GALÁPAGOS ISLANDS TO BRITISH COLUMBIA: SEABIRD COMMUNITIES ALONG A 9000 KM TRANSECT FROM THE TROPICAL TO THE SUBARCTIC EASTERN PACIFIC OCEAN

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SUMMARY

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Studies of seabird biogeography show that species distributions are related to wind conditions, the extent of water masses and ocean productivity patterns over scales of 1000s km. We document changes in the composition of marine bird communities in relation to remotely-sensed water mass properties and wind conditions along a 9,000 km transect across the northeastern Pacific Ocean during a 47 day (20 April – 5 June 1999) cruise from the Galápagos Islands, Ecuador (0º 43.4' S; 90º 32.7' W) to British Columbia, Canada (48º 49.5' N; 125º 8.22' W). We characterized three different marine bird communities along the transect: tropical (booby - tropicbird - frigatebird), subarctic (alcid - fulmar) and a widely-distributed cosmopolitan assemblage dominated by tubenoses (Procellariiformes) (albatrosses, shearwaters, and storm-petrels). These communities inhabit different oceanic regions characterized by distinct water mass properties (e.g., sea surface temperature, chlorophyll concentration). The shift from the tropical to the subarctic community occurred rather abruptly at approximately 20º N. In addition to the latitudinal gradient in community composition, we noted a change in the relative importance of different feeding guilds at higher latitudes, namely an increase in the relative abundance of diving seabirds and a concurrent decrease in plunge-divers. These results support previous evidence of spatial segregation of marine bird species and feeding guilds across the North Pacific Ocean. Our study also provided an opportunity to survey pelagic seabird distributions within a poorly studied region during an anomalous year. In 1999, wind patterns along the entire cruise deviated from the long-term average, with a virtual collapse of the trade winds typically found below 15° N. Moreover, cold-water conditions, associated with a strong La Niña event were apparent throughout the survey track. This paper highlights the continued importance of ocean exploration and standardized time series for the study of seabird biogeography. We encourage other investigators to retrace this survey track in the future.

Keywords: biogeography, community structure, seabird assemblages, fronts, water masses, Galápagos, North Pacific Ocean

RESUMEN

Previos estudios biogeográficos han revelado que las distributiones de las aves marinas estan relacionadas con los patrones de viento, la distribución de masas de agua y la productividad a grandes escalas espaciales (1000s km). En este artículo, relacionamos la composición de las comunidades de aves marinas con las propiedades de las masas de agua, a lo largo de un transecto de 9,000 km a través del Pacifico oriental, desde las Islas Galápagos, Ecuador (0º 43.4' S; 90º 32.7' W) a la Columbia Británica, Canada (48º 49.5' N; 125º 8.22' W).

Hemos documentado tres tipos diferentes de comunidades a lo largo de este transecto: una tropical (pajaro bobo - rabijunco - fregata), una subárctica (alcidos - fulmares) y otra compuesta de especies cosmopolitas dominada por los petreles (albatroses, paiños y pardelas). Estas comunidades habitan regions distintas del Oceano Pacífico, characterizadas por propiedades diferentes (e.g., temperatura en superficie, concentración de clorofila). En particular, recalcamos un cambio drástico de especies a una latitud de 20º N, con una abrupta transición de la comunidad tropical a la subárctica. Además, documentamos un cambio en la incidencia de distintos gremios de forrajeo. A medida que aumentó la latitud, incrementó la proporción de pajaros que se sumergen para pescar y disminuyeron las especies que se zanbullen desde el aire. Estos resultados refuerzan previa evidencia de la segregación espacial de distintas especies y gremios en el Pacífico Norte. Además, nuestro estudio proporcionó una gran oportunidad para estudiar las distribuciones de aves pelágicas en una zone poco estudiada con anterioridad, y durante un año de condiciones oceanográficas extraordinarias. En 1999, los patrones atmosféricos fueron anómalos, con un colapso de los vientos aliseos que normalmente se encuentran al sur de la latitud 15° N. Además, la temperatura del mar fue muy baja, debido al desarrollo de un fuerte La Niña. Este artículo subraya la importancia de la exploración de los oceanos y la necesidad de observaciones estandarizadas para el estudio de la biogeografía de las aves marinas. En particular, es necesario llevar a cabo cruceros en zonas poco estudiadas por los ornitólogos para aumentar nuestros conocimientos de las distribuciones de las especies. Sin embargo, aunque un solo crucero puede aportar interesantes resultados, repetidos muestreos estandarizados son esenciales para comprender como la avifauna marina responde a la

variabilidad temporal en las condiciones oceanográficas. Por lo tanto, incitamos a nuestros colegas a que repitan este trayecto en el futuro.

INTRODUCTION

The distributions of nektonic predators, including seabirds, marine mammals, and large predatory fishes, reflect the same large-scale oceanographic domains and current systems that influence ocean productivity and plankton biogeography (Fager & McGowan 1963, Gould & Piatt 1993, McKinnell & Waddell 1993, Brodeur *et al*. 1999, Springer *et al*. 1999). In particular, studies of marine bird communities over scales of >1000 km have revealed that species with different foraging methods, wing morphologies, and diving capabilities preferentially inhabit specific regions of the world's ocean (Ashmole 1971, Ainley 1977, Ballance *et al*. 1997). This ecological segregation suggests that distinct assemblages are adapted to exploit specific water masses (Schneider *et al*. 1987, Wahl *et al*. 1989, Spear & Ainley 1998). In the North Pacific Ocean, diving seabirds preferentially inhabit highly productive areas, characterized by cool ocean temperatures and high chlorophyll concentrations. Conversely, tropical and subtropical waters of lower productivity typically support species that feed at the surface or pursue prey by plunge diving (Ainley 1977, Wahl *et al*. 1989, Gould & Piatt 1993, Ballance *et al*. 1997).

The North Pacific is characterized by strong spatial gradients and substantial temporal variability in atmospheric and hydrographic properties, including wind and ocean productivity patterns (Venrick *et al*. 1987, Polovina *et al*. 1994, Schwing *et al*. 2000), which influence the dispersion of highly migratory marine predators and their prey (Polovina 1996, Lehodey *et al*. 1997, Hyrenbach & Veit 2003). In particular, two large-scale spatial gradients in ocean productivity, prey biomass, and seabird abundance are apparent: a latitudinal (North – South) and an onshore-offshore (East – West) ecotone. The highest ocean productivity levels and standing stocks of marine seabirds and their prey occur in subpolar coastal areas, while lower productivity and standing stocks are found in pelagic waters at lower latitudes (Gould & Piatt 1993, Vinogradov *et al*. 1997, Shimoto *et al*. 1998).

