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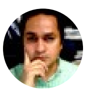
Sergio Hernández-Trujillo
Instituto Politécnico Nacional

Antonio Bode
Instituto Español de Oceanografia



Manuel Zetina-Rejón
Instituto Politécnico Nacional

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Community structure of pelagic copepods in the eastern tropical Pacific Ocean during summer and autumn

Gladis A. LÓPEZ-IBARRA[1], Sergio HERNÁNDEZ-TRUJILLO[1], Antonio BODE[2], and Manuel J. ZETINA-REJÓN[1,3]

(1) *Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional (CICIMAR-IPN), Av. I.P.N. s/n Col. Playa Palo de Sta. Rita, C.P. 23096, La Paz, B.C.S., México. E-mail: gibarra@ipn.mx*

(2) *Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo. 130, 15080 A Coruña, Spain*

(3) *Fisheries Centre, University of British Columbia, 2202 Main Mall, V6T 1Z4, Vancouver, British Columbia, Canada*

Abstract: The Eastern Tropical Pacific Ocean (ETPO) is a region of interest for commercial fisheries but is subject to high oceanographic variability, which affects primary and secondary production. Because pelagic copepods contribute significantly to secondary productivity, they were investigated to examine community structure variation both temporally and spatially. Zooplankton samples were collected from August to December 2003 using a bongo net (333 µm in mesh size). Ninety-six zooplankton samples were analysed, recording 94 copepod species from orders Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida. The study area could be divided into six geographical zones based on the numerically dominant species. The oceanographic conditions were relatively stable during summer and autumn. Total copepod abundance was higher (47,096 to 62,681 ind.100 m^{-3}) in stations near the coast, mostly in southern Baja California and the Gulf of Tehuantepec; the lowest densities were recorded towards the study area's oceanic regions. Similarly, ecological diversity was higher in zones influenced by tropical mass waters. The biogeographical affinity of copepod species was dominated by tropical species (75.5%), whereas subtropical and temperate species were far less abundant (15.7 and 8.6%, respectively).

Résumé : *Structure de la communauté des copépodes pélagiques dans l'Océan Pacifique tropical oriental en été et en automne.* L'est de l'océan Pacifique tropical (ETPO) est une région d'intérêt pour la pêche commerciale, mais il est sujet à une forte variabilité océanographique qui affecte la production primaire et secondaire. Les copépodes pélagiques contribuant de manière significative à la productivité secondaire, la variabilité spatio-temporelle de la structure de la communauté a été étudiée. Les échantillons de zooplancton ont été recueillis d'août à décembre 2003 à l'aide d'un filet bongo (333 µm de vide de maille). Quatre-vingt-seize échantillons de zooplancton ont été analysés, et 94 espèces de copépodes appartenant aux ordres des Calanoida , Cyclopoida , Harpacticoida et Poecilostomatoida ont été identifiées. La zone d'étude peut être divisée en six zones géographiques en fonction des espèces dominantes. Les conditions océanographiques ont été relativement stables au cours de l'été et de l'automne. L'abondance totale de copépodes était plus élevée (de 47096 à 62681 ind.100 m^{-3}) dans les stations près de la côte, principalement dans le sud de la Basse-Californie et le golfe de Tehuantepec ; les densités les plus faibles ont été enregistrées vers les régions océaniques de la zone d'étude. De même, la diversité écologique était plus élevée dans les zones influencées par les masses d'eaux tropicales. L'affinité biogéographique des espèces de copépodes est principalement tropicale (75,5% des espèces récoltées), tandis que les espèces subtropicales et tempérées étaient beaucoup moins nombreuses (15,7 et 8,6%, respectivement).

Keywords: Zooplankton ● Copepoda ● Biogeographical affinity ● Diversity ● ETPO

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Introduction

In the marine pelagic ecosystem, most of the secondary productivity derives from copepods. This group is characterized by high diversity and abundance; in some regions, copepods may account for up to 90% of zooplankton biomass, although most frequently, the abundance of this group ranges between 60 and 80% in oceanic and neritic regions (Palomares-García et al., 1998). Because of their high relative contribution to zooplankton biomass, these planktonic crustaceans represent a major biomass reservoir for energy transfers between primary producers and higher trophic levels. Copepods are characterized by a high diversity of habitat preferences, from an affinity for polar waters to a preference for tropical waters. Most larvae of small pelagic fish along with juveniles and adults of some nektonic fishes, which are ecologically important or commercially exploited in fisheries, feed on copepods (Olson et al., 2010).

To this respect, the Eastern Tropical Pacific Ocean (ETPO) is one of the regions of interest for commercial fisheries (especially of large pelagic species like tuna and billfish) and presents considerable oceanographic variability. This includes seasonal changes, such as upwelling processes, the influence of a number of currents that meet along Mexican coasts (including the California Current and Costa Rica Coastal Current) (Lluch-Cota et al., 2007), and other phenomena at intermediate scales, such as the El Niño or La Niña events, which affect vast areas of the western Pacific coast, influencing its species composition and ecosystem productivity according to the event's intensity and duration (Sydeman et al., 2014). These phenomena affect primary and secondary production across the region, hence influencing several higher trophic levels (Richardson & Schoeman, 2004; Hays et al., 2005), which results in recurrent consequences on some fishing resources throughout the region. For this reason, the main objective of this study is to analyze whether the community structure of pelagic copepods in the ETPO shows differences according to geographic variability. Because oceanographic conditions differ during summer and autumn and create distinctive geographic areas, we test the hypothesis that the community structure of pelagic copepods is different in different geographic areas. This is the first large-scale study describing pelagic copepods composition in this region.

