Planktonic copepods and environmental properties of the eastern equatorial Pacific: seasonal and spatial variations

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Abstract—Seasonal and areal distributions of copepod populations in the eastern equatorial Pacific were examined in relation to environmental properties (sea surface temperature, salinity, chlorophyll content, and vertical thermal structure). In the equatorial area between 4°S and 4°N, chlorophyll content reached its annual maximum in southern winter (August), when upwelling intensity was the strongest; a less distinct peak was observed between March and May. The two maxima were observed both to the north and to the south of the equator. Copepod populations had a single maximum in the same areas in southern winter. Diversity of the copepod populations was highest between 10 and 14°S.
   The variability of copepod populations is a function of area and season. Population data were assigned to three areas: (a) north equatorial (north of 2°N); (b) equatorial (between 2°N and 4°S); (c) south equatorial (south of 4°S). The seasonal effect is obvious only in the equatorial area where during southern winter there is a predominance of herbivorous species and, during southern summer, a predominance of carnivorous species.

INTRODUCTION

THE TROPICAL zones of the oceans usually are considered to have low organic production. Within this oligotrophic environment, trophic enrichments occur in response to wind-induced coastal upwelling along the continental shores, mainly in the east, and to circulation-related open-ocean upwelling in the equatorial area. Equatorial upwelling, which extends from 8 to 12°N to 6 or 8°S between the coast of South America and the date line, is more active in the eastern side of the oceans as shown by surface temperature distributions.

An analysis of copepod distributions, based on samples collected by ships of opportunity along the entire shipping route New Caledonia–Tahiti–Panama, has shown that, in the oceanic areas sampled [(1) the tropical South Pacific, (2) the central South Pacific, and (3) the eastern equatorial Pacific], the seasonal variations were maximal in the equatorial region (DESSIER, 1983). In this paper, we report results from a subsequent investigation of the relationship between the copepod populations and the environment in the equatorial eastern Pacific, using samples collected on the shipping routes, Tahiti or Mururoa to Panama (Fig. 1A). Species composition, geographic distribution, and productivity of planktonic communities in equatorial zones are influenced by upwelling. The transport and growth of the populations are particularly affected by zonal and meridian

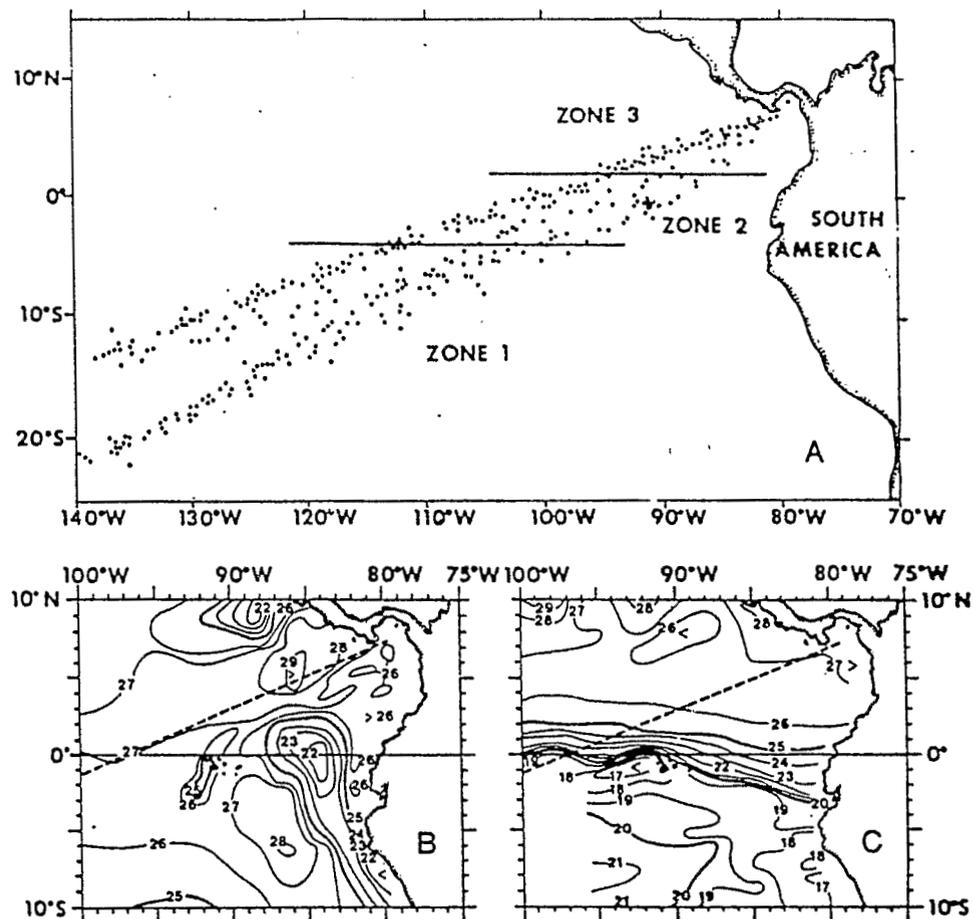* SURTROPAC Group, Centre ORSTOM de Nouméa, B.P. A5—Noumea, Nouvelle Calédonie.

Fig. 1. (A) Locations of the zooplankton sampling along the shipping route between Tahiti and Panama and of the three geographical zones. (B, C) Sea surface temperature from 75 to 100°W, February to March 1967 and August to September 1967, respectively (Love, 1972). The dashed line indicates the route of ships of opportunity.

fluxes from equatorial divergence. Consequently, it must be possible to compare variations of planktonic communities with physical properties. Except for papers by Black-burn et al. (1970) and Owen and Zeitzschel (1970), there has been limited research on temporal variations of planktonic communities in the tropical Pacific.

MATERIAL AND METHODS

Zooplankton and surface properties (except chlorophyll) and sampling methods used aboard ships of opportunity by the SURTROPAC Group from "Centre ORSTOM de Nouméa" have been described by Dessier (1983). Dandonneau's (1982) method was used for chlorophyll. Zooplankton samples were obtained nightly, 3 or 4 h after dark, when the swimming pool (20 to 25 m^3) was filled with water filtered on a 330 μm mesh net. Samples were preserved in 5% formalin.

In addition, every 6 h several other observations, including surface temperature salinity, and chlorophyll measurements, were made by the same ships; XBTs were used to determine thermal structure from the surface to 450 m. For each of these parameters, the monthly average by degree of latitude was calculated, using data collected from September 1974 to May 1982 for temperature and salinity, from January 1978 to May 1982 for chlorophyll, and from August 1979 to June 1982 for thermal profiles.