In addition to these spatial gradients, specific water masses, large-scale atmospheric pressure systems, and ocean productivity patterns undergo substantial variability in extent, location, and intensity at inter-annual and longer temporal scales (Venrick *et al*. 1987, Mantua *et al*. 1997, Chavez *et al*. 2003). These year-to-year shifts are particularly strong in the eastern Pacific Ocean, where periodic changes in sea surface temperature and primary productivity are associated with variability in the El Niño Southern Oscillation (ENSO) (Barber & Chavez 1986, Chavez *et al*. 2002). Approximately eight months prior to the observations described in this paper, one of the strongest La Niña events in several decades developed in the NE Pacific. By the start of this cruise, large masses of cool water extended across the Pacific Ocean, from 20-60º N, and from the West Coast of North America to 130º W (Hayward *et al*.1999, Bograd *et al*.2000, Schwing *et al*. 2000).
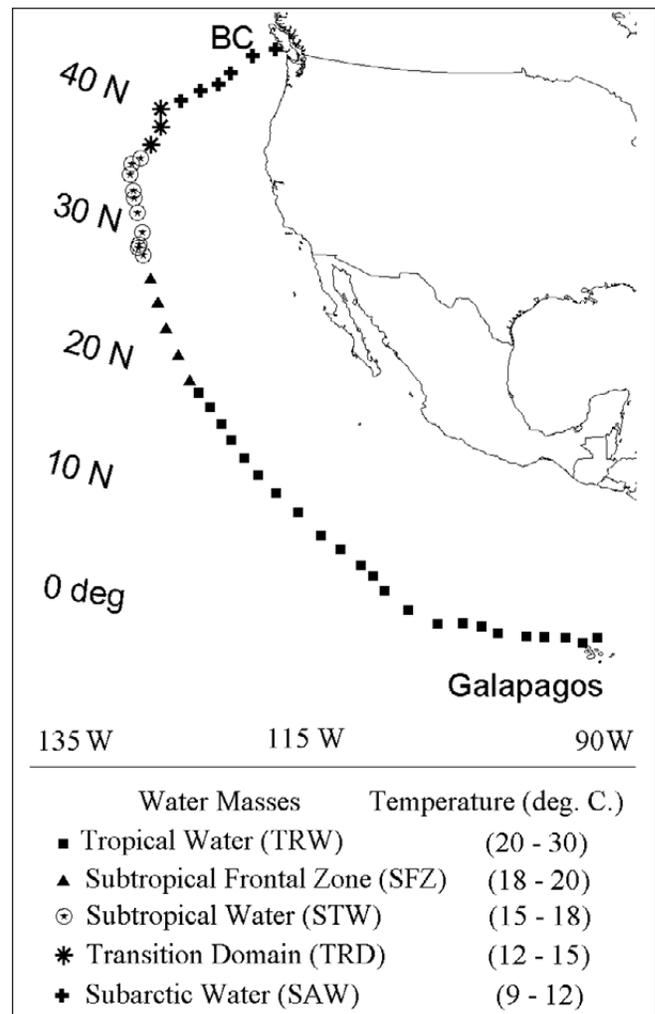
This paper documents seabird distributions and community structure along a 9,000 km transect across the northeast Pacific Ocean, extending from tropical to subarctic latitudes. We assess whether seabird species are closely or loosely associated into groups of recurrent species, and quantify their oceanographic

habitats (e.g., water depth, ocean temperature, chlorophyll concentration). This study provides a snapshot of marine bird dispersion and oceanic habitats during a single cruise. To better interpret this static perspective in the context of dynamic atmospheric and oceanographic processes, we discuss the environmental conditions during the spring of 1999 in relation to the climate of the northeast Pacific Ocean.

METHODS

Seabird observations

Data were collected during a 47 d (20 April - 5 June 1999) cruise of the 13-m vessel S.V. Minke I (cutter rig) from the Galápagos Islands, Ecuador (00.723° S; 90.545° W) to Bamfield, British Columbia, Canada (48.825° N; 125.137° W) (Fig. 1). The survey track followed a published route (three waypoints) that guides offshore sailors from the Galápagos Islands to British Columbia: (1) 2° N; 105° W, (2) 20° N; 125° W, and (3) 40° N; 135° W (Cornell 1992). Most of the track was completed under sail, tacking across the wind as required by local conditions. The actual distance traveled between successive noon-time locations and the daily sailing speeds were both influenced by the changing wind

Fig. 1. The survey track of 47 daily noon locations, coded on the basis of distinct water masses, defined in terms of the sea surface temperature.

conditions (mean daily distance: 183.3 ± 59.0 (SD) km, range: 33.3 to 59.0 km, n: 47; mean speed 7.8 ± 2.5 km hr^{-1}, range 1.4 km hr^{-1} to 12.4 km hr^{-1}, n: 47). The total survey line spanned over 9 000 km, while the linear track linking the 47 daily noon locations accounted for 5 600 km.

One of us (JS) surveyed marine birds from the cockpit, (approximately 2 m above the ocean surface) during daylight hours following a rotating schedule of 3-h watches and 6-h resting periods. Over the course of seven weeks, 240 hours were dedicated to seabird observations with an additional 160 hours done opportunistically during rest periods. Seabird observations ceased whenever visibility compromised the ability to detect and identify the birds (e.g., fog, high winds).

All seabirds sighted within 250 m of either side of the vessel were identified to the lowest taxonomic level possible, with the horizontal distance estimated by eye. Behaviour (e.g., sitting, flying, feeding), age class and gender were recorded for each sighting. Ship-following birds were recorded when they were first encountered, and ignored thereafter. Floating marine garbage and the neustonic invertebrate *Velella velella* were also recorded to examine their co-occurrence with convergence zones and foraging pelagic birds. The daily, local noon-time position of the vessel and the location of most seabird sightings were recorded using the onboard global positioning system (GPS).

Due to variable wind conditions and cruising speeds throughout the entire survey, each 3-h sampling period covered a different length of trackline. The estimation of standardized marine bird densities (number km^{-2}) was not possible due to the variability in the vessel's cruising speed, the irregular spacing and length of the survey bins, and the inability to quantify the movement of flying birds relative to that of the vessel (Tasker *et al*. 1984, Spear *et al*. 1992, Garthe & Hüppop 1999). However, the data were used to analyse marine bird community structure and habitat associations on the basis of the relative abundance of different taxa within specific oceanic regions and water masses. For each daily survey, we calculated the numerical importance of each taxon by dividing the number of individuals belonging to each species by the total number of birds sighted. Thus, our dataset expressed the daily proportional contribution of the different species to the total number of birds sighted along the survey track.

Seabird community structure
In addition to presenting the number and identity of the species recorded, we used multivariate statistics to determine whether certain species co-occurred in space and time, and whether distinct seabird assemblages inhabited different water masses. We combined the several 3-h watches completed each day and considered the 47 daily totals as independent samples. Thus, our community-level analyses considered 47 daily observations and the concurrent environmental conditions measured at each of the local noon-time positions.

We were interested in whether the avifauna observed on this cruise consisted of fixed communities or chance associations. If assemblages were predictable, then species that use the same area of the ocean would be significantly associated with each other. We used recurrent group analysis (RGA) to quantify the degree of co-occurrence between species in time and space (Fager & McGowan 1963, Veit 1995). This technique, originally proposed by Fager

(1957) and subsequently modified by Venrick (1982), identifies objective groups of recurrent species defined by the strength of their association ($\forall$):

$$\forall = [J (Na \ Nb)^{-1/2}] - [1/2 \ (Nb)^{1/2}]$$

where J is the number of joint occurrences; Na is the total number of occurrences of species A; Nb is the total number of occurrences of species B; and species are coded such that Na ≤ Nb. The first term of the equation above ranges from 0 to 1, and quantifies the degree of co-occurrence. The second term accounts for disparities in sample sizes (number of species occurrences) for different species pairs, and is always a number smaller than 1 (Fager 1957, Fager & McGowan 1963). The association value ($\forall$) provides a quantitative metric of species association. Investigators frequently select a "threshold" $\forall$ value and consider higher indices indicative of a "positive" inter-specific association, with all such species in the recurrent group forming a distinct community (Fager & McGowan 1963, Venrick 1982).