Methods

Zooplankton samples were collected on board of two ships, R/V David Starr Jordan and R/V MacArthur II, of the US National Oceanic and Atmospheric Administration (NOAA) in the ETPO. Sampling began in July near the Baja California peninsula and continued toward the equator until December 2003 (Fig. 1). Ninety-six zooplankton samples were collected with a 0.6 m diameter bongo net of 333 μm mesh size towed obliquely from 200 m for 15 min. A flowmeter was used on the out-board net, and an average of 438 m^3 of water was filtered per tow. Simultaneously, sea surface temperature (SST) was recorded at various depths using a SeaBird CTD. Additionally, we compared *in situ* SST data with temperature and chlorophyll *a* satellite images with a 9-km resolution averaged on a seasonal scale downloaded from NASA Ocean Color Web (http://oceancolor.gsfc.nasa.gov). The images consist of data from Aqua/Modis and SeaWIFS satellite sensors.

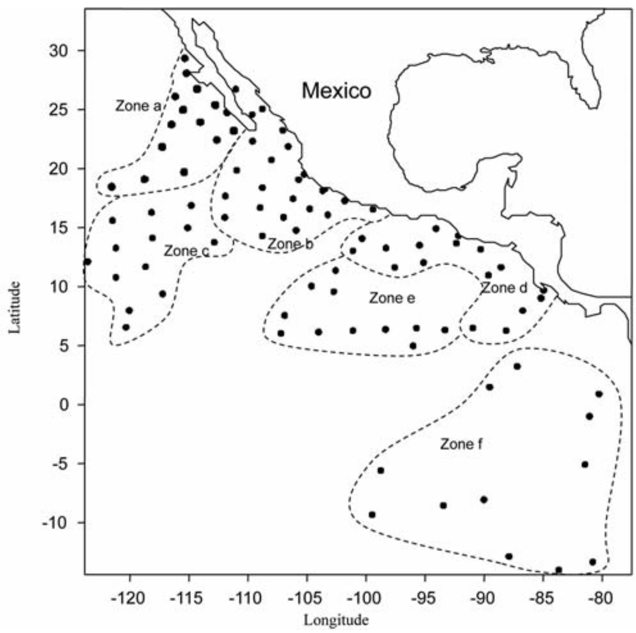

Figure 1. Study area and sampling stations in the Eastern Tropical Pacific Ocean. The six geographic zones identified in the analysis are shown: Western coast of the Baja California peninsula (*a*), Mexico's coastal region (*b*), Mexico's oceanic region (*c*), central coastal region (*d*), central oceanic region (*e*) and Equatorial oceanic region (*f*).

The sampling area comprises a large area in the ETPO located between the subtropical gyres of the North and South Pacific in Tropical Surface Water (TSW). This water mass is characterized by surface temperatures > 25°C and salinity < 34 (Fiedler & Talley, 2006). Sampling locations encompassed parts of the eastern Pacific warm pool, the North Equatorial Countercurrent, the North Equatorial Current, and the southern terminus of the California Current (Fiedler & Talley, 2006). The area is also influenced by the California Current (cold waters) and the Costa Rican Coastal Current (warm waters). In this sense, physical and chemical characteristics of the sea influence the community structure dynamics of pelagic copepods. In order to better discuss the geographical and oceanographic influence, we took into account the oceanographic dynamics reported by Fiedler & Talley (2006) and Kessler (2006) to classify the study area into six geographic zones: *a*) Western coast of the Baja California peninsula, *b*) Mexico's coastal region, *c*) Mexico's oceanic region, *d*) Central coastal region, *e*) Central oceanic region and *f*) Equatorial oceanic region.

Due to the large volume of samples, we subsampled using a Folsom splitter and then obtained a 20 ml aliquot from each subsample using a Stempel pipette according to Harris et al. (2000). The aliquot was then observed under a stereoscopic microscope for copepod identification; species names were in accordance with Walter & Boxshall (2014). Once specimens were identified and quantified, abundances were standardized to 1,000 m^3 of filtered water. The data matrices obtained were the basis for data analyses. The Shannon diversity index (H') was used for investigating ecological diversity.

The biogeographical affinity of pelagic copepod species was determined based on the criteria proposed by Raymond (1983), Bradford-Grieve (1994 & 1999), and Palomares-García et al. (1998).

The validity of the geographical zone classification was tested independently by using discriminant analysis based on logarithmically transformed total copepod abundance by area. Differences in mean values between groups were tested using ANOVA and 'a posteriori' Student-Neuman-Keuls tests.