A total of 354 plankton samples collected east of 140°W between the end of 1977 and July 1982 are considered in this study; however data collected before 1979 comprised only about 10% of the total. (Sampling in the vicinity of the Galapagos Islands was made before the 1980 prohibition on passing through the islands.) After sorting, copepod species were identified and enumerated, without, however, taking into account sex or developmental stages. Because of the imprecise amounts of water filtered, the species abundances are expressed as number of individuals per sample. The results were analysed using multivariate analysis (correspondence analysis or reciprocal averaging) and automatic classification (ascending hierarchical classification using distance of χ^2, LEBART et al., 1979). These procedures have been used for zooplankton studies in equatorial Africa (DESSIER and LAUREC, 1978; DESSIER, 1979) and for a previous study in the Pacific, based on the ships of opportunity sampling program from New Caledonia to Panama (DESSIER, 1983).

ENVIRONMENT

Surface properties

Equatorial upwelling is the basic hydrographic feature in the studied area (WYRTKI, 1981); it is responsible for the presence of a cold water tongue at the surface, extending usually from the Galapagos Islands to 180°W. The development of the cold tongue is related to seasonal and interannual variations in equatorial upwelling and to the horizontal advection of the cold surface water from the coast of Peru. The association with the Peruvian upwelling occurs mainly during southern winter (August to October) when the southeast tradewinds are strongest. With the weakening of the winds during austral summer (February to March), the intensity of the equatorial cooling decreases considerably, and the continuity between upwelling off Peru and equatorial upwelling seems to disappear, allowing the warm waters from the north to mingle with those south of the Galapagos Islands (Fig. 1B, C).

A thermal front located at about 3°N in the vicinity of the Galapagos Islands separates the warm, low salinity waters in the northern hemisphere from the cooler, equatorial waters resulting from equatorial and Peruvian upwelling. The front reaches its maximum intensity during southern winter (Fig. 1C). In the area where the shipping route crosses the equator (95 to 100°W), the front is located at 1 to 2°N. With the weakening of the south winds (HASTENRATH and LAMB, 1977), the front becomes weaker and practically disappears between January and March to April (Fig. 1B), allowing a southward extension of the northern warm waters. The southern limit of the equatorial cool waters is less clear; a thermal gradient extends along the shipping route over 6° or 7° of latitude (Fig. 2A). A salinity front (Fig. 2B) marks the boundary between the northern warm and low salinity waters and the southern cold and high salinity waters. Unlike the temperature front, it is particularly strong at 1 to 3°N during southern summer (January to April), when the low salinity waters from the northern hemisphere have a maximum southward extension; it disappears in May and appears again, but less intensely, between June and December.
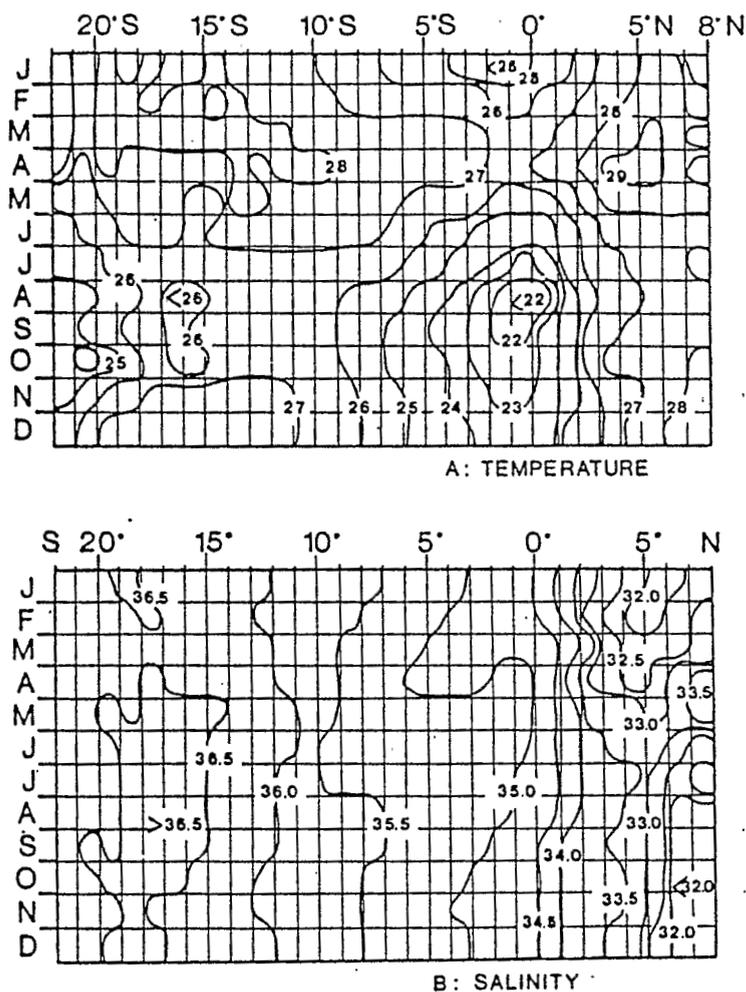
Fig. 2.   (A, B) Mean monthly temperature (°C) and salinity (10⁻³) along the shipping route
between Tahiti and Panama.

Seasonal variations of surface temperature and salinity along the shipping route Tahiti
to Panama have been analysed and discussed by DONGUY and HENIN (1980). In summary,
from July to December, cool waters are observed, whereas from January to June, warm
waters are seen south of 10°S, due to warming during southern summer and in the vicinity
of the equator, due to the lack of equatorial upwelling (Fig. 2A). In southern summer,
salinity is minimal and, from July to December, maximal (Fig. 2B).

Vertical thermal structures

Based on 1137 XBTs records from August 1979 to June 1982, sections showing monthly
mean thermal profiles have been obtained between 7°N and 20°S. Two typical seasonal
situations are shown in Fig. 3.