We used the empirically-derived distribution of observed $\forall$ values to identify those species that co-occurred more than would be expected by chance. We restricted our analysis to the 15 taxa that were sighted in more than 5% of the 47 survey days. We included unidentified frigatebirds because these were likely either Great Frigatebirds *Fregata minor* and Magnificent Frigatebirds *F. magnificens* (Harrison 1985) but excluded unidentified storm-petrels and shearwaters because these could include many different species with disparate biogeographic affinities. We computed the $\forall$ value for each of the possible 120 pair-wise comparisons, and defined the threshold value of "positive association" as the mean (0.023) plus one standard deviation (0.233) of the observed, pair-wise $\forall$ values.

We organized the positively associated species into the fewest number of recurrent groups by assembling the largest possible group first and then all smaller, subsequent ones. Group membership required that a species had a positive affinity with all other group members, while taxa not associated with all the members of an already existing group were linked as "associates". The links between recurrent groups and associate species were quantified using the proportion of group members that had a positive association with the "associate" species, ranging from 0 to 1 (Venrick 1982).

Environmental data
We characterized habitats using six variables: (1) sea-surface temperature (° C), (2) chlorophyll concentration (mg m^{-3}), (3) wind speed (m s^{-1}), (4) ocean depth (m), (5) latitude (° N), and (6) longitude (° W) (Table 1). Ocean temperature and chlorophyll concentration are useful proxies of water mass distributions and ocean productivity domains (Sverdrup *et al*. 1942, Longhurst 1998), and have been previously used to characterize the oceanographic habitats of North Pacific seabirds (Wahl *et al*. 1989, Hyrenbach *et al*. 2002). Additionally, wind speed is an important determinant of the composition of marine bird communities, since regions of high and low wind are preferentially inhabited by species with different wing morphologies, and prevailing wind conditions likely influence seabird migration routes (Spear & Ainley 1998, 1999). In particular, because wind speed and direction influence the ranging and activity patterns of marine birds, changing wind conditions may alter the number and identity of the

birds sighted within a given area (Weimerskirch *et al.* 2000). Similarly, water depth shapes seabird distributions, as indicated by the disparate communities that inhabit distinct bathymetric domains (e.g., shallow continental shelves versus deeper pelagic waters offshore) (Schneider *et al.* 1986).

In addition to these environmental variables, the distance to breeding colonies is an important determinant of pelagic bird distributions and community structure (Stahl *et al.* 1985, Veit 1995). As the cruise passed within 1000 km of several large seabird colonies, (e.g., Galápagos Islands, Clipperton Islands, and Isla de Revillagigedo), we used the location along the survey track to account for potential species range limits.

We used weekly averages of filtered sea surface temperature (SST) imagery from the Advanced Very High Resolution Radiometer (AVHRR), with a spatial resolution of 1 degree latitude x longitude, to quantify ocean temperatures along the survey track (Reynolds & Smith 1994). These data are available at the Pacific Marine Environmental Laboratory web-site (www.ferret.noaa.gov/fbin/climate_server). Global comparisons have revealed that AVHRR SST measurements are 0.3-0.4° C lower than concurrent vessel-based observations, with cross-correlations ranging between + 0.3 and + 0.7 (McClain *et al.* 1985).

Chlorophyll concentrations were derived from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) eight-day composites, with a spatial resolution of 9 km (seawifs.gsfc.nasa.gov/ SEAWIFS.html). Within the range of 0.05-50 mg m^{-3}, SeaWiFS estimates are within 35% of in-situ chlorophyll a concentrations (Hooker & McClain 2000), with the greatest discrepancies in waters between 1-10 mg m^{-3} (Kahru & Mitchell 1999). We discarded unreasonably high chlorophyll a concentrations beyond the range of SeaWiFS validation (> 50 mg m^{-3}) (Hooker & McClain 2000). Because the spatial resolution of the chlorophyll data was finer than the temperature imagery, we aggregated the SeaWiFS images into 100 x 100 km grids, comparable to the resolution of the temperature data (1 degree latitude x longitude). We calculated the median chlorophyll concentration of the 121 (11 x 11) pixels within each grid cell, and used this value for the subsequent habitat analyses.

We used 12-h averages of surface-wind magnitude data from the Fleet Numerical Oceanography Center (FNMOC), with a spatial resolution of 1° x 1° grids (Clancy 1992). These

observations are available twice daily (at 0 and 12 hours) at the Pacific Fisheries Environmental Laboratory web-site (las.pfeg.noaa.gov/las/main.pl). To match the timing of the concurrent day-time seabird observations, we used the 47 daily noon wind speed values in our analysis.

Finally, we obtained bathymetric data from NOAA's National Geophysical Data Center ETOPO 5-minute grid elevation dataset (NGDC 1998), and aggregated these fine-scale data into 1° x 1° grids. We calculated the average depth of the 144 (12 x 12) values within each grid cell, and used these data to quantify ocean depth along the survey track.

Analysis of seabird-habitat associations
In addition to the recurrent group analysis, we used non-metric multi-dimensional scaling (NMDS) to quantify the association between seabird distributions and the environmental variables described above. NMDS is a non-parametric ordination technique and does not impose any assumptions on the shape of the habitat-wildlife relationships, the number of explanatory variables defining the species ranges, or the degree of association required to define significant species clusters. Instead, NMDS plots each species on a multi-dimensional space defined by several habitat axes, which represent combinations of the environmental variables used in the analysis. This technique plots species along a multi-variable continuum. Thus, taxa with similar distributions are plotted closer together than those with different distributions (Kenkel & Orloci 1986, Brodeur *et al.* 1999). We used the PC ORD statistical software to perform the NMDS analysis and to create the plots of species distributions (McCune & Mefford 1999).

Segregation across water masses
We evaluated the correlations between the six variables used to characterize seabird habitats, measured at the 47 daily noon-time locations. We found that eight of the 15 possible pair-wise comparisons were significant. In addition to latitudinal ecotones (wind speed and ocean temperature) and longitudinal gradients (ocean depth, wind speed, and ocean temperature), these cross-correlations revealed that shallow, shelf-slope waters supported higher chlorophyll concentrations than deeper pelagic waters, and that higher wind speeds were associated with colder areas of the ocean (Table 1). Because many of the habitat variables were cross-correlated, we focused on the significance of sea surface temperature as a determinant of seabird community structure. This

TABLE 1
Summary of cross-correlations between the six environmental variables used to characterize oceanographic habitats, measured at 47 daily noon-time locations: sea surface temperature (SST), wind speed (WSP), depth (DPH), latitude (LAT), longitude (LON), and chlorophyll concentration (CHL). For each pair-wise combination, the matrix below shows the sign and the magnitude of the Pearson correlation coefficient, and the associated significance level. The bold font denotes significant results.