Results

Environmental conditions

Temperature *in situ* data reveal the influence of warm water derived from the Costa Rican Coastal Current across most of the study area, except in waters off the southern end of the Baja California peninsula, where temperatures below 25ºC prevail as a frontal zone oriented perpendicularly to the coastline (Fig. 2). Satellite images of the distribution of sea surface temperature and chlorophyll-a concentrations allow us to identify two relatively stable oceanographic structures prevailing from summer to autumn: a temperature front in the zone closest to the Baja California peninsula and an area with a high chlorophyll-a concentration off the Gulf of Tehuantepec (Fig. 3).

Analysis of the copepod community

A total of 94 copepod species were identified, which belonged to the orders Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida. The Order Calanoida included the highest number of species, 62 (67%), followed by Poecilostomatoida with 22 (23.4%), Cyclopoida with 5 (5.3%) and Harpacticoida with 4 (4.3%).

The highest values of total copepod abundance were observed close to the coast, mostly in the southern Baja California coastal region and the Gulf of Tehuantepec, contrasting with lower densities in oceanic regions (Fig. 4). The Shannon diversity index (H') ranged from 1.5 to 3.2 bits.ind^{-1}, which peaked in zones *b*, *c* and *d*, whereas the lowest diversity numbers were noted in zones *e* and *f* (Fig. 5). The warmer zones (28 to 31ºC) were the regions with the both the highest abundance and diversity of pelagic copepods and the highest proportion of copepod species of tropical affinity (73-79%).

The specific relative abundance of pelagic copepods in each zone displayed changes associated with the geographical zone (Fig. 6). In zone *a, Undinula vulgaris* (Dana, 1849) was, by far, the most dominant species, with over 50% of total abundance, but it was less or not dominant in other zones. Between one and three species dominated in all other zones (*b*, *c*, *d*, *e* and *f*), but no individual species represented more than 15% of total abundance. This fact illustrates a relatively diverse community structure in all areas except for zone *a*; for example, a larger number of species (17 and 19) was required to reach 80% of total abundance.

In general, the biogeographical affinity of pelagic copepod species was largely dominated by species of tropical affinity (75.7%), contrasting with a noticeably modest presence of subtropical and temperate species (15.7% and 8.6%, respectively). When analysing

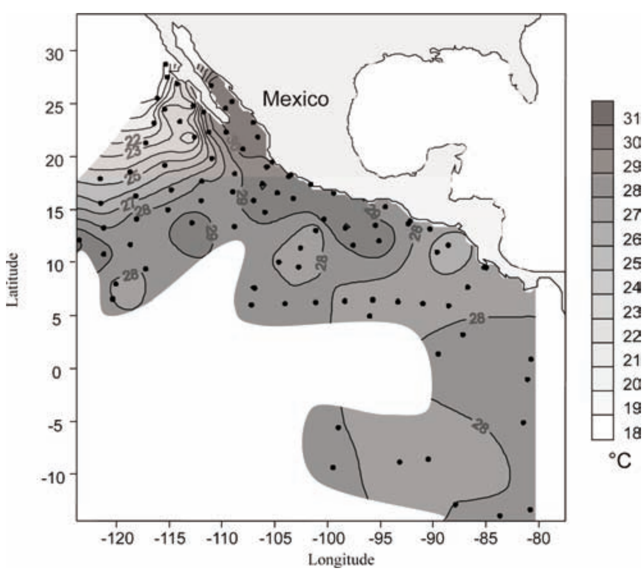

Figure 2. Seawater temperature at a depth of 5 m in the study area. The dots represent the sampling stations.

