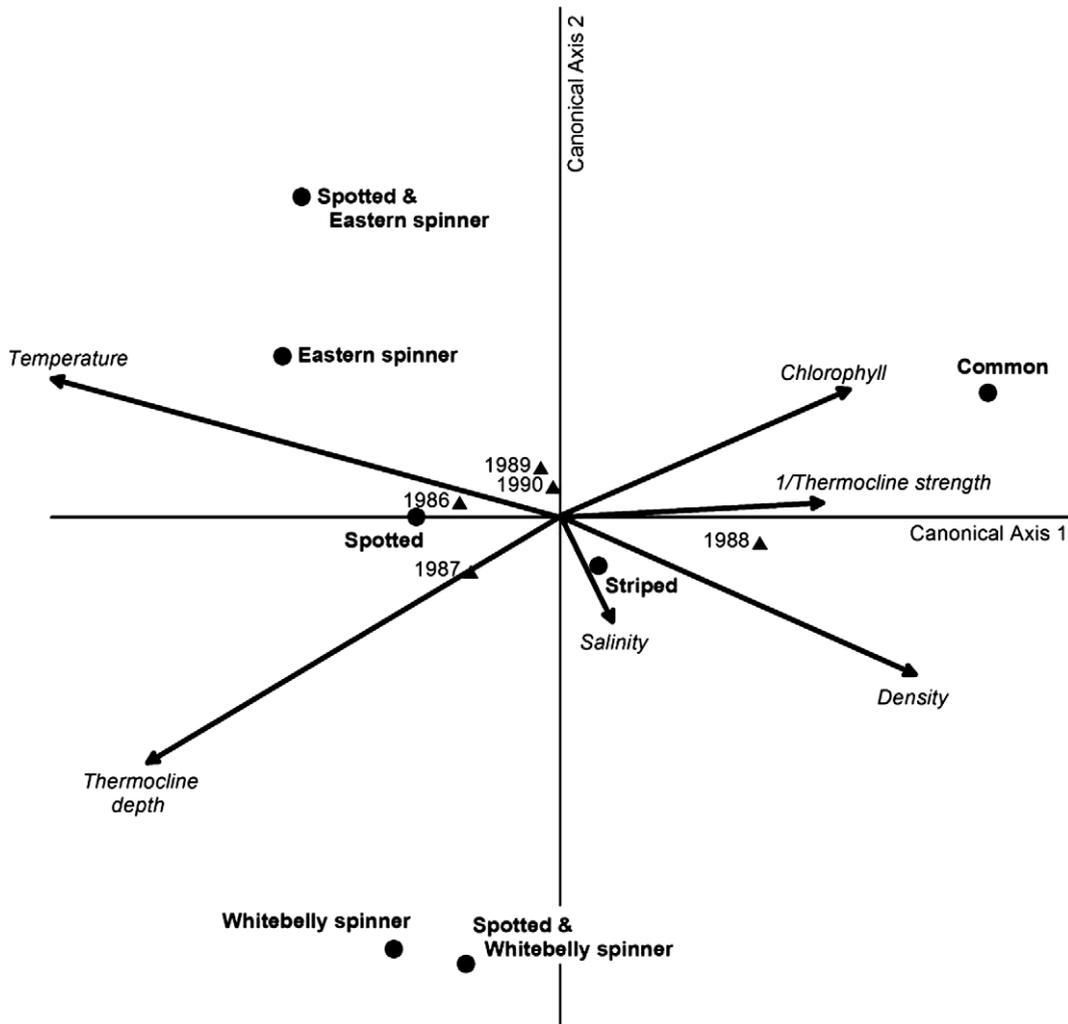


Fig. 8. Ordination results from Canonical Correspondence Analysis of cetacean species/sub-species and environmental conditions in the eastern tropical Pacific (primarily between 20°N and 5°S latitude, from the Central American coast to 125°W longitude). The two Canonical Axes represent those combinations of environmental characteristics that explain the greatest proportion of variance in density of seven dolphin species or school types. The direction and degree of influence of six oceanographic variables on the Canonical Axes are illustrated by the arrows. Points represent the location of seven dolphin species/sub-species or school types in the habitat space identified by the two axes. Clear habitat segregation is apparent between common, spotted and eastern spinner, and spotted and whitebelly spinner dolphins. (Distribution patterns for these species are illustrated in Fig. 3.) Centroids for each of five years are shown and clearly indicate interannual variation in the system. From Reilly and Fiedler (1994).

Spear et al. (1995) documented associations (1) between Townsend's Shearwater and cool surface waters with shallow and weak thermoclines over the continental slope, (2) between Galápagos Petrel and waters having shallow thermoclines, (3) between Hawaiian Petrel and waters of moderate temperature, and (4) between Newell's Shearwater and waters with moderate salinities.

Ribic and Ainley (1997) quantified species–habitat relationships within the region found between 105° and 140°W longitude, and 10°N to 10°S latitude, an area nominally encompassing Tropical, Equatorial, and Subtropical Surface Water. They found Sooty Terns and Wedge-tailed Shearwaters were most likely to be found where thermoclines were relatively deep (median = 60 m) and surface salinity relatively high (median values between 34.99 and 35.13 pss), Juan Fernandez Petrels where thermocline gradients were strong (median of 9.8 °C m⁻¹ [*sic*]), and Wedge-rumped Storm Petrel where thermoclines were relatively shallow

(median = 22 m). Within this region, these authors did not explicitly place species distribution or hydrography into a spatial context.

Spear et al. (2001) reported species–habitat relationships for a 4° latitudinal band encompassing the Equatorial Front (2° on both north and south sides) between 100° and 145° W longitude, and found that planktivores preferred waters with shallow thermoclines, whereas piscivores preferred waters where sea surface temperature was high, salinity low, and the thermocline deeper and strong.