	SST	WSP	DPH	LAT	LON	CHL
				p-value		
SST	-	**p < 0.001**	p > 0.50	**p < 0.001**	**p < 0.001**	0.20 < p < 0.10
WSP	- 0.544	-	0.50 < p < 0.25	**p < 0.001**	**p < 0.001**	p > 0.50
DPH	- 0.067	+ 0.113	-	0.20 < p < 0.10	**p < 0.001**	**p < 0.001**
LAT	- 0.949	+ 0.536	+ 0.208	-	**p < 0.001**	0.20 < p < 0.10
LON	+ 0.768	- 0.536	- 0.573	- 0.895	-	p > 0.50
CHL	- 0.216	+ 0.079	- 0.660	+ 0.212	+ 0.040	-
				r-coefficient		

approach facilitated the study of marine bird distributions and community structure with respect to distinct water masses (Wahl *et al.* 1989, Gould & Piatt 1993, Hyrenbach *et al.* 2002).

We characterized the seabird assemblages within six distinct water masses, defined on the basis of remotely-sensed sea surface temperature: the Tropical Water Mass (TRW) (SST > 20º C), the Subtropical Frontal Zone (STF) (SST: 20-18.01º C), the Subtropical or Central Pacific Water Mass (STW) (SST: 18-15.01º C), the Transition Domain (TRD: 15-12.01º C), and Subarctic waters (SAW) (12-9º C) (Lynn 1986, Roden 1991). We graphically contrasted the relative abundance of different types of seabirds within these five water masses. Additionally, we computed the proportion of divers, plunge-divers, and surface-foraging birds in each temperature range, and used the G statistic to test for significant differences in the composition of the avifauna (Zar 1984). We hypothesized that plunge-diving species would be numerically-dominant in warm tropical waters, while divers would be disproportionately more numerous in cool, subarctic waters (Ainley 1977, Wahl *et al.* 1989).

RESULTS

Seabird observations
We recorded 974 seabirds (814 identified individuals belonging to 32 species, 11 families, and three orders) during the 47 day survey (Tables 2, 3). The Sooty Shearwater *Puffinus griseus* and the Black-footed Albatross *Phoebastria nigripes* accounted for 28% of all identified birds (17 and 11%, respectively); all other species were each less than 10% of birds sighted. Most species (63.5%) were sighted more than once, with five taxa (Black-footed Albatross, Leach's Storm-petrel *Oceanodroma leucorhoa*, Sooty Shearwater, Masked Booby *Sula dactylatra*, and Northern Fulmar *Fulmarus glacialis*) observed during more than 10 survey days (Table 2).

Recurrent group analysis
Twenty-six of the 120 pair-wise comparisons involving the "common" taxa (species observed in at least three daily samples) yielded $\forall$ values larger than our assigned threshold (0.257). These fifteen species formed four recurrent groups characteristic of
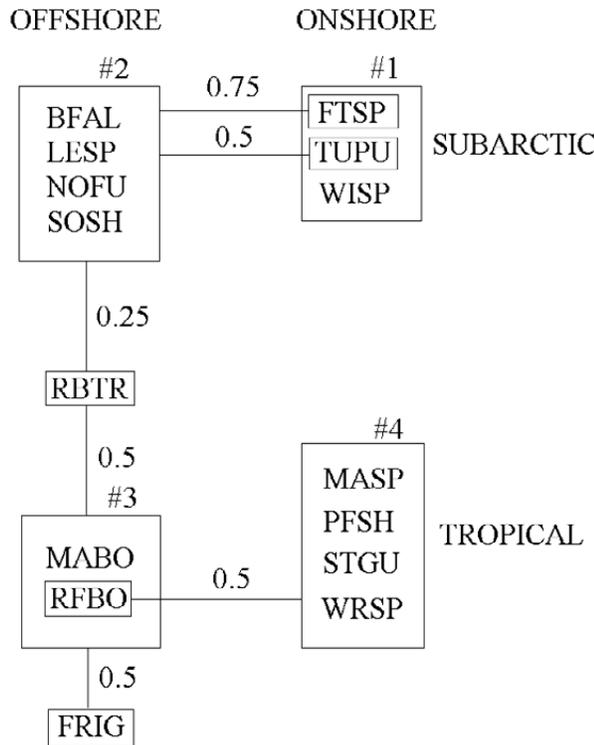
TABLE 2
Species list, foraging guilds, and relative occurrence and abundance of seabirds
observed during 47 day cruise in northeast Pacific, 20 April - 5 June 1999.

Species Name	Genus and species	Code	Guild	% Days	% Birds
Black-footed Albatross	*Phoebastria nigripes*	BFAL	surface	44.7	10.8
Short-tailed Albatross	*Phoebastria albatrus*	STAL	surface	2.1	0.1
Northern Fulmar	*Fulmarus glacialis*	NOFU	surface	21.3	6.5
Pink-footed Shearwater	*Puffinus creatopus*	PFSH	dive	6.4	1.3
Flesh-footed Shearwater	*Puffinus carneipes*	FFSH	dive	4.3	1.1
Wedge-tailed Shearwater	*Puffinus pacificus*	WTSH	dive	4.3	0.4
Sooty Shearwater	*Puffinus griseus*	SOSH	dive	34.0	16.8
Shearwater species	*Puffinus* spp.	SHEA	dive	31.9	4.8
Audubon's Shearwater	*Puffinus lherminieri*	AUSH	dive	4.3	0.2
Black Petrel	*Procellaria parkinsoni*	BLPE	surface	4.3	2.2
Galapagos Petrel	*Pterodroma phaeopygia*	DRPE	surface	2.1	0.1
Wilson's Storm-petrel	*Oceanites oceanicus*	WISP	surface	12.8	4.3
Fork-tailed Storm-petrel	*Oceanodroma furcata*	FTSP	surface	10.6	3.8
Leach's Storm-petrel	*Oceanodroma leucorhoa*	LESP	surface	34.0	6.3
Madeiran Storm-petrel	*Oceanodroma castro*	MASP	surface	6.4	0.3
Black Storm-petrel	*Oceanodroma melania*	BLSP	surface	2.1	0.1
Wedge-rumped Storm-petrel	*Oceanodrama tethys*	WRSP	surface	10.6	2.5
Elliott's Storm-petrel	*Oceanites gracilis gracilis*	ELSP	surface	4.3	0.2
Storm-petrel species	*Oceanodrama* spp.	STPE	surface	38.3	6.4
White-tailed Tropicbird	*Phaethon lepturus*	WTTR	plunge	2.1	0.3
Red-billed Tropicbird	*Phaethon aethereus*	RBTR	plunge	19.2	3.4
Masked Booby	*Sula dactylatra*	MABO	plunge	29.8	7.1
Red-footed Booby	*Sula sula*	RFBO	plunge	17.0	9.6
Brown Pelican	*Pelecanus occidentalis*	BRPE	plunge	2.1	0.1
Frigatebird species	*Fregata* spp.	FRIG	surface	8.5	0.5
Pomarine Jaeger	*Stercorarius pomarinus*	POJA	surface	2.1	0.1
Bonaparte's Gull	*Larus philadelphia*	BOGU	surface	2.1	0.1
Western Gull	*Larus occidentalis*	WEGU	surface	2.1	0.2
Glaucous-winged Gull	*Larus glaucescens*	GWGU	surface	2.1	1.5
Swallow-tailed Gull	*Creagrus furcatus*	STGU	surface	8.5	2.1
Common Tern	*Sterna hirundo*	COTE	plunge	4.3	0.5
Sooty Tern	*Sterna fuscata*	SOTE	plunge	2.1	0.8
Tern species	*Sterna* spp.	TERN	plunge	2.1	4.5
Noddy species	*Anous* spp.	NODD	plunge	4.3	0.3
Rhinoceros Auklet	*Cerorhinca monocerata*	RHAU	dive	2.1	0.1
Tufted Puffin	*Fratercula cirrhata*	TUPU	dive	6.4	0.6

different ecotones (onshore – offshore) and latitudinal regions (tropical – subarctic) (Fig. 2).