In August (southern winter), the equatorial upwelling is intense and the thermocline is
prominent on each side of the equator (Fig. 3A). South of the equator, extending
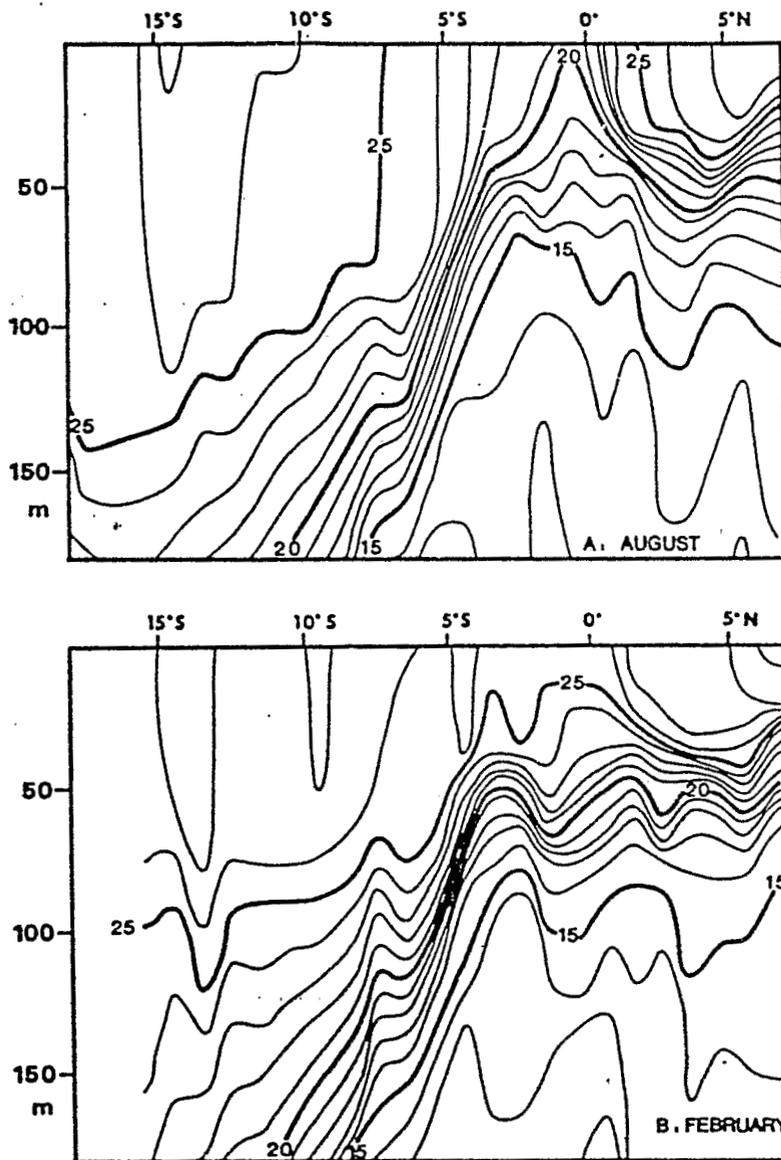
Fig. 3. (A, B) Mean thermal structure in August and February along the shipping route between
Tahiti and Panama.

southwestward along the shipping route, the thermocline deepens quickly and, starting at
6°S, weakens progressively. South of 10°S, the mixed layer is more than 100 m thick and
the thermal gradient in the underlayers is less than that north of 10°S, inducing a possible
enrichment of the surface layers by turbulent vertical mixing (DESSIER, 1983). Between the
equator and about 1°N, the thermocline shoals, intersecting the sea surface to form a
thermal front, and north of the equator the thermocline is found at <50 m.

Between 3°S and 1°N, the thermocline splits, with shallow isotherms shoaling to close to the surface and deep isotherms deepening. The 20°C isotherm reaches its minimum depth (10 m) between the equator and 1°S, whereas the 15°C isotherm reaches 70 m depth. The separation of the thermocline usually characterizes the presence of the equatorial undercurrent. Since the isotherm slope is upward on each side of the equator, the westward Equatorial Current prevails at the surface in the equatorial zone; north of 5°N the isotherm slope reverses and the surface current is eastward, characteristic of the North Equatorial Countercurrent (TSUCHIYA, 1974). In addition to the advection of nutrient-rich waters from off Peru, the equatorial upwelling and turbulence due to the undercurrent are an important source of enrichment in this area.

In February (southern summer), equatorial upwelling is much less intense than in August (Fig. 3B). The 20°C isotherm has a maximum depth of 40 m instead of 10 m (August). South of 4°S, the thermocline deepens and weakens quickly; the thickness of the mixed layer remains <100 m. The thermal structure appears less favorable for the enrichment of the euphotic layer than in winter. However at 3°S, a doming appears, and the 20°C isotherm extends to a depth of 50 m. North of the equator, because of the weak intensity of equatorial upwelling, the thermocline does not reach the surface and the Galapagos thermal front disappears. The thermocline, however, remains as intense as in August at 50 m depth. At the equator, the thermocline is not split as in August; the undercurrent is probably weak and close to the surface (JONES, 1969; TSUCHIYA, 1974). Considering the topography of the thermocline, it is clear that the Equatorial Current, although weaker than in August, persists at the equator. On each side of the equator, an eastward countercurrent occurs, particularly at 2 to 3°S latitude, which is in agreement with the findings of TSUCHIYA (1974). The intense doming at 3°S induced by the contact between the eastward South Equatorial Countercurrent and the westward South Equatorial Current, south of 3°S, may constitute an enrichment factor similar to equatorial upwelling in August.

Year-to-year variability

The main signal of low frequency climatic variability in the tropical Pacific is the "Southern Oscillation". In the eastern Pacific, the El Niño event is the most obvious regional manifestation of the Southern Oscillation.

During the surveyed period, two weak El Niño signals were indicated, one in 1978 to 1979, the other in 1981 to 1982 at the usual time of El Niño. Positive anomalies of surface temperature were observed in the eastern equatorial zone during the southern 1979 and 1982 summers (DONGUY and DESSIER, 1983). However, the zooplankton sampling was too sparse to investigate the biological consequences of these weak events. In August 1982, after the conclusion of this study, a major El Niño occurred.