Ballance et al. (2002) analyzed six years of data collected primarily between 20° N and 5° S latitude, from the Central American coast to 125° W longitude, and focused on a suite of nine species (Tahiti, Juan Fernandez, and White-winged petrels, Wedge-tailed Shearwater, Wedge-rumped and Leach's storm petrels, Red-footed Booby, Phalarope species, and Sooty Tern), chosen to represent a broad range of foraging ecology and phylogeny. Distributions clearly show taxon-specific patterns. For any given year, seven oceanographic and two geographic variables (sea surface temperature, salinity, and chlorophyll concentration, sigma-t, thermocline depth and strength, mean concentration of chlorophyll in the euphotic zone, and latitude and longitude) explained between 26% and 39% of the variance in species density of the community as a whole. These variables explained greater than 25% of the variance in density for six of these nine species when considered individually, with clear habitat preferences for four of these. Phalarope species associated with waters characterized by cool surface water, high in chlorophyll, with shallow and weak thermoclines, in the eastern region of the study area, whereas Juan Fernandez Petrel and Wedge-tailed Shearwater avoided this habitat. Wedge-rumped Storm Petrel associated with waters characterized by cool, high-density surface water, with shallow and weak thermoclines in southern latitudes in the eastern region of the study area.

Though quantified and, in some cases, statistically significant, these relationships present a complex picture of species-specific associations with physical and biological characteristics of water masses that is not always consistent across studies. We suspect there are multiple reasons for this, including improper choice of scale (for data collection and analysis), failure to tease out seasonal signals due to constraints related to breeding biology, and incorporation of habitat variables that presumably serve as proxies, rather than those that more directly measure prey distribution, abundance, and availability. We discuss this in more detail below.

4.3. Summary – associations with surface currents and water masses

It is difficult to identify the causal mechanisms for most of these associations, and most authors do not specifically address this issue. It is generally presumed that the easily-measured variables used in these analyses, such as depth or sea surface temperature, are proxies that are indirectly related to prey abundance or availability. Productivity is certainly a key factor. In a mega-scale study of Pacific seabirds, including Antarctic, subantarctic, subtropical, and tropical waters, Ainley and Boekelheide (1983) documented strong evidence for the widely accepted hypothesis that productivity affects seabird species composition, species number, morphology, and behavior. Ballance et al. (1997) confirmed this on a macro-scale for seabirds of the eastern tropical Pacific. But on a smaller scale, the relationships between physical variables used in most habitat studies and productivity, prey abundance, and prey availability are rarely investigated, though their significance is widely acknowledged. This is less the case for studies of higher latitude systems, where biological variables are more often directly measured along with physical oceanographic variables, and both are incorporated into species–habitat investigations. This approach can result in a clear picture of the mechanisms determining abundance and distribution. Particularly at coarse scales, we do understand how physics affects prey and consequently apex predators (e.g. Hunt and Harrison, 1990; Coyle et al., 1992). In addition to physical variables, future work in the eastern tropical Pacific should focus on incorporation of biological variables into species–habitat investigations.

5. Effects of temporal variation: seasonal, interannual, and the El Niño-Southern oscillation

Oceanic systems are not static in space or time. Fiedler and Reilly (1994) illustrated this nicely using habitat preferences identified by Reilly and Fiedler (1994) to map habitat quality for five dolphin species/sub-species. Using climatological fields of surface temperature, thermocline depth, and thermocline thickness over a

15-year period, from 1975 to 1990 (Fig. 9), they calculated variability on a number of time scales. Seasonal variability in habitat quality was generally higher than interannual variability (see below), and was greatest for species/sub-species with the most restricted ranges (Fig. 10). The strongest interannual variability could be attributed to the ENSO cycle in general and to two El Niño events in particular, 1982–83, and 1986–87 (Fig. 11). That exercise indicates that changes in the distribution of preferred habitat might explain changes in distribution, and perhaps in other parameters, for marine organisms at a variety of temporal scales. In many cases, this is exactly what we see – that seabirds and cetaceans track their preferred habitat (that is, distribution and abundance corresponds to distribution of their preferred habitat) as it moves spatially on seasonal, interannual, and longer-time scales.