The first group, offshore-tropical, included Masked and Red-footed Boobies *Sula sula* and two associated species (Red-billed Tropicbird *Phaethon aethereus* and frigatebirds). The second group, offshore-subarctic, included the Black-footed Albatross, Northern Fulmar, Sooty Shearwater, and Leach's Storm-petrel.

Fig. 2. Recurrent species groups formed using the daily observations of 15 "common" species sighted during the cruise. Individual species from one group may be linked to another group, if they have a positive affinity for some, but not all, of the taxa in the second recurrent group. These species – group linkages are labeled to show the magnitude (0-1) of these associations.

These two groups were linked by an associated species, the Red-billed Tropicbird. Additionally, each of these two offshore groups were linked with an onshore group with an affinity for tropical and subarctic waters. The third group, onshore-subarctic, included the Fork-tailed Storm Petrel *Oceanodroma furcata*, Wilson's Storm Petrel *Oceanites oceanicus* and Tufted Puffin *Fratercula cirrhata* and was linked with the offshore–subarctic group. The final group, onshore-tropical, included the Madeiran and Wedge-rumped Storm Petrel *Oceanodroma castro*, *O. tethys*, Pink-footed Shearwater *Puffinus creatopus* and Swallow-tailed Gull *Creagrus furcata* and was linked to the offshore-tropical taxa. We detected no associations between the species in the offshore-subarctic and onshore-tropical groups, or between the offshore-tropical and onshore-subarctic taxa (Fig. 2).

Oceanographic setting
The vessel was becalmed on 13 days from 0.35° N, 41.72° W to 38.43° N, 136.53° W, with extended no wind periods during 21-23 April and 18-21 May 1999. Average wind speeds at the 47 daily noon locations ranged from 1.58-9.64 m s^{-1} (Fig. 3A), with values 1-2 m s^{-1} lower than the long-term average along the tropics (10° S-15° N) and positive anomalies (1-2 m s^{-1} higher) off the West Coast of North America (30-40° N) (Fig. 3B).

The survey track traversed tropical, subtropical, and subarctic water masses, with surface temperatures at daily noon locations declining from 28.78 to 9.76° C moving northward (Fig. 4A). Ocean temperatures were largely cooler than the 50-year average for the NE Pacific, with the largest negative anomalies (1-2° C colder) north of 15° N latitude (Fig. 4B). We surveyed waters off the continental shelf, with ocean depth at the 47 daily locations ranging between 295 and 5,363 m. The daily SeaWiFS-derived median chlorophyll values ranged from 0.06 to 4.48 mg m^{-3} (Fig. 5).
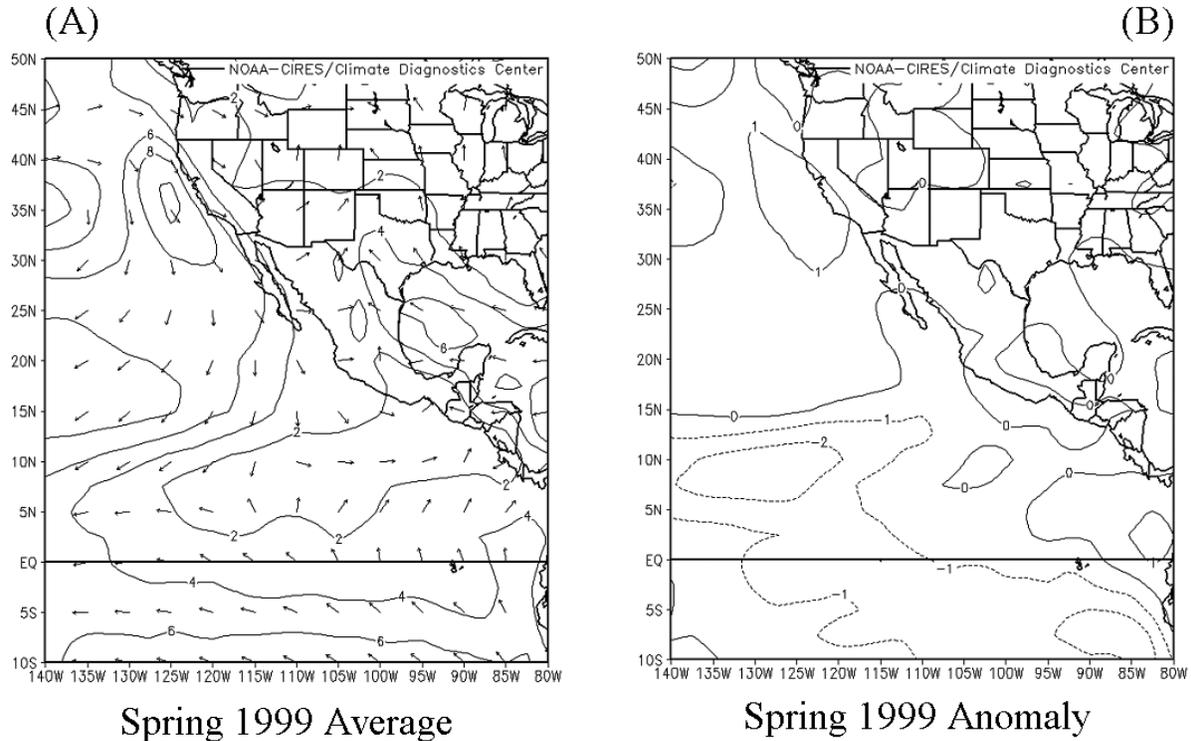
Multivariate analysis of seabird assemblages
The NMDS procedure selected three habitat axes, which accounted for 88% of the variability observed in the structure of the marine bird community (Fig. 6). The first axis described onshore – offshore gradients associated with concurrent changes in ocean depth and chlorophyll concentration, with shallow shelf-slope regions supporting higher phytoplankton standing stocks. The second axis illustrated latitudinal/longitudinal changes in sea
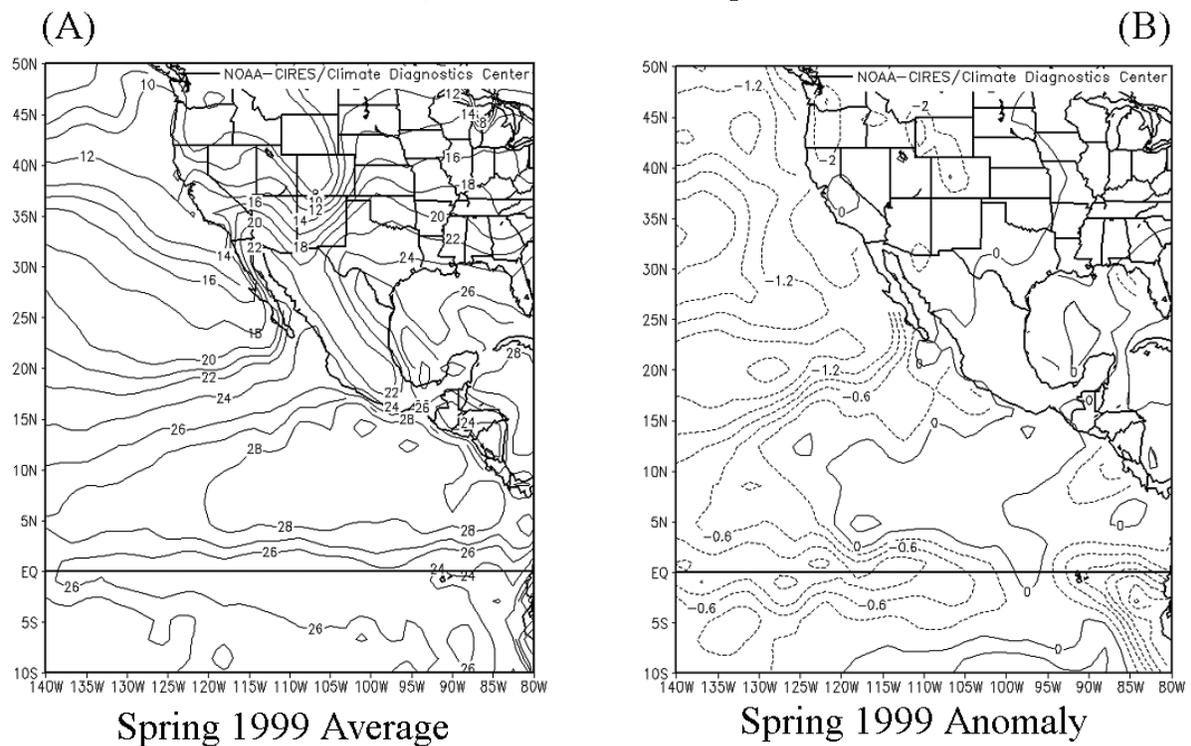
TABLE 3
Summary of seabird orders and families recorded across the northeast Pacific, 20 April - 5 June 1999,
showing the proportion of sighted birds that were identified to species level and the number of species identified.