Sea surface chlorophyll concentration

As the chlorophyll concentration of surface waters provides an index of the phytoplankton biomass, estimates of mean chlorophyll concentration, based on 1500 measurements (1978 to 1982), were calculated by 2° of latitude (Fig. 4A). Values increase regularly from 22 to 12°S, remain almost constant until 4 to 5°S, then increase again dramatically reaching a maximum at the equator. North of the equator chlorophyll concentration decreases quickly but increases again up to the Gulf of Panama, where a value a little greater than that recorded at the equator is reached.
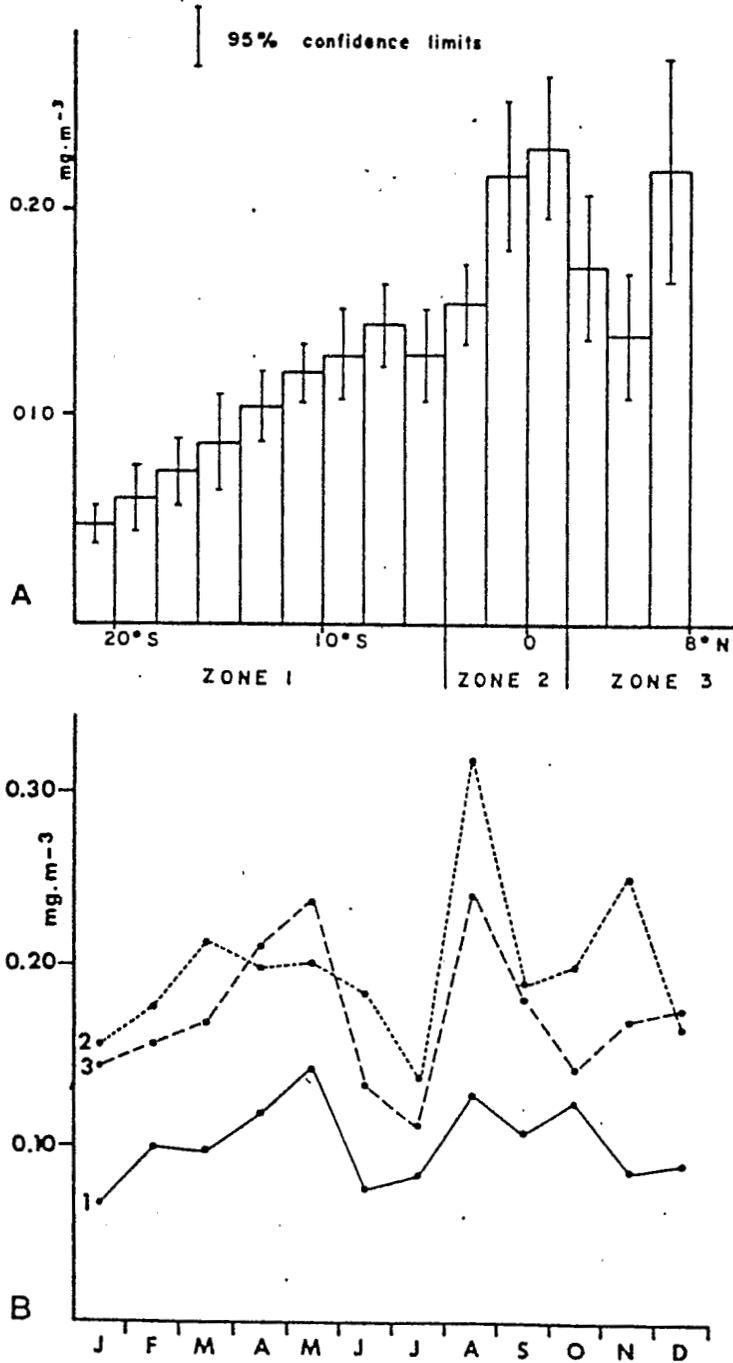
Fig. 4.   (A) Mean surface chlorophyll content per 2° of latitude along the shipping route between Tahiti and Panama. (B) Seasonal variation of surface chlorophyll content in zones 1, 2 and 3.

Seasonal variations of mean chlorophyll concentration (Fig. 4B) have been considered in three geographical zones (Fig. 1A): (1) south of 4°S, (2) between 4°S and 2°N (equatorial upwelling), and (3) north of 2°N (thermal and saline front). The first zone is heterogeneous; it includes the ecologically poorest and most stable zone of the South Pacific in the southern part and an equatorial influenced area in the northern part. In each of the three zones chlorophyll concentrations show minima, between March to May and in August. Seasonal variations are the least remarkable in zone 1 where the second peak is indistinct.

PLANKTONIC COPEPODS

Zooplanktonic populations in the equatorial Pacific exhibit spatial variability due to north–south distribution of the populations and temporal variability due to the seasonal
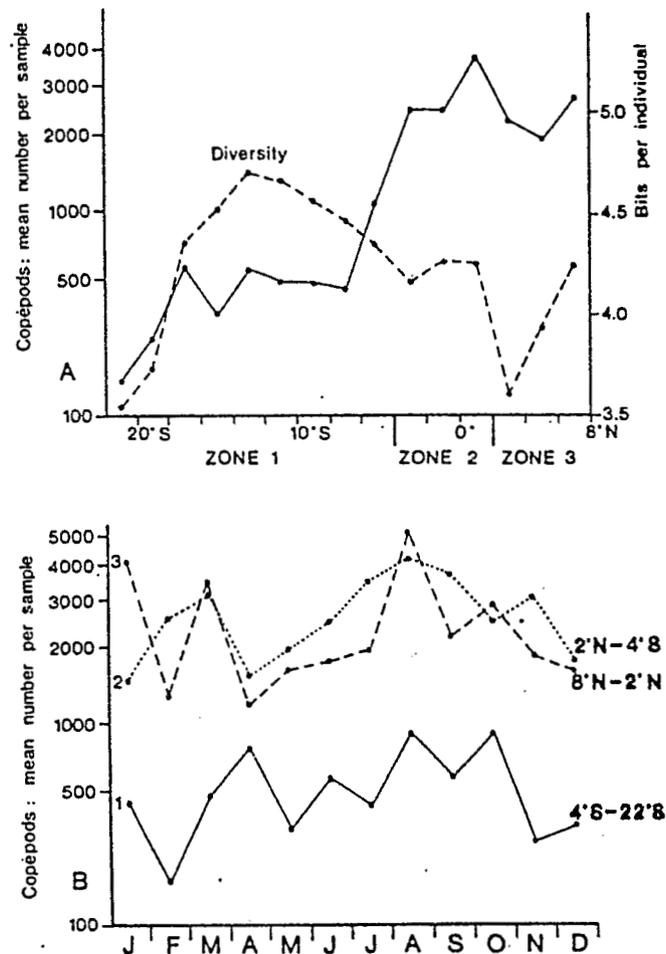

Fig. 5. (A) Mean number of copepods per sample (left scale and solid line) and Shannon diversity index by 2° of latitude (right scale and dashed line) along the shipping route between Tahiti and Panama. (B) Seasonal variation of mean number of copepods in zones 1, 2 and 3.

variations of the environment. We designed our data treatment to analyse the individual or combined influence of these two types of variability on some biological characteristics of the populations.

Standing stock

The total number of individuals was used to estimate standing stock of copepods. The meridional variation of the mean number of copepods per sample and per 2° latitude (Fig. 5A) is similar to that of chlorophyll (Fig. 4A), except the flat part between 5 and 12°S is more extended for copepods (6 to 14°S). The Shannon diversity index, calculated for samples averaged over 2° latitude, reaches maximum values at about 12 to 14°S and shows a weak diversity in the vicinity of 20°S where the mean number of copepods is lowest.