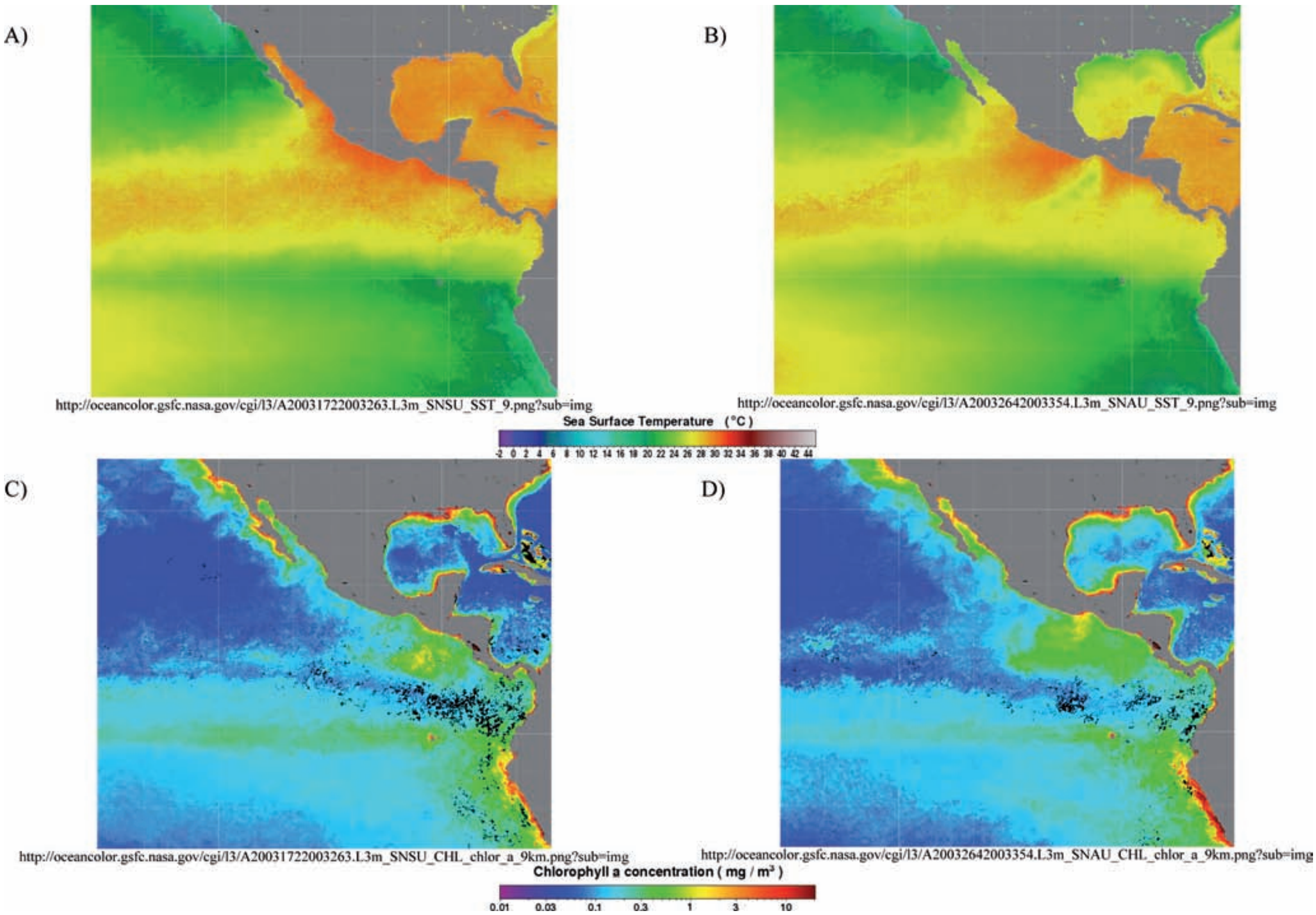

Figure 3. Satellite images for the average sea surface temperature (SST) and Chlorophyll-a concentration (Chl a) in the Eastern Tropical Pacific Ocean. **A.** SST: Summer/2003. **B.** SST: Autumn/2003. **C.** Chl a: Summer/2003. **D.** Chl a: Autumn/2003.

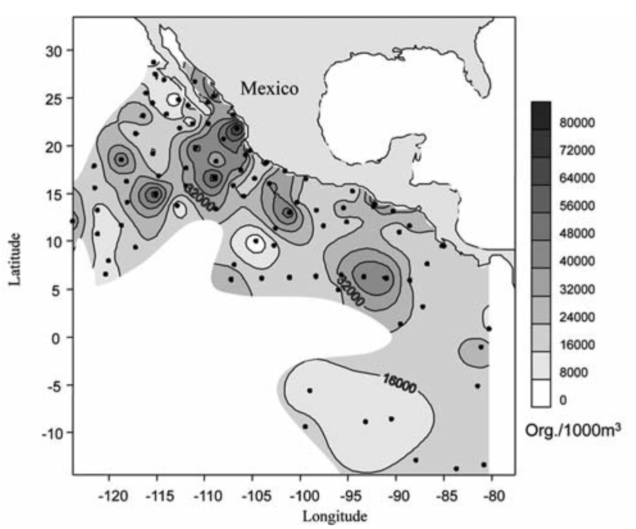

Figure 4. Total abundance of pelagic copepods recorded in the study area. The dots represent the sampling stations.

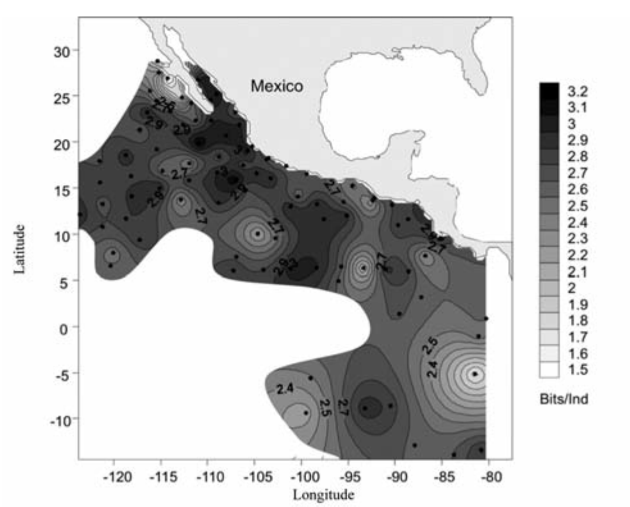

Figure 5. Map depicting the Shannon diversity index of pelagic copepods in the study area. The dots represent the sampling stations.