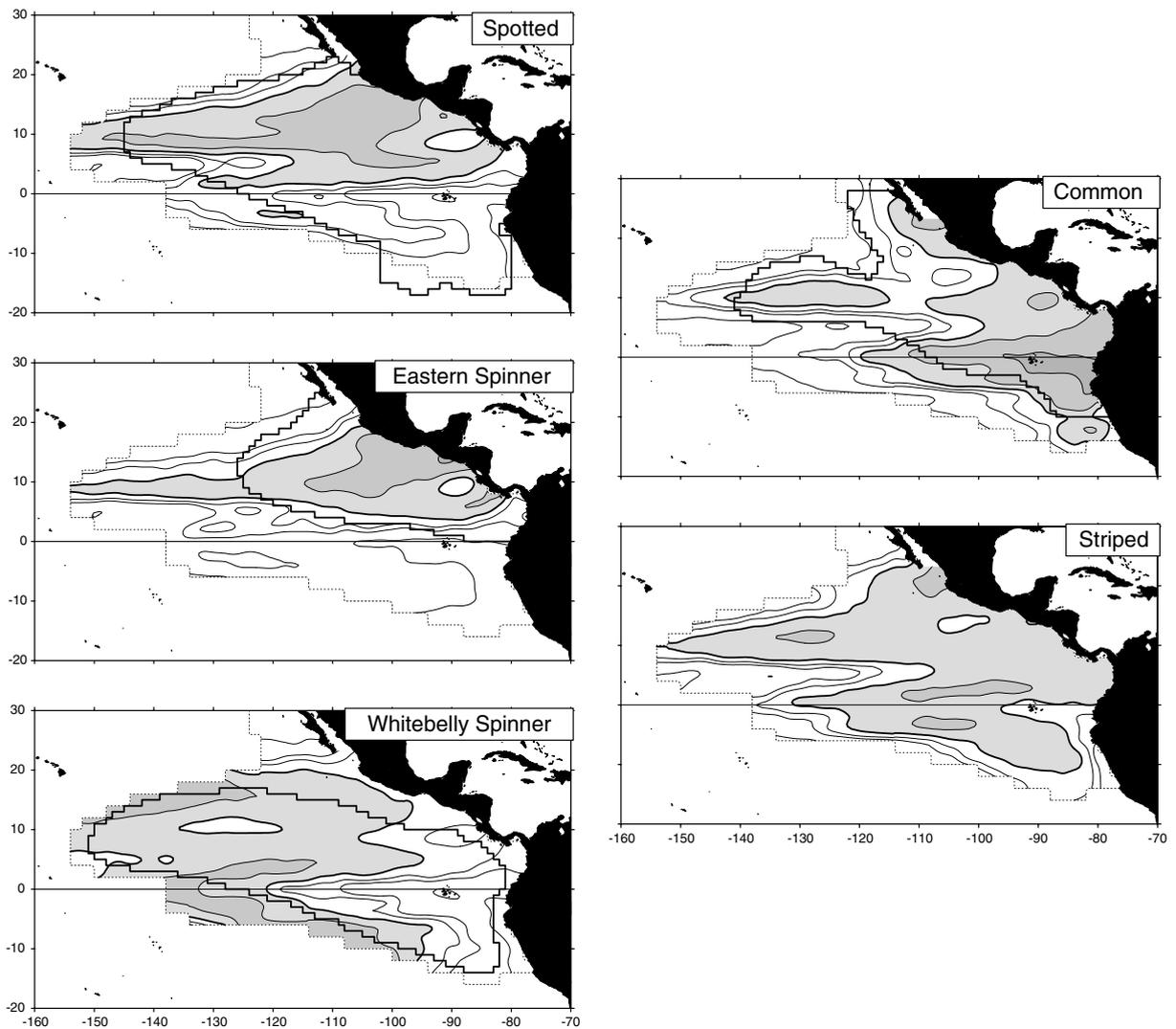


Fig. 9. Spatial variation in mean habitat quality (relative expected abundance based on local environmental conditions using habitat preferences identified by Reilly and Fiedler, 1994) for spotted, eastern spinner, whitebelly spinner, common, and striped dolphins, as calculated from a 15-year dataset of climatological fields of surface temperature, thermocline depth, and thermocline thickness. Shaded contours indicate favorable habitat (quality > 1). Thick lines are nominal species/sub-species boundaries. From Fiedler and Reilly (1994).

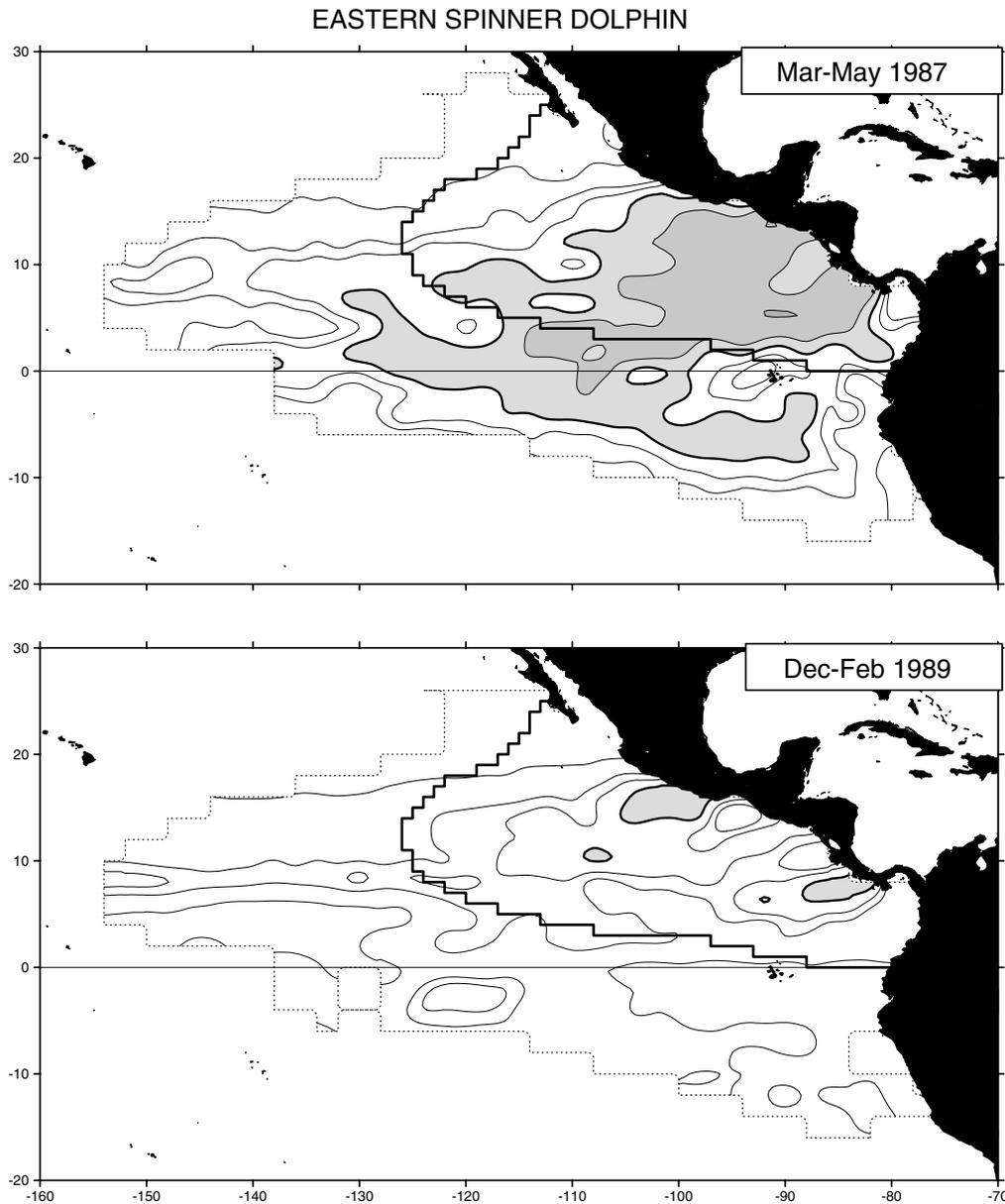


Fig. 10. Spatial variation in mean habitat quality (as in Fig. 9) for eastern spinner dolphin during two extreme periods: March–May 1983 (strong El Niño) and September–November 1985 (moderate La Niña). The figure illustrates how the distribution and abundance of high-quality habitat can change over time. From Fiedler and Reilly (1994).

