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Effects of El Niño and La Niña on seabird assemblages in the Equatorial Pacific

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ABSTRACT: Spring and autumn cruises in Equatorial and Subtropical Surface Waters were conducted from 1984 to 1989 in the eastern Equatorial Pacific. Assemblage characteristics of species richness and diversity during El Niño 1986-87 and La Niña 1988 were compared with the other years. The 3 genera that dominated the assemblages, storm-petrels (*Oceanodroma*), gadfly petrels (*Pterodroma*), and shearwaters (*Puffinus*), differed markedly in relative importance depending on season and water mass. During autumn, on the basis of biomass, gadfly petrels dominated assemblages in both water masses; on the basis of abundance, gadfly petrels shared dominance with storm-petrels. During spring, shearwaters and storm-petrels were important in both water masses while gadfly petrels were important only in the Equatorial Surface Water. Assemblage characteristics varied from year to year, but changed the most during El Niño and La Niña. Either event was manifested by a decrease in richness and a disappearance of genera and species, particularly those of medium-abundance. Generally, the common genera and species were not affected. For El Niño, assemblages changed more during autumn compared to spring. The effect of La Niña was strongest during spring.

INTRODUCTION

The biological effects of the warm-phase of the oceanographic-meteorological event called El Niño – Southern Oscillation (ENSO) have been known for some time (Murphy 1926, 1936, Wooster 1980). These effects include reductions in productivity of otherwise rich areas, especially those of upwelling regions, and the meteorological effects resulting from incursions of warm water into otherwise cool areas (Barber & Chavez 1983, 1986, McPhaden & Picaut 1990). Increases in productivity during ENSO are less common (Tarazona et al. 1988, Tershy et al. 1991). Effects of the anomalous cold-phase of the southern oscillation called La Niña (LNSO) are less well known though the potential for causing changes should be as great as for ENSO.

In recent decades, it has become increasingly apparent that seabird species, like fish and plankton, are constrained to reside in specific parts of the world ocean on the basis of the characteristics of marine climate. That is, each water mass or group of neighboring and similar water masses has a characteristic assemblage of seabird species (see Hunt & Schneider 1987, Wahl et al. 1989). This being the case, then events such as ENSO and LNSO that perturb marine climate in a region should produce changes in community characteristics consistent with climate alteration (Ainley 1976, Ainley et al. 1986, Briggs et al. 1987). However, it is difficult to predict the effects of such perturbations because the factors that constrain seabird species to a given region are poorly understood (Hunt & Schneider 1987).

From previous work on pelagic seabird communities, Ribic & Ainley (1988/89) found no effect of ENSO on seabird species assemblages at the mega-scale (> 3000 km; Hunt & Schneider 1987). From that work, it appeared that the strongest seabird associations for the common species were found during an ENSO event. No prediction was made concerning the effect of LNSO due to lack of information (the last LNSO occurred in 1975 before the data in Ribic & Ainley (1988/89) were collected). However, the data of Ribic & Ainley (1988/89) were collected to investigate events on the mega-scale; changes on a smaller scale, such as

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shifts in species distributions within water masses (the macro-scale, 1000 km; Hunt & Schneider 1987), would not be detected. The objective of our paper is to focus on the macro-scale (i.e. water masses) and investigate what changes in assemblage composition occurred during ENSO 1986-87 and LNSO 1988. In order to evaluate the changes, we defined species assemblages in non-ENSO/LNSO years as 'normal', calculated assemblage characteristics and variability, and compared these characteristics to those calculated from the assemblages in the ENSO and LNSO years.

METHODS

The study area consisted of the eastern tropical Pacific Ocean (ETP) between 10° N and 10° S and between 140 and 90° W. Three water masses are present in that area: Tropical Surface Water, Equatorial Surface Water (ESW), and Subtropical Surface Water (SSW) (Longhurst & Pauly 1987). For the purpose of the present analysis, we confined our analysis to the ESW and SSW owing to roughly equivalent representation of the 2 water masses for all study seasons. Single spring and autumn cruises were conducted for 6 years, 1984 to 1989, on research vessels of the National Oceanic and Atmospheric Administration (NOAA) as part of EPOCS (Equatorial Pacific Ocean Climate Study) and TOGA (Tropical Ocean-Global Atmosphere). We defined spring and autumn from the Northern Hemisphere perspective.

ENSO occurred from mid-1986 to the end of 1987 (McPhaden et al. 1990). Therefore, we defined cruises that occurred during autumn 1986, spring 1987, and autumn 1987 as ENSO 1986-87 cruises. LNSO occurred during 1988 when the coldest sea surface temperature anomalies since the mid-1970s were measured in the ETP (McPhaden & Hayes 1990, Climate Analysis Center 1989a to f). LNSO cruises, therefore, occurred during spring 1988 and autumn 1988. The other cruises are termed 'normal' in the sense that they did not occur during ENSO or LNSO.

Four oceanographic variables were measured during the cruises. Sea surface temperature (°C) and surface salinity (ppt) were measured every half-hour while conducting transects. Thermocline depth (m) and slope (°C) were determined from XBTs deployed 4 to 6 times daily as part of the EPOCS-TOGA projects. For each water mass/season combination, temperature-salinity plots were made to compare ENSO and LNSO cruises with normal cruises. For each water mass/season combination, 1-way analyses of variance with Scheffe's procedure (alpha = 0.05; Miller 1980) were used to test for differences in the 4 oceanographic variables among the various cruises. Scheffe's procedure was used to calculate confidence intervals for specified contrasts among ENSO, LNSO and the other cruises. Any interval not containing zero meant that the variable measured during LNSO or ENSO was significantly different.

Strip transects were conducted using the methodology described by Tasker et al. (1984) and modified slightly by Ainley & Boekelheide (1983). Only censuses made when the ship was moving at least 10 km h^{-1} were included. Total area surveyed and total number of transects made are reported in Tables 1 & 2. We conducted an average of 8 half-hour transects per day of observation (range: 7 to 10 transects d^{-1}).

Because we did not know which particular aspects of the assemblage might be affected during the ENSO and LNSO, we used a broad definition of assemblage to preclude any restriction to differences we might see. Thus, we used the following definition of assemblage (Giller & Gee 1987): the seabird assemblage in that water mass is comprised of all species encountered in a particular water mass during the cruises. This definition is similar to that used in other seabird studies (e.g. Griffiths et al. 1982, Haney 1986) and plankton studies (reviewed in Longhurst & Pauley 1987). This definition includes rare species. A bias in detecting changes may occur if the changes seen were only due to changes in rare species. We therefore analyzed the data with and without extremely rare species (i.e. species where only one individual was seen in the water mass); our conclusions drawn from the analyses did not change. Therefore, we do not believe our definition of assemblage biased our ability to detect changes. Rare species were included in the results presented in this paper.

Abundance (total number of birds) and biomass in each water mass were analyzed at the generic and species levels. Because results using biomass and abundance were similar, only those for abundance are presented in the tables with differences between biomass and abundance noted in the text. The tables for biomass are presented in the Appendix. We collected birds on the cruises and mean weights of birds were determined from specimens from which the digestive tracts had been removed. Biomass was then calculated as the mean weight times the count of the species.

Assemblage characteristics used for comparisons were richness and cumulative abundance curves as reflected by diversity indices. Richness and diversity are typical characteristics used to describe biogeographic areas as well as communities (Griffiths et al. 1982, Brown 1988, Magurran 1988).

