

KEY SPECIES IN THE PELAGIC COPEPOD COMMUNITY STRUCTURE ON THE WEST COAST OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

The community structure of pelagic copepods was obtained from 494 zooplankton samples collected on ten cruises made by CICIMAR in the northwest Mexican Pacific (31°N 118°W, 22°N 108°W) between 1984 and 1989. Of the 144 taxa identified, *Acartia danae* (temperate-tropical), *Calanus pacificus* (transitional), *Euchaeta marina* (tropical), and *Pleuromamma abdominalis* (tropical) were the most important species according to their frequency of occurrence, abundance, and contribution to total variance of the community. *C. pacificus* was dominant in almost every month sampled. The ratio of the abundance of this species to the other three decreased from north to south. The abundance of *A. danae*, *E. marina*, and *P. abdominalis* changed month by month and with latitude. The dominance of *C. pacificus* over the other species suggests resource partitioning favoring this species. The abundance of the two tropical species increased in summer and autumn, and that of the transitional species in winter and spring.

INTRODUCTION

Key species exploit a common resource in a similar way (Root 1967). Sometimes a single species is able to exploit most of the available resources. This means that the community structure depends on key species (Paine 1969) and that the dominant species controls the occurrence of other species. The number of species and their relative abundance is what community ecologists call species structure (McGowan and Miller 1980). An important aspect of a community species structure that seems highly variable is the constancy of the rank order of species abundance in time and space.

The rank order of plankton species changes dramatically from sample to sample, as McGowan and Miller (1980) showed in their paper on larval fish and zooplankton community structure in the California Current, as Hernández-Trujillo and Esquivel-Herrera (1997) showed for the copepod community along the west coast of Baja California, and as Palomares-García and Gómez-

Gutiérrez (1996) showed for the copepod community at Bahía Magdalena on the southwest coast of Baja California Sur. Other studies of the abundance and species composition of zooplankton have shown that a few species dominate the whole community structure (Longhurst 1967, 1995; McGowan and Miller 1980; Weikert 1982; Palomares-García 1996). These small species groups become recurrent groups when they occur in the same sample more often than can be attributed to chance (Fager and McGowan 1963), which means there are common factors systematically influencing the occurrence of these groups.

The purpose of this paper is to identify the key species in the copepod community along the west coast of the Baja California peninsula between 1984 and 1989 by examining abundance, hierarchies, and the constancy of the frequency of occurrence of particular species.

METHODS

A total of 494 zooplankton samples was obtained on 10 oceanographic cruises made by the Centro Interdisciplinario de Ciencias Marinas (CICIMAR; fig. 1). The sampling protocol was taken from Smith and Richardson (1977): oblique tows of bongo nets equipped with digital flowmeters and mesh sizes of 333 and 505 μm were made. The adult copepods in the 505 μm net were sorted, identified, and counted with the method of Hernández-Trujillo (1991a). Sea-surface temperature (SST) data were collected at each station with an Inter-Ocean CTD. Additional historical data were obtained from CD-ROM COAD (ORSTROM & NOAA). Cole and McLane (1989) divided the study area into three latitudinal blocks (21°–24°N, 24°–27°N, and 27°–30°N); I used their divisions.

I determined the key species by following three criteria: (1) occurrence in the cruises 100% of the time, (2) great abundance, and (3) contribution to total variance of the community according to principal components analysis (PCA). A two-way ANOVA was used to test for differences in the mean of key species abundance, phytoplankton abundance, SST variability among cruises and latitude, season, and latitude ($\alpha = 0.05$). The PCA

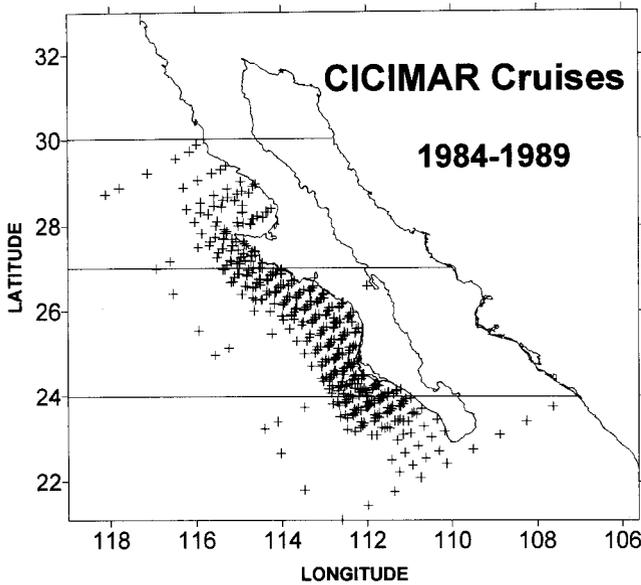


Figure 1. The CICIMAR station grid, 1984–89.

method was used to determine recurrent groups of the copepod species. I applied this analysis to a matrix with abundance values per sampling station after normalizing by log-transformation ($x + 1$).

Microphytoplankton (>20 μm , MF) and nannophytoplankton (5–20 μm , NF) data were from Hernández-Trujillo et al. (unpublished data). I analyzed the key species abundance with SST and phytoplankton (MF and NF)

by season using regression of Pearson product-moment ($P < 0.05$) to indicate trends between variables and not to represent the functional forms of causal mechanisms (Mullin 1998).

RESULTS

A total of 144 copepod species was identified. From this assemblage 11 species (*Pleuromamma abdominalis*, *Euchaeta marina*, *Paracalanus parvus*, *Calanus pacificus*, *Pleuromamma gracilis*, *Rhincalanus nasutus*, *Labidocera acutifrons*, *Euchaeta longicornis*, *Acartia danae*, *Subeucalanus subcrassus*, and *Scolecithrix danae*) were found in every cruise. I found that 4 were dominant, and named them *key species*: *Acartia danae*, *Calanus pacificus*, *Euchaeta marina*, and *Pleuromamma abdominalis*. Their mean abundances by cruise are shown in table 1.

The relative abundance of *A. danae*, *C. pacificus*, *E. marina*, and *P. abdominalis* showed high variability during the period studied (table 2). Those changes can be seen in the changes of species rank within the community structure.

The ANOVA for *A. danae*, *E. marina*, and *P. abdominalis* shows significant differences by month ($P < 0.05$) but not for latitude factor ($P > 0.05$). The ANOVA for *C. pacificus* showed that H_0 was rejected for both month and latitude factor ($P < 0.05$; table 3).