Order	Family	Birds Sighted	Birds Identified	Proportion Identified	Species Identified
Procellariiformes	Diomedeidae	106	106	100.00	2
	Hydrobatidae	230	170	73.91	6
	Procellariidae	328	280	88.33	9
Pelecaniformes	Fregatidae	5	0	0.00	0
	Pelecanidae	1	1	100.00	1
	Phaethontidae	36	36	100.00	2
	Sulidae	162	162	100.00	2
Charadriiformes	Alcidae	7	7	100.00	2
	Laridae	38	38	100.00	4
	Stercorariidae	1	1	100.00	1
	Sternidae	60	13	21.67	2
TOTAL		**974**	**814**	**83.57**	**32**

Surface Vector Wind (m/s) Composite Mean

(A)   (B)

Spring 1999 Average   Spring 1999 Anomaly

Fig. 3. Mean (A) and long-term anomaly (B) of wind speed during April-June 1999. The anomalies are calculated by subtracting the long-term seasonal climatology (1949-2003) from the mean values during 1999. Positive and negative values are indicative of anomalously higher and lower wind speeds during the 1999 cruise. Figure courtesy of NOAA's Climate Diagnostics Center (www.cdc.noaa.gov).

Surface Temperature (^{O}C) Composite Mean

(A)   (B)

Spring 1999 Average   Spring 1999 Anomaly

Fig. 4. Mean (A) and long-term anomaly (B) of sea surface temperature during April-June 1999. The anomalies are calculated by subtracting the long-term seasonal climatology (1949-2003) from the mean values during 1999. Positive and negative values are indicative of anomalously higher and lower wind speeds during the 1999 cruise. Figure courtesy of NOAA's Climate Diagnostics Center (www.cdc.noaa.gov).

surface temperature, with cooler ocean temperatures at more northern latitudes and western longitudes. The third axis included these same latitudinal/longitudinal ocean temperature gradients, as well as changes in mean ocean depth and wind speed (Table 4). Because sea surface temperature was strongly correlated with the second and third habitat axes selected by the NMDS procedure, we felt justified contrasting the composition of the avifauna within different water masses defined by specific SST ranges.

The NMDS plot reinforced the results of the recurrent group analysis. The seven species in the offshore-subarctic and the onshore-subarctic groups were associated with high wind speeds and cool water temperatures to the north and west of the area surveyed. A second cluster containing the seven tropical species occurred in warmer waters to the south and east of the study area. Furthermore, the Red-billed Tropicbird – a species associated with the two offshore recurrent groups – was plotted between the tropical and the subarctic NMDS species clusters (Figs. 2, 6).
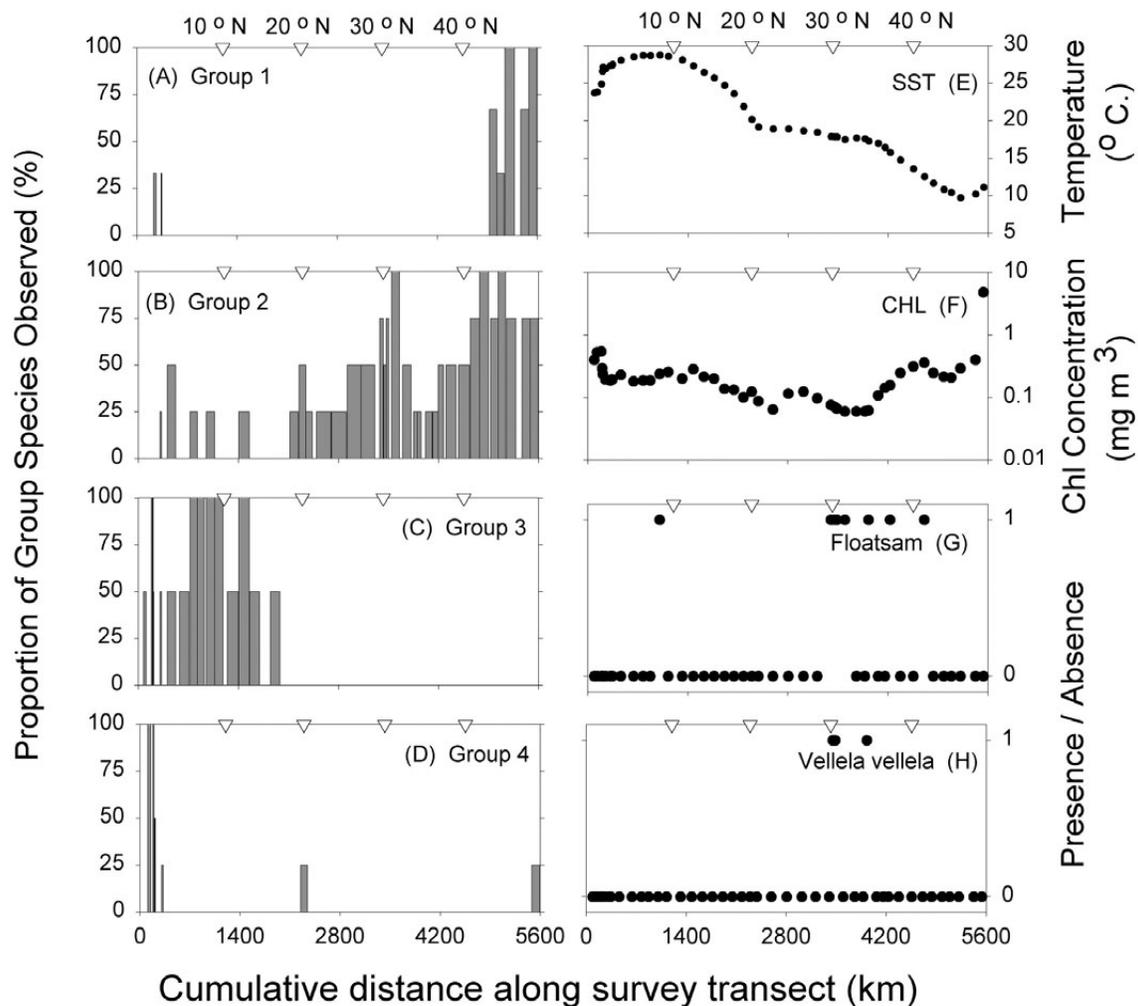
Segregation across water masses
We found three seabird communities based on water mass characteristics: (1) a tropical community (booby – tropicbird –