Because equal areas were not sampled and equal numbers of individuals were not sighted, generic and species richness were not directly comparable between cruises. Therefore, we calculated rarefacted numbers of genera and species (Tipper 1979) following James & Rathbun (1981). Rarefaction was used to calculate an expected richness by standardizing effort between cruises. This procedure is similar to the standardization procedure used by Haney (1986). However, Haney (1986) standardized on the smallest number of birds seen, while rarefaction standardizes on the smallest count and the smallest area sampled. The rarefacted numbers are directly comparable and differences were considered to be significant.

Cumulative abundance curves [cumulative species versus log(abundance)] cannot be directly compared due to variable species numbers among cruises, but diversity indices can be used to reflect differences between the curves (Legendre & Legendre 1983). We calculated the unbiased Shannon diversity index with standard errors calculated using a jackknife procedure (Adams & McCune 1979). Ninety-five percent confidence intervals (CI) were then used to assess differences among years for each water mass/season combination. If the confidence intervals for ENSO or LNSO cruises did not overlap those from the other cruises, the differences were considered to be significant. The use of the jackknife procedure produces variance estimates that tend to be too large (Efron & Tibshirani 1986); thus using the confidence intervals to judge differences is a conservative procedure. Changes in the percentages of the genera and species were used to explain any significant differences. We considered major genera to be those genera that comprised more than 20 % of the total abundance or biomass in at least 2 normal years. Major species were those comprising greater than 15 % of the total abundance or genera in at least 2 normal years.

Table 1. Mean and standard deviation (SD) for sea surface temperature, sea surface salinity, thermocline depth, and thermocline slope for cruises in Equatorial and Subtropical Surface Waters, 1984 to 1989. #: water mass not adequately sampled (less than 100 km^2 of the water mass sampled); n: number of half-hour transects. * LNSO or ENSO means significantly different from the normal years at alpha = 0.05 using Scheffe's method

Cruise	n	Sea surface temperature (°C)		Sea surface salinity (ppt)		Thermocline Depth (m)		Thermocline Slope (°C)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Spring									
Equatorial Surface Water									
1984	87	26.63	0.99	34.86	0.15	1.7	4.5	3.39	1.20
1985	63	27.06	1.25	34.72	0.30	49.0	19.7	6.26	3.42
1986	75	27.44	1.22	34.51	0.29	52.6	13.2	8.00	2.52
1987 (ENSO)	77	28.71*	0.64	34.75	0.24	44.8	16.0	4.70	2.02
1988 (LNSO)	106	25.62*	2.26	34.65	0.32	49.3	22.1	5.64	2.91
1989	211	26.83	0.83	34.66	0.23	40.0	29.4	5.63	2.65
Subtropical Surface Water									
1984	86	26.30	0.73	35.07	0.04	11.8	3.4	2.04	0.84
1985	108	25.77	1.03	35.13	0.07	44.1	21.6	3.11	1.21
1986	183	25.84	0.96	35.18	0.11	52.3	22.6	4.52	2.76
1987 (ENSO)	82	28.46*	0.21	35.17	0.07	54.3	14.2	4.58	1.63
1988 (LNSO)	128	22.60*	0.73	35.17	0.08	46.1	24.1	4.49	1.95
1989	134	26.27	0.79	35.14	0.10	48.0	28.8	3.87	1.81
Autumn									
Equatorial Surface Water									
1984	78	22.18	1.42	34.67	0.24	22.7	14.1	1.95	0.92
1985	108	22.24	2.34	34.75	0.18	28.2	17.4	2.23	1.66
1986 (ENSO)	122	26.67*	1.49	34.65	0.22	79.7*	25.0	3.56	1.56
1987 (ENSO)	90	26.44*	1.62	34.76	0.24	49.4	19.9	3.51	2.39
1988 (LNSO)	185	23.45	2.29	34.67	0.23	47.0	40.4	3.69	1.63
1989	195	26.11	1.71	34.59	0.33	69.6	30.0	4.41	2.33
Subtropical Surface Water									
1984	#	#	#	#	#	#	#	#	#
1985	63	24.20	1.44	35.12	0.13	68.0	20.3	2.60	1.22
1986 (ENSO)	98	25.92*	1.13	35.14	0.12	97.4*	17.9	4.24	1.60
1987 (ENSO)	85	25.98*	0.90	35.22	0.14	69.8	17.8	4.65	2.00
1988 (LNSO)	#	#	#	#	#	#	#	#	#
1989	98	24.70	1.46	35.15	0.10	75.2	27.6	5.13	2.33

Because the Shannon diversity index typically reflects the changes in the most abundant (i.e. dominant or common) species, we calculated a second diversity index, the inter-quartile slope (*Q*) of the cumulative abundance curve. *Q* tends to reflect the contribution of species with medium abundances (Magurran 1988). We will use the term 'moderately abundant' for genera or species that fall between the 25th and 75th percentiles of the log(abundance) curve. In addition, *Q* appears to be a more stable measure of diversity and is not dependent on the fitting of a particular distribution to the cumulative abundance data (Kempton & Wedderburn 1978). Low values of *Q* indicate low diversity and high values of *Q* indicate high diversity. Since there are currently no variance estimates available for *Q*, ENSO and LNSO cruises were considered to be different from the normal cruises if the ENSO and LNSO *Q* values fell outside the range of values during normal years. Differences in the percentage abundances of individual genera and species were used to interpret the results.

RESULTS

Oceanographic conditions

During spring, the major difference among the years was sea surface temperature (Table 1, Fig. 1). Temperatures were significantly warmer during ENSO and cooler during LNSO in both Equatorial Surface Water [$F = 55.8$, $df_1 = 5$, $df_2 = 613$, $p < 0.001$; ENSO CI: (5.2, 8.5), LNSO CI: (-6.9, -4.0)] and Subtropical Surface Water [$F = 574.9$, $df_1 = 5$, $df_2 = 715$, $p < 0.001$; ENSO CI: (8.1, 11.2), LNSO CI: (-15.1, -12.5)] (Table 1).

During autumn, sea surface temperatures were significantly warmer during ENSO (Fig. 1) for both Equatorial Surface Water [$F = 127.6$, $df_1 = 5$, $df_2 = 772$, $p < 0.001$; ENSO CI: (15.0, 21.5)] and Subtropical Surface Water [$F = 40.5$, $df_1 = 3$, $df_2 = 340$, $p < 0.001$; ENSO CI: (2.2, 3.8)] (Table 1). In addition, for early ENSO, the thermocline was significantly deeper in both water masses [ESW: $F = 20.2$, $df_1 = 5$, $df_2 = 243$, $p < 0.001$; ENSO CI: (50.9, 186.1); SSW: $F = 19.9$, $df_1 = 3$, $df_2 = 84$, $p < 0.001$; ENSO CI: (30.9, 102.5)] (Table 1). For LNSO during autumn, the oceanographic variables were not different from the values in the normal years (Table 1).