Seasonally, the ANOVA (table 4) showed that *A. danae* abundance was not different by temporal and geographical factors ($P > 0.05$). The remaining key species showed

TABLE 1
Average Abundance (Org · 1,000 m⁻³) of Copepod Key Species by Cruise on the West Coast of Baja California, 1984–89

Cruise number	8401	8405	8505	8508	8605	8611	8707	8710	8807	8906
Species (n_i) ^a	77	38	37	42	67	68	52	72	69	58
<i>Acartia danae</i>	705	9,719	1,420	118	503	48	4,954	474	279	252
<i>Calanus pacificus</i>	1,034	334,777	58,319	7,530	70,060	569	100,254	6,251	38,368	25,675
<i>Euchaeta marina</i>	1,325	1,402	324	825	354	1,023	345	1,786	757	339
<i>Pleuromamma abdominalis</i>	1,994	19,690	1,595	713	965	1,163	1,293	731	1,222	910

^a n_i = number of species identified by cruise.

TABLE 2
Relative Abundance and Rank of Key Species in the Copepod Community by Cruise on the West Coast of Baja California, 1984–89

Cruise	<i>Acartia danae</i>		<i>Calanus pacificus</i>		<i>Euchaeta marina</i>		<i>Pleuromamma abdominalis</i>	
	Percentage	Rank	Percentage	Rank	Percentage	Rank	Percentage	Rank
8401	4.8	5	8.9	4	13.7	2	18.9	1
8405	1.4	5	85.8	1	<1.0	11	3.3	3
8505	1.7	5	81.5	1	<1.0	17	1.6	6
8508	<1.0	16	60.2	1	13.3	2	3.1	5
8605	<1.0	4	96.2	1	<1.0	7	<1.0	3
8611	<1.0	38	9.4	4	13.8	1	6.4	7
8707	3.3	2	92.7	1	<1.0	8	<1.0	5
8710	<1.0	25	36.2	1	8.7	3	2.5	8
8807	<1.0	11	84.5	1	1.2	4	2.0	3
8906	<1.0	15	88.2	1	<1.0	7	1.9	2

TABLE 3
 Two-Way ANOVA of the Effect of Month and Latitude on the Variability of Key Species Abundance on the West Coast of Baja California, 1984–91

Source	DF	MS	F	P	H ₀
<i>Acartia danae</i>					
Month	10	2.6E09	3.530	<0.05	Rejected
Latitude	2	1.6E07	0.225	>0.05	Accepted
Residual	194	75359057			
Total	206				
<i>Calanus pacificus</i>					
Month	10	5.6E11	8.007	<0.05	Rejected
Latitude	2	1.0E11	1.494	<0.05	Rejected
Residual	450	7.1E10			
Total	462				
<i>Euchaeta marina</i>					
Month	10	8359116	2.410	<0.05	Rejected
Latitude	2	41191	0.012	>0.05	Accepted
Residual	300	3468813			
Total	312				
<i>Pleuromamma abdominalis</i>					
Month	10	1.3E09	3.246	<0.05	Rejected
Latitude	2	3.8E08	0.949	>0.05	Accepted
Residual	287	4.4E08			
Total	299				

TABLE 4
 Two-Way ANOVA of How Season and Latitude Affect the Variability of Key Species Abundance on the West Coast of Baja California, 1984–91

Source	DF	MS	F	P	H ₀
<i>Acartia danae</i>					
Season	3	1.5E08	3.530	>0.05	Accepted
Latitude	2	9.4E06	0.225	>0.05	Accepted
Residual	201	83639810			
Total	206				
<i>Calanus pacificus</i>					
Season	3	6.0E11	7.760	<0.05	Rejected
Latitude	2	1.7E11	2.223	>0.05	Accepted
Residual	457	7.8E10			
Total	462				
<i>Euchaeta marina</i>					
Season	3	16012152	4.568	<0.05	Rejected
Latitude	2	173327	0.049	>0.05	Accepted
Residual	307	3505532			
Total	312				
<i>Pleuromamma abdominalis</i>					
Season	3	1.1E09	2.753	<0.05	Rejected
Latitude	2	4.6E08	1.076	>0.05	Accepted
Residual	294	4.3E08			
Total	299				

significant differences between season ($P < 0.05$) but not for latitude ($P > 0.05$).

The PCA shows the spatial representation of the abundance and the relation of copepod species with the first two principal components. For each cruise the variance of the two first components, obtained by the PCA applied to the matrix of copepod abundance, is shown in table 5.

The first component is identified with a set of variables that determines the differential abundance of each species; therefore all species have a positive correlation with this component. The groups are separated according to the density of the species that constitute them. The second component is identified with the SST, separating the species that have high abundance in warm or cold waters.

Figures 2 and 3 illustrate the dispersion diagram of the first two components for each cruise. The graphs have a point for each species, and the disposition of points spatially represents the relation between the abundance distributions of the species with respect to the first two components, which account for between 92% (August 1986) and 51% (November 1986) of the total variance.

The graphs show the key species position in bidimensional hyperspace according to their relative abundance and distribution. For almost all cruises, the key species position is separate from the other copepod species.

Figure 4 shows the seasonal relation between key species abundance and the SST for all 10 cruises over the 6 years. On the basis of linear regression, in winter, spring, and autumn (except for *E. marina*), the abun-

TABLE 5
 Percent of Variance of First Two Principal Components (C1, C2), the Cumulative Percentage (Σ Variance), and Number of Samples by Cruise (n)

Cruise	C1	C2	Σ Variance	n
8401	47.02	9.75	56.78	47
8405	64.35	18.65	83.01	68
8505	74.13	7.98	82.11	38
8508	88.38	3.93	92.31	47
8605	87.16	4.67	91.83	61
8611	39.27	12.52	51.79	57
8707	86.26	5.61	91.87	39
8710	49.65	16.22	65.88	62
8807	44.55	23.39	67.94	37
8906	81.12	7.54	88.67	38

dance of the key species was inversely related to SST. In autumn there was a positive relation of the key species and SST (table 6).

The abundance of copepod key species related to phytoplankton abundance (figs. 5 and 6) shows that in winter the greater abundance of key species was observed mainly in the microphytoplankton abundance range of 500 to 5,000 cell/L and for nanophytoplankton between 2,000 and 5,000 cell/L. In spring there was a wide range in copepod abundance (10 to 500,000 org/1,000 m³) associated with microphytoplankton abundance between 100 and 25,000 cell/L. *Calanus pacificus* was clearly more abundant in comparison with the other key species. For nanophytoplankton, the highest copepod abundance was associated with 5,000 to 25,000 cell/L. Again, *C. pacificus* was more abundant than the other copepod species.