frigatebird) found exclusively in the warm subtropical frontal zone and tropical water mass (SST > 18° C); (2) a subarctic community (alcid – fulmar) largely restricted to subarctic and Transition Domain waters (SST: 9.7-17. 9° C); and (3) a widely-distributed, cosmopolitan community (storm-petrel – shearwater – albatross) occupying a broad range of ocean temperatures, from 9.7-28.8° C (Fig. 7).

In spite of the presence of diving birds in all water masses (due to the migratory movements of shearwaters), there was a significant segregation of seabird foraging guilds, as suggested by the number of pursuit diving, plunging, and surface foraging birds sighted in each of the five water masses we surveyed ($G_8 = 246.02$, $P < 0.001$). Plunge-divers were the numerically-dominant taxa in tropical waters, and divers were disproportionately more abundant in the cool waters of the Subarctic and Transition domains (Fig. 8). In addition to faunal disparities across water masses, we documented several frontal crossings along the survey track.

The SST gradients and the accumulation of marine debris and neustonic invertebrates suggest that we crossed two convergence zones associated with oceanic fronts: the Subtropical Frontal Zone

Fig. 5. Spatial distribution of recurrent group member species (A-D), water mass properties (E-F), floating debris (G) and neustonic zooplankton (H) along the 5,600 km track linking daily noon cruise positions (April 20-June 5, 1999). For each recurrent group, the proportion of the constituent species sighted on every survey day is plotted. Thus, the four recurrent group histograms for any given day need not add to 100%.

(SST: 18-20° C) at ~20° N, and the southern extent of the North Pacific Transition Zone (SST: 15-18° C) at ~35° N (Fig. 5E). Floating garbage (including discarded net, rope, styrofoam, plastic balls, buoys, and bottles) was observed beside the vessel on seven days, and was concentrated from 29° N; 133° W to 41° N; 137° W (Fig. 5G). Black-footed Albatross fed on small, floating plastic fragments, and fulmars and albatross found pelagic invertebrates that had accumulated on or near the flotsam. Large aggregations of *Velella velella* extended over 668 km (~ 30-35° N) in mid-May (Figure 5H).

Fig. 6. Non-metric multidimensional scaling (NMDS) plot, showing the oceanographic habitats of the 15 "common" seabird species sighted during the cruise.

TABLE 4

Correlation coefficients between the six environmental variables and the three non-metric multidimensional scaling (NMDS) axes used to characterize marine bird oceanographic habitats.

Environmental Variable	Axis 1	Axis 2	Axis 3
Sea surface temperature (SST)	0.117	- 0.602	- 0.714
Wind speed (WSP)	0.155	0.207	0.482
Depth (DPH)	0.286	0.266	0.440
Latitude (LAT)	0.002	0.535	0.770
Longitude (LON)	0.187	0.496	0.834
Chlorophyll concentration (CHL)	- 0.206	- 0.025	- 0.009

DISCUSSION

This is the first study to examine seabird assemblages along a latitudinal gradient extending from tropical to subarctic waters in the eastern Pacific Ocean. Our analysis of the avifauna along a 9 000 km survey complement previous studies of marine bird communities in this region (Wahl *et al*. 1989, Gould & Piatt 1993) and similar studies in the tropical and south Pacific (Pitman 1986, Ribic & Ainley 1988, Ballance *et al*. 1997). This study revealed the spatial segregation of different species types and foraging guilds across water masses, defined in terms of sea surface temperature. These patterns were particularly striking for alcids that are restricted to cool subarctic waters (SST 12-9° C) and frigatebirds and boobies in tropical waters (SST > 20° C). Furthermore, while some species were restricted to specific water masses, other taxa occupied a broad range of ocean temperatures. In particular, the Black-footed Albatrosses, Northern Fulmars, and Red-billed Tropicbirds inhabited several "adjacent" water masses characterized by similar properties. The fulmars were found in subarctic, Transition Domain, and subtropical waters, while the tropicbirds occupied warmer tropical and subtropical front waters. As suggested by both the recurrent group analysis and the multidimensional scaling plot, the Red-billed Tropicbird inhabits a "transitional" habitat between the tropical species to the south and the subarctic taxa to the north. The broad distribution of the Black-footed Albatross suggests that this species occupies a wide range of ocean temperatures but aggregates at the North Pacific Transition Domain and the subtropical frontal zone (Wahl *et al*. 1989, Hyrenbach *et al*. 2002). Finally, other cosmopolitan species groups, like storm petrels and shearwaters, were found in all water masses. This result is not unexpected, as these are very specious groups, including warm-water and cold-
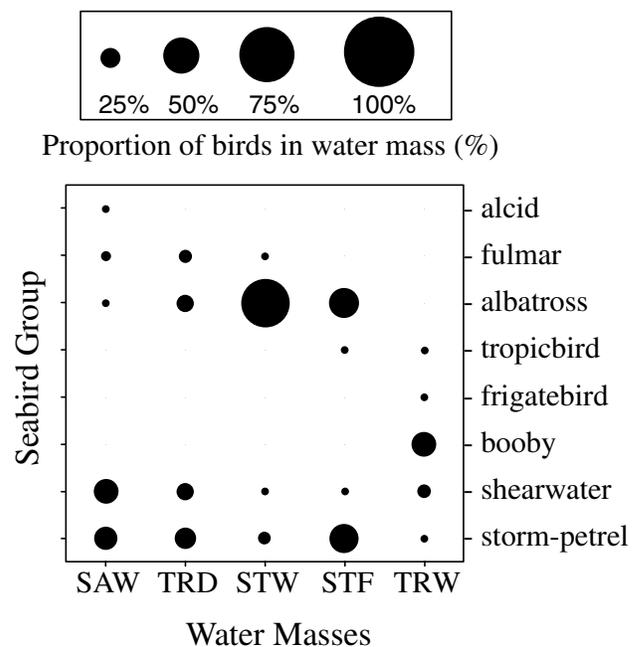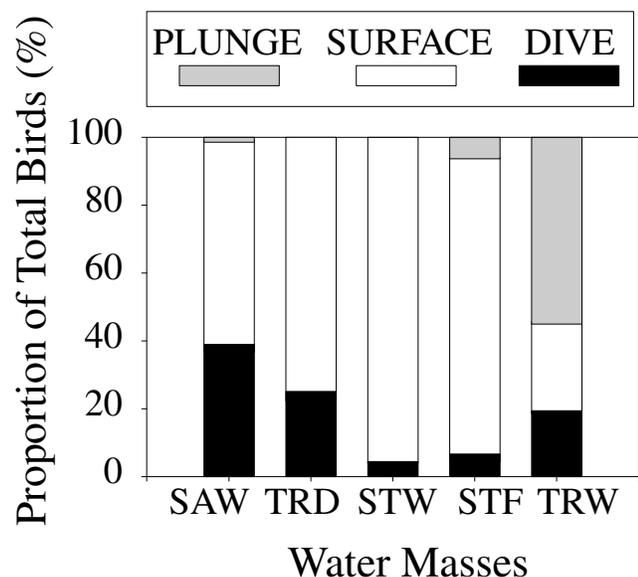