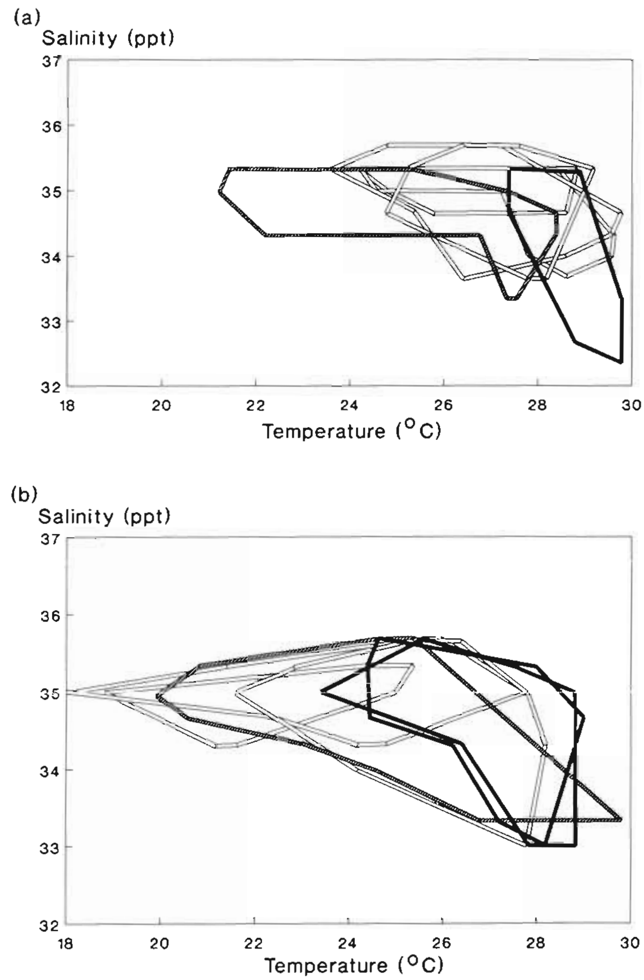

Fig. 1 Outline of sea surface temperature/salinity plots for cruises made during 1984 to 1989 for (a) spring and (b) fall. (▬) Cruises done during ENSO; (▭) cruises done during LNSO; (▭) all other cruises

Seabird assemblages during spring

Equatorial surface water

We encountered 15 to 33 species within 8 to 12 genera; rarefacted numbers were 6 to 8 genera and 11 to 18 species (Table 2). Major genera were storm-petrels (*Oceanodroma*) ($\bar{x} = 38.0$ %, SE = 12.8 %, n = 4), gadfly petrels (*Pterodroma*) ($\bar{x} = 23.2$ %, SE = 7.8 %, n = 4), and shearwaters (*Puffinus*) ($\bar{x} = 17.3$ %, SE = 5.8 %, n = 4), with predominance varying by year (Table 3). Terns (*Sterna*) were variable in importance contributing an average of 13.5 % of the total abundance in the normal years (SE = 6.3 %, n = 4). Boobies (*Sula*) and jaegers (*Stercorarius*) were of relatively minor importance and consistently made up less than 5 % of abundance during normal years. In terms of biomass, gadfly petrels and shearwaters were important in all years, together comprising an average of 63.5 % of the total biomass (SE = 11.1 %, n = 4) (Appendix Table A1). Major species were Leach's storm-petrel *Oceanodroma leucorhoa*, wedge-rumped storm-petrel *Oceanodroma tethys*, Juan Fernandez petrel *Pterodroma externa*, and wedge-tailed shearwater *Puffinus pacificus* (Table 4).

Table 2. Number of genera and species, and the area surveyed for cruises in Equatorial and Subtropical Surface Waters, 1984 to 1989. * Water mass not adequately sampled (less than 100 km^2 of the water mass sampled)

Cruise	Number Genera	Number Species	Area surveyed (km^2)	No. of birds seen	Rarefacted no. Genera	Rarefacted no. Species
Spring			Equatorial Surface Water			
1984	8	15	318.9	151	7	12
1985	8	21	245.8	327	7	15
1986	11	29	286.5	331	8	18
1987 (ENSO)	10	21	306.7	404	6	13
1988 (LNSO)	7	23	424.1	385	5	15
1989	12	33	820.1	1329	6	11
			Subtropical Surface Water			
1984	6	13	293.7	78	6	13
1985	8	15	412.5	289	5	9
1986	12	31	663.1	883	5	10
1987 (ENSO)	10	24	335.4	486	6	14
1988 (LNSO)	5	12	530.9	225	3	8
1989	9	25	512.9	341	6	12
Autumn			Equatorial Surface Water			
1984	12	20	302.9	260	9	16
1985	10	20	448.7	219	9	17
1986 (ENSO)	8	24	471.2	602	6	14
1987 (ENSO)	6	16	332.8	410	5	12
1988 (LNSO)	8	27	769.9	649	5	13
1989	8	27	791.7	1669	5	12
			Subtropical Surface Water			
1984	*	*	*	*	*	*
1985	7	12	242.8	94	7	12
1986 (ENSO)	8	17	400.1	679	5	9
1987 (ENSO)	8	20	318.3	311	6	13
1988 (LNSO)	*	*	*	*	*	*
1989	11	24	402.1	904	5	10

Variability in genera and species composition during normal years can be seen in Tables 3 & 4; patterns for biomass were similar (Appendix Tables A1 to A3). Composition during the 1984 cruise was unusual with the majority of abundance attributable to storm-petrels (67 % of all species seen). This dominance is reflected in the low values for generic and species diversity for 1984 (Fig. 2). The assemblage in the other normal years was relatively more diverse; dominance was shared among 2 or 3 genera (Table 3) and species (Table 4). The moderately abundant genera and species tended to have relatively high diversity (genera Q: 1.52 to 2.35; species Q: 4.57 to 7.51). In particular, many different species were consistently seen in low numbers.

During ENSO, no changes in numbers of genera and species were evident (Table 2, rarefacted numbers) and major genera did not change in percentage abundance or biomass (Table 3, Appendix Table A1). Neither did diversity of the common genera change (Fig. 2). However, among moderately abundant genera and species, diversity decreased compared to the normal years (ENSO: genera $Q = 1.14$; species $Q = 3.41$). The 3 most abundant genera during ENSO, storm-petrels, gadfly petrels and terns, comprised 91.8 % of the abundance compared to an average of 74.7 % (SE = 5.5 %, n = 4) in the normal years (Table 3). Boobies, normally of minor importance, were not observed during ENSO. Sooty terns *Sterna fuscata* and black-winged petrels *Pterodroma nigripennis* increased in percentage abundance during ENSO, comprising 49.3 % of the abundance compared to an average of 12.8 % (SE = 6.4 %, n = 4) during the normal years (Table 4). The 4 major species from the normal years (Leach's storm-petrel, wedge-rumped storm-petrel, Juan Fernandez petrel, and wedge-tailed shearwater) made up 33.6 % of the abundance during ENSO, compared to an average of 66.6 % (SE = 6.3 %, n = 4) during the normal years (Table 4).

During LNSO, fewer genera were seen (Table 2, rarefacted numbers). Boobies and jaegers, seen at low

Table 3. Percentage abundance for genera comprising at least 5 % of total abundance and/or biomass in Equatorial and Subtropical Surface Waters, 1984 to 1989. –: Genus not seen; • surface water not adequately sampled (less than 100 km^2 of the water mass sampled)