5.1. Seasonal Patterns

Much of the biology of seabirds and cetaceans cycles seasonally (e.g. migration, dispersal, or, in the case of seabirds, the annual replacement of feathers), cycling that is often related to reproduction. Many seasonal patterns in abundance, distribution, and behavior in the eastern tropical Pacific reflect this biology. For example, the Juan Fernandez Petrel is abundant along the countercurrent thermocline ridge at 10°N during the boreal summer and fall, but by November their abundance decreases and remains low through the boreal spring, when it begins to increase again (Smith and Hyrenbach, 2003; Pitman and Ballance, unpublished data). This seasonal pattern occurs because the Juan Fernandez Petrel breeds on islands off the coast of central Chile

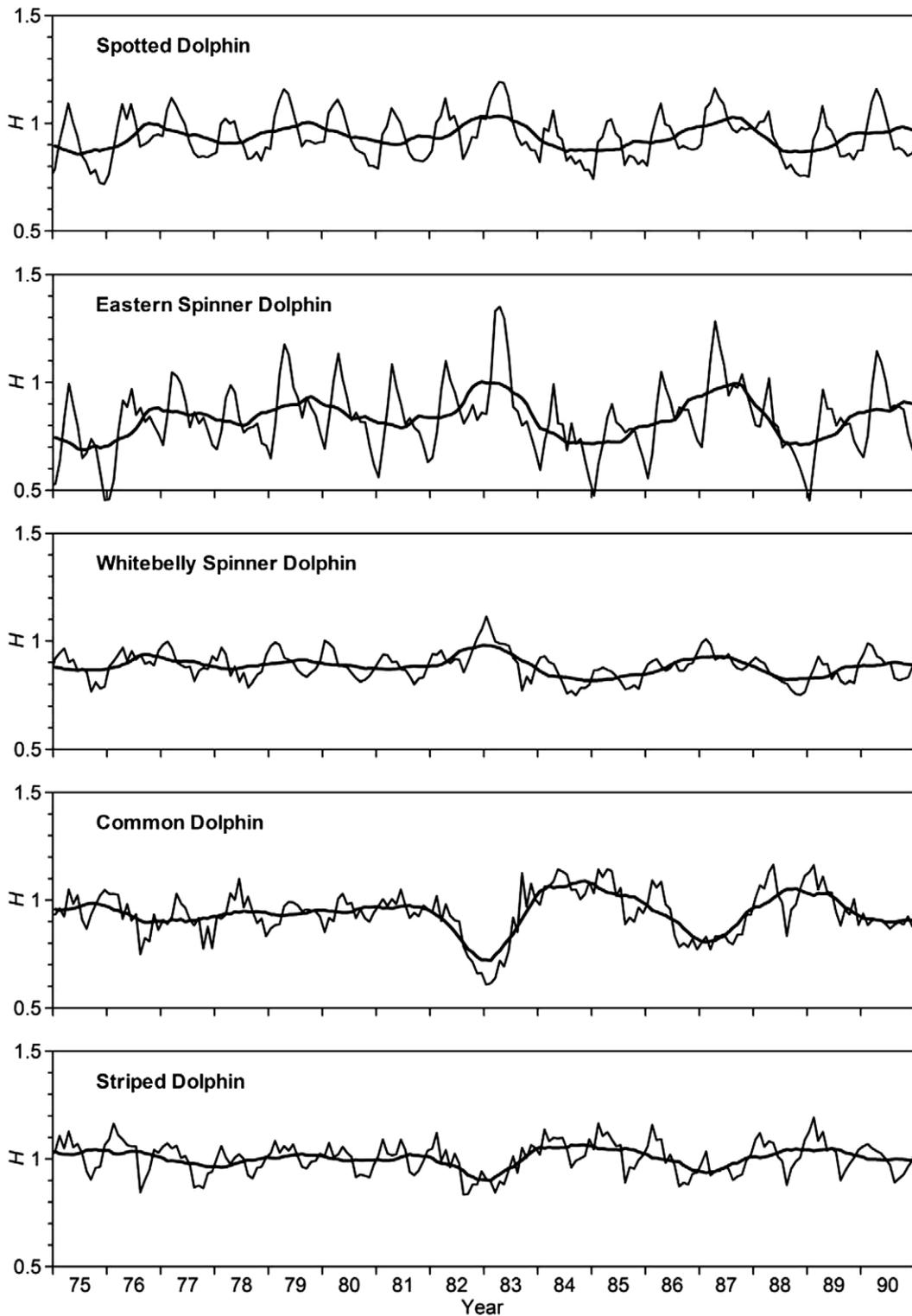


Fig. 11. Seasonal (3-month, thin line) and interannual (15-month running mean; thick line) variation in mean habitat quality, “H” on the ordinate (as in Figs. 10 and 11), for spotted, eastern spinner, whitebelly spinner, common, and striped dolphins. From Fiedler and Reilly (1994).

during the months of December to April and, therefore, moves out of the eastern tropical Pacific at that time. Sighting rates of seabirds feeding in flocks show a distinct seasonal pattern (Waldron, 1964), also likely related to reproductive constraints on distribution. Spear et al. (1995) offer additional examples of seasonal patterns in habitat relationships for seabirds that can be explained by breeding biology. Baleen whales migrate between the tropics and temperate latitudes to take advantage of seasonal prey increases in temperate and polar waters during the summer. The seasonal changes in distribution and abundance of blue whales along the coast of Baja California or around the Galápagos Islands, for example (Reilly and Thayer, 1990; Palacios, 1999), reflect these migration patterns.

It is likely that these seasonal patterns in biology have evolved to take advantage of oceanographic conditions, both in the eastern tropical Pacific and in the areas to which these animals migrate. Oceanographic conditions in one area only may provide the strongest selective force in producing these biological patterns. For example, the migration of blue whales out of the eastern tropical Pacific during the summer may reflect a seasonal increase in productivity of temperate waters more than a change in oceanographic conditions in tropical regions. So, a seasonal pattern shown by seabirds and cetaceans in the eastern tropical Pacific may not necessarily reflect oceanographic conditions there.