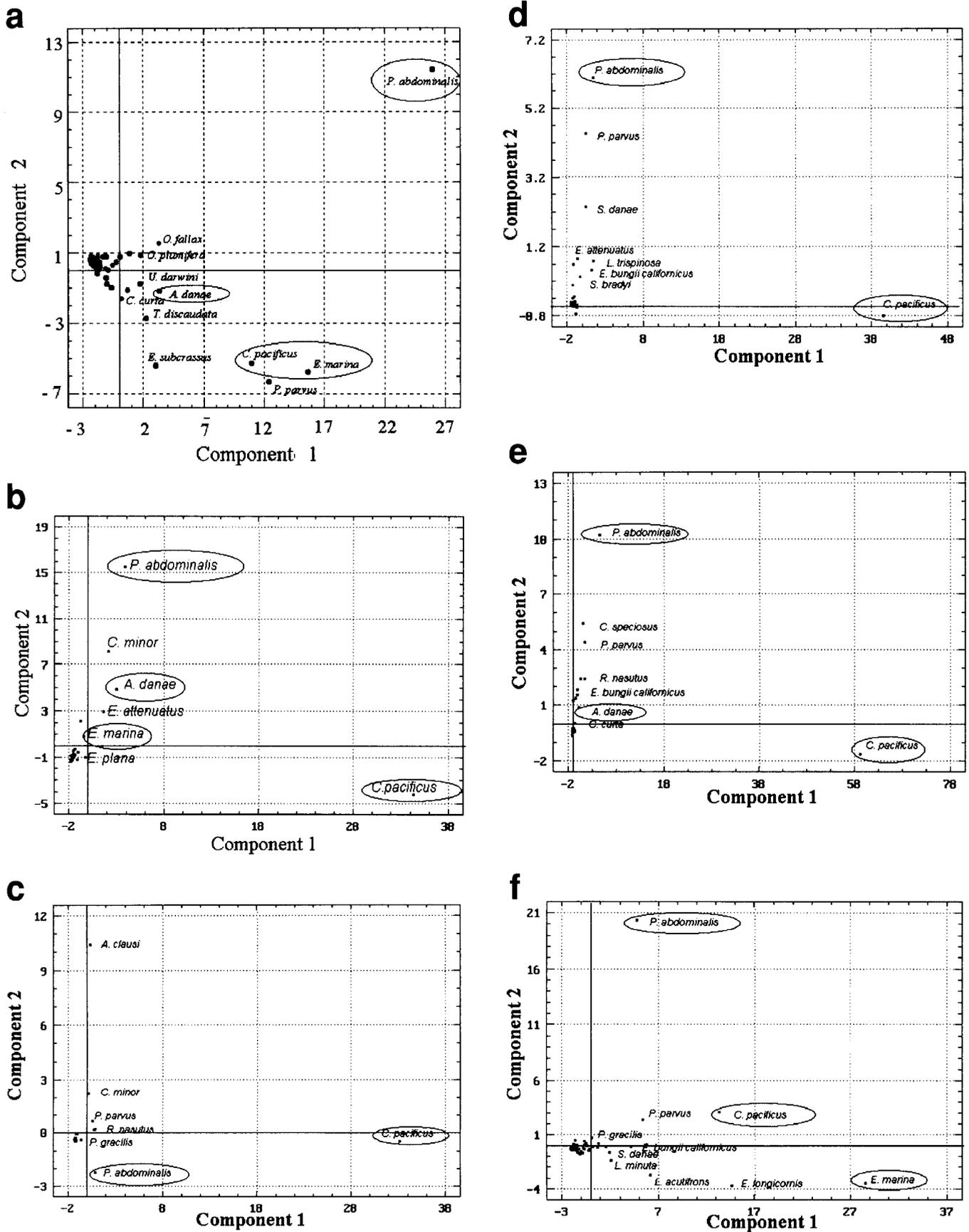


Figure 2. Dispersion diagrams of the two first principal components for cruises 8401 (a), 8405 (b), 8505 (c), 8508 (d), 8605 (e), and 8611 (f).