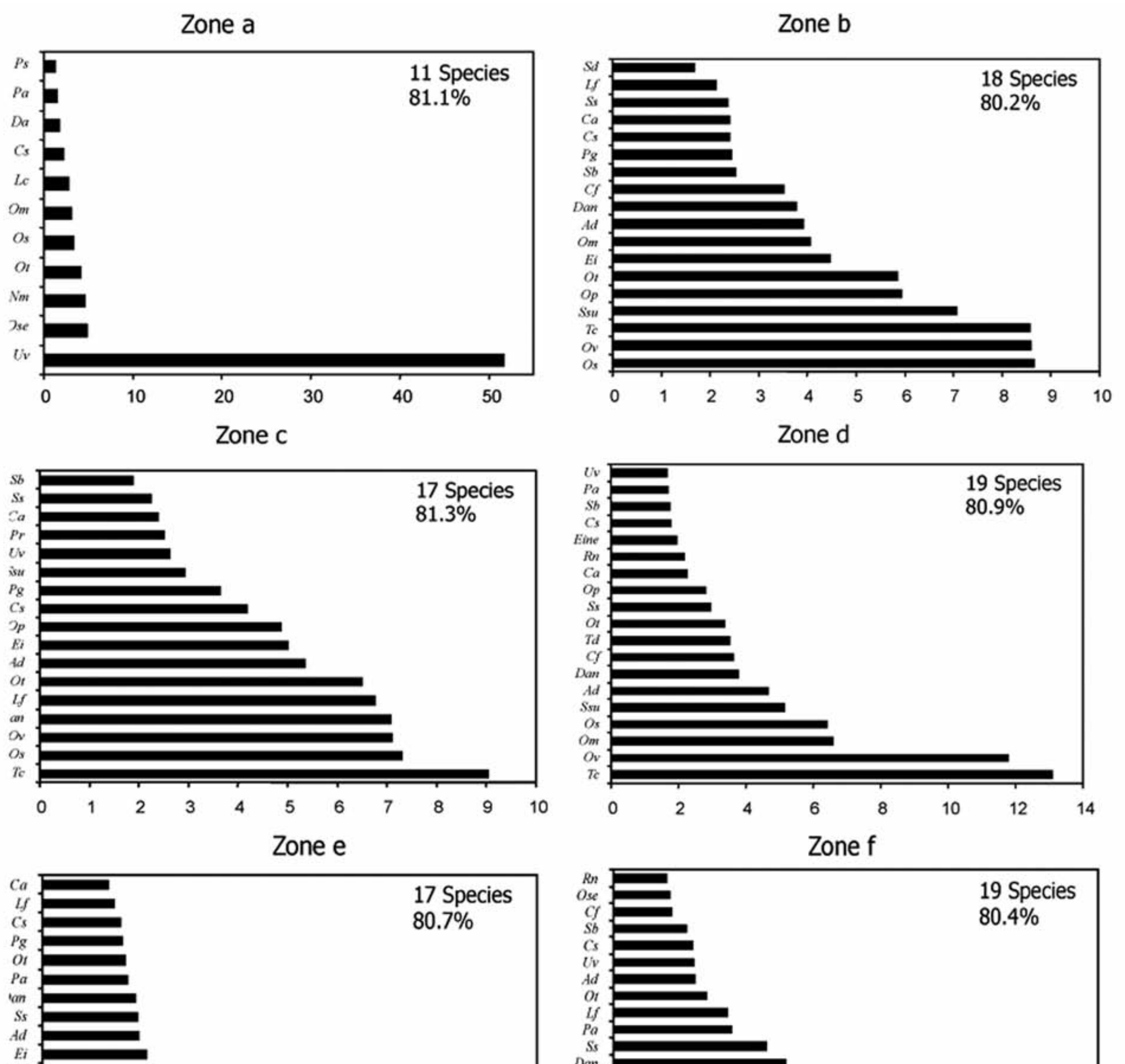

Figure 6. Relative abundance of dominant pelagic copepods per zone across the Eastern Tropical Pacific Ocean. Only species that contribute at least 80% of total abundance are shown. Ps: *Pareucalanus sewelli* (Fleminger, 1973), Pa: *Pleuromamma abdominalis abdominalis* (Lubbock, 1856), Da: *Ditrichocorycaeus amazonicus* (Dahl F., 1894), Cs: *Corycaeus speciosus* (Dana, 1849), Lc: *Lucicutia clausi* (Giesbrecht, 1889), Om: *Oncaea media* (Giesbrecht, 1891), Os: *Oithona similis* (Claus, 1866), Ot: *Oithona tenuis* (Rosendorn, 1917), Nm: *Nannocalanus minor* (Claus, 1863), Ose: *Oithona setigera* (Dana, 1849), Uv: *Undinula vulgaris* (Dana, 1849), Sd: *Scolecithrix danae* (Lubbock, 1856), Lf: *Lucicutia flavicornis* (Claus, 1863), Ca: *Clausocalanus arcuicornis* (Dana, 1849), Pg: *Pleuromamma gracilis* (Claus, 1863), Cf: *Centropages furcatus* (Dana, 1849), Ad: *Acartia danae* (Giesbrecht, 1889), Ei: *Euchaeta indica* (Wolfenden, 1905), Op: *Oithona plumifera* (Baird, 1843), Tc: *Triconia conifera* (Giesbrecht, 1891), Sb: *Scolecithricella bradyi* (Giesbrecht, 1888), Ov: *Oncaea venusta* (Philippi, 1843), Pr: *Pleuromamma robusta* (Dahl F., 1893), Eine: *Eucalanus inermis* (Giesbrecht, 1893), Ss: *Subeucalanus subtenuis* (Giesbrecht, 1888), Td: *Temora discaudata* (Giesbrecht, 1889), Dan: *Ditrichocorycaeus andrewsi* (Farran, 1911), Ssu: *Subeucalanus subcrassus* (Giesbrecht, 1888), Rn: *Rhincalanus nasutus* (Giesbrecht, 1888).