With this in mind, and as noted above, we expect that animals will track their preferred habitat over time. There are numerous examples of seasonal changes in distribution that reflect oceanographic changes and indicate that this is the case. For example, density of spotted and spinner dolphins along the countercurrent thermocline ridge increases during summer months, and is correlated with an intensification of thermocline ridging during that season (Au and Perryman, 1985; Reilly, 1990). The seasonal redistribution of spotted and spinner dolphins along the warm edge of the Peru Current and Equatorial Front is correlated with seasonal evolution of the equatorial cold tongue, with dolphins avoiding cool equatorial waters in all seasons (Au and Perryman, 1985; Reilly, 1990). Species-specific differences in habitat preferences for spotted and spinner versus common and striped dolphins persist year-round, despite seasonal variability in oceanographic conditions, and the seasonal changes in these distributions indicate that these species track their preferred habitat as it shifts spatially with time (Reilly, 1990).

The situation can be similar for seabirds. For example, Spear et al. (2001) found that seasonal differences in the Equatorial Front were correlated with shifts in distribution and density of seabirds. Specifically, the increased intensity of the front during northern autumn was accompanied by significant increases in density of the planktivorous species that typically associate with this feature.

It is interesting, however, that, for seabirds at least, many studies indicate inconsistent habitat associations on a seasonal time scale. For example, in the northern autumn, *Pterodroma* petrels dominated seabird assemblages (on the basis of biomass) in both Equatorial and Subtropical Surface Waters, and shared dominance (on the basis of abundance) with storm petrels in both water masses. However, in the northern spring, though storm petrels and shearwaters were still important in both water masses, *Pterodroma* petrels were dominant only in Equatorial Surface Water (Ribic et al., 1992). In the northern spring, Black-winged Petrel was seen most often in the South Equatorial Current, whereas in the northern fall it was seen most often on the other side of the Equatorial Front in the North Equatorial Countercurrent (Ribic et al., 1997a). In the northern spring, Leach's Storm Petrel and Wedge-tailed Shearwater were not consistently associated with a particular current system, whereas in the northern autumn, Leach's Storm Petrel was seen more often in the South Equatorial Current and Wedge-tailed Shearwater in the North Equatorial Countercurrent (Ribic et al., 1997a). Spear et al. (2001) documented increased densities of piscivorous seabirds in the eastern tropical Pacific as a whole during the northern spring, as compared with the northern fall. These seasonal inconsistencies may reflect seasonal changes in oceanographic features, for example, the equatorial cold tongue and Equatorial Front are both very strongly developed in August through October and are weak in February through April (Fiedler and Talley, 2006). Just as likely, seasonal variations result from distributional changes in seabird abundance associated with reproductive seasonality. Until breeding activity is teased out of these types of analyses, the picture of seasonal variation in habitat relationships for seabirds will remain complex.

Finally, it is interesting that seasonal patterns are apparently absent for some species. Reilly (1990) looked for seasonal differences in distribution of common dolphins but found none. He attributed this to the fact that these dolphins occupy upwelling-modified habitat (Au and Perryman, 1985), presumably with low seasonal

variation in this region. Reilly and Thayer (1990) found blue whales to be present in Costa Rica Dome waters year-round and noted that if these whales were residents, they could be feeding on zooplankton, also found in high abundance relative to surrounding waters year-round. Reilly and Thayer speculated that this pattern might ultimately be the result of sufficiently low temperature and high nitrate and chlorophyll of surface waters through all seasons.

5.2. Interannual patterns

Oceanographically, interannual variation in the eastern tropical Pacific tends to be dominated by ENSO cycles of 2–7 years (Wang and Fiedler, 2006); the effects on seabirds and cetaceans are reviewed below. In this section, we discuss interannual patterns in seabird and cetacean distribution and abundance that have not been specifically linked with ENSO effects.

Reilly and Fiedler (1994) found that adding “year” as a variable to a Canonical Correspondence Analysis of seven dolphin school types and six oceanographic variables observed over a five-year period, primarily between 20° N and 5° S latitude from the Central American coast to 125° W longitude, explained only an additional 0.3% of the variance in dolphin density. However, there was clear interannual variability in distribution of dolphin sightings, distribution of habitat types as identified by the analysis and in the location of the centroids representing each year when plotted on a biplot of all years together (Fig. 8). They concluded that the small but measurable interannual variation in the species data was effectively accounted for by interannual variation in the environmental explanatory variables. Their conclusions were supported by a follow-up analysis using similar methods and an additional three years of data (Reilly et al., 2002).

Based on the habitat preferences identified by Reilly and Fiedler (1994), Fiedler and Reilly (1994) documented interannual variability in habitat quality throughout the same region for the seven species of dolphins included in the analysis. This variability, essentially in environmental factors, was correlated with variability in estimated abundance, and these authors speculated that the correlations resulted from a sampling effect rather than a population effect. In other words, as the geographic distribution of preferred habitat shifted interannually, dolphins tracked this habitat, and in some years moved out of the area nominally defined as their range.

Similar conclusions were reached by Ballance et al. (2002) for seabirds using data collected primarily between 20° N and 5° S latitude, from the Central American coast to 125° W longitude, and focused on a suite of nine species (Tahiti, Juan Fernandez, and White-winged petrels, Wedge-tailed Shearwater, Wedge-rumped and Leach’s storm petrels, Red-footed Booby, Phalarope species, and Sooty Tern). These authors found that habitat association patterns (detailed above in section 4.2) remained broadly consistent across a 12-year time period (1988–2000). Adding “year” as a variable to their Canonical Correspondence Analysis explained less than 2% of the variance in species density, while adding “decade” (to represent data collected in the 1980s compared with those collected in the 1990s) explained a few tenths of a percent only. The strength of habitat associations for any particular species varied with year, but the specific combinations of physical, biological, and geographic variables that defined species-specific habitat associations remained consistent over time. Ballance et al. (2002) concluded that the observed interannual variation in species distribution patterns (e.g., Fig. 12) could be largely explained by species tracking their preferred habitat over time.