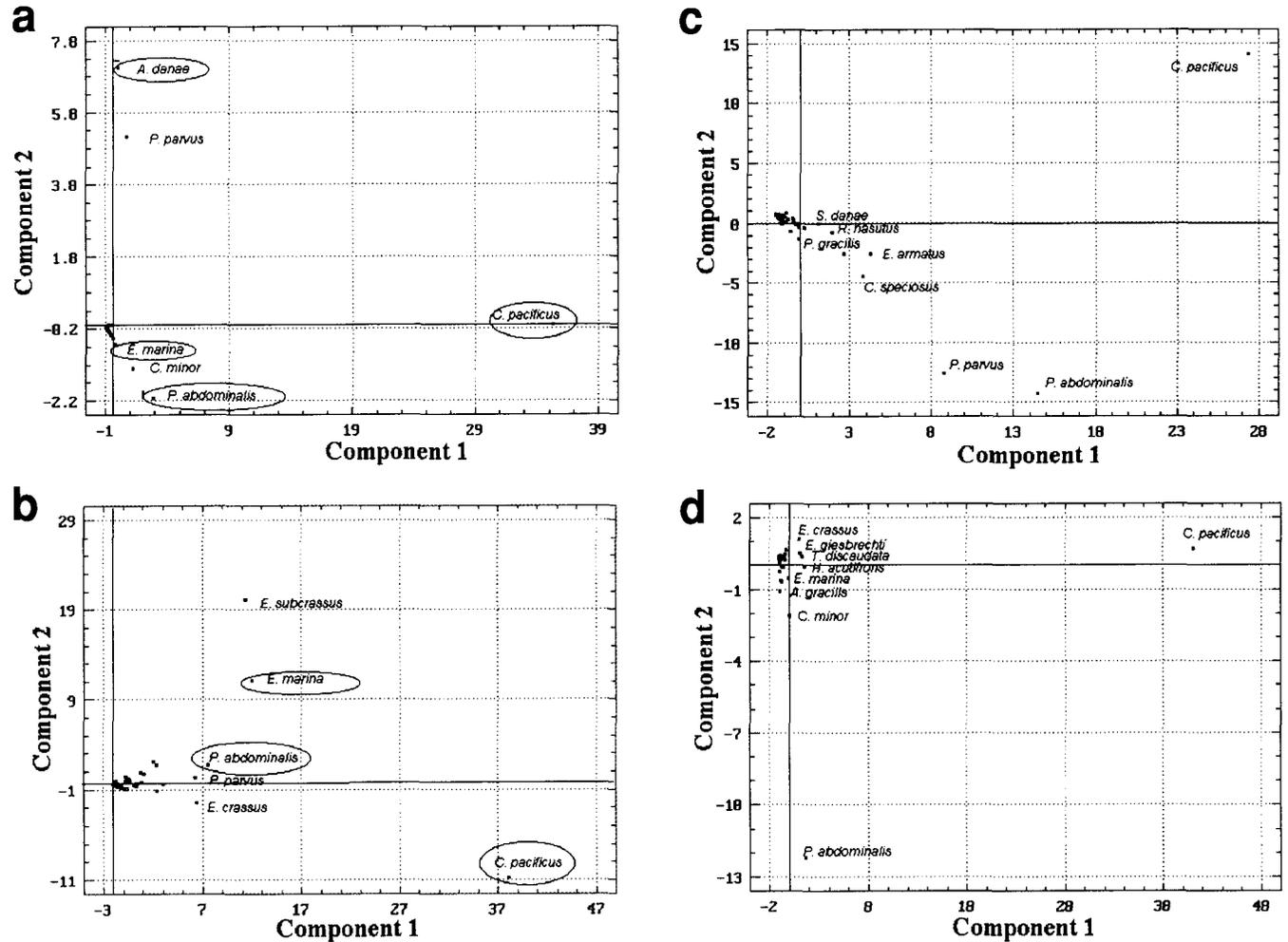


Figure 3. Dispersion diagram of the two first principal components for cruises 8707 (a), 8710 (b), 8807 (c), and 8906 (d).

In summer the key species abundance was similar to that in spring, and occurred with concentrations of microphytoplankton between 100 and $1 \cdot 10^6$ cell/L. For nanophytoplankton, abundance, as well as the key species, was similar to the microphytoplankton, but the main abundance of copepods occurred between 5,000 and 25,000 cell/L. For both phytoplankton size fractions, *C. pacificus* was the dominant species.

In autumn the abundance of copepods decreased to 10–25,000 org./1,000 m³ and occurred at concentrations of microphytoplankton between 125 and 5,000 cell/L. For nanophytoplankton, the larger key species abundance was observed in the range of 5,000 and 60,000 cell/L. For both size fractions, the key species abundance was similar, without dominance of any one species.

The linear regression of the abundance of key species and MF showed an inverse relation for all species in winter, and a positive relation in the other seasons. For NE, a similar situation was observed for winter but not for the other seasons, in which there were negative correlations for *A. danae* in summer and autumn, and for *P. abdominalis* in autumn (tables 7 and 8).

TABLE 6
 Product-Moment Correlation between Copepod
 Key Species and SST on the West Coast of
 Baja California, 1984–89

	Algebraic formula	<i>r</i>	<i>r</i> ²	<i>N</i>
Winter				
<i>A. danae</i>	$Y = 10.3 - 0.240x + eps$	-0.25	0.07	32
<i>C. pacificus</i>	$Y = 14.1 - 0.410x + eps$	-0.44	0.19	40
<i>E. marina</i>	$Y = 13.3 - 0.360x + eps$	-0.32	0.11	47
<i>P. abdominalis</i>	$Y = 14.5 - 0.430x + eps$	-0.42	0.18	42
Spring				
<i>A. danae</i>	$Y = 9.6 - 0.177x + eps$	-0.15	0.02	97
<i>C. pacificus</i>	$Y = 11.7 - 0.122x + eps$	-0.10	0.01	207
<i>E. marina</i>	$Y = 7.0 - 0.084x + eps$	-0.08	0	73
<i>P. abdominalis</i>	$Y = 8.6 - 0.105x + eps$	-0.09	0	126
Summer				
<i>A. danae</i>	$Y = 10.4 - 0.233x + eps$	-0.38	0.14	57
<i>C. pacificus</i>	$Y = 15.8 - 0.322x + eps$	-0.43	0.18	112
<i>E. marina</i>	$Y = 2.6 + 0.108x + eps$	0.20	0.04	77
<i>P. abdominalis</i>	$Y = 6.8 - 0.030x + eps$	-0.06	0	69
Autumn				
<i>A. danae</i>	$Y = 16.3 + 0.885x + eps$	0.83	0.69	17
<i>C. pacificus</i>	$Y = 1.9 + 0.20x + eps$	0.25	0.06	89
<i>E. marina</i>	$Y = 0.5 + 0.237x + eps$	0.40	0.16	98
<i>P. abdominalis</i>	$Y = 5.9 + 0.009x + eps$	0.01	0	56

Note: Bold type indicates significant ($P < 0.05$).