Table 1. Biogeographical affinity composition (%) of pelagic copepod species in the Eastern Tropical Pacific Ocean (July to December 2003).

	Zone a	Zone b	Zone c	Zone d	Zone e	Zone f
Tropical	73.1	75.4	74.5	77.2	76.1	79.2
Subtropical	19.2	17.5	14.9	17.5	17.4	16.7
Temperate	7.7	7	8.5	5.3	6.5	4.2

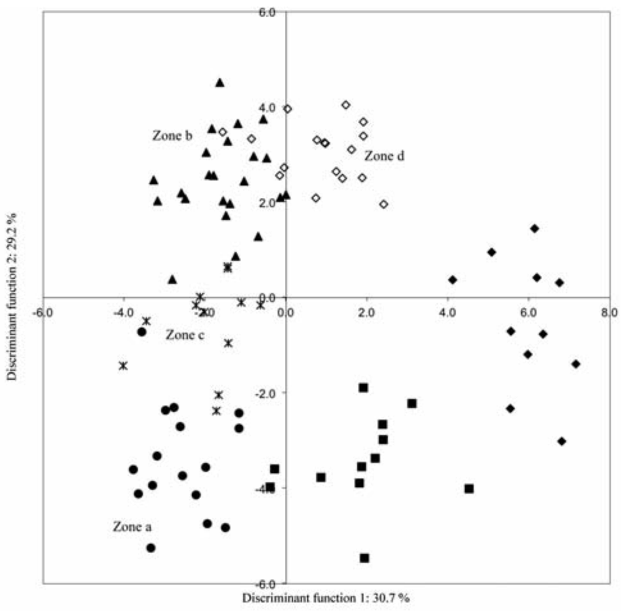

Figure 7. Plot of samples defined by two first discriminant functions; the variance explained by each axis is indicated of the copepod community between geographic zones (July to December, 2003).

biogeographical affinity by geographic zone, we found a similar pattern in all areas, in which tropical species were dominant, followed by subtropical and temperate species (Table 1). However, it is evident that northern areas have a slightly lower percentage of tropical species in contrast with all other geographical areas. This finding reveals a steady southward rise in the number of tropical species, as expected. For example, in contrast with the community in zone *a*, a more heterogeneous community was observed in all other zones in terms of biogeographical affinity and species size: zone *b* was characterized by the presence of tropical, carnivore and small-sized species (0.6-1 mm) (*Oithona similis, O. plumifera, Triconia conifera*), contrasting with larger (2-5.5 mm) omnivore species of temperate affinity in zones *d*, *e* and *f* (*Eucalanus inermis* and *Rhincalanus nasutus*).

The discriminant analysis revealed the separation of the 6 previously defined geographic areas, with the two first discriminant functions accounting for approximately 60% (Fig. 7). Significant differences were found between groups (Student-Neuman-Keuls test, $p < 0.0005$). The species with higher canonical coefficients associated with the two first discriminant functions are shown in table 2. We selected the first four species with higher canonical coefficients and plotted their abundance by zone (Fig. 8). A simple ANOVA reveals significant difference in all cases ($p < 0.05$).

Discussion

The abundance and species composition of the copepods observed were compared with data from other studies, and differences in both abundance and distributions emerged, likely due to the effect of the larger spatial scale involved in this study. The highest concentrations were observed in coastal areas, which coincide with large biomasses coupled with high species richness reported by several authors (Hernández-Trujillo, 1999; Franco-Gordo et al., 2001; Fernández-Álamo & Färber-Lorda, 2006). Although no new copepod species were registered in this study, a higher number of species was observed (94), compared with 63 species reported by Chen (1986) along a transect running from 23ºN to 3ºS across the ETPO, which identified *Subeucalanus subtenuis, S. subcrassus* and *Rhincalanus nasutus* as the dominant species. This result contrasts with our findings, where the dominant species in this same geographic region were small species such as *Triconia conifera, Oncaea venusta* (Philippi, 1843), *Oithona similis* and *O. plumifera*, which were not recorded by Chen (1986). This suggests that the difference in the number of species between these two investigations may have resulted from differences in the locations of the oceanographic stations and/or the number of stations in each study. Furthermore, in the present work, the study area comprised a wide variety of zones with different oceanographic and biogeographic characteristics, which contributed to the higher species richness observed. Additionally, the organic suspended matter could be different among years, affecting the efficiency of sampling small species inclusively when using the same mesh size.