5.3. The El Niño-Southern Oscillation

El Niño effects on seabirds and cetaceans in the California and Peru Current systems are well known. The most common responses are distributional shifts, changes in diet, partial or complete reproductive failures, and, in the most extreme cases, adult mortality (e.g. Schreiber and Duffy, 1986; Anderson, 1989; Ainley and Boekelheide, 1990; Oedekoven et al., 2001; Fiedler, 2002b; Schreiber, 2002; and references therein). Much less is known regarding effects of El Niño events and ENSO cycles on seabirds and cetaceans in the oceanic eastern tropical Pacific. It is clear, however, that ENSO affects oceanographic patterns and processes, and there is evidence that these cycles affect distribution and abundance of some species.

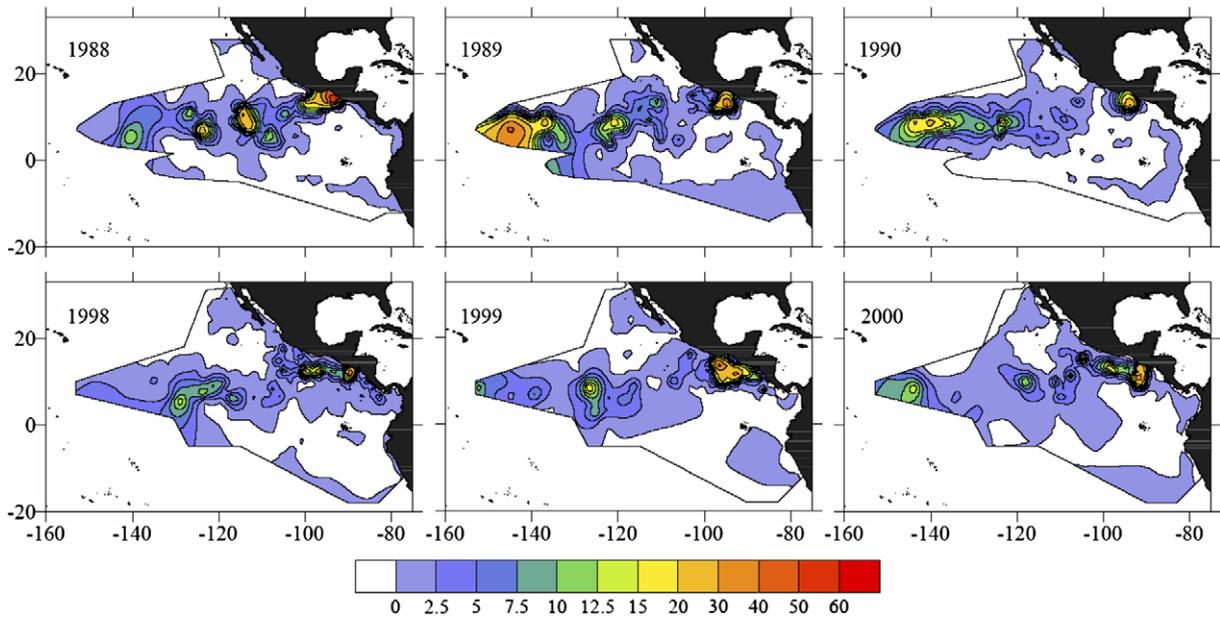


Fig. 12. Distribution of Tahiti Petrel. Color contours represent birds sighted/100 km²/day. From Ballance et al. (2002).

For example, Reilly and Fiedler (1994) found that interannual variation in distribution of dolphin habitat types, as identified by Canonical Correspondence Analysis, reflected ENSO cycles. Specifically, in 1986, cool upwelling habitat was found along the equator to 130°W, north of the equator to about 10°N along the coast of Central America, and off the coast of Baja California. In 1987, cool upwelling habitat south of Baja California did not extend west of 110°W or north of 4°N, except in the Gulf of Panama. This change was caused by a moderate El Niño event that began in late 1986 and lasted through 1987. In 1988, cool upwelling habitat extended far north of the equator and south of Baja California, considerably reducing the area covered by warm tropical water. This could be traced to the strong La Niña that occurred that year. The distribution of common dolphins changed interannually, more so than that of other dolphins, and Reilly & Fiedler concluded this was due to ENSO variability and its effects on distribution of their preferred habitat: cool, upwelling-modified waters (Au and Perryman, 1985; Reilly, 1990; Reilly and Fiedler, 1994). In summary, common dolphin distribution appeared to mirror the distribution of their preferred habitat, ultimately influenced by ENSO variability.

A greater number of studies have investigated the effects of ENSO cycles on seabirds than on cetaceans, and at a number of spatial scales. Species-environment relationships appear to be largely unaffected by ENSO at both the coarse scale (Ribic et al., 1997b), and at the meso-scale. For example, Spear et al. (2001) found the intensity of the Equatorial Front varied with the phase of ENSO, being most intense in La Niña years. Accordingly, the planktivorous species that associate with this front were found there at higher densities during La Niña years compared to El Niño years. Because planktivore abundance in the North Equatorial Countercurrent and the South Equatorial Current declined during La Niña years, the authors speculated that the increased density at the front was due to displacement of birds from these two current systems. These studies support the general idea that seabirds follow their preferred habitat through time, including shifts in habitat distribution and intensity due to ENSO cycles.

In contrast, at the macro-scale, habitat relationships appear to change with phase of ENSO cycles for some species, though not for others (Ribic et al., 1997b). Wedge-rumped and Leach's storm petrels and Juan Fernandez Petrels exhibited habitat relationships that were different during ENSO versus non-ENSO years (Ribic et al., 1997b), as was the case for Black- and White-winged Petrels (Ribic and Ainley, 1997). However, habitat relationships for Sooty Terns, Black-winged, and White-winged petrels remained the same; these species are associated with the South Equatorial Current across all years and regardless of ENSO cycle (Ribic et al., 1997b). These authors speculated that ENSO events would act to decrease productivity in general and would,

therefore, affect seabirds adapted to higher productivity habitats more than those species adapted to low productivity habitats. They reasoned that during El Niño or La Niña events, species adapted to higher productivity habitats would move in search of their preferred habitat, and this re-distribution would lead to changes in habitat relationships at the macro-scale.