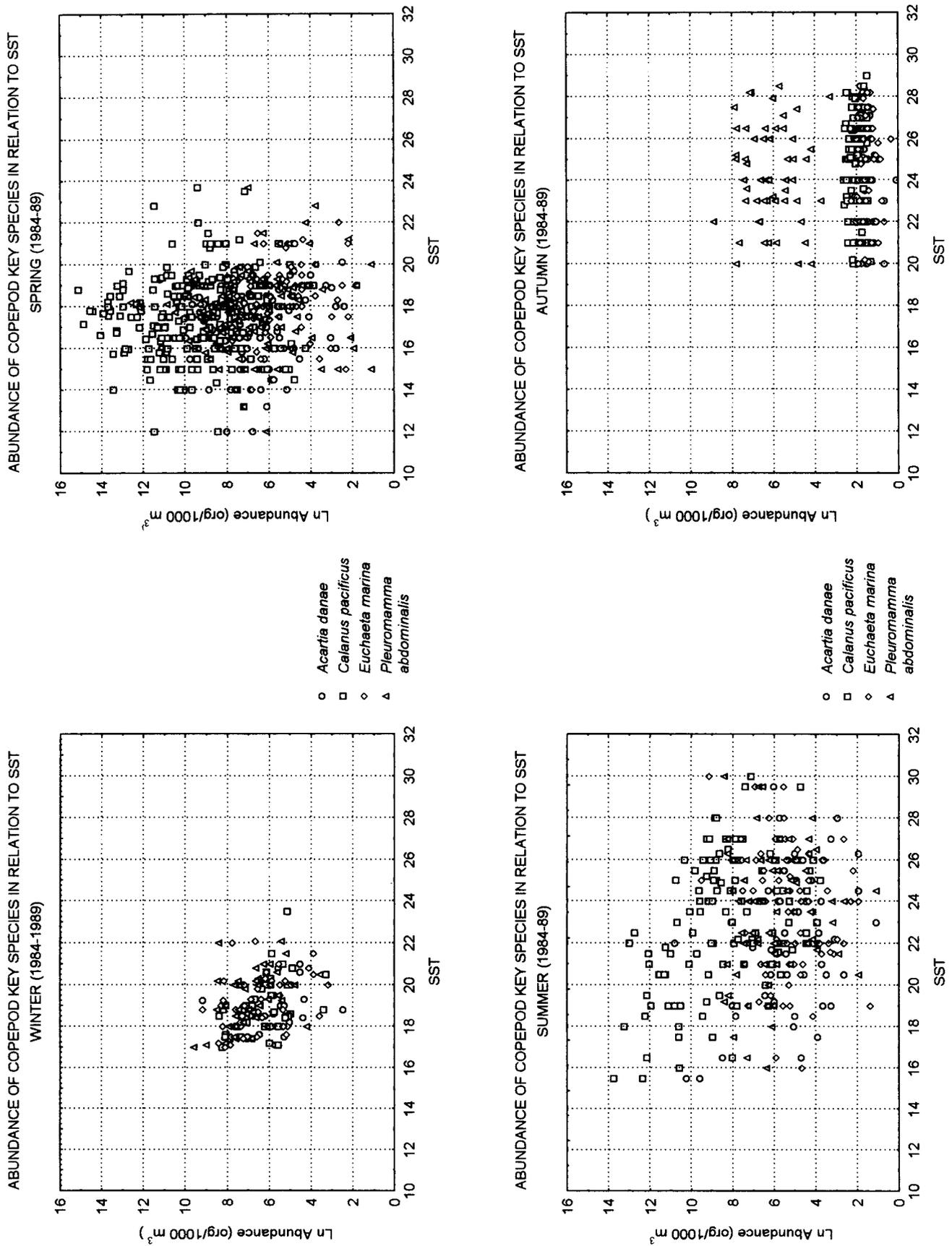


Figure 4. Seasonal relation between abundance of the copepod key species and the sea-surface temperature (SST).