The study area was characterized by marked contrasts in copepod abundance and diversity, especially between northern and southern areas, thus reflecting the large influence of oceanographic dynamics in the ETPO. Zone *a*

Table 2. Standardized canonical discriminant coefficients associated with the two first functions (DF1 and DF2). Only species having the highest absolute values of the coefficients are shown. Biogeographical affinity is indicated for each species (T = tropical; S = subtropical; TM = temperate).

Species	Coefficient DF1	Coefficient DF2	Biogeographical affinity
Acrocalanus gracilis Giesbrecht, 1888		-0.726	T
Aetideus bradyi Scott A., 1909	-0.735		T
Candacia catula (Giesbrecht, 1889)		-0.598	S
Centropages longicornis Mori, 1932		-0.771	T
Clausocalanus arcuicornis (Dana, 1849)		0.718	T
Ditrichocorycaeus andrewsi (Farran, 1911)	0.899		T
Eucalanus inermis Giesbrecht, 1893	0.753		T
Euchaeta indica Wolfenden, 1905		0.876	T
Euchaeta longicornis Giesbrecht, 1888	0.939		T
Euchaeta marina (Prestandrea, 1833)	0.757		T
Lucicutia flavicornis (Claus, 1863)	1.210	-0.813	T
Oithona plumifera Baird, 1843	-0.894		T
Oithona similis Claus, 1866	-1.063		S
Paracalanus parvus (Claus, 1863)		-0.732	TM
Pareucalanus sewelli (Fleminger, 1973)		-0.695	S
Pleuromamma gracilis Claus, 1863		-0.872	T
Pleuromamma robusta (Dahl F., 1893)	-1.029		T
Pontellina plumata (Dana, 1849)		0.860	T
Rhincalanus nasutus Giesbrecht, 1888	0.774		TM

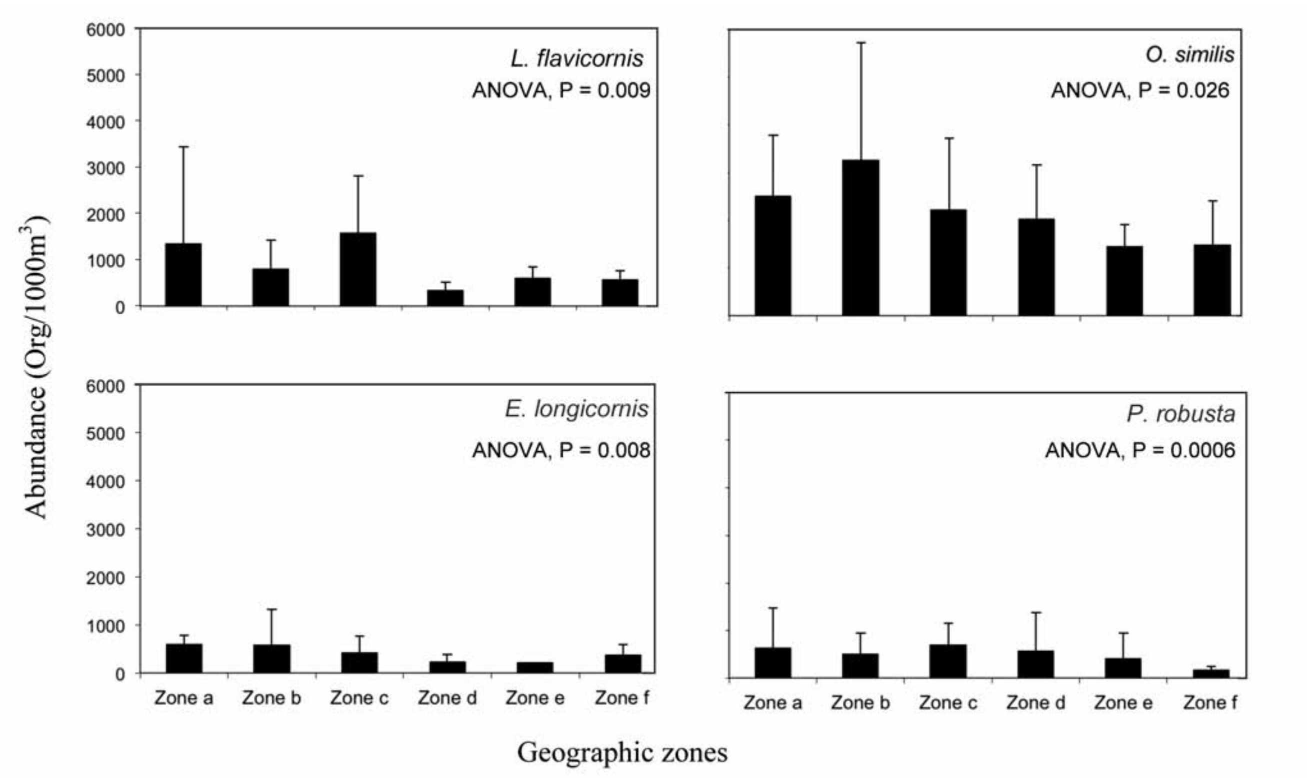

Figure 8. Abundance recorded in the geographic zones of the four species with the highest canonical coefficient on the first two axes of the discriminant analysis.