Genus	1984	1985	1986	1987	1988	1989
Spring			Equatorial Surface Water			
Storm-petrels (*Oceanodroma*)	71.5	10.7	28.1	19.8	13.8	41.9
Gadfly petrels (*Pterodroma*)	8.6	42.8	28.4	31.2	44.4	13.2
Terns (*Sterna*)	0.7	11.6	30.8	40.8	1.5	10.8
Shearwaters (*Puffinus*)	7.3	26.0	7.2	6.4	37.7	28.7
Boobies (*Sula*)	5.3	1.5	1.2	–	–	0.1
Jaegers (*Stercorarius*)	2.6	4.0	0.9	0.2	–	0.9
Gulls (*Larus*)	2.6	–	–	–	–	0.2
			Subtropical Surface Water			
Storm-petrels	41.0	14.2	26.4	30.6	37.8	42.8
Gadfly petrels	6.4	18.3	37.9	14.4	56.9	18.2
Terns	10.2	46.7	17.4	28.2	0.9	21.7
Shearwaters	39.7	19.0	14.6	16.7	0.9	7.3
Boobies	1.3	0.7	0.2	–	–	–
White-faced storm-petrel (*Pelagodroma*)	–	–	2.1	7.6	3.5	7.3
Autumn			Equatorial Surface Water			
Storm-petrels	67.3	67.1	39.0	21.0	37.4	14.7
Gadfly petrels	25.4	14.6	29.1	51.2	36.8	31.9
Terns	1.9	8.7	20.8	20.0	8.4	21.2
Shearwaters	0.4	2.3	9.0	7.3	13.7	29.9
Boobies	1.9	1.4	0.5	–	–	0.06
Jaegers	0.4	2.7	1.2	0.2	2.8	1.8
Frigatebirds (*Fregata*)	–	0.9	–	0.2	0.3	0.06
			Subtropical Surface Water			
Storm-petrels	•	19.1	29.0	28.0	•	36.1
Gadfly petrels	•	71.3	38.4	55.6	•	20.3
Terns	•	4.2	19.4	8.0	•	31.3
Shearwaters	•	–	11.5	2.2	•	9.9
Jaegers	•	1.1	1.0	3.2	•	0.8

levels in the normal years, were not observed during LNSO (Table 3). Diversity of the common genera did not change (Fig. 2). The LNSO assemblage was similar to the assemblage during normal years by having a few genera dominating the count. Diversity of the moderately abundant genera decreased, however, compared to the normal years (LNSO $Q = 0.88$). During LNSO, most of the species were either gadfly petrels or shearwaters; those 2 genera made up 82.1 % of the abundance compared to an average of 40.5 % (SE = 10.9 %, n = 4) in the normal years (Table 3). Species diversity did not change (Fig. 2, LNSO $Q = 5.32$).

Subtropical surface water

In general, 13 to 30 species within 6 to 12 genera were seen during spring in SSW; rarefacted numbers were 9 to 13 and 5 to 6, respectively (Table 2). Major genera were storm-petrels ($\bar{x}$ = 31.1 %, SE = 6.7 %, n = 4) and shearwaters ($\bar{x}$ = 20.1 %, SE = 6.9 %, n = 4) (Table 3). On the basis of biomass, gadfly petrels and terns were also major genera (Appendix Table A1). Major species included Leach's storm-petrel, sooty tern and wedge-tailed shearwater (Table 4), paralleling the major genera. This concentration of abundance in a few genera is reflected in relatively low generic diversity (Fig. 3; Q: 1.01 to 1.44). There was more diversity in the species (Fig. 3; Q: 2.67 to 5.86).

During ENSO, even though similar numbers of genera were seen (Table 2, rarefacted numbers), generic diversity was significantly higher (Fig. 3). Diversity increased because the storm-petrels, gadfly petrels, terns and shearwaters were more similar in percentage abundance during ENSO compared to the normal years (Table 3). Diversity of the moderately abundant genera during ENSO was similar to the normal

Table 4. Percentage abundance for species comprising at least 5 % of abundance and/or biomass in Equatorial and Subtropical Surface Waters for cruises done during spring 1984 to 1989. –: Species not seen

Species	1984	1985	1986	1987 (ENSO)	1988 (LNSO)	1989
			Equatorial Surface Water			
Storm-petrels:						
Leach's storm-petrel *Oceanodroma leucorhoa*	37.7	10.4	24.5	12.6	6.7	16.7
Wedge-rumped storm-petrel *Oceanodroma tethys*	29.1	0.3	3.6	7.2	6.2	16.0
Harcourt's storm-petrel *Oceanodroma castro*	4.6	–	–	–	0.2	8.7
Gadfly petrels:						
Juan Fernandez petrel *Pterodroma externa*	7.9	36.7	16.9	8.4	16.1	5.9
White-winged petrel *Pterodroma leucoptera*	0.7	0.6	2.7	7.4	5.4	0.1
Black-winged petrel *Pterodroma nigripennis*	–	–	5.7	10.9	10.6	0.4
Tahiti petrel *Pterodroma rostrata*	–	4.0	0.3	0.5	1.5	2.9
Terns:						
Sooty tern *Sterna fuscata*	0.7	9.2	25.1	38.4	1.5	10.1
Shearwaters:						
Wedge-tailed shearwater *Puffinus pacificus*	5.3	23.5	4.8	5.4	34.5	27.2
Sooty shearwater *Puffinus griseus*	1.3	1.5	0.9	0.5	0.2	1.1
Boobies:						
Masked booby *Sula dactylatra*	1.3	0.3	0.6	–	–	0.1
Red-footed booby *Sula sula*	4.0	0.3	0.3	–	–	–
Jaegers:						
Pomarine jaeger *Stercorarius pomarinus*	2.0	3.4	0.3	–	–	0.8
Gulls:						
Swallow-tailed gull *Larus furcatus*	2.6	–	–	–	–	0.2
			Subtropical Surface Water			
Storm-petrels:						
Leach's storm-petrel	32.0	10.7	6.0	13.0	15.1	34.3
Wedge-rumped storm-petrel	7.7	3.5	18.9	17.7	22.7	8.2
Gadfly petrels:						
Juan Fernandez petrel	1.3	2.8	11.7	1.4	12.9	1.5
White-winged petrel	–	10.0	2.4	0.6	33.3	0.6
Black-winged petrel	1.3	0.3	18.0	1.4	5.3	8.2
Tahiti petrel	3.8	4.8	0.9	5.8	3.5	4.4
Terns:						
Sooty tern	7.7	45.7	16.6	26.1	0.9	18.5
Shearwaters:						
Wedge-tailed shearwater	17.9	18.3	12.8	12.1	0.9	4.4
Sooty shearwater	20.5	0.7	0.1	3.5	–	2.9
Boobies:						
Masked booby	1.3	0.7	0.2	–	–	–
White-faced storm-petrel:						
White-faced storm-petrel *Pelagodroma marina*	–	–	2.1	7.6	3.5	7.3

years (ENSO $Q = 1.35$). More species were seen during ENSO (Table 2, rarefacted numbers) but there was no change in species diversity (Fig. 3, ENSO $Q = 5.84$).

During LNSO, fewer genera and species were seen (Table 2, rarefacted numbers), similar to the results of the comparisons in the Equatorial Surface Water. Abundance was concentrated in the storm-petrels and gadfly petrels (Table 3) and is reflected in a significantly lower generic diversity for the LNSO assemblage (Fig. 3; LNSO $Q = 0.67$). Even though fewer species were seen, diversity of common species did not differ (Fig. 3). However, diversity decreased in the moderately abundant species (LNSO $Q = 1.87$). The major species from the normal years (Leach's storm-petrel, sooty tern, and wedge-tailed shearwater) comprised only 16.9 % of the abundance during LNSO compared to an average of 56.2 % (SE = 8.0 %, n = 4) in the normal years (Table 4).