Proportion of birds in water mass (%)

Fig. 7. Make-up of the seabird communities inhabiting different North Pacific water masses, defined in terms of sea surface temperature characteristics. The circles are proportional to the relative abundance of different seabird species groups. The totals for each water mass need not add to 100% if other taxa were sighted.

water taxa with tropical and subpolar distributions (Harrison 1985). In particular, our survey overlapped with the spring, northward migration of the southern hemisphere shearwaters and we found these birds scattered throughout the study area (Gould & Piatt 1993, Spear & Ainley 1999).

Significance of distinct water masses

The segregation of species types and foraging guilds across water masses underscores the notion that seabirds with different life-styles preferentially occupy specific oceanic domains (Ainley 1977, Wahl *et al*. 1989, Ballance *et al*. 1997, Spear & Ainley 1998). Previously, Wahl and coworkers (1989) documented similar segregation patterns of pursuit diving and plunge diving species across the North Pacific during summer, with pursuit divers preferentially inhabiting cool and highly-productive subarctic waters and plunge divers being most numerous in the warmer and less productive waters of the Subtropical Gyre. Similar patterns have been observed for breeding seabird communities along the eastern North Pacific, from the Galápagos (0º N) to Olympic Island (48º N) (Ainley 1977). Ultimately, the dispersion of prey resources and the energetic constraints of foraging influence whether seabird species can inhabit specific water masses.

In this study, we found that three habitat axes accounted for a large proportion (88%) of the structure of the marine avifauna. Additional environmental variables not addressed in this study (e.g. the distribution of prey resources and the distance to breeding colonies) probably account for the unexplained variance. Sea surface temperature proved to be a very strong determinant of seabird community structure, as previously documented by other studies in the Pacific Ocean (e.g., Ribic & Ainley 1988, Wahl *et al*. 1989, Hyrenbach & Veit 2003). Because the habitat axes were strongly correlated with water temperature, we investigated the distribution of different species and foraging guilds across specific water masses. These water mass associations seemed particularly relevant given the fluid nature of oceanic systems, and the well-established temperature associations of many of the prey exploited by marine birds. Moreover, because the location of frontal systems

Fig. 8. Proportion of different seabird foraging guilds inhabiting different North Pacific water masses, defined in terms of sea surface temperature characteristics.

and the extent of water masses shift seasonally and from year to year, the study of temperature associations facilitates comparisons across time and space (McKinnell & Waddell 1993, Lehodey *et al*. 1997, Hyrenbach & Veit 2003).

Significance of frontal systems

The sea surface temperature (SST) gradients, and the presence of floating debris and *Velella velella* along the track suggest our survey crossed two frontal systems: one at ~20º N and another one at ~35º N. We observed a very striking latitudinal shift in seabird community structure over a relatively short distance (~200 km) in the vicinity of 20° N, which was associated with the Subtropical Frontal Zone (SST: 20-18° C). This observation underscores the significance of oceanic fronts and water mass boundaries as important biogeographic features in the open ocean (Sverdrup *et al*. 1942, Fager & McGowan 1963, Longhurst 1998). In pelagic systems, changes in the types and abundances of nektonic organisms (marine mammals, seabirds, large predatory fishes) often occur at frontal systems, where waters of different temperature and salinity meet (Gould & Piatt, 1993, Brodeur *et al*., 1999). Previously, researchers documented changes in seabird communities across similar hydrographic fronts in the eastern North Pacific. A narrow (40-44º N) region of strong temperature and salinity gradients, termed the Transition Domain, delimits the ranges of subarctic and subtropical species, and influences the distribution of far-ranging fish, seabirds, and marine mammals (McKinnell & Waddell 1993, Brodeur *et al*. 1999, Springer *et al*. 1999).

Frontal systems and convergence zones concentrate marine debris and neustonic prey across the North Pacific Ocean (Dahlberg & Day 1985, Galt 1985). Procellarids may ingest small pieces of plastic while foraging in these areas (Blight & Burger 1997), leading to a decline in body condition (Sileo *et al*. 1990).

Significance of prevailing wind patterns

In addition to water mass distributions and frontal systems, prevailing wind patterns are potentially important determinants of seabird distributions and community structure (Spear & Ainley 1998, Weimerskirch *et al*. 2000). In the northeast Pacific, there is a marked reduction in surface winds from 25-35° N associated with a subtropical anticyclone, a zone typically referred to as the 'horse latitudes' by offshore sailors. As expected, there were very light winds from 15-30° N during the spring of 1999. However, winds were also exceptionally light south of 15° N, an area known for favourable tradewinds. The collapse of the climatological wind patterns, with relatively light winds across the entire track, might explain the relatively low number of total birds seen during this cruise.

Large-scale oceanographic context

Ocean conditions are dynamic and change from year to year, thus it is essential that we place our observations in a larger, oceanographic context. During the fall of 1998, a strong La Niña event developed in the northeast Pacific. By August 1998, the multivariate ENSO index changed from a positive value, indicative of El Niño conditions, into a negative value, suggestive of a developing La Niña event. By September, the eastern tropical Pacific (5º N-5º S; 90-150º W) was characterized by anomalously shallow thermocline depths (Bograd *et al*. 2000); and strong negative SST anomalies (exceeding 1° C) were apparent along the tropics and off the West Coast of North America (Hayward *et al*. 1999). Unusually high coastal upwelling off the West Coast of

North America (21-51° N) persisted from the fall of 1998 to the fall of 1999, resulting in the unusually cold SSTs observed during this cruise (Bograd *et al*. 2000, Schwing *et al*. 2000). However, it is unclear to what extent these atmospheric and oceanographic perturbations influenced the avifauna of the northeast Pacific Ocean. Additional cruises will be required to determine whether the anomalous conditions during the spring of 1999 lead to unusual seabird distributions and marine bird community structure.

Our study suggested that, over macro-mega spatial scales (1000s km), marine bird communities of the northeast Pacific Ocean are associated with distinct water masses. Moreover, the observed segregation of different foraging guilds suggests that marine bird communities are structured by the interplay of ocean productivity and the costs of foraging. This cruise followed an unusual track during an anomalous year. Thus, additional surveys are required to assess how the marine bird communities of the northeast Pacific Ocean shift spatially and temporally.

ACKNOWLEDGEMENTS

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