Seasonal changes in standing stock in each of the three geographic zones were determined (Fig. 5B). The bimodal characteristics of the chlorophyll curves exist for
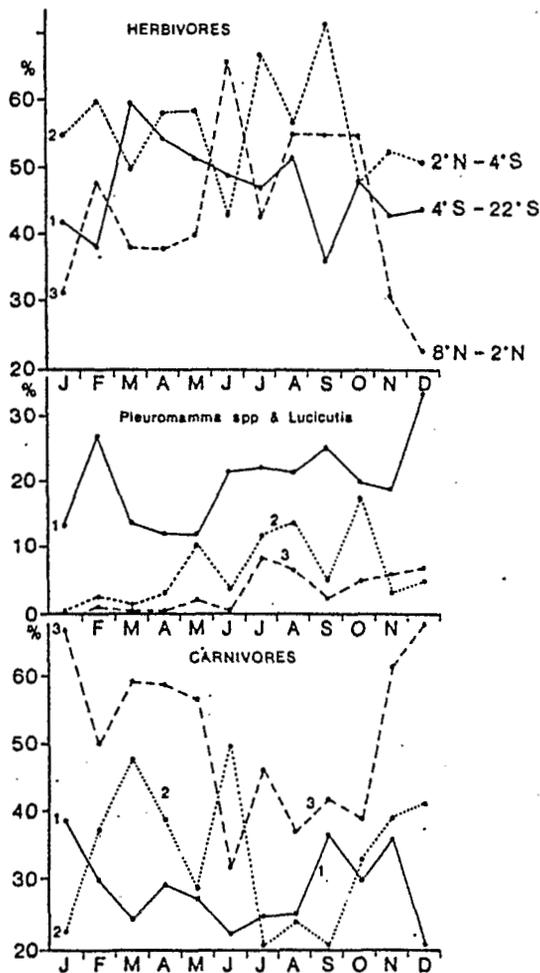

Fig. 6.   Seasonal variation of three categories of zooplankton in zones 1, 2 and 3; herbivores (weakly or not migrating); *Pleuromamma* spp. and *Lucicutia* sp. (migrating herbivores–omnivores); and carnivores.

copepods only between 4°S and 4°N (zone 2). Elsewhere a maximum occurs only during the southern winter (August to October).

Trophic structure

Only late copepodite stages and adults were considered in the determination of the trophic structure, which is very coarse. Three categories of copepods were characterized (Fig. 6): (1) herbivores–omnivores, weakly or not migrating (e.g., *Undinula, Paracalanus, Clausocalanus, Calanus, Eucalanus, Acrocalanus*), (2) migrating herbivores–omnivores (*Pleuromamma, Lucicutia*), and (3) carnivores (e.g., *Euchaeta, Candacia, Oncaea, Corycaeus*). North of 4°S, carnivores are proportionally more numerous than both types of hervivores–omnivores during southern summer. However, the proportion of migrating copepods, relative to nonmigrating ones, is always greater south of 4°S than to the north.

Types of spatial–temporal variation

An average sample has been calculated by month and by 2° latitude between 22°S and 8°N. Overall 180 latitudinal sections are defined but only 159 contained one or more samples. Schematically two main types of geographical abundance may be distinguished: (1) A single maximum abundance peak. Species were located approximately in the three zones, i.e., south of the equator (e.g., *Euchaeta marinella, Rhincalanus cornutus*), equatorial area (*Paracalanus* spp., *Clausocalanus* spp., *Euchaeta rimana*), and north of the equator (*Centropages furcatus, Oncaea venusta*). (2) Two maxima in abundance, either one peak equatorial, and the other subequatorial (*Calanus minor, Lucicutia flavicornis*) or both subequatorial (*Pleuromamma piseki*).

RESULTS OF MULTIVARIATE ANALYSIS: IDENTIFYING POPULATIONS

A correspondence analysis was carried out using the 70 most abundant species in the 354 samples (Table A1). The first five factors extract 38% of the total variance; an automatic clustering method in the space of the five first axes allows identification of eight main classes of observations but of unequal importance. As shown by the dendrogram (Fig. 7) the classes can be distributed in two sets; the first includes equatorial (classes 1 and 2) and north equatorial populations (classes 3 and 4), while the second set consists of south equatorial populations (classes 6, 7, and 8). The first axis distinguishes the two sets (Fig. 7, plan defined by the first and second axes). Classes 1 and 2 seem to correspond only to a temporal succession (austral summer and winter, respectively) as indicated by their position along the second axis (Fig. 7). Classes 3 and 4, which contain observations from north of the equator, are close to class 1 on the plan of the two first axes and are discriminated by the other axis.

Spatial and temporal distributions of copepod samples (per 2° latitude) for each class are shown in Fig. 8. The most abundant species were determined for each class and are listed by decreasing density in Table A2.