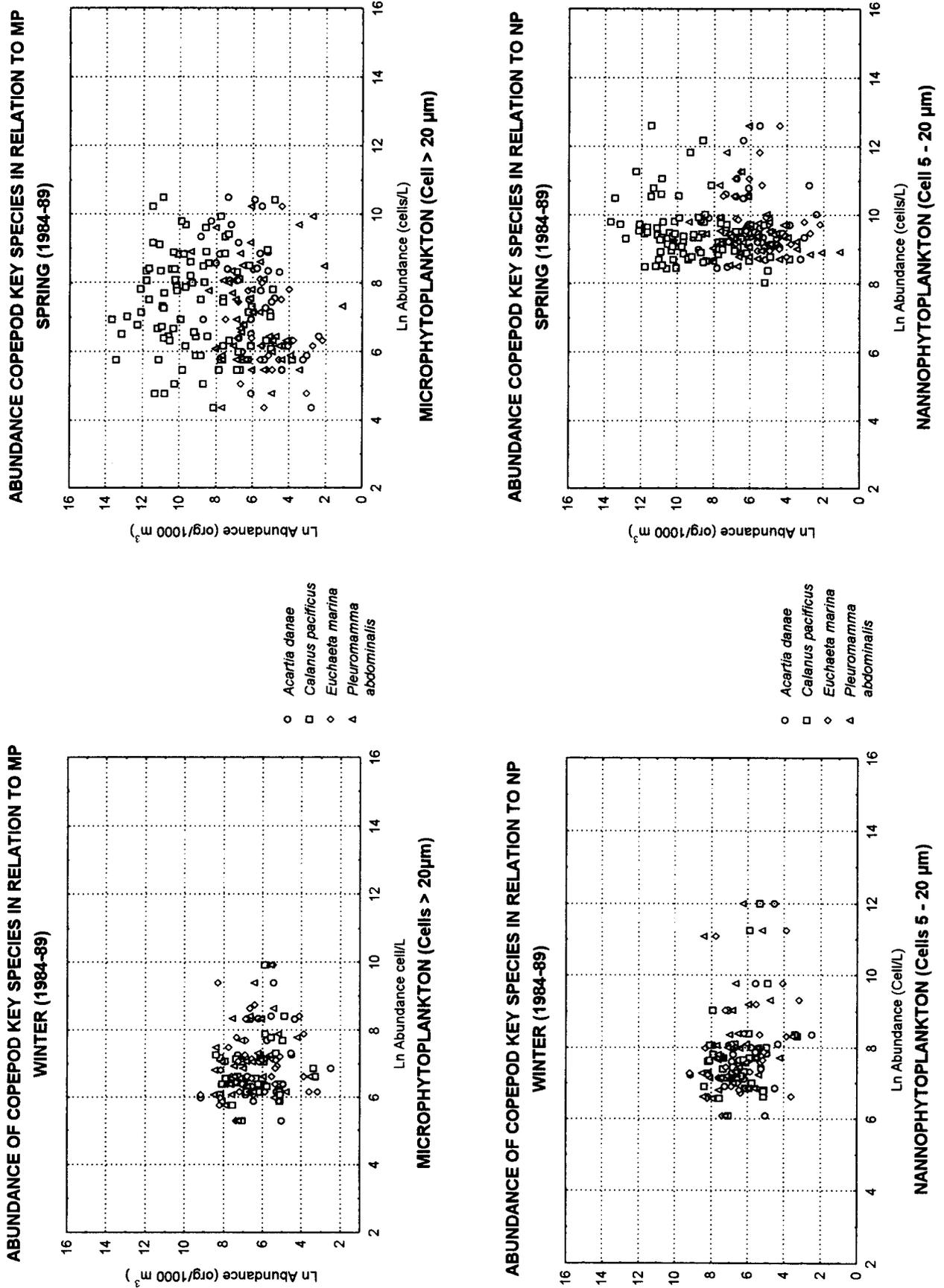
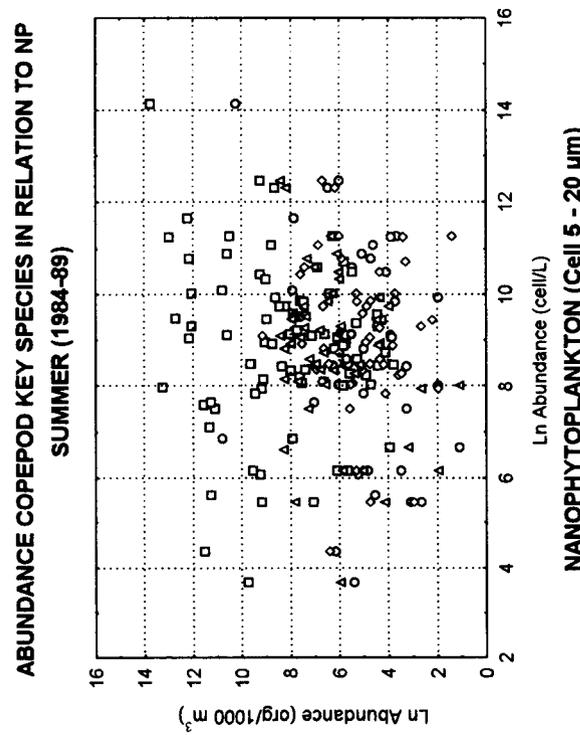
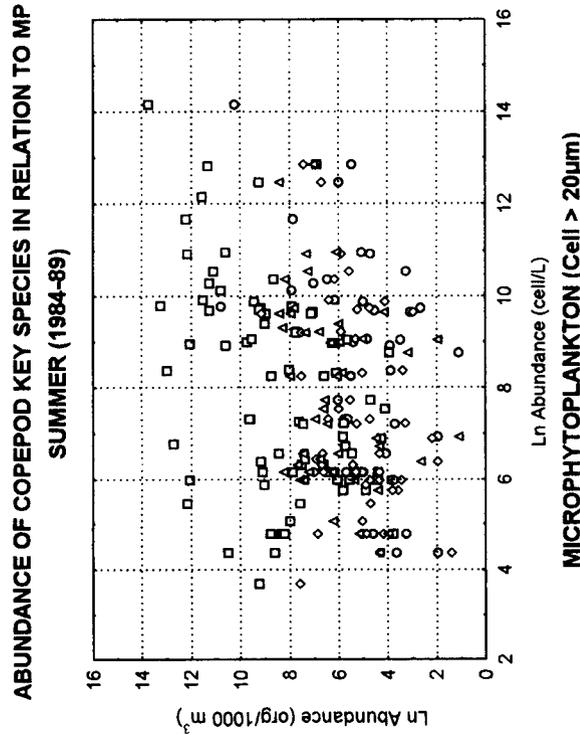
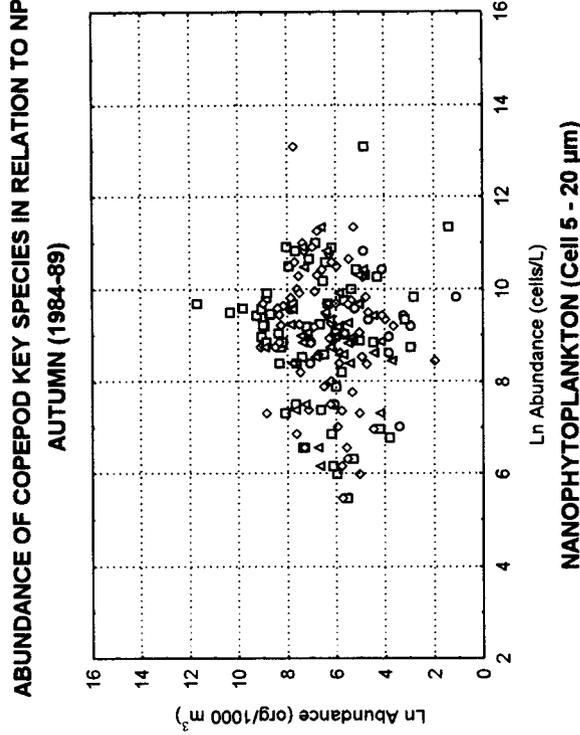
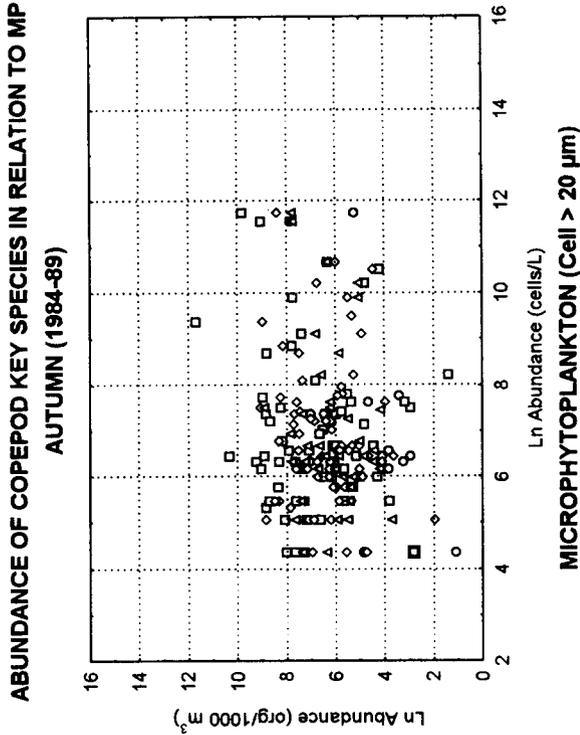


Figure 5. Winter and spring relation between abundance of the copepod key species and the abundance of micro- and nanophytoplankton.



- *Acartia dense*
- *Calanus pacificus*
- ◇ *Euchaeta marina*
- △ *Pleuromamma abdominalis*

- *Acartia dense*
- *Calanus pacificus*
- ◇ *Euchaeta marina*
- △ *Pleuromamma abdominalis*

Figure 6. Summer and autumn relation between abundance of the copepod key species and the abundance of micro- and nanophytoplankton.