and the region north of zones *b* and *c* displayed the highest abundance and diversity indices, likely due to the presence of a semi-permanent oceanic front in the transition zone (detected through *in-situ* and satellite sea surface temperature data) located southwest of the Baja California peninsula. This front likely delimitates two communities differing in zoogeographical affinity. Etnoyer et al. (2006) described this front as one of the most permanent fronts in the Pacific Ocean, and it travels north or south forward throughout the year depending on the influence of the prevailing currents in the region, such as the California Current and the Costa Rican Coastal Current (Badan, 1997). This oceanographic dynamic would foster a higher species diversity resulting from the mixture of groups of species with temperate, transitional or tropical zoogeographic affinity. In this study, similar conditions were observed during the summer and autumn. Pennington et al. (2006) also categorized the ETPO as an area with high primary production, thus favoring a large abundance of secondary producers; however, no investigations on zooplankton secondary production are currently available for this area, and the present study is the first one conducted at a large scale in the ETPO that addresses the quantification of the abundance of pelagic copepods.

The southern oceanic zones (*e* and *f*) displayed relative lower abundance and diversity, given their oceanic and tropical characteristics that are less influenced by continental runoff and coastal upwelling events, which translates into lower phytoplankton abundance and, hence, limited food sources. It is reasonable to infer that in addition to regional differences, coastal areas show relatively higher copepod abundance and diversity compared with oceanic areas, coinciding with reports by Haedrich & Judkins (1979). Additionally, our findings confirm the existence of higher diversity in the coastal areas than in the oceanic region. Furthermore, different groups of species were recorded in each zone: coastal regions were characterized by small-sized species with short life cycles, likely resulting from greater resource availability, in contrast with larger, longer-living copepod species in oceanic zones, likely due to their energy expenditure being allocated primarily to search for food rather than to reproduce.

The high abundance and species diversity found in the southern Baja California peninsula and the Gulf of Tehuantepec may result from two factors. First, the wind-driven upwelling events, which may be more intense in the fall, lead to nutrient resuspension that in turn leads to phytoplankton blooms and abundant food for higher trophic levels. In this sense, Kiǿrboe (1991) and Arcos & Fleminger (1986) have detected increases in abundance or in the presence of some species in deep waters. Second, these are areas influenced by several different water masses, such as those from the California Current, the Costa Rican Coastal Current, the North-Equatorial Current, the Equatorial Counter-current and from the Eastern Tropical Pacific Ocean, which might contribute to concentrate a large number of organisms. However, the concentration of organisms of any given biogeographical affinity depends on the intensity of the prevailing currents because these may vary in intensity and travel either north (Costa Rican Coastal Current) or south (California Current) with seasonal periodicity. Furthermore, the circulation patterns of these currents may also be altered by inter-annual events like El Niño, when warm waters from the Costa Rican Coastal Current advance longer distances (Van der Spoel & Pierrot-Bults, 1979; Parés-Sierra et al., 1997).

Regarding the biogeographical affinity of species in the pelagic copepod community across the ETPO, the prevalence of tropical species is not surprising, although species of subtropical and temperate affinity were also found, likely carried by sea currents running through the study area. Although a larger number of tropical species was recorded during the summer when the region is dominated by warm waters from the Tropical Pacific Ocean and the Costa Rica Coastal Current (Van der Spoel & Pierrot-Bults, 1979; Badan, 1997), the temperate species recorded are associated mostly with regions around the California Current or close to the temperature front off the southern Baja California peninsula (Etnoyer et al., 2006). This suggests that both cosmopolitan and transitional species are coexisting in the study area after being transported by different water masses (Van der Spoel & Pierrot-Bults, 1979). Additionally, cosmopolitan species like *Eucalanus elongatus* and *E. inermis* occurred in oceanic stations, where food availability is limited, but these species are able to feed on recycled particulate organic matter (Hidalgo et al., 2005).

The Mexican Pacific coasts are acknowledged as a key portion of the so-called Panamanian Province, comprising one district that ranges from the Gulf of California to the southern border of Mexico, followed by a second district stretching from the southern border of Mexico to Central America. In the present investigation, this vast zone was included in the study area. From a biogeographical standpoint, the community structure of copepods found in this study coincides with earlier reports dealing with copepods, euphausiids and polychaetes, where the prevalence of tropical and subtropical species is highlighted (Fernández-Álamo & Färber-Lorda, 2006).

It can be concluded that tropical pelagic copepods dominated from July to December 2003 in the study area (comprising 80 to 90% of total abundance) and were associated with seawater temperatures between 28 and 30ºC. No ETPO-endemic species were recorded, nor was any apparent biogeographical association of provinces

(Panamanian and Mexican, as described for other planktonic taxa), as copepods usually display broad distribution patterns not restricted to the ETPO. Separately, both abundance and specific diversity of copepods were higher in geographic areas influenced by the oceanic temperature front off the southern Baja California peninsula and the Gulf of Tehuantepec, coinciding with the influence of oceanographic events like temperature fronts and upwellings.

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