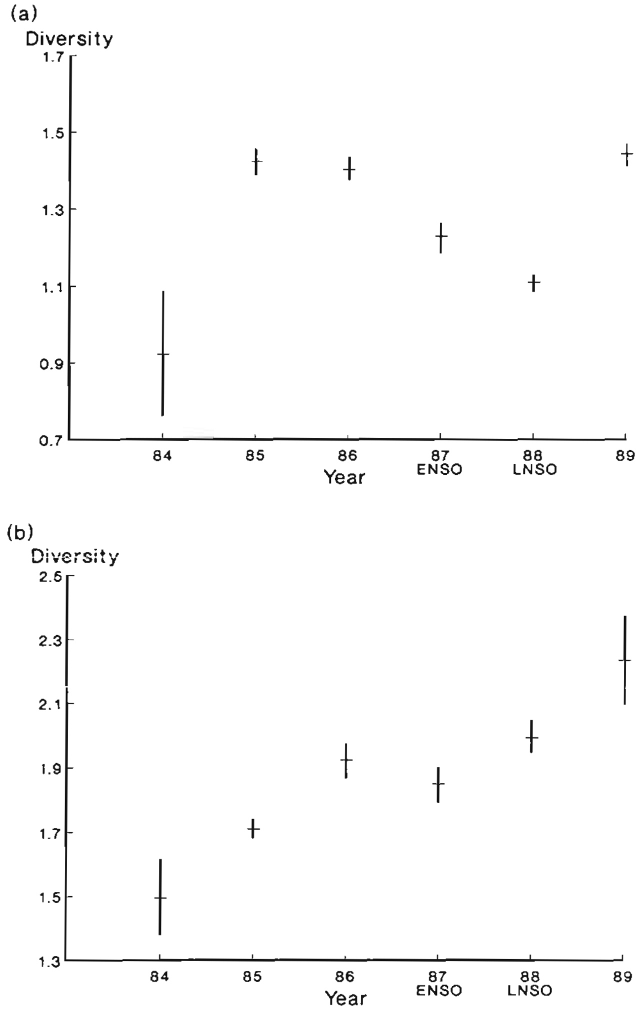

Fig. 2. Shannon index ± 95 % confidence intervals for (a) genera and (b) species seen during spring 1984 to 1989 in Equatorial Surface Water

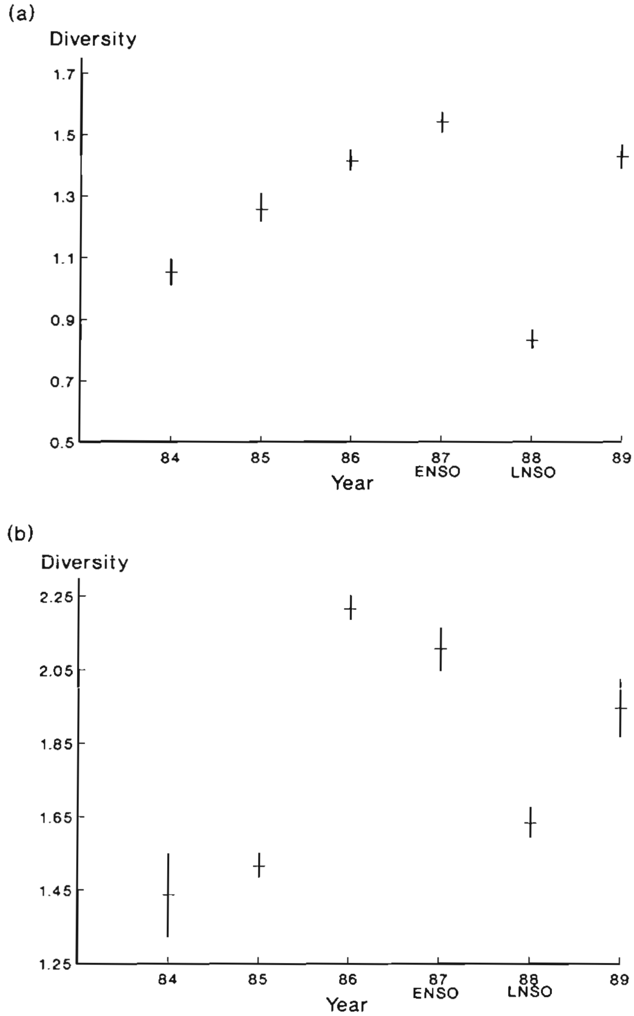

Fig. 3. Shannon index ± 95 % confidence intervals for (a) genera and (b) species seen during spring 1984 to 1989 in Subtropical Surface Water

Seabird assemblages during autumn

Equatorial surface water

We recorded 20 to 27 species within 8 to 12 genera; rarefacted numbers were 12 to 17 and 5 to 9, respectively (Table 2). Major genera were storm-petrels ($\bar{x}$ = 49.7 %, SE = 17.5 %, n = 3) and gadfly petrels ($\bar{x}$ = 24.0 %, SE = 5.0 %, n = 3) (Table 3). Boobies and jaegers were of minor importance, except when biomass was considered (Table 3, Appendix Tables A1 & A3). Major species were Leach's storm-petrel and wedge-rumped storm-petrel (Table 5). Domination by a few genera or species was reflected in low values for the Shannon index (Fig. 4). Moderately abundant genera ranged in diversity from 0.77 (1989 *Q*) to 3.25 (1984 *Q*). Species diversity for moderately abundant species was consistently high (species *Q*: 4.92 to 7.93).

Few changes in the assemblage characteristics were evident during ENSO. Similar numbers of genera and species were seen (Table 2, rarefacted numbers). Generic diversity was similar to the normal years (Fig. 4; ENSO *Q* = 0.97, 0.78), though boobies, normally seen at low levels, were not seen during late ENSO (Table 3). Even though diversity of common species did not change (Fig. 4), that of moderately abundant species decreased (ENSO *Q*: 3.88, 2.39). In early ENSO, the major species were Leach's storm-petrel and sooty tern, and they made up 49.2 % of the abundance. During the normal years, those 2 species comprised an average of 34.9 % of the abundance (SE = 0.2 %, n = 3) (Table 5). During late ENSO, the major species were Juan Fernandez petrel and sooty tern, and they made up 52.7 % of the abundance. During normal years, the 2 species comprised an average of 24.1 % of the abundance (SE = 11.2 %, n = 3) (Table 5).

Table 5. Percentage abundance for species comprising at least 5 % of abundance and/or biomass in Equatorial and Subtropical Surface Waters during autumn, 1984 to 1989. –: Species not seen; * surface water not adequately sampled (less than 100 km^2 of the water mass sampled)

Species	1984	1985	1986 (ENSO)	1987 (ENSO)	1988 (LNSO)	1989
			Equatorial Surface Water			
Storm-petrels:						
Leach's storm-petrel	33.8	30.6	28.9	11.2	28.0	14.2
Wedge-rumped storm-petrel	31.5	26.9	10.1	9.7	8.6	0.5
Gadfly petrels:						
Juan Fernandez petrel	14.6	5.9	13.1	32.7	25.6	25.5
White-winged petrel	8.1	4.6	7.1	8.5	4.2	0.1
Black-winged petrel	0.8	0.9	6.1	1.9	0.6	2.5
Tahiti petrel	0.8	–	1.3	2.2	3.4	2.0
Hawaiian petrel *Pterodroma phaeopygia*	0.4	3.2	0.2	0.2	0.1	–
Stejneger's petrel *Pterodroma longirostris*	–	–	0.3	4.9	0.5	0.3
Terns:						
Sooty tern	0.8	4.6	20.3	20.0	8.3	20.8
Shearwaters:						
Wedge-tailed shearwater	–	–	6.1	3.4	10.5	21.0
Sooty shearwater	–	–	0.3	3.9	1.2	2.3
Newell's shearwater *Puffinus auricularis*	–	–	1.2	–	1.7	5.4
Boobies:						
Masked booby	–	1.4	0.5	–	–	0.06
Jaegers:						
Parasitic jaeger *Stercorarius parasiticus*	0.8	2.7	1.2	0.2	0.3	0.3
			Subtropical Surface Water			
Storm-petrels:						
Leach's storm-petrel	*	9.6	25.0	15.4	*	34.1
Wedge-rumped storm-petrel	*	9.5	4.0	12.5	*	2.0
Gadfly petrels:						
Juan Fernandez petrel	*	11.7	20.8	12.9	*	12.4
White-winged petrel	*	56.4	10.4	31.5	*	4.7
Black-winged petrel	*	1.1	4.6	1.6	*	1.8
Tahiti petrel	*	1.1	1.2	0.6	*	0.9
Stejneger's petrel	*	–	1.2	6.1	*	0.1
Terns:						
Sooty tern	*	4.2	19.0	6.1	*	30.5
Shearwaters:						
Wedge-tailed shearwater	*	–	11.5	0.6	*	5.4
Sooty shearwater	*	–	–	1.6	*	0.7
Jaegers:						
Parasitic jaeger	*	–	0.9	2.6	*	0.2