DISCUSSION AND CONCLUSIONS

The oceanic area considered in this study has a great ecological heterogeneity, since it extends from the central South Pacific to the Gulf of Panama (22°S to 8°N). The diversity of environmental conditions in the area results in a very strong geographic zonation of the
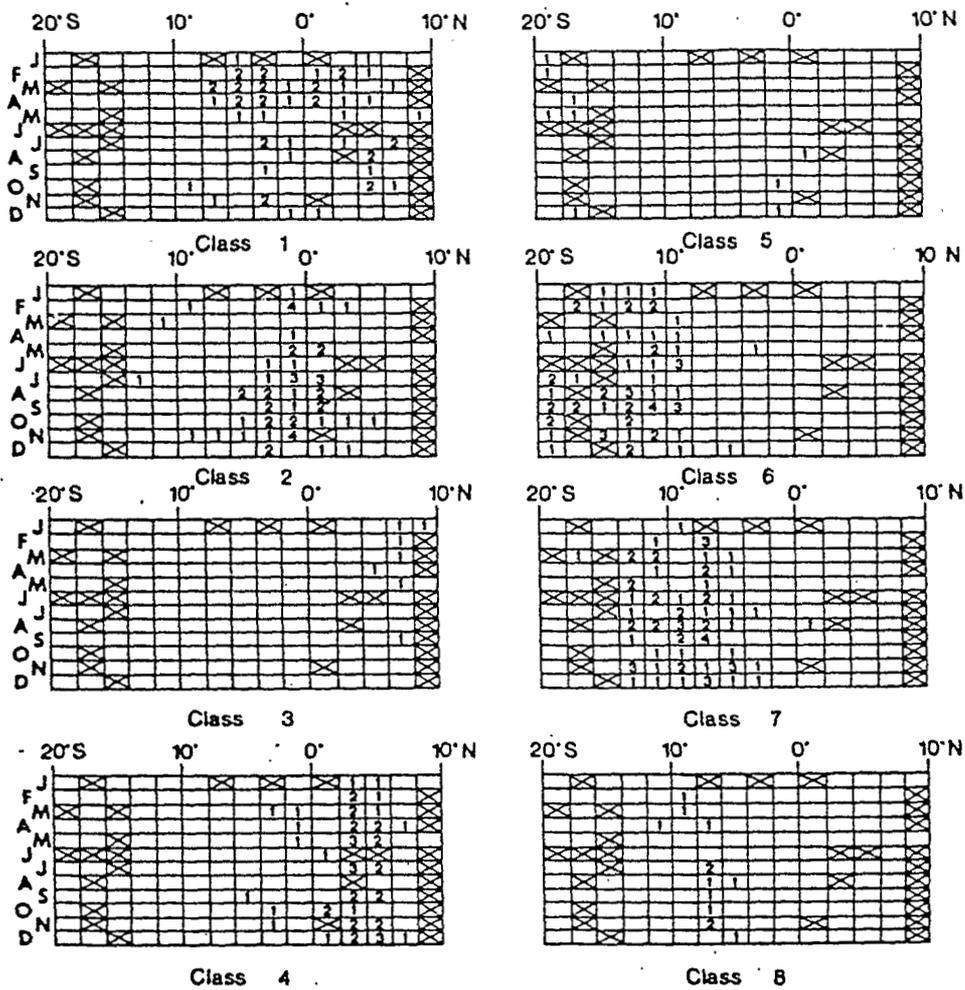
Fig. 7. Results of multivariate analysis: distribution of the eight classes of samples along the two axes and grouped into two sets (dendrogram).

copepod species distributions (BEKLEMISHEV, 1981). Because of this, we have stratified our data into three zonal areas in this study. Year-to-year variability cannot be seen clearly and consequently seasonal aspects were considered.

Temporal variability

The seasonal variation (Fig. 4) of surface chlorophyll content shows two maxima, one in southern summer and the other in southern winter. KING and HIDA (1957) did not find significant seasonal variation of plankton abundance in the central Pacific. However, results similar to ours were reported for the 1967 to 1968 Eastropac cruises, which showed temporal fluctuations of the planktonic biomass (chlorophyll content of the water column) and of primary production (OWEN and ZEITZSCHEL, 1970; BLACKBURN *et al.*, 1970) with two more or less clear maxima, also one each in summer and winter. The agreement with the present observations (Fig. 4) is surprising as the sampling methods were very different,
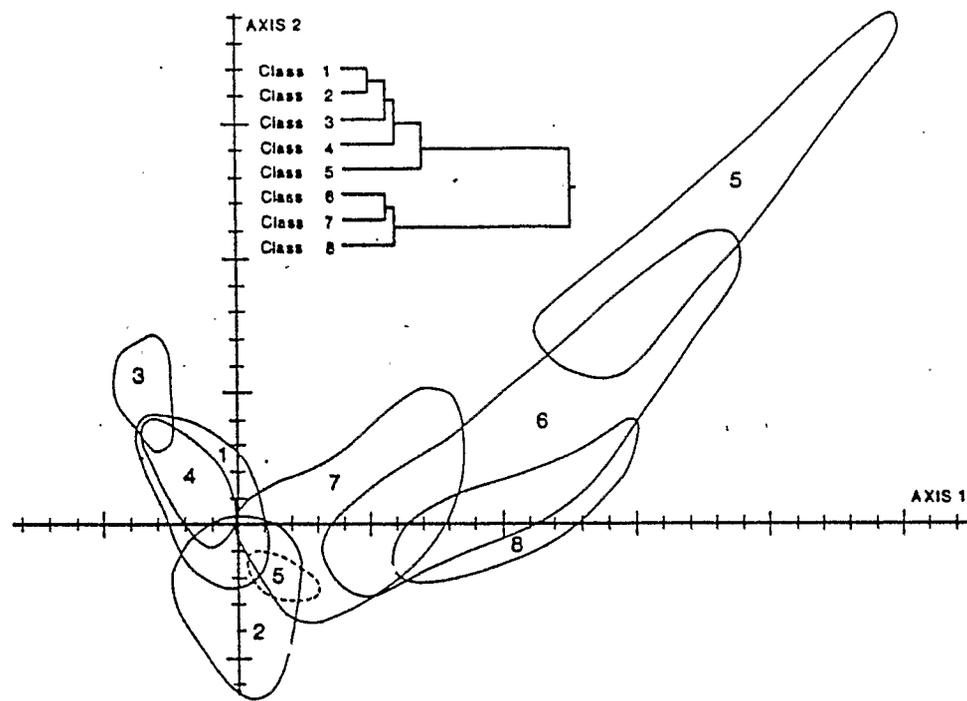
Fig. 8. Results of multivariate analysis: temporal–spatial distribution of each of the eight classes.

which could explain the shifting in time of the peaks. The change with time of the total number of copepods (Fig. 5B) also shows two maxima, similar to those of chlorophyll. It is remarkable that in the equatorial zone in July, zooplankton populations (Fig. 5B) are abundant at the time of strong equatorial upwelling, but chlorophyll concentration exhibits a minimum. This feature is consistent with the conclusion of THOMAS (1979), based on Eastropac data, that the excess of grazing by zooplankton is the main limiting factor for the development of a phytoplankton bloom. However, his findings of zooplankton biomass variations in phase with chlorophyll variations are based on daytime zooplankton sampling.