Seabird assemblage characteristics also appear to be affected by ENSO cycles, perhaps because species respond to El Niño and La Niña in different ways. Ribic et al. (1992) analyzed data collected between 10°N and 10°S latitude, and from 90° to 140°W longitude and found that both El Niño and La Niña were correlated with a decrease in assemblage richness throughout the area and with the disappearance of genera and species from these assemblages, particularly those of medium abundance: terns, boobies, and jaegers. Common taxa, the storm petrels, *Pterodroma* petrels, and shearwaters, were less affected. El Niño effects were most pronounced in Subtropical Surface Water during the autumn, and the authors speculated that this was due to the impact of El Niño on equatorial upwelling, noting that the equatorial thermocline deepening associated with El Niño was significant only during the autumn. The effects of La Niña were most pronounced in the spring, in both Equatorial and Subtropical Surface Water. The authors noted that the largest differences in mean sea surface temperature occurred during the spring, but did not speculate as to the mechanism for the assemblage effects. At the mega-scale, species associations appear to persist during El Niño and non-El Niño years (Ribic and Ainley, 1988/1989).

Finally, at the mega-scale, Spear et al. (2001) noted an increase in abundance of planktivores in the eastern tropical Pacific as a whole during El Niño years and speculated that this was due to increased dispersal of these species away from temperate regions and into the tropics. Perhaps this was a result of a general decrease in productivity in temperate waters, leading them to search for more favorable foraging areas. Or perhaps they were skipping a year of breeding or suffered breeding failures. This study also documented effects of ENSO cycles on distribution and abundance of piscivorous seabirds, with densities being higher during La Niña years and lower during El Niño years in the eastern part of the region; the opposite pattern was documented for the western part of the region.

To summarize, little work has been conducted to investigate ENSO effects on cetaceans in the eastern tropical Pacific, and results of the few investigations focusing on ENSO effects on seabirds are complex and not easy to interpret. We suspect this is because a number of factors interact to produce these effects, and the magnitude of factor-specific effects and the precise nature of their interactions remain unknown. These factors include not only seasonal and ENSO effects on oceanography, but also seasonal patterns in breeding biology. Many seabirds inhabit the eastern tropical Pacific for part of the year only, coming from regions well outside including the California and Peru currents, where ENSO effects on seabirds may be intensified. Much has been made of the detrimental effects of ENSO cycles, and particularly El Niño events, on tropical seabirds. A seminal paper by Schreiber and Schreiber (1984) documenting complete reproductive failure and disappearance of the entire seabird community of Christmas Island in the equatorial central Pacific following the 1982–83 El Niño likely set the stage for this. In addition, most early seabird studies (1900–1965) were conducted during El Niño events, undoubtedly influencing marine ornithologists' interpretations, though unknowingly prior to 1982 (Schreiber, 2002). However, even strong El Niño events may not always be bad for tropical seabirds. The Masked Booby population on Clipperton Island has increased by three orders of magnitude during the last 45 years, a period that included two “El Niño events of the century” (Pitman, unpublished data). Certainly, much more research is needed to understand the effects of ENSO cycles on cetaceans and seabirds.

6. Summary and conclusions

Species distributions are among the most basic patterns that biologists attempt to understand. Oceanography has helped marine ecologists to interpret these distributions for seabirds and cetaceans; species-specific distributions may be seen in the context of species-specific habitat relationships. In the eastern tropical Pacific, these relationships are identified through species associations with physical features, water masses, and surface currents. For some species, these associations appear to persist over time; species follow preferred habitats as they move in space and time, and even through perturbations such as ENSO cycles.

Nevertheless, species–habitat relationships are far from simple, and our understanding of the associations is far from complete. Few have attempted to tease out the confounding effects of seasonal patterns in biology

(e.g., migration for reproduction) from those due to oceanographic influences (i.e., tracking of preferred habitat as it moves through space and time). In many cases, the relationships are not with a specific physical feature, water mass, or surface current, but with combinations of physical variables along complex gradients. The confounding factor that spatial and temporal patterns due to oceanographic influences might be masked by population abundance changing to a greater extent interannually due to anthropogenic depletion or recovery is rarely addressed. Perhaps most significantly, the mechanisms underlying species–habitat associations are not well understood. This is likely due, at least in part, to the fact that seabirds and cetaceans may not be responding directly to the physical variables used in studies of species–habitat relationships, but to prey that respond to physical features and processes. Hypotheses proposed to explain habitat associations tend to focus on the significance of prey abundance and availability, though incorporation of direct measures of prey into habitat investigations are entirely lacking for eastern tropical Pacific studies to date. Incorporation of these variables into species–habitat investigations has proved fruitful in other systems and should be a promising avenue for future research in the eastern tropical Pacific.

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Appendix A

Cetacean species recorded in the oceanic (off the continental shelf) eastern tropical Pacific. Symbols represent resident status (R = resident; SR = seasonal resident; M = migrant; as in Reeves et al., 2002) and endemic status (E = endemic). From Holt and Sexton (1989); Sexton et al. (1989); Hill et al. (1990a,b); Hill et al. (1991a); Hill et al. (1991b); Kinzey et al. (1999); Kinzey et al. (2000); Kinzey et al. (2001).

Common name	Latin name	
Humpback Whale	<i>Megaptera novaeangliae</i>	SR
Minke Whale	<i>Balaenoptera acutorostrata</i>	SR?
Bryde's Whale	<i>Balaenoptera edeni</i>	R
Sei Whale	<i>Balaenoptera borealis</i>	SR?
Fin Whale	<i>Balaenoptera physalus</i>	R?
Blue Whale	<i>Balaenoptera musculus</i>	SR?
Sperm Whale	<i>Physeter macrocephalus</i>	R
Pygmy Sperm Whale	<i>Kogia breviceps</i>	R
Dwarf Sperm Whale	<i>Kogia sima</i>	R
Cuvier's Beaked Whale	<i>Ziphius cavirostris</i>	R
Baird's Beaked Whale	<i>Berardius bairdii</i>	SR?
Longman's Beaked Whale	<i>Indopacetus pacificus</i>	R?
Pygmy Beaked Whale	<i>Mesoplodon peruvianus</i>	R E
Blainville's Beaked Whale	<i>Mesoplodon densirostris</i>	R
Rough-toothed Dolphin	<i>Steno bredanensis</i>	R
Bottlenose Dolphin	<i>Tursiops truncatus</i>	R
Pantropical Spotted Dolphin	<i>Stenella attenuata</i>	R
Offshore Spotted Dolphin	<i>Stenella attenuata</i>	R
Coastal Spotted Dolphin	<i>Stenella attenuata graffmani</i>	R E
Spinner Dolphin	<i>Stenella longirostris</i>	R
Eastern Spinner Dolphin	<i>Stenella longirostris orientalis</i>	R E