The assemblage characteristics during LNSO did not differ from the normal years. Numbers of genera and species were the same (Table 2, rarefacted numbers) though boobies were not seen (Table 3). Genera and species diversity did not change (Fig. 4; LNSO: genera $Q = 1.00$, species $Q = 5.50$).

Subtropical surface water

We did not sufficiently sample the Subtropical Surface Water during 1984 and 1988, and, therefore, no LNSO results are presented. In the 2 normal years, 12 and 24 species of 7 and 11 genera, respectively, were seen during autumn in SSW; rarefacted numbers of genera and species were 5 and 7, and 10 and 12 (Table 2). Major genera were storm-petrels and gadfly petrels (Table 3). No consistent major species was found during the 2 normal years though Juan Fernandez petrel comprised about 10 % of the abundance in both years (Table 5). Even though the identities of the dominant genera and species changed among the normal years, percentage abundances were domi-

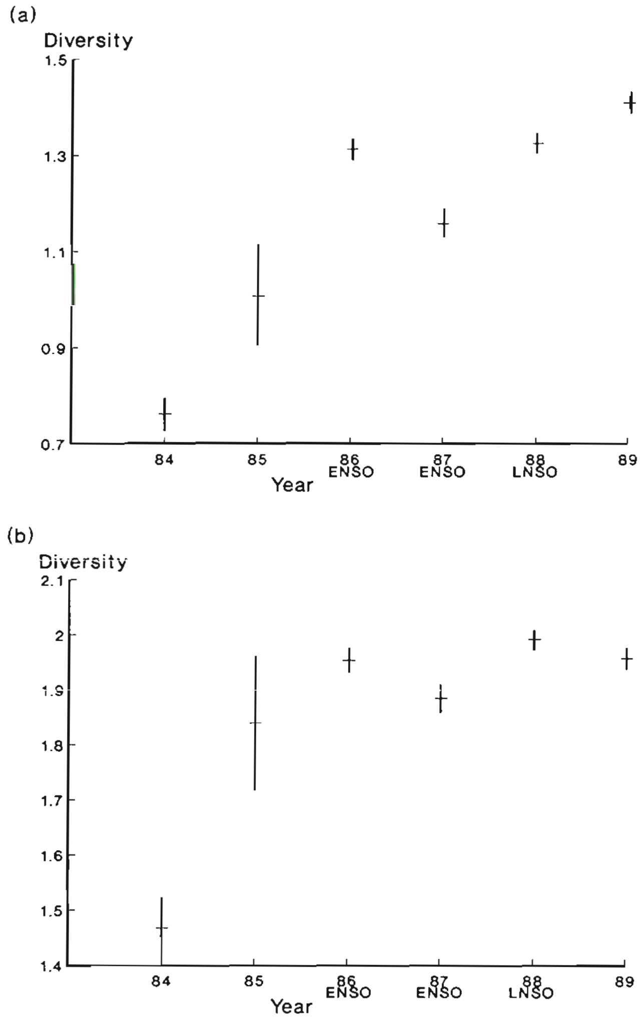

Fig. 4. Shannon index ± 95 % confidence intervals for (a) genera and (b) species seen during autumn 1984 to 1989 in Equatorial Surface Water

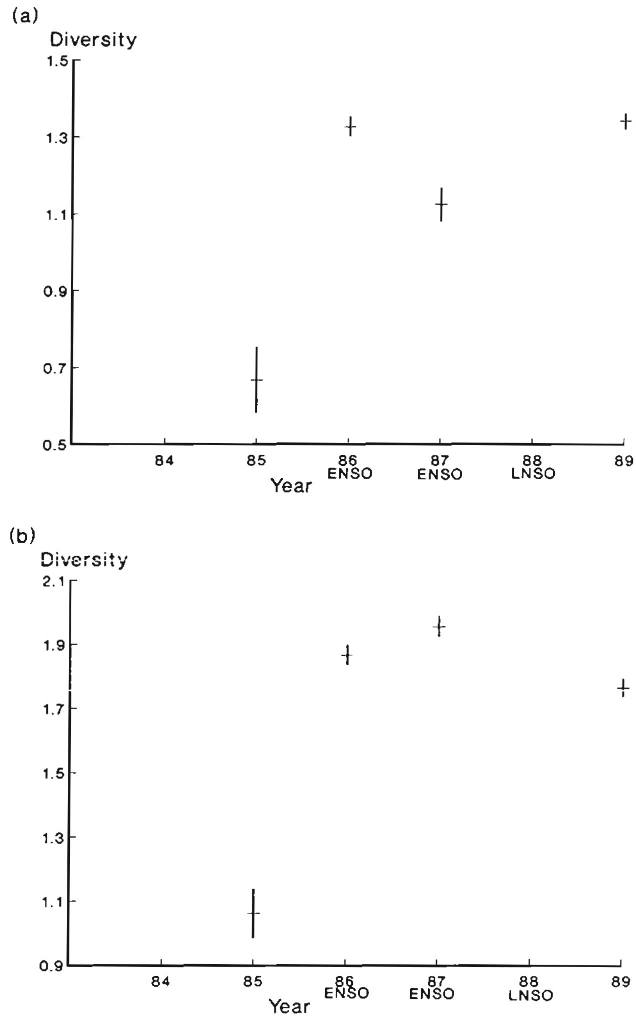

Fig. 5. Shannon index ± 95 % confidence intervals for (a) genera and (b) species seen during autumn 1984 to 1989 in Subtropical Surface Water

nated by a few genera or species (Tables 3 & 5). This dominance was reflected in the low diversity for common genera and species (Fig. 5). Diversity for moderately abundant genera was low (Q = 1.38, 1.25), although species diversity was higher (Q = 2.73, 5.01).

During early ENSO, similar numbers of genera but fewer species were seen compared to the normal years (Table 2, rarefacted numbers). Major genera were similar to the normal years (Table 3), and diversity for common genera did not change (Fig. 5). However, moderately abundant genera decreased (early ENSO Q = 0.92). At the species level, diversity of common species increased (Fig. 5) and that of moderately abundant species decreased (early ENSO Q = 2.34). This change can be seen in the composition of the assemblage. During early ENSO, 86.7 % of abundance was spread relatively evenly among 5 species, Leach's storm-petrel, Juan Fernandez petrel, white-winged petrel *Oceanodroma leucoptera*, sooty tern and wedge-tailed shearwater (Table 5). During 1985, only 1 species, white-winged petrel, dominated the assemblage, making up 56.4 % of abundance (Table 5). During 1989, 2 species, Leach's storm-petrel and sooty tern, dominated the assemblage, making up 64.6 % of abundance (Table 5).