As expected, seasonal variations in total copepod number are related to variations in equatorial upwelling and to variations in horizontal advection of water upwelled off Peru (WYRTKI, 1981). The copepod maximum observed during July to September (Fig. 5B) is correlated with the maximum intensity of upwelling and of advection (Figs 2 and 3). The class 2 populations, where herbivores are dominant, are mostly responsible for this southern winter maximum, whereas their zonal extension increases during the winter season (Fig. 8). The interpretation of the second maximum (southern summer) is more difficult. It clearly precedes the maximum of the surface chlorophyll content which lasts for a longer time. During the southern summer (WYRTKI, 1981), the connection between the equatorial waters and the cold waters from Peru does not seem to exist; on the contrary, the equatorial surface circulation could possibly flow eastward during this season (TSU-CHIYA, 1974). On the other hand, the disappearance of the Galapagos thermal front allows

surface waters warmer than 26°C to extend into the whole equatorial zone (Fig. 2A), since the saline front occurring at 2 to 3°N does not seem to form an obvious ecological barrier. During the southern summer, class 1 populations (Fig. 8) extend from 8°S to 8°N, whereas during winter, they mostly remain north of 4°N. Among these populations, carnivorous species, with *O. venusta* predominating, constitute almost 36% of the total number vs 25% for class 2 and 66% for class 4. Consequently, the summer peak could be due partly to the ageing of the equatorial communities and to their mixing with north equatorial populations. North of the Galapagos front, planktonic communities have a long evolution period due to the stability of the environment and the disappearance of the front which allows their extension to the south. The intense doming of nutrient-rich waters to near the surface, occurring at 3°S, might also be an important source of enrichment and could increase the chlorophyll maximum in southern summer.

Spatial variability

Spatial variability cannot be separated from temporal variability. Distributions of the communities in an equatorial upwelling regime depend on the zonal circulation: in austral winter the westward Equatorial Current prevails; in austral summer eastward countercurrents (North Equatorial Countercurrent, South Equatorial Countercurrent and a shallowing undercurrent) prevail. The meridional circulation also can be important: in southern winter the surface water drifts poleward from the equator and, in southern summer, equatorward, whereas under the thermocline level the directions are reversed in both seasons. Contrary to other findings (e.g., VINOGRADOV, 1981), our observations have not shown that the maximum development of zooplankton is distant from the upwelling location where the phytoplanktonic bloom occurs. VINOGRADOV (1981) found that the maximum abundance of the herbivore copepods, *R. cornutus* and *Undinula darwinii*, occurred within two narrow bands located on each side of the equatorial divergence. We did not observe this kind of distribution in *R. cornutus*, which had its maximum abundance at 10°S; however, we did find some shift in space and time relative to the maximum surface cooling in the distribution of species of another herbivore, *Clausocalanus*, which had maxima between 2 and 4°S and 0 and 2°N. Unfortunately the frequency and accuracy of our sampling were not sufficient to describe these phenomena. Nevertheless, it is possible to observe some southwestward drifting (the Galapagos front prevents northward drifting) of the winter maximum of the carnivorous species, *Corycaeus crassiusculus* and *Onychocorycaeus pacificus*, located downstream in the community scale. However, for the carnivore, *Euchaeta rimana*, the maximum abundance occurs during the summer between 2°S and 2°N.

Meridional transport of water in the equatorial zone (zone 2) may be responsible for the southward extension of class 2 populations at the end of the southern winter (Fig. 8). The populations of class 1 that replace them in summer keep this wide north–south extension in distribution. South of 4°S (zone 1) the seasonal variability is very limited for biomass, trophic structure, and species composition. Two (6, 7) of the three classes (6, 7 and 8) identified in this zone seem to be affected by a meridional transport. Class 7 populations clearly benefit from the equatorial enrichment as suggested by the finding that 64% of the observations of this class were sampled during the second half-year. The dominant species (20.2%) in class 7 is *U. darwinii*, whereas small herbivorous copepods (*Clausocalanus* and *Paracalanus*) represent no more than 7% of the total number of copepods vs 36.4% in class 2 (Table A2). Small herbivores probably have a short biological cycle that prevents the

persistence of populations far away from the enrichment zones. Moreover, the high value of the Shannon index of diversity (4.5 bits/individual) between 8 and 16°S is consistent with the conclusion that the population of this area results from the mixing of equatorial zone populations with central South Pacific populations. Class 6 represents the southern edge of the population inventory. It probably has a composite characteristic since *U. darwinii* represents 9% of all copepods, 31.6% are migrating species and 33.3% carnivores.

In conclusion, this paper attempts to relate ocean productivity with the physical environment in an extensive area. During the sampling time (1977 to July 1982), the year-to-year variability was low and the features described may be considered as normal. Although a major El Niño did not occur during the present study, additional sampling was being carried out in August 1982 when a strong El Niño appeared so that a description of the effects of this event on zooplankton will be available.

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APPENDIX

The 70 most abundant copepod species in the 354 samples collected along the shipping route Tahiti to Panama were used in the statistical analyses. The data are presented in Tables A1 and A2.

Table A1. The 70 most abundant copepod species, listed by decreasing density (%) within all samples (354)

Species	%	Species	%
Oncaea venusta	17.60	Centropages calaninus	0.11
Clausocalanus spp.	11.30	Pontellina plumata	0.09
Undinula darwinii	8.20	Microsetella spp.	0.08
Paracalanus spp.	6.17	Paracandacia simplex	0.08
Acrocalanus gracilis	6.16	Rhincalanus nasutus	0.08
Euchaeta rimana	4.10	Candacia bipinnata	0.07
Canthocalanus pauper	3.94	Centropagea elongatus	0.07
Onychocorycaeus pacificus?	3.48	Oithona plumifera	0.07
Lucicutia flavicornis	2.76	Monocorycaeus robustus	0.07
Scolecithrix danae	2.74	Neocalanus robustior	0.07
Corycaeus crassiusculus	2.65	Centropages elegans	0.06
Temora discaudata	2.18	Labidocera acutum	0.06
Acrocalanus longicornis	2.17	Candacia pachydactyla	0.05
Pleuromamma gracilis	2.17	Ditrichocorycaeus dubius	0.05
Pleuromamma piseki	1.77	Labidocera acutifrons	0.04
Corycaeus speciosus	1.72	Urocorycaeus longistylis	0.03
Pleuromamma borealis	1.61	Copilia mirabilis	0.03
Euchaeta indica	1.56		
Eucalanus subtenuis	1.17		
Centropages furcatus	1.10		
Calanus minor	1.08		
Pleuromamma abdominalis	0.98		
Farranula concinna	0.93		
Acartia negligens	0.78		
Agetus typicus	0.71		
Calocalanus pavo	0.66		
Acartia danae	0.64		
Oncaea mediterranea	0.61		
Eucalanus attenuatus	0.60		
Euchaeta longicornis	0.58		
Euchaeta marinella	0.54		
Undinula vulgaris	0.53		
Eucalanus subrassus	0.45		
Farranula gibbula	0.44		
Rhincalanus cornutus	0.43		
Candacia catula	0.40		
Onychocorycaeus agilis	0.39		
Ditrichocorycaeus andrewsi	0.39		
Oncaea conifera	0.37		
Acrocalanus monachus	0.33		
Neocalanus gracilis	0.27		
Agetus flaccus	0.23		
Centropages gracilis	0.19		
Eucalanus pileatus	0.18		
Paracandacia truncata	0.18		
Urocorycaeus lautus	0.17		
Corycaeus clausi	0.16		
Candacia curta	0.15		
Ditrichocorycaeus asiaticus	0.14		
Oncaea curta	0.13		
Candacia ethiopica	0.13		
Ischnocalanus plumulosus	0.12		
Paracandacia bispinosa	0.12		