TABLE 7
 Product-Moment Correlation between Copepod
 Key Species and Microphytoplankton on the West Coast
 of Baja California, 1984–89

	Algebraic formula	r	r ²	N
Winter				
<i>A. danae</i>	$Y = 7.1 - 0.179x + eps$	-0.15	0.02	30
<i>C. pacificus</i>	$Y = 7.9 - 0.224x + eps$	-0.15	0.02	35
<i>E. marina</i>	$Y = 6.6 - 0.054x + eps$	-0.03	0.01	42
<i>P. abdominalis</i>	$Y = 8.9 - 0.322x + eps$	-0.27	0.07	37
Spring				
<i>A. danae</i>	$Y = 1.7 + 0.538x + eps$	0.54	0.30	43
<i>C. pacificus</i>	$Y = 8.5 + 0.079x + eps$	0.05	0	88
<i>E. marina</i>	$Y = 4.1 + 0.143x + eps$	0.13	0.01	26
<i>P. abdominalis</i>	$Y = 5.8 + 0.006x + eps$	0	0	47
Summer				
<i>A. danae</i>	$Y = 1.9 + 0.367x + eps$	0.42	0.18	38
<i>C. pacificus</i>	$Y = 4.6 + 0.465x + eps$	0.42	0.17	77
<i>E. marina</i>	$Y = 3.5 + 0.227x + eps$	0.31	0.09	53
<i>P. abdominalis</i>	$Y = 4.4 + 0.222x + eps$	0.25	0.06	47
Autumn				
<i>A. danae</i>	$Y = 1.9 + 0.398x + eps$	0.46	0.21	15
<i>C. pacificus</i>	$Y = 6.1 + 0.094x + eps$	0.08	0	62
<i>E. marina</i>	$Y = 5.7 + 0.092x + eps$	0.10	0	72
<i>P. abdominalis</i>	$Y = 5.5 + 0.094x + eps$	0.14	0.02	40

Note: Bold type indicates significant ($P < 0.05$).

TABLE 8
 Product-Moment Correlation between Copepod
 Key Species and Nannophytoplankton on the West Coast
 of Baja California, 1984–89

	Algebraic formula	r	r ²	N
Winter				
<i>A. danae</i>	$Y = 7.4 - 0.211x + eps$	-0.18	0.03	30
<i>C. pacificus</i>	$Y = 8.3 - 0.256x + eps$	-0.23	0.05	35
<i>E. marina</i>	$Y = 9.5 - 0.42x + eps$	-0.32	0.10	42
<i>P. abdominalis</i>	$Y = 8.3 - 0.204x + eps$	-0.22	0.05	37
Spring				
<i>A. danae</i>	$Y = 1.7 + 0.538x + eps$	-0.01	0	44
<i>C. pacificus</i>	$Y = 8.5 + 0.079x + eps$	0.27	0.07	88
<i>E. marina</i>	$Y = 4.1 + 0.143x + eps$	0.18	0.03	26
<i>P. abdominalis</i>	$Y = 5.8 + 0.006x + eps$	0.22	0.04	46
Summer				
<i>A. danae</i>	$Y = 3.0 + 0.234x + eps$	0.26	0.07	39
<i>C. pacificus</i>	$Y = 6.9 + 0.154x + eps$	0.10	0.01	79
<i>E. marina</i>	$Y = 4.6 + 0.062x + eps$	0.06	0	54
<i>P. abdominalis</i>	$Y = 3.6 + 0.296x + eps$	0.29	0.08	48
Autumn				
<i>A. danae</i>	$Y = 6.9 - 0.246x + eps$	-0.13	0.01	15
<i>C. pacificus</i>	$Y = 6.3 + 0.054x + eps$	0.04	0	62
<i>E. marina</i>	$Y = 4.8 + 0.167x + eps$	0.17	0.03	72
<i>P. abdominalis</i>	$Y = 6.3 - 0.017x + eps$	-0.01	0	40

Note: Bold type indicates significant ($P < 0.05$).

DISCUSSION

During the period studied in central and southern Baja California, a large proportion of the variability in the abundance of the copepod community was attributed to the 11 most frequent species, and more particularly to the named key species. These species never disappeared from the studied area; on the contrary, their abundance exhibited an important fraction of the total copepod community.

Calanus pacificus has been characterized as a transitional species of oceanic and subsurface distribution (Fleminger 1967). They occur, and are abundant, along the California and Baja California coasts. This holds true in the present study for the central and southern Baja California areas. The copepods *A. danae* (temperate-tropical species of wide north-south and inshore-offshore distribution), and *P. abdominalis* (tropical species, oceanic and epipelagic distribution) have been characterized as the most frequent species between central California and southern Baja California (Fleminger 1964; Bowman and Johnson 1973). The copepod *E. marina* (tropical-subtropical species, oceanic and subsurface distribution) has also been found in the study area, where it is less abundant than the other three copepod species.

In the study area *A. danae*, *E. marina*, and *P. abdominalis* predominated in the copepod community, had similar abundances, and showed changes of rank, month to month and by latitude. The latitudinal monthly abundance differences found for three key species mean that the change of the dominant species was affected by the

season of sampling and not by the geographic position of the sampling stations.

The assemblage reflects the complexity of the copepod community in the area studied, as well as its structural dynamics. The three key species maintained their abundance below that of *C. pacificus* during the study period (except for summer) in each of the latitudinal blocks. For *C. pacificus*, I found spatial and temporal abundance heterogeneity in the study area. The dominance of *C. pacificus* over the remaining key species was shown in time and space. Its abundance was higher in the north, decreasing to the south. However, the seasonal pattern differed because *A. danae* abundance did not differ over time or space, and the remaining key species had temporal, but not geographic differences.

Temperature was found to be significant for all copepods. The type of correlation, either positive or negative, relies on the species' ecological habits: for tropical-subtropical species, maxima occurred during the warm period, and for the transitional species during cold periods. The PCA also suggests that the first component was temperature, influencing the variation of abundance and geographical distribution of the copepods. The abundance of key species related to the SST shows this effect. The habitat of the key species was another factor contributing to the species assemblages. Colebrook (1977) found similar results for the copepods in the California Current system in 1955–59.

The variance of the first factor obtained by PCA in each cruise shows that the variability of the abundance

of copepod species in the Baja California peninsula area is linked to the structure of the environment, as Dessier and Donguy (1987) showed for epiplanktonic copepods in the eastern tropical Pacific. The greatest abundance of *C. pacificus* along the west coast of Baja California coincides with the strongest equatorward surface flow of the California Current, March through May, and their lowest abundance with an equally strong poleward flow, July through September (Lynn and Simpson 1987; Parés et al. 1997). The SST had an important effect on the seasonal spatial distribution and abundance of the key species, because in each season they were limited to waters in a specific temperature range.

The observed relations of micro- and nannophytoplankton with the fluctuations in copepod abundance probably reflect changes in the hydrological regime of the area. The abundance of micro- and nannophytoplankton showed a negative correlation with the abundance of all key species in winter; this could indicate that in the studied area the copepods showed some preference for food other than phytoplankton. For the remaining seasons the abundance of phytoplankton showed positive relations with almost all copepod abundances, especially for *C. pacificus*.