During late ENSO, a different pattern was observed. Even though similar numbers of genera were seen, more species were present compared to the normal years (Table 2, rarefacted numbers). Diversity of common genera did not differ from the normal years (Fig. 5) but an increase in the diversity of moderately abundant genera occurred (late ENSO Q = 1.78). An increase in the diversity of the common species was observed (Fig. 5) though no change was evident in that of the moderately abundant species (late ENSO Q = 3.74). During late ENSO, a total of 72.3 % of the abundance was spread relatively evenly among 4 species, Leach's storm-petrel, wedge-rumped storm-petrel, Juan-Fernandez petrel and white-winged petrel (Table 5). This more even composition was similar to that seen in the early ENSO assemblage.

DISCUSSION

The general distribution of seabirds in the eastern Equatorial Pacific is fairly well known (King & Pyle 1957, King 1970, 1974, Gould 1971, Au & Pitman 1986, Pitman 1986), though our study is the first to consider between-year differences in assemblage characteristics (see also Ribic & Ainley 1988/89) and to consider assemblage characteristics on the macro-scale (i.e. water mass). Previous work on seabirds in the ETP emphasized meso-scale or smaller features (100 to 1000 km; Hunt & Schneider 1987) such as associations of species in feeding flocks, usually over tuna (*Thunnus* spp.), rather than by habitat type (i.e. water masses; see Reilly 1990 for dolphin species distribution in relation to water masses). To be sure, all of the above studies noted the correspondence of various individual species to sea-surface temperature and noted that particular species were apparently associated with meso-scale features such as convergence zones. Our study, by considering assemblage characteristics rather than individual species, is most similar to the studies of Abrams & Griffiths (1981) and Griffiths et al. (1982) who studied species richness and diversity of seabird communities off South Africa. Our focus on the macro-scale and water masses is most similar to that of Pocklington (1979) and Wahl et al. (1989) who described seabird assemblages in the Indian Ocean and northern North Pacific, respectively, although these studies as well did not consider annual differences in species composition.

The seabird assemblages in the different water masses of the ETP normally varied from year to year. This variability is exemplified by the differences seen in the spring assemblages of the normal years. The most extreme normal year was 1984, which followed the severe 1982-83 ENSO. Even though the physical oceanographic conditions were considered to be in the normal range in 1984, there may have been carryover effects of the ENSO into the spring of 1984 which may have been reflected in the seabird assemblage characteristics. However, we did not consider this a compelling enough reason for removing 1984 from the 'normal' years and we chose to keep 1984 in the set. Our decision resulted in a conservative approach to detecting ENSO/LNSO changes since the variability of the seabird assemblage characteristics in the normal years was increased.

Even with the normal variability in the assemblage characteristics, the assemblage characteristics still changed the most during both ENSO and LNSO (Tables 6 & 7). The typical impact of either event was to decrease diversity of the genera and species normally in the moderately abundant class, generally the terns, boobies and jaegers. The common taxa, storm-petrels, gadfly petrels and shearwaters, were not affected.

For ENSO, the changes in the assemblage depended on water mass and season. The most marked changes occurred in Subtropical Surface Water during autumn. This effect during autumn but not spring is likely due to the impact of ENSO on equatorial upwelling. Even though mean sea-surface temperature was significantly warmer during ENSO in both seasons in our study area, the thermocline was significantly depressed only during autumn (early in ENSO). During early ENSO, the seabird assemblage in both water masses showed changes but more changes were seen in the Subtropical Surface Water where the depression of the thermocline was the greatest. Equatorial upwelling, normally strongest during autumn, was disrupted during the warm phase of ENSO (McPhaden & Hayes 1990). In the upwelling domain of the California Current, Ainley (1976) and Briggs et al. (1987) also noted marked changes in species distributions during ENSO in conjunction with geographical shifts in marine climate. In the Equatorial Pacific, diversity and richness increased in Subtropical Surface Water during late ENSO when the thermocline was not depressed. In addition, equatorial waters apparently remained nutrient rich during August-November 1987 (Fiedler et al. in press).

Terns, boobies, 1 shearwater (wedge-tailed shearwater), and jaegers are closely associated with tuna schools (the jaegers by virtue of kleptoparasitizing the terns and boobies; Ainley, Spear & Ribic unpubl. data) (Au & Pitman 1986). In our study, boobies were frequently missing from the seabird assemblage during ENSO, particularly in the Equatorial Surface Water. However, the sooty tern and wedge-tailed shearwater did not decrease during ENSO. Boobies are more dependent on the presence of land (Au & Pitman 1986); thus the stress from ENSO may have caused the boobies to contract their range to more central areas (i.e. areas closer to land). Sooty terns, adapted to the open ocean (Au & Pitman 1986), were already in their central range and thus no contraction would be expected.

The effect of LNSO appeared to be strongest during spring compared to autumn. During spring, a major decrease in diversity and richness, particularly in the

Table 6. Summary of changes during 1986-87 ENSO

Season	Equatorial Surface Water	Subtropical Surface Water
Spring	Decreased diversity: medium-abundant genera and species	Increased species richness
	Increased presence of terns; boobies not seen	Increased diversity: common genera
Autumn	Early ENSO:	Early ENSO:
		Decreased species richness
	Decreased diversity: medium-abundant species	Increased diversity: common species
		Decreased diversity: medium-abundant genera and species
	Late ENSO:	Late ENSO:
		Increased species richness
	Decreased diversity: medium-abundant species	Increased diversity: medium-abundant genera and common species
	Increased presence of gadfly petrels; boobies not seen	

genera, was seen regardless of water mass. It appeared as if the assemblages consolidated into the major taxa with less abundant taxa disappearing. The largest differences in mean sea-surface temperatures in our study area occurred during spring as well. This is similar to the results of McPhaden & Hayes (1990) who found that the coldest equatorial temperature anomalies developed in early 1988 in response to a large-scale, remotely forced upwelling. However, little is known about the productivity of the area during LNSO in the spring. In the autumn, August to November 1988, Fiedler et al. (in press) found that nutrients and chlorophyll had increased in equatorial waters compared to 1986 and 1989. In the Equatorial Surface Water of our study area, sea-surface temperatures were not different from the normal years and no changes in the autumn assemblage characteristics were found during LNSO.

Our previous work (Ribic & Ainley 1988/89) hypothesized no impact on composition of species assemblages due to ENSO at the mega-scale. However, that analysis emphasized common species leaving any changes in moderately abundant species undetected. As Brown (1988) points out, the less common species may be as interesting as the dominant species in a community. On a macro-scale in the present study, we found differences that depended on water mass and season manifested by changes in minor taxa with few changes found in the major taxa. These results emphasize the importance of considering scale when investigating the characteristics of seabird assemblages (Hunt & Schneider 1987). Our results here also indicate a need to quantify the relative productivity of equatorial water masses during climatic perturbations and to understand better the ecology of individual species within the assemblages.

Table 7. Summary of changes during 1988 LNSO

Season	Equatorial Surface Water	Subtropical Surface Water
Spring	Decreased generic richness	Decreased generic and species richness
	Decreased diversity: medium-abundant genera	Decreased diversity: common genera, medium-abundant genera and species
	Decreased presence of terns; boobies not seen	Increased presence of gadfly petrels; decreased presence of terns and shearwaters
Autumn	Boobies not seen	[not covered]

The minor taxa in our study area are generally more abundant elsewhere. Thus, the reason for their small representation was likely related to being at the periphery of their normal range or habitat. Changes in marine climate, then, were enough to discourage their presence with, perhaps, movement to more productive areas (e.g. ENSO refugias of Tershy et al. 1991). As we have been amassing much data on differences in feeding ecology of seabirds among years and water masses, this will be the subject of future contributions.