Table A2. Distribution of the 70 most abundant copepod species in eight classes, listed by decreasing density (%) within each class

Species	%	Species	%
Class 1		**Class 4**	
Oncaea venusta	16.81	Oncaea venusta	47.60
Acrocalanus gracilis	12.94	Euchaeta rimana	5.17
Undinula darwinii	10.45	Clausocalanus spp.	4.63
Paracalanus spp.	7.79	Acrocalanus gracilis	4.05
Canthocalanus pauper	7.17	Scolecithrix danae	3.77
Euchaeta rimana	6.21	Paracalanus spp.	3.76
Clausocalanus spp.	4.75	Euchaeta indica	3.69
Acrocalanus longicornis	3.80	Undinula darwinii	3.43
Onychocorycaeus pacificus	3.42	Onychocorycaeus pacificus	2.59
Scolecithrix danae	2.77	Corycaeus crassiusculus	2.51
Temora discaudata	2.53	Corycaeus speciosus	2.19
Corycaeus crassiusculus	2.36	Canthocalanus pauper	2.16
Euchaeta indica	2.25	Temora discaudata	1.76
Farranula concinna	1.64	Pleuromamma gracilis	1.38
Corycaeus speciosus	1.46	Candacia catula	1.20
Centropages furcatus	1.19	Lucicutia flavicornis	1.15
Undinula vulgaris	1.04		
Pleuromamma gracilis	1.00	**Class 5**	
		Pleuromamma borealis	13.10
		Oncaea venusta	9.53
Class 2		Lucicutia flavicornis	7.61
Clausocalanus spp.	26.03	Clausocalanus spp.	6.69
Paracalanus spp.	10.39	Euchaeta marinella	6.41
Oncaea venusta	8.17	Oncaea mediterranea	5.33
Undinula darwinii	7.86	Pleuromamma abdominalis	5.27
Onychocorycaeus pacificus	5.20	Scolecithrix danae	4.05
Acrocalanus gracilis	4.20	Paracalanus spp.	3.96
Eucalanus subtenuis	2.83	Centropages furcatus	2.39
Euchaeta rimana	2.80	Undinula darwinii	2.39
Pleuromamma gracilis	2.78	Acrocalanus gracilis	2.38
Corycaeus crassiusculus	2.64	Temora discaudata	2.35
Acrocalanus longicornis	2.58	Calanus minor	2.34
Lucicutia flavicornis	2.32	Corycaeus crassiusculus	2.27
Temora discaudata	2.12	Pleuromamma gracilis	2.07
Calanus minor	1.66	Eucalanus subcrassus	1.86
Pleuromamma borealis	1.58	Onychocorycaeus pacificus	1.59
Scolecithrix danae	1.56	Euchaeta rimana	1.39
Acartia danae	1.50	Corycaeus speciosus	1.36
Euchaeta longicornis	1.39	Eucalanus subtenuis	1.24
Calocalanus pavo	1.19	Acrocalanus monachus	1.03
Farranula concinna	1.01		
Canthocalanus pauper	1.00	**Class 6**	
		Lucicutia flavicornis	12.18
Class 3		Undinula darwinii	8.59
Canthocalanus pauper	25.66	Agetus typicus	8.21
Centropages furcatus	10.59	Pleuromamma piseki	7.85
Onychocorycaeus pacificus	10.24	Pleuromamma gracilis	4.79
Temora discaudata	8.02	Clausocalanus spp.	4.74
Oncaea venusta	8.02	Pleuromamma borealis	4.38
Ditrichocorycaeus andrewsi	6.08	Calanus minor	4.27
Eucalanus subrassus	5.78	Acartia negligens	3.32
Acrocalanus longicornis	5.72	Corycaeus speciosus	3.22
Acrocalanus gracilis	4.66	Corycaeus crassiusculus	2.89
Clausocalanus spp.	1.67	Euchaeta marinella	2.84
Paracalanus spp.	1.63	Euchaeta rimana	2.62
Undinula vulgaris	1.40	Pleuromamma abdominalis	2.35
Scolecithrix danae	1.21	Oncaea venusta	2.27
Corycaeus speciosus	1.09	Agetus flaccus	2.07
Corycaeus crassiusculus	1.07	Scolecithrix danae	1.97
Labidocera acutum	1.05	Rhincalanus cornutus	1.77
Undinula darwinii	1.01		

To Table A2. *Continued*

Species	%	Species	%
Class 6 (cont.)		*Rhincalanus cornutus*	1.82
Farranula gibbula	1.71	*Eucalanus attenuatus*	1.51
Urocorycaeus lautus	1.66	*Agetus typicus*	1.20
Paracandacia bispinosa	1.48	*Oncaea conifera*	1.18
Acrocalanus gracilis	1.37	*Pleuromamma abdominalis*	1.03
Oncaea conifera	1.29		
Neocalanus gracilis	1.27	Class 8	
Oncaea mediterranea	1.06	*Pleuromamma piseki*	33.73
Canthocalanus pauper	1.04	*Rhincalanus cornutus*	12.05
		Pleuromamma gracilis	9.00
Class 7		*Undinula darwinii*	5.29
Undinula darwinii	20.21	*Clausocalanus* spp.	5.22
Pleuromamma piseki	8.87	*Corycaeus crassiusculus*	3.94
Clausocalanus spp.	6.53	*Lucicutia flavicornis*	3.28
Lucicutia flavicornis	5.53	*Corycaeus speciosus*	2.76
Oncaea venusta	5.31	*Oncaea venusta*	2.66
Scolecithrix danae	5.06	*Scolecithrix danae*	2.16
Acrocalanus gracilis	4.67	*Agetus typicus*	1.78
Corycaeus crassiusculus	4.43	*Acartia negligens*	1.55
Euchaeta rimana	4.38	*Calanus minor*	1.35
Pleuromamma gracilis	3.52	*Agetus flaccus*	1.32
Corycaeus speciosus	3.42	*Eucalanus subtenuis*	1.27
Canthocalanus pauper	3.29	*Pleuromamma abdominalis*	1.23
Acartia negligens	2.25	*Euchaeta rimana*	1.21