The importance of the seasonal phytoplankton abundance differed for each key species over the study period, especially for *C. pacificus*, whose abundance was higher than the other copepod species at low and high concentrations of cells (except in winter for both MF and NF fraction size). The relation between the abundance of the key species and the phytoplankton suggests that resource distributions and niches were slanted to *C. pacificus* to maintain high abundance levels for almost all concentrations of phytoplankton recorded, according to Hernández-Trujillo (1991b) and Mullin (1991, 1994, 1995).

Other oceanographic variables could be expected to influence the variability of abundance of the copepods in the study area. One is the warming and cooling by El Niño and La Niña episodes in the eastern Pacific, which affect the fauna and flora of the study area (Palomares-García and Gómez-Gutiérrez 1996; Hernández-Trujillo and Esquivel-Herrera 1997; Gárate-Lizárraga and Siqueiros-Beltrones 1998). In addition, more observations on the copepod community structure have to be made to demonstrate whether the key species extracted really represent the most important species.

To explore the functional relation between copepod species and environmental factors, we need a complete and continuous data set. The data indicated, at least during the period studied, that an important proportion of the variability of copepod abundance, represented by the 4 key species, can be associated with SST and phytoplankton abundance, both associated with the strength of the California Current.

CONCLUSIONS

Acartia danae, *Calanus pacificus*, *Euchaeta marina*, and *Pleuromamma abdominalis* were the key copepod species in the 1984–89 period. The dominance of *C. pacificus* in comparison to the other key species was the most important feature of the copepod community. The variability of the key species abundance was dependent on the SST and the phytoplankton abundance. The warm and cool episodes should be isolated to get the normal pattern of variation of the key species. The variability of distribution and abundance of *C. pacificus* suggests extensive resource partitioning along the west coast of the Baja California peninsula.

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LITERATURE CITED

- Bowman, T. W., and M. W. Johnson. 1973. Distributional atlas of Calanoida in the California Current region. Calif. Coop. Oceanic Fish. Invest. Atlas 19. La Jolla, Calif.
- Cole, D. A., and D. R. McLain. 1989. Interannual variability of temperature in the upper layer of the North Pacific eastern boundary region, 1971–1987. NOAA Tech. Memo. NMFS-SWFC-125, 9 pp. + 5 figs. + appendix.
- Colebrook, J. M. 1977. Annual fluctuation in biomass of taxonomic groups of zooplankton in the California Current, 1955–59. Fish. Bull. 75(2): 357–368.
- Dessier, A., and J. R. Donguy. 1987. Response to El Niño signals of the epiplanktonic copepod populations in the eastern tropical Pacific. J. Geophys. Res. 92(C13):14,393–14,403.
- Fager, E. W., and J. A. McGowan. 1963. Zooplankton species groups in the North Pacific. Science 140(3566):453–460.
- Fleminger, A. 1964. Distributional atlas of Calanoid copepods in the California Current region. Part 1. Calif. Coop. Oceanic Fish. Invest. Atlas 19. La Jolla, Calif. 313 pp.
- . 1967. Distributional atlas of Calanoid copepods in the California Current region. Part 1. Calif. Coop. Oceanic Fish. Invest. Atlas 19. La Jolla, Calif. 300 pp.
- Garate-Lizárraga, I., and D. Siqueiros-Beltrones. 1998. Time variations in phytoplankton assemblages in a tropical lagoon system after the 1982–1983 “El Niño” event (1984 to 1986). Pac. Sci. 52(1):79–97.
- Hernández-Trujillo, S. 1991a. Variación latitudinal de la diversidad de copépodos en la costa occidental de B.C.S. (1982–1984). Ciencias Marinas 17(4): 83–103.
- . 1991b. Patrones de distribución y abundancia de *Calanus pacificus* en relación a la temperatura superficial en el Pacífico de Baja California Sur, México (1982–1986). Rev. Inv. Cient. UABCS, 2(1):56–64.
- Hernández-Trujillo, S., and A. Esquivel-Herrera. 1997. Asociaciones interespecíficas de copépodos en la costa oeste de Baja California Sur, México. Hidrobiológica 7:65–74.
- Longhurst, A. 1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393–408.
- . 1995. Seasonal cycles of pelagic production and consumption. Prog. Oceanogr. 36:77–167.
- Lynn, R. J., and J. J. Simpson. 1987. The California Current system: the seasonal variability of its physical characteristics. J. Geophys. Res. 92(C12): 12,947–12,966.

- McGowan, A. J., and C. B. Miller. 1980. Larval fish and zooplankton community structure. Calif. Coop. Oceanic Fish. Invest. Rep. 21:29-36.
- Mullin, M. M. 1991. Production of eggs by the copepod *Calanus pacificus* in the southern California sector of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 32:65-90.
- . 1994. Distribution and reproduction of the planktonic copepod *Calanus pacificus*, off southern California during winter-spring of 1992, relative to 1989-91. Fish. Oceanogr. 3:142-157.
- . 1995. The Californian El Niño of 1992 and the fall of *Calanus*. Calif. Coop. Oceanic Fish. Invest. Rep. 36:175-178.
- . 1998. Biomasses of large-celled phytoplankton and their relation to the nitricline and grazing in the California Current system off southern California, 1994-1996. Calif. Coop. Oceanic Fish. Invest. Rep. 39:117-123.
- Paine, R. T. 1969. A note on trophic complexity and community stability. Am. Nat. 103:91-93.
- Palomares-García, R. 1996. Estructura espacial y variación estacional de los copépodos en la ensenada de La Paz. Océánides 11(1):29-43.
- Palomares-García, R., and J. Gomez-Gutierrez. 1996. Copepod community structure at Bahía Magdalena, Mexico during El Niño 1983-84. Estuarine, Coastal Shelf Sci. 43:583-595.
- Pares, S. A., A. Lopez, and E. G. Pavia. 1997. Oceanografía física del Océano Pacífico Nororiental, In Contribuciones a la oceanografía física en México, monografía no. 3, Unión Geofísica Mexicana, M. F. Lavín, ed., pp. 1-24.
- Root, R. B. 1967. The niche exploitation pattern on the blue-gray gnat-catcher. Ecol. Monogr. 37:317-350.
- Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish eggs and larval survey. FAO Fish. Tech. Pap. 175, 100 pp.
- Weikert, H. 1982. Some features of zooplankton distribution in the upper 200 m in the upwelling region off Northwest Africa. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 180:280-288.