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The research described herein was developed by one of the authors, an employee of the U.S. EPA, on her own time. It was conducted independent of EPA employment and has not been subjected to the Agency's peer and administrative review. Therefore, the conclusions and opinions drawn are solely those of the author and should not be construed to reflect the views of the Agency.

APPENDIX

Table A1. Percentage biomass for genera comprising at least 5 % of total abundance and/or biomass in Equatorial and Subtropical Surface Waters 1984 to 1989. –: Genus not seen; • water mass not adequately sampled (less than 100 km^2 of the water mass sampled)

Genus	1984	1985	1986	1987	1988	1989
Spring						
			Equatorial Surface Water			
Storm-petrels	12.9	1.3	5.1	3.4	1.6	6.8
Gadfly petrels	19.1	53.3	38.5	40.7	44.2	26.1
Terns	0.7	5.6	27.4	38.9	0.9	8.6
Shearwaters	17.7	31.1	15.2	13.9	51.7	53.0
Boobies	32.6	1.0	7.2	–	–	0.8
Jaegers	7.0	5.9	2.4	0.9	–	2.0
Gulls	9.2	–	–	–	–	0.7
			Subtropical Surface Water			
Storm-petrels	4.7	2.1	3.8	4.9	7.7	10.6
Gadfly petrels	7.4	20.6	49.5	24.0	87.6	31.0
Terns	5.1	36.3	14.7	25.8	1.4	25.4
Shearwaters	71.4	34.5	26.6	40.6	2.4	26.3
Boobies	8.0	4.2	1.6	–	–	–
White-faced storm-petrel	–	–	0.4	1.5	0.9	1.9
Autumn						
			Equatorial Surface Water			
Storm-petrels	18.3	15.8	8.0	2.8	5.3	1.9
Gadfly petrels	68.9	31.2	49.2	67.3	56.7	41.7
Terns	2.2	9.0	15.2	13.4	6.0	12.0
Shearwaters	1.3	6.2	19.3	15.0	24.6	40.4
Boobies	1.0	5.1	2.4	–	–	0.1
Jaegers	3.0	13.2	4.4	0.6	5.4	2.9
Frigatebirds	–	0.9	–	0.9	1.3	0.4
			Subtropical Surface Water			
Storm-petrels	•	3.4	5.2	5.1	•	7.6
Gadfly petrels	•	83.7	55.9	67.6	•	37.1
Terns	•	4.4	15.8	6.8	•	29.1
Shearwaters	•	–	19.2	7.6	•	22.0
Jaegers	•	2.9	2.8	12.0	•	1.9

Table A2. Percentage biomass for species comprising at least 5 % of abundance and/or biomass in Equatorial and Subtropical Surface Waters during spring 1984 to 1989. –: Species not seen

Species	1984	1985	1986	1987 (ENSO)	1988 (LNSO)	1989
			Equatorial Surface Water			
Leach's storm-petrel	8.3	1.3	4.8	2.5	1.0	3.3
Wedge-rumped storm-petrel	3.5	0.02	0.4	0.8	0.5	1.7
Harcourt's storm-petrel	1.1	–	–	–	0.05	1.7
Juan Fernandez petrel	18.5	46.8	29.5	19.0	23.6	12.1
White-winged petrel	0.6	0.3	2.1	6.1	3.1	0.06
Black-winged petrel	–	–	3.6	8.9	6.2	0.8
Tahiti petrel	–	4.9	0.5	1.1	2.2	5.4
Sooty tern	0.7	4.8	24.4	37.6	0.9	8.3
Wedge-tailed shearwater	11.2	26.4	8.5	10.7	47.3	48.2
Sooty shearwater	5.8	3.5	3.8	1.9	0.7	4.2
Masked booby	10.2	0.4	4.2	–	–	0.8
Red-footed booby	22.4	0.3	1.5	–	–	–
Pomarine jaeger	4.8	4.7	0.7	–	–	1.8
Swallow-tailed gull	9.2	–	–	–	–	0.7
			Subtropical Surface Water			
Leach's storm-petrel	4.0	1.8	1.3	2.7	4.2	9.2
Wedge-rumped storm-petrel	0.6	0.3	2.2	2.2	3.6	1.2
Juan Fernandez petrel	1.7	4.7	26.2	3.2	35.8	4.0
White-winged petrel	–	6.4	2.0	0.5	33.3	0.6
Black-winged petrel	0.6	0.2	14.2	1.2	5.5	8.7
Tahiti petrel	5.0	8.8	1.9	13.3	9.9	11.6
Sooty tern	4.3	35.9	14.3	24.7	1.4	23.0
Wedge-tailed shearwater	21.4	32.1	22.3	24.2	2.4	11.3
Sooty shearwater	48.8	2.4	0.4	14.7	–	15.0
Masked booby	8.0	4.2	1.6	–	–	–
White-faced storm-petrel	–	–	0.4	1.5	0.9	1.9

Table A3. Percentage biomass for species comprising at least 5 % of abundance and/or biomass in Equatorial and Subtropical Surface Waters during autumn 1984 to 1989. –: Genus not seen; * water mass not adequately sampled (less than 100 km^2 of the water mass sampled)

Species	1984	1985	1986 (ENSO)	1987 (ENSO)	1988 (LNSO)	1989
			Equatorial Surface Water			
Leach's storm-petrel	11.4	8.3	6.7	1.8	4.5	1.8
Wedge-rumped storm-petrel	6.2	4.3	1.3	1.0	0.7	0.03
Juan Fernandez petrel	51.4	16.8	32.8	53.0	44.4	35.9
White-winged petrel	10.2	4.7	6.3	5.0	2.4	0.1
Black-winged petrel	0.9	1.0	5.1	1.2	0.4	1.3
Tahiti petrel	2.8	–	3.0	3.6	5.8	2.8
Hawaiian petrel	1.2	8.8	0.3	0.5	0.3	–
Stejneger's petrel	–	–	0.3	2.8	0.2	0.1
Sooty tern	1.2	5.8	14.9	13.4	5.9	11.9
Wedge-tailed shearwater	–	–	12.5	4.5	16.8	26.1
Sooty shearwater	–	–	1.5	10.5	4.4	5.4
Masked booby	–	5.1	2.4	–	–	0.1
Newell's shearwater	–	–	2.5	–	3.1	7.4
Parasitic jaeger	3.0	13.2	4.4	0.6	0.8	0.6
			Subtropical Surface Water			
Leach's storm-petrel	*	2.1	4.8	3.6	*	7.4
Wedge-rumped storm-petrel	*	1.2	0.3	1.5	*	0.2
Juan Fernandez petrel	*	28.3	42.1	30.4	*	27.9
White-winged petrel	*	51.3	7.3	26.2	*	3.8
Black-winged petrel	*	0.8	3.3	1.3	*	1.5
Tahiti petrel	*	2.5	2.2	1.5	*	2.1
Stejneger's petrel	*	–	0.7	4.4	*	0.1
Sooty tern	*	4.4	15.6	5.7	*	28.7
Wedge-tailed shearwater	*	–	19.2	1.4	*	10.8
Sooty shearwater	*	–	–	6.2	*	2.7
Parasitic jaeger	*	–	2.5	10.5	*	0.8

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