(continued on next page)

Appendix A (continued)

Common name	Latin name	
Central American Spinner Dolphin	<i>Stenella longirostris centroamericana</i>	R E
Whitebelly Spinner Dolphin	<i>Stenella longirostris orientalis/longirostris</i>	R
Gray's Spinner Dolphin	<i>Stenella longirostris longirostris</i>	R
Striped Dolphin	<i>Stenella coeruleoalba</i>	R
Fraser's Dolphin	<i>Lagenodelphis hosei</i>	R
Short-beaked Common Dolphin	<i>Delphinus delphis</i>	R
Long-beaked Common Dolphin	<i>Delphinus capensis</i>	R
Pacific White-sided Dolphin	<i>Lagenorhynchus obliquidens</i>	R
Dusky Dolphin	<i>Lagenorhynchus obscurus</i>	R
Risso's Dolphin	<i>Grampus griseus</i>	R
Melon-headed Whale	<i>Peponocephala electra</i>	R
Pygmy Killer Whale	<i>Feresa attenuata</i>	R
False Killer Whale	<i>Pseudorca crassidens</i>	R
Killer Whale	<i>Orcinus orca</i>	R
Short-finned Pilot Whale	<i>Globicephala macrorhynchus</i>	R

Appendix B

Seabird species recorded in the oceanic (off the continental shelf) eastern tropical Pacific. Symbols represent resident status (R = resident; SR = seasonal resident; M = migrant) and endemic status (E = endemic). Only those species for which at least 100 individuals were recorded in at least 1 year are listed. Data from Harrison (1985); Pitman (1986); Pitman and Jehl (1998); Olson et al. (2000); Olson et al. (2001a,b). *Waved albatross feeds in Peru-Chile Current.

Common name	Latin name	
Waved Albatross	<i>Phoebastria irrorata</i>	R* E
Tahiti Petrel	<i>Pseudobulweria rostrata</i>	SR
Cook's Petrel	<i>Pterodroma cooki</i>	M
Stejneger's Petrel	<i>Pterodroma longirostris</i>	M
Phoenix Petrel	<i>Pterodroma alba</i>	SR
Pycroft's Petrel	<i>Pterodroma pycrofti</i>	SR?
White-winged Petrel	<i>Pterodroma leucoptera</i>	SR
Black-winged Petrel	<i>Pterodroma nigripennis</i>	SR
Juan Fernandez Petrel	<i>Pterodroma externa</i>	SR
Herald Petrel	<i>Pterodroma heraldica</i>	SR
Hawaiian Petrel	<i>Pterodroma sandwichensis</i>	R E
Galapagos Petrel	<i>Pterodroma phaeophygia</i>	R E
Kermadec Petrel	<i>Pterodroma neglecta</i>	SR
Murphy's Petrel	<i>Pterodroma ultima</i>	M
Defilippe's Petrel	<i>Pterodroma defilippiana</i>	SR
Bulwer's Petrel	<i>Bulweria bulweri</i>	SR
Parkinson's Petrel	<i>Procellaria parkinsoni</i>	SR
Wedge-tailed Shearwater	<i>Puffinus pacificus</i>	SR/R
Pink-footed Shearwater	<i>Puffinus creatopus</i>	SR/M
Sooty Shearwater	<i>Puffinus griseus</i>	M
Christmas Shearwater	<i>Puffinus nativitatis</i>	SR

Appendix B (continued)

Common name	Latin name	
Townsend's Shearwater	<i>Puffinus auricularis</i>	R E
Newell's Shearwater	<i>Puffinus newelli</i>	SR
Audubon's Shearwater	<i>Puffinus lherminieri</i>	R
White-vented Storm Petrel	<i>Oceanites gracilis</i>	R
Least Storm Petrel	<i>Oceanodroma microsoma</i>	SR
Wedge-rumped Storm Petrel	<i>Oceanodroma tethys</i>	R E
Band-rumped Storm Petrel	<i>Oceanodroma castro</i>	R
Leach's Storm Petrel	<i>Oceanodroma leucorhoa</i>	SR
Markham's Storm Petrel	<i>Oceanodroma markhami</i>	R
Black Storm Petrel	<i>Oceanodroma melania</i>	SR
Red-billed Tropicbird	<i>Phaethon aethereus</i>	R
Red-tailed Tropicbird	<i>Phaethon rubricauda</i>	SR
White-tailed Tropicbird	<i>Phaethon lepturus</i>	SR
Masked Booby	<i>Sula dactylatra</i>	R
Nazca Booby	<i>Sula granti</i>	R E
Red-footed Booby	<i>Sula sula</i>	R
Brown Booby	<i>Sula neboxii</i>	R
Magnificent Frigatebird	<i>Fregata magnificens</i>	R
Great Frigatebird	<i>Fregata minor</i>	R
Red Phalarope	<i>Phalaropus fulicarius</i>	SR
Northern Phalarope	<i>Phalaropus lobatus</i>	SR
South Polar Skua	<i>Catharacta maccormicki</i>	SR/M
Pomarine Jaeger	<i>Stercorarius pomarinus</i>	SR
Parasitic Jaeger	<i>Stercorarius parasiticus</i>	SR
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	SR
Swallow-tailed Gull	<i>Creagrus furcatus</i>	R E
Common Tern	<i>Sterna hirundo</i>	M/SR
Arctic Tern	<i>Sterna paradisaea</i>	M/SR
Sooty Tern	<i>Sterna fuscata</i>	R/SR
Black Tern	<i>Chlidonias niger</i>	SR
White Tern	<i>Gygis alba</i>	R/SR
Brown Noddy	<i>Anous stolidus</i>	R
Black Noddy	<i>Anous minutus</i>	R

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